

Chapter 12

Cyanobacterial Dominance in the Polar Regions

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Summary

Although cyanobacteria are often thought of as warm water organisms, they are the predominant biota in cold polar environments such as ice shelves, glaciers, glacial meltwater streams and ice-capped lakes. Cyanobacteria are the primary colonizers of glacial moraines after the retreat of ice sheets, and they play an important role in the carbon and nitrogen economy of tundra and polar desert soils. Various communities dominated by cyanobacteria inhabit exposed rock surfaces, while others occur within fissures and the interstitial spaces between crystals in certain Arctic and Antarctic rock types (See Chapter 13). Highly pigmented microbial mats dominated by *Nostoc* or oscillatoriaceans (Oscillatoriaceae) are a feature of streams, lakes and ponds in both polar regions, with extreme accumulations up to 90 cm thick and $> 40 \mu\text{g Chl}a \text{ cm}^{-2}$ at some sites. Picocyanobacteria often dominate the phytoplankton of polar and subpolar lakes. In the coastal saline lakes of Antarctica picocyanobacteria achieve some of the highest natural concentrations on record, up to $8 \times 10^6 \text{ cells mL}^{-1}$. However, picocyanobacteria are conspicuously absent or rare in the adjacent polar oceans. The ecophysiological characteristics of high-latitude cyanobacteria that contribute to their success and dominance include: an ability to grow over a wide temperature

range (but at slow rates); tolerance of desiccation, freezing and salinity stress; a variety of adaptive strategies against high levels of solar radiation (including ultraviolet radiation) in exposed habitats; and acclimation to shade allowing net growth in protected dim light environments. In many polar habitats, the large standing stocks of cyanobacterial biomass are the result of gradual accumulation over many seasons, with only minor losses via biotic and abiotic removal processes. Cyanobacteria are not successful in the polar oceans where slow, temperature-depressed and light-limited growth rates are unable to keep pace with the continuous losses due to grazing, advection and mixing.

I. Introduction

"When I persuaded our botanist, Dr. Berggren, to accompany me in the journey over the ice, I joked with him on the singularity of a botanist making an excursion into a tract, perhaps the only one in the world, that was a perfect desert as regards botany. This expectation was, however, not confirmed. Dr. Berggren's keen eye soon discovered, partly on the surface of the ice, partly in the above mentioned [cryoconite] powder, a brown, polycellular alga, which small as it is, together with the powder and certain other microscopic organisms by which it is accompanied, is the most dangerous enemy to the mass of ice, so many thousand feet in height and hundreds of miles in extent." (p.163 in Leslie, 1879)

These observations by the Swedish explorer Adolf Erik Nordenskiöld describe a remarkable discovery made during his 1870 expedition across the Greenland Ice Sheet. In certain regions of the interior, the surface of the ice sheet is coated by "cryoconite", literally "cold rock dust". These particulates are trapped by black, mucilage-producing cyanobacteria and the resultant dark patches absorb radiation. This in turn influences the local heat balance, producing holes, ponds and streams that accelerate local melting and the degradation of ice. Nordenskiöld proposed several potential origins for the extensive cryoconite powder, but his initial suggestion based on chemical analyses that it might be composed of cosmic dust (micro-meteorites) subsequently proved correct (Maurette et al., 1986). These communities of cyanobacteria in the Greenland interior thus hold the unusual distinction of growing on ice, meltwater and extra-terrestrial substrates.

As explorers began to roam more widely in the polar regions there was increasing evidence, often anecdotal, that cyanobacteria were well established throughout the Arctic and Antarctic. A Swedish expedition to Spitsbergen in 1861 noted cyanobacteria growing in fellfield pools: "and here and there the beautiful *Phalaropus* [northern

phalarope] was seen to pluck the alga *Nostoc commune* (See Chapter 17) which is plentiful in these waters" (p. 65 in Leslie, 1879). James Murray, the biologist on Shackleton's 1907-9 expedition to Ross Island, Antarctica, dug through the ice of a frozen lake and found benthic mat material "that on careful thawing released a multitude of living things for study" (Murray, 1910), notably filamentous cyanobacteria and the rotifers which feed on them. These and earlier collections from the Ross Sea region revealed many species of cyanobacteria as well as diatoms and other organisms (Fig. 1). Some two years later, Griffith Taylor, a geographer on the British Antarctic Expedition was sent by Captain Robert Falcon Scott to explore the "Dry Valley", one of a series of largely ice-free valleys at latitude 78°S in the McMurdo Sound region.

As Taylor crossed one of the frozen lakes he looked down and made note of the "extensive water plants" (brightly colored mats of cyanobacteria) beneath him (Taylor, 1916). He also commented on the medicinal taste of one of the ponds, perhaps the first evidence of taste and odor compounds (Persson, 1996) produced by the mat-forming species in this region.

Cyanobacteria are now known to colonize a remarkably diverse range of high latitude environments including rocks, glaciers, ice shelves, streams, ponds and lakes. In polar desert soils these micro-organisms are amongst the primary colonizers, and they continue to play an important role in the overall nitrogen and carbon economy of well-vegetated sites such as tundra and moss banks. At the bottom of certain Antarctic lakes, the biomass accumulation can be spectacular with up to a 90 cm thick layer of biomass and mucilage; some of the thickest microbial biofilms to be found in the natural environment. In the more extreme polar habitats, cyanobacteria constitute not only the dominant phototrophs but also most of the microbial ecosystem biomass. A notable exception to this general trend is the polar marine environment where picocyanobacteria are conspicuously rare or absent.

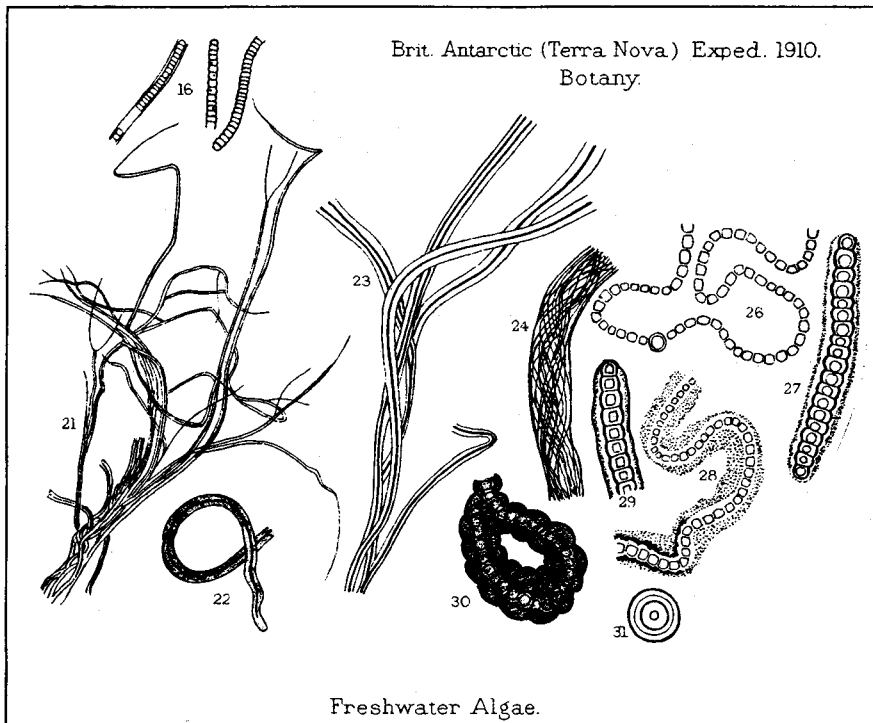


Fig. 1. Drawings of cyanobacteria collected from Ross Island, Antarctica (latitude 77°S) during Scott's Terra Nova expedition. The newly described taxa were *Phormidium priestleyi* (16), *Schizothrix antarctica* (21-24) and *Nostoc fuscescens* var. *mixta* (25-31). From Plate I, Fritsch (1917)

This review first describes the range of cyanobacterial communities and habitats in the polar regions, and considers some of the general issues regarding their distribution and biodiversity. It then examines some of the eco-physiological characteristics that distinguish these assemblages of cyano-bacteria. The final section considers cyanobacterial dominance, and questions why this group of organisms is pre-eminently successful in non-marine high latitude environments yet is so poorly represented in the polar oceans.

II. Habitats and Communities

A. Marine Environments

Chroococcoid forms of cyanobacteria generally ascribed to the genus *Synechococcus* are widely distributed throughout the world oceans, and in many temperate and tropical regions they contribute a major, sometimes dominant, fraction of total phytoplankton biomass and productivity (Waterbury et al., 1986). The polar oceans are a notable

exception. In the Arctic as well as Antarctic, concentrations of *Synechococcus* fall to low values, often below 10^2 cells mL^{-1} . Higher concentrations occur in sea ice, although such populations may simply represent cells which were trapped in the ice during freezing, with little *in situ* growth (Walker and Marchant, 1989).

In the Southern Ocean, two types of picocyanobacteria were distinguished on the basis of their cell wall ultrastructure, indicating the likely presence of genetically different strains (Marchant et al., 1987). There was a strong North-South trend in the concentration of these phycoerythrin-containing picocyanobacteria (Fig. 2), with a four order-of-magnitude drop between latitudes 45 and 60°S to a minimum of < 10 cells mL^{-1} . There was also a strong correlation between cell concentration and sea surface temperature, suggesting that low temperatures were the principal determinant of the low abundance in this part of the ocean.

