CHAPTER 6

Ice-based freshwater ecosystems

**Ian Hawes, Clive Howard-Williams, and
Andrew G. Fountain**

Outline

Ice is a dominant component of polar landscapes which melts seasonally where combinations of solar energy flux, ice albedo, and air temperature permit. The resulting liquid water can persist on, and in, ice structures and these can support various types of ice-based aquatic ecosystem. We discuss the physical, chemical, and biotic features of the main types of ice-based aquatic ecosystems. We describe how dark-colored sediments on and in ice enhance absorption of solar radiation, and promote melting and the formation of habitats of varying sizes and longevity. We show how these range from 'bubbles' within glacial and perennial lake ice (≈10^{-2} m diameter), and cryoconite holes (≈10^{-1}–10^{0} m diameter) on ice surfaces to large melt lakes (≈10^{1}–10^{2} m diameter) and rivers on ice shelves and ice sheets. We describe the shared physical, chemical, and biological properties, notably those that relate to their alternating liquid–frozen state, and how similar species assemblages tend to result, often shared with neighboring terrestrial habitats where extreme conditions also occur. Although there are tantalizing suggestions that microbial metabolism may occur within polar glacial ice, for the most part development of ice-based aquatic ecosystems depends on liquid water. Communities are predominantly microbial, with cyanobacteria and algae dominating the phototrophs, whereas microinvertebrates with stress-tolerating strategies (rotifers, tardigrades, and nematodes) are also present. We argue that while most of these ice-based systems are oligotrophic, with low concentrations of salts and nutrients supporting low rates of production, they are found across large areas of otherwise barren ice in polar regions and that to date their contributions to polar ecology have been underestimated. We suggest that they represent important biodiversity elements within polar landscapes, and would have been essential refugia from which polar-region ecosystems would have recovered after periods of extended glaciation.

6.1 Introduction

Ice and snow, the dominant features of polar landscapes, contribute to aquatic ecosystems through seasonal melting. Although much meltwater ultimately feeds land-based aquatic ecosystems, liquid water can also persist on and in ice itself long enough for aquatic ecosystems to develop (Howard-Williams and Hawes 2007). That meltwater systems develop on ice is in part due to latent heat of fusion. Raising a cubic decimeter (10^{-3} m^3) of ice from a winter temperature of −30ºC to 0ºC requires acquisition of approximately 58 kJ of heat, but turning ice at 0°C to water at the same temperature requires a further heat gain of approximately 333 kJ. This energy can come from absorption of solar radiation or from conductive transfer from the overlying atmosphere; on local scales it is absorption of solar radiation that tends to play a major role in determining ice melt. The albedo of snow and ice is normally high, reflecting 70–90% of the incoming solar energy (Paterson 1994). It has, however, long been recognized that melting of ice is promoted where accumulations of dark-colored material reduce this albedo and thus increase the absorption of solar energy relative to the adjacent ice (e.g. Sharp 1949; Gribbon 1979).

The manner in which deposits of wind-blown or avalanche-derived sediments evolve to form cylindrical cryoconite holes in glacier ice is now well established (e.g. Wharton *et al.* 1985; Fountain *et al.* 2004). In addition, the low-gradient, undulating surfaces of ice shelves are particularly favorable for the accumulation of sediment and large, long-lived, pools can be found associated with surface sediments on suitable ice shelves in both the Arctic and Antarctic (Howard-Williams *et al*. 1989; Vincent *et al*. 2000). Similarly, where the ice covers of perennially frozen lakes incorporate dark-colored material, liquid water may form during the summer months either on the surface or within ice covers, and these pockets of liquid water, or 'ice bubbles' *sensu* Adams *et al*. (1998), in turn support microbial ecosystems (Pearl and Pinckney 1996; Fritsen and Priscu 1998).

A somewhat different type of ice-based aquatic habitat, not dependent on sediment absorption of radiation, occurs where melt generated on the surfaces of glaciers coalesces to form flowing streams and supraglacial pools on the ice itself (Heywood 1977). Gradations exist between these categories of ice-based freshwater systems, but in this chapter we recognize ice bubbles, cryoconite holes, supraglacial pools, and streams to describe ice-bound freshwater habitats. The special category of ice-based lake and river systems that develop underneath ice sheets and glaciers are described in Chapter 7 of this volume.

6.2 Ecosystems on and in glacial ice

6.2.1 Types of glacier-based ecosystem

Our categorization of freshwater habitats on glaciers is based primarily on their hydrology; *cryoconite holes* tend to be small, more or less isolated water pockets that generate their liquid water internally, *supraglacial pools* are fed from a catchment larger then the pool itself and not necessarily dependent on sediment, while *streams* are channelized pathways of flowing water. We currently know more about cryoconite holes than about the large meltwater pools and streams that are now known to occur on many polar glacier surfaces.

6.2.2 Cryoconite holes

Cryoconite holes are vertical cylindrically shaped melt holes in the glacier surface, which have a thin layer of sediment at the bottom and are filled with water (Figure 6.1). Although the holes have been known by a variety of names, including dust wells, dust basins, sub-surface melt pools, and baignoire (Agassiz 1847; Hobbs 1911; Sharp 1949), cryoconite hole is the term in most common use today. Cryoconite holes are common to ice-surfaced (as

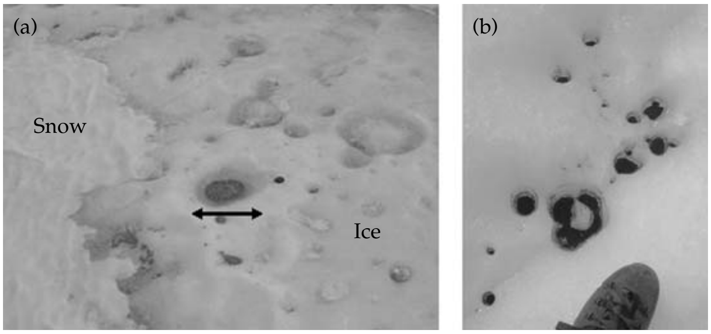

Figure 6.1 Cryoconite holes. (a) Holes with frozen lids on the surface of Canada Glacier, McMurdo Dry Valleys, Antarctica. The dark sediment patch is melting in, other holes are entirely frozen over. The scale arrow is about 20 cm. (b) Open holes on Storglaciaren, Sweden with a boot for scale.

opposed to snow-surfaced) zones of glaciers worldwide, including the Arctic (Von Drygalski 1897; Mueller *et al.* 2001; Säwström *et al.* 2002), temperate glaciers of the mid-latitudes (McIntyre 1984; Margesin *et al.* 2002), and the Antarctic (Wharton *et al.* 1985; Mueller *et al.* 2001; Fountain *et al.* 2004).

6.2.2.1 Physical processes in cryoconite holes

Cryoconite holes first form when small patches of sediment (wind-blown or avalanche-derived) accumulate in small depressions on the ice surface (Wharton *et al.* 1985; Fountain *et al.* 2004, 2008). The sediment absorbs solar radiation and initially melts into the surrounding ice faster than surrounding ice ablates, forming a water-filled hole (Figure 6.2). Cryoconite-hole width is probably determined by the size of the original sediment patch and can be a few centimeters to a meter or more in diameter. As the sediment melts deeper into the ice, the attenuation of radiation by absorption and scattering reduces heat gain and rate of melting and an equilibrium depth (typically 30–50 cm) is reached when the melt-rate in the hole matches the ablation rate of the ice surface (Gribbon 1979).

