

Biodata of **Warwick F. Vincent**, author of the chapter “*Cold Tolerance in Cyanobacteria and Life in the Cryosphere*”

Dr. Warwick F. Vincent is Professor of Biology and Canada Research Chair in Aquatic Ecosystem Studies at Laval University, Quebec City, Canada. He obtained his BSc (hons) in Botany and Cell Biology from the University of Auckland, New Zealand, in 1974, and his PhD in Ecology from the University of California, Davis, in 1977. He is a Fellow of the Royal Society of Canada and an Honorary Fellow of the Royal Society of New Zealand. His current research concerns underwater light, aquatic microbial biodiversity, the ecology of Cyanobacteria, and the effects of climate on high latitude lakes, wetlands, rivers and coastal seas.

E-mail: warwick.vincent@bio.ulaval.ca



COLD TOLERANCE IN CYANOBACTERIA AND LIFE IN THE CRYOSPHERE

WARWICK F. VINCENT

*Centre d'Études Nordiques & Département de Biologie,
Laval University, Quebec City, Quebec G1K 7P4, Canada*

1. Introduction

Cyanobacteria are commonly thought of as microbial phototrophs that are characteristic of warm water environments such as hot springs (Steunou et al., 2006), stratified lakes during summer (Vazquez et al., 2005) and tropical oceans (Johnson et al., 2006). It is less widely known that many cyanobacterial taxa achieve their greatest ecological success at the opposite thermal extreme, in polar and alpine environments. One of the first discoveries of the prolific growth of cyanobacteria in the cryosphere (the ensemble of cold environments containing snow and ice) was by the Swedish-Finnish explorer Adolf Erik Nordenskiöld. In his expedition across the Greenland Ice Cap in 1870 his team discovered black sediment that he called 'cryoconite', cold rock dust collecting in melt holes (Leslie, 1879). On closer inspection they observed that this material was composed of not only inorganic sediments but also black-pigmented cyanobacteria, now known to be mostly the heterocystous species *Calothrix parietina* (Gerdell and Drouet, 1960). They concluded that because of its dark colouration, this cyanobacteria and its bound sediment absorbs radiation and hastens melting of the ice, a process more recently documented on glaciers (Takeuchi et al., 2001) and ice shelves in the Canadian High Arctic (Mueller and Vincent, 2006).

The early expeditions to Antarctica such as those by Scott and Shackleton also brought back evidence of cyanobacteria forming extensive communities in some south polar habitats (Vincent, 2000). Current research shows that cyanobacteria are the phototrophic dominants in many types of communities in both Polar Regions. In some meromictic lakes, picocyanobacteria are the most common photosynthetic cell type, for example in lakes of the Vestfold Hills Antarctica (Powell et al., 2005) and at the northern coastline of High Arctic Canada (Van Hove et al., 2006). They are also abundant in many arctic rivers (Rae and Vincent, 1998), although are much less common in coastal and offshore marine waters (Waleron et al., 2007). Viable cyanobacteria are a frequent constituent of permafrost soils (Vishnivetskaya et al., 2005) and also occur commonly within and on the outside of rocks in the desert landscapes of both Polar Regions (Cockell and Stokes, 2004). The cyanobacteria-dominated assemblages that form in cryoconite holes and pools on glaciers continue to be of great interest to microbial ecologists to address questions concerning microbial distribution and diversity, biogeochemical

processes in microbial consortia and microbial strategies for survival and success in the cryosphere (Wharton et al., 1981; Christner et al., 2003; Mueller and Pollard, 2004; Porazinska et al., 2004; Stibal et al., 2006; Tranter et al., 2004) The most luxuriant growth of cyanobacteria in the Polar Regions occurs as benthic mats and films in shallow thermokarst (eroded permafrost) lakes (Vézina and Vincent, 1997; Rautio and Vincent, 2006), in ice shelf ponds of the Arctic (Vincent et al., 2004a, b; Mueller et al., 2005) and Antarctica (Howard-Williams et al., 1989; Sabbe et al., 2004; Jungblut et al., 2005), in rivers and streams (Vincent et al., 1993; Elster et al., 1997; McKnight et al., 1999; Fernández-Valiente et al., 2007) and in ice-covered lakes (Wharton et al., 1983; Hawes and Schwarz, 2001; Singh and Elster, 2007; Taton et al., 2006; Vopel and Hawes, 2006). Littoral communities of benthic cyanobacteria are also well known from cold, alpine habitats (Vinebrooke and Leavitt, 1996; Sommaruga and Garcia-Pichel, 1999).

The common occurrence of cyanobacteria in cold habitats has implications for the development of microbial ecosystems on early Earth. Although debate continues as to the thermal regime throughout the Precambrian, there is mounting evidence that extreme cold and freeze-up was experienced during several glacial periods, perhaps even during the earliest stages in the appearance and evolution of microbial life (Vincent et al., 2004a, b, and references therein). Major freeze-up of much of the planet is believed to have occurred during the Proterozoic Era, specifically during the Paleoproterozoic 2.3 billion years bp (Melezhik, 2006) and during the Neoproterozoic, 600–700 million years bp (Hoffman and Schrag, 2002). The fossil record suggests that cyanobacteria would have been present throughout these Proterozoic events, and perhaps during earlier periods of global cooling. There is evidence for the continuity of life throughout these glacial episodes, and cyanobacteria-dominated ecosystems in the modern cryosphere are increasingly viewed as analogues for such conditions (Olcott et al., 2005; Corsetti et al., 2006).