There are many records of picocyanobacteria in the seas of the north polar region, however they are rarely major components of the plankton. There is also

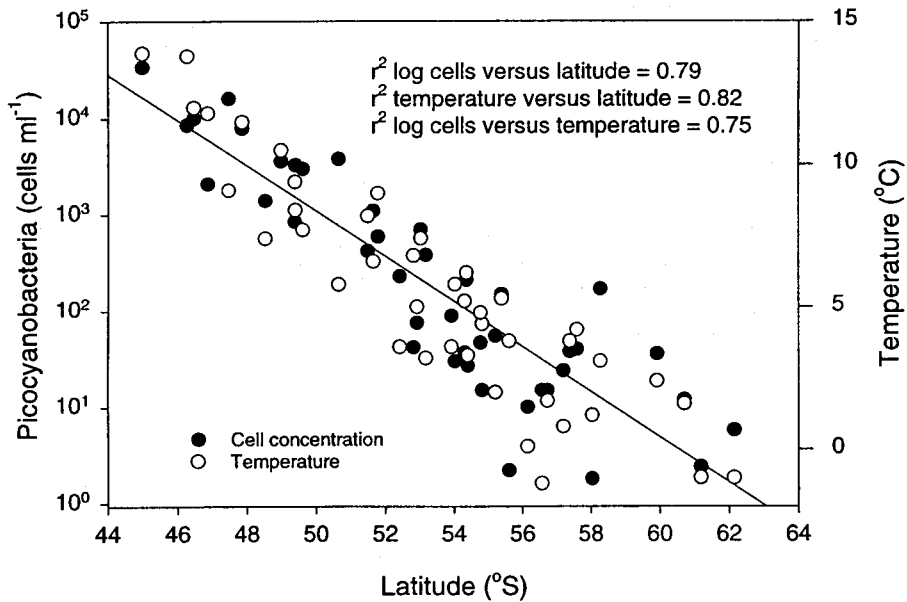


Fig. 2. Relationship between picocyanobacterial abundance (solid circles) and latitude in the Southern Ocean. The data are for 4 transects over the period Sept 1989-Feb 1986, from Table 1 in Marchant et. al. (1987). Also shown are the corresponding water temperature measurements (open circles) and r^2 values for the relationships between variables.

some controversy over to what extent these low density populations represent communities that are actively growing *in situ* versus populations that are transported from lower latitudes by advection. Mishitina et al. (1994) reported that phycoerythrin-rich populations were present at all times during their sampling of the open waters of the Barents, Norwegian and Greenland Seas, implying that there were resident communities of actively growing cells. *Synechococcus* also occurred as an epiphyte on the blades of brown algal macrophytes in the littoral zone of the Barents Sea.

In another study of northern waters, strong seasonal, spatial and depth variations in abundance of picocyanobacteria in the Greenland Sea were measured, with highest concentrations (up to 5470 cells mL⁻¹) in Arctic Intermediate Water. However, they were virtually absent from water collected inside the central Arctic Ocean, leading Gradinger and Lenz (1995) to conclude that picocyanobacteria had little impact on pelagic carbon and energy flux in the Arctic Ocean, and that their periodic appearance in the Greenland Sea was due to a high survival ability during advection from the North Atlantic. Several studies in the northern hemisphere reported a similar trend to that recorded on the Southern Ocean of a decreasing abundance of phycoerythrin-containing

cells with increasing latitude; for example in the North Atlantic (Murphy and Haugen, 1985) and the Greenland Sea (Legendre et al., 1993).

B. Ice and Snow

The cryoconite features that were first discovered during Nordenskiöld's expedition over the Greenland Ice Cap are now known to occur in the lower part of many glaciers in the polar regions as well as on alpine glaciers of the temperate zone (Wharton et al., 1985). The holes, ponds and streams form in the wastage zone and are readily colonized by micro-organisms, particularly cyanobacteria. The Greenland cryoconite communities are dominated by *Calothrix parietina*, a cyanobacterium known from Antarctica as a producer of the black UVR-absorbing pigment scytonemin (See Chapter 21). All of the samples of cryoconite examined by Gendel and Drouet (1960) from the Thule area contained fine mineral particulates loosely bound by the filaments of this cyanobacterium.

Complementary studies on cryoconite communities in the south polar region, specifically on the Canada Glacier in the McMurdo Dry Valleys, showed that the communities were dominated by filamentous cyanobacteria, specifically *Phormidium frigidum*, *Lyngbya martensiana*, *Microcoleus paludosus* var.

acuminatus and *Nodularia harveyana*. Cylindrical cells of the chroococcalean *Synechococcus aeruginosa* were also common. These taxa are found throughout the valleys in other terrestrial and aquatic habitats, and the communities are likely to be derived from wind blown microbial mats (Wharton et al. 1981).

Cyanobacteria appear to be relatively rare in melting snow banks by comparison with other phototrophs, notably the chlorophyte *Chlamydomonas nivalis*, which often dominates snow assemblages in temperate as well as polar latitudes (Vincent, 1988). Cyanobacterial growth rates may be too slow for these transient habitats. However, they are found in a broad range of other ice-dominated systems including ice sheets, glaciers and lake ice. In the ice-covered lakes of the McMurdo Dry Valleys, Antarctica, benthic mats of cyanobacteria can detach and float up to become incorporated in the ice cap during winter freeze-up. These patches of microbial mat then remain within the ice for many years where they continue to be metabolically active in an ice-bubble of gas and melt water. With subsequent freezing at the bottom of the ice cap and ablation at its upper surface the mats gradually move up through the ice over a period of several years and are finally released at the surface. Parker et al. (1982) calculated that this "escape mechanism" of biomass and mineral materials could result in a quantitatively significant loss of nutrients from the lakes each year. Another *Phormidium*-dominated community is also found growing within the liquid water inclusions of the lake ice, and appears to be inoculated from the surface by wind-blown material (Priscu et al. 1998).

One of the most extensive developments of cyanobacteria in the polar regions occurs over an area of 1500 km² on the McMurdo Ice Shelf (lat. 78°S). This ablation zone consists of an interconnected complex of meltwater lakes, ponds and streams which contain thick (several mm to cm) microbial mats dominated by oscillatorians or, less commonly, by *Nostoc commune* and *N. microscopicum* with subdominant diatom assemblages (Vincent, 1988; Howard-Williams et al., 1989, 1990; Hawes et al., 1993). The ponds are chemically diverse, ranging from dilute, low conductivity meltwaters (< 200 $\mu\text{S cm}^{-1}$) to sulfate-rich brines (See Chapter 10) with several times the salinity of sea water (de Mora et al., 1994). Some of the ponds are inundated by a single daily tide (Hawes et al., 1997). The microbial mats are correspondingly varied, but typically consist of an orange or red surface layer which is rich in carotenoid

pigments, and a deep blue-green layer which has high concentrations of chlorophyll *a* (Chl*a*) and phycocyanin (Fig. 3).

Studies on the physiological ecology of the ice shelf mats revealed that they act as "compressed euphotic zones" where there are large changes in spectral quality down through the vertical profile (Quesada and Vincent, 1993). Ultraviolet radiation (UVR) and high energy photosynthetically active radiation (PAR) are strongly attenuated by the surface layer of the mat, and most of the photosynthesis takes place in the "deep Chl *a* maximum" layer (DCM) growing towards the base of the profile in an orange or red dim light regime. Some of the microbial mats contain species capable of gliding motility that vertically migrate through the light gradient of the mat in response to changes in ambient solar radiation (Vincent et al., 1993c; Vincent and Quesada, 1994; Quesada and Vincent, 1997).

C. Rock and Soils

Cyanobacteria are the primary colonizers of exposed moraines after the retreat of glaciers and they are widely distributed throughout the soils of both polar regions. Species that fix dinitrogen play an especially important role in the nitrogen economy of these habitats and permit colonization by other microorganisms and higher plants (Bliss and Gold, 1994). Various types of rock environment provide a favorable habitat for cyanobacteria. The communities form dark surface crusts over the rock (epiliths), and blue-green colored biofilms under translucent stones (subliths or hypoliths). Well-developed communities can also grow within rock fissures (chasmoendoliths) or in the interstitial spaces beneath the surface of porous rocks, particularly sandstones (cryptoendoliths; See Chapter 13; Plates 20 and 21). The severe microclimate of many of these exposed rock habitats contrasts with the more benign conditions experienced by cyanobacteria that grow on (as epiphytes) or in association with moss, lichens and vascular plants.

Dark crusts are found on rock throughout the Arctic and Antarctic and are particularly conspicuous in the polar desert and semi-desert regions (e.g., Aleksandrova, 1988). These occur in habitats that are periodically supplied with snow melt and the assemblages are commonly dominated by *Gloeocapsa* spp. The dark coloration is due to the UVR-screening pigment scytonemin (see Chapter 21). Although this community can withstand bright solar radiation and

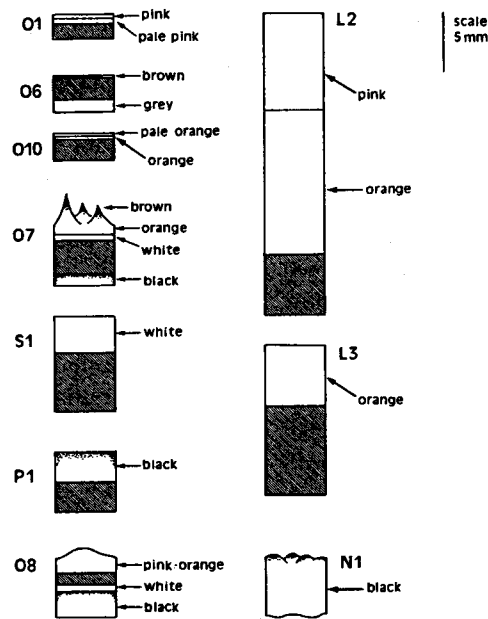


Fig. 3. Schematic diagram of vertical sections through Antarctic microbial mats dominated by cyanobacteria. The shaded area is the blue-green colored DCM. All profiles have been drawn to the same scale, from Vincent et al. (1993b).

desiccation it appears to be intolerant of saline conditions (Broady, 1996). The community is absent, for example, from Signy Island in the maritime Antarctic region, and from coastal areas influenced by sea spray.

Hypolithic communities are commonly found wherever translucent stones occur over the soil surface as they do, for example, in the Vestfold Hills and Schirmacher Oasis regions in the Antarctic continent. At the latter site, the hypolithic environment is colonized exclusively by *Aphanocapsa endolithica*. The Vestfold Hills communities are more diverse with *Chroococcidiopsis*, *Plectonema* and two green algal species (*Desmococcus* and *Prasiococcus*) as the dominant genera (Broady 1996). *Chroococcidiopsis* appears to be completely absent from salt-influenced areas and is limited to mineral, low salinity soils.

Endolithic communities are best described from the south polar region but are also known to occur in the Arctic, for example in fissures within the exposed dolomite sections at Resolute Bay (lat. 74°N), and at 1-5 mm depth within in the sandstones of Ellesmere Island (lat. 81°N). Extensive research on the cryptoendolithic communities of the McMurdo Dry Valleys region, Antarctica, showed that the

communities are typically composed of cyanobacteria (in particular the genus *Chroococcidiopsis*), microscopic lichens or the green alga *Hemichloris antarctica* (Nienow and Friedmann, 1993 and refs therein). The chasmoendolithic communities appear to be more diverse and *Chroococcidiopsis* co-exists with a variety of eukaryotic taxa. Vertical zonation is a feature of many of the endolithic communities and cyanobacteria typically form the lowermost stratum. In coastal chasmoendolithic communities the outer green layer of *Desmococcus* or *Prasiococcus* is underlain by an interior blue-green stratum of *Chroococcidiopsis* (Broady, 1981).

