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Perennial Antarctic Lake Ice: A refuge for Cyanobacteria in an Extreme Environment

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INTRODUCTION AND BACKGROUND

The polar deserts of Antarctica form one of the driest and coldest ecosystems known and have, until recently, been thought to harbor little life (69). The diaries of Captain Robert Falcon Scott, one of the earliest explorers of the McMurdo and South Polar regions of Antarctica, referred to the McMurdo Dry Valleys as the "Valley of the Dead" during his first visit in 1903 (79). Recent studies in Antarctica have now revealed new information on the presence of microbial life in environments such as surface snow near the South Pole (9), 3.5 km deep Vostok ice (43,75), exposed soils (92), sandstones (22), melt water ponds (91), the liquid water column of permanently ice-covered lakes (74), and the ice covers of permanent lake ice (73, 76). Most of the microbes found in these habitats are prokaryotic (5, 30, 87). A large portion of these prokaryotes are photosynthetically active cyanobacteria that can provide new carbon and nitrogen to the ecosystem. As in all desert ecosystems, the production of new carbon and nitrogen compounds is critical given the general lack of liquid water and the dearth of allochthonous production. Without new carbon and new nitrogen entering the system, the presence of higher trophic levels and biodiversity in general is compromised.

Numerous studies on cyanobacteria-dominated systems have occurred in the McMurdo Dry Valleys. These valleys form the largest (~ 4,000 km^2) ice- free expanse of land on Antarctica and are the centerpiece of an NSF- funded Long Term Ecological Project aimed at integrating the understanding of meteorological, geophysical, hydrological and biogeochemical processes in the area. Meteorological conditions in the dry valleys (Table 1) reveal the extreme conditions that organisms must overcome to survive. Surface air temperatures average –27.6 ^oC, but range widely from 10 ^oC to –65.7 ^oC. Air temperatures above freezing are rare averaging 6.2 degree days per year. Soil temperatures show similar averages and minimums but, owing to direct solar heating, reach almost 23 ^oC during cloud-free summer days. Hence, soil microbes must have the capability to withstand perhaps the most extreme temperature range on Earth. Given the persistent and often high winds characteristic of the dry valleys in concert with low and seasonal stream flow, most organic matter is mobilized throughout the region by wind.

Perhaps the first description of cyanobacteria in the McMurdo Dry Valleys was by Griffith Taylor during the 1911 British expedition to southern Victoria Land. Taylor noted the existence of "water plants" through the clear moat ice on a McMurdo Dry Valley lake (86). Since Taylor's early observations, little research on cyanobacteria in the McMurdo Dry Valleys occurred until the 1960's when Wilson (98) studied the cyanobacterial mats associated with lake and pond ice. Wilson observed pieces of cyanobacterial mat consisting of *Oscillatoria* and *Nostoc* moving upward through the ice in the lakes and ponds of Wright and Taylor Valleys in the McMurdo Dry Valleys. These mats were 1-5 cm^2 in area and each was associated with a gas bubble. The phenomenon was observed only in small ponds and the shallow parts of lakes. Wilson used a thermodynamic model to show that the upward movement was a function of gas-induced

buoyancy coupled with absorption of solar radiation by the mat itself, which melts the overlying ice. Meyer-Rochow confirmed Wilson's observations. Following these initial reports, a considerable amount of research was conducted on benthic mats within the lakes (e.g. 62, 80, 93), streams (e.g. 39, 89) and ponds (e.g., 34, 35, 40). Except for the observation of pieces of mat within the lake ice of Lake Hoare by Squyres et al. (83), cyanobacteria within lake ice received little direct attention since its early description by Wilson and Meyer-Rochow. During studies on the biogeochemistry of nitrous oxide in McMurdo Dry Valley lakes, Priscu and co-workers observed a peak in nitrous oxide associated with a sediment layer 2 m beneath the surface of the 4 m thick ice cover of Lake Bonney (67, 72, 73). This observation together with elevated levels of chlorophyll-a (chla), particulate organic carbon, particulate organic nitrogen, ammonium, and dissolved organic carbon (100) led to the hypothesis that the cyanobacteria within the lake ice were not passive but grew actively within the ice cover. Subsequent research showed that adequate liquid water was present (2, 25) to support an active prokaryotic ecosystem within the ice consisting of cyanobacteria and a diversity of bacterial species (e.g. 30, 59, 66, 73).

Cyanobacteria in Antarctic systems are adapted and acclimated to their environment in terms of temperature, freeze/thaw survival, photoprotection and light acquisition for photosynthesis (52, 53, 84, 85, 89) and provide adequate fixed carbon via photosynthesis to drive a well-developed ecosystem (87). Despite their significance to Antarctic ecosystem dynamics, very few cyanobacteria can be considered true psychrophiles (24, 84). Their high growth and photosynthetic optima (>20 ^{o}C) in concert with their ability to metabolize near 0 ^{o}C best classifies them as psychrotolerant or psychrotrophic. Interestingly, the same cyanobacterial species (to a large extent *Phormidium, Oscillatoria* and *Nostoc*) occur across habitats that have highly divergent environmental extremes. For example, the cyanobacteria in melt ponds and ephemeral streams face high radiation and frequent freeze/thaw cycles whereas those inhabiting the benthos of lakes with perennially liquid water columns receive low radiation and are constantly bathed in liquid water.

Analysis of particulate organic carbon (POC) and DNA sequence distribution (5, 6, 7, 27, 30) provides strong evidence that microbes are distributed widely throughout the McMurdo Dry Valleys via aeolian processes. Primary sources of this organic carbon are cyanobacterial mats located in ephemeral streams and associated with the benthos of lakes and ponds. Parker et al. (61) suggested that cyanobacterial mats lift off the bottom of the larger permanently ice covered lakes and freeze onto the underside of the lake ice. Annual freezing of new ice to the bottom of the lake ice together with ablation at the surface (2) eventually brings the mats to the surface where aeolian processes distribute them to the surrounding environment. Parker et al. (61) further proposed that this mechanism reduces organic carbon within the lakes leading to oligotrophy over time. Burkins et al. (6), based on stable isotope signatures, concluded that lacustrine-derived

particulate organic matter together with marine and endolithically derived material contributes significantly to the organic carbon content of the Taylor Valley. Hence, cyanobacteria provide an important source of carbon that supports contemporary soil metabolism (7, 47, 50). DNA hybridization studies between cyanobacteria and other prokaryotes found in the permanent lake ice in the McMurdo Dry Valleys have revealed that cyanobacterial mats in ephemeral streams provide the biological seed for the lake ice cyanobacteria (29, 30, 73). It is clear that cyanobacterially colonized lakes and streams are the " life support system" of Antarctic polar deserts, providing organic carbon to the surrounding areas and seeding numerous habitats with microbes.

This paper will focus on the organisms and ecosystem processes associated with a novel habitat that exists within the permanent ice covers of lakes within the area. Our specific objectives are to: (1) describe the microbes that exist within the lake ice; (2) present biogeochemical data to reveal the structure and function of this unique ecosystem; and (3) define the conditions that produce liquid water to support microbial growth and associated biogeochemical processes.

STUDY AREA

The McMurdo Dry Valleys, southern Victoria Land ($76^{o}30^{'}$ to $78^{o}30^{'}$S; 160^{o} to 164 ^{o}E) consist of a number of valleys that extend from the Polar Plateau to McMurdo Sound (Fig 1). The valleys are ice-free because the Transantarctic Mountains block the flow of ice from the polar plateau and low precipitation and strong katabatic winds (14) lead to little accumulation of snow in the area. The valleys harbor some of the only permanently ice- covered lakes on Earth (e.g., 31, 68). The lakes occupy closed basins and vary in surface area (1 to about 6 km^2), depth (20-85 m), and ice-cover thickness (3-5 m) (82). The permanent ice covers greatly influence wind-driven mixing in the liquid water column (81, 82), gas exchange between liquid water and the atmosphere (67, 72, 95), light penetration (26, 46, 60) and sediment deposition into the water column (3, 55). Consequently, ecosystem properties in the water columns of the lakes are largely controlled by the presence of the perennial ice cover (23, 96). A majority of the research presented in this paper was derived from three lakes in the Taylor Valley, particularly Lake Bonney (Fig. 1).

The dry valley lakes are perennially ice-covered due to a combination of cold mean annual air temperatures (see Table 1) and seasonal glacial melt that flows into the lakes during the summer (49). McKay's model shows that the latent heat entering the lake in the melt water plays a key role in the maintenance of a liquid water body beneath the permanent ice cover. Hence, the presence and thickness of the ice cover depends to a large extend on air temperature, which controls both freezing and melting processes. The ice thickness of most of the lakes that contain substantial liquid water bodies ranges from 3 to 5 m and varies with air temperature and the degree of mixing within the lakes (18, 82, 96). The thickness of the lake ice

is ultimately governed by the dynamic equilibrium between lake water accretion (freeze) at the bottom of the ice and ablation at the surface. Hence, the ice can be depicted in a gross sense as an upward moving conveyor belt carrying newly frozen ice from the bottom to the top where it is lost through ablation (15).

Sediment layers exist in most of the ice covers (2, 3, 25, 73, 83) as a result of aeolian deposition followed by summer melting. The sediments melt to a depth where solar radiation can no longer supply adequate energy to generate melt, i.e., the downward melting is balanced by the upward conveyer motion of the ice described above. Based on the balance between these processes, the sediment layers reach an equilibrium depth in the ice between 0.5 and 2 m (2, 24). Losses of sediment from the ice are not completely understood, but appear to be through cracks or conduits in the lower portion of the ice column (2, 80, 83).

WHY STUDY CYANOBACTERIA IN ICE?

Earth's biosphere is cold, with 14% being polar and 90% (by volume) cold ocean <5 ^{o}C. More than 70% of Earth's freshwater occurs as ice, and a large portion of the soil ecosystem exists as permafrost. Expectations of commercial applications and interest in the early evolution of life have led many researchers to examine microbes, including cyanobacteria, in thermal systems. Based on the occurrence of evolutionarily old microbes in extreme thermal systems, in concert with extensive geothermal activity during the early evolution of our planet, it is generally thought that life on Earth evolved in hot environments (42, 63). Recent considerations about the evolution of life, however, have suggested that a "hot start" was probably not the only alternative for the origin of life. Though there are strong arguments for a thermal origin of life based on small subunit ribosomal RNA (16S rRNA) phylogenetic relationships, the validity of this relationship is questioned by researchers who believe that phylogenies are strongly biased by the use of just a single gene for the construction of the tree of life. If lateral gene transfer is common among all prokaryotic organisms (56), then a hierarchical universal classification is difficult or impossible (64, 65) and evolutionary patterns must be reassessed (16). A hot origin of life also is not supported by new results from phylogenetic trees based on genes that do not code for ribosomal RNA, chemical experiments with alternative structure for the nucleic acid backbone (19), considerations about the thermal stability of basic molecules found in all organisms, and statistical analysis of the GC content of DNA (28). Adaptation to life in hot environments may even be a late adaptation (4).