This chapter considers the range of conditions that cyanobacteria may have had to contend with in the cryosphere during glacial periods on Precambrian Earth, and the range of ecophysiological strategies that modern-day cyanobacteria in culture or in polar and alpine regions employ to deal with such conditions. There are two distinct sets of stresses imposed by a glacial environment: (i) the freeze-up process and resultant ice regime and (ii) the persistence of cold temperatures for metabolism, growth and survival in aqueous habitats. These two sets of environmental conditions are treated separately below.

2. Freeze-up and the Implications of Ice Formation

The phase transition from liquid water to ice poses a number of challenges for phototrophic growth and survival. These include the osmotic and mechanical stresses during ice formation, the need to retain viability during periods of prolonged dormancy, and an ability to capture light and achieve net growth despite the attenuating effects of the overlying ice and snow cover.

2.1. ICE FORMATION

Many polar and alpine habitats such as shallow ponds and streams freeze solid each year. During this process, solutes are excluded from the ice and the remaining water surrounding the cells can achieve high osmolarities. This process is well known in sea ice where the freeze-concentrated brines within channels between the ice crystals may achieve salinity values many times that of sea water (Thomas and Dieckmann, 2002). This process is also known in polar lakes and ponds where benthic microbial mats experience relatively freshwater conditions in late summer to salinities up to five times that of seawater, and liquid water temperatures down to -12°C , during the final stages of freeze-up in winter (Schmidt et al., 1991). Additionally, the formation of ice can destroy membranes, particularly if the crystals are formed intracellularly (Vincent, 1988; Fuller, 2004).

Cyanobacteria have a variety of strategies to minimize the osmotic and mechanical stresses of freeze-up. Like sea ice microbiota, the mat-forming species in cold environments such as on the McMurdo Ice Shelf (de los Ríos et al., 2004) form copious quantities of mucopolysaccharides (exopolymeric substances, EPS). This material likely slows the flow of liquid water during freeze-up and thaw, and may also force ice crystal formation to occur well away from the cells. Experiments on *Nostoc commune* indicate that EPS is critical to surviving desiccation as well as freeze-up (Tamaru et al., 2005).

Many cyanobacteria produce compatible solutes (Mackay et al., 1984) that reduce the osmotic effects of freeze-up, although this has not been examined in detail in polar and alpine taxa. Some of these osmoregulatory substances protect proteins from denaturation and deactivation, for example glycine betaine (*N*-trimethyl glycine) protects the photosystem II complex against dissociation (Papageorgiou and Murata, 1995).

Like other phototrophs, cyanobacteria from some polar environments are known to produce macromolecular substances that cause pitting and other modifications of growing ice crystals. The exact role of these ice-active substances is not known at present, but they are thought to play a cryoprotective role (Raymond and Fritsen, 2000).

2.2. PROLONGED DORMANCY

One of the prerequisites for life in a seasonally frozen environment is the ability to maintain viability until the next period of thaw. Freeze-drying is a method to preserve microbes, and cyanobacterial strains in some culture collections are stored in this way. In Antarctica, freeze-dried mats have been shown to resume photosynthesis and other physiological processes within minutes to hours after rethawing. It is less clear however, what the upper limit may be to survival at much longer time scales. For example, the postulated 'snowball Earth' scenario suggests that microbes could be frozen for up to millions of years. There is a variety of

evidence that ancient microbes immured in glacial ice, permafrost soils or salt crystals can be brought to life (e.g. Vishnivetskaya et al., 2005). In part this may strongly depend on the physical and chemical properties of the surrounding environment during dormancy, for example the extent of exposure to UV radiation and to reactive oxygen species (ROS).

2.3. LOW IRRADIANCE

Clear ice allows a high transmittance of photosynthetically available radiation (PAR) as well as UV radiation. However, bubbles, particles and snow cover have a strong effect on albedo (back reflection) and scattering, and can result in a severe reduction in underwater energy supply (Belzile et al., 2001). Some eukaryotic algal species are known to be highly adapted to such extreme shade conditions. One of the best studied examples is the chlorophyte *Chlamydomonas raudensis* UW0241 isolated from a permanently ice-covered Antarctic lake where it is one of the dominant phototrophs. This psychrophilic species has a growth optimum at 8°C and is unable to grow at temperatures above 18°C. It is a shade species adapted to optimal growth in its ambient environment of extremely low, blue-green irradiance. Among its many features tuned towards this low light regime are a low Chl*a*:Chl*b* ratio, a reduction in PSI light-harvesting Chl-proteins, a high concentration of the Chl*b* light-harvesting protein complex and a limited ability to adjust to high irradiances (Morgan-Kiss et al., 2006; and references therein).