Much of what we know about the algal ecology of polar soils comes from more than 25 years of microbiological research on Signy Island (lat. 60°S) in the maritime region of Antarctica. Soil samples from this region contained from 4 to 57 taxa, with most assemblages dominated by cyanobacteria (Broady, 1996). Filamentous cyanobacteria are the primary colonizers of fellfield soils recently exposed by receding ice (Wynn-Williams, 1990); detailed epifluorescence studies showed how these species bind together the soil particles and increase the retention and stability of mineral fines (Wynn-Williams, 1991). There is a high degree of spatial

variability between and within frost polygons, with a seasonal succession from chlorophytes in spring to filamentous cyanobacteria in summer (Davey, 1991). The most common form in the Signy Island fellfield soils is *Phormidium autumnale* and it occurs throughout the upper 5 mm of the soil profile. Davey and Clarke (1991) found that *Nostoc* had a median depth of 150 μm while *P. autumnale* had a median depth of 1110 μm . They interpreted this deeper location of *P. autumnale*, as well as the migration behavior of these assemblages, as adaptive responses to avoid desiccation.

Soils on the Antarctic continent that are flushed by meltwater often support visible growths of cyanobacteria (Broady, 1996). Common forms include *Nostoc commune* (see Chapter 17) and members of the Oscillatoriales, with subdominant genera such as *Nodularia*, *Calothrix*, *Scytonema* and *Tolypothrix*. Water availability and salinity appear to be the major determinants that influence distribution of these cyanobacteria. For example, in the Vestfold Hills heterocystous cyanobacteria are absent from soils which are moist but not subject to flowing water, while *Gloeocapsa* becomes locally abundant only where the salinities are low.

Antarctic bryophyte communities often contain an associated epiphytic flora dominated by filamentous and coccoid cyanobacteria. Some species form crusts over the mosses, for example, *Stigonema minutum* at Schirmacher Oasis and *Nostoc* and oscillatorians at the Vestfold Hills; in areas subject to sea spray where birds are prevalent these surface communities are replaced by green crusts of chlorophytes (Broady, 1986).

D. Rivers and Streams

A variety of flowing water environments occur around the margins of Antarctica and these often contain a well developed periphyton dominated by cyanobacteria or, at some locations, by chlorophytes (Vincent et al., 1993a and refs therein). Three groups of stream cyanobacteria were distinguished: surface crusts; cohesive microbial mats; and moss epiphytes; all three types occur over a wide range of substrates including irrigated rock faces, flushed mineral soils and the channels of perennial streams.

The epilithic crusts are typically rich in scytonemin or other UVR-screening pigments and are colored black or brown. The common dominants are *Gloeocapsa*, *Schizothrix* and at some localities (e.g., the Alph River system in southern Victoria Land), the

heterocystous genus *Calothrix*. In the latter community, *Gloeocapsa* is subdominant and grows epiphytically over the *Calothrix* as well as directly over the rock substrate.

Two types of microbial mats are found in Antarctic streams. The most common mat is dominated by oscillatorians (particularly *Phormidium*, *Oscillatoria* and *Schizothrix*) in which the filaments are embedded in mucilage where they bind together silt and sand grains. The mats occur up to several mm in thickness (up to 40 $\mu\text{g Chl a cm}^{-2}$) and are often red or orange colored, with a blue-green bottom layer that is rich in phycobilin pigments (e.g., Ellis-Evans and Bayliss 1993; see also Fig. 3). The second group of mats is composed primarily of *Nostoc commune* and form black mucilaginous layers up to 20 mm thick. The *Nostoc* communities tend to occur in more ephemeral environments than do oscillatorian mats such as at the edge of stream beds and in the slow-moving flush areas.

Moss communities are especially common on the bank of streams in the maritime regions of Antarctica as well as on the continent. They generally contain a diverse flora dominated by cyanobacteria, but there are large regional differences in the forms present. For example, at one coastal location in east Antarctica (Strandnebbba) the stream-bank moss communities were sometimes completely coated by *Stigonema minutum* and *Plectonema* to the exclusion of other forms, whereas 30 km further to the North the communities were more diverse with five species of diatoms and a desmid as subdominants (Ohtani and Kanda, 1987).

Rivers and streams are also a major component of the Arctic landscape and, as in Antarctica, their periphytic assemblages are often dominated by cyanobacteria. Sheath et al. (1996) recognized two groups of riverine streams in the Arctic tundra: those which flow solely in the Arctic; and those which originate further to the south in the boreal forest. They noted that the latter were typically too deep and turbid to support benthic autotrophs, while the former often contained an extensive, macroscopic growth of periphyton. In their analysis of algal community structure and distribution in 150 segments of tundra streams across North America they recorded 83 taxa, of which 39% were cyanobacteria and 42% were chlorophytes. The most widespread forms were *Rivularia minutula*, *Nostoc commune* and *Tolypothrix tenuis*. Oscillatorian communities also occur in Arctic streams (Croasdale, 1973; Hamilton and Edlund, 1994; Vézina and Vincent, 1997; Sheath and

Müller 1997). The mats are rarely as well developed and extensive as those in Antarctica, perhaps reflecting the increased grazing pressure in the Arctic. Insects, for example, are absent from continental Antarctica but can achieve high population densities in the Arctic. Differences in nutrient supply may also contribute to the contrast between Arctic and Antarctic mat communities.

E. Lakes and Ponds

1. Plankton

Early studies on the limnology of the polar regions drew attention to the apparent lack of cyanobacteria in the plankton despite the eutrophic conditions which would favor blooms of cyanobacteria in water bodies of temperate latitudes (Kalff and Welch, 1974; Kalff et al., 1975). This earlier work on polar phytoplankton tended to emphasize nanoplankton and net plankton species. More recent studies confirmed that the larger colonial and filamentous bloom-forming taxa were relatively rare in polar lakes. However, the advent of fluorescence microscopy revealed that picoplanktonic species of cyanobacteria are abundant and can be the biomass dominants in the phytoplankton community of lakes in both polar regions.

Small, single-celled taxa of planktonic cyanobacteria were recorded in many lakes throughout Antarctica. *Synechococcus* and *Synechocystis* were noted in the plankton of the permanently ice-covered McMurdo Dry Valley lakes during the first investigation of their biological limnology (Goldman et al., 1967). A subsequent study determined that *Synechocystis* was a dominant component of the deep Chla maximum (DCM) in Lake Vanda, the deepest, most oligotrophic of the Dry Valley lake series (Vincent and Vincent, 1982). Further to the north but still within the Antarctic Ross Sea sector, studies on the lakes of the Terra Nova Bay region indicated that up to 50% of the phytoplankton Chla was in the <2 µm fraction. Cultures of picoplankton samples from these lakes contained *Synechococcus* as well as eukaryotic species and two unidentified taxa that were tentatively identified as prochlorophytes (Andreoli et al., 1992). Picocyanobacteria also appeared to be important elements of lakes of the maritime zone of Antarctica. In five lakes on Signy Island, *Synechococcus*-like cells were the dominant phytoplankton in terms of cell concentrations and Chla, but nanoplankton

(mostly flagellates and chlorophytes) dominated the total primary production (Hawes, 1990; Ellis-Evans, 1991).

The most detailed study to date on picocyanobacteria in Antarctic inland waters is from a meromictic, marine-derived lake in the Vestfold Hills (Ace Lake, lat. 68.5°S). *Synechococcus* cells in this lake had dimensions of 0.9 x 1.5 µm and were readily distinguished in flow cytometric analyses through their phycoerythrin fluorescence (Rankin et al., 1997). Cell concentrations were less than 10⁴ cells mL⁻¹ during winter, but increased rapidly in the DCM to peak concentrations of 8 x 10⁶ cells mL⁻¹ at 11 m depth in mid-December. The latter values are almost an order of magnitude higher than the maximum concentrations found in tropical and temperate oceans. The temperature at this depth in the lake remained relatively constant at around 6°C, with a salinity approximately that of sea water, and PAR irradiances less than 1% of those at the surface. Net population growth rates calculated from the cell concentration data for 10 m depth presented by Rankin et al. (1997) averaged 0.03 d⁻¹ during spring and early summer, with negative values in the period Jan-July (Fig. 4). Recent studies on isolates from these lakes confirmed that they were rich in phycobilins and devoid of Chlb, but also suggested genetic affinities with *Prochlorococcus* (Rankin and Bowman, unpublished data).

Picocyanobacteria are also important components in oligotrophic lakes of the subarctic and Arctic (See Chapters 5 and 7). In the cold, subarctic lakes of northern Québec the <2 µm fraction typically accounts for 30-60 % of the total planktonic Chla (Bergeron and Vincent, 1997) and is dominated by picocyanobacteria. Similarly, in Arctic lakes picocyanobacteria are often the phytoplankton dominants. A comparison of the growth rates and pigment characteristics of five isolates of *Synechococcus* from Arctic lakes showed differences between strains, and evidence of considerable genetic diversity within this component of the microbiota (Vézina and Vincent, 1997).

Oscillatorian cyanobacteria are often found as a major element of the phytoplankton in polar lakes. Many of these taxa have extremely thin trichomes (ca. 1 µm in diameter), and because of these morphological characteristics their light absorbing properties are as efficient as small coccoid or ovoid cells such as those of *Synechococcus*. These filamentous populations were found in Dry Valley lakes (Vincent and James, 1996) and in Arctic ponds

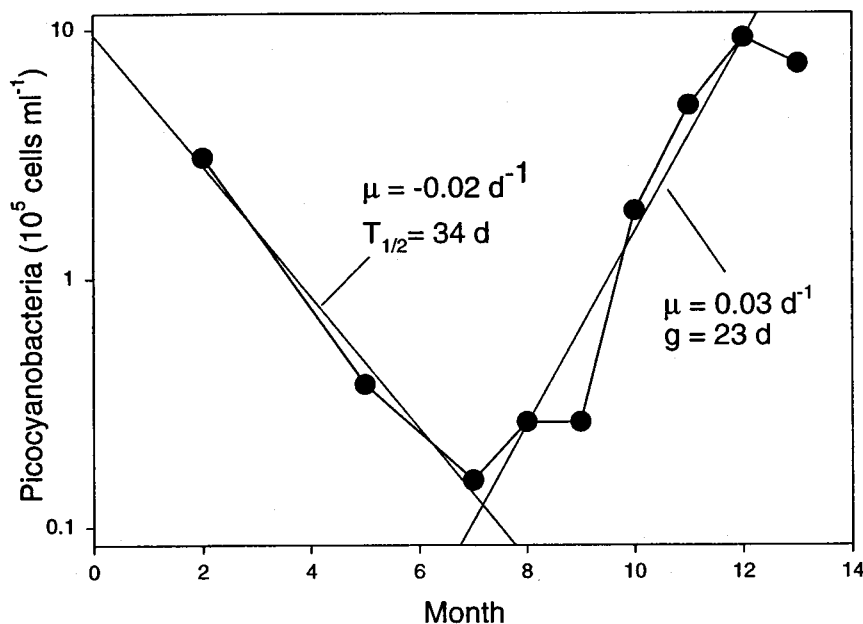


Fig 4. The seasonal distribution of picocyanobacteria at 10 m depth in Ace Lake, Antarctica. The net population loss or growth rates were calculated from natural log regressions of the cell count data versus time. Redrawn from Rankin et. al. (1997).