Though much more research is required to determine whether life originated in hot or cold environments, it is highly probable that cold environments have acted as a refuge for life during major glaciations. Recent evidence has indicated that around 600 millions years ago during the Neoproterozoic, early microbes endured an ice age with such intensity that even the tropics froze over (37, 38, 78). According to this so-called "Snowball Earth Hypothesis", the Earth

would have been completely ice covered for 10 million years or more, with ice thickness exceeding 1 km. Only the deepest oceans would have contained liquid water. One of the primary criticisms of the Snowball Earth Hypothesis is that the thick ice cover over the world ocean would cut off the supply of sunlight to organisms in the seawater below and thereby eliminate photosynthesis and all life associated with photosynthetic carbon production. Others have concluded that global-scale freezing would extinguish all surface life (97). Only the hardiest of microbes would have survived this extreme environment. Hoffman and Schrag (38), Vincent and Howard-Williams (88) and Vincent et al. (91) suggest that photosynthetic cyanobacteria and bacteria, similar to those found in the permanent ice covers of contemporary polar systems, may have acted as an icy biotic refuge during this period. The resultant high concentration of microbes in these icy environments would favor intense chemical and biological interactions between species, which would force the development of symbiotic associations, and eventually eukaryotic development through evolutionary time (91). Though this "density- speeds- evolution" theory has been considered primarily in the context of thermal microbial mat communities (48), it is highly probable that ice-bound habitats also provided opportunities for microbial evolution, inducing the radiation of the eukaryotic cell type at the onset of the Neoproterozoic (38, 45).

Studies of Earthly ice-bound microbes also are relevant to the evolution and persistence of life on extra-terrestrial bodies. During the transition from a clement to an inhospitable environment on Mars, liquid water may have progressed from a primarily liquid phase to a solid phase and the Martian surface would have eventually become ice-covered (95). Evidence from Martian orbiter laser altimeter images has revealed that water ice exists at the poles of Mars. Habitats in polar ice may serve as a model for life on Mars (59, 73, 74) as it cooled and may assist us in our search for extinct or extant life on Mars today (94). Surface ice on Europa, one of the moons of Jupiter, appears to exist in contact with subsurface liquid water (8, 32). Solar heating of the subsurface could result in melt layers similar to those described in Earth's polar habitats (74, 91). With reports of life almost 4 km beneath the Antarctic ice sheet and implications for life in Lake Vostok, an enormous lake ~1 km deep and about 14,000 km^2 in surface area (13, 43, 75) it is clear that we must extend the bounds of what is currently considered the "Earth's biosphere" to include subsurface ice environments.

THE LAKE ICE ENVIRONMENT

Vertical Profiles

A majority of research on microbes in permanent lake ice has focused on the east lobe of Lake Bonney (see Fig. 1), though studies have encompassed at least seven other lakes in the McMurdo Dry Valleys. Particulate organic carbon (POC) in the ice cover of the east lobe of Lake Bonney is concentrated at 2 m in association with maximum sediment levels (Fig 2). Chlorophyll-a, primary productivity, bacterial density, and bacterial activity (uptake and metabolism of organic

matter) also coincide with the depth of maximum sediment concentration indicating that viable phototrophs and heterotrophs are present in the ice and can become active after a short exposure to liquid water.

Dissolved organic carbon (DOC), dissolved inorganic carbon (DIC) and ammonium show maxima in the region of highest sediment and POC concentration, suggesting active biogeochemical cycling of these constituents. The DOC, presumably from extracellular photosynthate released from cyanobacteria following photosynthetic inorganic carbon fixation, can supply the heterotrophic component of the microbial assemblage with an energy and carbon source for growth which, in turn, recycles CO_2 to support photosynthesis by the cyanobacteria. The ammonium maximum associated with the sediment layer implies active regeneration of nitrogen, ammonium leakage following atmospheric nitrogen (N_2) fixation, leaching from sediments, or a combination of these sources (in excess of sinks). The lack of a clear vertical trend in soluble reactive phosphorus (SRP) is related to adsorptive processes that occur between SRP and the inorganic sediment material. The general trends in the east lobe of Lake Bonney are evident in most lake ice covers in the McMurdo Dry Valleys. Combined data from seven lakes show increases in POC and particulate organic nitrogen (PON), primary and bacterial production, chlorophyll-a, and bacterial biomass with sediment concentration (Fig. 3). The ratio of POC to PON for the combined data from all ice covers in the region averages 8.9 (g:g), which is higher than the ratio of 5.7 (g:g) that occurs during balanced growth of photoautotrophs (77).

Growth Rates and Photosynthetic Activity

Cyanobacteria dominate the biomass (e.g., POC) within the ice covers. Pinckney and Paerl (66), using chlorophyll-a normalized pigment markers, showed that myxoxanthophyll, echinenone, zeaxanthin and canthaxanthin, which are all markers for cyanobacteria, were the most abundant phytopigments in ice aggregates from the Lake Bonney ice cover. These pigments resemble those measured in shoreline soil samples more closely than in the underlying lake water implying a terrestrial origin for the lake ice assemblage. Pinckney and Paerl used $^{14}CO_2$ photopigment- labeling experiments to further show that carbon-specific growth rates are less than 0.10 d^{-1} during the first 24 hours after thawing. Fritsen and Priscu (24), using $^{14}CO_2$ labeling of cellular macromolecules, showed that despite low photosynthetic rates a large proportion (41%) of the photosynthate was incorporated into protein, indicating that the cyanobacteria were undergoing efficient net cellular growth. $^{14}CO_2$ incorporation into polysaccharide, lipid, and low molecular weight metabolites averaged 39%, 4.1% and 15.9%, respectively, during the same experiments. Photosynthesis versus irradiance experiments revealed that the cyanobacterial assemblages had variable maximum biomass-specific rates of photosynthesis, ranging from 0.0043 to 0.0406 µgC (µg chlorophyll-a)$^{-1}$ h^{-1} among the six ice

covers studied. $^{14}CO_2$ incorporation into protein was used to compute carbon-specific growth rates ranging from 0.001 to 0.012 d^{-1}, in agreement with the pigment labeling results (66).

During the months of continuous sunlight during summer, *in situ* irradiances are above that required to saturate the photosynthetic capacity of the cyanobacteria without causing inhibition (23). Hence, *in situ* growth rates are not likely to be light limited when liquid water is present. The light- saturated rate of photosynthesis normalized to chlorophyll-a for the cyanobacterial assemblage in Lake Fryxell increased about 10-fold when incubation temperature was increased from 2° to 20 °C corresponding to a Q_{10} value of 3.46. The temperature response of light- saturated photosynthesis is near 20 °C, with about 10% of the maximum rate occurring at *in situ* growth temperatures (23, 24). These data support the results of Tang et al. (84) and Tang and Vincent (85) who contend that few true cyanobacterial psychrophiles are associated with polar freshwater systems. Nadeau and Castenholz (53, 54) recently isolated one of the first true polar psychrophilic cyanobacteria from a pond on the Ross Ice Shelf, Antarctica. Based on genetic analysis Nadeau and Castenholz concluded that psychrotolerant forms are more closely related to temperate cyanobacteria, whereas the true psychrophiles probably evolved in the polar habitat. The temperature response of light-saturated photosynthesis in the permanent lake ice and stream cyanobacteria of the McMurdo Dry Valleys indicates that these assemblages are psychrotrophic or psychrotolerant whereas sea ice diatoms and the chlorophyte *Chlamydomonas subcauda* isolated from the liquid water column of Lake Bonney (51) are true psychrophiles (Fig. 4). The relatively high temperature thresholds evident in the stream cyanobacteria would allow them to cope with the high soil temperatures that often occur during summer (see Table 1). The lack of cyanobacterial psychrophiles in lake ice assemblages may be related to selection factors other than temperature (e.g., freeze-thaw tolerance, tolerances to high fluxes of solar radiation) that dictate which organisms survive and grow in icy environments (84, 87, 90).

In contrast to most of the dry valley lakes that have maximum concentrations of cyanobacteria and sediment located 1 - 2 m below the ice surface, the cyanobacterial aggregate layer in Lake Fryxell is concentrated in the upper 0.5 m. Presumably this difference is the result of elevated snow accumulation in Lake Fryxell, which lies close to the relatively moisture rich coast of McMurdo Sound (20, 21). The snow effectively blocks incident radiation at the ice surface hindering the downward melting of sediments and associated microorganisms. As the result of near- surface sediment accumulation, surface melt pools up to 20 cm deep and 1 m in diameter form during the summer and support dense cyanobacterial mats. These near- surface cyanobacteria exist as loose aggregates or flakes measuring 0.5 to 2 cm in diameter that coat 60 to 90 % of the ice surface within the melt pools. Records of *in situ* temperatures within the shallow melt pools at the surface of Lake Fryxell show diurnal changes of 10 °C within the ice cyanobacterial aggregates (Fig. 5a). The absolute value of temperatures within the aggregates is dependent on the orientation of the mat relative to the solar disk throughout the day. The

aggregates within the north-facing melt pool experienced temperatures about 4 ^{o}C higher than those in the south-facing pools reaching a maximum of 6.3 ^{o}C. Since the temperature probes were placed horizontally 0.5 to 1 cm inside the mats these temperatures are not likely to be artifacts caused by direct solar heating of the probes. Cores (2.8 cm diameter) of aggregates in the small-surface pools yielded chlorophyll-a concentrations of 15.34 µg chla cm^{-2} (Standard error = 2.38; n = 6). When extrapolated from the centimeter to meter scale this represents about 90 to 153.4 mg chla m^{-2} because there was only partial coverage of cyanobacterial aggregates in the pools.

Photosynthesis-irradiance relationships changed in response to freezing (Fig 5b). Maximum rates of photosynthesis were approached at irradiances greater than 600 µmoles of photons m^{-2} s^{-1} in the experiments conducted. Compensation irradiances (where photosynthesis = respiration) were 202 µmol photons m^{-2} s^{-1} before and 308 µmol photons m^{-2} s^{-1} after experimental freezing, which equals a 53% increase induced by freezing. The rates of respiration (O_2 consumption in the dark) were 33% lower following freezing (-1.6 x 10^{-3} mg O_2 mg l^{-1} s^{-1} after freezing versus -2.15 x 10^{-3} mg O_2 mg l^{-1} s^{-1} before freezing). Despite the changes that occurred following an experimental freeze-thaw cycle, freezing and thawing does not appear to have a major adverse affect on the cyanobacteria in the ice over long time scales. Rather, freezing may be the environmental parameter that allows biota and ecosystems to live within polar environments where low-light (< 200 µmol photons m^{-2} s^{-1}) or complete darkness (spanning days to months) would otherwise be dominated by the loss of reduced carbon and ecosystem energy.

Phylogenetic Affiliation

The phylogenetic diversity of bacteria and cyanobacteria colonizing sediment particles at a depth of 2.5 m in the permanent ice cover of Lake Bonney was characterized by analyses of 16S rRNA genes amplified from environmental DNA (29, 30). A rRNA gene clone library of 198 clones was made and characterized by sequencing and oligonucleotide probe hybridization. The library was dominated by representatives of the cyanobacteria, proteobacteria, and Planctomycetales, but also contained diverse clones representing the Acidobacterium/Holophaga division, the Green Non-Sulfur division, and the Actinobacteria. Of the cyanobacterial gene clusters characterized, only one was closely (>97% similarity) affiliated with a well-characterized cyanobacterial species, *Chamaesiphon subglobosus*. The remaining cyanobacterial gene clusters were less than 93% similar to any characterized sequences in public databases although they resembled *Leptolyngbya* sp. and *Phormidium* sp. Oligonucleotide probes made from three lake ice cyanobacterial clusters were used to screen environmental 16S rDNA samples obtained from the terrestrial (soil and stream) environment in the vicinity of Lake Bonney and Lake Fryxell. The probes designed to hybridize to cyanobacterial 16S rRNA genes effectively hybridized to each sample, indicating that the cyanobacterial sequences present in the lake ice of Lake Bonney are

also found in terrestrial cyanobacterial mat samples. Sequence analysis together with physiological data indicate that the cyanobacterial (and bacterial) community within the lake ice is dominated by organisms not uniquely adapted to the lake ice ecosystem. Instead, the strong katabatic winds common to the region (see Table 1) act to disperse microorganisms in the desert environment and provide the biological seed for the lake ice microbial assemblage (30, 73).

