Ecological processes in Antarctic inland waters: interactions between physical processes and the nitrogen cycle

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Abstract: In this review we consider the physical processes that shape inland aquatic ecosystems and how these affect ecosystem processes, with particular focus on the nitrogen cycle. Inland Antarctica is dominated by microbial communities that are usually concentrated in, or adjacent to, habitats with free water. The presence of free vs frozen water is dependent on very small changes in temperature around 0ºC, so significant variability in the distribution of free water can be expected in response to variations in climate over diel, decadal, to millennial time scales and a range of spatial scales. Antarctic inland waters take many forms: snow-surface melt pockets, cryoconites, basal regions of wet-based glaciers, ponds (varying in salinity and degree of desiccation), melt streams, perennially and seasonally ice covered lakes and even hypersaline, ice free lakes. The important processes and transformations that characterize the nitrogen cycle worldwide have all been identified in Antarctic inland waters and in some cases (e.g. N-uptake, N-fixation), rates are similar to those at lower latitudes. The unique features of Antarctic ecosystems stem from the extreme and variable physical conditions under which these processes operate rather than any unique ecosystem processes *per se*.

Introduction

The extreme climate of Antarctica places severe limitations on the inland aquatic ecosystems that develop there. While much of the world's reservoir of freshwater is tied up in the Antarctic ice cap, the prevailing subzero temperatures mean that for most of the time very little of it is in liquid form. Liquid water is required for ecosystems to function, and what sets Antarctic ecosystems aside from other water bodies outside of the polar regions is their dependence on the phase change of water between solid and liquid. Thus Antarctic inland waters differ from other aquatic ecosystems in arid climates in that availability of water is driven not by episodic and poorly predictable rainfall events, but rather by the melting and freezing of water. These processes are controlled by heat balance rather than precipitation and tend to follow predictable cycles, albeit of varying amplitude and periodicity. For example, Antarctic inland water ecosystems (and those in the high Arctic) can experience withdrawal of liquid water through daily freeze thaw cycles in summer and long periods of deep freezing with temperatures to -50ºC over seasonal timescales. Over longer term climatic oscillations, which drive larger scale ice formation and retreat, aquatic ecosystems may exist for decades, centuries or millennia and then disappear, only to reappear as conditions again become favourable (McKnight *et al.* 1999). Figure 1 illustrates the annual variability in temperature within a freshwater pond at Bratina Island (78ºS). The short period of liquid water occurs in summer

when the combined effect of insolation and relatively warm air temperatures permit ice melt and temperatures to exceed 0ºC.

Placing Antarctic aquatic ecosystems within a global context requires that we understand how the extreme nature of the physical environment, including its variability, affects ecosystem processes. For ecosystems to persist, the organisms inhabiting them must have attributes that are sufficient and diverse enough to provide all the basic pathways that allow ecosystem processes to function. Such processes include nutrient cycling, photosynthesis, the range of catabolic pathways (aerobic and anaerobic), nitrogen fixation, the nitrogen and sulphur cycles and trace-element metabolism. In this review we show that the principal microbially mediated metabolic pathways are present in Antarctic aquatic systems, using the nitrogen cycle as our example. These include: N-uptake (inorganic and organic); N-fixation; N-release; transformations (e.g. inorganic to organic, particulate to dissolved forms); ammonification; nitrification; denitrification and dissimilatory nitrate reduction. We argue that Antarctic conditions do not exclude any essential microbial processes, so long as liquid water is present. We review how the extreme and variable climate has created a range of extraordinary aquatic habitats within which these ubiquitous microbial processes operate, and go on to show how the extremity of the habitats affects the way in which the processes are expressed.
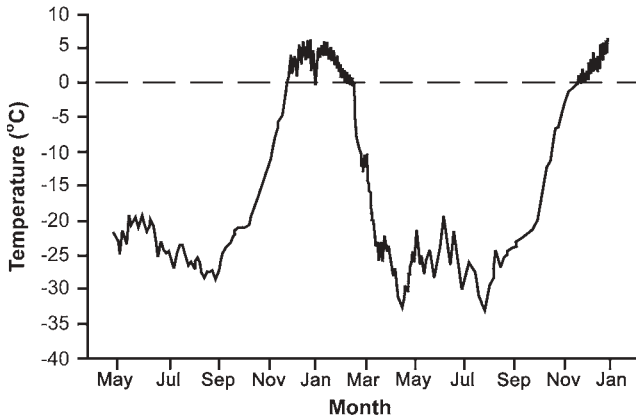
Fig. 1. Annual cycle of temperature in Fresh Pond, Bratina Island, 2001–2002 at a depth of 0.4 m. The summer melt period is a short part of the year.

Sensitivity of polar systems to climate variability

Inland waters are driven by the hydrological cycle, which in turn responds to the climate over a range of time scales. The sensitivity of Antarctic inland waters to very small changes in climate is due to the closeness of these systems to the phase change transitions between solid and liquid water. Diel, seasonal and longer-term variability in temperature, solar radiation and snowfall influence the hydrological cycle through changes in snow and ice melt (Doran *et al.* 2002, Welch *et al.* 2003). There are, for instance, significant reservoirs of water in the glaciers poised above or adjacent to inland waters which will melt if the climate ameliorates; conversely these reservoirs will expand and deliver less
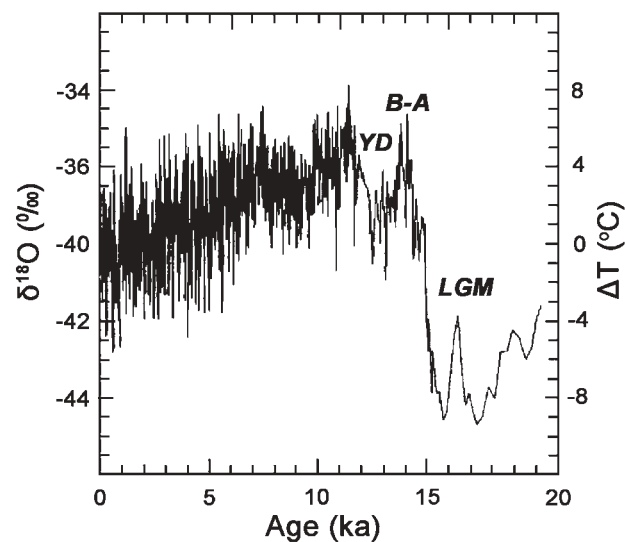
Fig. 2. Oxygen isotope ratios and inferred temperatures relative to present from Taylor Dome ice core over the last 20 Kyr. B-A = Bølling-Allerød Event; YD = Younger Dryas cooling, LGM = Last glacial Maximum. Modified from Steig *et al.* (2000).

liquid water if the annual melt should decrease (Doran *et al.* 2002). Meltstreams, ponds and even large lakes therefore exist in a tenuous environment where small changes in heat balance either provide meltwater or result in desiccation. Small changes to the production of liquid water "cascade' through aquatic ecosystems and where trends in climatic change result in monotonic trends in meltwater production, small changes can translate over time to large effects.

