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Algae and extreme environments

# Glacial cryoconite ecosystems: A bipolar comparison of algal communities and habitats

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with 7 figures and 1 table

**Abstract:** Meltwaters on glaciers contain a variety of aquatic biota, particularly within the habitat formed by cryoconite holes in the glacial ablation zone. These holes consist of cylindrical cavities filled with meltwater and a basal layer of dark sediment. They are initiated when wind-blown dust gathers in small depressions in the ice and causes vertical melting by absorbing more radiation than the surrounding ice. These holes are typically 10-50 cm deep and provide a suitable habitat for microbial colonization, growth and succession. The communities are complex microbial consortia of heterotrophic bacteria, cyanobacteria, eukaryotic algae, and protists, and may also contain micro-invertebrates such as tardigrades and rotifers. We undertook a bipolar comparison to evaluate whether there are biogeographical differences between the two polar regions in this type of cryo-ecosystem. Samples were taken from cryoconite holes on Canada Glacier, Taylor Valley, Antarctica (77°37′S, 162°55′E) and on White Glacier, Axel Heiberg Island, Nunavut Territory, Canada (79°27′N, 90°40′W). The two sites have approximately the same mean annual temperature, although the White Glacier has higher summer temperatures. Water from Canada Glacier cryoconite holes contained significantly higher concentrations of ammonia, nitrate and DRP. The pH of White Glacier water was significantly below that for the Canada Glacier meltwaters, possibly reflecting the anthropogenic input of acidic materials via the north polar atmosphere. Communities from Canada Glacier were dominated by cyanobacteria (either Chroococcales or Oscillatoriales). Two species of saccoderm desmids plus oscillatorian cyanobacteria were prominent in White Glacier cryoconite holes. Communities from both glaciers also contained heterotrophic bacteria, flagellates, ciliates, rotifers and tardigrades. These results indicate a high prokaryotic and eukaryotic biodiversity despite the extreme nature of the glacial meltwater habitat.

**Keywords:** Arctic, Antarctic, cryoconite, glacial biology, bipolar, algal habitat, cyanobacteria, polar ecology.

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## Introduction

In 1870 the Swedish explorer A.E. NORDENSKJÖLD coined the term cryoconite during the second Swedish expedition to Greenland (LESLIE 1879). He described being inconvenienced by numerous holes that contained a black powder, and after an examination of the grains, he concluded that this powder was cosmic dust. He chose to name it from the Greek: *kruos* (ice) and *konis* (dust) (GAJDA 1958). Some cryoconite is indeed of cosmic origin (WRIGHT et al. 1996), however, in general, it can be defined as any fine-grained material transported by wind onto ice surfaces. This dust gathers in small depressions in the ice and, due to its lower albedo, it preferentially absorbs solar radiation, melting a vertical hole (SHARP 1947). The hole is thereby filled with melt water and this provides an environment suitable for life to exist (GERDEL & DROUET 1960).

Cryoconite holes are known to occur in the weathering crust of glacial ablation zones (KEELER 1964). They can be very small (< 1 cm) to rather large (1 m) in width and they seldom grow deeper than 60 cm (VON DRYGALSKI 1897, STEINBÖCK 1936). Cryoconite hole distribution within the ablation zone appears to be random and limited solely by the availability of aeolian materials (GERDEL & DROUET 1960). They have been described from polar glaciers at sites in Greenland (POSER 1934), Svalbard, (DE SMET & VAN ROMPU 1994), Canada (ADAMS 1966a, BROCHU 1975), and Antarctica (WHARTON et al. 1985). Cryoconite holes have also been described in temperate glaciers of the Rocky Mountains (MCINTYRE 1984) and the Himalayas (TAKEUCHI et al. 2000).

Between the 1870s and the 1930s, several German glaciologists described cryoconite holes (WEGENER 1930), speculated on mechanisms of hole development (PHILIPP 1912), analyzed the cryoconite grain size and mineralogy (VON DRYGALSKI 1897), and even recognized the significance of this microhabitat for biological activity (STEINBÖCK 1936). During the 1950's, the United States Army investigated routes to drive vehicles up onto the Greenland Ice Cap. To this end, they examined the glaciology of ice ramps in the Thule region (WILSON 1955, NOBLES 1960). As these features were within the ablation zone, cryoconite holes were also described and discussed. Some papers delved into the biology of these holes, listing the species present and hypothesizing that biothermal heat production plays a part in the thermodynamics of these holes (GERDEL & DROUET 1960). Several studies have elucidated the heat budget of cryoconite holes by empirical and modeling approaches (MCINTYRE 1984, PODGORNY & GRENFELL 1996). Other papers have described the fauna associated with some cryoconite holes, showing the presence of rotifers and tardigrades that graze on cyanobacteria and algae (DE SMET & VAN ROMPU 1994).

Studies by WHARTON focused on the occurrence of cryoconite holes on the Canada Glacier, Taylor Valley, Antarctica (WHARTON et al. 1981, 1985). Cryoconite features were described (WHARTON et al. 1985) and the species present were documented (WHARTON et al. 1981). WHARTON hypothesized that reciprocity exists between the Taylor Valley lake/soil communities and the glacier cryoconite communities. Aeolian transport seems to play a role in moving dried biological materials to and from the glacier. Melting glaciers may also deposit biological materials from the cryoconite communities during their retreat and by way of meltwater flow. Cryoconite hole production has also been suggested as a mechanism of accelerated ablation, for example, on the Greenland Ice Cap (LESLIE 1879) and White Glacier, Axel Heiberg Island

(ADAMS 1966b). The latter study also included a preliminary survey of the distribution and biological content of cryoconite holes in the high Arctic.

In the current study, we examined the nature of cryoconite holes as an algal habitat by comparing two glaciers at similar latitudes but in different polar regions. Our aims were to describe the physical, chemical and biological properties of the cryoconite habitats at the two contrasting sites, and to determine whether there are fundamental differences between the Arctic and Antarctica in this type of cryo-ecosystem. Below we first provide a review of the literature concerning the physical dynamics of cryoconite holes and their characteristics as an extreme microbial habitat. We then present our new results from the bipolar comparison.

## Dynamics in the cryoconite environment

An understanding of cryoconite hole form and evolution must precede any further discussion on cryoconite as a habitat. Sediment blows onto glacier surfaces where it collects in small depressions (such as sun cups or thin snow patches), then melts downward into the ice due to its relatively low albedo. In some cases, numerous small, closely spaced cryoconite holes only a few centimetres in width give the glacier surface a 'Swiss cheese' appearance. Over time, the cryoconite holes grow to a maximum diameter of between 46 and 100 cm and a maximum depth of 60 cm (GERDEL & DROUET 1960, NOBLES 1960, ADAMS 1966b). Enlargement may be either through coalescence or by the trapping of more material into the hole. Most of the holes in our study were roughly circular to elliptical, since solar radiation comes from 360 degrees in polar regions. In contrast, non-polar alpine cryoconite holes are 'D' shaped (rounded on poleward side) resulting from more variable solar angles and the effect of daily sunset during the melt season (MCINTYRE 1984).

Since the ablation zone of the glacier is, by definition, downwasting, cryoconite must absorb more energy than the glacier surface itself, in order to grow. For this process to occur at relatively low sun angles, oblique radiation must penetrate white glacier ice, water surfaces, or, cryoconite hole ice-cover to warm the sediment at the bottom (GERDEL & DROUET 1960). Deepening of the hole is carried out via conduction from sediment to subjacent ice, whereas conduction and convection through water could be responsible for enlargement of cryoconite hole girth (SHARP 1947). Most cryoconite holes have a seasonal ice cover, which, being 'black ice', has a lower albedo than glacier ice. This cover allows light to penetrate, while simultaneously reducing the transfer of sensible and latent heat from the hole.

The resulting structure behaves like a greenhouse because ice is relatively impervious to long-wave radiation (OKE 1987). Incoming short-wave radiation then becomes the most important energy flux to the system and is controlled chiefly by the albedo of the admitting surface. The albedo of still water varies greatly with solar angle so it is important to consider that polar regions have small solar angles, which increase water reflectivity (VINCENT 1988). An increase in albedo from the whitening of ice progresses during melting of the ice cover, reversing only when the ice melts completely (FRITSEN et al. 1998).