Molecular characterization (PCR amplification of the nifH fragments) of the nifH gene (encoding for the highly conserved Fe-protein subunit) of nitrogenase in lake ice sediments from Lake Bonney also demonstrated the presence of a diverse diazotrophic assemblage (57). The nifH analysis suggested that phototrophic cyanobacteria and heterotrophic microorganisms have the potential to fix atmospheric nitrogen when liquid water is present in the ice cover. The expression of nitrogenase was confirmed by the acetylene reduction assay for nitrogenase activity (33, 57, 59).

Biogeochemistry

Nutrient bioassay experiments showed that cyanobacterial photosynthesis was stimulated by the addition of inorganic nitrogen, either as ammonium or nitrate (Fig 6). Iron in the presence of a chelator and phosphorus did not stimulate photosynthesis. These results imply that cyanobacterial photosynthesis, and presumably growth, is limited by inorganic nitrogen, a contention that is supported by the POC:PON ratios in the ice (see Fig 3). The ability to fix atmospheric nitrogen could offset the apparent photosynthetic inorganic nitrogen deficiency. Nitrogenase activity was stimulated by phosphorus and iron addition and showed little effect from the addition of mannitol (Fig. 6). Even though molecular analysis showed that both cyanobacteria and bacteria in the ice aggregates have the potential to fix atmospheric nitrogen, the stimulatory effect of nitrogenase by light implies that cyanobacteria are responsible for a majority of the phenotypic expression of this enzyme in nature (59).

Another source of inorganic nutrients to the ice assemblage is the sediment. A considerable amount of ammonium and phosphate can be leached from soils surrounding the lake (Fig. 7). These data, particularly the more complete phosphorus data set, show that most of the adsorbed nutrient is bound to small soil particles. Interestingly, a significantly higher quantity of phosphorus was leached from the soils when salty deep water (see 82) from the Lake Bonney water column was used as the solvent relative to freshwater from just beneath the ice cover. Sediments within the ice cover itself have relatively little leachable phosphorus implying that most of the phosphorus was desorbed as the sediments melted through the ice, a process that could explain the vertical profile of inorganic phosphorus in the lake ice (see Fig. 2). The apparent nitrogen deficiency in the ice cyanobacterial assemblage can be explained by the relative amounts of nitrogen and phosphorus that can be leached from the terrestrial soils following aeolian deposition on the ice surface by wind. Based on the available data, the average amounts

of ammonium and phosphorus that can be leached from surrounding soils is 7.1 µgN g sediment^{-1} (16.2 in KCl extracts) and 4.1 µgP g sediment^{-1}, respectively. The ratio of leachable N:P is 1.7 (3.9 if KCl exchangeable ammonium is included), which is well below that required for balanced cyanobacterial growth. The low N:P ratio resulting from differential N and P leaching would provide a selective advantage for microorganisms that have the ability to fix atmospheric nitrogen.

Despite apparent cyanobacterial nitrogen deficiency in the ice, the ammonium maximum associated with the sediment layer in Figure 2 indicates that sources of ammonium exceed sinks. Results from ^{15}N-ammonium based isotope dilution experiments show that uptake of ammonium either equaled or exceeded microbial ammonium regeneration for the samples and size fractions analyzed (Table 2). Under these conditions the ammonium pool should be depleted. The absolute rates of ammonium uptake and regeneration relative to the PON pool range from 0.7% d^{-1} to 22.0% d^{-1} and 0.1% d^{-1} to 22.1% d^{-1}, respectively. The lowest activity occurred in the <63 µm size class from the Lake Hoare ice cover. These values are similar to those measured within the water column of Lake Vanda (70). Apparently, a combination of ammonium leaching and ammonium release following atmospheric nitrogen fixation replenishes the ammonium pool faster than it is consumed. Based on the size-fractionated data from Lake Bonney, the bacterial (<63 µm) fraction is responsible for a majority of the ammonium regeneration. Half-saturation constants for ammonium are generally below the ammonium levels within the ice (compare Figure 2 and Table 2) corroborating the results of the ^{14}C-based bioassay experiments, which show nitrogen deficiency.

The peak in dissolved inorganic carbon (DIC) associated with the sediment layer also suggests active cycling of the organic and inorganic carbon pools. Leaching experiments revealed little DIC production from the sediments alone (unpublished data). Conversely, $^{14}CO_2$ release experiments showed pronounced mineralization of organic carbon from radiolabeled cyanobacteria collected from various soil locations in the dry valleys (Fig. 8). Interestingly, *Nostoc* and *Phormidium* dominated mats from the Lake Bonney basin were more labile than a *Phormidium* dominated mat from the Lake Vida basin. The turnover of particulate organic carbon in these mat samples ranged from 17.5% d^{-1} in the *Nostoc* mat to 57.8% d^{-1} in the *Phormidium* mat collected from the Lake Vida basin, which are on average higher than the turnover rates of PON.

Microbial Consortia

A majority of the cyanobacterial and bacterial activity was associated with sediment aggregates, as opposed to individual microorganisms embedded in the ice matrix. A core of Lake Bonney ice collected from 0.2 to 0.25 m showed considerable differences between clean and sediment- laden layers based on epifluorescence counts of material stained with SYBER gold, a probe specific for DNA (12). Based on the SYBER gold -staining study, the average bacterial and

virus-like particle (VLP) densities in clear ice were $2.29x10^3$ cells ml^{-1} and $1.23x10^4$ VLPs ml^{-1}, respectively. The sediment- laden portion of this ice core had a bacterial density of $1.15x10^4$ cell ml^{-1} and a VLP count of $2.77x10^4$ ml^{-1}. The virus:bacteria ratio was 5.37 for the clear ice and 2.41 for the sediment sections of the core. These ratios are within the range of those seen in more temperate climates that include eutrophic and oligotrophic waters (101) but lower than those in the water columns of freshwater lakes of Signey Island, Antarctica (99) and Lake Hoare, Antarctica (44). Tomato mosaic tobamovirus RNA also has been detected but not quantified using molecular methods in 140,000 year old Greenland ice cores (10). There were on average 5.02 fold more bacteria and 2.25 fold more VLPs in the Lake Bonney ice core sample that included the sediment than in the clear ice section of the core. The virus:bacteria ratio for sediment laden ice was less than half of that observed in the clear ice, implying there are fewer viruses per bacterium in the sediment- containing section of the core. It remains unclear if the VLPs were bacteriophage or cyanobacteriophage. However, the presence of viral particles in the ice indicates that phage may play a major role in genetic transfer and overall survival of prokaryotes in the ice. Castello et al. (11) isolated phage from *B. subtilis* isolated from deep ice cores from Greenland.

Figure 9 shows the lake ice assemblage on several scales. Microautoradiographic studies reveal that both bacterial and cyanobacterial activities were tightly associated with sediment particles corroborating experimental results. Microautoradiographs also indicated that virtually all of the incorporation of radiolabeled organic substrates was mediated by non-autofluorescent (non-chlorophyll containing) bacterial-size rods (0.5-1 µm length) and filaments (0.5 µm width) closely associated with aggregates whereas $^{14}CO_2$ incorporation was limited to filamentous cyanobacteria (59). Heterotrophic bacteria were attached to soil particles and associated with cyanobacterial colonies and aggregates. These observations are similar to those reported for temperate and tropical cyanobacteria- dominated systems (58). Tetrazolium salt (TTC) reduction assays further revealed that, when melting occurs, localized O_2 consumption associated with aggregates is sufficient to create reduced microzones. These microzones are associated with regions colonized by bacteria and cyanobacteria, suggesting they may be potential sites for O_2-sensitive processes such as atmospheric nitrogen fixation (57, 59). Pinkney and Paerl (66) showed that cyanobacterial and bacterial biomass and activities were heterogeneously distributed among aggregates, promoting the development of O_2 and, possibly, other biogeochemical gradients. Biogeochemical zonation and diffusional O_2 and nutrient concentration gradients likely result from microscale patchiness in microbial metabolic activities (i.e., photosynthesis, respiration). These gradients, in turn, promote metabolic diversity and differential photosynthetic and heterotrophic growth rates.

Phototrophy, heterotrophy and diazotrophy (N_2 fixation) can occur simultaneously in ice - aggregate microbial communities. Key environmental factors controlling the rates and

biogeochemical significance of these processes include: (i) the presence of radiant energy and liquid water; (ii) N, P and trace metals sufficient for phototrophy; (iii) adequate organic matter for heterotrophic activity; and (iv) energy (light or organic C), P, Fe and other trace metals sufficient for diazotrophy (59).

Mineralization of POC and PON is highly dependent on organic matter availability, the main source being cyanobacterial photosynthesis. Therefore, close spatial proximity of heterotrophs to phototrophs is essential for completion of carbon, nitrogen and phosphorus cycling. The paucity of higher trophic levels in the ice (e.g., protozoans) magnifies the importance of microbial interactions within the ice assemblage and amplifies the role played by virus in terms of microbial survival and possibly diversity. Clearly, the spatial and temporal relationships within the ice produce a microbial consortium that is of fundamental importance for initiating, maintaining, and optimizing essential life-sustaining production and nutrient-transformation processes. Close spatial and temporal coupling of metabolite exchange among producers and consumers of organic matter existing within the ice appears to be the limiting ecological factor enabling microbial process to coexist in what appears to be an otherwise inhospitable environment. To accomplish this feat, the microbes must exist in a highly cooperative and efficient manner. The basic consortial relationships that we believe exist within Antarctic lake ice are outlined in Fig. 10. We stress that without these close spatial linkages, the microbial assemblage may not be able to survive the extreme conditions posed by the ice environment.

Liquid Water Production

Virtually all of the metabolic data that exist on the dry valley lake ice is based on melted ice samples. Clearly, no biological and biogeochemical process would occur without the presence of liquid water, a contention that has been confirmed by the lack of activity obtained in experiments on cyanobacterial photosynthesis and atmospheric nitrogen fixation in solid ice samples (59, Priscu and Fritsen, and Priscu unpublished data). Since the discovery of a cyanobacterial/bacterial consortium within the permanent ice covers of the dry valley lakes (57,59,73) internal water production in permanent ice covers has become an important issue. In addition to life support within the ice, the permanent ice covers influence the exchange of momentum, thermal energy, and materials between the water column and the atmosphere (e.g. 26,41,72,83,96). The first evidence for the presence of liquid water in the ice covers was reported by Henderson et al. (36) who noted that a liquid “water table” developed within the ice cover of Lake Fryxell during summer. Subsequently, Squyres et al. (83) encountered liquid water 2.1 m below the surface while constructing sampling holes in Lake Hoare during early summer, and noted that the depth of the liquid water coincided with the bottom of the in-ice sediment. Adams et al. (1) observed the presence of liquid water near a sediment inclusion 2.5 m below the ice surface in otherwise dry ice from the Lake Bonney ice cover. Within days of the observation,

liquid saturated ice was encountered approximately 1.0 m below the surface in the same vicinity. Adams et al. (2) later noted dynamic relationships in gas bubbles within the ice cover indicating differential melting associated with the sediment layer.