Millenium time-scale changes

The polar regions are now changing rapidly, but within a framework of longer-term change. The last 20 000 years in particular has seen considerable change, characterized by the ice cores at Taylor Dome (Fig. 2) as follows (Fountain & Lyons 2003):

> The Last Glacial Maximum (LGM) ended at 15 Kyr BP with a very rapid warming (Bølling-Allerød Event) when mean annual temperature at Taylor Dome increased by almost 12ºC over 1 Kyr (Steig *et al.* 2000) and the accumulation rate of snow increased.

> The Younger Dryas cooling event from 13–11 Kyr BP then dropped temperatures by *c.* 4ºC, after which temperatures rose again to Bølling-Allerød values.

> Since 10 Kyr BP there has been a gradual cooling of about 5ºC with sharp cooling events 9.5 and 6.5 Kyr BP.

> Over the last 1000 yrs there has been a warming of *c.* 2ºC.

This general setting provided the environment for the development of inland aquatic habitats that persist today. Of the various types of extant aquatic ecosystem, the larger lakes of Antarctica preserve the best records of the effects of change on these timescales.

While lakes affected by these events are no doubt to be found throughout coastal Antarctica, the lakes of the McMurdo Dry Valleys are the closest to the Taylor Dome core site, and have shown long-term changes that correlate with the Taylor zone climate record. These lakes are thought to have been at their maximum extent about 10–12 Kyr BP, during the warming that ended the LGM. At that time, the expanded Ross Ice Shelf effectively dammed the valleys and sufficient water accumulated behind this dam to result in two very large lakes filling the Wright and Taylor valleys – Great Lake Vanda (> 200 m deep) and Lake Washburn (> 100 m deep) respectively. As the Ross Ice Shelf retreated, the large lakes drained, leaving a series of small lakes in the rock depressions that remained. Relative cooling in the valley up to about 1000 yr ago was accompanied by further lake evaporation to a minimum water volume at that time (Wilson 1964, Lyons *et al.* 1998). Since then the lakes have refilled as temperatures in the McMurdo Dry Valleys have increased about 2ºC in the last 1000 years.

Detailed information of lake level changes over the last century show a trend of increasing lake levels from 1903 to
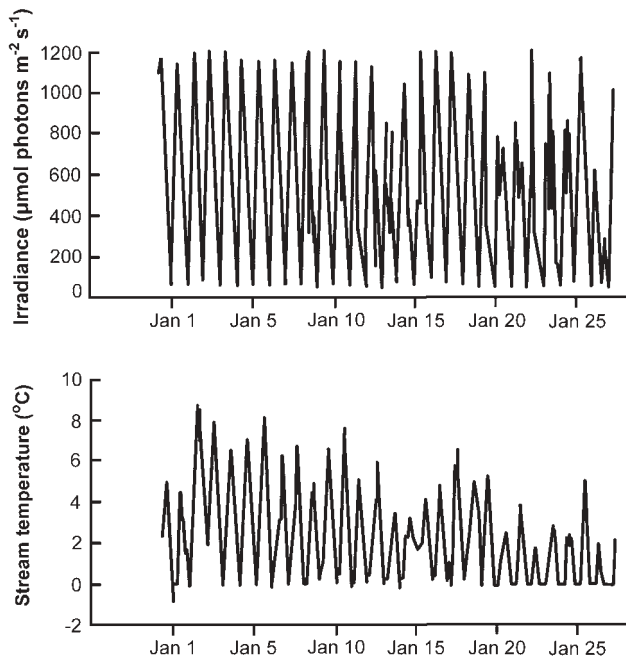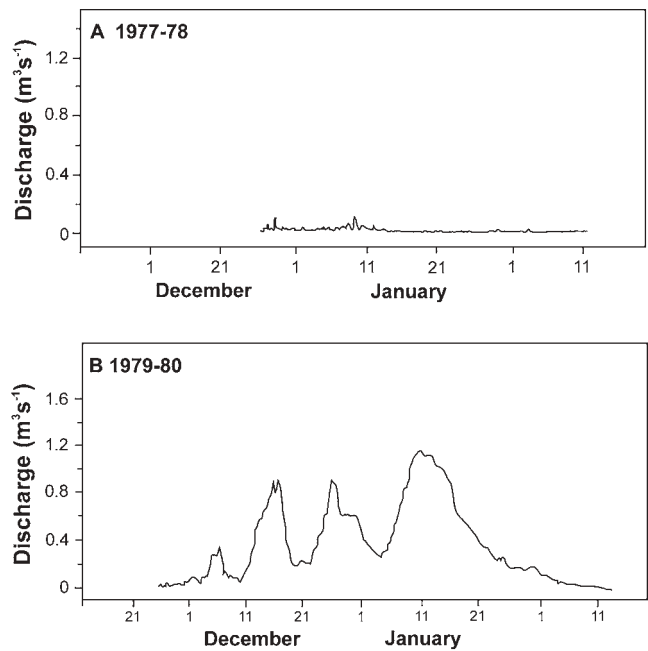
Fig. 3. Daily irradiance (top panel) and water temperature (lower panel) for the Onyx River over 26 days in mid-summer.

Fig. 4. Onyx River flows in two contrasting years (1977–1978 and 1979–1980) showing extremes of interannual variability Modified from Chinn (1993).

the late 1980s (Chinn 1993). However, between 1996 and 2000 air temperatures in the Taylor Valley decreased by 0.7ºC (Fountain & Lyons 2003) resulting in a slowing of glacier runoff and stable lake levels (Welch *et al.* 2003) until 2001 when significant lake level rises occurred as a response to a "high-flow" year (Lawson *et al.* 2004).

Other lake areas of the continental margins have shown millennium-scale changes that can also be related to long-term climate variability and its resultant effects of deglaciation, isostatic uplift and warming temperatures such as those of the Larseman Hills (Burgess *et al.* 1994), the Vestfold Hills (Pickard 1986) and the Schirmacher Oasis (Bormann & Fritzsche 1995).