Cyanobacteria lack the light-harvesting chlorophyll proteins that are characteristic of *Chlamydomonas*, however their phycobilisomes provide a highly efficient protein complex of multiple phycobiliproteins for capturing light deep in the water column, within microbial mats or under ice. For example, Hawes and Schwarz (1999) have shown that microbial mats on the benthos of ice-covered Antarctic lakes are coloured pink as a result of their high levels of the phycobiliprotein phycoerythrin. Laboratory gas-exchange measurements showed that the communities have an unusually efficient light-capturing capacity, with photosynthetic quantum yields close to the theoretical maximum (Hawes and Schwarz, 2001). These results were subsequently confirmed by in situ measurements in perennially ice-covered Lake Hoare in the McMurdo Dry Valleys using oxygen micro-electrodes (Vopel and Hawes, 2006).

Cyanobacteria mats growing in exposed polar and alpine lakes are often enriched in light-protecting pigments in their surface layers (Bonilla et al., 2005), while their basal layers are deep blue-green associated with high concentrations of the phycobiliprotein phycocyanin (PC). For example, a microbial mat from Skeleton Lake in the Canadian High Arctic had a surface 1-mm thick pink layer rich in carotenoids, and a basal 2–3 mm blue-green layer that contained more than seven times the quantity of PC than in the surface layer and a 50% higher PC:Chl*a* ratio (Quesada et al., 1999).

Phycobilisomes are now known to be dynamic light-capturing systems that are free to diffuse horizontally in the photosynthetic membranes of cyanobacteria (Joshua et al., 2005). The physical association between phycobilisomes and reaction centers modulates the distribution of excitation energy, and influences the degree of spillover between PSI and PSII. Spillover was initially thought to be a rapid bright light acclimation response, but there is increasing evidence that in cyanobacteria it is an adaptive physiological response to low light conditions (Mullineaux and Emlyn-Jones, 2005).

2.4. PROLONGED DARKNESS

In some respects, prolonged darkness in liquid water conditions may be a much greater constraint on viability than freeze-up. Respiration may continue throughout such periods and the energetic costs of basal metabolism, maintenance and repair may ultimately deplete cellular reserves. It is not known whether there may be a threshold for such metabolism, with a loss of viability below which the cells are unable to recover even when returned to available light conditions.

3. Implications of Persistent Low Temperatures

Low temperatures exert an obvious dampening effect on all metabolic processes, although the magnitude of this cold inhibition varies greatly among species. The net result is slow net growth rates, but this may not be an ecological constraint in many habitats. For example mat communities in perennial ice-covered lakes, ice shelf ponds and polar desert streams gradually accumulate biomass each year, and this biomass then overwinters to provide a large inoculum for the next year of microbial activity. In this way, cyanobacteria maintain their perennial coverage of benthic substrates, resulting in pre-emptive competitive success at the beginning of each season.

The cyanobacterial strategy of slow growth is likely to be much less successful in ephemeral habitats and in ecosystems where loss processes are more severe. For example, melting snowbanks offer a habitat for microbial growth for only few weeks each year. These ephemeral meltwaters are subject to continuous losses by percolation, and are more typically colonized by eukaryotic snow algae than slower growing cyanobacteria (Vincent, 1988). Similarly, in the marine environment of both Polar Regions, cyanobacteria are conspicuously sparse or absent, and this may reflect an inability to keep pace with substantial loss rates via turbulent diffusion, advection and grazing by a diverse spectrum of zooplankton (Vincent, 2000). In these oceanic environments, picoplanktonic phototrophs are often abundant, but they are highly adapted psychrophilic eukaryotes that can achieve much faster growth rates than cold-tolerant cyanobacteria. In earlier times, such as the Paleoproterozoic before the emergence and radiation of

eukaryotes, psychrotolerant cyanobacteria may have played a more important role in cold ocean ecosystems.

A variety of other problems are imposed by persistent low temperatures. Firstly, cells may be especially prone to photobiological damage due to ultraviolet radiation and bright PAR irradiances. Photobiological effects can be direct (e.g. DNA damage through UV-B absorption) or indirect (through the production of ROS) and while these photochemical reactions are dependent on radiation exposure, they are largely independent of temperature. On the other hand, cellular repair mechanisms such as DNA and photosystem II repair processes are likely to depend on metabolic rates, and therefore reduced under low temperatures. Persistent cold therefore has the potential to shift the damage–repair balance towards net cellular damage (Rae et al., 2000). Cyanobacteria show a remarkable suite of mechanisms to reduce such effects, including the production of a great variety of photoprotective pigments. Additional challenges in the cold are to maintain membrane fluidity, transport functions and enzymatic activities, and cold-tolerant cyanobacteria provide excellent examples of this suite of acclimation abilities.

