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CYANOBACTERIAL ASSEMBLAGES IN PERMANENT ICE COVERS ON ANTARCTIC LAKES: DISTRIBUTION, GROWTH RATE, AND TEMPERATURE RESPONSE OF PHOTOSYNTHESIS[1]

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ABSTRACT

The proliferation of microalgae in the McMurdo Dry Valleys of Antarctica is intricately linked to the seasonal cycle involving the freezing and melting of water. Anecdotal observations and preliminary sampling have found cyanobacterial cells in ice covers on lakes in the McMurdo Dry Valleys, and several of these ice covers are known to undergo seasonal freeze–thaw cycles. Therefore, we sought to determine the distribution and abundance of cyanobacterial assemblages in several permanent ice covers throughout the McMurdo Dry Valleys and to determine their rates of growth and their photosynthetic physiologies upon encountering liquid water. We found that the majority of the permanent ice covers contained cyanobacterial assemblages in close association with sedimentary material. Cyanobacterial biomass was conspicuously absent in sediment-free ice covers, suggesting that the seasonal interaction between the sediments, ice, and solar radiation present the necessary liquid water environment for cyanobacterial growth. All assemblages exhibited extremely low rates of photosynthesis when first exposed to liquid water. Despite the low rates of photosynthesis, a large proportion (41%) of the photosynthate was incorporated into protein, indicating that the cells were undergoing efficient net cellular growth. The short-term response (24 h) of photosynthesis to a range of temperatures showed optimum rates occurring at temperatures >15° C, which is similar to those of psychrotrophic cyanobacteria isolates from soil and stream habitats, which we believe provides the inoculum for the in- ice habitats.

Key index words: Antarctica, cyanobacteria, extreme environments, ice, lakes, photosynthesis

Abbreviations: CN, cellular nitrogen; E_d, downwelling irradiance; E_o, scalar irradiance; G, generation time; G′, in situ *generation time; I_k, photoacclimation index;* P^b, *biomass-specific photosynthetic rate;* P^b_m, *maximum biomass-specific photosynthetic rate; PC, protein carbon; PON, particulate organic nitrogen; α, photosynthetic efficiency; ρ′, biomass-specific rate of nitrogen incorporation; μ, specific growth rate*

Microalgae proliferate within a variety of environments throughout Antarctica's freshwater and terrestrial ecosystems. Habitats supporting active cyanobacterial populations include ephemeral streams and ponds, the water column and benthos of permanently ice-covered lakes, permafrost, soils, and rocks, as well as ice shelves and glaciers (e.g. Heywood 1977, Vincent 1988, Friedmann 1993). These habitats exhibit characteristics, such as long periods of darkness, low temperature, and low water activities, and resident cyanobacteria exhibit a range of physiological characteristics enabling them to proliferate within these extreme environments (e.g. Holm-Hansen 1963, Davey 1989, Hawes et al. 1992, Nienow and Friedmann 1993).

Permanent ice covers on Antarctic lakes also contain cyanobacterial cells (Wilson 1965, Vincent 1988, Wing and Priscu 1993), and preliminary studies at Lake Bonney, Antarctica, revealed that they are viable and capable of photoautotrophic production in the presence of liquid water (Wing and Priscu 1993, Priscu et al., unpubl.). Liquid water has been observed both within and on the surface of some of the permanent ice covers during summer months (e.g. Calkin and Bull 1967, Fritsen et al. 1998). Recent studies have estimated that ice covers may contain between 20% and 60% liquid water at the end of the austral summer season in areas associated with sediment inclusions (Fritsen et al. 1998). The presence of liquid water and viable cyanobacteria in this extreme and unique environment prompted us to gather fundamental ecological information on the physical dynamics of the ice environment as well as the distribution and physiological characteristics of the ice-bound cyanobacterial assemblages. This information is used to determine the cyanobacterial assemblage's potential for growth and primary production within the permanent ice covers in major lakes of the McMurdo Dry Valleys. Because the ice covers provide a perennial cold-water environment, we further investigated the photosynthetic metabolism of the ice-cyanobacteria over a range of temperatures to determine if they possessed photophysiological characteristics of cold-adapted cells.

MATERIALS AND METHODS

Study area and site description. The lakes that were studied are located in the McMurdo Dry Valleys adjacent to McMurdo Sound (77°43′ S, 162°23′ E) (except Lake Morning, which is adjacent to Mount Morning located in the Ross ice shelf area south of McMurdo Sound). The Transantarctic Mountains impede the flow of the polar ice cap into this region, making these valleys the largest ice-free area (~4000 km^2) on the Antarctic continent. The lakes are fed by glacier meltwater and maintain perennial ice covers, except for small (<3% of total lake area) seasonal (<10 weeks·year^{-1}) moats. Most lakes have ice covers ranging in thickness from 3 to 5 m overlying liquid water columns 15–75 m deep

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(e.g. Lakes Bonney, Hoare, Fryxell, Joyce, Vanda, and Miers). Some lakes have ice covers exceeding 10 m and contain little or no liquid water (e.g. Lakes Vida and Morning).

Previous studies on the relatively thin ice covers (3–5 m) overlying liquid water indicate that the ice thickens during the austral winters when temperature gradients in the ice are sufficient to produce ice growth at the ice–water interface (McKay et al. 1985, Adams et al. 1998, Fritsen et al. 1998). Whereas ice growth occurs during the winter months, evaporation and sublimation from the ice surface occurs primarily during the spring and summer (Clow et al. 1988). This balance effectively creates a conveyor system wherein new ice, grown at the ice–water interface, is transported upward with the theoretical residence time of ice in the 3–5-m ice covers being 10–15 years (Clow et al. 1988). The mass balance and thermodynamics of deeply frozen lakes (lakes with ice covers exceeding 10 m) are unknown at this time. However, it has been suggested that these lakes attained their deep ice covers by flooding of the ice surfaces by stream water followed by freezing (Calkin and Bull 1967).

Instrumentation. Thermocouples were placed in the east lobe of Lake Bonney in 1992 at initial depths of 0.5, 1.0, 2.0, and 3.5 m. Temperature readings from each of these thermocouples were logged at 1-h intervals using a Campbell 21X data logger (Logan, Utah). Coincident with the temperature readings, incident fluxes (E_d) of photosynthetically active radiation (PAR) were measured and logged at the surface of the ice with a LiCor 192SA cosine collector mounted and leveled at 1 m above the ice surface. Spherical PAR sensors (LiCor 193S) were frozen into a 10-cm-diameter auger hole at depths of 1, 2, 3, and 4 m in August 1995, and the scalar irradiances of PAR (E_c) were then logged over 20-minute intervals using a Campbell CR10 data logger.

Sample collection and analysis. Ice cores were collected from the middle portion of the ice covers on Lakes Bonney (both east and west lobes), Hoare, Fryxell, Vanda, Vida, and Miers from August to October 1995 and from Lakes Bonney, Joyce, Vida, and Morning during August 1996 (using both SIPRE and PICO coring devices, 10 cm diameter). The areas of ice core collections were over 100 m distant from seasonal moat ice; therefore, samples are representative of the ice within the permanent ice areas of these lakes. Cores were sectioned at approximately 30 cm intervals and placed in 4-L high-density polyethylene (HDPE) jars and melted slowly. Ice meltwater never exceeded 2° C during processing.

Subsamples of ice core meltwater were immediately filtered through precombusted GF/F filters (Whatman Corp.) and extracted in a cold DMSO:Acetone:H_20 solution (50:45:5 by volume) for 12–24 h. Chlorophyll *a* (chl *a*) concentrations in the extract solutions were then determined fluorometrically (Holm-Hansen et al. 1965) using a Turner 111 fluorometer calibrated with standard concentrations of purified chl *a* (Sigma Chemical, St. Louis, Missouri). When present, approximately 2 g of sediments in the ice core meltwater were subsampled with a clean spatula and extracted in the DMSO–acetone solution for determination of chl *a* contents. The extracted sediments were then dried (90° C for 24 h) and weighed in order to normalize chl *a* concentrations to the sediment dry weights. The remainder of the sediments in the ice core meltwater also were dried and weighed to yield the total sediment concentrations ($g \cdot L^{-1}$) in each ice core section.