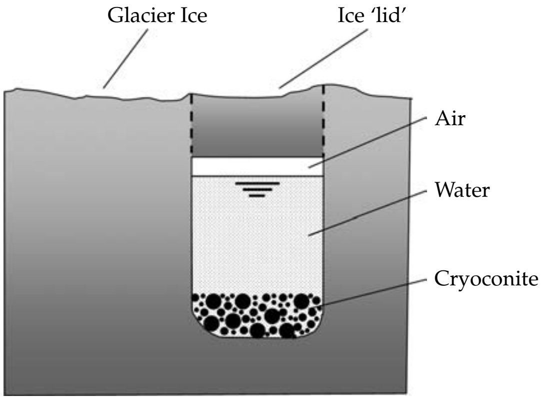

Figure 6.2 Cross-section schematic of a sealed cryoconite hole. Cryoconite holes freeze entirely during winter. The freezing process concentrates the solutes, possibly resulting in a delay of complete freezing of the entire hole as increasing salt concentration depresses the freezing point. The return of summer solar radiation again preferentially warms the sediment, which, if there has been winter or spring sublimation of surface ice, is now closer to the ice surface and again melts its way down through the ice according to the amount of heat it receives. In this way the sediment and associated biota may remain just beneath the ice surface, more or less isolated from the surrounding hydrologic system and the atmosphere for years and in some cases decades (Fountain *et al.* 2004).

Two types of cryoconite hole are now recognized: those normally open to the atmosphere in summer, and those normally sealed with an ice lid. Closed holes are found where freezing air temperatures and persistent winds maintain a frozen ice surface over the liquid phase. In the Ross Sea sector of Antarctica, closed cryoconite holes occur at least as far north as 72°S (I. Hawes, personal observations). Closed holes have severely restricted exchange of water, solutes and gases and, unless surface conditions change dramatically, the cryoconite hole becomes entombed, freezing and melting beneath the glacier surface for years and capable of developing unusual biogeochemistries (Tranter *et al.* 2004). In some cases, however, apparently closed cryoconite holes can be hydrologically connected to a subsurface system of drainage passages (Fountain *et al.* 2004, 2008).

Open holes occur where the surface energy balance is close to melting and appear to be more common in the Arctic and temperate glaciers, where summers are warmer, than in the Antarctic (Mueller *et al.* 2001). Open holes tend to act like small ponds. Their water chemistries, while different from the host ice due to sediment dissolution and biological processes, are regularly diluted with fresh meltwater from the surface and exchange gases readily with the atmosphere.

6.2.2.2 Ecosystem processes in cryoconite holes

That cryoconite holes develop their own biota is not surprising, given that the snow that forms glacial ice encapsulates many propagules, including Archaea, bacteria, fungi, algae, and protozoa (Abyzov 1993; Christner *et al.* 2005; Castello and Rogers 2005) which can remain viable for long periods of time. Winds also carry such particles directly on to snow and ice surfaces as aeroplankton (Nkem *et al.* 2006). For open holes this is supplemented by surface meltwater and direct deposition into the holes. The microbial biota includes bacteria, virus-like particles, nanoflagellates, cyanobacteria, algae, and protozoa (Wharton *et al.* 1981, 1985; Mueller *et al.* 2001; Säwström *et al.* 2002; Christner *et al.* 2003). A metazoan census includes nematodes, tardigrades, rotifers (De Smet and Van Rompu 1994; Grongaard *et al.* 1999; Takeuchi *et al.* 2000; Christner *et al.* 2003; Porazinska *et al.* 2004), protozoans, copepods, and insect larvae (Kikuchi 1994; Kohshima 1984).

Studies of metabolic activity and nutrient analyses in cryoconite holes confirm the presence of active microbial consortia (Tranter *et al.* 2004; Foreman *et al.* 2007). Hodson *et al.* (2005) point to the loss of ammonium ions in the meltwaters on the glacier ice surfaces in Svalbard as evidence of microbial activity (photosynthesis) in the organic-rich sediments within the cryoconite holes. The water chemistry of the closed cryoconite holes of the McMurdo Dry Valleys also provides evidence of microbial activity. Photosynthesis in the holes, presumably by the green algae and cyanobacteria, is indicated by high saturations of oxygen (160%) and low values of pCO2 (Tranter *et al*. 2004). Values of net primary production, based on ^{14}C uptake, range from 67 to 146 mg C m^{-3} day^{-1} (C.M. Foreman, unpublished results) compared with 14–3768 mg C m^{-3} day^{-1} in open holes on Svalbard (Säwström *et al.* 2002).

In some closed holes, the chemistries can be extreme, with pH approaching 11 (Fountain *et al.* 2004), although Mueller *et al*. (2001) recorded an average pH of 8 for Canada Glacier cryoconite holes. This contrasts with the more dynamic, open holes on Arctic glaciers, where pH can be acidic (Mueller *et al*. 2001). High pH results first from hydrolysis of carbonates during the spring thaw that can increase pH to approximately 10.5, saturate the water with calcium carbonate and decrease pCO2. Photosynthesis further decreases pCO2 and increases pH to the observed extreme levels and can supersaturates the water with calcium carbonate. Ultimately, low pCO2 and high pH may limit photosynthesis. Thus in these poorly pH-buffered closed systems, photosynthesis may be constrained because of limitations on nutrients and new carbon dioxide sources. In-hole biogeochemical processes raise electrical conductivities in closed systems to several hundred µS cm^{-1}, substantially higher than melted ice.

Food webs in cryoconite holes are simple, with net flux of critical nutrients (inorganic carbon, nitrogen, and phosphorus) being dependent on external exchange and mineralization of sediment. Tranter *et al*. (2004) hypothesize that the cyanobacteria and algae in closed cryoconite holes must acquire nutrients scavenged from the sediments in the hole, although nitrogen fixation is a feature of several of the identified cyanobacterial taxa (Mueller *et al.* 2001). Phosphorus is almost certainly the limiting nutrient for growth. Heterotrophic bacteria found in the holes are comparable in abundance with those in high alpine lakes (Foreman *et al.* 2007), and these and fungi (Vincent *et al.* 2000) are together capable of exploiting different carbohydrates, amino acids, carboxylic acids, and aromatic compounds, suggesting that the cryoconite holes of dry-valley glaciers support metabolically diverse heterotrophic communities. The mixture of phototrophic and heterotrophic strategies, combined with the ability to survive in a frozen state through the dark winter months, produces a robust ecosystem capable of surviving many freeze–thaw cycles in isolation from the atmosphere and from subsurface water sources.

6.2.3 Supraglacial pools and streams

Aerial and satellite imagery shows that networks of supraglacial pools and interconnecting meltwater streams are widespread and common on ice shelves and on the Greenland Ice Sheet (e.g. Heywood 1977; Reynolds 1981; Maurette *et al.* 1986; Thomsen 1986; Säwström *et al.* 2002; Hodgson *et al.* 2004). Despite this abundance, little is known of these ecosystems. Whereas they are likely to share many features with cryoconite holes, their principal differences are hydrological and sediment-related. Pools will tend to have a much higher surface-area-to-volume ratio than cryoconite holes, a higher water-to-sediment ratio, and advective gains and loss of materials that do not occur in at least some cryoconite holes. In the 2005–2006 austral summer we sampled supraglacial ponds on the Tucker Glacier, Antarctica (72°S). Data from a typical pond are summarized in Table 6.1 and show an ultra-oligotrophic system, with even lower organic content and a lower pH than nearby cryoconite holes. Perhaps the best information on biological processes in supraglacial waters comes from the

Table 6.1 Characteristics of a typical supraglacial pond, and two nearby cryoconite holes (Cryo) on the Tucker Glacier Antarctica, January 2006. PC, particulate carbon; DOC, DON, DOP, dissolved organic carbon, nitrogen and phosphorus; DIN, dissolved inorganic nitrogen; DRP, dissolved reactive phosphorus. From I. Hawes, unpublished results

Site	Chlorophyll *a* (mg m^{-3})	PC (mg m^{-3})	pH	Conductivity (μS cm^{-1})	DON (mg m^{-3})	DOP (mg m^{-3})	DOC (g m^{-3})	DIN (mg m^{-3})	DRP (mg m^{-3})
Pond 1	0.04	63	8.3	7.8	31	2	2.9	6	1
Cryo 1	0.70	229	9.2	27	171	3	4.7	11	2
Cryo 2	0.49	285	9.3	26	284	3	3.1	17	3

Arctic (Säwström *et al.* 2002), where phytoplankton were found actively photosynthesizing at a rate of 7–8 mg C m^{-3} h^{-1}.