Once the ice cover is melted, the cryoconite hole can gain more sediment and organisms by trapping wind blown material. Also, melt and rainwater may flow into the hole, and direct lateral inputs may occur through englacial piping. Cryoconite holes can coalesce into bigger holes or become connected by meltwater channels (WHARTON et al. 1985, TAKEUCHI et al. 2000). In an extreme case, this type of growth can result in broad, shallow depressions with

large amounts of sediment. Depending on thickness, the sediment layer can insulate the subjacent ice, preventing further downward melting (Sharp 1949). Once exposed, sediments may be washed off the glacial surface, or may dry up and blow away, initiating more cryoconite holes elsewhere on the glacier.

As solar radiation decreases towards the autumnal equinox, an ice cover forms at the water surface and grows downwards. During the freezing process solutes are rejected because they impede the formation of a regular hexagonal crystal structure. The phenomenon of freeze-out is responsible for concentrating solutes until the temperature drop stabilizes, or the solutes precipitate out and the remaining water freezes (Lock 1990). This process is less effective with faster freezing rates, since solutes do not have a chance to fractionate and can become trapped in bubbles or brine pockets.

Research conducted in two freshwater ponds over an Antarctic winter show increasing salinity in the water column up to values of 189 to 268 mS $cm^{-1}$ (up to 5 times the salinity of seawater). These ponds froze solid in July and August after reaching minimum brine temperatures of –12.1 and –13.0 °C, respectively (Schmidt et al. 1991). An important finding of this research was the continued respiration of the microbial community for at least part of the winter despite these harsh conditions. In contrast, McMurdo Ice Shelf microbial mats appear to freeze quickly with the onset of colder temperatures without appreciable freeze concentration or freezing depression (Hawes et al. 1999). This latter scenario is more likely to be also the case for cryoconite holes.

Water that freezes in the cryoconite holes forms black ice that is easily distinguished from glacier ice. Without solar radiation, winter glacial ablation can only occur via wind-induced sublimation (Fountain et al. 1998). As a result, cryoconite holes will become shallower throughout the dark season due to the lowering of the glacier surface relative to the cryoconite sediment. During the twilight conditions of the shoulder seasons, the extremely high albedo and extinction coefficient of snow keeps the transmission of solar radiation at a minimum and prevents them from melting until the snow cover disappears (Vincent 1988).

As the solar input becomes strong enough to penetrate the ice covering the cryoconite, preferential melting takes place at the sediment-ice contact zone, thereby melting downwards, away from the ice cover, deepening the hole to summer equilibrium level. Sediment will absorb heat faster than ice, due to its lower albedo and heat capacity (Oke 1987). As soon as this material is above the melting point, heat can be conducted to the ice, ultimately causing its phase change to liquid water. The result is a sediment inclusion, immersed in water, surrounded by ice. Since ice is less dense than water, the liquid water will occupy 90% of the resultant cavity, with the remaining head space filled with air.

## Cryoconite holes as an extreme habitat

In spite of the extreme nature of the surface glacial environment, cryoconite holes are known to harbour a variety of life. In part, this is attributable to the seasonal availability of liquid water, although other environmental factors may further limit biological processes in these microcosms. Potentially low levels of nutrients, high levels of light (including UV radiation), freeze concentration of solutes and freeze-thaw cycles are all likely to impede biological processes in such habitats.

One potential problem faced by organisms in the cryoconite habitat is the quantity and quality of light. Photoautotrophic organisms require adequate PAR (400 to 700 nm), yet both autotrophs and heterotrophs are sensitive to the effects of ultraviolet radiation (UVR) (300–400 nm) (VINCENT & QUESADA 1997). Therefore, cryoconite biota may receive excessive UVR, although this effect maybe offset by higher albedos for the shorter wavelengths in ice environments. In polar environments, the added advantage of 24-hour sunlight during the growing season is somewhat offset by low-angle solar radiation. UVR must penetrate ice obliquely and may be largely reflected due to increased albedo, which is enhanced by the radiation's low incidence angles on water and ice surfaces (VINCENT 1988). Organisms contend with high levels of UVR through four basic strategies. The first is avoidance of incoming radiation, which presumes organisms are motile. The second adaptation is screening with pigments that can protect cells from damage (QUESADA et al. 1999). The third mechanism involves quenching reactive oxygen species (e.g., superoxide and hydroxyl radicals) with the assistance of carotenoids. Finally, the organism can attempt to repair damaged DNA and other cellular components by increasing the activity of nucleic acid repair enzymes (VINCENT & QUESADA 1997).

Low concentrations of nutrients create a challenge for cryoconite hole organisms. Relatively high concentrations of nitrates have been reported in snow and snow-derived ice and water (VINCENT & HOWARD-WILLIAMS 1994). Although some sites contain elevated concentrations of nitrogen levels are elevated, the vast majority of cryoconite habitats can be classed as ultra-oligotrophic. A tight recycling of nutrients through a shortened food web composed of microbial autotrophs, heterotrophs and detrivores (i.e., the microbial loop) may help deal with this environmental shortcoming (VINCENT 1988, BELL 1998). In cases where fixed nitrogen levels are low, cyanobacteria capable of nitrogen fixation would be favoured (VINCENT & HOWARD-WILLIAMS 1994), and this nitrogen could eventually become available for the rest of the community through microbial decomposition. No such mechanism exists to increase phosphorus levels ice habitats must rely on phosphorus inputs from atmospheric, hydrologic and mineral sources, making this nutrient a probable limiting factor for the growth of these communities.

Despite the harsh environmental conditions, cryoconite holes harbour a surprising variety of organisms. In general, the dominant organisms in ice habitats are cyanobacteria, typically filamentous mat-formers of the order Oscillatoriales (WHARTON et al. 1981, TAKEUCHI et al. 2000, VINCENT 2000a). However, chlorophytes are also regularly found in these environments along with heterotrophic bacteria, diatoms and fungi (e.g., GERDEL & DROUET 1960, ADAMS 1966a). Ciliate and flagellate protists (some mixotrophic) and even metazoans such as tardigrades and rotifers have been observed in cryoconite (SØMME 1996). The occurrence of a carnivorous rotifer in a cryoconite hole shows that a modest three level trophic hierarchy can exist in an ice habitat (DE SMET & VAN ROMPU 1994). In the Himalayas, a cold-adapted midge was found in the cryoconite environment of the Yala Glacier (KOHSHIMA 1984) and, "ice worms" (the annelid *Mesenchytraeous solifugus*) exist on the glaciers of Alaska and British Columbia (ODELL 1949, MCINTYRE 1984).

The basic similarity between most reported cryoconite habitats is the prevalence of desmids and filamentous cyanobacteria. It has been supposed that cyanobacteria may dominate this environment because of their tolerance to a wide variety of conditions and ubiquitous distribution in aquatic environments and soils of the cold regions (ELSTER et al. 1999, VINCENT

2000a). While other organisms can out-compete cyanobacteria in more clement environments, the stress of an ice habitat favours an autotrophic, slow growing, yet tolerant type of organism. It has been demonstrated that cyanobacteria have appropriate mechanisms to deal with nutrient deficiency (e.g., nitrogen fixation; KOMÁREK & ANAGNOSTIDIS 1989), desiccation (HAWES et al. 1992) and high UVR (e.g., pigmentation, avoidance, etc.) (QUESADA et al. 1999) while they remain tolerant of a wide range of temperatures (i.e., eurythermal; SEABURG et al. 1981, TANG et al. 1997). These characteristics, coupled with the ubiquitous distribution of cyanobacteria, make these organisms a relatively important part of ice habitat communities throughout the world.

Certain species prevalent in cryoconite literature (e.g., *Mesotaenium berggrenii* and *Chlamydomonas nivalis*) are restricted to snow and ice habitat (BROOK 1981). Despite this evidence, there is an apparent rarity of confirmed psychrophiles (growth optimum at < 15 °C) in polar habitats (VINCENT 2000a). While organisms have been isolated from polar environments that are cold adapted, most algal isolates from these regions show temperature-growth relationships that are characteristic of psychrotrophs (SEABURG et al. 1981, TANG et al. 1997). This trend is paralleled by a theoretically low proportion of endemism in polar regions (VINCENT & JAMES 1996, VINCENT 2000b). Since ice habitats can be occupied by tolerant exotic species, there is no expectation that specialization is required and thus endemism should be relatively low. The fact that many of these habitats are seeded by aeolian transport of individuals, either locally or regionally but ultimately long-range, explains how species with growth optima at >15 °C can be delivered to ice habitats and surrounding areas (VINCENT 2000a). This type of dispersal is by no means uniform, giving rise to potentially large differences in ice habitat species composition on a global level. It is therefore interesting to ask to what extent and why these differences occur, bearing in mind issues of climate, transportation, speciation and species tolerance on the local, regional and global scales.