Sediment samples also were collected from the surface of the ice and from the shores of Lake Bonney using clean stainless steel spatulas and HDPE collection jars during the 1995 field season. The chl *a* contents of these sediments were determined as described above.

Photosynthesis versus irradiance experiments. Photosynthetic rates were determined from the uptake of ^{14}C-bicarbonate into organic material. Meltwater suspensions were inoculated with ^{14}C-bicarbonate (ICN Pharmaceuticals) to a final activity of 1 $\mu Ci \cdot mL^{-1}$ and incubated under irradiances varying from 0 to 545 μmol photons$\cdot m^{-2} \cdot s^{-1}$ PAR. Variable irradiances were achieved using neutral-density screening of cool-white fluorescent lighting. Temperatures were held between 0° and 2° C during incubations that lasted approximately 4 h. Incubations were terminated by acidifying with 0.5 mL 6 N HCl followed by drying at 95° C. Ten milliliters of Cyctocint (ICN Pharmaceuticals) liquid scintillation cocktail were then added and radioactivity was determined with a Beckman model LS 6800 liquid scintillation counter. Counts per minute were corrected to disintegrations per minute based on sample quench and a quench curve prepared with a ^{14}C-toluene standard with acetone as the quenching agent. Dissolved inorganic carbon was determined by sparging ice meltwater in 6 N H_2SO_4 in a stream of nitrogen gas with subsequent measurement of the liberated CO_2 by infrared gas analysis. The hyperbolic tangent equation (Jassby and Platt 1976) fitted with Marquardt's algorithm was used to model chl *a*-normalized uptake rates (P^b) as a function of irradiance. Photosynthetic efficiencies (α) and maximum biomass- specific rates of photosynthesis (P^b_m) were obtained from the model. The ratio of P^b_m to α, known as I_k or the photoacclimation index (Talling 1957, Lizotte and Priscu 1992), was derived from the model solutions for α and P^b_m. Photoinhibition was not included in our analysis because initial inspection of the data showed no decrease in photosynthesis at the highest irradiances tested.

Photosynthate partitioning. Experiments determining the partitioning of the incorporated ^{14}C into cellular macromolecules (protein, polysaccharide, lipid, and low molecular weight compounds [LMWC]) were conducted over time- courses extending up to 66 h. Samples were exposed to a continuous saturating irradiance of 140 μmol photons$\cdot m^{-2} \cdot s^{-1}$ and temperature of 0°–2° C during incubations. Subsamples were drawn during the time course, filtered through GF/F filters, and frozen at $<-20°$ C until biochemical fractionation was performed as outlined by Priscu et al. (1987). Rates of total photosynthesis compared to the combined synthesis of the photosynthetic end products showed >90% recovery of ^{14}C in all analyses. The changes in the relative incorporation of label over time were linearly modeled as gradients in proportions (Fleiss 1981).

Growth rates. Biomass-specific rates of nitrogen incorporation (ρ', μg N$\cdot$(mg chl *a*)$^{-1} \cdot h^{-1}$) were estimated from rates of protein carbon synthesis (μg PC$\cdot$(mg chl *a*)$^{-1} \cdot h^{-1}$) assuming a N:C ratio of 0.3 (w/w) in proteins (DiTullio and Laws 1983) and a conversion factor for protein nitrogen to total cellular nitrogen of 0.34 (Priscu and Goldman 1983). A model II linear regression analysis of particulate organic nitrogen (PON) versus chl *a* showed that particulate nitrogen in ice meltwater covaried significantly with chl *a* at a ratio of 19 mg PON:mg chl *a* with a positive intercept of 25 mg PON ($r^2 = 0.58$, n = 115). Making the first-order assumption that the PON covarying with chl *a* was primarily cyanobacteria cellular nitrogen (CN) allows use of the biomass-specific nitrogen production rates to solve for specific growth rates, μ (units, h^{-1}; or d^{-1} when applied to a 24 hour time period), from the exponential growth equation in the form

$$\mu = \ln[(CN_0 + \rho' Chla)/CN_0]$$

(Peterson 1978), where CN_0 is the initial concentration of cellular nitrogen estimated from chl *a* (Chla). Specific growth rates are also expressed as generation times (G, expressed in days) based on the relationship

$$G = 0.693\mu^{-1}.$$

In situ generation times (G′) were calculated by estimating the number of days that cyanobacterial growth could occur during a year and the generation times measured in liquid water. Growth was assumed to occur only when the temperatures of the ice were 0° C (the temperature of the ice when liquid water is presumed to be available) at the depth of the cyanobacterial biomass. Because ice temperature measurements have not yet been made in all of the lakes, we used temperature records from the east lobe of Lake Bonney (Fritsen et al. 1998) in order to derive first-order estimates of the number of days during which liquid water is available at different depths in the ice covers.

RESULTS

Irradiances, temperatures, and liquid water cycles. Indirect solar radiation first reaches Lake Bonney in the McMurdo Dry Valleys in August (Fig. 1A). The