3.1. PHOTOPROTECTIVE-SCREENING PIGMENTS

One of the first lines of protection against UV and high energy PAR exposure is the production of light-screening pigments. Cyanobacteria of the cold regions show two classes of such compounds. The first are the lipid-soluble sheath pigments gloeocapsin and scytonemin. The former is present in the sheaths of some *Gloeocapsa* species, for example the taxon *G. ralfsiana* that forms rust-coloured crusts over rock in streams of the McMurdo Dry Valleys Antarctica (Vincent, 1988). This compound has been known for almost a century, with interest in the way it changes colour with pH. However it is still not characterized either ecologically, physiologically or chemically. In contrast there is a large literature on the sheath pigment scytonemin that is found in several cyanobacteria. This compound absorbs maximally in the UV-A end of the spectrum (Garcia-Pichel and Castenholz, 1991; Proteau et al., 1993) and can be in such high concentrations, for example in *Nostoc* colonies, that the cyanobacterial mats or crusts are black. High concentrations of this pigment occur in mat-forming communities in many types of antarctic, arctic and alpine communities (Vincent and Quesada, 1993).

The second class of screening pigments is mycosporine-like amino acids (MAAs). These water-soluble compounds are found within the cells and absorb maximally at the UVB end of the incident solar spectrum (Garcia-Pichel and Castenholz, 1993; Cockell and Knowland, 1999). Studies on a High Arctic cyanobacterial mat showed that these compounds were four times higher per unit Chl *a* in the surface relative to bottom layer (Quesada et al., 1999). A novel oligosaccharide-mycosporine-amino acid found in *Nostoc* (Böhm et al., 1995) has recently been identified in microbial mats on arctic ice shelves (Mueller et al., 2005).

3.2. PHOTOPROTECTIVE-QUENCHING PIGMENTS

One of the most severe damaging effects of exposure to high solar radiation is the production of ROS such as singlet oxygen, superoxide and hydrogen peroxide. Cyanobacteria have a variety of enzymatic and pigment strategies for quenching these highly toxic photochemically produced products, including the production of superoxide dismutase and ROS-quenching carotenoids (Vincent and Quesada, 1993; Hirschberg and Chamovitz, 1994). The latter is immediately apparent in cyanobacterial mats in streams, thermokarst lakes, ice shelf ponds and other shallow, brightly lit habitats that are often pigmented orange or pink with high carotenoid pigmentation. For example, in the Skeleton Lake mat, the bright orange surface layer had a fivefold high carotenoid concentration per unit *Chl a* relative to the phycocyanin rich bottom layer (Quesada et al., 1999). An antarctic mat-forming cyanobacterium in culture showed major increases in carotenoid pigmentation with decreasing temperature, increasing PAR and exposure to UV radiation. After a period of acclimation, the cultures growing under UV radiation had almost as high a growth rate as the controls not exposed to UV, and the observed production of photoprotective carotenoids is likely to have been one of the acclimation mechanisms allowing this near-optimal growth (Roos and Vincent, 1998).

3.3. OTHER PHOTOPROTECTIVE STRATEGIES

Several other adaptive mechanisms allow cyanobacteria to deal with bright PAR and UV radiation at the low temperatures that characterize the cryosphere. These include the choice of habitat, or exclusion from more severe, highly exposed habitats. For example, cyanobacteria in both Polar Regions are successful in habitats in rock cracks, as layers beneath the surface of rocks and underneath translucent rocks in which solar exposure is greatly attenuated (Smith et al., 2000; Cockell and Stokes, 2004). Deep ice-covered lakes and the UV-screened habitat at the base of optically thick biofilms similarly provide refugia from the damaging effects of surface insolation. Another strategy seen in many mat communities is that of motility in which trichomes are able to change their position in the vertical light gradients by way of a gliding ability. A striking example of this response has been recording in a meltpool microbial mat on the surface of the McMurdo Ice Shelf, Antarctica (Nadeau et al., 1999).

3.4. MEMBRANE STRATEGIES

Microorganisms have a variety of adaptive strategies to maintain membrane fluidity at low temperatures. The most common mechanism observed in cyanobacteria is fatty acid desaturation to increase the production of unsaturated fatty acids that remain fluid even in the cold. Specifically, saturated fatty acids such as C16:0 and

C18:0 are converted to C16:1 and C18:1 unsaturated fatty acids, respectively, by acyl-lipid desaturases as a post-biosynthetic modification (Chintalapati et al., 2004). Considerable interest is now focused on how cyanobacteria sense the cold and initiate this process. The current model is that the signal transduction pathway involves a two component system, a histidine kinase (Hik33) sensor located in the membrane, and a response regulator (Rer1) located in the cytoplasm. Cold-shock activates Hik33 that in turn activates Rer1. This interacts with DNA and activates the transcription of the *desB* gene that produces acyl-lipid desaturatase. The resultant increase in cellular concentrations of this enzyme leads to increased desaturation of lipids that are inserted into the membrane to reduce fluidity (Suzuki et al., 2001). Other mechanisms that modulate membrane fluidity at low temperature include: alteration of the lipid head group; increased synthesis of polar lipids (e.g. zeaxanthin) that stabilize the membrane relative to non-polar lipids (e.g. β -carotene); decreases in membrane protein content, resulting in less protein-lipid interactions that limit acyl chain flexibility; decreases in fatty chain length to produce short chains that have lower melting points and that are unable to span the membrane, making it less gel-like; and an increase in the proportion of *cis*-relative to *trans*-fatty acids (Chintalapati et al., 2004).