Typical temperature profiles in the ice cover of the east lobe of Lake Bonney are shown in Figure 11a for the period January 1995 to January 1996. The most significant feature of these data in terms of liquid water production is the almost isothermal temperatures near 0 ^{o}C during the summer. These isothermal temperatures persist for approximately 85 days from November to February (see also 2, 25). In contrast, midwinter temperature gradients were typically 6 ^{o}C m^{-1}. Fritsen et al. (25) used the ice temperature records to develop an energy budget for the period when freezing fronts were propagating through the ice in the austral autumn. The energy budget was used to calculate the changes in latent heat for depth intervals defined by thermocouple placement. The change in latent heat was then used to estimate the fractional volume (V_w, expressed as a percent) of liquid water generated during the proceeding summer melt season. Maximum values of V_w (approaching 25% in 1995) occurred near 2 m, coinciding with the depth of maximum sediment concentration. They also modeled ice temperature from Lake Hoare collected between 1986 and 1988 that showed a similar trend with maximum V_w coinciding with the sediment layer. V_w values in Lake Hoare approached 60%, considerably higher than that computed for the mid-1990's in Lake Bonney reflecting warmer air temperatures that occurred in the 1980's (17, 18). The thermodynamic data indicate that the absorption of solar radiation by the lithogenic material is a primary process generating liquid water in the ice covers.

Gas bubbles associated with sediment in the ice provide further evidence for the presence in summer of liquid water pockets or lenses within the ice (2, see Fig. 9a). Assuming the arching bubbles are remnant traces of liquid water, their dimensions are proxies for the size of the melted region. Arching bubbles have been shown to extend 20 to 50 cm above sediment inclusions, which indicate that water pockets formed during the previous year with volumes averaging 0.3 m^3 (per m^2 of sediment area). These dimensions are on the same order as the 0.39 m^3 of liquid water (per m^2 of sediment area) predicted from the model of Fritsen et al. (25).

Direct measurements have been made in the ice cover in Lake Bonney using time-domain reflectometers (TDR) (Fig. 11b), which detect changing dielectric permittivity in porous media allowing indirect measurements of volumetric water content. TDR data from late 1998 through July 2000 show that liquid water is present in the ice cover of Lake Bonney from mid-November through early May. The 2 m TDR sensor, placed directly in a sediment aggregate during the 1998-1999 austral summer, shows that this layer is one of the first to melt and the last to freeze. The extended period of melt at 2 m is also evident in the 1999-2000 austral summer.

Thermodynamic modeling and TDR data show that the liquid water produced by solar radiation induced melting associated with lithogenic material exists for approximately 150 days during the austral summer in Lake Bonney. Based on the length of this period, the cyanobacterial

doubling time has been estimated to be about 9 years in Lake Bonney. Estimates of cyanobacterial doubling time, growth rates, growing days, and annual primary production for a number of lakes in the McMurdo Dry Valleys are summarized in Table 3. These data show that cyanobacterial growth in the ice covers is slow, with generation times ranging from 0.43 to 9 years. The long generation times are directly related to the length of liquid water in the ice covers and vary with climatic conditions.

CONCLUSIONS

The permanent ice covers of liquid water- based lakes in the McMurdo Dry Valleys are thermodynamically active and display a well defined but transitory stratigraphy in sediment content, bubble morphology and liquid water. The unique combination of physical features produces liquid water deep within the permanent ice covers when the air temperature is well below the freezing point. A conceptual model of the processes within the ice covers in relation to organic carbon production is shown in Figure 12. About 30 cm of new ice growth takes place annually on the bottom of the ice cover with roughly an equal amount lost each year from ablation at the top (1,14). Terrestrial sediment, including cyanobacterial and bacterial cells, is deposited on the ice surface by aeolian processes, primarily by strong katabatic winds that occur during winter. As the sun rises above the horizon in late September, the sediments absorb radiant energy and melt through the surface layers of the ice. The sediments reach a level in the ice where downward melting is balanced by the general upward movement of the ice due to accretion of meltwater at the bottom and ablation at the surface. The sediments generally accumulate in pockets about 2 m beneath the ice surface with clean ice above and below. During the summer, an “aquifer” is created within the ice, with its lower boundary marked by the sediment layer. The aquifer is connected to the lake water through discrete conduits and the lower ice remains essentially dry. The presence of liquid water and adequate solar radiation during austral summer produces a cascade of microbial processes within the ice cover. Cyanobacterial photosynthesis and atmospheric nitrogen fixation produces reduced carbon and nitrogen that in turn fuel heterotrophic processes. The heterotrophs remineralize the organic matter producing raw materials to support further cyanobacterial activity. The close spatial and temporal coupling of metabolites within the microbial consortium appears to be essential for the microbes to survive and replicate in what has been characterized as “the edge of life” (59). Data on microbial activity for the ice assemblage indicate that metabolic complementation among functionally diverse, but structurally simple, prokaryotic consortia along microscale biogeochemical gradients is a unique and effective strategy for meeting the requirements of life in this extreme habitat. Sediment mounds noted on the bottom of certain lakes (55, 80, 83) and coarse sediments collected in sediment traps deployed in the lake water indicate that sediments and associated organic matter are lost from the ice covers, presumably during late summer and

early autumn when the liquid water content of the ice is at a maximum. The exact mechanism for this loss remains unclear, but owing to the patchiness of the benthic sediment mounds, it seems that the loss is through discrete cracks or conduits within the ice cover rather than downward melting.

Given the dynamic processes shown in Figure 12, it is conceivable that the organic matter accumulates within the ice covers by physical processes alone (i.e., aeolian sources exceed loss to the lakewater) rather than via cyanobacterial production. This is an important distinction in terms of defining the viability of the ecosystem. Are the microorganisms merely "freeloaders" passing through the ice or do they form a viable and self-sustaining ecosystem? The balance between biological and physical processes was determined through the following relationship:

$$?C/?t = (\mu ? C_i) + Q_a - Q_w$$

where:

$?C/?t$ = change in POC (mg C m^{-2} y^{-1})

μ = biological growth rate (0.5 y^{-1})

C_i = standing stock of cyanobacterial POC in the ice (375 mg C m^{-2})

Q_a = aeolian flux of POC onto the lake ice (43 mg C m^{-2} y^{-1})

Q_w = sinking flux of POC fro the ice (2.3 mg C m^{-2} y^{-1})

Values used for the various model parameters represent the best estimates from studies conducted during the 1995-1996 austral spring and summer. Solving the equation with the noted parameters yields ?C/?t = 229 mg C m^{-2} y^{-1} which is within the range of values for annual production shown in Table 3. The contribution from cyanobacterial primary production (μ?C_i) is about 80% of the total annual accumulation of POC in the ice, indicating that biological production exceeds POC accumulation via physical processes. Hence, the unique combination of physical and microbial processes that occur in the permanent lake ice in the McMurdo Dry Valleys produces an oasis for life in a polar desert where there is an overall paucity of liquid water and associated production of new carbon and nitrogen.

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Figure Legends

Fig. 1 Map of Antarctica showing the general location of the McMurdo Dry Valleys and a 3000 m aerial view of the Taylor Valley where three large permanently ice- covered lakes exist. Note the differences in the sediment concentration (denoted by dark coloration) on the ice covers of the lakes.

Fig 2. Vertical profiles of selected constituents within the ice cover of the east lobe of Lake Bonney. POC = particulate organic carbon; DIC = dissolved inorganic carbon; SRP = soluble reactive phosphorus; DOC = dissolved organic carbon; bacterial activity represents the rate of tritiated thymidine incorporation (TdR) into cellular DNA. Methodological details can be found in Priscu et al. (73) and Fritsen and Priscu (24).

Fig 3. Collective relationships between sediment concentration and various cyanobacterial (photosynthesis; chlorophyll-a) and bacterial (thymidine incorporation; cell density) parameters from seven lakes in the McMurdo Dry Valleys. Relationships between sediment concentration and POC also are shown. The regression of POC on PON has a slope of 8.89 (g:g), which is higher than that reported for balanced microbial growth.

Fig. 4. Photosynthetic temperature response by various microbial assemblages in the McMurdo Sound area. The samples of McMurdo Sound fast ice, lake water from Lake Bonney, stream samples from the Fryxell basin and lake ice from Lake Bonney were dominated by diatom algae, the chlorophyte *Chlamydomonas subcaudata*, *Phormidium* plus *Nostoc,* and *Phormidium*, respectively. Experimental details can be found in references 24 and 71. Note the similarity in temperature responses between stream and lake ice cyanobacteria, both of which show psychrotolerant characteristics; sea ice and lake water algae show typical psychrophilic characteristics.

Fig 5. (A) Temperature variation for north-facing and south-facing cyanobacterial mats on the surface of Lake Fryxell during a 2.5 day period in February 2000 (days labels are centered at 0000h). (B) Rates of oxygen exchange (+/- one standard deviation) measured at 0 ^{o}C in a gas

tight chamber for cyanobacterial mats collected from the surface of Lake Fryxell before freezing and following freezing for 10 hours at –15°C. The curves were fitted with a modified equation for a hyperbola where oxygen change = a - b/(1+ c · irradiance) $^{(1/d)}$; a (y-intercept), b, c and d are parameters fitted with the Marquadt algorithm.

Fig. 6. Results of nutrient enrichment bioassays on cyanobacterial photosynthesis (A, B) and atmospheric nitrogen fixation (C) in the Lake Bonney ice assemblage. Panel A: N = 20 µM NH_4^+, P = 2 µM PO_4^{3-}; Panel B: N = 10 µM NO_3^-, P = 5 µM PO_4^{3-}, Fe = 2 µM $FeCl_3$, EDTA = 2 µM; Panel C: P = 5 µM PO_4^{3-}, Fe = 0.5 µM $FeCl_3$, EDTA = 0.5 µM, mannitol = 2 mM. All incubations were between 72 and 119 h at 0-3 °C and 100 µmol photons m^{-2} s^{-1} except CONT-D in panel D, which was incubated in the dark. Error bars = standard deviation.

Fig. 7. Experimental ammonium (A) and phosphorus (B) leaching data from terrestrial soils surrounding Lake Bonney, and soils and sediment on and within (2 m) the ice cover of Lake Bonney. Deionized water (DIW) and KCl (5 mg l^{-1}) were used as the solvents in the ammonium experiments. Phosphorus leaching used water from just beneath the ice cover (5 m) and 30 m beneath the ice cover of Lake Bonney. The values on the x-axes represent the size fraction of sediments (µm) analyzed in each experiment. Error bars = standard deviation.