Studies of ponds on the George VI and Amery ice shelves provide insight into how critical snowfall and density of underlying firn are to meltwater accumulation. On those ice shelves, meltwater accumulates in surface irregularities where snowfall is below a threshold of 2×10^5 g m^{-2} $year^{-1}$ and when firn density exceeds 820 kg m^{-3}, when it becomes impermeable to water (Reynolds 1981). Once a melt pool has formed, it becomes self-reinforcing in that the surface has a lower albedo and rapidly absorbs radiation penetrating overlying snow. The George VI Ice Shelf contains not only open pools, but also what appear to be ice-sealed englacial pools that lie within a meter of the glacier surface and can be tens of centimeters deep. All persist for at least several years (Reynolds 1981). As far as we are aware the biological communities and ecosystem processes in these waters remain unstudied.

6.3 Ecosystems on floating ice shelves

6.3.1 Types of ice-shelf ecosystem

The mass balance of the floating ice shelves of the Arctic and Antarctic regions is maintained by various processes. Some are fed from high altitude, with down-slope flow feeding ice to the lower, floating parts; others represent long-term accumulation of sea ice or are sustained by basal freezing of underlying waters. Ice is lost by calving, melting, and ablation. Ice shelves with substantial ablation zones include Antarctica's George VI, Amery, and McMurdo ice shelves and the collection of remnant ice shelves along the northern coastline of Ellesmere Island in High Arctic Canada. Ablation zones allow sediment that has been deposited on, or incorporated into, the ice to migrate and accumulate towards the surface and thus promote the generation of surface meltwater that can in turn support aquatic ecosystems. Ice shelves support some of the most spectacular ice-based aquatic ecosystems on Earth (Plates 2 and 3).

The McMurdo Ice Shelf may be the most extensive surface-ablation area in Antarctica (Swithinbank 1970); it is virtually static, balanced by freezing of sea water beneath and ablation and melting on the surface. Basal freezing incorporates marine debris into the ice (Debenham 1920) and this is transported up through the ice as the surface ablates. Distribution of uplifted sediment on the surface varies and gives rise to a gradation of surfaces from almost fully covered with sediment that is 100 mm or more thick to a sparse sediment cover (Kellogg and Kellogg 1987). Differences in sediment cover determine the nature of the ice surface. Thick sediment cover (≥100 mm; Isaac and Maslin 1991) insulates underlying ice and prevents melting, thus creating a very stable ice surface within which large, long-lived, sediment-lined ponds develop (Howard-Williams *et al.* 1989). Patchy layers of sediment typically are a mosaic of bare ice, thin sediments that enhance melting, and thicker sediments that retard melting; the net effect being a highly dynamic and irregular surface with mobile sediments and generation of copious meltwater (Debenham 1920).

The Ward Hunt Ice Shelf (83°N, 74°W) and nearby Markham Ice Shelf in the Canadian Arctic are ablation zones that also derive sediment from aeolian transported terrestrial sources and from the underlying seabed (Vincent *et al.* 2004a, 2004b; Mueller and Vincent 2006). As with the McMurdo Ice Shelf, the undulating surfaces of these ice shelves accumulate meltwater in a series of streams and pools (Figure 6.3). Satellite imagery (see Figure 17.4) and aerial photos of the Ward Hunt Ice Shelf (Plate 2) show an alignment of these ponds with the prevailing winds (Vincent *et al.* 2000). A feature of Arctic ice shelves is that they are shrinking. They underwent considerable break-up over the twentieth century, with further loss in recent years (Mueller *et al.* 2003). Since 2000, extensive fractures have appeared in the 3000-year-old Ward Hunt Ice Shelf (83°N, 75°W) and large sections have disintegrated (Figure 17.4; see also Chapter 1 in this volume). The nearby Ayles Ice Shelf broke out completely in August 2005. The recent 30-year period of accelerated warming is implicated, as it has also been in loss of ice shelves from western Antarctica. Notable among these losses was the Larsen B Ice Shelf, which was known to have large meltwater ponds on its surface in its final stages (Shepherd *et al.* 2003) but we know of no details on the limnological characteristics of these.

6.3.2 Physical processes in ice-shelf ponds

Pond freezing is a gradual process with the ice front gradually moving down through the pond water as heat accumulated over the summer is slowly lost (Figure 6.4). The delay in freezing at depth results in the liquid-water phase extending several months after surface ice forms (Mueller and Vincent 2006). In spring, ice-based systems can become liquid long before air temperatures are above freezing (Hawes *et al.* 1999; Figure 6.4) while during summer, pond temperatures can reach over 10°C (Figure 6.5). Thus liquid water, at moderate temperature, can be present for more than 3 months, whereas the ice-free period ranges from zero to a little over 1 month (Hawes *et al.* 1993, 1997, 1999).

The process of salt concentration during freezing described for cryoconite holes is important in ponds, where stratification verging on meromixis can develop (Wait *et al.* 2006; Figure 6.5). Exclusion of salts from the ice matrix results in formation of a brine in the pond bottom which may be so saline that it remains liquid below –20°C. During this process, sequential precipitation of different minerals, first mirabilite and then gypsum, results in a change in ionic ratios as the brine volume

Figure 6.3 Sampling a meltwater pond on the Markham Ice Shelf, Canadian High Arctic. Photograph: W.F. Vincent.

and temperature decrease. The following summer a layer of melted ice overlies the brine pool which, where the density difference is sufficient to resist mixing, may persist all summer (Wait *et al.* 2006; Figure 6.5) and even to allow an inverse thermal gradient to develop (Hawes *et al.* 1999). Summer photosynthesis results in the monimolinia providing supersaturation of dissolved oxygen and extreme high pH with a corresponding marked depletion in dissolved inorganic carbon (Hawes *et al.* 1997). This situation is reversed in winter when oxygen is depleted through respiration in the dark and the deep layers of these ponds provide a sequentially variable environment for microbial populations. Freeze-concentration and evaporative concentration of salts, and dynamic water levels, result in ponds with an array of salinities and ionic compositions, from near fresh to hypersaline.

6.3.3 Ecosystem processes in ice-shelf ponds

Where sediments are patchy, water bodies are small and dynamic and support communities of low biomass, dominated by fast-growing 'colonizers' such as diatoms, particularly *Pinnularia cymatopleura*, and coccoid chlorophytes (Howard-Williams *et al.* 1990). The biota of more stable and long-lived ice-shelf ponds is often dominated by mats of algae and cyanobacteria (Howard-Williams *et al.* 1989, 1990; Vincent *et al.* 2000, 2004a, 2004b; Mueller and Vincent 2006) with biomass of the cyanobacterial mats on the McMurdo Ice Shelf as high as 400 mg chlorophyll *a* m^{-2} (Howard-Williams *et al.* 1990; Hawes *et al.* 1993, 1997). The cyanobacteria that dominate the more long-lived ponds show a degree of variation in species between ponds of different salinities (Howard-Williams *et al.* 1990). Mats are mostly dominated by species of *Phormidium*, *Oscillatoria*, *Nostoc*, and *Nodularia*. *Nodularia* is particularly common in brackish waters, while *Oscillatoria* cf. *priestleyi* was the dominant in a highly saline pond (>70 mS cm^{-1}). Phylogenetic diversity is much higher than morphological diversity and salinity appears to be a major factor determining diversity structure (Jungblut *et al.* 2005). The diatoms *Pinnularia cymatopleura*, *Nitzchia antarctica*, and *Navicula* spp. were