3.5. GROWTH RATES IN THE COLD

Cyanobacteria are often conspicuous components of the modern-day cryosphere and are also likely to have been a major component of frigid ecosystems in Earth's past. Yet the growth rates of extant species in the Polar Regions show no evidence of an impressive performance at low temperatures. All species tested in our own laboratory have been found to be psychrotolerant rather than psychrophilic, with slow growth rates at the low ambient temperatures in their native habitats (Tang et al., 1997). Even under optimal conditions for growth, these species have long doubling times relative to psychrophilic, eukaryotic algae, and relative to psychrophilic, heterotrophic bacteria. A small number of psychrophilic cyanobacteria have been identified, but although these show a temperature optimum below that of most cyanobacteria and inhibition by moderately warm conditions, their growth rates are still quite low at temperatures below 10°C. Two oscillatorian strains isolated from the McMurdo Ice Shelf had growth optima at 8°C and did not grow at 24°C. However, even at the optimal temperature for growth, their doubling times were long, ranging from 8.3 to 12.5 days (Nadeau and Castenholz, 2000).

4. Conclusions

Cyanobacteria do not seem to be specifically adapted to low temperatures in that they are unable to maintain fast growth rates in the cold. On the other hand, studies in the modern-day cryosphere show that they have a wide range of adap-

tive mechanisms that allow them to survive freeze-up, growth under low irradiances such as that produced by ice cover, and periodic exposure to UV radiation and bright PAR. These mechanisms include light-harvesting pigments, light-screening pigments, ROS-quenching compounds such as carotenoids, membrane fluidity at low temperatures and cold-stable proteins. Despite the cold, polar and alpine cyanobacteria can maintain slow but steady growth. This strategy of cold tolerance has been highly successful in some habitats such as in the benthos where communities can gradually accumulate over many seasons of growth to attain prolific biomass stocks. However, psychrotolerance and slow growth in the cold is not successful in ephemeral environments such as melting snowbanks, or in ecosystems where losses are substantial, for example as a result of strong grazing pressure or removal by advection.

5. Acknowledgements

This chapter has been written under the auspices of research programmes funded by NSERC, the Canada Research Chair program and the NCE program ArcticNet.

6. References

- Belzile, C., Vincent, W.F., Gibson, J.A.E. and Van Hove, P. (2001) Bio-optical characteristics of the snow, ice and water column of a perennially ice-covered lake in the high Arctic. *Can. J. Fish. Aquat. Sci.* **58**: 2405–2418.
- Böhm, G.A., Pfeiderer, W., Böger, P. and Scherer, S. (1995) Structure of a novel oligosaccharide-mycosporine-amino acid ultraviolet A/B sunscreen pigment from the terrestrial cyanobacterium *Nostoc commune*. *J. Biol. Chem.* **270**: 8536–8539.
- Bonilla, S., Villeneuve, V. and Vincent, W.F. (2005) Benthic and planktonic algal communities in a high arctic lake: pigment structure and contrasting responses to nutrient enrichment. *J. Phycol.* **41**: 1120–1130.
- Chintalapati, S., Kiran, M.D. and Shivaji, S. (2004) Role of membrane lipid fatty acids in cold adaptation. *Cell. Mol. Biol.* **50**: 631–642.
- Christner, B.C., Kvitko, B.H. II and Reeve, J.N. (2003) Molecular identification of bacteria and Eukarya inhabiting an Antarctic cryoconite hole. *Extremophiles* **7**: 177–183.
- Cockell, C.S. and Knowland, J. (1999) Ultraviolet radiation screening compounds. *Biol. Rev. Camb. Philos. Soc.* **74**: 311–345.
- Cockell, C.S. and Stokes, M.D. (2004) Widespread colonization by polar hypoliths. *Nature* **431**: 414.
- Corsetti, F.A., Olcott, A.N. and Bakermans, C. (2006) The biotic response to Neoproterozoic snowball earth. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **232**: 114–130.
- de los Ríos, A., Ascaso, C., Wierzchos, J., Fernández-Valiente, E. and Quesada, A. (2004) Microstructural characterization of cyanobacterial mats from the McMurdo Ice Shelf, Antarctica. *Appl. Environ. Microbiol.* **70**: 569–580.