Seasonal and diel timescale changes

Overlain on the longer term climatic oscillations are seasonal and diel variability. These are also driven by the hydrological cycle, but reflect short term excursions above and below the combinations of solar radiation and air temperature that determine the ice-water phase change. In many cases, high summer irradiance allows melting of frozen water bodies to occur while air temperature remains below zero (Hawes *et al.* 1999) and meltstreams deriving their flow from glaciers and snow banks tend to have flows which follow insolation of their sources rather than air temperature and flow may cease at times during the day (e.g. Howard-Williams *et al.* 1986, Conovitz *et al.* 1998). Temperatures of small water bodies may show strong diel variation, and, as the end of the liquid period nears, marked diel freeze-thaw cycles may be evident (Fig. 3). Interannual

variability in such melt-driven systems is also common, due to small interannual variability of climate amplified through the ice-water transition effect (Fig. 4).

Seasonal impacts are greatest for small water bodies which, lacking the ability to store heat, may freeze completely (often accompanied by increasing salinity during the freezing process) and streams which typically freeze and dry over the winter period. The capacity of larger water bodies to store heat buffers temperature change and may allow a proportion of the water to remain unfrozen in winter, with the most dramatic seasonal change therefore being the shift from continual daylight to continual darkness.

Temporal variability affects ecosystem processes in two ways. Firstly, it affects the physical and chemical structure of the environment in which processes operate and, secondly, it affects ecosystem processes directly (e.g. though rates of biogeochemical cycling). We now discuss variability in several common ecosystem types in relation to their physical structure and the nitrogen cycle.

Lakes (water bodies ≥ 1 ha)

Consequences of temporal variability on lake physical structure

Long-term climatic variability has resulted in unique water column structures in many Antarctic lakes. Many are wholly or partly saline. For example, Deep Lake in the Vestfold Hills with a salinity of about 10x seawater (270 kg

total dissolved solids m^{-3}; Ferris & Burton 1988) remains ice free year round even when winter water temperatures reach -18ºC. This lake was created by evaporation of seawater within a large isolated lake basin following isostatic uplift on deglaciation after the LGM.

In other continental Antarctic lakes, events associated with glacial expansion and retreat have had yet more complex effects. As discussed above, the end of the LGM in the McMurdo Dry Valleys was followed by evaporation of large lakes to small relict pools, and associated with this was a huge increase in ion content of the water. Since then these lakes have refilled to some extent, but perennial ice cover has prevented wind-induced mixing of the lake water columns and preserved the hypersaline layers that may have formed as a result of past climate-driven hydrological processes. Along with the preserved physical structure, legacies of past microbial activity are preserved.

This has some extraordinary effects. For example, in Lake Bonney, dissolved oxygen at depths below 20 m is very low, but a small oxygen peak at 35 m (Priscu *et al*. 1999) is thought to be a legacy of a drawdown event that occurred 1200 years BP (Lyons *et al*. 2000). Lake Vanda has a relict brine pool at its base with salt concentrations increasing markedly below 55 m to over three times that of seawater at the bottom of the lake. The age of the current brines is again estimated at 1200 yrs BP but sediment cores suggest at least three cycles of evaporative concentration over the history of the lake. The distinct salinity profile of Lake Vanda is matched by layers of microorganisms with different biogeochemical processing. The upper highly transparent fresh waters are ultra-oligotrophic with low rates of photosynthesis (0.03–0.09 mg C m^{-3} hr^{-1}) by phosphorus-limited phytoplankton (Vincent & Vincent 1982). Phytoplankton and bacterial biomass is low to *c*. 60 m depth, followed by a marked peak in primary production with values increasing five-fold to 0.2 mg C m^{-3} hr^{-1}. This deep chlorophyll maximum is fuelled by phosphorus diffusing upwards from an anoxic brine near the lake bed, into a zone where there is just enough light for photosynthesis. The lake chemical stratification is only possible because of the current ice cover and the historical, climate-driven fluctuations in lake level that generated the brine. The chemical stratification relates to all biologically active compounds, generated by stratification of a series of dominant biogeochemical cycles with depth and is well illustrated by the components of the nitrogen cycle.

Consequences of temporal variability on the lake nitrogen cycle

Lake Vanda provides an excellent example of the complex nitrogen cycle in ice-covered lakes, where biogeochemical processes are spatially separated due, in this case, to physical stability that is a legacy of past climate change. The lake is fed by the inland-flowing Onyx River that runs
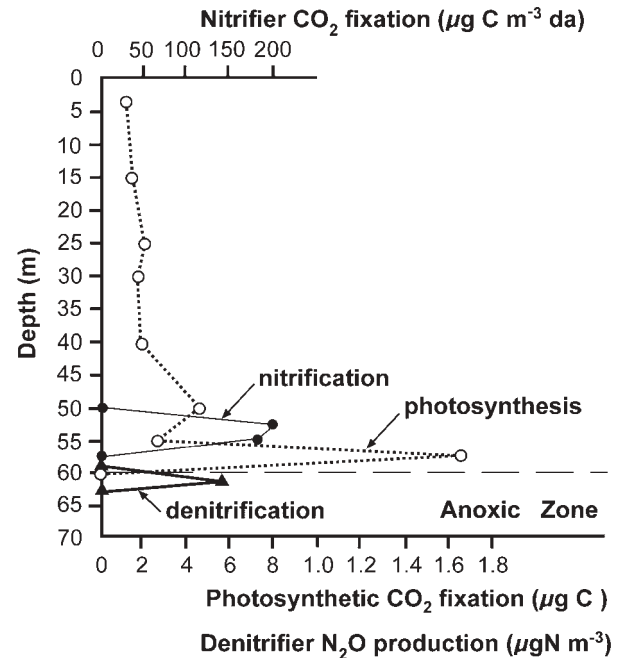
Fig. 5. The magnitude of several important ecosystem processes in the water column of Lake Vanda. Data after Vincent *et al*. 1981.

for *c*. 34 km from Lake Brownworth adjacent to the Lower Wright Glacier, through the Wright Valley to Lake Vanda. Inorganic nitrogen enters the lake from the Onyx River during its two month summer flow period mostly as NO_3-N and is trapped or efficiently recycled in the upper waters. Dense cyanobacteria dominated microbial mats cover the lake bed to at least 50 m acting as a net sink for nitrogen (uptake rates are approx 1 mg N m^{-2} day^{-1}, based on an C:N ratio of 10 and a C-fixation rate of 10 mg C m^{-2} day^{-1}, Hawes & Schwarz 1999).