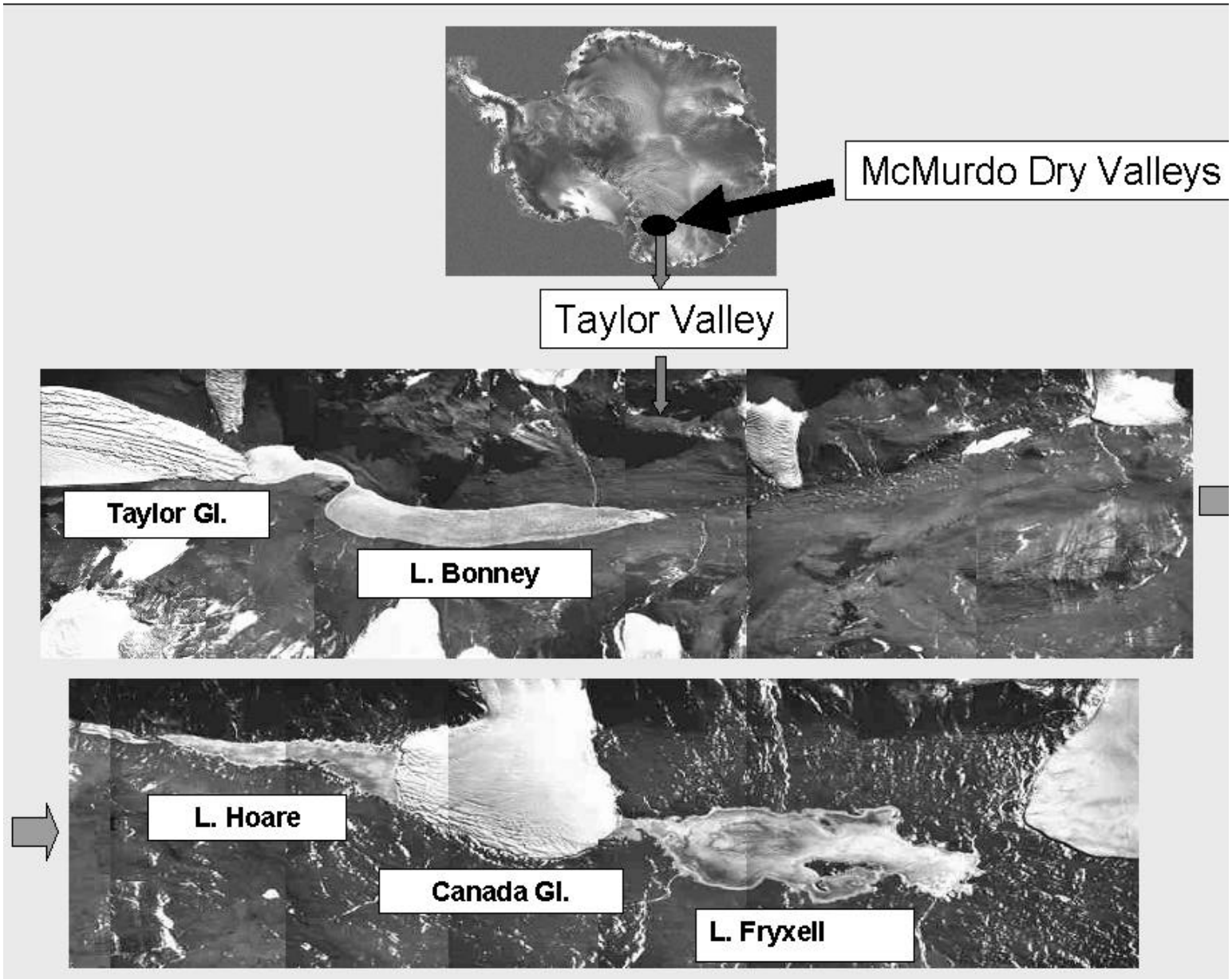
Fig. 8. Mineralization ($^{14}CO_2$ release) of ^{14}C-labeled cyanobacteria collected from the Bonney or Vida lake basins. Incubations were conducted in filtered (~0.7µm) surface water (5 m) from Lake Bonney. The slope of each response in concert with the specific activity of the labeled cyanobacteria was used to compute the turnover rates for the individual species.

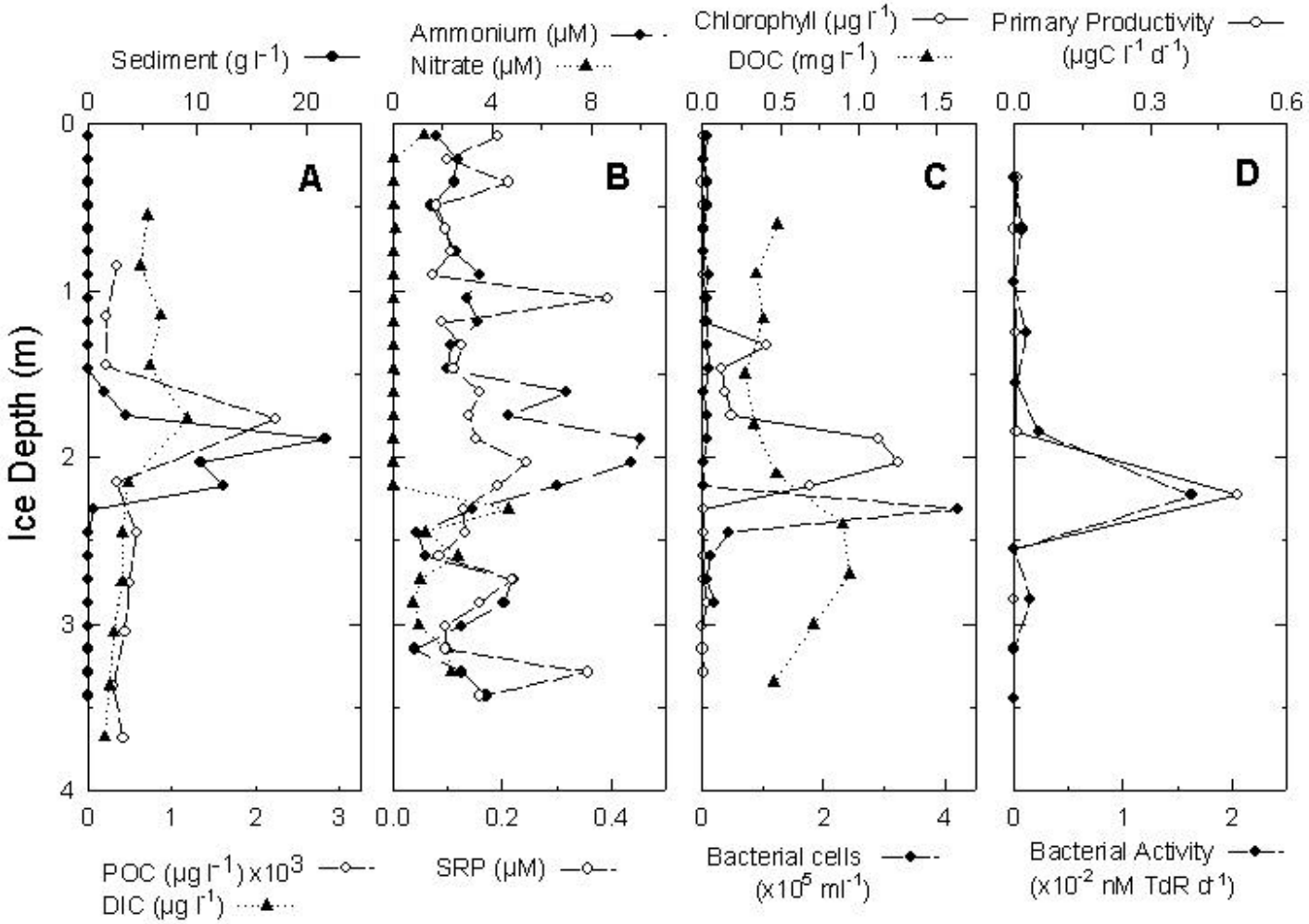
Fig. 9. Selected images of Lake Bonney ice sediments and associated organisms collected from ~2 m beneath the ice surface (A-D), and organisms associated with the sediments from dry stream beds surrounding Lakes Fryxell (E) and Lake Bonney (F). A: bubbles associated with sediment aggregates; B: laser confocal photomicrograph of *Nostoc*; C: SEM image showing microbially produced exopolymeric substance forming a fabric in the sediments; D: $^{14}CO_2$ microautoradiograph of filamentous cyanobacteria (dark material resulting from CO_2 incorporation) attached to sediment particles; E: trichomes of *Phormidium* (smaller filaments) and *Nostoc* (larger filaments) attached to sediment surfaces; F: a thick biofilm of *Nostoc* attached to sediment. Note the large heterocysts, presumably the primary site for N_2 fixation within the *Nostoc* filaments in E and F.

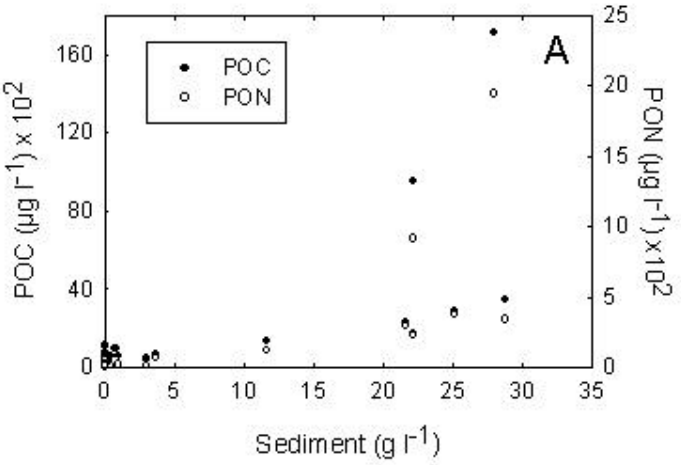
Fig 10. Consortial relationships between photosynthetic and heterotrophic prokaryotes found within the ice covers of the McMurdo Dry Valley lakes. Note that all of these exchanges take place on micron or smaller scales. Such a consortium is necessary for the survival and proliferation of life in the extreme environment posed by permanent Antarctic lake ice.

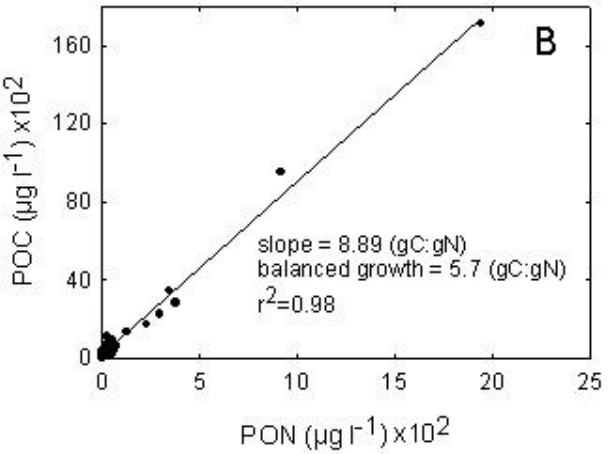
Fig 11. A: Vertical profiles of ice temperature in the East Lobe of Lake Bonney for 1995. Note the near isothermal temperatures that are reached during the summer months (late November through February). B: Relative water estimates obtained from time domain reflectometers (TDR) deployed in the ice cover of Lake Bonney during 1999 and 2000. The TDR data show the presence of liquid water when ice temperatures are isothermal near 0 °C.