## Site descriptions

For the present study, two sites were selected based on their accessibility and availability of base data. They are examples of glaciers in their respective regions. There is insufficient information to assess how representative these sites might be for each region, however they have no obvious features to suggest that they are anomalous in any way.

## The southern study site

The Canada Glacier (CG) (77°37′S, 162°55′E) is located between Lakes Fryxell and Hoare in Taylor Valley, Antarctica (Fig. 1). This valley is part of the McMurdo Dry Valleys, a rare terrestrial ice free 'oasis' compared to the rest of the continent (MOOREHEAD & PRISCU 1998). The valleys are characterized by perennially frozen lakes, ephemeral streams, soils and glaciers. The lakes harbour luxuriant microbial mats composed of cyanobacteria and diatoms that coat the sediments (PARKER et al. 1981) and highly stratified planktonic communities dominated by flagellates and cyanobacteria. The stream algal communities are frozen and desiccated for much of the year but photosynthesize upon rewetting (HAWES et al. 1992, MCKNIGHT et al. 1999). The soils are considered some of the least productive in the world, yet they are grazed by several species of nematodes (WALL-FRECKMAN & VIRGINIA 1998). The

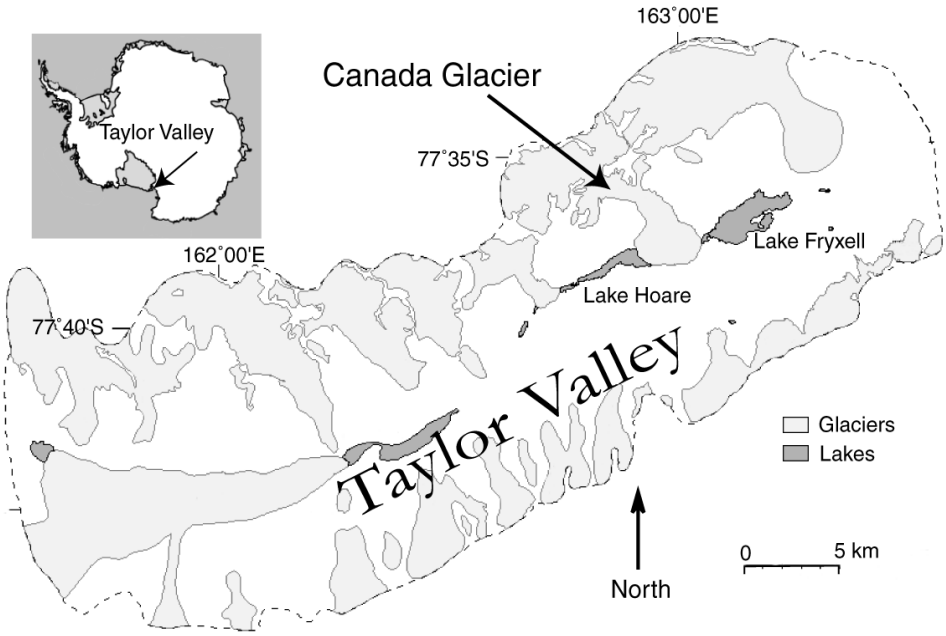


**Fig. 1.** Location of the Antarctic study site. (Modified from McMurdo LTER Display Map)

Dry Valleys are one of the coldest and driest terrestrial habitats on earth, with a mean temperature of –20 °Celsius and a mean annual precipitation of less than 100 mm (FOUNTAIN et al. 1998). Incoming solar radiation is similar to the northern study site owing to the similarity in latitude, however the climate of the Dry Valleys is more continental and often cloud free (ANDREWS 1964, BULL 1966, DANA et al. 1998). These radiation conditions skew the energy balance, as do the strong, yet relatively warm katabatic winds that flow down valley, especially in the winter months (CLOW et al. 1988). These effects combine to lessen the duration of temperature extremes during winter in the Dry Valleys. A total of 159.6 freezing degree-days were recorded on the Canada Glacier during the month prior to sampling (November 24 to December 24). Over this same period thawing degree days amounted to 1.18 (PETER DORAN, unpublished data).

The Canada Glacier is roughly 27 $km^2$ in area, flowing from an accumulation zone (1750–450 m.a.s.l.) in the Asgaard Range south-eastwards (N.B. a southern aspect in the Southern Hemisphere) through a narrow constriction and then onto a wide valley floor. The equilibrium zone is adjacent to a heavily crevassed icefall, below which the ablation zone spreads in a lobate fashion. The glacier terminates with high cliffs (80 m tall; LEWIS et al. 1998). The ablation zone is roughly 3 km wide by 3 km long. It dams both Lake Hoare to the west and Lake Fryxell to the east. For the most part the slope of the ablation zone is a constant and gentle rise (6 %). However, in the southernmost quarter, a series of meltpools lie at the bottom of 30 m depressions (FOUNTAIN et al. 1998). The Canada Glacier, like many glaciers in the Dry Valleys, is advancing (FOUNTAIN et al. 1998).

The Canada Glacier cryoconite holes appeared to be less numerous, larger and deeper than those on the White Glacier. Although they had melted out in previous summers, the vast majority of these holes were ice covered throughout the field season of the present study. Meltwater channels were present during the height of melt, but they were not as widespread as on the White Glacier. Studies reveal that Canada Glacier ablation occurs mainly through sublimation (70 %) rather than the more typical process of melting (FOUNTAIN et al. 1998). This phenomenon likely sets Dry Valley cryoconite holes apart from other cryoconite holes at warmer locations on Earth, such as the Arctic.

## The northern study site

The White Glacier (WG) (79°27′N, 90°40′W) is located at the head of Expedition Fiord on the western side of Axel Heiberg Island, Nunavut Territory, Canada (Fig. 2). The biota of Expedition Fiord includes mammals, birds, plants and insects (BESCHEL 1963, MACPHERSON 1963). The region's valley floors are covered by typical meadow tundra of the High Arctic. Nearby Colour Lake has had a residual ice cover in past years (DORAN et al. 1996), however, unlike Taylor Valley lakes, it contains no cyanobacterial mats (I. HAWES, pers. comm.) likely due to a naturally low pH (SCHIFF et al. 1991). Despite this anomaly, streams in the area have higher pH and do contain cyanobacteria (SHEATH & MÜLLER 1997). Expedition Fiord has a mean annual temperature of −15.2 °C with high summer temperatures that may reach above 10 °C (DORAN et al. 1996). Precipitation in the region is sparse (58 mm to 117 mm at sea level), however, orographic effects cause a higher snowfall on the White Glacier than on the valley floor (COGLEY et al. 1995).

A meteorological station at the McGill Arctic Research Station gives an idea of the weather in the Expedition Fiord area throughout the field season. Caution must be exercised in comparing these data with the Canada Glacier meteorological data since the Expedition Fiord station is located several kilometres from the White Glacier (the White Glacier energy balance would be affected by ice albedo and would therefore be cooler than these temperatures indicate; ANDREWS 1964). During the month prior to sampling (June 11 to July 11), there were 147.5 thawing degree-days and no freezing degree-days (PETER DORAN, unpublished data). The temperatures experienced during this field season appear to be similar to other temperature records for other summers (DIEM 1963, MÜLLER & ROSKIN-SHARLIN 1967, DORAN et al. 1996), therefore, it is assumed that this field season's data are not anomalous in this regard.

The White Glacier has a length of 15 km and a maximum width of 5 km in its accumulation zone. The equilibrium zone lies near 800 m.a.s.l. and from just above this elevation, the glacier narrows as it flows south-eastward (N.B. a southern aspect in the Northern Hemisphere) down a narrow valley to its terminus at 75 m.a.s.l. The ablation zone is approximately 5 km long and roughly 1 km wide with a slope that varies considerably (from 5 to 30 %). In contrast with the Canada Glacier, the White Glacier ends with a steep slope but does not terminate with a vertical cliff. The glacier has been studied since the 1960's and an ongoing mass balance record documents the retreat of the glacier since then (COGLEY et al. 1995). The rapid retreat of the White Glacier is manifested in a shift in ablation and equilibrium zone positions (COGLEY et al. 1995). These changes may be important for cryoconite communities as they respond to the changes in their environment.