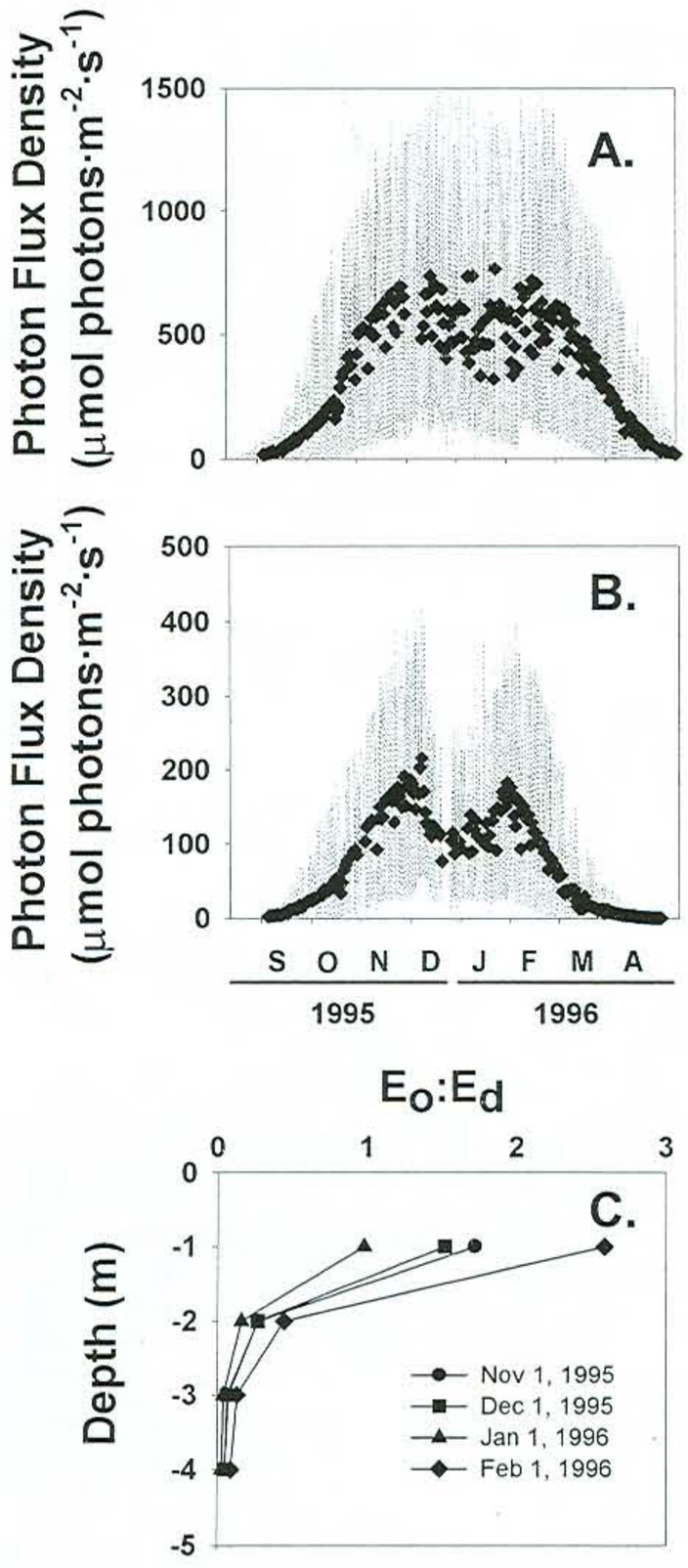

FIG. 1. Incident downwelling irradiances of PAR (A) and scalar irradiances of PAR at 2 m from the ice surface (B) in the east lobe of Lake Bonney from August 1995 to May 1996. Diamond symbols denote the average daily irradiances; grey lines are hourly values. Note the different scales on the y-axis in Fig 1B. Incident irradiances measured on the shore (rather than on the ice) are shown in panel A due to instrument failure on the ice from February to October 1996. (C) The ratio of scalar irradiances of PAR at different depths (E_o) to incident irradiances (E_d) at local noon illustrating the relative decrease in irradiances with depth in the ice and the seasonal variability in the transmission of PAR into the ice cover.

first direct solar radiation received at the surface of the ice covers each season varies from lake to lake due to local shading by topography (Dana et al. 1998). Solar radiation at Lake Bonney persists throughout the day by late October (Fig. 1A). Although solar radiation exists throughout the day, a diurnal cycle is present that varies by approximately an order of magnitude over a 24-h period. Incident downwelling irradiances of PAR reached a seasonal daily maximum of ~1500 μmol photons·m^{-2}·s^{-1} in January 1995.

Scalar irradiances of PAR (E_o) in the ice showed a different seasonal pattern relative to the seasonal progression of surface downwelling irradiances (Fig. 1B). When surface downwelling irradiances were still increasing in early December, irradiances at 2 m in the ice actually began to decrease, and by late December irradiances in the ice were ~30% lower than in late November. This seasonal decrease has been attributed to the "whitening" of the ice from the development of scattering features (e.g. Tyndal figures, fine fractures, etc.) in the near-surface layer of the ice (Priscu 1991, McKay et al. 1994, Howard-Williams et al. 1998). Later in the season (late January to early February), irradiances in the ice began to increase and reached a second seasonal maximum in February (Fig. 1B).

Irradiances at 1 m in the ice ranged from 1 to 2.8 times the incident downwelling irradiances (E_d) and decreased to 0.05–0.1 times incident irradiances at 4 m (Fig. 1C) indicating that the habitats within the ice at Lake Bonney during 1995– 1996 were within the 1% level, which is typically used to define the euphotic zones of aquatic ecosystems. During the austral summer (December–January), absolute values of PAR at 2 m in the ice ranged from an average minimum of 20 μmol photons·m^{-2}·s^{-1} at local midnight up to an average of ~200 μmol photons·m^{-2}·s^{-1} at local noon (Fig. 1B).

Temperature records at Lake Bonney from 1993 to 1995 (Fig. 2) show the autumnal propagation of a cold wave into the ice, which established a temperature gradient averaging 7° C·m^{-1}. The austral winter temperatures at mid-depth in the ice ranged from −10° to −20° C. The ice became isothermal at 0° C during the late spring to early summer (November–December) and remained isothermal until the austral autumn when the seasonal freezing fronts again propagated into the ice. The progression of the freezing fronts from the top to the bottom of the ice allowed the deeper ice to remain at 0° C for longer periods of time compared to the ice at shallower depths. For instance, the ice at 2 m remained at 0° C (and presumably contained liquid water) until April in 1994, whereas temperatures at 0.5 m dropped below 0° C in January.

The number of days that ice temperatures are 0° C is likely to be a fair estimate of the number of days that liquid water is available. Solutes in the ice meltwater were low (e.g. $Na^+ < 2$ mg·L^{-1}, $Cl^- < 5$ mg·L^{-1}). Therefore, estimates of the duration of liquid water availability that are based on the duration of the ice being isothermal are not likely to be in error due to solute depression of the freezing point. During the years examined thus far, portions of the ice covers at Lakes Bonney and Hoare have had temperatures at 0° C from 80 to 150 days a year (Fritsen et al. 1998).

Chlorophyll a *distributions.* Chl *a* concentration in ice core meltwater suspensions (a measure of cyanobacterial biomass) ranged from <0.05 μg·L^{-1} to 58 μg·L^{-1} (Fig. 3). The maxima in each ice core always corresponded to the sections of the core containing

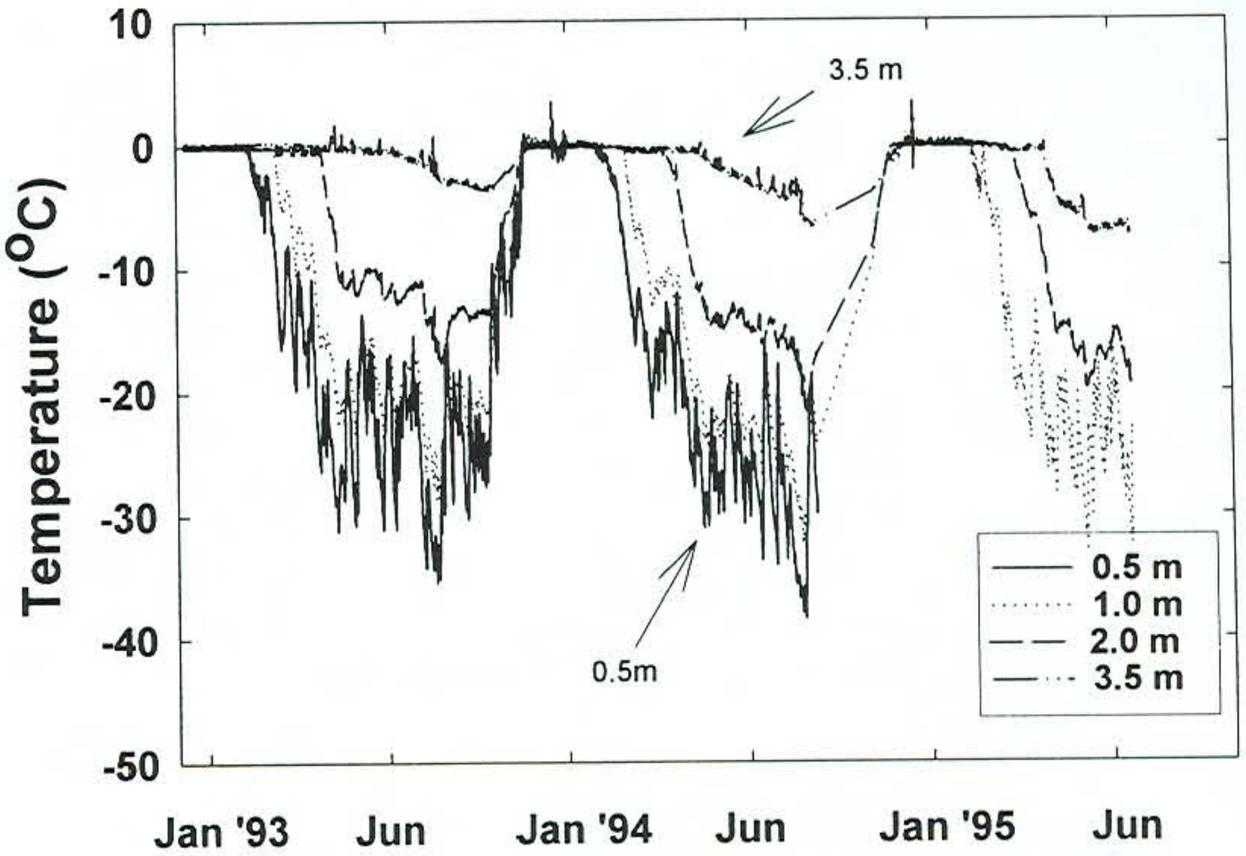

FIG. 2. Temperatures in the ice cover on the east lobe of Lake Bonney, Antarctica, between February 1993 and April 1995 (modified from Fritsen et al. 1998).

aggregates of sedimentary material (Fig. 3) in association with bubbles having distinctive arching morphologies (Adams et al. 1998). Ice cores taken in close proximity within the east lobe of Lake Bonney (<5 m distant, Table 1) showed a fourfold difference in their chl *a* contents, which was coincident with a 20-fold difference in sediment load (Table 1). During 1995, a 3.5-m pit was excavated in the ice cover on the east lobe of Lake Bonney in which the sediments and bubble morphologies were easily viewed (Adams et al. 1998). From these observations, we estimated that the sediment aggregates ranged between 2 and 20 cm in diameter and were horizontally dispersed at 10–100-cm intervals throughout the ice at ~1.5–3 m depth.