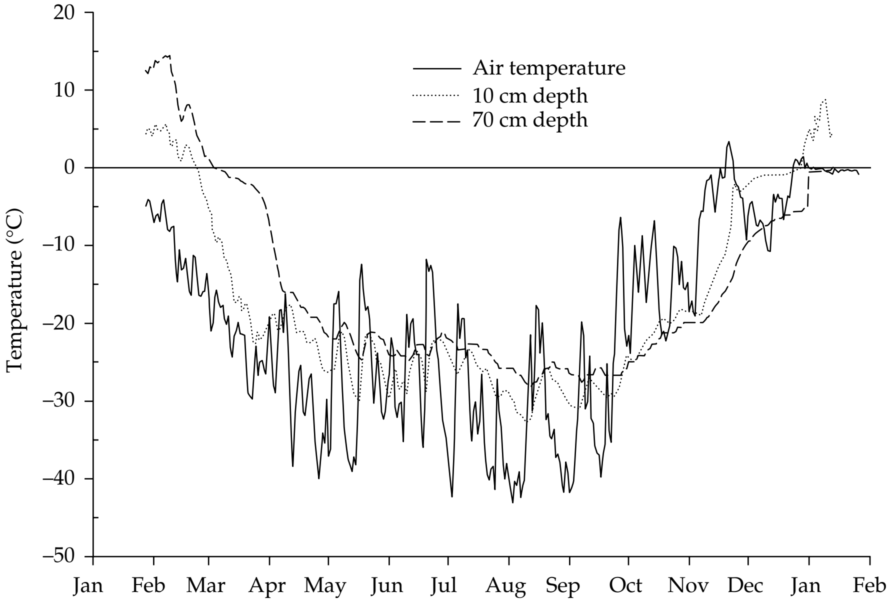

Figure 6.4 Thermistor records of temperatures in air and at two depths in a pond on the McMurdo Ice Shelf, during 1999. I. Hawes and C. Howard-Williams, unpublished results.

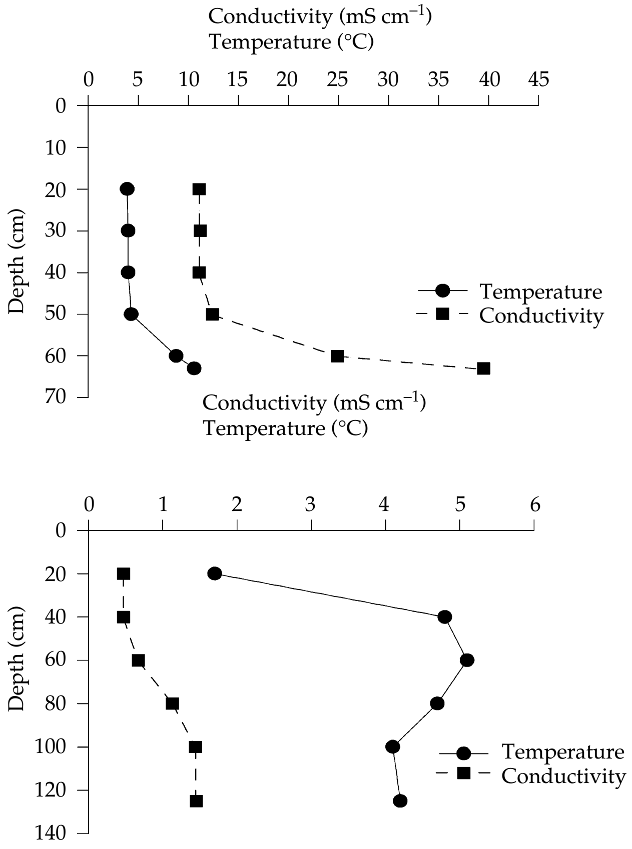

Figure 6.5 Vertical profiles of temperatures and conductivity in two ponds on the McMurdo Ice Shelf. The upper figure is for P70E, a pond which was ice-free at the time of sampling, and the lower figure is for Fresh Pond, which was frozen over all summer. Note the differences in scales of the *x* axes. I. Hawes and C. Howard-Williams, unpublished results.

associated with fresh waters, other naviculoids inculding *Navicula shackletonii* and *Navicula muticopsis* with fresh to brackish (11 mS cm^{-1}) waters and *Tropidoneis laevissima* and *Amphiprora* sp. with the most saline (Vincent and James 1996; Hawes *et al.* 1997). Benthic primary productivity is dealt with in detail in Chapter 10.

One species of tardigrade (probably a *Macrobiotus* sp.), three nematodes (three species of *Plectus*, *Plectus frigophilus* and two unidentified species) and seven rotifers (six bdelloids and one monogonontid) have been found associated with the cyanobacterial mats. Of the invertebrates, the rotifers were most abundant (4×10^5 m^{-2}) and of these, a *Philodina* species, is most abundant by far, with dense aggregations often forming orange spots on microbial mats (Suren 1990). In addition to the benthic communities, ice shelf ponds support a planktonic community with phytoflagellates, *Chlamydomonas*, *Chroomonas*, and *Ochromonas*; the latter dominating the most saline ponds (James *et al.* 1995). James *et al.* (1995) found that 'benthic' cyanobacteria were frequently entrained into the plankton. Twenty-two species of protozoa were also found in this survey, of which 15 could be considered truly planktonic. These fed primarily on bacteria-sized prey, with none showing any ability to consume particles of 5 µm diameter or greater.

Microbial mats dominate biomass and productivity in most ice-shelf ponds (Chapter 10). These typically take the form of cohesive layers of cyanobacteria overlying anoxic sediments. An orange-brown surface layer contains high concentrations of photoprotective pigment that shield lower, phycocyanin-rich blue-green layers (Vincent *et al.* 1993, 2004b) where both dissolved oxygen concentration and oxygen evolution reach their peaks (Hawes *et al.* 1997). A feature of ice-shelf ponds, as well as many other ice-based systems, is the high pH that can result from photosynthetic depletion of carbon dioxide and bicarbonate. Twelve ponds sampled on the McMurdo Ice shelf in 2002 had a mean pH of 9.7 (±0.5 S.D.). At such high a pH photosynthesis might be expected to be carbon-limited, but mat communities are well positioned to take advantage of any inorganic carbon/nutrients that are generated from their underlying sediments where pH is much lower and inorganic carbon and other nutrient concentrations are higher (Hawes *et al.* 1993). Physiologically, the mat-forming filamentous cyanobacteria consistently are primarily psychrotolerant, with temperature optima above 20°C (Hawes *et al.* 1997; Mueller and Vincent 2006). Phylogenetic analysis using molecular techniques suggests that the psychrotolerant trait occurs widely in the cyanobacterial lineage and that polar strains are often closely related to temperate ones. Psychrophily, in contrast, is confined to a narrow branch of the cyanobacteria, which includes bipolar strains (Nadeau *et al.* 2001).

A full suite of microbiological processes occurs within the ice-shelf ponds, allowing effective recyling of carbon, nitrogen, sulphur, and other elements within the semi-closed systems. Nutrient dynamics are exemplified by a nitrogen budget for a pond on the McMurdo Ice Shelf (Table 6.2). Autotrophic fixation of nitrogen (average 12.8 mg m^{-2} day^{-1} and similar to those at temperate latitudes) accounted for 67% of total nitrogen inputs whereas nitrogen release from the sediments as recycled ammonium/nitrogen, was 32%. Snow and ice melt provided the remaining 1%. Unlike nitrogen, other essential nutrients such as phosphorus cannot be biologically fixed and must come from weathering of minerals or atmospheric deposition.

Retention of nitrogen was high at 98%, much of it as biota, but retention as dissolved organic nitrogen (DON) appears to be very marked in pond waters. At the McMurdo Ice Shelf, DON concentrations can exceed 13 g m^{-3}, very high values for natural, unpolluted waters. Observations suggest that DON in these ponds is relatively refractory (Vincent and Howard-Williams 1994) and accumulates over time similarly to the major ions (Figure 6.6). The sources, sinks, and dynamics of DON in ice-based systems still need to be adequately addressed.