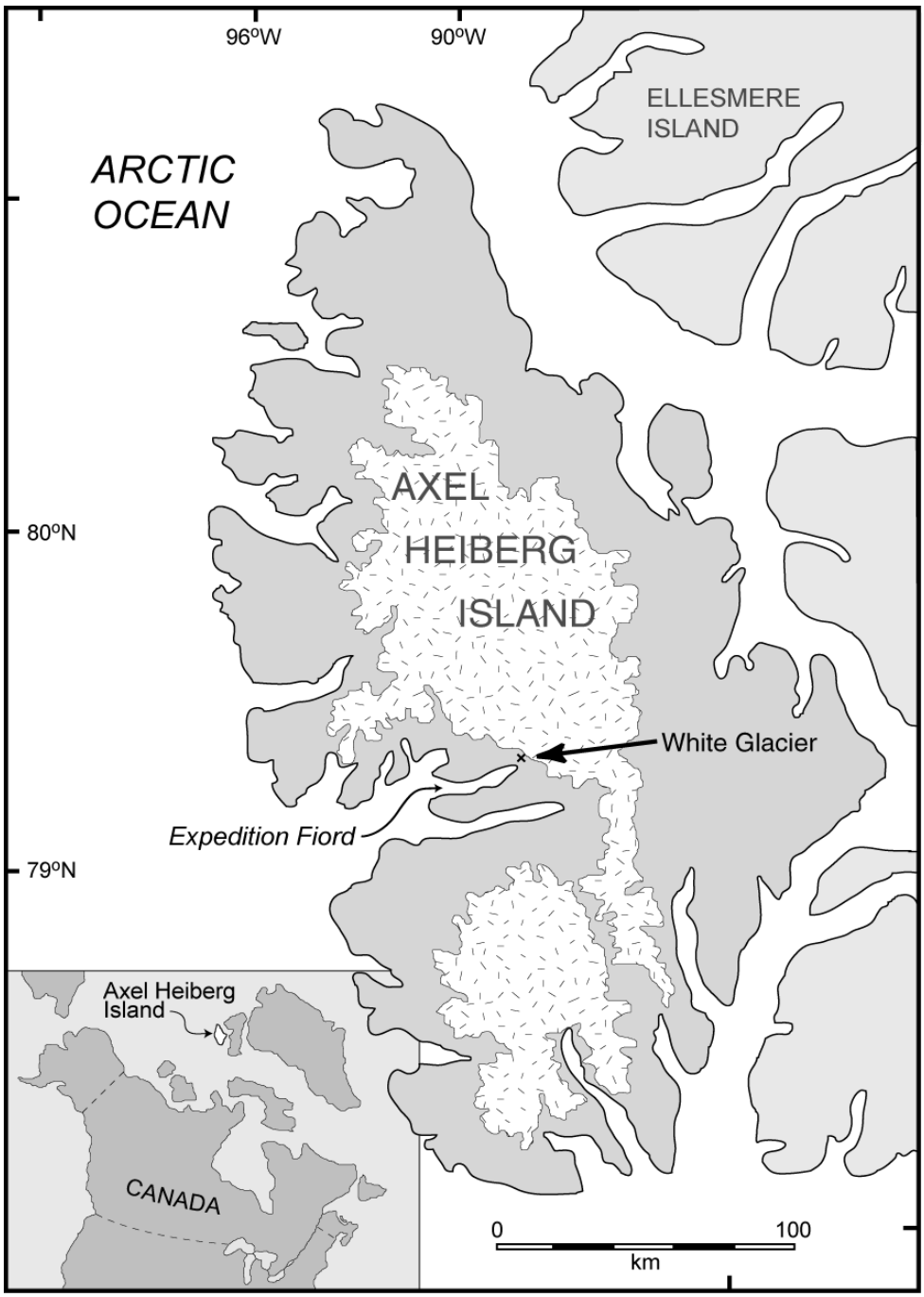


**Fig. 2.** Location of the Arctic study site. Map courtesy of Chris Omelon, Department of Geography, McGill University.

In general, cryoconite holes on the White Glacier were numerous and smaller relative to their southern counterparts and were free of ice for a longer period of summer. In July, large meltwater streams flowing on the glacier surface, many smaller tributary streams and over-glacier sheeting of meltwater were observed. This hydrologic regime kept many cryoconite holes filled with water and may promote the coalescence of holes.

## Methods

Transects were established on the surface of each glacier, one up the middle of the glacier (transect A), the other across the glacier (transect B) (Figs. 3 and 4). Forty samples were taken along transect A, whereas 10 (CG) or 7 (WG) samples were taken on transect B. Cryoconite holes that were less than 10 cm in diameter were excluded from the sampling design, as they did not contain enough water to pump the sediment out of the hole.

When present, ice cover of cryoconite holes was penetrated using a Kovacs hand auger (5 cm in diameter). Cryoconite sediment and water was pumped into a 500 ml HDPE Nalgene bottle (Fig. 5). The sampling equipment was then rinsed with de-ionized water to prevent cross contamination of samples. A tape measure was lowered down from the glacier surface

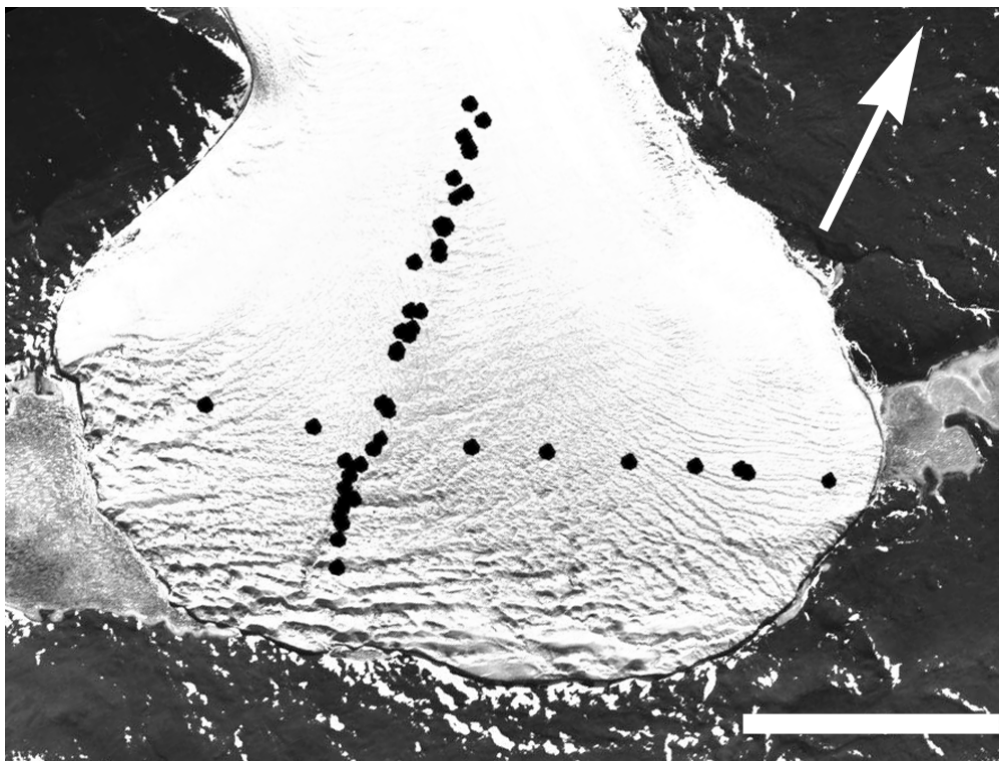

**Fig. 3.** Aerial photograph of the Canada Glacier ablation zone. Dots indicate cryoconite sample locations. [Scale Bar indicates 1 km and arrow indicates north.] (Modified from McMurdo LTER Photo ID: 3083-064, 1993).