In the lower water column of Lake Vanda various microbes associated with nitrogen cycling are separated by depth within a very small zone associated with the switch from oxic to anoxic water. At this oxycline, nitrifying bacteria produce nitrate from ammonium diffusing up from the anoxic deep layers, together with the intermediate product nitrous oxide which accumulates in the lake's layered structure. In 1985, the abundance of nitrifying bacteria reached a sharp maximum at *c*. 55 m (Fig. 5) with a sharp peak in nitrate and nitrite just above the oxic-anoxic boundary at 58 m. In this layer, nitrous oxide accumulated to global extreme values of > 20 000% of air equilibrium (*c*. 1400 μM L^{-1}), equivalent to the nitrate-N concentration (Vincent *et al*. 1981). This layer is directly above the deep chlorophyll maximum and photosynthetic maximum at 56–57 m where oxygen production is maximal. While N_2O is generally regarded as an intermediate in denitrification it is also produced in high redox conditions in the dissimilatory reduction of nitrate to ammonium. However, Lee *et al*. (2004) calculated that conditions in the N_2O peak were such that nitrification was the likely pathway for N_2O

production. Nitrate and N_2O then both diffuse down into the anoxic layer at the top of the brine pool (58–62 m) where a peak in denitrification activity occurs, utilizing both nitrate and N_2O as denitrification substrates. In the brine pool itself ammonium-N is released predominantly through the process of sulphate reduction as part of the decomposition process (Canfield & Green 1985, Purdey *et al.* 2001, Lee *et al.* 2004). At the sharp boundary of the oxic-anoxic zone (60 m) in 1985 NH_4-N was shown to diffuse upwards and was converted to NO_3-N by the nitrifier layer at 55 m. Between the discrete layers in the lakes, vertical transport of inorganic ions and gasses is predominantly through molecular diffusion owing to the lack of wind-induced turbulence under the thick ice cover.

Thus, once the physical structure of the lakes was established as a response to millennial and decadal climate change, and the ice-covers became permanent preventing turbulent mixing, then conditions related to redox controlled environments determined the apparently unusual layers and concentrations of compounds formed by biogeochemical reactions (Lee *et al.* 2004).

Ponds (water bodies less than 0.1 ha that usually freeze completely each winter)

Ponds are the most common type of water body in inland Antarctica, occurring in glacial moraines and in glacial ice depressions from high altitudes to the coast and from the margins of the continent to at least 86ºS. They occur at the edges of nunataks on the polar plateau and are common on ice shelves along the coast. Some have a permanent ice cover, but many have some, or complete, open water in summer. Most are oligotrophic but ponds at coastal sites near bird and seal activity may be highly eutrophic. In almost all cases Antarctic ponds are characterized by the presence of dense microbial mats that cover the base. Examples are found in Antarctic Penninsula (Ellis-Evans 1996), Schirmacher Oasis (Bormann & Fritzsche 1995), King George Ice Shelf (Heywood 1977), McMurdo Ice Shelf (Howard-Williams *et al.* 1990), Larseman Hills (Hodgson *et al.* 2001), Vestfold Hills (Pickard 1986), La Gorce Mountains (Broady & Weinstein 1998), north Victoria Land (Borghini & Bargagli 2004), and form the dominant life forms of these ecosystems.

Antarctic pond environments are variable in a number of scales, reflecting their dependence on melting of snow and ice to replenish water lost by ablation and evaporation. At decadal scales ponds may desiccate and refill. Desiccation provides a range of drying times for the pond mats from weeks, to years (Hawes *et al.* 1992). Salinity and hydrochemical conditions vary seasonally with freeze thaw cycles. One hypersaline pond, Don Juan Pond in the Wright Valley, does not freeze, rather the high salinity (TDS > 500 kg m^{-3}) depresses the freezing point so that liquid water remains in winter air temperatures of -50ºC, the predominant salt being Antarctite-$CaCl_2.6H_2O$ (Torii & Osaka 1965). The hydrological balance of Don Juan Pond is maintained through evaporative losses versus precipitation from snow and inflow from a confined saline aquifer. This balance results in highly variable hydrological and chemical regime.

Consequences of temporal variability on pond physical structure

A wide range of biogeochemical processes has been measured in Antarctic ponds during summer months. There have been very few studies of these systems during the freeze-up and over-winter periods. However, seasonal temperature curves (Fig. 1) illustrate that the summer melt periods are but a small part of the year. For most of the year pond-dwelling organisms are subjected to water and ice temperatures below 0ºC, they must withstand the common freeze-thaw regimes, and they must also be able to tolerate high levels of variability in a wide range of chemical conditions. These are brought about by two processes; freeze-thaw and biological activity. Freezing in late summer results in nutrients and major ion concentrations increasing by several orders of magnitude in the bottom waters (Schmidt *et al.* 1991). Simultaneously, the increasing salinity depresses the freezing point. Liquid water was recorded at -14ºC in June in two ponds at Cape Evans (Schmidt *et al.* 1991). Once a complete ice cover had formed and the ponds were sealed from the atmosphere, photosynthesis resulted in an initial depletion of CO_2 while sufficient light prevailed for net photosynthesis. As light disappeared the P/R ratio fell and respiratory pathways controlled pond metabolism. Oxygen was depleted, pH rapidly decreased and DIC increased. With oxygen depletion in darkness, sulphate reduction dominated in winter. Hydrogen sulphide was produced which, in combination with anoxia, high salinity, liquid water at well below freezing and pressure exerted as ice expanded, provided for an extremely inhospitable environment. Organisms that grow and reproduce in the benign conditions in summer (water temperatures *c.* 5ºC) must withstand severe osmotic, pH and temperature conditions for the remainder of the year. To add to the difficulties, the initial melt in the following summer may be provided by very low salinity water. Schmidt *et al.* (1991) suggested that this abrupt shift may be a greater stress than the gradual worsening of conditions toward winter.

In sheltered ponds turbulent mixing during the open water period is often not sufficient to break down salinity gradients that establish when high salinity melt forms on the bottom of the ponds and is overlain by low salinity melt from the surface ice. The pycnocline may be strong enough to isolate the pond bottom waters throughout summer resulting in a lower layer of warmer, higher pH, brackish water (Hawes *et al.* 1997, 1999). These cryogenic mini-

Table I. Nitrogen budget for the water column of a pond on the McMurdo Ice Shelf (data compiled from Hawes e*t al*. 1993, Downes *et al*. 2000, Fernandez-Valiente *et al*. 2001).

Water column nitrogen budget		
Process	Flux (mg m^{-2} day^{-1})	% of inflow
In: 1. Precipitation	0.2	1.0
2. N Fixation	12.8	67
3. Recycled N	6.0	32
Total in	19	100
Out: 4. Denitrification	0.4	2
5. Phytoplankton uptake	3.8	20
6. Benthic uptake	4.8	26
7. Burial*	10	52
Total out	19	100

* By difference

meromictic systems are often only 50 cm deep, or less, but are common in both the Antarctic and Arctic (Vincent *et al.* 2000).