Table 6.2 Nitrogen budget for the water column of a pond on the McMurdo Ice Shelf. Data compiled from Hawes *et al.* (1997), Downes *et al.* (2000) and Fernandez-Valiente *et al.* (2001)

Process	Flux (mg m^{-2} day^{-1})	Percentage of inflow
In		
1. Precipitation	0.2	1
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. Storage*	10	52
Total out	19	100

*By difference.

Steep biogeochemical gradients are a feature of microbial mats. Oxygen concentration falls from supersaturated to anoxia a few millimeters into the microbial mats (Hawes *et al.* 1997). Mountfort *et al.* (2003) examined the anaerobic processes occurring in the underlying anoxic sediments. They found that, while nitrate reduction and methanogensis did occur, sulphate reduction was the dominant process. Interestingly these authors reported that all of these processes continued after freeze-up, with methanogenesis showing less sensitivity to subzero temperatures than sulphate reduction. This resulted in a gradual shift in dominant terminal electron acceptors with declining temperature.

6.4 Lake-ice ecosystems

6.4.1 Introduction

Although perennially ice-covered lakes are found through many regions of Antarctica and the colder parts of the Arctic, the only ice-covered lakes from which extensive information on ice-bound communities has been obtained are those from the McMurdo Dry Valleys. Living material within the ice of these lakes was first reported by Wilson (1965) and further investigated by Parker *et al.* (1982). Since

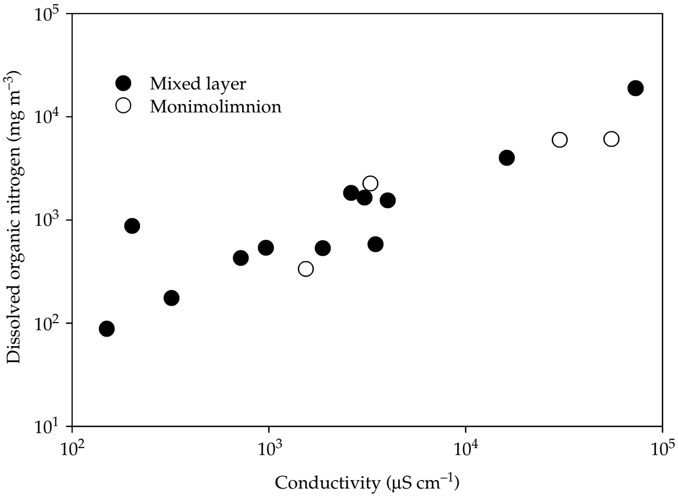

Figure 6.6 Dissolved organic nitrogen and conductivity in ponds on the McMurdo Ice Shelf. Note the logarithmic scales. Closed circles are the values from the upper mixed layer, open circles are from the lower layers when these were present at the time of sampling.

then investigations have revealed a variety of biota trapped within lake ice covers (Fritsen *et al.* 1998). As well as systems within lake ice, the sediment-rich surface of some perennially ice-covered lakes facilitates surface melting and the generation of freshwater systems on top of the ice, analogous to the sediment-lined surfaces of the McMurdo and Ward Hunt Ice Shelves.

6.4.2 Physical processes in lake ice

Ice temperatures vary with depth into the lake ice, being close to ambient air temperature close to the ice surface (surface pools will freeze to temperatures of −40°C), while at increasing depths into ice they are buffered from extremes. At 2 m into the ice, temperatures below −20°C are rare, whereas at 3 m depth −10°C is the lowest experienced each year (Priscu and Christner 2004).

The dynamics of perennial lake ice, with basal freezing balancing surface ablation, means that materials may enter lake ice from above, as with cryoconite holes on glaciers, but also from below, should materials be trapped in the ice cover during freezing, as with some ice shelves. Materials that freeze into the ice from above migrate downwards under the influence of solar heating and seasonal warming, leaving a liquid trail behind, until reaching a depth to which insufficient solar radiation penetrates to allow further migration (Adams *et al.* 1998). Materials that freeze into the ice from below include fragments of the microbial mats that grow on the beds of these lakes and these will move upwards as ice ablates at the surface (Wilson 1965; Parker *et al.* 1982).

Regardless of direction of movement, dark materials in lake ice will tend to accumulate at the depth where melting rate balances surface ablation. The lower attenuation of radiation by lake ice compared to the firn ice of glaciers allows lake-ice ecosystems to sink meters rather than the decimeters of cryoconite holes into glacial ice. Thus lake ice communities form deeply entombed 'bubbles' of water, gas, and mineral and biotic inclusions within the ice. These undergo complex physico-chemical changes during the multiple seasonal freeze–thaw cycles that they are exposed to (Adams *et al.* 1998).

6.4.3 Ecosystem processes in lake ice

Communities within lake ice occupy a habitat similar to cryoconite holes in many ways (Priscu *et al.* 1998) but differ in that, while lake ice bubbles exist, they are never open to atmospheric exchange. Few measurements have been made, but it is apparent that communities within lake ice bubbles are photosynthetically active, although light-saturated rates of chlorophyll *a*-specific photosynthesis were 1–100-fold lower in the ice bubbles than in the lake water below (Fritsen and Priscu 1998). This may be due to the long period of subzero temperatures (at least −20°C) over the winter months, although the chemical conditions in the bubbles, after long periods (possibly years) of enclosure in repeatedly frozen and thawed lake ice, make these waters chemically extreme. Carbon dioxide limitation is almost certainly a constraint on photosynthesis, in waters where pH rises to 10 or more (Fritsen *et al.* 1998).

As with cryoconite holes (see 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 once again the degree of similarity between communities in ice-based and ice-derived communities in that dominant members of the diverse lake-ice microbial community are also found in adjacent microbial mats in melt streams, cryoconite holes, and other local habitats from which they probably originated.

6.5 The significance of ice-based systems

Despite their widespread distribution within ablation zones, the significance of ice-based systems in polar landscapes has received relatively little attention. Mueller *et al.* (2001) noted that cryoconite holes covered 12% of the surface of the lower ablation zone of White Glacier on Axel Heiberg Island, Nunavut, and up to 8% of that of the Canada Glacier in Antarctica. Fountain *et al.* (2004) found 3–15% coverage on four different glaciers in the dry valleys including Canada Glacier. Multiplying the total area of cryoconite holes by the average biomass within a hole, Mueller *et al.* estimated ice-based biomass (as loss on ignition) of the two glaciers to be 10.0 and 1.5 g C m^{-2} respectively. Although these are low values, even in comparison with surrounding polar soils (216 g C m^{-2} was measured in soils close to the Canada Glacier; Moorhead *et al.* 1999), there are several reasons why this pool of living material may have disproportionately significant ecosystem roles.

First, numerous authors have alluded to the potential of cryoconite holes to act as refugia for the biota within an otherwise hostile landscape, and point to the broad similarities between the flora and fauna of cryoconite holes to each other and to surrounding terrestrial and aquatic systems (e.g. Wharton *et al.* 1985). Recent molecular studies have confirmed the close relationships between organisms in these various locales (Priscu and Christner 2004). The supposition that aeolian and perhaps other transport mechanisms link these small elements of the watershed follows naturally from these observations and it becomes sensible to think of an the extensive, if fragmented, ice-based ecosystem as forming a continuum between distant, soil-based habitats. Aeolian transport of sediment and biota have been shown to be important processes in polar regions (Lancaster 2002; Nkem *et al.* 2006), and windblown dust has been shown to contain abundant propagules of cyanobacteria, eukarotic algae, and bryophytes (Hawes 1991).