(Vézina and Vincent, 1997). In part, however, these populations may represent filaments washed in from stream beds or the littoral zone where thick mats of cyanobacteria occur.

2. Benthos

The richest biomass accumulations of cyanobacteria in the polar regions occur in the benthic habitats of lakes and ponds. The communities form highly pigmented layers over the bottom substrata and may gradually accumulate as mucilaginous films and mats up to several cm or even several tens of cm in thickness. In the lakes of the McMurdo Dry Valleys region five types of benthic mat were distinguished (Parker and Wharton, 1985):

Moat mats – these form around the edge of the lake where the ice melts each season. They are characterized by thick, spongy layers, and are often pigmented bright orange or brown.

Columnar lift-off mats – these are produced by the trapping of nitrogen and oxygen bubbles within the surface mat, and they grow as upright columnar structures. Portions of the mat may break off and float up under the permanent ice cover of the lake so that they become incorporated into the ice when it

freezes (see above). In one lake of the Dry Valleys, Lake Fryxell, the columnar mats precipitate calcium carbonate and remain in place with a hard calcite interior.

Pinnacle mats – these occur to at least 30 m depth within the relatively well illuminated environment of Lake Vanda and form conical structures 2-5 cm high and 3-5 cm wide. These structures incorporate sand grains and calcite crystals and resemble the fossil Precambrian stromatolite *Conophyton* (Chapter 2).

Aerobic prostrate mats – these occur over the surface sediments at depth and precipitate calcite.

Anaerobic prostrate mats – these occur in deep anoxic basins of the lakes.

The mats were typically dominated by filamentous cyanobacteria, usually members of the Oscillatoriaceae. In lakes of the Dry Valleys the dominant form was *Phormidium frigidum* in all mat types, sometimes in association with *Lyngbya martensiana*.

More recent studies in the Larsemann Hills of eastern Antarctica revealed a similarly wide diversity of mat types (Ellis-Evans, 1996, and refs therein):

a) In deeper lakes (> 10 m depth), black *Nostoc* mats several mm in thickness occurred to a depth of c. 1 m.

b) At greater depth *Nostoc* was replaced by orange pigmented mats up to 8 mm thick and dominated by *P. frigidum*. Small surface protrusions of the mat were associated with oscillatorian filaments that overgrew spherical *Nostoc* colonies. These mixed assemblages are morphologically similar to communities reported from elsewhere in Antarctica, specifically at Ablation Point, Alexander Island and in ponds on the McMurdo Ice Shelf which contained *Nostoc microscopicum*. The surface carotenoid pigmentation of the mats diminished with depth in the lake and was absent from communities in water deeper than 6 m, consistent with the role of these pigments as a defense against bright solar radiation (see below).

c) In lakes with a maximum depth of 3-10 m the mats formed circular plates 1-2 cm thick and 10-15 cm in diameter. The plates accumulated in the bottom waters, formed a layer at least 50 cm in thickness, and were dominated by oscillatorians with *Nostoc*, *Gloeocapsa* and *Chroococcus* as subdominants. Similar plate- or disc-shaped growths of cyanobacteria are known to occur in shallow ponds in the southernmost part of Victoria Land (the Pyramid Trough area).

d) In shallow ponds of higher salinity, red pigmented mats covered the bottom and were periodically detached by wind. These mats also contained spherical *Nostoc* colonies on their upper surface, but without the filamentous overgrowth.

Thick benthic mats of cyanobacteria were reported from many other Antarctic locations. For example, divers who examined the bottom of Priyadarshani Lake (maximum depth of 6.5 m) in the Schirmacher Oasis region found 25-90 cm thick cyanobacterial mats that were dominated by oscillatorians as well as *Synechocystis* and *Chroococcus* (Ingole and Parulekar, 1990). Benthic cyanobacteria occur in association with mosses in the maritime lakes of Signy Island. Unlike the lake communities of continental Antarctica these maritime cyanobacterial communities are dominated by *Phormidium* in shallow waters and by *Tolypothrix tenuis* and *Plectonema* (and sometimes the xanthophyte *Tribonema*) at depth (Ellis-Evans, 1996).

III. Biodiversity and Endemism

The biodiversity of polar cyanobacteria is at present a subject of considerable debate and uncertainty. In large part this reflects the inadequacy of current taxonomic criteria for these organisms. Broady

(1996) pointed to the lack of consistent taxonomic criteria in analyses of the Antarctic microflora in general, but particularly with respect to the cyanobacteria. Most investigators use the traditional taxonomic scheme of Geitler (1932) and work with samples of freshly collected or preserved field material. Some authors adopted the highly simplified Drouet classification, in which much information was sacrificed. Few studies of polar regions to date have used the criteria of Anagnostidis and Komárek, (1988) that are based on morphological features and attributes of strains in culture. A notable example of this approach in Antarctica was the work of Broady and Kibblewhite (1991); similar studies are only just beginning in the Arctic (Vézina and Vincent, 1997).

The slow rates of speciation by cyanobacteria in general (Castenholz, 1992), in combination with the efficient dispersal abilities of this group of microorganisms, and the relatively young age of ice-free environments in the Arctic and Antarctic, suggest that endemism is likely to be rare amongst polar cyanobacteria. Most of the forms identified to date appear to be cosmopolitan taxa. However, the morphological simplicity of cyanobacteria masks a high level of genetic variability. For example, *Phormidium autumnale* is a commonly encountered species in both polar regions, and recent studies on lakes in the Bylot Island region of the Arctic (Lat. 73°N) demonstrated that several isolates which conformed to the morphological criteria for this taxon differed greatly in their pigment and growth characteristics (Fig. 5).

The application of molecular tools to polar communities (e.g. PCR fingerprinting; sequence analysis of phylogenetically-relevant genes such as 16S rRNA) will be of special interest in determining the genetic relationships between such isolates, and for determining the affinity of the Arctic cyanobacterial flora with that of lower latitudes and Antarctica.

IV. Ecophysiology of Polar Cyanobacteria

A. Temperature Relations

Many observations from temperate lakes and rivers support the tenet that cyanobacteria prefer warm temperatures. For example, bloom-forming species have temperature optima for growth and photosynthesis above 20°C and generally achieve

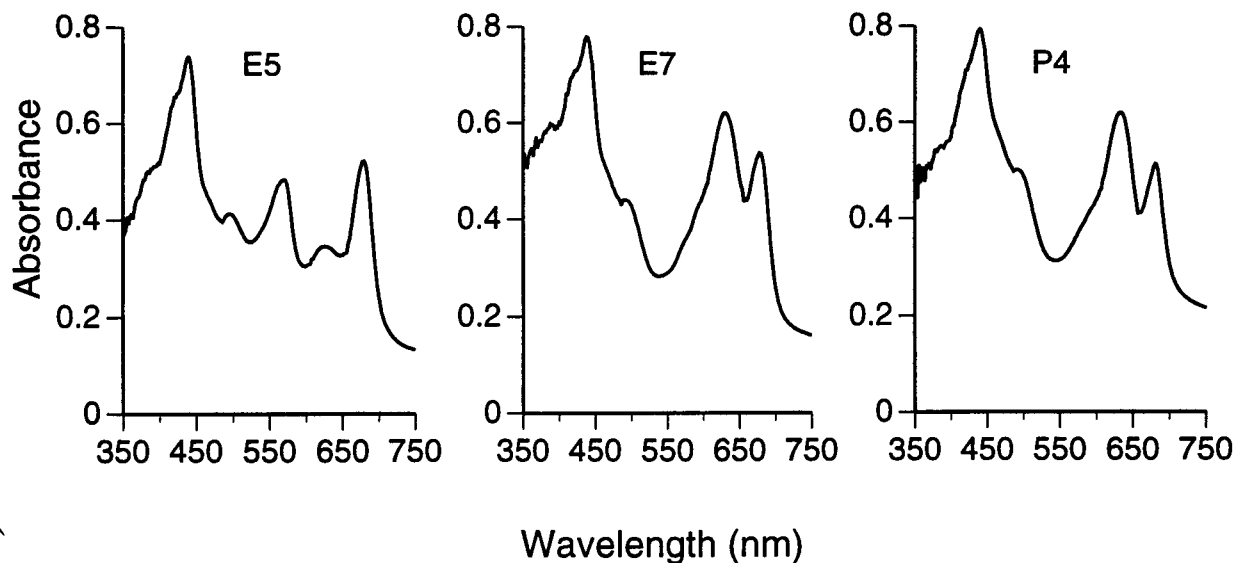


Fig. 5. In vivo absorbance characteristics of three isolates of Arctic cyanobacteria. E5 and E7 are both oscillatorians identified as *Phormidium autumnale*, but E5 contains both phycoerythrin and phycocyanin while E7 contains only phycocyanin. P4 is a picoplanktonic isolate containing phycocyanin but not phycoerythrin (Vézina and Vincent, 1997).

their peak abundance in late summer during the period of highest temperatures (Robarts and Zohary, 1987). Freshwater picocyanobacteria increase in numbers with increasing water temperature in rivers, lakes and the ocean (Bertrand and Vincent, 1994; and refs therein). Although these correlative relationships imply that low temperatures in the polar regions may severely inhibit cyanobacterial growth and abundance, they do not constitute proof of cause and effect, particularly in view of the range of other environmental variables which often co-vary with temperature such as nutrient supply and water column stability.

Field and laboratory measurements on one group of polar cyanobacteria, the mat-formers, indicate that although the low ambient temperatures may not completely inhibit metabolism and growth, they are strongly limiting. In controlled temperature studies on a microbial mat dominated by oscillatorians in a McMurdo Dry Valley stream, photosynthesis increased with increasing temperature, to maximum

rates at 25°C. However, respiration rates also increased and in the dark the mats were rapidly destroyed by bacterial decomposition under warmer temperatures (Vincent and Howard-Williams, 1986). Similar assays for photosynthesis in *Phormidium*-dominated mats in the maritime zone (Signy Island) gave an optimum temperature for net photosynthesis of 15°C (Davey, 1989).