- Elster, J., Svoboda, J., Komárek, J. and Marvan, P. (1997) Algal and cyanoprocarvate communities in a glacial stream, Sverdrup Pass, 79°N, Central Ellesmere, Canada. *Arch. Hydrobiol. Algol. Stud.* **85**: 57–93.
- Fernández-Valiente, E., Camacho, A., Cochera, C., Rico, E., Vincent, W.F. and Quesada, A. (2007) Community structure and physiological characterization of microbial mats in Byers Peninsula, Livingston Island (South Shetland Islands, Antarctica). *FEMS Microb. Ecol.* **59**: 377–385.
- Fuller, B.J. (2004) Cryoprotectants: the essential antifreezes to protect life in the frozen state. *Cryo Letters* **25**: 375–388.
- García-Pichel, F. and Castenholz, R.W. (1991) Characterization and biological implications of scytonemin, a cyanobacterial sheath pigment. *J. Phycol.* **27**: 395–409.
- García-Pichel, F. and Castenholz, R. (1993) Occurrence of UV absorbing mycosporine-like compounds among cyanobacterial isolates and an estimate of their screening ability. *Appl. Environ. Microbiol.* **59**: 163–169.
- Gerdel, R.W. and Drouet, F. (1960) The cyanobacteria of the Thule area, Greenland. *Trans. Am. Microsc. Soc.* **79**: 256–272.
- Hawes, I. and Schwarz, A.-M. (1999) Photosynthesis in an extreme shade environment: benthic microbial mats from Lake Hoare, a permanently ice-covered Antarctic lake. *J. Phycol.* **35**: 448–459.
- Hawes, I. and Schwarz, A.-M. (2001) Absorption and utilization of irradiance by cyanobacterial mats in two ice-covered Antarctic lakes with contrasting light climates. *J. Phycol.* **37**: 5–15.
- Hirschberg, J. and Chamovitz, D. (1994) Carotenoids in cyanobacteria. In: D.A. Bryant (ed.), *The Molecular Biology of Cyanobacteria*. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 559–579.
- Hoffman, P.F. and Schrag, D.P. (2002) The snowball Earth hypothesis: testing the limits of global change. *Terra Nova* **14**: 129–155. doi: 10.1046/j.
- Howard-Williams, C., Pridmore, R.D., Downes, M.T. and Vincent, W.F. (1989) Microbial biomass, photosynthesis and chlorophyll a related pigments in the ponds of the McMurdo Ice Shelf, Antarctica. *Antarct. Sci.* **1**: 125–131.
- Johnson, Z.I., Zinser, E.R., Coe, A., McNulty, N.P., Malcolm, E., Woodward, S. and Chisholm, S.W. (2006) Niche partitioning among *Prochlorococcus* ecotypes along ocean-scale environmental gradients. *Science* **311**: 1737–1740.
- Joshua, S., Bailey, S., Mann, N.H. and Mullineaux, C.W. (2005) Involvement of phycobilisome diffusion in energy quenching in cyanobacteria. *Plant Physiol.* **138**: 1577–1585.
- Jungblut, A.D., Hawes, I., Mountfort, D., Hitzfeld, B., Dietrich, D.R., Burns, B.P. and Neilan, B.A. (2005) Diversity within cyanobacterial mat communities in variable salinity meltwater ponds of McMurdo Ice Shelf, Antarctica. *Environ. Microbiol.* **7**: 519–529.
- Leslie, A., (1879) *The Arctic Voyages of Adolf Erik Nordenskiöld*. MacMillan and Co., London, UK, 447 pp.
- Mackay, M.A., Norton, R.S. and Borowitzka, L.J. (1984) Organic osmoregulatory solutes in cyanobacteria. *J. Gen. Microbiol.* **130**: 2177–2191.
- McKnight, D.M., Niyogi, D.K., Alger, A.S., Bomblies, A., Conovitz, P.A. and Tate, C.M. (1999) Dry Valley streams in Antarctica: ecosystems waiting for water. *Bioscience* **49**: 985–995.
- Melezhik, V.A., (2006). Multiple causes of Earth's earliest global glaciation. *Terra Nova* **18**: 130–137.
- Morgan-Kiss, R.M., Priscu, J.C., Pockock, T., Gudynaite-Savitch, L. and Huner, N.P.A. (2006) Adaptation and acclimation of photosynthetic microorganisms to permanently cold environments. *Microbiol. Mol. Biol. Rev.* **70**: 222–252.
- Mueller, D. and Pollard, W.H. (2004) Gradient analysis of cryoconite ecosystems from two polar glaciers. *Polar Biol.* **27**: 66–74.
- Mueller, D.R. and Vincent, W.F. (2006) Microbial habitat dynamics and ablation control on the Ward Hunt Ice Shelf. *Hydrological Processes* **20**: 857–876.