It should be noted that the concentration of pigments and sediments in ice meltwater represent an integrated average over the core section and can be

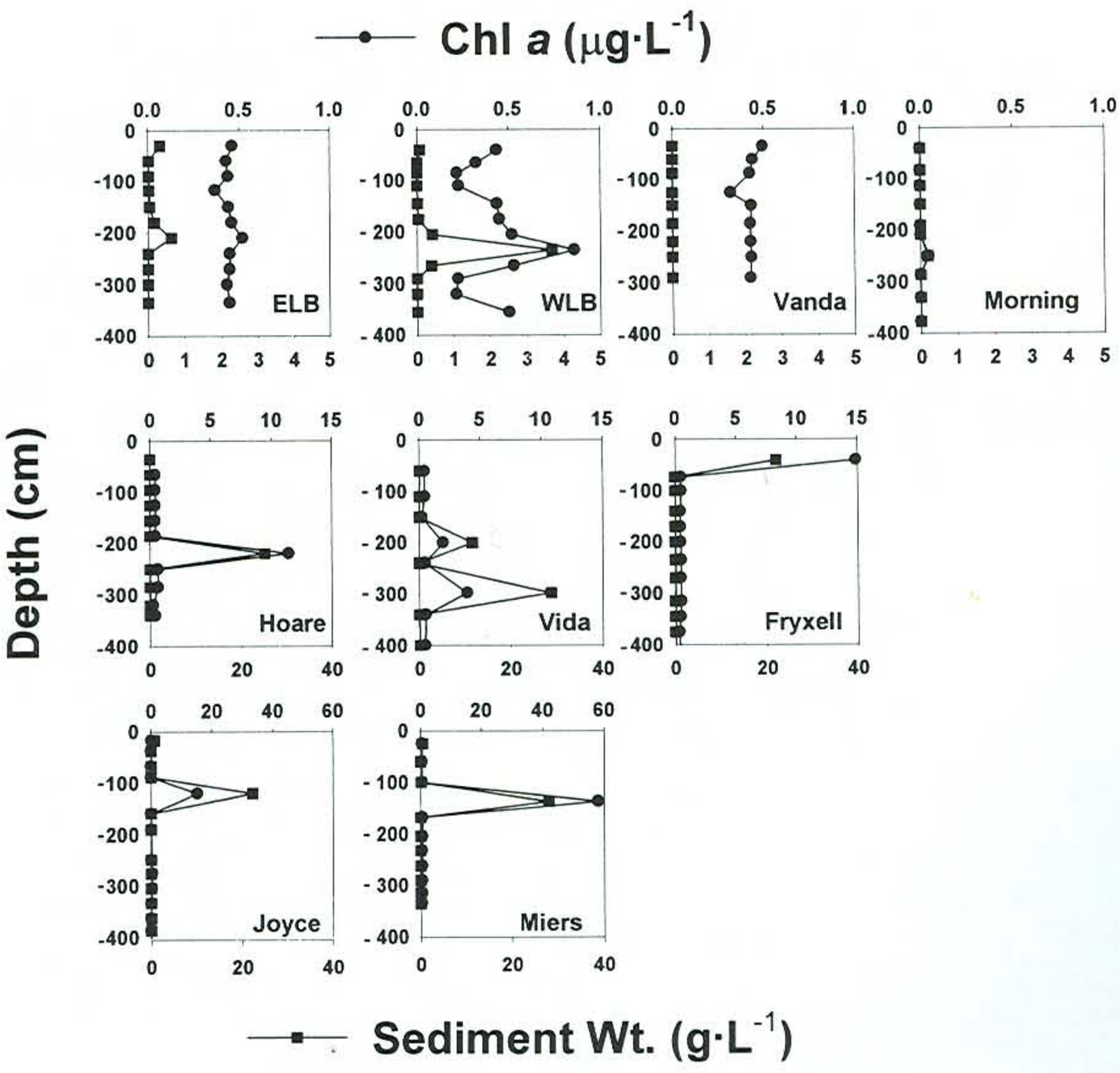

FIG. 3. Profiles of chl *a* and sediment concentrations within ice covers of lakes throughout the McMurdo Dry Valleys. ELB, east lobe of Lake Bonney; WLB, west lobe of Lake Bonney; all other lakes' names are complete. The data represent averages from ice core sections approximately 30 cm long. Note the different scales on the x-axes.

TABLE 1. *Depth-integrated sediment and chl* a *contents in ice cores collected from lakes throughout the McMurdo Dry Valleys, Antarctica. ELB, east lobe of Bonney; WLB, west lobe of Bonney. Chl* a *in the Lake Miers ice core represents a minimum because chl* a *concentrations were not measured on one section of the core.*

Lake/core	Sediment load ($kg \cdot m^{-2}$)	Standing stock of chl *a* (mg chl $a \cdot m^{-2}$)
ELB/core 1	0.37	1.6
ELB/core 2	8.28	6.3
WLB	1.39	1.7
Hoare	8.81	8.2
Fryxell	8.88	39.9
Joyce	7.23	>5.08
Vanda	0	1.2
Vida	22.24	8.6
Miers	11.40	41.7
Morning	0	0

much higher on smaller scales. For instance, in Lake Miers the 58 μg chl $a \cdot L^{-1}$ represents a 30-cm section of the ice core subsampled from 1.0 to 1.3 m depth; visual inspection indicated that sediments were concentrated in a 5–10-cm layer within this core section. Therefore, the actual *in situ* concentration may have been more on the order of 175–350 $\mu g \cdot L^{-1}$.

The chl *a* suspended in the ice meltwater did not represent all of the microalgal biomass in the ice. Sediment particles that settled in the sampling jars also contained attached algae and associated pigments in substantial quantities. Chl *a* contents of these sediments (Sed) ranged from 0.05 μg chl $a \cdot$(g Sed dry wt)$^{-1}$ at Lake Vida to 3.63 μg chl $a \cdot$(g Sed dry wt)$^{-1}$ at Lake Fryxell (Fig. 4a). Sediment loads in the ice cores ranged from <0.1 $kg \cdot m^{-2}$ at Lakes Vanda and Morning to 22.2 $kg \cdot m^{-2}$ at Lake Vida (Table 1), and the chl *a* in the sediments contributed an average of 39% of the total standing stocks of chl *a*. The total depth-integrated chl *a* contents of the different ice cores ranged from <0.1 mg chl $a \cdot m^{-2}$ at Lake Morning to 41.7 mg chl $a \cdot m^{-2}$ at Lake Miers (Table 1). Comparison of the chl *a* contents of sediments collected from the surface of the ice and the shores of Lake Bonney to those within the ice cover shows the sediments within the ice had significantly higher chl *a* content (Fig. 4b).