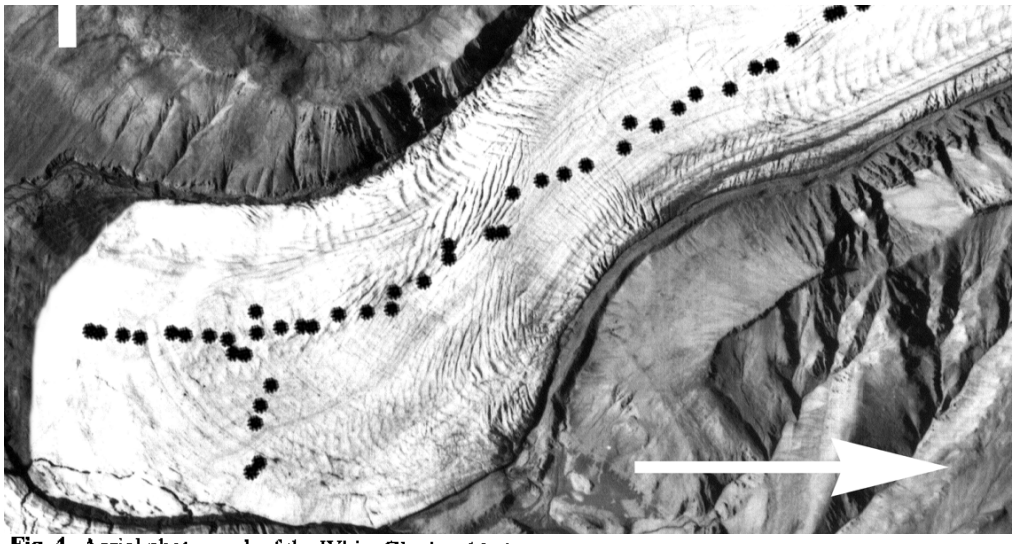

**Fig. 4.** Aerial photograph of the White Glacier ablation zone. Dots indicate cryoconite sample locations. [Scale Bar indicates 1 km and arrow indicates north.] (Modified from National Airphoto Library of Canada, photo number A16864-36, 1959)

to measure the thickness of the ice cover, water level and hole depth. The diameter was also recorded for each hole. The spatial coordinates of each site were obtained by using a hand-held global positioning system (Trimble Geo (CG) and Trimble Flight-Mate (WG)). The units were accurate in the order of 10s of metres in the horizontal and 100s of metres in elevation despite averaging 180 positions.

Percent cover of the cryoconite holes on each glacier was determined by measuring the diameter of all holes that fell within plots taken at different locations on the glacier. On the Canada Glacier, the plot was 78 $m^2$ whereas on the White Glacier a two-dimensional plot was not practical due to the small size of many of the holes. Instead, several linear measurements were made using a tape. The percentage of a measuring tape that was underlain by cryoconite was recorded and four of these 'transects' were averaged to obtain the percent cover for that location.

Each sample was kept chilled (1 to 5 °C) until it could be processed in the lab. Samples were homogenized by shaking then, quickly poured into filter towers containing a glass fibre filter (CG – Whatman GF/F, WG – Whatman GF/C). One filter per sample was immediately frozen for Chlorophyll *a* analysis. The filtered cryoconite water was frozen to preserve it for nutrient analysis. Sub-samples were preserved with buffered formalin (WG) or gluteraldehyde (CG) fixative (1 % final concentration v/v). The pH was taken with an Orion pH probe at each hole on the White Glacier. The pH of Canada Glacier holes was taken in the lab, after sub-sampling, using a Beckman pH probe. Conductivity was measured after sub-sampling for both glaciers. Ammonia, nitrate, nitrite and dissolved reactive phosphorus (DRP) were measured colourmetrically, using an autoanalyzer (Antarctic Support Associates, Crary Lab, McMurdo, Antarctica – CG and National Laboratory for Environmental Testing, Burlington, Ontario, Canada – WG). Detection limits were 2 $\mu g\text{-}N\ l^{-1}$ for Canada Glacier ammonia,

**Fig. 5.** Sampling a cryoconite hole on the White Glacier.

10 µg-N $l^{-1}$ for nitrate, 5 µg-N $l^{-1}$ for nitrite and 2 µg $l^{-1}$ for DRP. For the White Glacier, detection limits were 5 µg-N $l^{-1}$ for ammonia, 10 µg-N $l^{-1}$ for nitrate, 1 µg-N $l^{-1}$ for nitrite and 0.2 µg $l^{-1}$ for DRP. Chlorophyll *a* was determined fluorometrically following extraction in DMSO:acetone (50 % DMSO, 45 % Acetone, 5 % Water; Fritsen & Priscu 1998) using purified *Anacystis* Chlorophyll *a* (Sigma corporation) to calibrate the Turner Designs 10 AU fluorometer. For both glaciers, several samples of cryoconite sediment were dried to constant weight and combusted at 500 °C to determine organic content via loss on ignition.

A known volume from 20 samples for each glacier was scanned using a bright field phase haemacytometer with an improved Neubauer ruling (Hauser Scientific). After concentration by centrifuge, each sample was thoroughly mixed and sub-sampled with a pipette for loading into the counting chamber. Each preparation was scanned prior to counting to assess for an even distribution over the surface of the grid. Preparations were counted at 320 times magnification (NA 1.32) using bright-field illumination on a Leitz Diaplan microscope.

The focus of this study was on cyanobacteria, algae and protists; the presence of heterotrophic bacteria, fungi, rotifers and tardigrades was also noted but these organisms were not quantified. In addition, only living individuals were recorded, which excluded the empty diatom frustules that occurred with some regularity. Individuals were confirmed to have been living (at the time of preservation) by a visible cytoplasm, nucleus or chloroplast.

Due to many problems with the taxonomy of cyanobacteria, (e.g., limited morphological differentiation and the need for high magnification to see diagnostic detail, identification to the species level was not carried out (ANAGNOSTIDIS & KOMÁREK 1985, CASTENHOLZ 1992). Instead, certain morphotypes were recognized and described. Each morphotype may represent a species (*sensu stricto*), a variant/ecophene of a certain species, or may include several species that were morphologically undifferentiated. Species names were assigned to morphotypes if they could be confidently identified (see BROADY 1982, MCKNIGHT et al. 1998). We adopted the cyanobacterial nomenclature of ANAGNOSTIDIS & KOMÁREK (1985), and the diatom nomenclature of KRAMMER & LANGE-BERTALOT (1986).

It was assumed that individuals in each sample were randomly distributed according to the Poisson distribution (VENRICK 1978a). Since these samples contained colonial forms, individual cells were not always enumerated; rather only natural units (colonies or cells, depending on habit) were considered (SMAYDA 1978). Counting proceeded until 400 natural units were enumerated which, according to Poisson theory, would yield a sample error of 10 % (VENRICK 1978a). Each natural unit was measured in at least one dimension from which a biovolume was obtained using standard geometrical formulae (sphere, cylinder, and hemispherical rod). The morphotype biovolume data were used to calculate SIMPSON's diversity index (SIMPSON's D; YOSHIMURA et al. 1997) and provide an overview of species abundance.

It should be noted that this methodology was prone to several different sources of error. Every effort was made to treat each sample in the same manner, however errors are associated with sub-sampling (VENRICK 1978b), with counting (STUDENT 1907, VENRICK 1978a), identification, measurement and extrapolation. Recounting of several samples was undertaken at a higher magnification using a solution of fluorochrome DAPI (4',6-diamidino-2-phenylindole, Sigma Scientific) at 1000 times magnification on an inverted microscope. The total biovolume obtained with the standard method was between 109 to 441 % higher (mean = 192%) than the totals from DAPI recounts (n = 9). In addition, the relative proportions of morphotypes obtained from the recount were different than the previous measurement, although there were no systematic differences. Relative to large differences between cryoconite hole community assemblages, this error did not appear detrimental to the overall conclusions of the study.

## Results and discussion

Both glacial ablation zones in this study contained an abundance of cryoconite habitats. Cryoconite hole percent cover ranged from 0 to 12.2 % in the White Glacier ablation zone (mean = 5.3 %, n = 15 sites), whereas Canada Glacier cryoconite cover was slightly lower ranging from 0 % at the snow line to a maximum of 8.6 % at the lower end of the ablation zone (mean = 3.5 %, n = 5 sites). The average diameter (mean = 38.7 cm, SD = 27.0, n = 50) of Canada Glacier cryoconite holes was larger than White Glacier cryoconite holes (mean = 27.1 cm, SD = 11.1, n = 47) (N.B. average represents holes over 10 cm in diameter). It is important to note that the size distribution of the White Glacier cryoconite holes is positively skewed, resulting in a large number of small holes (< 10 cm) that are under-represented in average dimension measurements. As expected, the average surface area is significantly smaller

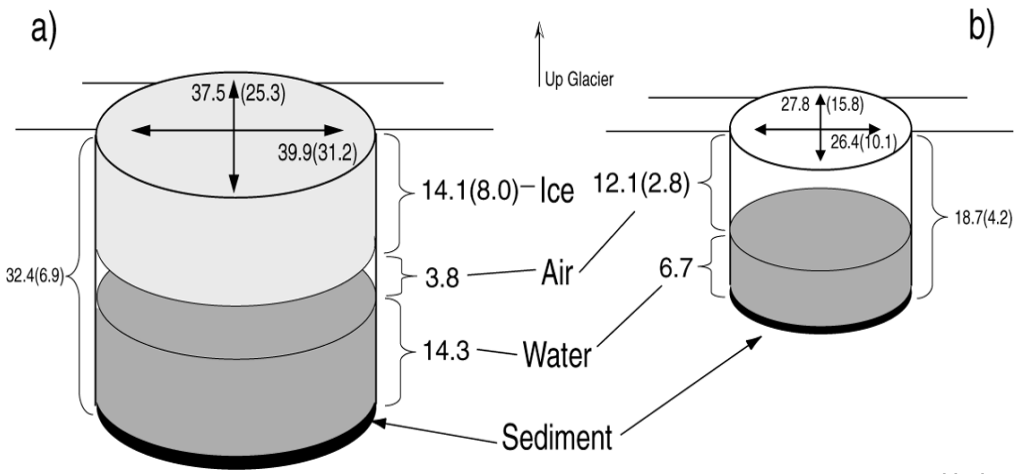


**Fig. 6.** Dimensions of an 'average' cryoconite hole on the Canada Glacier (**6a**) and the White Glacier (**6b**). Each measurement represents the mean of 50 holes for the Canada Glacier and 47 holes for the White Glacier (SD in parentheses). [All measurements are in cm.] Holes less than 10 cm in diameter were excluded from the analysis.