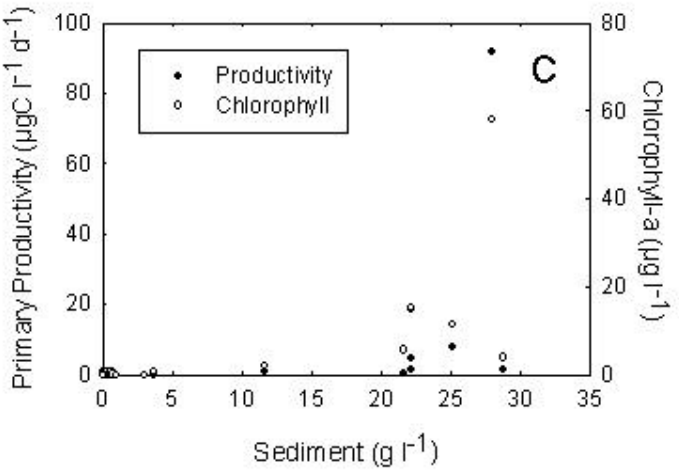
Fig. 12. Conceptualization of particulate organic matter and associated sediment fluxes within the permanent ice covers of dry valley lakes. Note that numerical models based on empirical date indicate that the accumulation layer is a source of organic carbon resulting from cyanobacterial photosynthesis in excess of physical sinks (see text for details).

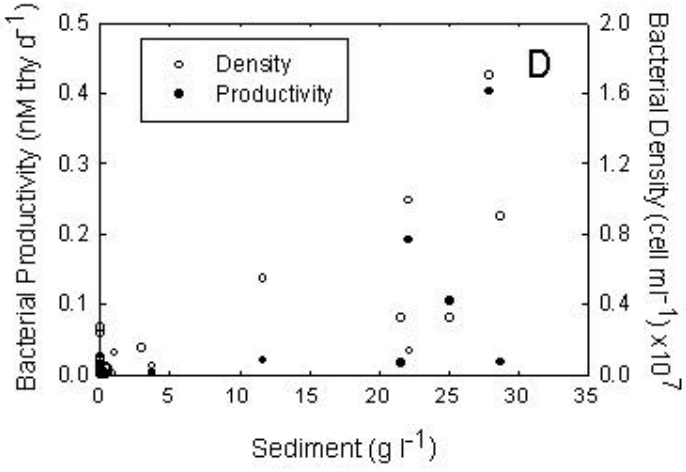

McMurdo Dry Valleys
Taylor Valley
Taylor Gl.
L. Bonney
L. Hoare
Canada Gl.
L. Fryxell

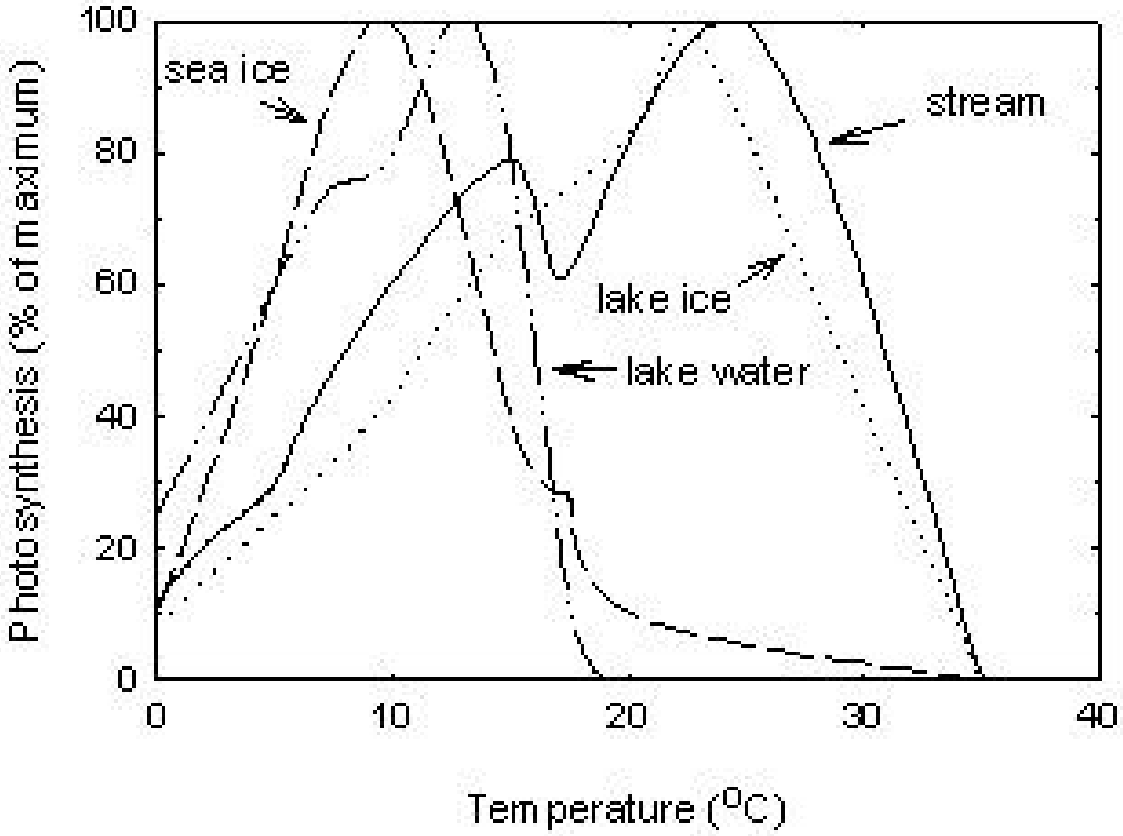

Ice Depth (m)
A
B
C
D
Sediment (g l-1)
Ammonium (µM)
Nitrate (µM)
Chlorophyll (µg l-1)
DOC (mg l-1)
Primary Productivity
(µgC l-1 d-1)
POC (µg l-1) x10-3
DIC (µg l-1)
SRP (µM)
Bacterial cells
(x10-5 ml-1)
Bacterial Activity
(x10-2 nM TdR d-1)

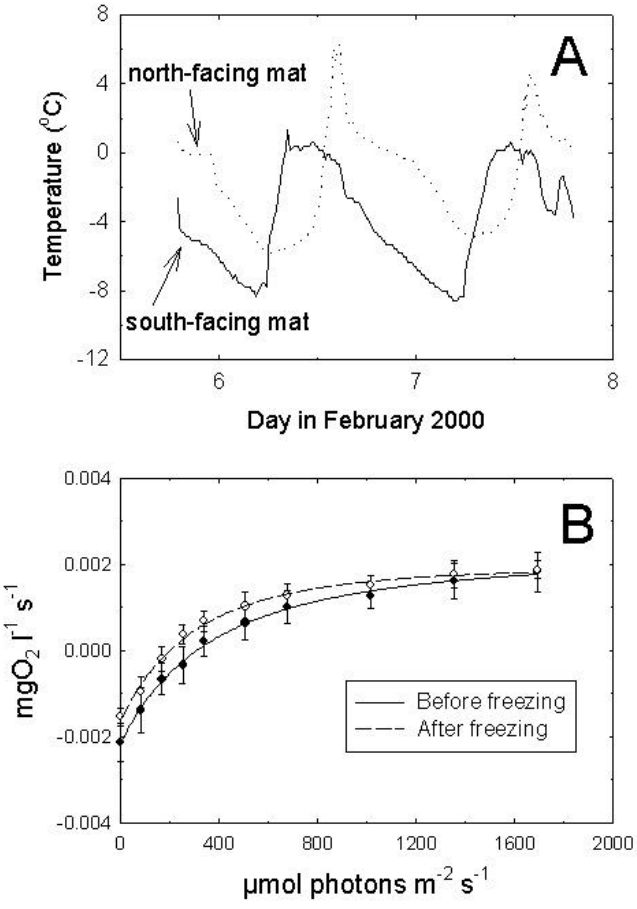

A
POC
PON
POC (µg l-1) x 10-2
PON (µg l-1) x10-2
Sediment (g l-1)

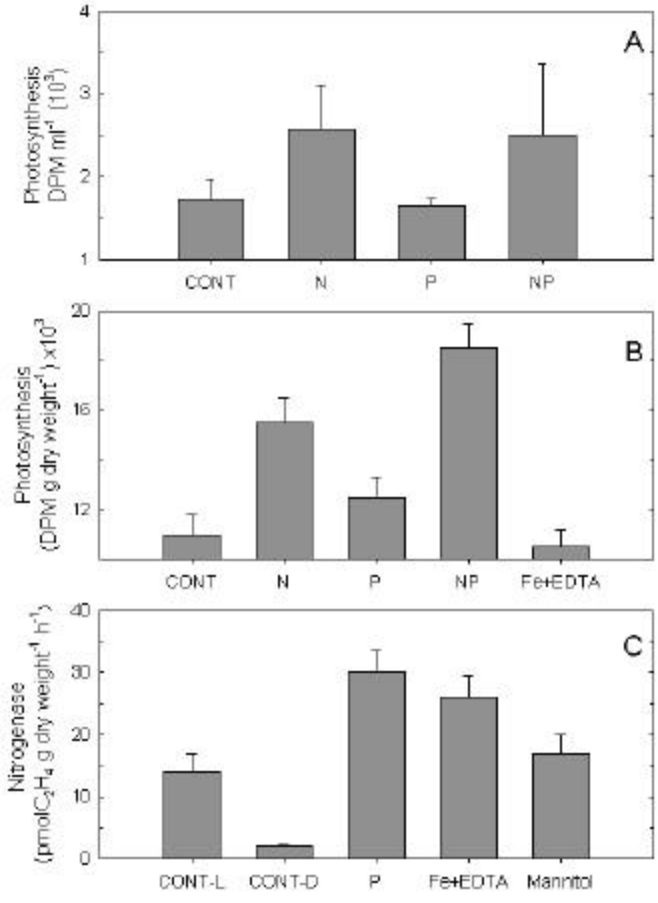

B
slope = 8.89 (gC:gN)
balanced growth = 5.7 (gC:gN)
r2=0.98
POC (µg l-1) x10-2
PON (µg l-1) x10-2

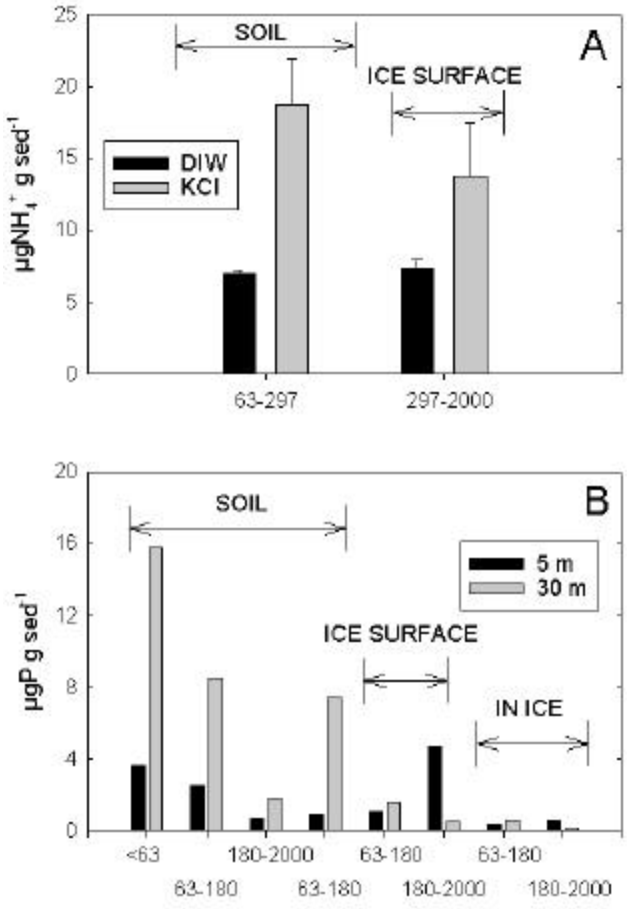

C
Productivity
Chlorophyll
Primary Productivity (µgC l-1 d-1)
Chlorophyll-a (µg l-1)
Sediment (g l-1)