Photosynthesis versus irradiance relationships. More than 98% of the microalgal biomass (determined as chl *a*, see above) in any given ice core was associated with the sections of the cores that contained sedi-

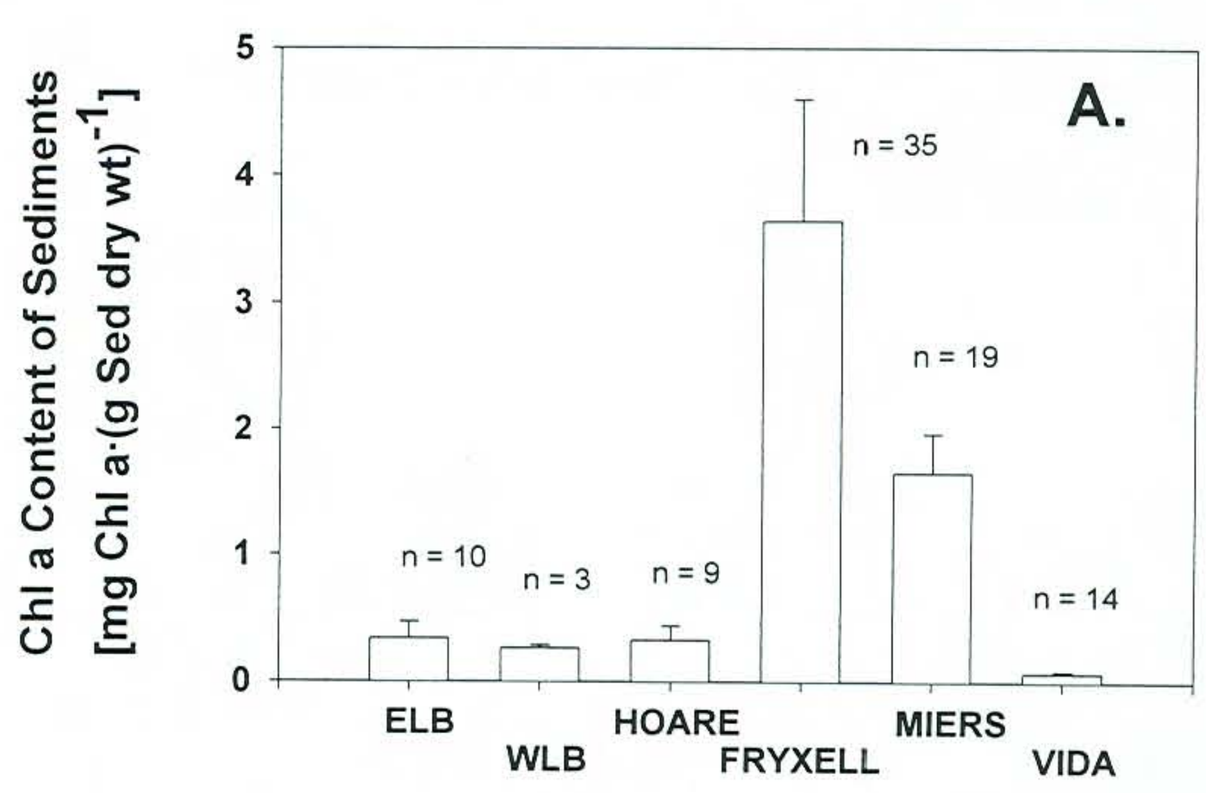

FIG. 4. (a) Average (±SE) chl *a* content of sediments in ice cores collected from permanent ice covers throughout the McMurdo Dry Valleys. Notation same as in Fig. 3. Lakes Vanda and Morning are not shown because sediments were virtually absent (<0.5 $g \cdot L^{-1}$) in these ice covers. (b) Average (±SE) chl *a* content of sediments collected from shoreline soils, from sediments on the surface of the ice, and within the ice cover on the east lobe of Lake Bonney.

TABLE 2. *Photosynthesis–irradiance parameters determined at 0°–2° C for cyanobacterial assemblages collected from ice samples containing sedimentary aggregates (±SD). Notation for lake names the same as in Table 1. Units:* P^b_m, *μg C·(μg chl a^{-1})·h^{-1}; α, μg C·(μg chl a^{-1})·h^{-1}·(μmol photons·m^{-2}·s^{-1})$^{-1}$; I_k, μmol photons·m^{-2}·s^{-1}. Standard deviations on I_k were obtained by propagation of the variances according to Taylor (1982), assuming independent and random errors.*

Lake	P^b_m (×10^{-3})	α (×10^{-4})	I_k
ELB	4.3	4.9	8.7
	(0.23)	(1.55)	(2.8)
WLB	5.9	4.5	13.0
	(0.46)	(1.60)	(4.9)
Hoare	4.6	1.6	28.8
	(0.35)	(0.35)	(6.72)
Fryxell	14.2	17.0	8.4
	(0.97)	(3.31)	(3.0)
Miers	40.6	18.2	22.3
	(2.6)	(3.92)	(5.0)
Vida	4.6	1.1	41.8
	(0.28)	(0.20)	(8.1)

ments. Experiments on ice core meltwater also showed that more than 95% of the total potential photosynthetic activity was associated with these same sections.

Photosynthesis versus irradiance experiments showed the cyanobacterial assemblages had variable maximum biomass-specific rates of photosynthesis, ranging from 0.0043 to 0.0406 μg C·(μg chl *a*)$^{-1}$·h^{-1} (Table 2). Photosynthetic efficiencies in the light-limited portion of the PI curves (α) also varied 10-fold, ranging from 0.0001 to 0.0017 μg C·(μg chl *a*)$^{-1}$·h^{-1}· (μmol photons·m^{-2}·s^{-1})$^{-1}$. I_k values ranged from 8.7 to 41.2 μmol photons·m^{-2}·s^{-1} (Table 2). The highest biomass-specific rates of photosynthesis and photosynthetic efficiencies occurred in Lakes Fryxell and Miers, being two- to 10-fold higher than those in Lakes Bonney, Hoare, and Vida.

Photosynthate partitioning. The proportion of ^{14}C incorporated into specific macromolecular groups changed over time during several of the time series assays. Most notable were the significant decreases in the relative labeling of the LMWC fraction over the first 40 h (Fig. 5) in almost all of the experiments (the exception being the time series for the west lobe of Bonney). The magnitude of the decreases in labeling of the LMWC fractions was typically near 10% of total photosynthate produced. However, the Lake Miers assemblage showed a substantial decrease from an initial value of 38% at 4 h to 12% at 55 h (Fig. 5).

Relative labeling of the lipid fraction increased over the first 40 h of the experiments on the samples from Lakes Hoare, Fryxell, Miers, and Vida, whereas it remained constant during the time series experiments on the Lake Bonney samples. The incorporation of ^{14}C into the lipid fraction never exceeded 10% at any time during any of the assays.

Relative partitioning of $^{14}CO_2$ into proteins and polysaccharides remained invariant during the Lake Miers, Hoare, and west lobe of Bonney time courses (Fig. 5). Changes in the partitioning into the protein fraction were evident in the Lake Fryxell assemblage, showing an increase from 24% at 15 h to 44%–51% at 50–60 h (average rate of increase, 0.4% h^{-1}; $r^2 = 0.70$, $P < 0.05$). Increases in the percent incorporation of ^{14}C into protein from Lakes Vida and the east lobe of Lake Bonney, though less substantial, still increased over the duration of the time course (average rate of increase, 0.21%–0.22% h^{-1}; $r^2 = 0.35$–0.43, $P < 0.1$).