In cultures of mat-forming cyanobacteria isolated from the polar regions the temperature optima for growth were consistently above the near-freezing temperatures that typically occur in the natural environment. Several clones of cyanobacteria isolated from southern Victoria Land, Antarctica were unable to grow at temperatures less than or equal to 5°C. This implies that these organisms originated from warmer temperate latitudes (Seaburg et al., 1981). A strain of *Oscillatoria priestleyii* isolated from the McMurdo Ice Shelf had a growth optimum in the range 21-24°C (Castenholz and Schneider,

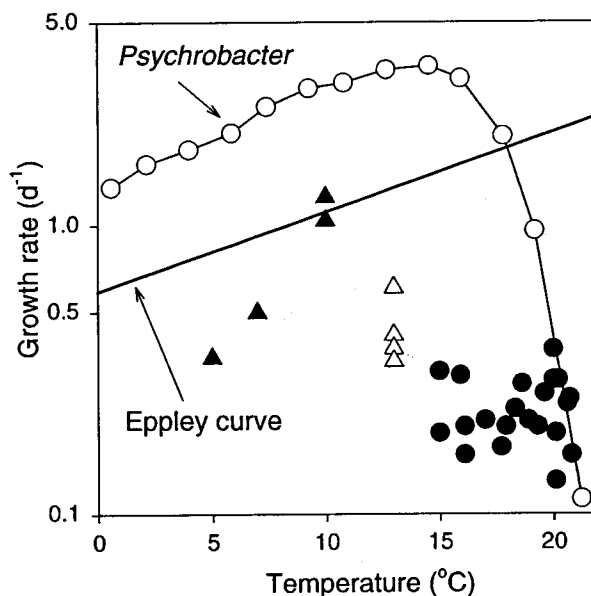


Fig. 6. Growth versus temperature relationships. The black symbols are maximum growth rates (μ_{\max}) at optimum temperatures for polar mat-forming cyanobacteria with T_{opt} at or below 20°C (from Tang et al., 1997). The line is the upper bound for marine phytoplankton given by Eppley (1972). The open symbols are for a marine bacterium isolated from congelation ice in East Antarctica, from Bowman et al. (1997). The open triangles are for picocyanobacterial isolates from Arctic lakes grown at 13°C and optimal light (Vézina & Vincent 1997). The closed triangles are μ_{\max} and T_{opt} values for marine diatoms from the Arctic and Antarctic (Jacques, 1983).

1993), well above the summer pond temperatures which were typically in the range 0-8°C.

In the most extensive survey to date, Tang et al. (1997) found that 27 isolates of oscillatoriids from lakes, streams and ponds in the Arctic, subarctic and Antarctic were consistently psychrotrophic. Temperature optima for growth were in the range 15-35°C, with some species showing insignificant growth at 5°C. Most isolates, however, grew over a wide temperature range (5-30°C) and, although they were not genetically adapted to low temperatures, they were likely to be tolerant of the variable temperature regime which characterizes their environment. These characteristics contrast with Arctic and Antarctic marine diatoms and sea ice bacteria whose temperature optima for photosynthesis and growth are much lower than those of polar cyanobacteria (Fig. 6). These psychrophilic attributes of the marine communities may reflect the persistent low and stable temperature of these environments, in contrast to the variable thermal regime of non-marine polar habitats (Tang et al., 1997).

B. Desiccation, Freezing and Salinity Tolerance

A primary factor that contributes to the success of polar cyanobacteria is their ability to withstand freezing and the related stresses of high salinity and low water activity. The streams and shallow ponds may dry completely in late summer, or freeze solid and then ablate to leave dry, frozen communities. These later experience elevated salinities as the remaining solutes are re-dissolved and mobilized at the onset of the thaw of the next season. Such freeze-concentration effects may be especially severe for the microbial mats living at the bottom of high latitude ponds that freeze completely in winter. Studies on two Antarctic coastal ponds during the time of freezing revealed the magnitude of salinity variations experienced by their biota (Schmidt et al., 1991). These waters had a relatively low conductivity in summer, but the dissolved salts were largely excluded from the ice during winter freezing, and there was a gradual concentration of solutes in the remaining water. In mid-winter the benthic cyanobacterial mats were covered by a thin layer of concentrated brine with salinities more than six times that of sea water

and liquid water temperatures of -12°C (See Chapter 10).

The cyanobacteria of streams in southern Victoria Land are capable of maintaining large populations of viable cells on the dry frozen stream bed throughout winter. These populations provide a large inoculum that may contribute a substantial percentage of the total standing stock during the next growing season. For example, in Fryxell Stream the percent cover of cyanobacteria was $61 (\pm 19)\%$ prior to summer streamflow and rose slightly to $84 (\pm 5)\%$ by the end of summer flow. These overwintering assemblages began photosynthesis, respiration and nutrient uptake within 30 minutes to a few hours of rehydration (Vincent and Howard-Williams, 1986).

Studies at two sites in Antarctica confirmed the highly resilient nature of polar cyanobacteria subjected to water stress (Hawes et al., 1992). Mats dominated by *Nostoc commune* placed in the dry atmosphere on the McMurdo Ice Shelf dehydrated rapidly and were completely desiccated within 5 hours (see Chapter 17). Photosynthesis and respiration was measured in the mats within 10 minutes of rewetting. *Phormidium*-dominated mats appeared to be less tolerant of dehydration and took much longer to recover their physiological activity after rewetting.

C. Defenses Against UVR

Many of the polar cyanobacteria inhabit surface or shallow-water environments in which the exposure to continuous UVR in summer may play a role in limiting microbial colonization and growth. Such effects may now be exacerbated by the stratospheric ozone depletion that is occurring over Antarctica as well as increasingly in the high latitudes of the northern hemisphere (Kerr, 1994). Like other phototrophic organisms, cyanobacteria have four lines of defense against UVR, and these strategies are well represented in the polar communities studied to date (Vincent and Quesada, 1994, 1997; Quesada and Vincent 1997):

a) Cyanobacteria can avoid UVR by their choice of habitat such as beneath rock surfaces or deep within microbial mats. The consequence of adopting such a strategy is that only low PAR is available for growth. Examples of polar cyanobacteria in perennial shade environments include sublithic and endolithic communities, phytoplankton and benthos in permanently ice-covered lakes, and the bottom communities of optically-thick microbial mats. Some

cyanobacterial species are motile and are capable of migration up and down the mat profile to avoid UVR exposure while ensuring adequate PAR; for example, *Oscillatoria priestleyii* from the McMurdo Ice Shelf (Quesada and Vincent 1997). In some environments, however, this strategy may be more closely linked to water supply and desiccation tolerance than UVR avoidance (Davey and Clarke, 1991).

b) A second type of avoidance strategy is the production of screening compounds that filter out UVR (See Chapter 21). The black or dark gold pigmentation associated with many cyanobacterial communities in the polar regions is due to the pigment scytonemin which absorbs maximally at 390 nm but with a broad absorbance spectrum that extends into the UVB and low energy PAR. Scytonemin is a dimeric molecule (molecular weight of 544) that is probably formed from a condensation of tryptophan and phenylpropanoid derivatives (Proteau et al., 1993). Dark pigmented communities of Arctic cyanobacteria include *Nostoc* colonies and sheets in the shallow waters of lakes and ponds (Fig. 7); stream communities of *Rivularia*, *Stigonema* and *Scytonema* (Sheath et al., 1996); black films and crusts over desert and semi-desert soils (Aleksandrova, 1988) and *Gloeocapsa* crusts on exposed rock faces (Konhauser et al., 1994). Similar communities occur in Antarctica and include *Nostoc* at the edge of streambeds or in slowly flowing flush environments; *Calothrix* and *Gloeocapsa* at the edge of streams; and black crusts over soils. A dark red pigment occurs in the sheaths of *Gloeocapsa* that forms brown crusts over the rocks in Arctic (Sheath et al., 1996) as well as Antarctic streams; this pigmentation was ascribed to gloeocapsin, but its UVR-absorbing and other molecular properties have yet to be studied. Water soluble pigments that absorb UV-A/B are also well known in cyanobacteria, particularly mycosporine-like amino acids such as asterina-330, shinorine, porphyra-334 and palythene which absorb maximally in the range 320-335 nm (Vincent and Roy, 1993). Aqueous extracts of *Nostoc commune* from Alaska (Fig. 7) and oscillarian isolates from the McMurdo Ice Shelf (Quesada and Vincent, 1997) have spectra that suggest the presence of this group of sunscreens. These compounds may be responsible for the strong UVR attenuation in the upper few hundred μm of Antarctic *Phormidium* mats (Quesada and Vincent, 1993).

c) UVR damage of biological systems can be the result of direct photochemical degradation of cellular

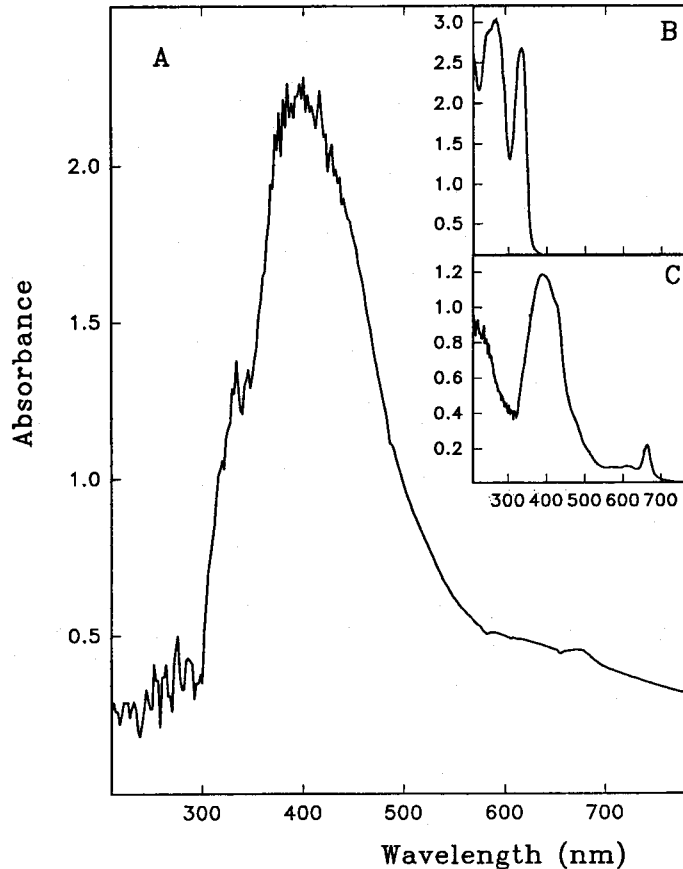


Fig. 7. UV-screening capability of *Nostoc commune* from Toolik Lake, Alaska. Curve A is the *in vivo* absorbance spectrum; curve B is a scan of a 90% methanol-water extract showing the presence of compounds with the absorption characteristics of mycosporine-like amino-acids; curve C is a scan of a 90% acetone-water extract showing the characteristic spectrum of scytonemin (Vincent and Quesada, 1997; Plate 24e).

components, or indirect effects mediated by reactive oxygen species (ROS) (Vincent and Neale, 1999; and refs therein). These latter secondary effects can be substantially offset or eliminated by cellular quenching agents that react with and neutralize ROSs. Carotenoids are well known in this regard, and surface populations of cyanobacteria in the polar regions are often highly pigmented with canthaxanthin, myxoxanthophyll and related compounds. The carotenoid:Chl*a* ratios of polar cyanobacteria in culture are maximal under low temperatures, bright PAR and moderate UVR (Vincent and Quesada, 1997; Tang et al., 1997; Roos and Vincent, unpublished data).

d) Further protection against the long-term effects of UVR exposure is conferred by an ability to identify and repair the photochemical damage to DNA or to

the photosynthetic apparatus (See Chapters 15 and 21). These repair mechanisms are stimulated by long wavelength UVR or blue light. Studies on two isolates of oscillarian cyanobacteria from the McMurdo Ice Shelf showed that there were large differences in UVB sensitivity between species, but for the growth of both strains UVA exposure substantially offset the inhibitory effects of UVB (Quesada et al., 1995).