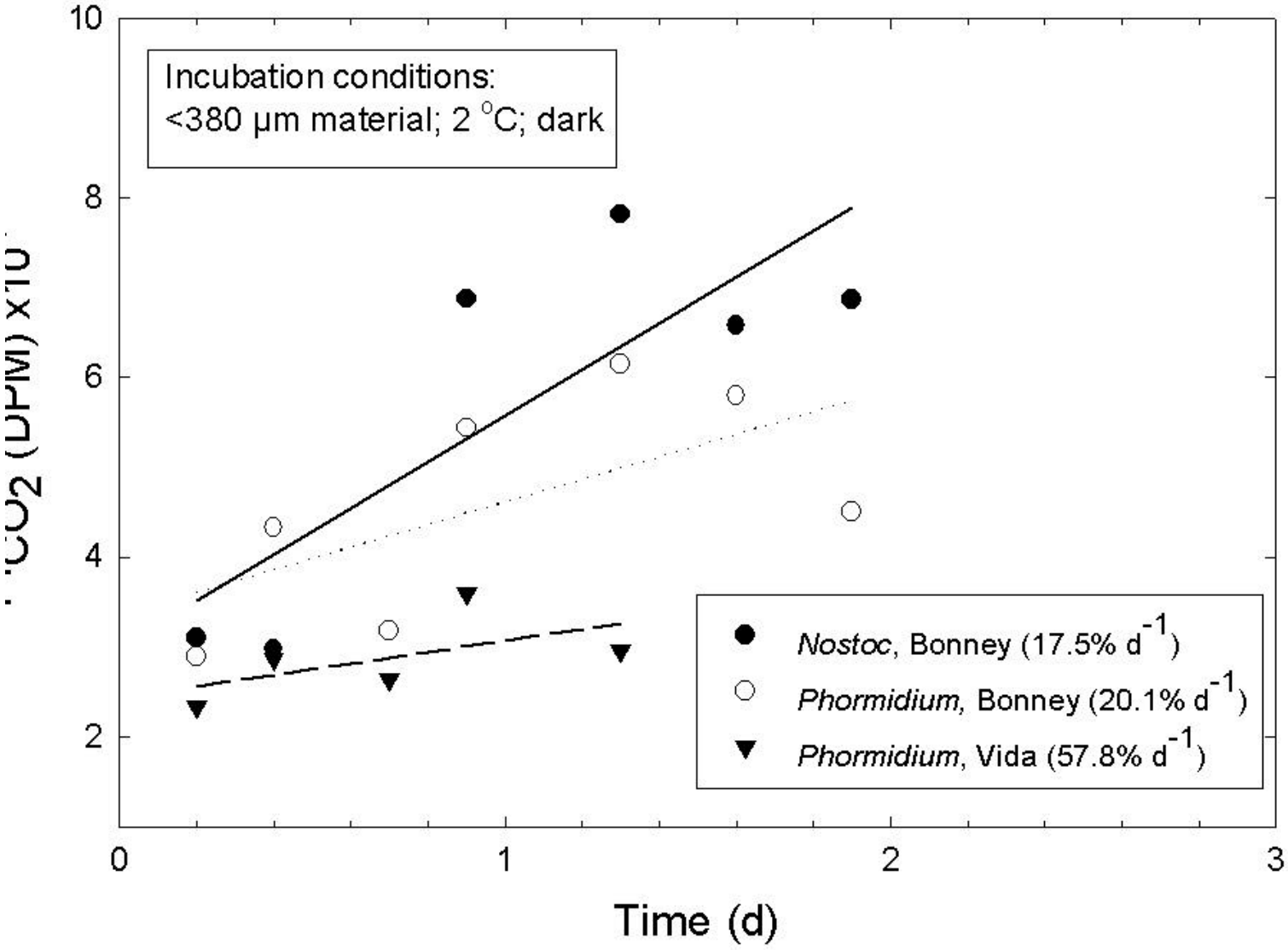

D
Density
Productivity
Bacterial Productivity (nM thy d-1)
Bacterial Density (cell ml-1) x10-7
Sediment (g l-1)

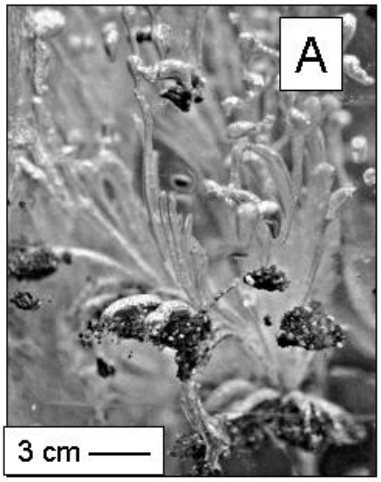

100
80
60
40
20
0
0
10
20
30
40
Photosynthesis (% of maximum)
Temperature (°C)
sea ice
stream
lake ice
lake water

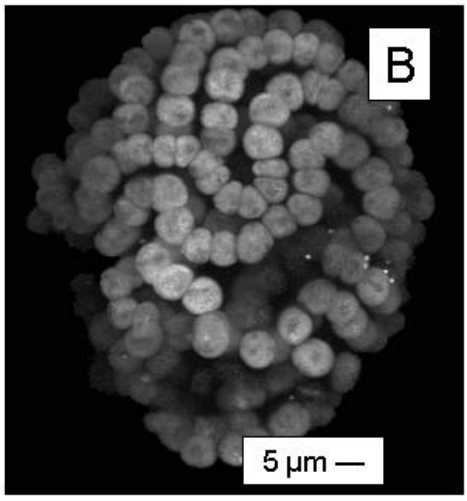

A
north-facing mat
south-facing mat
Temperature (°C)
8
4
0
-4
-8
-12
6
7
8
Day in February 2000
B
0.004
0.002
0.000
-0.002
-0.004
mgO2 l-1 s-1
Before freezing
After freezing
0
400
800
1200
1600
2000
µmol photons m-2 s-1

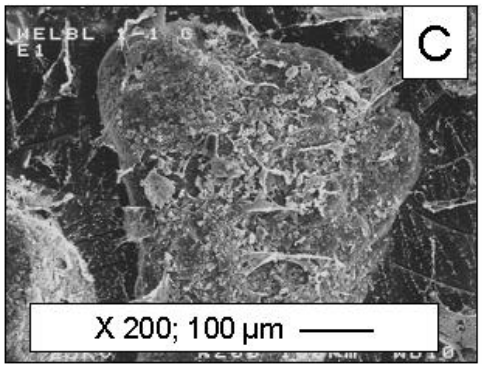

A
Photosynthesis
DPM ml-1 (10³)
4
3
2
1
CONT
N
P
NP
B
Photosynthesis
(DPM g dry weight-1) x10³
20
16
12
CONT
N
P
NP
Fe+EDTA
C
Nitrogenase
(pmol C2H4 g dry weight-1 h-1)
40
30
20
10
0
CONT-L
CONT-D
P
Fe+EDTA
Mannitol

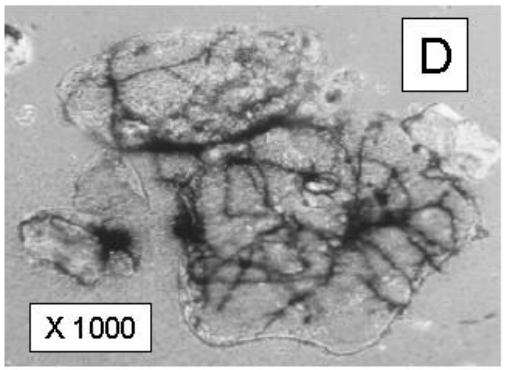

A
SOIL
ICE SURFACE
DIW
KCl
µgNH4+ g sed-1
25
20
15
10
5
0
63-297
297-2000
B
SOIL
5 m
30 m
ICE SURFACE
IN ICE
µgP g sed-1
20
16
12
8
4
0
<63
180-2000
63-180
63-180
63-180
63-180
180-2000
180-2000

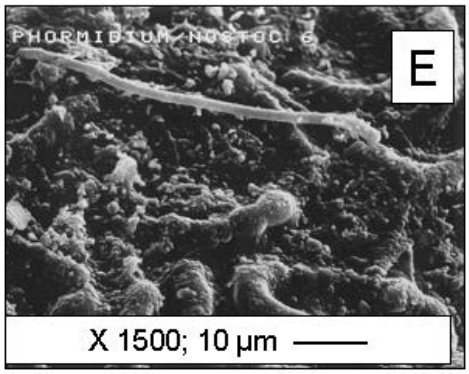

Incubation conditions:
<380 µm material; 2 °C; dark
Nostoc, Bonney (17.5% d-1)
Phormidium, Bonney (20.1% d-1)
Phormidium, Vida (57.8% d-1)
Time (d)
0
1
2
3
2
4
6
8
10