- Mueller, D.R., Vincent, W.F., Bonilla, S. and Laurion, I. (2005) Extremophiles, extremotrophs and broad-band pigmentation strategies in a high arctic ice shelf ecosystem. *FEMS Microbiol. Ecol.* **53**: 73–87.
- Mullineaux, C.W. and Emlyn-Jones, D. (2005) State transitions: an example of acclimation to low-light stress. *J. Exp. Bot.* **56**: 389–393.
- Nadeau, T.L. and Castenholz, R.W. (2000) Characterization of psychrophilic oscillatorians (cyanobacteria) from antarctic meltwater ponds. *J. Phycol.* **36**: 914–923.
- Nadeau, T.L., Howard-Williams, C. and Castenholz, R.W. (1999) Effects of solar UV and visible irradiance on photosynthesis and vertical migration of *Oscillatoria* sp (cyanobacteria) in an Antarctic microbial mat. *Aquat. Microb. Ecol.* **20**: 231–243.
- Olcott, A.N., Sessions, A.L., Corsetti, F.A., Kaufman, A.J. and de Oliveira, T.F. (2005) Biomarker evidence for photosynthesis during Neoproterozoic glaciation. *Science* **310**: 471–474.
- Papageorgiou, G.C. and Murata, N. (1995) The unusually strong stabilizing effects of glycine betaine on the structure and function of the oxygen-evolving photosystem II complex. *Photosynth. Res.* **44**: 243–252.
- Porazinska, D.L., Fountain, A.G., Nylen, T.H., Tranter, M., Virginia, R.A. and Wall, D.H. (2004) The biodiversity and biogeochemistry of cryoconite holes from McMurdo Dry Valley glaciers, Antarctica. *Arct. Antarct. Alp. Res.* **36**: 84–91.
- Powell, L.M., Bowman, J.P., Skerratt, J.H., Franzmann, P.D. and Burton, H.R. (2005) Ecology of a novel *Synechococcus* clade occurring in dense populations in saline Antarctic lakes. *Mar. Ecol. Prog. Ser.* **291**: 65–80.
- Proteau, P.J., Gerwick, W.H., 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., Vincent, W.F. and Lean, D.R.S. (1999) Community and pigment structure of Arctic cyanobacterial assemblages: the occurrence and distribution of UV-absorbing compounds. *FEMS Microbiol. Ecol.* **28**: 315–323.
- Rae, R., and Vincent, W.F. (1998) Effects of temperature and UV radiation on microbial food web structure: potential responses to global change. *Freshw. Biol.* **40**: 1–12.
- Rae, R., Howard-Williams, C., Hawes, I. and Vincent, W.F. (2000) Temperature-dependence of photosynthetic recovery from solar damage in Antarctic phytoplankton. In: W. Davison, C. Howard-Williams and P.A. Broady (eds.), *Antarctic Ecosystems: Models for Wider Ecological Understanding*. The Caxton Press, Christchurch, New Zealand, pp. 183–189.
- Rautio, M., and Vincent, W.F. (2006) Benthic and pelagic food resources for zooplankton in shallow high-latitude lakes and ponds. *Freshw. Biol.* **51**: 1038–1052.
- Raymond, J.A., and Fritsen, C.H. (2000) Ice-active substances associated with Antarctic freshwater and terrestrial photosynthetic organisms. *Antarct. Sci.* **12**: 418–424.
- Roos, J.C., and Vincent, W.F. (1998) Temperature dependence of UV radiation effects on Antarctic cyanobacteria. *J. Phycol.* **34**: 118–125.
- Sabbe, K., Hodgson, D.A., Verleyen, E., Taton, A., Wilmotte, A., Vanhoutte, K. and Vyverman, W. (2004) Salinity, depth and the structure and composition of microbial mats in continental Antarctic lakes. *Freshw. Biol.* **49**: 296–319.
- Schmidt, S., Moskall, W., de Mora, S.J.D., Howard-Williams, C., and Vincent, W.F. (1991) Limnological properties of Antarctic ponds during winter freezing. *Antarct. Sci.* **3**: 379–388.
- Singh, S.M., Elster, J. (2007) Cyanobacteria in antarctic lake environments: A mini-review in: J. Seckbach (ed.) *Algae and Cyanobacteria in Extreme Environments*. Springer, Dordrecht. (the volume) pp. xxx–yyy.
- Smith, M.C., Bowman, J.P., Scott, F.J., and Line, M.A. (2000) Sublithic bacteria associated with Antarctic quartz stones. *Antarct. Sci.* **12**: 177–184.
- Sommaruga, R., and Garcia-Pichel, F. (1999) UV-absorbing mycosporine-like compounds in planktonic and benthic organisms from a high-mountain lake. *Arch. Hydrobiol.* **144**: 255–269.
- Steunou, A.-S., Bhaya, D., Bateson, M.M., Melendrez, M.C., Ward, D.M., Brecht, E., Peters, J.W., Köhl, M. and Grossman, A.R. (2006) *In situ* analysis of nitrogen fixation and metabolic switching in unicellular thermophilic cyanobacteria inhabiting hot spring microbial mats. *Proc. Natl. Acad. Sci. U.S.A.* **103**: 2398–2403.