Consequences of temporal variability on the pond nitrogen cycle

For some inland ponds atmospheric sources of nitrogen (as nitrate in snow) appears to be the principal source with inland ponds having concentrations of nitrate–N of < 13 g m^{-3} (Vincent & Howard-Williams 1994). However, a nitrogen budget for a pond on the McMurdo Ice Shelf (Table I) shows that the autotrophic fixation of nitrogen accounted for 67% of total nitrogen inputs while nitrogen release from the sediments as recycled NH$_4$-N, was 32%. Snow precipitation and ice melt provided the remaining 1%. Pond N-fixation rates (12.8 mg m^{-2} day^{-1}) were very rapid, similar to those at temperate latitudes (Fernandez-Valiente *et al*. 2001)

Nitrogen transformations between the sediments, the benthic mats and the pond water column were dominated by uptake processes in the plankton (20%) and the benthic microbial mats (26%) with uptake following first order kinetics (Downes *et al*. 2000). Transformations from inorganic nitrogen to dissolved organic nitrogen (DON) appear to be very marked in pond waters. Vincent & Howard-Williams (1994) showed a correlation between pond salinity and DON in isolated ponds suggesting DON is relatively refractory and accumulates with time like the major ions. High DON concentrations in some supra-glacial ponds (Vincent & Howard-Williams 1994) are still not explained.

In Victoria Land, ponds are often nitrogen-limited. Attempts have been made to measure nitrification of recycled ammonium, but while the process was detected the rates were too slow to accurately quantify (M. Downes, personal communication 1993). However, in the anaerobic conditions below microbial mats denitrification has been measured at rates of 0.4 mg N m^{-2} day^{-1}, constituting a small proportion (2%) of nitrogen lost from pond waters. As in the lakes, nitrogen loss from this process is as N$_2$ gas or as N$_2$O (Downes *et al*. 2000). N$_2$O concentrations, while measurable, do not have a chance to build up in ponds to the extreme concentrations found in the deep stratified lakes described above. However, this may be because measurements have only been carried out during summer. With winter ice cover we hypothesize that concentrations of N$_2$O in the pond waters may be significant before final freeze up.

Meltstreams (including groundwaters of the hyporheic zone)

The existence of, and hydrology of, Antarctic streams is determined not by immediate precipitation, but by the temperature of the glacier surfaces where melt is generated (Fountain *et al*. 1999). Stream flow variability is dependent on glacier surface melt which in turn is dependent on the small changes to the heat budget on the glacier surface. As all melt is generated in summer, and in Antarctica most summer days are close to the freezing point of water, very small changes in glacier surface temperature are needed to switch the phase change from ice to water and reverse. At some times of the year, such as just prior to the maximum surface temperatures of glaciers, flow off the glaciers can start and stop with passing cloud banks. Several reviews of Antarctic melt stream systems have been published in the last decade or so (Vincent *et al*. 1993, Hawes & Howard-Williams 1998, McKnight *et al*. 1999) showing that typically streams flow for 4–8 weeks in the year with maximum discharge being in December and January, (Vincent & Howard-Williams 1986, McKnight *et al*. 1999) with considerable diel (Fig. 3) seasonal and interannual variability (Fig. 4) (Bomblies *et al*. 1998, Pizarro & Vinocur 2000, Mataloni *et al*. 2005).

Consequences of temporal variability on melt stream physical structure

Most melt streams show strong daily signals of flow, with minimum in the early hours of the morning and maximum in the afternoons (Howard Williams *et al*. 1986, Conovitz *et al*. 1998). Small streams often cease flow and the stream surfaces freeze at least once a day (Fig. 3) unless drainage from the adjacent and sub channel hyporheic zone continues to provide water (Conovitz *et al*. 1998).

Thus organisms inhabiting stream surfaces must be tolerant of daily freeze thaw cycles, daily and seasonal desiccation. As stream channels change course in the glacial landscapes and as interannual flow variability is high, some channels may dry or flood over longer (decadal) time scales. Thus communities in stream channels may be adapted to desiccation for years at a time (McKnight *et al*. 1999) and recover quickly once water is available. Interannual stream flow variability is a function of interannual climate
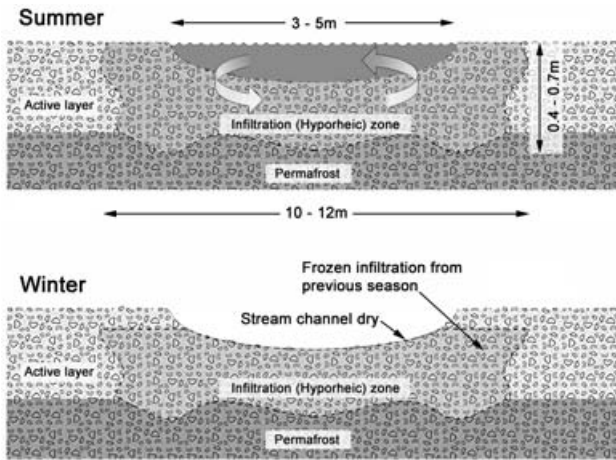
Fig. 6. Schematic diagram of hyporheic exchanges in a dry valley stream in summer and winter (After Gooseff *et al.* 2003).

Table II. Nitrogen budget for a cyanobacterial mat community in Canada Stream, Taylor Valley. Rate units are µg N (mg mat N)$^{-1}$ h^{-1}. Percentages are of total gains to, or losses from, the mat. (After Howard-Williams *et al.* 1989)

	Process	Rate	%
Gains	Nitrate uptake	0.370	72
	Ammonium uptake	0.021	4
	Urea uptake	0.074	14
	Nitrogen fixation	0.046	10
	Total gains	0.515	100
Losses	Coarse particulate organic-N	0.001	< 1
	Fine particulate organic-N	0.031	10
	Dissolved organic N	0.280	90
	Total losses	0.312	100
	Net accumulated in mat	0.203	

variability (Fig. 4). For instance *c.* 50% of the streams marked on topographic maps drawn in the 1970s did not appear to flow in 1990 during a cooler climatic period (McKnight *et al.* 1999, Doran *et al.* 2002).

In glacial alluvial landscapes significant lateral and vertical interaction occurs between the water in the stream channel and surrounding soils above the permafrost (Fig. 6). The recent works of McKnight and colleagues (Conovitz *et al.* 1998, Runkel *et al.* 1998, McKnight *et al.* 1999) have shown the importance of the hyporheic zone below the stream channel and the lateral wetted zones on either side of the channel in determining Antarctic stream flow processes. Seasonal variability in these channel/soil interactions depends on the winter freeze-up (Fig. 6). Stream channels dry out in winter and the wetted and hyporheic soil zones freeze. Where the ratio of hyporheic zone to stream channel volume is large, the hyporheic zone may smooth out some variability in stream flow (Gooseff *et al.* 2003, 2004).