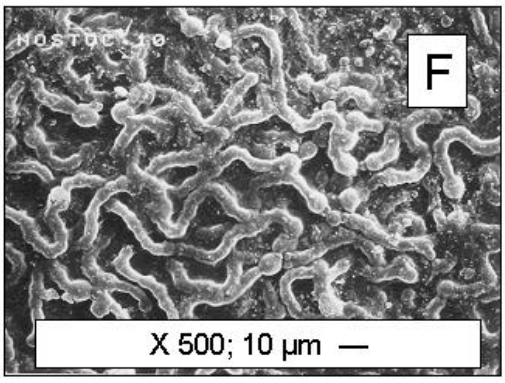

A
3 cm


B
5 µm

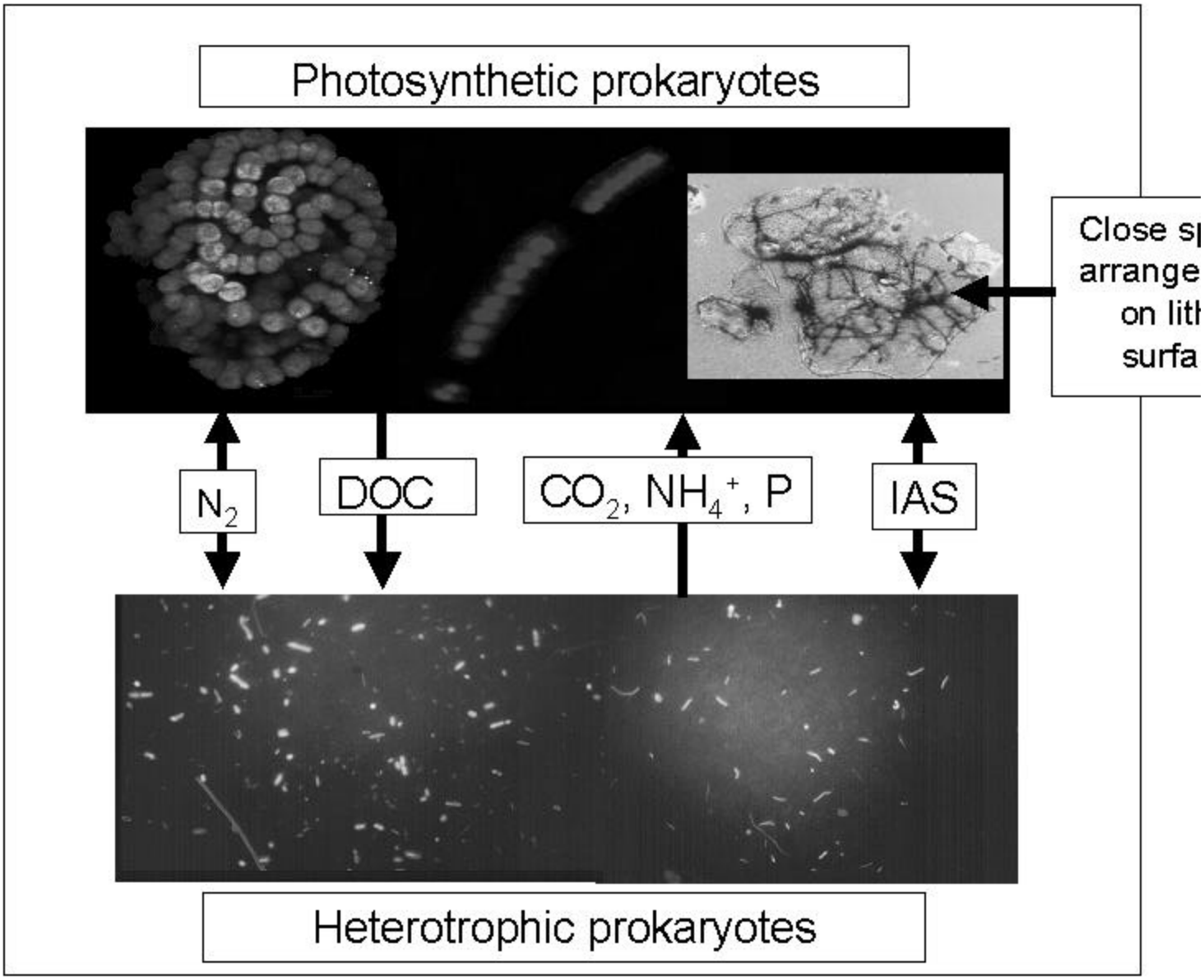

C
X 200; 100 µm

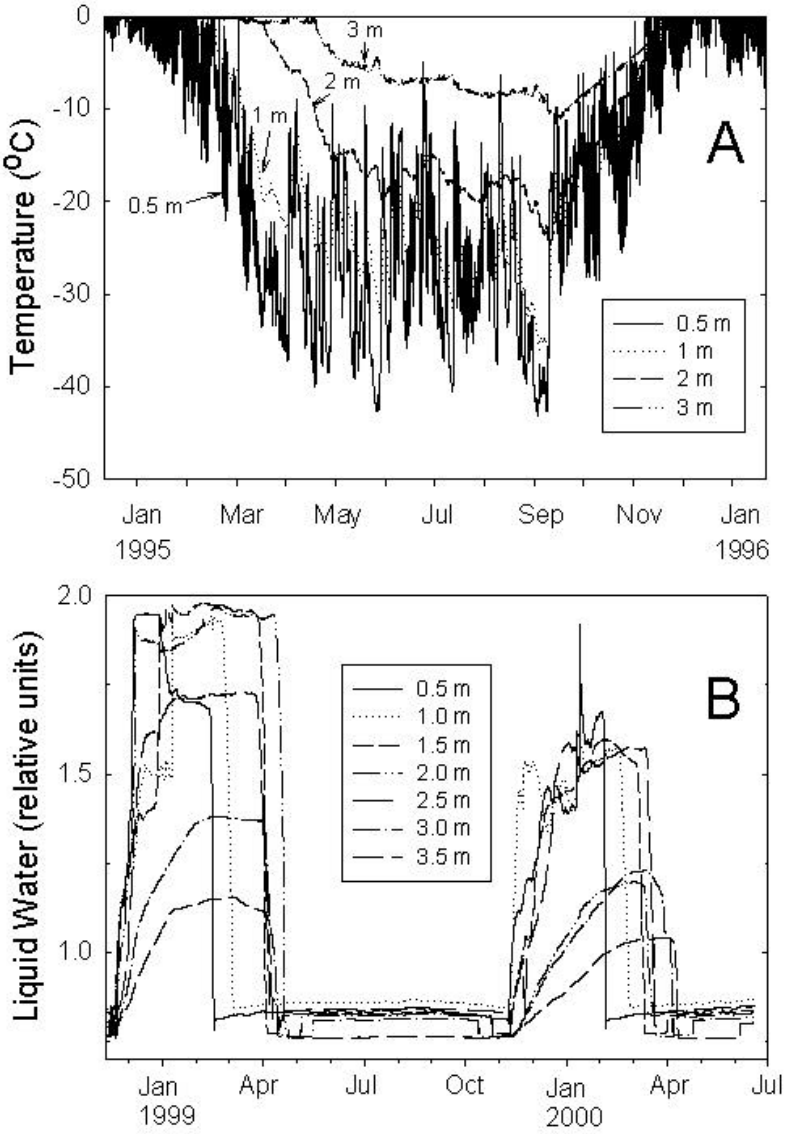

D
X 1000


E
X 1500; 10 µm


F
X 500; 10 µm

LAKE ICE MICROBIAL CONSORTIUM




0
-10
-20
-30
-40
-50
Temperature (°C)
3 m
2 m
1 m
0.5 m
A
0.5 m
1 m
2 m
3 m
Jan
1995
Mar
May
Jul
Sep
Nov
Jan
1996
2.0
1.5
1.0
Liquid Water (relative units)
0.5 m
1.0 m
1.5 m
2.0 m
2.5 m
3.0 m
3.5 m
B
Jan
1999
Apr
Jul
Oct
Jan
2000
Apr
Jul

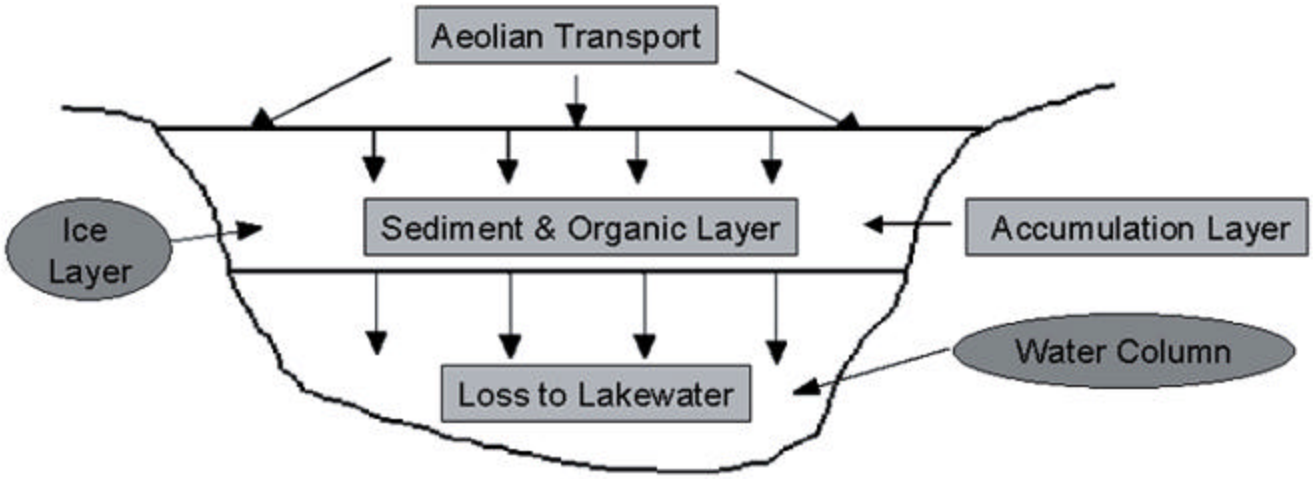

Aeolian Transport
Ice Layer
Sediment & Organic Layer
Accumulation Layer
Water Column
Loss to Lakewater

Table 1. McMurdo Dry Valley averages and extremes in selected meteorological parameters. Data are from 1985 to 2000 and represent information collected from Taylor, Wright and Victoria valleys. (see also Doran et al., submitted).

Parameter	Value
Surface air temperature (^{o}C)	
average mean annual	-27.6
absolute maximum	10.0
absolute minimum	-65.7
Degree days above freezing	
mean annual	6.2
Soil temperature at surface (^{o}C)	
average mean annual	-26.1
absolute maximum	22.7
absolute minimum	-58.2
Surface wind speed (m s^{-1})	
average mean annual	4.1
maximum	37.8

Table 2. Ammonium uptake (U) and regeneration (R) rates determined by ^{15}N isotope dilution experiments for lake ice assemblages in Lakes Bonney, Fryxell, Hoare, Miers and Vida. Half-saturation constants (K_s) and maximum uptake velocities (V_{max}) were determined using ^{15}N-ammonium incorporation and the Michaelis-Menten model. Isotope dilution experiments were conducted on < 63 µm, < 297 µm and unfractionated (total) samples. Michaelis-Menten parameters were determined on unfractionated samples only.

Sample	Uptake ($\mu M\ h^{-1}$)	Uptake (h^{-1})	Regeneration ($\mu M\ h^{-1}$)	Regeneration (h^{-1})	U:R	K_s (μM)	V_{max} (h^{-1})
East Bonney < 63 µm	0.0030	0.00383	0.0031	0.00399	0.98	0.82	0.0003
East Bonney < 297 µm	0.0051	0.00384	0.0011	0.00084	4.73	--	--
Fryxell < 297 µm	0.0209	0.00224	0.0031	0.00033	6.81	--	--
Hoare < 63 µm	0.0059	0.00029	0.0011	0.00005	5.53	2.68	0.0006
Miers Total	0.0754	0.00899	0.0183	0.00219	4.11	11.09	0.0010
Vida Total	0.0403	0.00917	0.0405	0.00912	0.99	4.67	0.0003

Table 3. Growth related measurements for cyanobacterial assemblages associated with the sediment layer of various lakes in the McMurdo Dry Valleys.μ (d^{-1}) = growth rate based on the rate of protein synthesis; Growing days = estimated number of days during a year when liquid water is available for growth; Generation time (years) = *in situ* generation time based on growth rates and the number of growing days; Annual primary production (mg C m^{-2} y^{-1}) = *in situ* primary production based on $^{14}CO_2$ fixation rates and the number of growing days. Growth rate and primary production were measured when cyanobacteria were exposed to liquid water at irradiances saturating to photosynthesis (~200 μmol photons m^{-2} d^{-1}) and 0 – 2 ^{o}C. NA = not applicable; -- = not measured. Modified from Fritsen and Priscu (1998).

Lake	μ	Growing days	Generation time	Annual primary production
EL Bonney	0.001	150	9.0	86-340
WL Bonney	0.003	130	2.0	120
Hoare	0.006	130	0.96	843
Fryxell	0.008	80	0.64	5891
Joyce	--	130	--	--
Vanda	NA	NA	NA	0
Vida	2.71	130	1.92	617
Miers	12.0	100	0.43	10,447