($p = 0.01$) for White Glacier cryoconite holes (639 $cm^2$) than for Canada Glacier holes (1677 $cm^2$). The mean depth of Canada Glacier cryoconite holes was significantly greater than for the White Glacier holes ($p < 0.01$), and the former usually had an ice cover, whereas the White Glacier holes were all open (Fig. 6). This reflects a difference in the energy budget between these two sites. On the Canada Glacier radiative heating of the cryoconite is likely to dominate, while sensible heat melting through warmer air and moving water would dominate on the White Glacier. The differences in heat exchange are indicated by the morphology of White Glacier holes, which show evidence of coalescence as multi-leveled basal ice inter-spaced with small pinnacles. All White and Canada Glacier cryoconite hole dimensions were within literature values.

Nutrient levels were low and often below detection limits (especially for Canada Glacier nitrite and White Glacier ammonia and nitrate) pointing to the oligotrophic status of the holes (Fig. 7). The Canada Glacier cryoconite water was similar in nutrient levels to those previously measured on the glacier face (ammonia 16.0 μg-N $l^{-1}$, nitrate 17.8 μg-N $l^{-1}$, DRP 4.0 μg $l^{-1}$) and icicle meltwater (ammonia 17.3 μg-N $l^{-1}$, nitrate 95.8 μg-N $l^{-1}$, 6.0 DRP μg $l^{-1}$) (Howard-Williams et al. 1986).

Contrary to expectations, White Glacier cryoconite water contained lower concentrations of nutrients (with the exception of nitrite) than the Canada Glacier (Fig. 7), which may be due to the flushing or dilution effect brought about by increased meltwater production. The Canada Glacier cryoconite holes, which had relatively little interaction with meltwater, were also covered with an ice cover that expelled a certain amount of nutrients during freezing. These two reasons are also likely to have been responsible for the high conductivity of Canada Glacier cryoconite water, which was more than twice that of the White Glacier on average (Fig. 7).

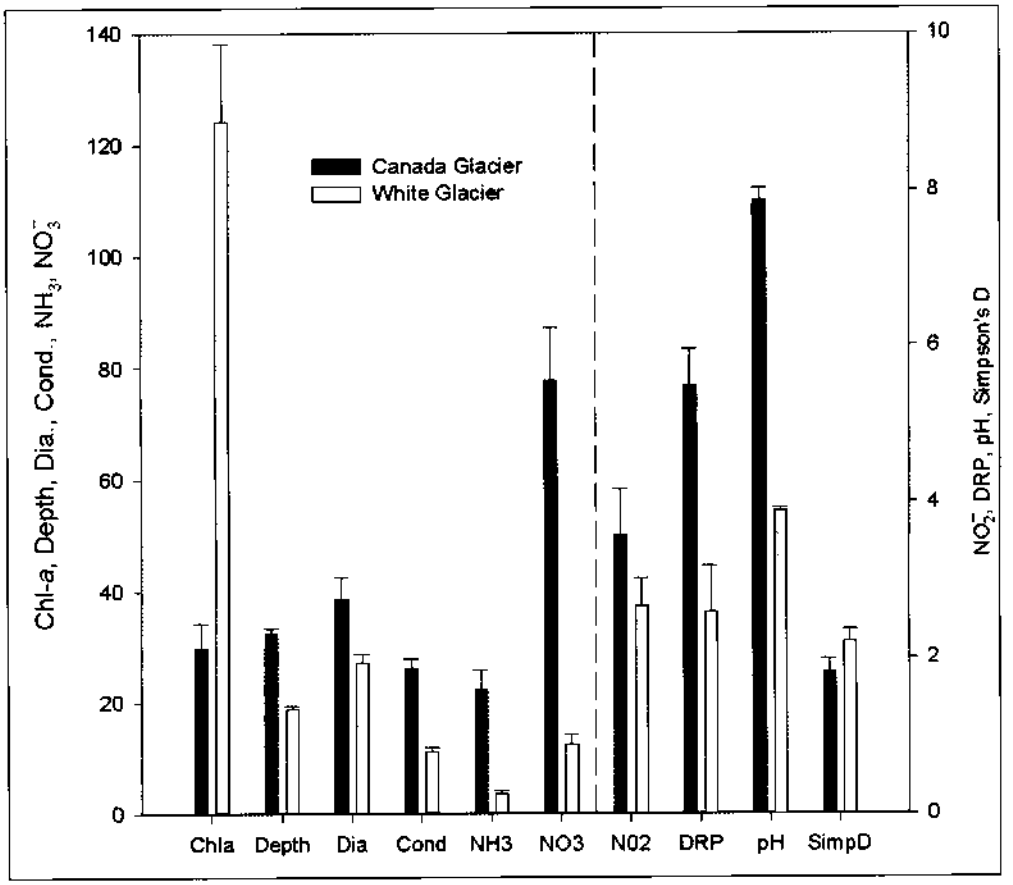


**Fig. 7.** Mean values of cryoconite hole properties in the Canada and White Glaciers. Error bars indicate SE. Chla = Chlorophyll *a* [µg $l^{-1}$], Depth = Cryoconite hole depth [cm], Dia = Cryoconite hole diameter [cm], Cond = Conductivity [µS $cm^{-1}$], NH3 = $NH_3$ [µg-N $l^{-1}$], NO3 = $NO_3^-$ [µg-N $l^{-1}$], NO2 = $NO_2^-$ [µg-N $l^{-1}$], DRP = DRP [µg $l^{-1}$], SimpD = Simpson's Diversity Index. For ammonia, nitrate, nitrite, DRP and conductivity, the sample size was 50 for Canada Glacier and 20 for White Glacier. Depth, diameter and pH were measured for 50 holes on the Canada Glacier and for 47 holes on the White Glacier. Chlorophyll *a* sample size was 20 for the Canada Glacier and 47 for the White Glacier. The Simpson's diversity index was computed for 20 samples on each glacier.

The pH of Canada Glacier cryoconite water (mean = 7.9) exceeded ($p < 0.01$) that of the White Glacier (mean = 3.9) by a wide margin (Fig. 7). This marked difference is consistent with pH measurements in other parts of the cryosphere. For example in Antarctica, ponds on the McMurdo Ice Shelf are pH 7–10 (Hawes et al. 1993), and Dry Valley lakes adjacent to Canada Glacier are pH 7–8.9 (Wharton et al. 1993). In high Arctic Canada and Svalbard, pH measurements of cryoconite water and ice shelf surface water were all acidic (pH between 3.8 and 5.0; Adams 1966b, De Smet & Van Rompu 1994, Vincent et al. 2000). This may reflect acid deposition from the Arctic atmosphere (Wadleigh 1996).

A comparison between species found in cryoconite holes from previous studies and the current study is given in Table 1. Both White Glacier (ADAMS 1966b) and Canada Glacier (WHARTON et al. 1981) cryoconite holes have been examined before. The results are listed showing several taxa in common with those found here, but the current study identified more morphotypes from both glaciers than were previously known to occur. Cryoconite holes in the White Glacier contained fewer morphotypes than in the Canada Glacier (Tab. 1). The groups most common in cryoconite holes, in the current and other studies, are cyanobacteria, chlorophytes, and metazoans (Tab. 1). Only the non-polar cryoconite holes contained macroscopic organisms in addition to microalgae and cyanobacteria.