As well as creating spatial continua, cryoconite-type habitats may also play a role in providing temporal continuity by acting as refugia through climatic excursions, including ice ages, facilitating rapid recolonization with cold-tolerant organisms when the ice retreats (Wharton *et al.* 1985). Recently there has been growing acceptance that during its early history the Earth went through one or a series of so-called snowball Earth phases, when almost the whole planet froze over (Hoffman *et al.* 1998). Vincent *et al.* (2000) argued that supraglacial habitats would have been among the few that would have provided suitable conditions for the survival of the microbial organisms and communities that are thought to have existed at the time of the largest event (600 million years before present, BP), including the cyanobacteria which still dominate the flora of ice-based ecosystems. Indeed, arguments have been advanced that the concentration of organisms into low-volume compartments within icy systems that would have accompanied the snowball Earth phases, coupled with the long-term stability of biota under cold conditions, may have provided ideal conditions for the development of symbiotic associations and eukaryotic development in the Precambrian (Vincent *et al.* 2000). Even in Quaternary glacial cycles, ice covered 11–18% of the Earth's surface and ice-based ecosystems must have been more extensive than at present (Hoffman and Schrag 2000).

The evidence for long-term viability of bacteria, viruses, fungi, and eukaryotes in polar ice is becoming increasingly strong (Castello and Rogers 2005). Whether these organisms are metabolically active at ambient temperatures or merely preserved is not yet clear, but it does seem likely that some organisms trapped in ice during its formation do retain viability and may form part of the early colonists of ice-based systems as they begin to melt. This is another way whereby ice-based systems may form an important intermediary for recolonization of terrestrial habitats during periods of glacial retreat.

Ice-based systems also play a role in the flux of matierals through polar landscapes. Hodson *et al.* (2005) showed how microbial activity within supraglacial freshwater systems on Arctic glaciers could make significant contributions to evolution of the chemistry of water draining glacial surfaces. They attributed the unexpectedly large fluxes of dissolved and particulate organic nitrogen from the glacier surfaces to nitrogen assimilation by microbial communities in cryoconite holes. The only measurement of the productivity of polar cryoconite holes of which we are aware (Säwström *et al.* 2002) indicates that rates of photosynthesis can be at least as high as water from nearby lakes, particularly in hole bottom water, and, whereas individual holes may have small volumes, the possibility that the large area occupied by cryoconite holes on some glaciers may result in substantial total carbon fixation requires further investigation. For the ice-shelf-based ecosystems there is no question that they represent substantial foci for biomass accumulation and productivity, far exceeding that of other habitats with the regions that they occupy.

6.6 Conclusions

In this review a surprising congruity between what are often treated as different types of ice-based system has emerged. We have shown how aquatic ecosystems can develop on and in any kind of perennial ice, most usually in ablation areas of relatively impermeable ice. In many cases, the existence of an aquatic ecosystem is triggered by an exposure of dark material on the ice surface that promotes melting through absorption of solar radiation; the type of system that develops, regardless of type of ice, is determined by the thickness, size, and stability of these sediment deposits. Indeed, there is a such an overlap between ice bubbles, ice-lidded and open cryoconites, ice-covered and ice-free ponds, and ice-bound lotic ecosystems as to make our splitting of these habitats a convenience rather than a reality. All share the seasonal fluctuations between frozen and unfrozen, and the common mechanism of ice formation means that the freeze-concentration effects in gas and salt contents are similar.

Whether ice, water, or land is the 'natural' abode of the organisms that are shared and exchanged with nearby terrestrial, ice-based, and aquatic ecosystems is perhaps an unanswerable and irrelevant question. The dominance of psychrotrophs over psychrophiles (Nadeau *et al.* 2001) supports the view that the ability to tolerate a varied range of habitats rather than to specialize in ice-bound systems is an important trait among the ice community. Our tendency to think of ice-based aquatic ecosystems, even in polar regions, as suboptimal oddities is perhaps more a reflection of our bias as warm-zone, terrestrial animals than a realistic assessment of their niche. It is better to think of these biota as a dynamic group of extremotrophs that are able to occupy whatever habitats are available at any given time. At both poles, and in most kinds of habitat, they are dominated by cyanobacteria, although a wide range of other organisms – including algae, fungi, protists, rotifers, nematodes, and tardigrades – is present. The required characteristics of successful colonists include tolerance of freezing and desiccation (Hawes *et al.* 1992), of high irradiance during summer (usually through synthesis of photoprotective pigments; Vincent *et al.* 1993, 2004a) and in some cases tolerance to high salinities (Hawes *et al.* 1997) and, wherever gas exchange is restricted, high pH (e.g. Fritsen *et al.* 1998). Therefore, similarities among biota between Arctic and Antarctic, glacier, and lake-ice habitats should not be surprising. Cold conditions are neither new nor rare on Earth. In the past they have been more and less widespread, but the ability of organisms to both tolerate the extremes of cold environments and extract sufficient resources from an inhospitable and often isolated habitat to grow and reproduce have clearly enabled them to persist.

This picture of dynamic interaction between land and ice becomes yet more logical when the relative timescales of biological evolution and habitat change are superimposed. Over evolutionary (millennial) time scales the relative abundance of ice and land in both polar regions has undergone substantial change. An example sequence from Victoria Land (Doran *et al.* 1994) is shown below.

- 15 000–10 000 years BP: during the last glaciation there were few if any ice-free areas. The main refuges for microbial life were ice-bound ecosystems (cryoconites, glacial ice ponds, and ice shelves).
- 10 000–5000 years BP: in the early interglacial during glacial retreat from small parts of the continent the ice-free areas would have been colonized from the ice-bound ecosystems by washout from **cryoconite** holes and aeolian dispersal from ice shelves.
- 5000 years BP–present: in mid to late interglacials the above process may be balanced by a 'reverse' colonization of glaciers from aeolian dispersal from ecosystems that have subsequently developed on ice-free land.

Over long time periods we may expect a mixing back and forth of communities between ice-bound systems and ice-free land. A major ecosystem stressor over millennia are the glaciations and it is the ice-bound systems that provide the genetic pools of microbial consortia that allow for ecosystem biogeochemical pathways, and presumably the soil-based systems when the ice retreats. This existing balance in favor of ice-bound systems may be changing rapidly with warming of the polar regions and glacial retreat (e.g. Schiermeier 2004) which will allow a greater diversity of organisms to colonize the ice-free lands and marked changes to existing ecosystems. The consequences for ice-based habitats will be complex and potentially severe, perhaps resulting in elimination from some areas. However, if our hypothesis that the ice biota is less a specialized one and more part of an assemblage of stress-tolerant opportunists which cross-colonize between and across ice- and soil-based systems prove correct, we can expect ice-bound ecosystems to return as soon as ice does. Testing these hypotheses may be significant to our full understanding of whether polar climate amelioration threatens unique ice-based ecosystems or whether there is sufficient long-term resilience to cope with long-term change.

Acknowledgments

Thanks are due to those people, too many to list by name, with whom we have shared experiences of ice-based aquatic ecosystems and have contributed through their support, ideas and stimulating discussions over the years. Many agencies have supported our research; we would particularly acknowledge the New Zealand Foundation for Research, Science and Technology (CO1X0306) and the US National Science Foundation (ANT-0423595). Logistic support has come from the New Zealand and US Antarctic Research Programs and Polar Shelf Canada.

References

Abyzov, S.S. (1993). Microorganisms in Antarctic ice. In Friedmann, E.I. (ed.), *Antarctic Microbiology*, pp. 265–296. Wiley, New York.

Adams, E.E., Priscu, J.C., Fritsen, C., Smith, S.R., and Brackman, S.L. (1998). Permanent ice covers of the McMurdo Dry Valley Lakes, Antarctica: Bubble formation and metamorphism. In Priscu, J.C. (ed.), *Ecosystem Dynamics in a Polar Desert: the McMurdo Dry Valleys, Antarctica*, pp. 281–295. Antarctic Research Series vol. 72. American Geophysical Union, Washington DC.

Agassiz, L. (1847). *Nouvelles études et expériences sur les glaciers actuels leur structure leur progression, et leur action physique sur le sol*. Victor Masson, Paris.