D. Light Harvesting and Photosynthesis

Arctic and Antarctic cyanobacteria experience extreme variations in PAR supply from continuous light in summer to continuous winter darkness. Many of the communities inhabit subsurface environments that remain highly shaded, even in mid-summer; for

example, well beneath the surface of rocks, deep within microbial mats, at the bottom of perennially ice-covered lakes and beneath the surface crust of soils. Other communities occur beneath ice or snow early in the growing season and are then exposed to full sunlight during summer melt. Polar cyanobacteria must therefore be capable of acclimation to a broad range of PAR regimes.

Cultures of Antarctic oscillatorians showed a high level of adaptive flexibility in pigmentation in response to changes in ambient PAR (Quesada and Vincent, 1993). Incubation under dim light ($20 \mu\text{mol photons m}^{-2} \text{s}^{-1}$) resulted in a large increase in cellular Chl *a* and phycobilin content and a corresponding decrease in the carotenoid to Chl *a* ratio. A comparison of incubations under full waveband PAR with those under color filters (which simulated the spectral conditions at the base of the mats) showed that these changing pigment ratios were primarily a response to changes in incident light quantity rather than quality down the mat profile.

The small cell diameter of some polar species may confer a light-capturing advantage under dim PAR conditions by minimizing self-shading effects within the cell. Optically thin cells are a feature not only of the picocyanobacteria but also of members of the Oscillatoriaceae with narrow (1-2 μm) trichomes. Recent studies with isolates of this latter group from Arctic microbial mats indicate that their cellular absorption coefficients ($\mu\text{m}^2 \text{cell}^{-1}$) span two orders of magnitude and are a function of cell size and the PAR conditions that they acclimate to during growth. The narrow trichome species from mat communities have similar optical characteristics to the picocyanobacteria from Arctic lakes (Vézina and Vincent, unpublished).

One of the intriguing features of the thick microbial mats found in the polar regions is the apparently precarious balance between photosynthesis and respiration. Although the maximum photosynthetic rates can be high per unit area (up to $4 \mu\text{g C cm}^{-2} \text{h}^{-1}$), the Chl *a* specific carbon uptake is low and reflects the low ambient temperature and the high degree of self-shading within the optically thick mats (Hawes, 1993). Assays of CO_2 -exchange performed on cyanobacteria from Antarctic streams indicated that net photosynthesis was generally well below gross photosynthesis, and sometimes near-zero or even negative (Vincent and Howard-Williams, 1986; Hawes and Howard-Williams, 1997). These observations imply that the large accumulations of biomass are the result of many seasons of slow net

growth, with relatively little biomass loss through processes such as grazing or sloughing.

E. Nitrogen Fixation

Nitrogen-fixing cyanobacteria, particularly *Nostoc commune*, are contributors of soil nitrogen and carbon in both polar regions, and may play an important role in the primary successional stage of colonization after the retreat of an ice sheet or glacier (Chapin et al., 1992) as well as in mature communities (Henry and Svoboda, 1986). In the Vestfold Hills, Antarctica, and probably other terrestrial sites, nitrogenase activity is strongly regulated by temperature and moisture availability, with maximum activity in December and January when the N_2 -fixing mats are well supplied with meltwater and when ground temperatures rise to 8-10°C (Davey and Marchant, 1983). Fixation of dinitrogen by cyanobacteria can be an important contribution to the nitrogen budget of polar lakes, ponds and streams (Alexander et al. 1980, 1989; Hawes et al. 1993).

Nitrogen-fixing cyanobacteria are often found in close association with moss communities. In the maritime Antarctic (Signy Island) nitrogen fixation rates varied from a mean of 46 (dry turf) to 192 (wet carpet) $\text{mg N m}^{-2} \text{y}^{-1}$. These rates were comparable to the amount of inorganic nitrogen entering these systems by precipitation; about $65 \text{mg N m}^{-2} \text{y}^{-1}$ (Christie, 1987). On Svalbard, at latitude 79°N, the ability to support cyanobacteria, in particular *Nostoc*, varied greatly between bryophyte communities and there were concomitant variations in nitrogen-fixation rates as measured by the acetylene reduction assay technique (Solheim et al., 1996). Nitrogenase activity was stimulated greatly (probably by phosphorus) in regions grazed by geese and the rates in these areas were as much as one order-of-magnitude higher than those measured in cyanobacterial mats in the warmer low latitude mires of the sub-Arctic (Karagatzides et al., 1985) and sub-Antarctic (Smith and Russell, 1982).

V. Why Do Cyanobacteria Dominate (Or Not)?

The large and rapidly expanding literature on high latitude cyanobacteria continues to reinforce a striking dichotomy in their pattern of distribution and abundance. In cold, non-marine habitats such as ice-

caps, polar desert soils, glacial streams and ice-capped lakes, cyanobacteria are often the dominant phototrophs. In environments such as shallow ponds and rock faces they may contribute most of the total ecosystem standing stock, with spectacular biomass accumulations at some sites. Yet in the marine environment of both polar regions cyanobacteria are rare or conspicuously absent. Any explanation of the pre-eminent success of cyanobacteria in the terrestrial biomes of the Arctic and Antarctica must also consider their weak representation in cold oceanic waters. This concluding section briefly considers five aspects of the eco-physiology of polar cyanobacteria that might account for this fascinating pattern of presence and absence.

A. Temperature Effects

The strong latitude-dependent decrease in marine picocyanobacteria (Fig. 2), and the correlative relationships between cyanobacterial abundance and temperature in the polar regions as well as elsewhere, point to temperature as a likely overall control. The non-marine isolates examined to date have broad tolerances to temperature but lack the adaptive goodness-of-fit to cold that is characteristic of many diatoms and bacteria in the polar ocean. Polar cyanobacteria have extremely slow growth rates at near-zero temperatures relative to psychrophilic species. Even the maximum growth rates of polar cyanobacteria are slow relative to phytoplankton in general with μ_{\max} values that fall well below the Eppley curve (Fig. 6). In apparent contradiction to these observations is the dramatic success of cyanobacteria, including picocyanobacteria, in cold non-marine habitats such as cryoconite ponds, polar desert lakes and high latitude streams. The water temperature in some of these non-marine ecosystems fluctuates considerably over the 24 h cycle because of solar heating. The eurythermal capacity of cyanobacteria may provide a competitive advantage in these systems, but not in the polar oceans or in ice-capped lakes where cold temperatures persist throughout the year.

B. Salinity Responses

The greater presence of cyanobacteria in polar freshwaters versus marine habitats might simply reflect their limits of tolerance to salinity. Wright and Burton (1981) noted that the combined extreme of salinity plus low temperatures exerts a severe

physiological stress on organisms and could account for the absence of cyanobacteria from some of the hypersaline lake environments in Antarctica. However, this seems an unlikely explanation for the absence of picocyanobacteria in the polar oceans. Picocyanobacteria achieve spectacularly high densities in Ace lake, Antarctica, at salinities similar to seawater and at relatively low temperatures (6°C). On the McMurdo Ice Shelf, mat-forming cyanobacteria occur in ponds that remain cold ($< 5^{\circ}\text{C}$) throughout the year at salinities at or above seawater (Howard-Williams et al., 1989), and in ponds on Ross Island, microbial mats survive the seasonal extreme of sub-zero liquid water temperatures and salinities up to many times that of seawater (Schmidt et al., 1991).

C. Nutrient Requirements

Bloom-forming and picoplanktonic species of cyanobacteria are extreme in terms of their nutrient requirements. The former group occurs mostly in nutrient-rich environments, while the latter has a high nutrient-scavenging ability and is more typical of oligotrophic conditions. Consistent with this general pattern, picocyanobacteria occur throughout the oligotrophic lakes of both polar regions however, even in enriched lakes of the Arctic and Antarctica, bloom-forming species are rarely present. These latter forms are typically gas vacuolate and can adjust their position in the water column; this strategy would not be favored in the cold unstable waters of polar lakes. A consideration of nutrient-size relationships suggests that picocyanobacteria would have less of a competitive advantage under nutrient-replete conditions than under conditions of nutrient deficiency. Nevertheless, picoplanktonic taxa (but eukaryotes) are often a dominant component of the phytoplankton in the nutrient-rich Arctic Ocean (Gradinger and Lenz, 1995) and Southern Ocean (Vincent, 1988), indicating that picocyanobacteria are not precluded simply on the basis of their small size. In these environments, the success of picoplankton-sized phototrophs is more likely to be the result of selection for organisms which have a superior light-capturing ability and that are less prone to grazing losses than larger cells.

The availability of iron was identified as a potentially important control on phytoplankton production in certain parts of the world ocean, including the seas around Antarctica. Cyanobacteria as a group are known to have a high requirement for

iron and therefore may be especially prone to limitation effects. However, this explanation seems unlikely for the absence of picocyanobacteria in the Arctic Ocean where there is a strong freshwater influence from the surrounding land masses, and where terrigenous inputs of iron are probably substantial. Furthermore, picocyanobacteria have a strong scavenging ability for Fe relative to other algal groups.

Polar lakes, ponds and streams which contain mat-forming species of cyanobacteria span a broad range of nutrient conditions, although concentrations within the mats may be orders of magnitude higher than in the overlying water (e.g. up to 1000 μg dissolved reactive P L^{-1} in mats on the McMurdo Ice Shelf; Vincent et al., 1993c). The N_2 -fixing ability of *Nostoc* is likely to be a factor that contributes to the widespread distribution of this form in nitrogen-deficient habitats such as glacial moraines and certain meltwater streams.