Stream channels are characterized by thick cohesive microbial mats dominated by cyanobacteria whenever stable substrates occur. In the absence of grazing and disturbance these communities can develop over years to achieve high biomass. In streams with shifting sediment filled channels, stream biomass is restricted to armoured banks where some geomorphological stability may be found. In the Antarctic Peninsula area, stream channels may also be dominated by eukaryotic filamentous species (Hawes & Brazier 1991) but in the Ross Sea region, while filamentous chlorophyes *Binuclearia tectorum* and *Prasiola calophylla* are found they are sparsely distributed, the latter confined to deep shade environments under rocks perched in stream channels. As nutrients have been shown to be non-limiting to growth in Antarctic melt streams (Vincent & Howard-Williams 1986, Howard-Williams *et al.* 1989, Vincent *et al.* 1993) the primary controls on carbon processing are water temperature and the length of the free water period (this defines the growing season). Elster &

Komarek (2003) found that the optimum length of time for periphyton accumulation on glass slides was 65 days after which sloughing and dieback caused a decrease in accumulated biomass. Modelling of natural biomass accumulations shows that several years of biomass accumulation are needed to reach that seen in mature stream communities (Hawes & Howard-Williams 1998).

Consequences of temporal variability on the melt stream nitrogen cycle

Nitrogen cycling in Antarctic streams was studied initially in the Canada Stream in the Dry Valleys (Howard-Williams *et al.* 1989). A preliminary nitrogen budget for the stream benthic mat community on a midsummer day when flows were 0.06 m^{-3} s^{-1} is described by gains and losses (Table II). Gains to the cyanobacterial mat community in the channel were 0.515 µg N (mg mat N)$^{-1}$ h^{-1} of which 72% was NO$_3$-N uptake, 10% was N-fixation and ammonium and urea uptake combined was 18%. Thus N-fixation was a much lower proportion of input nitrogen in the stream compared with ponds (see section above). Losses from the mat were 0.312 µg N (mg mat N)$^{-1}$ h^{-1}, of which 90% was as DON, 10% as fine particulate N and less than 1% was coarse particulate N. The remainder (0.203 µg N (mg mat N)$^{-1}$ h^{-1}) was presumably accumulated in the mat. Subsequently a number of elegant studies by McKnight and colleagues have added a new dimension to these stream nutrient studies by incorporating the flux to and from the hyporheic zone below and alongside the streams (McKnight *et al.* 1999, 2004, Gooseff *et al.* 2004).

The N-cycle can be viewed in a number of steps; sources, hyporheic exchange, in-channel transformations, sinks and out flow. Of the sources, glacier melt or snow melt provides the principal source of nitrogen, mostly in the form of nitrate. Howard-Williams *et al.* (1986) provide a table of stream N concentrations from a wide range of Antarctic glaciers. As examples, small melt streams directly on the Canada Glacier surface showed concentrations of DIN in the meltwater that varied with flow from 145 mg m^{-3} during

low flow periods to 30 mg m^{-3} at high melt periods.

Snow melt as a source of DIN was demonstrated by McKnight *et al*. 2004, with NH$_4$-N concentrations of 28 µg L^{-1} and NO$_3$-N of 11.2 µg L^{-1}.

Hyporheic exchanges have recently been recognized as important in melt stream nitrogen dynamics. The high permeability of the glacial moraine alluvium over which Antarctic streams flow provides a matrix for hyporheic exchange of water and solutes. Nutrient concentrations in stream hyporheic zones and so-called parafluvial seeps flowing into streams from adjacent moraine had higher nitrogen concentrations than meltwater from snow banks. For instance concentrations of NO$_3$+NO$_2$ were below detection in meltwater and up to 168 µg L^{-1} in seep hyporheic zones and 126 µg L^{-1} in the sub-stream hyporheic zones (McKnight *et al*. 2004).

In-channel transformations are dominated by microbial uptake. Downstream attenuation of dissolved inorganic nitrogen has been recorded in several Antarctic streams and microbial uptake and transformation of this to particulate and dissolved organic nitrogen is shown in Table II (Howard-Williams *et al*. 1989, Moorhead & Priscu 1998, McKnight *et al*. 1999). Recent tracer injection experiments into streams, show that microbial uptake can be separated into that occurring in the stream channel and that occurring in the sub-channel hyporheic zone. McKnight *et al*. (2004) found that 84.5–93.5% of the uptake occurred in the main channel zone and 6.5–15.5% in the hyporheic zone. The uptake rate coefficients were similar between the two zones but clearly flows were considerably greater in the main channel. Microbial nitrogen uptake from the water in the hyporheic zone may be due to direct assimilation by biofilms, and by denitrification. A third possible pathway, dissimilatory reduction, was found to be a very minor pathway in two study streams (Gooseff *et al*. 2004). Denitrifying bacteria have been detected in the base of microbial mats in Antarctic ponds (Downes *et al*. 2000) and in the hyporheic zone of Antarctic streams (Maurice *et al*. 2002). Denitrification was found to be a minor sink when compared with biotic assimilation of N by the benthic microbial mats in the stream channel, but in the hyporheic zone it was assumed by Gooseff *et al*. (2004) to be the single most important process in N removal. Denitrification potential experiments showed that NO$_3$ concentration was the limiting substrate rather than labile carbon.

Gooseff *et al*. (2004) found that nitrate was the rate limiting substrate for denitrification in the Taylor Valley streams. Potential denitrification assays (PDA) with non-limiting substrates showed rates from 7 nmol N cm^{-2} h^{-1} for *Phomidium* mat to 16 nmol N cm^{-2} h^{-1} for *Nostoc* dominated mats. These are in the same range as uptake rates for these mat types. Actual rates (no added substrate) of denitrification were at least an order of magnitude lower. It appears that denitrification is *c*. < 10% of benthic uptake in the study stream. This is of the same order as found in the McMurdo Ice Shelf ponds where denitrification was found to be 9% of the benthic uptake rate in the whole pond nutrient budget (Table I).

McKnight *et al*. (2004) found that nitrate concentrations in streams containing abundant microbial mats were almost an order of magnitude less than those with sparse mats (cf. 5–17 µmol NO$_3$ in sparsely colonized streams vs 0.2–1.4 µmol NO$_3$ where abundant mats were present). The main sink for the nitrate from the water column was therefore uptake by autotrophic benthic microbial communities. In the Onyx River, Howard-Williams *et al*. (1997) showed that 80% of the nitrate flux was removed by the benthic microbial communities in a wide section of the river above Lake Vanda.