The Canada Glacier cryoconite communities contained a large proportion of coccoid and filamentous cyanobacteria (Tab. 1). These organisms belong to the order Oscillatoriales and were comprised chiefly of *Leptolyngbya* spp., *Phormidium* spp., *Lyngbya* spp. and *Oscillatoria* spp., which were divided into 5 morphotypes according to their size, colour and cross wall visibility. One particularly conspicuous species was *Crinalium glaciale* and a variant, *C. glaciale* var. *helicoides* (BROADY & KIBBLEWHITE 1991). Surprisingly, microscopic examination of the Canada Glacier cryoconite did not reveal a great proportion of *Nostoc* spp. Others have found *Nostoc* spp. in abundance in the Canada Glacier and in the surrounding environment (WHARTON et al. 1981, HOWARD-WILLIAMS et al. 1986). The cryoconite also contained *Chroococcus* sp., *Gloeocapsa* sp., cf. *Aphanothece nidulans*, cf. *Synechococcus aeruginosus* and unidentified coccoid cyanobacteria. *Chlamydomonas* spp. was the only identified chlorophyte, however, there were several different kinds of ciliates and flagellates. While many different diatom frustules were observed, only *Muellaria peraustralis* and *M. meridionalis* were regularly noticed to be living. Rotifers and tardigrades were observed frequently but not identified (Tab. 1).

**Table 1.** Organisms found in cryoconite holes. Presence is indicated by + or the letter corresponding to a study. Numbers indicate the mean percent abundance (by biovolume) of each morphotype found in cryoconite holes on the Canada and White Glaciers (n=20 holes on each glacier; SD in parentheses). Key: a = BROADY 1989a, b = BROADY 1989b, c = BROADY & KIBBLEWHITE 1991, d = WHARTON et al. 1981, e = WHARTON & VINYARD 1983, f = MCINTYRE 1984, g = TACHEUCHI et al. 2000, h = DE SMET & VAN ROMPU 1994, i = ADAMS 1966b, j = VON DRYGALSKI 1897, k = GERDEL & DROUET 1960, l = WILSON 1955. † includes 2 distinct morphotypes, ‡ includes 5 distinct morphotypes, § includes 3 identified species.

| Species/Morphotype | This study | | Other studies | | |
|---|---|---|---|---|---|
| | Canada Gl. | White Gl. | Antarctic | Non-polar Alpine | Arctic |
| **Bacteria** | | | | | |
| Heterotrophic Bacteria | + | + | | | i |
| **Cyanophyta** | | | | | |
| Unidentified cyanobacterial unicell | 0.3 (0.05) | 0.2 (0.28) | | | |
| *Aphanothece* cf. *nidulans* (RICHTER) | 0.9 (1.69) | | | | |
| cf. *Synechococcus aeruginosa* NÄGELI | 6.3 (12.6) | | d | | |
| *Aphanocapsa* sp. | | | | | j |
| cf. *Gloeocapsa* spp. | 11.3 (19.0) † | | b | | j |
| cf. *Microcystis* spp. | 3.8 (11.1) | 1.1 (4.88) | | | |

| Species/Morphotype | This study | | Other studies | | |
|---|---|---|---|---|---|
| | Canada Gl. | White Gl. | Antarctic | Non-polar Alpine | Arctic |
| *Chroococcus* spp. | 20.6 (21.7) | 0.4 (0.69) | | | |
| Oscillatoriales (may include *Oscillatoria* spp., *Lyngbya* spp., *Phormidium* spp., *Leptolyngbya* spp. and *Microcoleus* spp.) | 35.7 (35.5)‡ | 24.1 (19.9)‡ | a b d§ | g † | |
| *Schizothrix heufleri* GRUN. | | | | | k |
| *Schizothrix* sp. | | | | | j |
| cf. *Spirulina* spp. | 2.9 (5.2)† | | | | |
| *Crinalium glaciale* BROADY | 6.8 (12.6) | | c | | |
| *Crinalium glaciale* var. *helicoides* BROADY | 2.11 (5.07) | | c | | |
| *Plectonema nostocorum* BORN. | | | | | k |
| *Homoeothrix* cf. *rivularis* | | | b | | |
| cf. *Scytonema* sp. | | 2.6 (10.4) | | | |
| *Calothrix parietina* (NÄGELI) THURET | | | | | k |
| *Calothrix drygalskiana* BORN. | | | | | j |
| *Anabaena* spp. | 0.3 (0.82)† | | | | |
| *Nodularia harveyana* (THURET) | | | d | | |
| *Nostoc* sp. | | | b | | |
| *Nostoc* cf. *commune* VAUCHER | <0.1 (0.14) | | | | |
| *Nostoc* cf. *punctiforme* (KÜTZING) HARIOT | <0.1 (0.16) | | d | | |
| **Chlorophyta** | | | | | |
| Unidentified chlorophyte | 0.57 (1.07) | 0.5 (1.04) | a | | |
| *Tetracystis* sp. | | | d | | |
| cf. *Chloromonas* sp. | | <0.1 (0.24) | | e | |
| *Chlamydomonas* spp. | 2.0 (3.93) | | d | e f | l |
| *Scotiella* sp. | | | | f | |
| *Palmella* sp. | | | | | j |
| *Cryocystis granulosa* KOL | | | | e | |
| *Actinotaenium cucurbita* WEST | | | | e | |
| *Cylindrocystis brebissonii* (RALFS) DE BARY (Syn. *C. cylindrospora*) | | 44.7 (28.8) | | g | h k |
| *Mesotaenium berggrenii* (WITTROCK) LAGERHEIM (Syn. *Ancylonema nordenskioldii*) | | 22.8 (26.6) | | e g | h k |
| *Raphidonema* sp. | | | | g | |
| cf. *Dictyochloropsis* sp. | | | b | | |
| *Stichococcus bacillaris* | | | b | | |
| *Trochiscia* sp. | | | | | j k |
| *Protococcus nivalis* (BAUER) | | | | | k |
| **Bacillariophyta** | | | | | i |
| *Achnanthes* spp. | | | | e | |
| *Synedra* spp. | | | | e | |
| *Eunotia curvata* (KÜTZ.) LAGERST. var. *curvata* | | | e | | |
| *Gomphonema acuminatum* EHR. | | | | e | |

| Species/Morphotype | This study | | Other studies | | |
|---|---|---|---|---|---|
| | Canada Gl. | White Gl. | Antarctic | Non-polar Alpine | Arctic |
| *Luticola* cf. *gaussii* (HEIDEN) D.G. MANN | <0.1 (0.02) | | | | |
| *Luticola* cf. *murrayi* WEST et WEST | 0.3 (1.18) | | | | |
| *Luticola* cf. *mutica* KÜTZING | <0.1 (0.03) | | | | |
| *Muellaria* spp. in SPAULDING et STOERMER 1997 | 2.8 (7.94) | | | | |
| *Navicula* sp. | | | | | l |
| *Navicula muticopsis* v. HEURCK | | | a | | |
| *Pinnularia cymatopleura* WEST et WEST | | | a | | |
| *Pinnularia hilseana* JAN. var. *hilseana* | | | e | | |
| *Caloneis ventricosa* var. *truncatula* (GRUNOW) | | d | | | |
| **Chrysophyta** | | | | | |
| cf. *Dinobryon* EHRENBERG | <0.1 (0.09) | | | | |
| **Protozoa** | | | | | |
| Heterotrophic flagellates | 0.2 (0.39) | <0.1 (0.01) | | | |
| Ciliates | 3.0 (12.1) | 3.5 (4.39) | | | h |
| *Trachelomonas* sp. | | | | | l |
| **Eumycota** | | | | | |
| Fungi | + | + | | | ik |
| **Metazoa** | | | | | |
| Rotifers | + | + | b | g | h k |
| Tardigrades | + | + | | g | h |
| Nematodes | + | | | | |
| **Other** | | | | | |
| *Mesenchytraeus solifugus* – annelid worm | | | | f | |
| *Glaciella yalensis* – copepod | | | | g | |
| *Diamesa* sp. – insect | | | | g | |
| **Taxon Richness** | 31 | 19 | | | |

White Glacier cryoconite communities also contained filamentous cyanobacteria similar to Canada Glacier cryoconite (Tab. 1). Most of these organisms were under 3 μm in diameter and were identified as cf. *Leptolyngbya* spp. However, there were some Oscillatoriales that were larger in diameter, although they were less abundant (e.g., cf. *Oscillatoria* sp., cf. *Microcoleus* sp., and cf. *Plectonema* sp.). White Glacier cryoconite contained some cf. *Chroococcus* sp. and several different species of ciliates, flagellates, rotifers and tardigrades (unidentified). Diatoms in White Glacier cryoconite were observed very infrequently, and none were observed with chloroplasts. In contrast with Canada Glacier cryoconite, northern cryoconite contained desmids, including *Mesotaenium berggrenii* (synonym = *Ancyclonema nordenskiöldii*; LING et al. 2000) and *Cylindrocystis brebissonii*. Despite a high average abundance, the prevalence of desmids varied between samples from virtually absent to dominant

(Tab. 1). This variation could be due to population dynamics from seasonal desmid blooms, rather than environmental differences between cryoconite holes.