The proportion of ^{14}C recovered in the major cellular pools at the end of the time series incubations averaged 41.0 ± 4.4% protein, 39.0 ± 3.8% polysaccharide, 4.1 ± 1.4% lipid, and 15.9 ± 2.4% LMWC among all experiments (±2 SD, n = 5). Because cyanobacteria contain relatively few membranes and associated membrane lipids with respect to eukaryotic cells, the pattern of ^{14}C incorporation supports preliminary autoradiographic results (Paerl and Pinckney 1996) showing that the autofluorescent flagellates (common in the water column of these

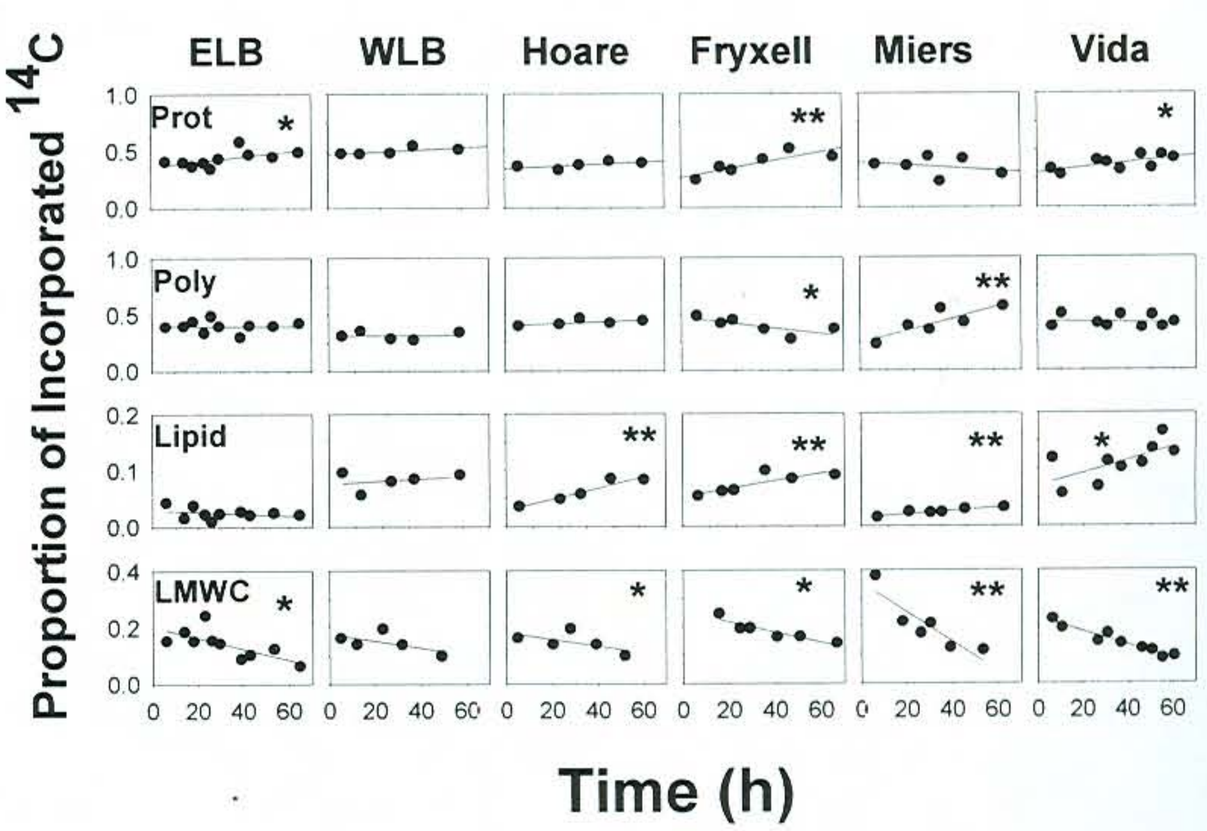

FIG. 5. Proportion of ^{14}C incorporated into proteins (Prot), polysaccharides (Poly), lipids, and low molecular weight compounds (LMWC) as a function of time for cyanobacterial assemblages collected from different ice covers. *, slope is greater than zero at $P < 0.1$; **, slope is greater than zero at $P < 0.05$. Note different scales on the y-axis for the different macromolecular pools.

TABLE 3. *Measured activities and estimates of primary production potential of cyanobacterial assemblages collected from the different lakes' ice covers within the McMurdo Dry Valleys. Rates of protein synthesis expressed as protein carbon (μg PC·[mg chl* a*]$^{-1}$·h^{-1}) and specific growth rates (μ, d^{-1}) when cyanobacteria were exposed to liquid water, temperatures of 0°–2° C, and irradiances saturating to photosynthesis (140–200 μmol photons·m^{-2}·s^{-1}). Growing days are the estimated number of days during a year when liquid water is available for growth.* In situ *generation times (G′, years) and annual primary production (mg C·m^{-2}·year^{-1}) estimates. NA, not applicable because biomass was not present at sufficient quantities to determine growth rates based on protein synthesis; NM, protein synthesis was not measured, therefore growth rates and generation times could not be derived.*

Lake	Protein synthesis	μ	Growing days	G′	Annual primary production
ELB	0.58	0.001	150	9.0	86–340
WLB	2.54	0.003	130	2.0	120
Hoare	5.44	0.006	130	0.96	843
Fryxell	8.08	0.008	80	0.64	5891
Joyce	NM	NM	130	NM	NM
Vanda	NA	NA	NA	NA	0
Vida	2.71	0.003	130	1.92	617
Miers	12.0	0.012	100	0.43	10,447
Morning	NA	NA	NA	NA	0

lakes) and diatoms (observed in some of the ice samples) did not substantially contribute to the rates of primary production within any of the lake ice environments studied.

Growth rates. Light-dependent rates of protein carbon synthesis ranged from 0.58 to 8.08 μg PC·(mg chl *a*)$^{-1}$·h^{-1} (Table 3), which translates to nitrogen uptake rates of 0.51–10.6 μg N·(mg chl *a*)$^{-1}$·h^{-1} and specific growth rates of 0.001–0.012 d^{-1} (Table 3). Expressed as generation times, these rates indicate the cyanobacterial biomass would double every 0.15–3.2 years in the presence of liquid water and saturating irradiances.

Depending on the vertical location of the cyanobacterial assemblage (Fig. 3), cyanobacteria would have experienced 80 to 130 days of ice temperatures of 0° C between November 1994 and February 1995 (Fig. 2, Table 3). In the same time period during the 1995–1996 season, *in situ* irradiances were above those levels that would have saturated the assemblages' maximum photosynthetic capacities. Therefore, the combination of the physiological data and the environmental data suggests that *in situ* growth rates are not likely to be light limited when liquid water is present. However, liquid water is present for only a fraction of the year and *in situ* generation times are estimated to be 2–3 times longer than those measured in the ice meltwater (i.e. on the order of 0.4 to 9 years; Table 3). Scaling these estimates of *in situ* generation times to the standing stocks of chl *a* within the ice and assuming a 50:1 C:chl *a* ratio (g:g) yields annual production estimates of 80 to 10,000 mg C·m^{-2}·y^{-1} (Table 3). Note that these calculated growth and production rates are likely to be underestimates if portions of the PON covarying with chl *a* are associated with nonviable cells.

Temperature effects on photosynthesis. Increasing temperature from 2° to 20° C increased P^b_m of a Lake Fryxell cyanobacterial assemblage approximately 10-fold (from 0.014 to 0.172 μg C·[μg chl *a*]$^{-1}$·h^{-1}) and α approximately threefold (from 0.0018 to 0.0037) (Fig. 6). Corresponding Q_{10} values were 3.46 for P^b_m and 1.45 for α. Concomitant with the differential change in P^b_m and α was a 3.5-fold increase in I_k, from 13.2 to 46.1 μmol photons·m^{-2}·s^{-1}.

Biomass-specific rates of light-saturated photosynthesis (irradiances >150 μmol photons·m^{-2}·s^{-1}) also were measured over a range of temperatures (from 0° to 40° C) on samples of ice aggregates from Lakes Miers and Fryxell. These experiments showed that the maximum rates of photosynthesis occurred near 20° C (Fig. 7).

DISCUSSION

A distinct association was found between algal pigments and sediments in the permanent ice covers.