D. Growth Rates

One of the most striking features of polar cyanobacteria is their slow growth rate in culture as well as in the natural environment. In part this is an effect of low temperature, perhaps compounded by osmotic stress in some habitats. In the polar oceans these temperature-depressed growth rates may be further slowed by light-limitation in the deep mixed layer. However even at the optimum temperature for growth, μ_{max} values for polar cyanobacteria lie well below the Eppley curve (Fig. 6) and in some communities such as the lake and stream microbial mats the net balance between photosynthesis and respiration is close to zero through much of the growing season. This implies that the selection pressure in non-marine polar environments is not for an ability to out-compete other organisms via fast growth. On the other hand, cyanobacteria are able to achieve net growth over a broad range of pH, nutrient concentrations, PAR and UVR fluxes, and temperatures. These broad physiological tolerances are likely to be important in the highly variable non-marine habitats such as soils and ephemeral streams, but may be less useful in the thermally and chemically more stable oceanic environments.

E. Loss Rates

Slow growth can only be one component of an overall strategy for microbial success; it must also be

accompanied by an ability to minimize biotic and abiotic processes which remove biomass. In the polar non-marine environment there are many examples of resistance to abiotic loss through processes such as tolerance to freeze-up and desiccation, and the persistence of an overwintering inoculum on dry stream beds or in the bottom waters of lakes. Grazing losses are minimal in these habitats in Antarctica where the only herbivores are microscopic species such as tardigrades, nematodes and rotifers, and these rarely achieve a large population size. Insect grazers are important in Arctic streams and ponds, and may be responsible for the reduced standing stocks in these environments relative to Antarctic communities. In Ace Lake, Antarctica, populations of picocyanobacteria begin to decline well before the ambient light conditions begin to deteriorate, perhaps in response to increased populations of protozoan grazers which are known to occur seasonally in these lakes (Laybourne-Parry and Marchant, 1992). This resistance to loss is likely to be much less effective in the polar marine environment where there is a more diverse assemblage of herbivores capable of grazing picocyanobacteria (e.g., choanoflagellates and tunicates), and where continuous advection and mixing may further prevent the accumulation of cells.

In summary, cyanobacteria are able to dominate the microflora at many sites in the polar regions through slow growth, tolerance of severe conditions (e.g., winter freeze-up) and persistence. This strategy is successful in extreme environments in which multi-trophic level communities are poorly developed, and where competition, herbivory and other biological interactions are only weakly expressed. This approach fails, however, in cold oceanic environments where only faster growing, more thermally adapted species are able to keep pace with the continuous removal of biomass via biotic and abiotic loss processes.

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References

- Aleksandrova VD (1988) Vegetation of the Soviet polar deserts. Cambridge University Press, Cambridge
- Alexander V, Stanley DM, Daley RJ and McRoy CP (1980) Primary producers. In: Hobbie JE (ed) Limnology of Tundra Ponds, pp179-250. Dowden, Hutchinson and Ross Inc, Stroudsburg, PA
- Alexander V, Whalen SC and Klingensmith KM (1989) Nitrogen cycling in Arctic lakes and ponds. *Hydrobiologia* 172: 165-172
- Anagnostidis K and Komárek J (1988) Modern approach to the classification system of cyanophytes, 3.-Oscillatoriales. *Archiv für Hydrobiol Supplement band 71 (Algological Studies, 38-39):* 291-302
- Andreoli C, Scarabel L, Spini S and Grassi C (1992) Picoplankton in Antarctic lakes of northern Victoria Land during summer 1989-1990. *Polar Biol* 11: 57-82
- Bergeron M and Vincent WF (1997) Microbial food web responses to phosphorus and solar UV radiation in a subarctic lake. *Aquatic Microbial Ecol* 12: 239-249
- Bertrand N and Vincent WF (1994) Structure and dynamics of photosynthetic picoplankton across the saltwater transition zone of the St. Lawrence River. *Can J Fish Aquat Sci* 51: 161-171
- Bliss LC and Gold WG (1994) The patterning of plant communities and edaphic factors along the a high Arctic coastline- implications for succession. *Can J Bot* 72: 1095-1107
- Bowman JP, Nichols DS and McMeekin TA (1997) *Psychrobacter glacicola* sp. nov., a halotolerant, psychrophilic bacterium isolated from Antarctic sea ice. *System Appl Microbiol* 20: in press
- Broady PA (1981) The ecology of chasmolithic algae at coastal locations of Antarctica. *Phycologia* 20: 259-272
- Broady PA (1986) Ecology and taxonomy of the terrestrial algae of the Vestfold Hills. In: Pickard J (ed) *Antarctic Oasis*, pp 165-202. Academic Press, Sydney
- Broady PA (1996) Diversity, distribution and dispersal of Antarctic terrestrial algae. *Biodiversity and Conservation* 5: 1307-1335
- Broady PA and Kibblewhite AL (1991) Morphological characterization of Oscillatoriales (Cyanobacteria) from Ross Island and southern Victoria Land, Antarctica. *Ant Sci* 3: 35-45
- Broady PA and Smith RA (1994) A preliminary investigation of the diversity, survivability and dispersal of algae into Antarctica by human activity. *Proceedings of the National Institute of Polar Research (NIPR) Symposium on Polar Biology* 7: 185-197
- Castenholz RW (1992) Species usage, concept, and evolution in the Cyanobacteria (blue-green algae) *J Phycol* 28: 737-745
- Castenholz RW and Schneider AJ (1993) Cyanobacterial dominance at high and low temperatures: optimal conditions or precarious existence? In: Guerrero R and Perdos-Alio (eds) *Trends in Microbial Ecology*, pp 19-24. Spanish Society for Microbiology, Barcelona
- Chapin FS, Jeffries RL, Reynolds JF, Shaver GR and Svoboda J (1992) Arctic Ecosystems in a Changing Climate: An Ecophysiological Perspective. Academic Press, San Diego, California
- Christie P (1987) Nitrogen in two contrasting Antarctic bryophyte communities. *J Ecol* 75: 173-193
- Croasdale H (1973) Freshwater algae of Ellesmere Island, N.W.T. National Museums of Canada Publications in Botany 3: 1-131
- Davey MC (1989) The effects of freezing and desiccation on photosynthesis and survival of terrestrial Antarctic algae and cyanobacteria. *Polar Biol* 10: 29-36
- Davey MC (1991) The seasonal periodicity of algae on Antarctic fellfield soils. *Holarctic Ecol* 14: 112-20
- Davey MC and Clarke KJ (1991) The spatial distribution of microalgae on Antarctic fell-field soils. *Antarctic Science* 3: 257-263
- Davey A and Marchant HJ (1983) Seasonal variation in nitrogen fixation by *Nostoc commune* Vaucher at the Vestfold Hills, Antarctica. *Phycologia* 22: 337-385
- de Mora SJ, Whitehead RF and Gregory M (1994) The chemical composition of glacial melt water ponds on the McMurdo Ice Shelf, Antarctica. *Ant Sci* 6: 17-27
- Ellis-Evans JC (1991) Numbers and activity of bacterio- and phytoplankton in contrasting maritime Antarctic lakes. *Verh Internat Verein Theor Angew Limnol* 24: 1149-54
- Ellis-Evans JC (1996) Microbial diversity and function in Antarctic freshwater ecosystems. *Biodiversity and Conservation* 5: 1395-1431
- Ellis-Evans JC and Bayliss PR (1993) Biologically active microgradients in cyanobacterial mats of Antarctic lakes and streams. *Verh Internat Verein Limnol* 25: 948-952
- Eppley RW (1972) Temperature and phytoplankton growth in the sea. *Fish Bull* 70: 1063-1085
- Fritsch FE (1917) Freshwater algae. British Antarctic ("Terra Nova") Expedition, 1910, Natural History Report. British Museum (Natural History) p 1-16
- Geitler L (1932) Cyanophyceae. In: Kolkwitz R (ed) *Dr. L Rabenhorst's Kryptogamenflora von Deutschland, Osterreich und der Schweiz*. Akademische Verlagsgesellschaft, Leipzig
- Gendel RW and Drouet F (1960) The cyanobacteria of the Thule Area, Greenland. *Trans Am Microscop Soc* 79: 256-272
- Goldman CR, Mason DT and Hobbie JE (1967) Two Antarctic desert lakes. *Limnol Oceanogr* 12: 295-310
- Gradinger R and Lenz J (1995) Seasonal occurrence of picocyanobacteria in the Greenland Sea and central Arctic Ocean. *Polar Biol* 15: 447-452
- Hamilton PB and Edlund SA (1994) Occurrence of *Prasiola fluviatilis* (Chlorophyta) on Ellesmere Island in the Canadian Arctic. *J Phycol* 30: 217-221
- Hawes I (1990) Eutrophication and vegetation development in maritime Antarctic lakes. In Kerry KR and Hempel G (eds) *Antarctic Ecosystems. Ecological Change and Conservation*, pp 83-90. Springer-Verlag, Berlin
- Hawes I (1993) Photosynthesis in thick cyanobacterial films: a comparison of annual and perennial Antarctic mat communities. *Hydrobiologia* 252: 203-209
- Hawes I and Howard-Williams C (1997) Primary production processes in streams of the McMurdo Dry Valleys, Antarctica. In: Prisco J (ed) *Dry Valley a Cold Desert Ecosystem*. Antarctic Research Ser, in press
- Hawes I, Howard-Williams C and Pridmore RD (1993) Environmental control of microbial biomass in the ponds of the McMurdo Ice Shelf, Antarctica. *Arch Hydrobiol* 127: 27-287
- Hawes I, Howard-Williams C, Schwarz A-MJ and Downes MT (1997) Environment and microbial communities in a tidal lagoon at Bratina Island, McMurdo Ice Shelf, Antarctica. In: Battaglia B, Valencia J and Walton D (eds), *Antarctic Communities: Species, Structure and Survival*, in press. Cambridge University Press, UK
- Hawes I, Howard-Williams C and Vincent WF (1992) Desiccation and recovery of cyano-bacterial mats. *Polar Biol* 12: 587-594