Cryoconites

Cryoconite holes are formed when groups of particles (organic or inorganic) on the surface of glaciers absorb heat and melt into the ice. The hole that forms is filled with melt water during the summer months and provides a habitat for microbial life. Cryoconites range in size from less than 1 cm in diameter to 1 m and may be as deep as 0.6 m in some conditions (Gerdel & Drouet 1960). In parts of Antarctica groups of cryoconites merge to form supraglacial ponds several metres in diameter. Most Antarctic cryoconites have a persistent ice cover during the melt period which allows light to penetrate but minimizes gas transfer and the conductive transfer of heat from the hole. Solar radiation penetrates from above and the sides through the ice so these are characterized as high light environments (Vincent & Quesada 1997).

Cryoconites behave as ponds during winter with marked changes in solute concentration as the ice freezes down from the surface, concentrating the salts to form brines which, in turn, lower the freezing point. In some conditions the cryoconite water column remains stratified (Vincent *et al*. 2000) with high concentrations of major ions and nutrients at the base. In any given location, the depth to which cryoconite sediments will melt into the ice tends to be similar, and is set by the balance between absorption of solar radiation, which declines as the sediment sink into underlying ice, and heat dissipation to the ice.

The restrictions to gas exchange by the ice cover results in extremely depleted dissolved CO$_2$ and correspondingly high pH (> 10.0) together with a super-saturation of dissolved oxygen (160%). The combination of low pCO$_2$ (down to 10$^{-7.6}$ (cf near atmospheric values of 10$^{-3.7}$), coupled with low nutrient flux. (dissolved nitrogen exists mostly in the form of DON (Tranter *et al*. 2004) although nitrate was detected in some cryoconite holes by Porazinska *et al*. 2004) makes these waters highly inhospitable regimes that are unique on the planet (Tranter *et al*. 2004). As in the case with lake ice cover aquatic habitats (see section below), the high pH and low pCO$_2$ will almost certainly inhibit

photosynthesis although measurable C-fixation does occur. P/R ratios between 0.01 and 1.3 have been found (Tranter *et al*. 2004) suggesting net photosynthesis and complex linkages between these metabolic processes and pH, DIC, DOC and DON.

With liquid water, light and nutrients, cryoconites are commonly colonized by a variety of microbial life forms similar to those in ponds and streams of the adjacent landscapes (Christner *et al*. 2003, Porazinska *et al*. 2004). These are frequently dominated by filamentous cyano-bacteria (Mueller *et al*. 2001) and mat communities with a high biodiversity of rotifers, nematodes, tardigrades, ciliates, protozoa and a wide range of heterotrophic bacteria may occur on the sediment particles at the base of the hole (Christner *et al*. 2003). Nitrogen fixation is a feature of several of the identified cyanobacterial taxa (Mueller *et al*. 2001) with phosphorus almost certainly the limiting nutrient for growth. Cryoconite microbial biomass was estimated as 45.2 g (organic matter) m^{-2} on the Canada Glacier (Mueller *et al*. 2001). Molecular identification using 16S rDNA amplification has shown that seeding of cryoconites at the Canada Glacier occurs via aeolian transport from the surrounding local environment.

At present there is very little information on how microbial processes are constrained by the extreme conditions within cryoconites. Given the abundance of the habitat and its extreme features, this is an area where more research would likely be fruitful.

Lake ice

Lake ice itself, particularly as it warms in summer, is relatively porous and bubbles of varying sizes and shapes filled with liquid water and gases form in complex patterns throughout the ice (Adams *et al*. 1998). Minerals, nutrients and microbial communities associated with sediments blown on to the lake ice surface, or liftoff mats from the lake bed rising up through the ice form the habitats in the ice bubbles. These are similar to cryoconites in many ways but while the bubbles exist the gaseous exchange with the atmosphere will be minimal. Light saturated rates of Chl *a*-specific photosynthesis were 1–100-fold lower in the ice bubbles than in lake water below (Fritsen & Priscu 1998). This may be due to the long period of low temperature in the ice bubbles (at least -20ºC) for the six months prior to the measurements. No measurements were made but it is likely that hydrochemical processes in lake ice bubbles are similar to those in cryoconites (Tranter *et al*. 2004) although long periods (possibly years) of enclosure in lake ice may make these waters even more extreme. CO_2 limitation was almost certainly a constraint on photosynthesis.

As with cryoconites (Christner *et al*. 2003), molecular characterization of the diversity of bacteria and cyanobacteria in the ice bubbles has shown a wide variety of microbial groups (Gordon *et al*. 2000). 16S rDNA

hybridization experiments demonstrated that dominant members of this diverse lake ice microbial community are found in adjacent microbial mats in melt streams and other local habitats.

Basal regions of wet-based glaciers

Since Sharp *et al*. (1999) suggested that life existed in subglacial flows in Arctic glaciers, evidence for these microbial communities has been gathering pace. Indeed, the microbially mediated processes of methanogenisis, nitrate reduction and sulphate reduction have been recorded (Skidmore *et al*. 2000). Blood Falls (so called because of its red iron-oxide derived colour) at the terminus to the Taylor Glacier is a surface expression of an Antarctic saline sub glacial flow (Mikucki *et al*. 2004). Reduced iron in the low redox water of the flow was rapidly oxidized at the surface of the outflow. Inorganic nitrogen was found in reduced form only and dissolved organic carbon levels were high (9.25 g C m^{-3}) implying either an ancient or contemporary microbial metabolic system. Microbiology of the outflow showed an active microbial assemblage comprised of a diversity of prokaryotic cell morphologies with an average density of 10^4 cells ml^{-1}. Doubling times of the organisms ranged from 37–54 days at 0ºC. Optimum temperature (based on leucine incorporation) was 15ºC. The presence of dimethyl sulphide in the outflow also suggests chemosynthetic pathways of energy acquisition (J. Priscu personal communication 2006).

Discussion

The above review highlights how basic ecosystem processes are present in all of the microbe-dominated inland aquatic ecosystems that have yet been studied in Antarctica. There is no need to suggest that these ecosystems function any differently from those in other parts of the earth, but simply that the unique features of their physical environments allow these basic ecosystem processes to be expressed in different ways to elsewhere. Above all it seems that the variability of the physical processes in Antarctica, over a range of scales, defines the ways in which microbial processes are expressed.