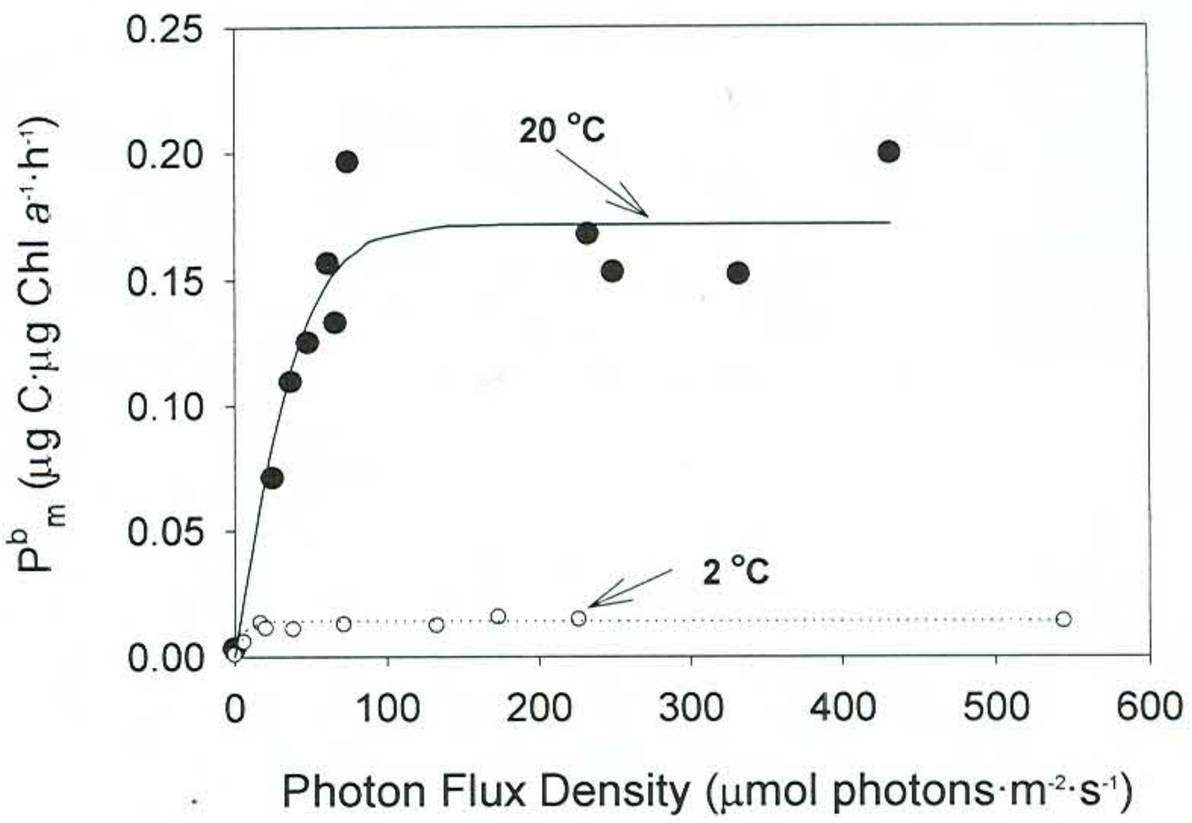

FIG. 6. Photosynthesis–irradiance curves for cyanobacteria collected from the permanent ice cover on Lake Fryxell and incubated at 0°–2° C and 20° C. P^b_m at 20° C = 0.172 μg C·(μg chl *a*)$^{-1}$·h^{-1}; α at 20° C = 0.004 μg C·(μg chl *a*)$^{-1}$·h^{-1}·(μmol photons·m^{-2}·s^{-1})$^{-1}$; I_k at 20° C = 46.1 μmol photons·m^{-2}·s^{-1}. Photosynthetic parameters at 2° C given in Table 2.

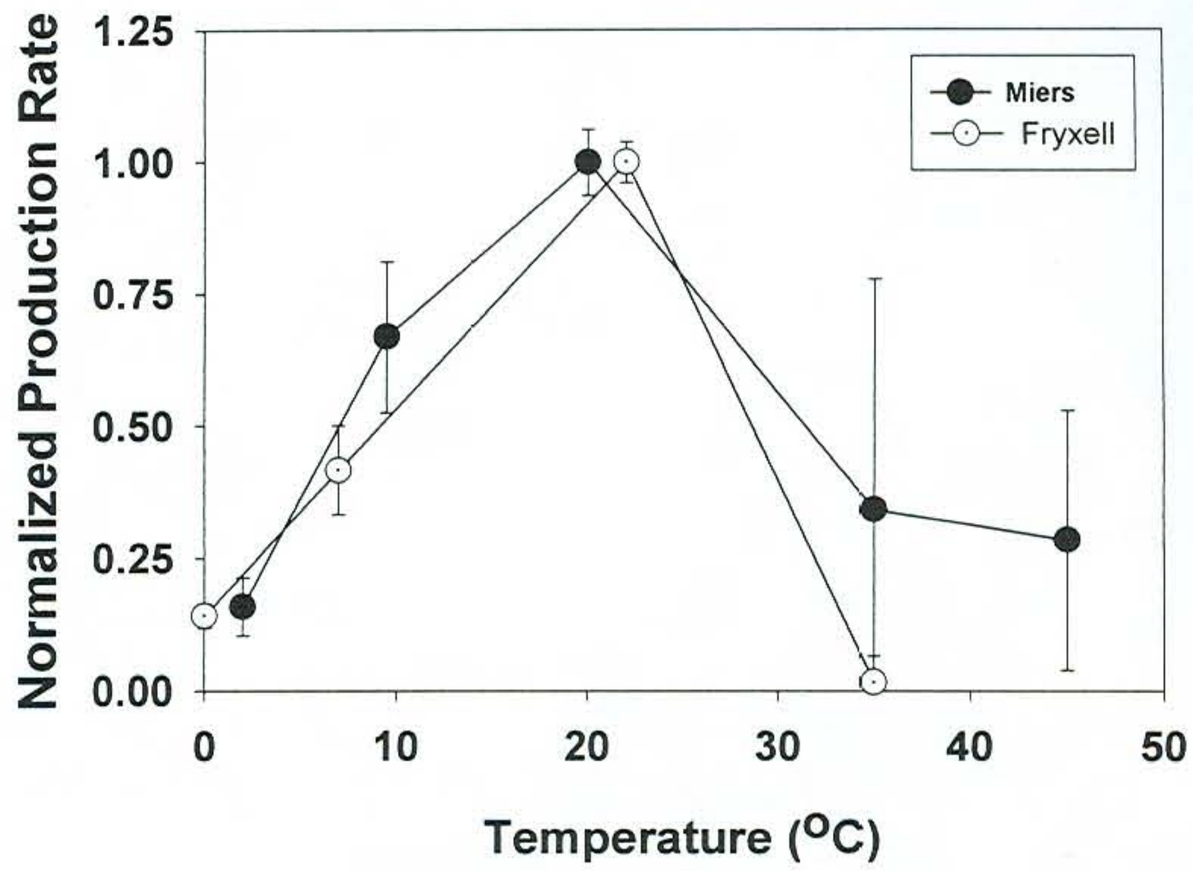

FIG. 7. Response of light-saturated photosynthesis by cyanobacterial assemblages collected from Lakes Fryxell and Miers and incubated at temperatures between 0° and 45° C. Rates are expressed normalized to the rate at the temperature yielding the maximum photosynthetic rate in order to demonstrate the optimal temperature for photosynthesis. Error bars for Lake Fryxell data represent range of replicates (n = 2), whereas error bars for Lake Miers data represent standard errors of the relationship between ^{14}C incorporation and time over 24 h (n = 6- -8 time points).

Ice covers that were devoid of sediments throughout their profiles (Vanda and Morning) also were devoid of chl *a* (i.e. chl $a < 0.5\ \mu g \cdot L^{-1}$). Because the lower portions of the ice covers were free of chl *a* (Fig. 3), it is unlikely that cyanobacterial mats were frozen into the bottom of the ice (with subsequent transport into the ice interior). However, we concentrated our sampling in the pelagic regions of the lakes; therefore, we did not sample benthic cyanobacterial mats entrapped in the seasonal moat ice or those benthic mats that may have been frozen into the underside of the permanent ice in the littoral zones of the lakes (Wilson 1965, Vincent 1988).