- Henry GHR and Svoboda J (1986) Dinitrogen fixation (acetylene reduction) in high arctic sedge meadow communities. *Arctic Alpine Res* 18: 181-187
- Howard-Williams C, Pridmore RD, Broady PA, and Vincent WF (1990) Environmental and biological variability in the McMurdo Ice Shelf ecosystem. In: Kerry KR and Hempel G (eds) *Antarctic Ecosystems. Ecological Change and Conservation*, pp 23-31. Springer-Verlag, New York
- Howard-Williams C, Pridmore R, Downes MT and Vincent WF (1989) Microbial biomass, photosynthesis and chlorophyll *a* related pigments in the ponds of the McMurdo Ice Shelf, Antarctica. *Ant Sci* 1: 125-131
- Ingole BS and Parulekar AH (1990) Limnology of Priyadarshani Lake, Schirmacher Oasis, Antarctica. *Polar Rec* 26: 13-17
- Jacques G (1983) Some ecophysiological aspects of the Antarctic phytoplankton. *Polar Biol* 2: 27-33
- Kalff J, Kling HJ, Holmgren SH and Welch HE (1975) Phytoplankton, phytoplankton growth and biomass cycles in an unpolluted and in a polluted polar lake. *Verh Internat Verein Limnol* 19: 487-495
- Kalff J and Welch HE (1974) Phytoplankton production in Char Lake, a natural polar lake, and in Meretta Lake, a polluted polar lake, Cornwallis Island, Northwest Territories. *J Fish Res Board Can* 31: 621-636
- Kerr JB (1994) Decreasing ozone causes health concern. *Environ Sci Technol* 28: 514-518
- Konhauser KO, Fyfe WS, Schultze-Lam S, Ferris FG and Beveridge TJ (1994) Iron phosphate precipitation by epilithic microbial films in Arctic Canada. *Can J Earth Sci* 31: 132-1324
- Karagatzides JD, Lewis MC, Schulman HM (1985) Nitrogen fixation in the high arctic tundra at Sarcpa Lake, Northwest territories. *Can J Bot* 63: 974-79
- Laybourne-Parry J and Marchant HJ (1992) The microbial plankton of freshwater lakes in the Vestfold Hills, Antarctica. *Polar Biol* 12: 405-410
- Legendre L, Gosselin, M, Hirsch HJ, Katner G and Rosenberg G (1993) Environmental control and potential fate of size-fractionated phytoplankton production in the Greenland Sea (75 °N). *Mar Ecol Prog Ser* 98: 297-313
- Leslie A (1879) *The Arctic Voyages of Adolf Erik Nordenskiöld*. MacMillan and Co, London
- Marchant HJ, Davidson AT and Wright SW (1987) The distribution and abundance of chroococcoid cyanobacteria in the Southern Ocean. *Proceedings of the National Institute of Polar Research (NIPR) Symposium on Polar Biology* 1: 1-9
- Maurette M, Hammer C, Brownlee DE, Reeh N and Thomsen HH (1986) Placers of cosmic dust in the blue ice lakes of Greenland. *Science* 233: 869-872
- Mishistina IE, Moskvina MI, Rodikova LP and Severina II (1994) Cyanobacteria of the genus *Synechococcus* in Arctic Seas (in Russian). *Dokl-Ran* 336: 562-565
- Murray J (1910) On collecting at Cape Royds. In: Murray J (ed) *British Antarctic Expedition 1907-1909 Reports on Scientific Expeditions, Vol. 1 Biology*, pp 1-15 Heinemann, London
- Murphy LS and Haugen EM (1985) The distribution and abundance of phototrophic ultraplankton in the North Atlantic. *Limnol Oceanogr* 30: 47-58
- Nienow JA and Friedmann EI (1993) Terrestrial lithophytic (rock) communities. In: Friedmann EI (ed) *Antarctic Microbiology*, pp 343-412. Wiley-Liss Inc, New York
- Ohtani S and Kanda H (1987) Epiphytic algae on the moss community of *Grimmia lawiana* around Syowa Station, Antarctica. *Proceedings of the National Institute of Polar Research Symposium on Polar Biology* 1: 255-264
- Parker BC, Simmons GM, Wharton RA, Seaburg KG and Love FG (1982) Removal of organic and inorganic matter from Antarctic lakes by aerial escape of bluegreen algal mats. *J Phycol* 18: 72-78
- Parker BC and Wharton RA (1985). Physiological ecology of blue-green algal mats (modern stromatolites) in Antarctic oasis lakes. *Arch Hydrobiol (Suppl)* 71: 331-348
- Persson P-E (1996) Cyanobacteria and off-flavours. *Phycologia* 35: 168-71
- Priscu, JC., Fritsen, CH, Adams, EE, Giovannoni, SJ, Paerl, HW, McKay, CP, Doran, PT, Gordon, DA, Lanoil, BD and Pinckney JL (1998) Perennial Antarctic lake ice: an oasis for life in a polar desert. *Science* 280: 2095-8.
- Proteau PJ, Gerwick WH, Garcia-Pichel F and Castenholz R (1993) The structure of scytonemin, an ultraviolet sunscreen pigment from the sheaths of cyanobacteria. *Experientia* 49: 825-829
- Quesada A, Mouget J-L and Vincent WF (1995) Growth of Antarctic cyanobacteria under ultraviolet radiation: UVA counteracts UVB inhibition. *J Phycol* 31: 242-248
- Quesada A and Vincent WF (1993) Adaptation of cyanobacteria to the light regime within Antarctic mats. *Verh Internat Verein Limnol* 25: 960-965
- Quesada A and Vincent WF (1997) Strategies of adaptation by Antarctic cyanobacteria to ultraviolet radiation. *Eur J Phycol* 32: 335-42
- Rankin LM, Franzmann PD, McMeekin TA and Burton HR (1997) Seasonal distribution of picocyanobacteria in Ace lake, a marine-derived Antarctic lake. In: Battaglia B, Valencia J and Walton D (eds), *Antarctic Communities: Species, Structure and Survival*, pp 178-184. Cambridge University Press, United Kingdom
- Roberts RD and Zohary T (1987) Temperature effects on photosynthetic capacity, respiration, and growth rates of bloom-forming cyanobacteria. *New Zealand Journal of Marine and Freshwater Research* 21: 391-399
- Schmidt S, Moskal W, de Mora SJ, Howard-Williams C and Vincent WF (1991) Limnological properties of Antarctic ponds during winter freezing. *Ant Sci* 3: 379-388
- Seaburg KG, Parker BC, Wharton RA and Simmons GM (1981) Temperature growth responses of algal isolates from Antarctic oases. *J Phycol* 17: 353-60
- Sheath RG and Müller KM (1997) Distribution of stream macroalgae in four high Arctic drainage basins. *Arctic* 50: 355-64.
- Sheath RG, Vis ML, Hambrook JA and Cole KM (1996) Tundra stream macro-algae of North America: composition, distribution and physiological adaptations. *Hydrobiologia*. 336: 67-82
- Smith V and Russell (1982) Acetylene reduction by bryophyte-cyanobacteria associations. *Polar Biol* 1: 153-7
- Solheim B, Endal A and Vigstad H (1996) Nitrogen fixation in Arctic vegetation and soils from Svalbard, Norway. *Polar Biol* 16: 35-40
- Tang EPY, Tremblay R and Vincent WF (1997) Cyanobacterial dominance of polar freshwater ecosystems: are high-latitude mat-formers adapted to low temperature? *J Phycol* 33: 171-181
- Taylor G (1916) *With Scott: The Silver Lining*. Dodd, Mead and Co, New York
- Vézina S and Vincent WF (1997) Arctic cyanobacteria and limnological properties of their environment: Bylot Island,

- Northwest Territories, Canada (73° N, 80° W) *Polar Biol* 17: 523-534
- Vincent WF (1988) *Microbial ecosystems of Antarctica*. Cambridge University Press, UK
- Vincent WF, Castenholz RW, Downes MT and Howard-Williams C (1993c) Antarctic cyanobacteria: light, nutrients, and photosynthesis in their microbial mat environment. *J Phycol* 29: 745-755
- Vincent WF, Downes MT, Castenholz RW and Howard-Williams C (1993b) Community structure and pigment organisation of cyanobacteria-dominated microbial mats in Antarctica. *Eur J Phycol* 28: 213-221
- Vincent WF and Howard-Williams C (1986) Antarctic stream ecosystems: physiological ecology of a blue-green algal epilithon. *Freshwater Biol* 16: 219-223
- Vincent WF, Howard-Williams C and Broady PA (1993a) Microbial communities and processes in Antarctic flowing waters. In: Friedmann EI (ed) *Antarctic Microbiology*, pp 543-569, Wiley-Liss Inc, New York
- Vincent WF and James MR (1996) Biodiversity in extreme aquatic environments: lakes ponds and streams of the Ross Sea sector, Antarctica. *Biodiversity and Conservation* 55: 1451-1471
- Vincent WF and Neale PJ (1999) Mechanisms of UV damage in aquatic biota. In: de Mora S (ed) *UV radiation in the marine environment*. Cambridge University Press, in press
- Vincent WF and Quesada A (1994) Ultraviolet radiation effects on cyanobacteria: implications for Antarctic microbial ecosystems. *Antarctic Res Ser* 62: 111-124
- Vincent WF and Quesada A (1997) Microbial niches in the polar environment and the escape from UV radiation in non-marine habitats. In: Battaglia B, Valencia J and Walton D (eds), *Antarctic Communities: Species, Structure and Survival*, pp 388-395. Cambridge University Press, UK
- Vincent WF and Roy S (1993) Solar UV-B effects on aquatic primary production: damage, repair and recovery. *Environ Rev* 1: 1-12
- Vincent WF and Vincent CL (1982) Factors controlling phytoplankton production in Lake Vanda (77°S). *Can J. Fish Aquat Sci* 39: 1602-9
- Walker TD and Marchant HJ (1989) The seasonal occurrence of chroococcoid cyanobacteria at an Antarctic coastal site. *Polar Biol* 9: 193-196
- Waterbury JB, Watson SW, Valois FW and Franks DG (1986) Biological and ecological characterization of the marine unicellular cyanobacterium *Synechococcus*. *Can Bull Fish Aquat Sci* 214: 71-120
- Wharton RA, Parker BC and Simmons GM (1983) Distribution, species composition and morphological algal mats (stromatolites) in Antarctic dry valley lakes. *Phycologia* 22: 355-365
- Wharton RA, McKay CP, Simmons GM and Parker BC (1985) Cryoconite holes on glaciers. *Bioscience* 35: 499-503
- Wharton RA, Vinyard WC, Parker BC, Simmons GM and Seaburg KG (1981) Algae in cryoconite holes on Canada Glacier in southern Victoria Land, Antarctica. *Phycologia* 20: 208-11
- Wright SW and Burton HR (1981) The biology of Antarctic saline lakes. *Hydrobiologia* 82: 319-338
- Wynn-Williams DD (1990) Ecological aspects of Antarctic microbiology. *Adv. Microb Ecol* 11: 71-146
- Wynn-Williams DD (1991) Epifluorescence image analysis of the 3D structure of phototrophic microbial biofilms at Antarctic soil surfaces. *Binary Comput Microbiol* 4: 53-57