- Stibal, M., Šabacká, M. and Kaštovská, K. (2006) Microbial communities on glacier surfaces in Svalbard: Impact of physical and chemical properties on abundance and structure of cyanobacteria and algae. *Microb. Ecol.* **52**: 644–654.
- Suzuki, I., Kanasaki, Y., Mikami, K., Kahnehisa, M. and Murata, N. (2001) Cold regulated genes under the control of *hik33* in *Synechocystis*. *Mol. Microbiol.* **40**: 235–245.
- Takeuchi, N., Kohshima, S.S., Goto-Azuma, K. and Koerner, R.M. (2001) Biological characteristics of dark colored material (cryoconite) on Canadian Arctic glaciers (Devon and Penny ice caps). *Mem. Natl. Inst. Polar Res. Special Issue* **54**: 495–505.
- Tamaru, Y., Takani, Y., Yoshida, T. and Sakamoto, T. (2005) Crucial role of extracellular polysaccharides in desiccation and freezing tolerance in the terrestrial cyanobacterium *Nostoc commune*. *Appl. Environ. Microbiol.* **71**: 7327–7333.
- Tang, E.P.Y., Tremblay, R. and Vincent, W.F. (1997) Cyanobacteria dominance of polar freshwater ecosystems: are high latitude mat-formers adapted to low temperature? *J. Phycol.* **33**: 171–181.
- Taton, A., Grubisic, S., Balthasart, P., Hodgson, D.A., Laybourn-Parry, J. and Wilmotte, A. (2006) Biogeographical distribution and ecological ranges of benthic cyanobacteria in East Antarctic lakes. *FEMS Microbiol. Ecol.* **57**: 272–289.
- Thomas, D.N., and Dieckmann, G.S. (2002) Antarctic sea ice – a habitat for extremophiles. *Science* **295**: 641–644.
- Tranter, M., Fountain, A.G., Fritsen, C.H., Lyons, W.B., Priscu, J.C., Statham, P.J. and Welch, K.A., (2004) Extreme hydrochemical conditions in natural microcosms entombed within Antarctic ice. *Hydrological Processes* **18**: 379–387.
- Van Hove, P., Belzile, C., Gibson, J.A.E. and Vincent, W.F. (2006) Coupled landscape-lake evolution in the Canadian High Arctic. *Can. J. Earth Sci.* **43**: 533–546.
- Vazquez, G., Jimenez, S., Favila, M.E. and Martinez, A. (2005) Seasonal dynamics of the phytoplankton community and cyanobacterial dominance in a eutrophic crater lake in Los Tuxtlas, Mexico. *Ecoscience* **12**: 485–493.
- Vézina, S. and Vincent, W.F. (1997) Arctic cyanobacteria and limnological properties of their environment: Bylot Island, Northwest Territories, Canada. (73°N, 80°W). *Polar Biol.* **17**: 523–534.
- Vincent, W.F. (1988) *Microbial Ecosystems of Antarctica*. Cambridge University Press, Cambridge, UK, 304 pp.
- Vincent, W.F. (2000) Cyanobacterial dominance in the Polar Regions. In: B.A. Whitton and M. Potts (eds.), *The Ecology of Cyanobacteria*. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 321–340.
- Vincent, W.F. and Quesada A. (1993) Cyanobacterial responses to UV radiation: implications for antarctic microbial ecosystems. *Antarct. Res. Ser.* **62**: 111–124.
- Vincent, W.F., Howard-Williams, C. and Broady P.A. (1993) Microbial communities and processes in Antarctic flowing waters, In: I. Friedmann (ed.), *Antarctic Microbiology*. Wiley-Liss, New York, pp. 543–569.
- Vincent, W.F., Mueller, D.R. and Bonilla, S. (2004a) Ecosystems on ice: the microbial ecology of Markham Ice Shelf in the high Arctic. *Cryobiology* **48**: 103–112.
- Vincent, W.F., Mueller, D.R., Van Hove, P. and Howard-Williams, C. (2004b) Glacial periods on early Earth and implications for the evolution of life In: J. Seckbach (ed.), *Origins: Genesis, Evolution and Diversity of Life*. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 481–501.
- Vinebrooke, R.D. and Leavitt, P.R. (1996) Effects of ultraviolet radiation on periphyton in an alpine lake. *Limnol. Oceanogr.* **41**: 1035–1040.
- Vishnivetskaya, T., Erokhina, L.G., Spirina, E.V., Shatilovich, A.V., Vorobyova, E.A., Tsapin, A.I. and Gilichinsky D.A. (2005) Viable phototrophs: cyanobacteria and green algae from the permafrost darkness. In: J.D. Castello and S.O. Rogers (eds.), *Life in Ancient Ice*. Princeton University Press, Princeton, USA, pp.140–158.
- Vopel, K. and Hawes I. (2006) Photosynthetic performance of benthic microbial mats in Lake Hoare, Antarctica. *Limnol. Oceanogr.* **51**: 1801–1812.

- Waleron, M., Waleron, K., Vincent, W.F. and Wilmotte, A. (2007) Allochthonous inputs of riverine picocyanobacteria to coastal waters in the Arctic Ocean. *FEMS Microbiol. Ecol.* **59**: 356–365.
- Wharton, R.A., Parker, B.C. and Simmons, G.M. (1983) Distribution, species composition and morphology of algal mats in Antarctic dry valley lakes. *Phycologia* **22**: 355–365.
- Wharton, R.A., Vinyard, W.C., Parker, B.C., Simmons, G.M. and Seaburg, K.G. (1981) Algae in cryoconite holes on Canada Glacier in Southern Victoria land, Antarctica. *Phycologia* **20**: 208–211.