Cryoconite hole community assemblages from both glaciers varied considerably in terms of species relative abundance as shown by the high standard deviations in Table 1. In the Canada Glacier cryoconite holes filamentous cyanobacteria dominated nine, and coccoid cyanobacteria an additional nine, of twenty samples. The remaining two samples contained a high proportion of ciliates and diatoms, respectively. On the White Glacier the majority of cryoconite samples (15/20) were dominated by desmids while the remaining contained a prevalence of filamentous cyanobacteria.

The species observed in the Canada Glacier cryoconite holes were all reported from nearby habitats and, as proposed by WHARTON et al. (1985), there appears to be reciprocity between the cryoconite, terrestrial and lacustrine environments. The absence of *Cylindrocystis brebissonii* in the cryoconite samples is notable. This genus has been reported in the littoral benthic mat of Lake Hoare (SEABURG et al. 1979), seems to be common to northern cryoconite communities (GERDEL & DROUET 1960, TAKEUCHI et al. 2000) yet was never recorded in our Antarctic cryoconite samples.

The White Glacier cryoconite samples are quite similar to other described cryoconite communities in the Northern Hemisphere. This includes the observation of desmids, in particular *Ancylonema nordenskiöldii* and *Cylindrocystis* spp. (GERDEL & DROUET 1960, YOSHIMURA et al. 1997, TAKEUCHI et al. 2000). In addition, most cryoconite literature makes reference to filamentous cyanobacteria, a major constituent of cryoconite communities at both sites in the present study.

Contrary to expectation, the White Glacier cryoconite contained fewer morphotypes than the Canada Glacier. One would surmise that, a greater landmass at high northern latitudes and warmer temperatures would lead to higher biodiversity among northern hemisphere cryoconite communities. There are several possible reasons for this apparent anomaly. Firstly, the available species present in the Dry Valleys might be already tolerant of cryoconite conditions and therefore many of them can live in cryoconite habitat without difficulty. On the White Glacier, lower nutrients, the possible ephemeral nature cryoconite holes and more flushing by meltwaters may create a habitat that only specialists can compete within. In this case, only faster growing filamentous cyanobacteria and desmids may survive, thereby lowering the equitability and apparent species richness.

No significant difference ($p = 0.093$, $n = 20$) in the Simpson's index of diversity existed between the White Glacier and Canada Glacier cryoconite holes (Fig. 7). The values for SIMPSON'S D ranged from 1.3 to 3.5 in White Glacier samples, with a mean of 2.2, (SD = 0.70, $n = 20$). The range for Canada Glacier samples was 0.36 to 3.0 with a mean of 1.8 (SD = 0.74, $n = 20$). In their study of snow algae on the Yala Glacier, Nepal, YOSHIMURA et al. (1997) found species diversity (between 1.1 and 4.3) to be affected by elevation. However, although their study examined a large elevation gradient, spanning from the equilibrium zone to well into the accumulation zone, it did not include the cryoconite environment.

Differences in biological characteristics between the two sites were also indicated by measurements of Chlorophyll *a*. Concentrations of this pigment were significantly ($p < 0.01$) lower on Canada Glacier (mean = 29.6 $\mu g\ l^{-1}$, SD = 20.7, $n = 20$) (White Glacier mean = 124.2 $\mu g\ l^{-1}$, SD = 95.7, $n = 47$, or mean = 0.995 $\mu g\ cm^{-2}$, SD = 0.655, $n = 20$)(Fig. 7). The reason for low biomass in Canada Glacier cryoconite probably stems from the source material: the

soil of Taylor Valley. This terrestrial environment is known to contain extremely low levels of organic materials (Horowitz et al. 1972, Fritsen et al. 2000). It is obvious that cryoconite microhabitat cannot be as clement as the most productive environments in the Dry Valleys, lakes and streams. Despite this, a first order approximation of biomass on the ablation zone of the Canada Glacier is 11 metric tons (based on an average of 45.2 g $m^{-2}$ lost on ignition and the average cryoconite percent cover of 3.5 %). The flow of biomass between glaciers and other Dry Valley ecosystems has not yet been considered important (Moorehead & Priscu 1998). The additive effect of all Dry Valley cryoconite biomass could amount to a previously unaccounted carbon sink/source for the valley ecosystems.

The White Glacier cryoconite biomass is over three times as high on a per unit area basis (mean = 189.6 g $m^{-2}$ loss on ignition). Such figures are in keeping with the overall biological richness of this region relative to the Dry Valleys. The White Glacier's ablation zone may not contain a significant biomass (estimated at 50 metric tons, based on the average percent cover of 5.3 %) as compared to the biomass in the Expedition Fiord area. However, the amount of glacial biomass may be far more important elsewhere in the Northern Hemisphere, such as on the Greenland Ice Cap, or during ice ages, where the proportion of terrestrial habitat to cryoconite habitat was far less than today.

The organic content of the Canada Glacier cryoconite communities was far less than White Glacier communities despite their higher species (morphotype) richness. Many ice habitats and lake benthic environments contain cohesive mats (Parker & Wharton 1985, Vincent et al. 1993). In general, the Canada Glacier microbial consortia are not structured in cohesive mats, likely due to a low biomass value in addition to a relatively lower proportion of mat-forming cyanobacteria. In larger, open cryoconite holes (not sampled due to random selection) a brown, gelatinous mass was observed. However, in the smaller ice-covered holes only loosely bound sand sized particles were observed interspersed with small (< 2 mm) pieces of cohesive mat. White Glacier cryoconite were also devoid of structured microbial mats. This Arctic material consisted of a brown-coloured, cohesive gelatinous mass with a lumpy texture, containing silt sized particles.

Several authors who have studied cryoconite holes have commented on the ephemeral nature of this environment. Whether or not cryoconite holes will endure several days, weeks or seasons seems to depend largely on the melt regime of the glacier surface. Slope, aspect, radiation, precipitation and meltwater have a role to play in the creation and destruction of cryoconite holes (Adams 1966b, Takeuchi et al. 2000). On some stable glaciers, cryoconite holes are thought to remain at least a hundred years, (Nobles 1960) this may be the case for the Canada Glacier, for example. However, for glacial surfaces with high slopes, meltwater production and precipitation, cryoconite holes may only last for days or weeks (Adams 1966b, Takeuchi et al. 2000). Regardless of the age that cryconite holes attain prior to their demise, cryoconite material may become redistributed to form new holes or may exit the glacier.

## Conclusions

Cryoconite holes constitute an important habitat type for extremophilic, cold-tolerant communities in both polar regions as well as in some alpine environments at lower latitudes. Our Arctic-Antarctic comparisons show that cryoconite holes can be physically, chemically and biologically different despite similar, albeit antipodal latitudes.

Wider, deeper and ice covered holes were found in the southern study site (Canada Glacier) relative to the smaller ice-free cryoconite holes from the northern study site (White Glacier). Cryoconite hole water was found to have higher conductivity, pH and nutrients on the Canada Glacier. However, the northern cryoconite holes contained more biomass per unit area and a greater percent coverage than their southern counterparts. A rough estimate of total biomass for the surface of each glacier's ablation zone is 11 metric tons for the Canada Glacier and 50 metric tons for the White Glacier. The cryoconite hole community assemblage from both study sites contained an abundance of filamentous cyanobacteria. However, the southern cryoconite holes were also dominated by coccoid cyanobacteria whereas the cryoconite holes from the northern study site were often dominated by desmids. There were a greater number of taxa observed in the Canada Glacier cryoconite holes relative to the White Glacier cryoconite holes. However, there was no significant difference in Simpson's diversity index between the sites.

The results of this study show that the cryoconite habitats on glaciers from different polar regions show some similarities, but also show some important differences. The energy balance and surface hydrology of each glacier are the likely cause of variations in cryoconite habitat morphology, longevity and chemistry. These factors plus regional biogeography may account for much of the biological differences observed between each glacier's cryoconite communities.

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