Castello, J.D. and Rogers, S.O. (2005). *Life in Ancient Ice.* Princeton University Press, Princeton, NJ.

Christner, B.C., Kvitko, B.H., and Reeve, J.N. (2003). Molecular identification of Bacteria and Eukarya inhabiting an Antarctic cryoconite hole. *Extremophiles* **7**, 177–183.

Christner, B.C., Mosley-Thompson, E., Thompson, L.G., and Reeve, J.N. (2005). Classification of bacteria from polar and non-polar glacial ice. In Castello, J.D. and Rogers, S.O. (eds), *Life in Ancient Ice*, pp. 227–239. Princeton University Press, Princeton, NJ.

Debenham, F. (1920). A new mode of transportation by ice: the raised marine muds of South Victoria Land (Antarctica). *Quarterly Journal of the Geological Society of London* **75**, 51–76.

De Smet, W.H. and Van Rompu, E.A. (1994). Rotifera and Tardigrada from some Cryoconite holes on a Spitsbergen (Svalbard) glacier. *Belgian Journal of Zoology* **124**, 27–37.

Doran, P.T., Wharton, Jr, R.A., and Lyons, W.B. (1994) Paleolimnology of the McMurdo Dry Valleys, Antarctica. *Journal of Paleolimnology* **10**, 85–114.

Downes, M.T., Howard-Williams, C., Hawes, I., and Schwarz, A.-M.J. (2000). Nitrogen dynamics in a tidal lagoon at Bratina Island, McMurdo Ice Shelf, Antarctica. In Davison, W., Howard-Williams, C., and Broady, P. (eds), *Antarctic Ecosystems: Models for Wider Ecological Understanding.* Proceedings of the VII SCAR Biology Symposium, pp. 19–25. Caxton Press, Christchurch.

Fernandez-Valiente, E., Quesada, A., Howard-Williams, C., and Hawes, I. (2001). N_2-Fixation in cyanobacterial mats from ponds in the McMurdo Ice Shelf, Antarctica. *Microbial Ecology* **42**, 338–349.

Foreman, C.M., Sattler, B., Mikucki, J., Porazinska, D.L., and Priscu JC. (2007). Metabolic activity and diversity of cryoconites in the Taylor Valley, Antarctica. *Journal of Geophysical Research* **112,** G04S32, doi:10.1029/2006JG000358.

Fountain, A.G., Tranter, M., Nylen, T.H., Lewis, K.J., and Mueller, D.R. (2004) Evolution of cryoconite holes and their contributions to meltwater runoff from glaciers in the McMurdo Dry Valleys, Antarctica. *Journal of Glaciology* **50**, 35–45.

Fountain, A.G., Nylen, T.H., Tranter, M., and Bagshaw, E. (2008). Temporal variations in physical and chemical features of cryoconite holes on Canada Glacier, McMurdo DryValleys, Antarctica. *Journal of Geophysical Research* **113**, G01S92, doi:10.1029/2007JG000430.

Fritsen, C.H. and Priscu, J.C. (1998). Cyanobacterial assemblages in permanent ice covers on Antarctic lakes: distribution, growth rate and temperature response to photosynthesis. *Journal of Phycology* **34**, 587–597.

Fritsen, C.H., Adams, E.E., McKay, C.P., and Priscu, J.C. (1998), Permanent ice covers of the McMurdo dry Valleys lakes, Antarctica: Liquid water contents. In Priscu, J.C. (ed.), *Ecosystem Dynamics in a Polar Desert: the McMurdo Dry Valleys, Antarctica*, pp. 269–280. Antarctic Research Series vol. 72. American Geophysical Union, Washington DC.

Gordon, D.A., Priscu, J.C., and Giovannoni, S. (2000). Origin and phylogeny of microbes living in permanent Antarctic lake ice. *Microbial Ecology* **39**, 197–202.

Gribbon, P.W. (1979). Cryoconite holes on Sermikaysak, West Greenland, *Journal of Glaciology* **22**, 177–181.

Grongaard, A., Pugh, P.J.A., and McInnes SJ. 1999. Tardigrades and other cryoconite biota on the Greenland Ice Sheet. *Zoologischer Anzeiger* **238**, 211–214.

Hawes, I. (1991). Airborne propagule sampling on the McMurdo Ice Shelf, 1990/91 – a comparison of samplers. *BIOTAS Newsletter* **6**, 7–10.

Hawes, I., Howard-Williams, C., and Vincent, W.F. (1992). Desiccation and recovery of Antarctic cyanobacterial mats. *Polar Biology* **12**, 587–594.

Hawes, I., Howard-Williams, C., and Pridmore, R.D. (1993). Environmental control of microbial biomass in the ponds of the McMurdo Ice Shelf, Antarctica. *Archiv für Hydrobiologie* **127**, 271–287.

Hawes, I., Howard-Williams, C., Schwarz, A.-M.J., and Downes, M.T. (1997). Environment and microbial communities in a tidal lagoon at Bratina Island, McMurdo Ice Shelf, Antarctica. In Battaglia, B., Valencia, J., and Walton, D. (eds), *Antarctic Communities: Species, Structure, and Survival*, pp. 170–177. Cambridge University Press, Cambridge.

Hawes, I., Smith, R., Howard-Williams, C., and Schwarz, A.-M.J. (1999). Environmental conditions during freezing, and response of microbial mats in ponds of the McMurdo Ice Shelf, Antarctica. *Antarctic Science* **11**, 198–208.

Heywood, R.B. (1977). Limnological survey of the Ablation Point area, Alexander Island, Antarctica. *Philosophical Transactions of the Royal Society of London Series B Biological Sciences* **279**, 39–54.

Hobbs, W.H. (1911). *Characteristics of Existing Glaciers.* Macmillian Co., New York.

Hodgson, D.A., Doran, P.T., Roberts, D., and McMinn, A. (2004). Paleolimnological studies from the Antarctic and sub antarctic islands. In Pienitz, R., Douglas, M.S.V., and Smol, J.P. (eds), *Long-term Environmental Change in Arctic and Antarctic Lakes*, pp. 419–474. Springer, Dordrecht.

Hodson, A.J., Mumford, P.N., Kohler, J., and Wynn, P.M. (2005). The high Arctic glacial ecosystem: new insights from nutrient budgets. *Biogeochemistry* **72**, 233–256.

Hoffman, P.F. and Schrag, D.P. 2000. Snowball Earth. *Scientific American*, **68**, 68–75.

Hoffman, P.F., Kaufman, A.J., Halverson, G.P., and Schrag, D.P. (1998). A Neoproterozoic snowball Earth. *Nature* **281**, 1342–1346.

Howard-Williams, C. and Hawes I. (2007) Ecological processes in Antarctic inland waters: interactions between physical processes and the nitrogen cycle. *Antarctic Science* **19**, 205–217.

Howard-Williams, C., Pridmore, R., 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. *Antarctic Science* **1**, 125–131.

Howard-Williams, C., Pridmore, R.D., Broady, P.A., and Vincent, W.F. (1990). Environmental and biological variability in the McMurdo Ice Shelf ecosystem. In Kerry, K.R. and Hempel, G. (eds), *Antarctic Ecosystems: Ecological Change and Conservation*, pp. 23–31. Springer Verlag, Berlin.

Isaac, P. and Masli, D. (1991). *Physical Hydrology of the McMurdo Ice Shelf.* Science Report to the New Zealand Antarctic Research Programme. Antarctica New Zealand, Christchurch.

James, M.R., Pridmore, R.D., and Cummings, V.J. (1995). Planktonic communities of melt pools on the McMurdo Ice Shelf, Antarctica. *Polar Biology* **15**, 555–567.

Jungblut, A.-D. *et al.* (2005). Diversity of cyanobacterial mat communities in three meltwater ponds of different salinities, McMurdo Ice Shelf, Antarctica. *Environmental Microbiology* **7**, 519–529

Kellogg, D.E. and Kellogg, T.B. (1987). Diatoms of the McMurdo Ice Shelf, Antarctica: implications for sediment and biotic reworking. *Palaeogeography, Palaeoclimatology and Palaeoecology* **60**, 77–96.