The distinct association of cyanobacterial biomass with the ice-bound sediments can be explained by two hypotheses that are not mutually exclusive. First, cyanobacterial cells attached to sediments within the surrounding desert soils (Seaburg et al. 1982) and ephemeral stream beds may be passively transported onto and into the ice via aeolian deposition and subsequent melting. Second, the cyanobacterial cells may be associated with the sediments in the ice because the sediments are the primary location within the ice covers where liquid water exists and promotes *in situ* growth.

If passive transport with sediments (hypothesis one) is the primary process whereby cyanobacterial cells enter the ice, then the ice-bound sediments should have similar chl *a*:sediment weight ratios to their source materials. Sediments collected from within the ice were significantly enriched in chl *a* compared to the soils surrounding the lake and those sediments lying on the surface of the ice (Fig. 4b). This enrichment is presumably the result of *in situ* growth when liquid water becomes available within the ice—a contention supported by the experiments showing light- dependent uptake of ^{14}C-bicarbonate and synthesis of cellular macromolecules in ice core meltwater (Fig. 5, Table 2). Therefore, the processes leading to liquid water generation in association with the sediment aggregates (i.e. solar radiation trapping) are likely to be governing the association of the cyanobacteria with the sediments in the ice covers.

Rates of light-saturated biomass-specific photosynthesis (P^b_m) and photosynthetic efficiencies (α) were 10- to 100-fold lower than those of the low-light- adapted phytoplankton in the underlying water column of these lakes (Lizotte and Priscu 1992) and those of sea ice algae adapted to low-light (e.g. Palmisano et al. 1985, Kirst and Wiencke 1995). Samples were collected during September and October 1995; the ice covers had been experiencing temperatures below 0° C (ca. −20° C at 2 m) since April 1995 (Fig. 2). The existence of liquid water in the ice and active photoacclimation by the ice-bound cyanobacteria was highly unlikely at this time; therefore, it is inappropriate to interpret the measured photosynthetic parameters in the context of photoadaptive strategies. Rather, the low photosynthetic versus irradiance parameters represent the photophysiological status of the cells as they enter the austral spring and a period when liquid water may become available for photometabolic processes. It is unknown at this time if the cells are able to shift-up their rates of photometabolism during a more prolonged exposure to liquid water.

The relative partitioning of photosynthate into carbohydrates versus protein is often indicative of the relationship between rates of carbon fixation and nutrient assimilation (Konopka and Schnur 1980). Relative incorporation of photosynthate into protein should be high when the rates of the two processes are comparable. Alternatively, when rates of carbon fixation exceed the rates of nutrient assimilation (in particular nitrogen), the excess carbon and energy are stored as polysaccharide and the

relative incorporation into protein should decrease as the relative incorporation into polysaccharide increases. Such patterns of preferential incorporation of CO_2 into polysaccharide have been found to occur at high light intensities within both cultures and natural populations (Konopka and Schnur 1980). Despite the fact that polysaccharide synthesis was optimized by our experimental design (light intensities were always saturating for photosynthesis), the ratio of protein to polysaccharide synthesis was higher than nutrient-sufficient cultures of a temperate oscillatorean (*Oscillatoria rubescens,* 35% protein:50% polysaccharide; Konopka and Schnur 1980) and higher than natural populations of *Phormidium* (36% protein:50% polysaccharide) or *Nostoc* (22% protein:62% polysaccharide) from Fryxell Stream within the Taylor Valley of McMurdo Sound (Vincent and Howard-Williams 1989). This comparison indicates that the ice cyanobacteria exhibited net cellular growth within hours of exposure to ice meltwater and suggests that growth was probably not limited by nutrient acquisition processes under these conditions. The relatively high proportion of protein synthesis relative to temperate Oscillatoriaceae also may be indicative of increased enzyme production in order to compensate for suboptimal enzyme temperatures (Thompsen et al. 1992). Such compensation would result in a higher protein cell content that is consistent with several studies showing higher protein contents of microalgae growing at low temperatures (e.g. Eppley 1972, Darley 1982, Thompsen et al. 1992).

Environments that exhibit temperatures continually below 5° C promote the establishment of psychrophilic (defined as having optimal growth temperatures <15° C) microbial populations (Morita 1975). Therefore, in the initial stages of our studies, we believed that the lake ice, with temperatures continually at or below 0° C (Fig. 2), was a habitat likely to harbor a psychrophilic population of cyanobacteria. However, all of our temperature experiments showed that rates of photosynthesis were optimal at temperatures >15° C. This psychrotrophic response (defined as having optimal temperatures above 15° C, yet having the ability to grow at temperatures <5° C) could be caused by a general lack of psychrophilic genotypes among the organisms colonizing the ice covers. Sediment transport onto and into the ice covers (Squyres et al. 1991, Fritsen and Priscu, pers. observ.) makes it likely that the cyanobacteria colonizing the lake ice habitats were originally derived from the soils and ephemeral streams and ponds throughout the valleys, which have a preponderance of psychrotrophic cyanobacteria with inherently slow growth rates at 0° C (Seaburg et al. 1982, Tang et al. 1997).

Tang et al. (1997) suggested that the lack of cyanobacterial psychrophiles in polar freshwater systems may be attributed to selection factors other than temperature that dictate which organisms survive and grow within these extreme environments. Selection factors such as freeze–thaw tolerance, tolerance to high fluxes of solar radiation, and desiccation are among those that could determine survival. Therefore, selection may not be specifically for low-temperature growth adaptations. We would add that obligate psychrophilic microbes are often sensitive to even moderate increases in environmental temperatures because their membranes (often comprised of highly unsaturated lipids) may irreversibly lose their integrity on heating, causing cell mortality. Despite low annual mean temperatures in the soils and ephemeral streams of Antarctica, temperatures can be highly variable during the austral summer months and may reach temperatures in excess of 15° C for short periods (Campbell et al. 1998, Dana et al. 1998). High temperatures in the lake ice are not likely to be eliminating psychrophiles. However, obligate psychrophilic cyanobacteria may not be available for colonizing the ice habitat because they are eliminated from the habitats that provide the inoculum populations. Therefore, even the short-term increases in environmental temperatures in the polar desert soils, ephemeral stream beds, and ephemeral ponds may ultimately be controlling the dominance of psychrotrophic cyanobacteria throughout the polar desert's environments, including the ice covers.

The estimates of annual *in situ* growth and annual primary production by the ice assemblages in each of the lakes have considerable uncertainty because they are based on a small number of samples, uncertainty in the length of the growing season, and assumptions that remain untested (e.g. the absence of metabolic acceleration during the growth season, the absence of nutrient limitation, the presence of chl *a* in nonviable material, etc.). Placing these estimates into a broader ecosystem perspective will require a much larger compilation of long-term productivity measurements in the lakes, streams, and soils. However, the contribution of the ice assemblages to each lake's annual primary production is likely to span the range of less than 1% (in lakes with relatively thin ice covers, extensive benthic mat communities, and phytoplankton populations; e.g. Lakes Hoare, Vanda, and Bonney) to 100% (in lakes with thick [>15 m] ice covers; e.g. Vida).

Overall, primary production within the ice covers of these lakes probably does not represent a substantial portion of the present-day total primary production in the desert and may not contribute significantly to the trophodynamics of the McMurdo Dry Valleys. However, the growth of cyanobacteria in these ice covers is likely to have consequences for other aspects of the ecosystem's biogeophysical dynamics and evolutionary processes. For example, ice-grown cyanobacteria may be the primary contributors to the burial of organic carbon in sediments in the regions of the lakes that do not support the growth of benthic mats. Several lakes have dense

bodies of bottom water (due to the high salt content) that retard sedimentation of the soft-bodied phytoplankton that grow within the upper euphotic zones of these lakes. Therefore, a large portion of the primary production in the euphotic zones may be regenerated within the water column and may not be buried in the lake's present-day sediments. Organic carbon flux to the bottom of these lakes may be dominated by the flux of organic carbon produced in the ice that maintains an association with the dense sediments as they settle to the lake's benthos. This contention is supported by high sediment and chl *a* loads in deep water sediment trap collections in these regions (Priscu, unpubl.).

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