As we increasingly realise that Antarctic biological diversity is richer than first thought (Vincent & James 1996, Vincent 2000) so we now realise that ecosystem processes are more complex and varied. To what extent can this be so in a place where life is at the edge of its existence? We argue that, given the basic ecosystem processes that we see in temperate environments are largely present in Antarctic inland ecosystems, microbial groups capable of all of these processes are clearly able to survive the extreme conditions we see today. In many cases the organisms of habitats with specific physical and chemical conditions that place them at global extremes of environmental conditions are the same
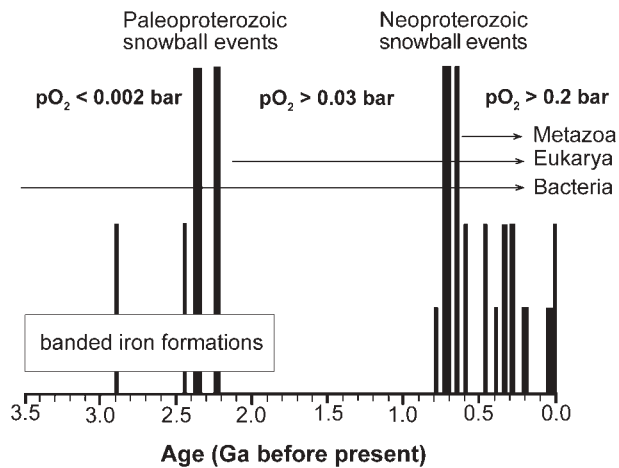
Fig. 7. Glacial events during the last 3.5 Gy (vertical bars). After Vincent *et al.* 2004, modified from Hoffman & Schrag (2002).

ones that are widespread throughout Antarctica. For instance the 16S rDNA hybridization experiments described in Gordon *et al.* (2000) and Christner *et al.* (2003) demonstrated that dominant members of the strange lake ice bubble and cryoconite microbial communities are the same as those common in adjacent microbial mats in widespread melt streams and other habitats. This situation indicates that the microbial communities are highly opportunistic colonizers of free water habitats. It also demonstrates the broad tolerance ranges of these organisms, inhabiting not only physically demanding sites in freeze-thaw, and desiccation regimes, but also regimes where the chemical environment is at a planetary extreme. The lack of psychrophily in many populations argues for a broad tolerance base of organisms that have survived many types of habitat and climatic change in the past. This is because of the set of physical extremes (particularly freezing and thawing) that characterize the region.

Vincent & James (1996) suggested that biodiversity in the Ross Sea region is mostly limited to species which have broad tolerances rather than an ability to grow fast. Antarctica's strong katabatic winds may blow these organisms across wide areas providing continual recruitment and their tolerance to extreme conditions that have allowed them to survive through earth's history, now allow them to inhabit almost every site where free water is found in the polar regions. Wind is an important integrating factor for inland Antarctic ecosystems (Fountain & Lyons 2003). Aeolian processes transport sediment and organic material (much living) across the landscape (Nkem *et al.* 2006). Algal mats have been found 300 m up on the Commonwealth Glacier. Mats that have lifted off from the bottom of lakes are torn off from lake ice and transported, ponds that vary in water level each year provide marginal mats that dry and are blown away (Hawes *et al.* 1992) and stream mats are also uplifted and blown.

New developments in the study of Earths history suggest

that not only has cold tolerance been a feature of earth's life forms since life began, but that this cold tolerance was an obligatory feature for the survival of life during the global freeze-ups or near freeze-ups that have been termed "Snowball Earth" periods (Fig. 7). There is now wide acceptance in the earth science literature of the planetary scale glaciations that have embraced Earth in at least two periods, *c*. 2.4 Gyr BP (Palaeoproterozoic Snowball Events) and between 750 and 590 Myr BP - Proterozoic Snowball Events (Hoffman *et al.* 1998, Hoffman & Schrag 2000). There is still some debate on the true extent of the Snowball Earth periods but one particular area that is of obvious interest to biologists is how life survived during global glaciations. It is clear that in modern polar regions there are marine and non-marine habitats that provide for the continuous existence of the resilient life forms that have been known to occur since the palaeoproterozoic. In inland areas, Antarctica demonstrates many habitats that are colonized by microorganisms involving a wide range of biogeochemical cycles, prokaryotic autotrophs (cyanobacteria), eukaryotic algae and metazoans (rotifers, nematodes and tardigrades). Ecosystem processes in these cryo-ecosystems are diverse and frequently concentrated in thin surface layers associated with microbial mats. Fossil evidence shows that microbial mats have been in existence for at least 3.5 Gyr, well before the first of the Snowball Earth periods began. There are many areas in Antarctica where autotrophic microbial mats similar to those in the Precambrian fossil record exist in abundance, as described in this paper.

Layered mats such as those found on the McMurdo Ice Shelf and the McMurdo Dry Valley Lakes are similar to the ancient fossil mats preserved as stromatolites in various geological formations. These are some of the oldest known microfossils, indicating that mats such as those in Antarctic inland waters have been present on earth for several billion years. When these mats were forming, the environment on earth was highly stressful compared with that which we see today. Oxygen was absent, high concentrations of reduced metals (usually the most toxic forms) and high levels of UV radiation would have been present. It is tempting to suggest that the ability of bacterial/cyanobacterial mats to thrive in the extreme conditions of inland waters in Antarctica today stems from genetic lessons learnt in the early period of life on earth. As it is now, the oldest forms of life on Earth, in the oldest known community structure, remain amongst the only ones capable of bringing life to the inland parts of Antarctica.

The organisms that currently inhabit and dominate Antarctic inland waters are tolerant of extremely wide ranges of:

temperature (few true psychrophiles have been identified),

light (ability to adapt to both extreme low and highlight

conditions - including UV),

chemical conditions (some waters are global extremes in combinations of eg. high pH, low pCO$_2$, high dissolved oxygen, virtual absence of DIN - but DON present)

redox (highly variable redox conditions in space and time)

salinity (highly varied spatial and temporal changes - in a single year salinity changes of several orders of magnitude at the base of ponds)

Large areas of aquatic habitat such as the McMurdo Ice Shelf with its 1500 km^2 of ponds lakes and streams and wide range of biogeochemical cycles (Howard-Williams *et al.* 1990, Fernandez-Valiente *et al.* 2001, Mountfort *et al.* 2003) and ice-bound areas like the Schirmacher Oasis (Bormann & Fritzche 1995) will provide long-term refuges for regional biodiversity and hence ecosystem function. Hence biodiversity is controlled by environmental heterogeneity and the heterogeneity present today is a legacy of past conditions.

Ecosystem processes including dispersal, recruitment, establishment, growth, reproduction, export (dispersal?) and many biogeochemical cycles are present on ice shelves and in inland waters that can survive glaciations and even expand during glacial periods (e.g. Lake Washburn, Great Lake Vanda) providing refuges and ecosystem continuation during wider glaciations.

Acknowledgements

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