Kikuchi, Y. (1994). *Glaciella*, a new genus of freshwater *Canthyocamyidae* (*Copepoda Harpacticoida*) from a glacier in Nepal, Himalayas. *Hydrobiologia* **292/293**, 59–66.

Kohshima, S. (1984). A novel cold-tolerant insect found in a Himalayan glacier. *Nature* **310**, 225–227.

Lancaster, N. (2002). Flux of eolian sediment in the McMurdo Dry Valleys, Antarctica: a preliminary assessment. *Arctic, Antarctic and Alpine Research* **34**, 318–323.

Margesin, R., Zacke, G., and Schinner, F. (2002). Characterization of heterotrophic microorganisms in alpine glacier cryoconite. *Arctic, Antarctic and Alpine Research* **34**, 88–93.

Maurette, M., Hammer, C., Brownlee, D.E., Reeh, N., and Thomsen, H.H. (1986). Traces of cosmic dust in the blue ice lakes of Greenland. *Science* **233**, 869–872.

McIntyre, N.F. (1984). Cryoconite hole thermodynamics. *Canadian Journal of Earth Sciences* **21**, 152–156.

Moorhead, D.L. *et al.* (1999). Ecological legacies: Impacts on ecosystems of the McMurdo Dry Valleys. *Bioscience* **49**, 1009–1019.

Mountfort, D.O., Kaspar, H.F., Asher, R.A., and Sutherland, D. (2003). Influences of pond geochemistry, temperature and freeze-thaw on terminal anaerobic processes occurring in sediments of six ponds of the McMurdo Ice Shelf, near Bratina Island, Antarctica. *Applied and Environmental Microbiology* **69**, 583–592.

Mueller, D., Vincent, W.F., Pollard, W.H., and Fritsen, C.H. (2001). Glacial cryoconite ecosystems: A bipolar comparison of algal communities and habitats. *Nova Hedwigia* **123**, 173–197.

Mueller, D.R., Vincent, W.F., and Jeffries, M.O. (2003). Ice shelf break-up and ecosystem loss in the Canadian high Arctic. *Eos* **84**, 548–552.

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.

Nadeau, T., Millbrandt, E.C., and Castenholz, R.W. (2001). Evolutionary relationships between cultivated Antarctic Oscillatorians (cyanobacteria*). Journal of Phycology* **37**, 650–654.

Nkem, J.N. *et al.* (2006). Wind dispersal of soil invertebrates in the McMurdo Dry Valleys, Antarctica. *Polar Biology* **29**, 346–352.

Parker, B.C., Simmons, G.M., Wharton, R.A., Seaburg, K.G., and Love, F.G. (1982). Removal of organic and inorganic matter from Antarctic lakes by aerial escape of blue-green algal mats. *Journal of Phycology* **19**, 72–78.

Paterson, W.S.B. (1994). *The Physics of Glaciers*, 3rd edn. Pergamon, Oxford.

Pearl, H.W. and Pinckney, J.L. (1996). Ice aggregates as a microbial habitat in Lake Bonney, dry valley lakes, Antarctica: nutrient-rich microzones in an oligotrophic ecosystem. *Antarctic Journal of the United States* **31**, 220–222.

Priscu, J.C. and Christner, B.C. (2004). Earth's icy biosphere. In Bull, A. (ed.), *Microbial Diversity and Bioprospecting*, pp. 130–145. ASM Press. Washington DC.

Priscu, J.C. *et al.* (1998). Perennial Antarctic lake ice: an oasis for life in a polar desert. *Science* **280**, 2095–2098.

Reynolds, J.M. (1981) Lakes on George VI Ice Shelf, Antarctica. *Polar Record* **20**, 435–432.

Säwström, C., Mumford, P., Marshall, W., Hodson, A., and Laybourn-Parry, J. (2002). The microbial communities and primary productivity of cryoconite holes in an Arctic glacier (Svalbard 79° N), *Polar Biology* **25**, 591–596.

Schiermeier, Q. (2004). Greenland's climate, a rising tide. *Nature* **428**, 114–115.

Sharp, R.P. (1949). Studies of superglacial debris on valley glaciers, *American Journal of Science* **247**, 289–315.

Shepherd, A., Wingham, D., Payne, T., and Skvarca, P. (2003). Larsen Ice Shelf has progressively thinned. *Science* **302,** 856–859.

Suren, A. (1990). Microfauna associated with algal mats in melt pools of the Ross Ice Shelf. *Polar Biology* **10**, 329–335.

Swithinbank, C. (1970). Ice movement in the McMurdo Sound area of Antarctica. *Proceedings of the International*

Symposium on Antarctic Glaciological Exploration, pp. 472–486. International Association of Scientific Hydrology, Ghentbrugge.

Takeuchi, N., Kohshima, S., Yoshimura, Y., Seko, K., and Fujita, K. (2000). Characteristics of cryoconite holes on a Himalayan glacier, Yala Glacier Central Nepal. *Bulletin of Glaciological Research* **17**, 51–59.

Thomsen, H.H. (1986). Photogrammetric and satellite mapping of the margin of the inland ice. West Greenland. *Annals of Glaciology* **8**, 164–167.

Tranter, M. *et al.* (2004). Extreme hydrochemical conditions in natural microcosms entombed within Antarctic ice. *Hydrological Processes* **18,** 379–387.

Vincent, W.F., Downes, M.T., Castenholz, R.W., and Howard-Williams, C. (1993). Community structure and pigment organisation of cyanobacteria-dominated microbial mats in Antarctica. *European Journal of Phycology* **28**, 213–221.

Vincent, W.F. and Howard-Williams, C. (1994). Nitrate-rich inland waters of the Ross Ice Shelf region, Antarctica. *Antarctic Science* **6**, 339–346.

Vincent, W.F. and James, M.R. (1996). Biodiversity in extreme aquatic environments: lakes, ponds and streams of the Ross Sea sector, Antarctica. *Biodiversity and Conservation* **5**, 1451–1471.

Vincent, W.F., Mueller, D., and Bonilla, S. (2004a). Ecosystems on ice: the microbial ecology of the Markham Ice Shelf in the high Arctic. *Cryobiology* **48**, 103–112.

Vincent, W.F., Mueller, D., Van Hove, P., and Howard-Williams, C. (2004b). Glacial periods on early Earth and implications for the evolution of life. In Seckbach, J. (ed.), *Origins: Genesis, Evolution and Diversity of Life*, pp. 483–501. Kluwer Academic Publishers, Dordrecht.

Vincent, W.F. *et al.* (2000). Ice shelf microbial ecosystems in the high Arctic and implications for life on snowball Earth. *Naturwissenschaften* **87**, 137–141.

Von Drygalski, E. (1897). *Grønland-Expedition der Gesellschaft für Erdkunde zu Berlin 1891–1893*. W.H. Kuhl, Berlin.

Wait, B.R., Webster-Brown, J.G., Brown, K.R., Healy, M., and Hawes, I. (2006). Chemistry and stratification of Antarctic meltwater ponds I: Coastal ponds near Bratina Island, McMurdo Ice Shelf. *Antarctic Science* **18**, 515–524.

Wharton, Jr, R.A., Vinyard, W.C., Parker, B.C., Simmons, Jr, G.M., and Seaburg, K.G. (1981). Algae in cryoconite holes on Canada Glacier in Southern Victoria Land, Antarctica. *Phycologia* **20**, 208–211.

Wharton, R.A., McKay, C.P., Simmons, G.M., and Parker, B.C. (1985). Cryoconite holes on glaciers. *Bioscience* **35**, 499–503.

Wilson, A.T. (1965). Escape of algae from frozen lakes and ponds. *Ecology* **46**, 376.