Benthic diatom flora in supraglacial habitats: a generic-level comparison

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ABSTRACT. Meltwaters on the surface of glaciers have been identified as hot spots for microbial activity. Records indicate that cyanobacteria and green algae dominate the autotrophic assemblages found in the benthic debris in cryoconite holes. Diatoms are commonly recorded in lentic and lotic ecosystems within polar habitats and, in line with the ubiquity principle for microbial communities, potentially, diatoms should be frequently found in the cryoconite of supraglacial environments. In this study, we cultured debris from cryoconite material collected in Svalbard and Greenland, to promote the growth of diatoms. Diatom generic richness varied between 12 and 17 between sites and was ~5-fold higher than previously reported. Cryoconite supported aerophytic, halophytic, epipelic and bryophilic diatoms, suggesting multiple origins of colonizing cells. Twenty-seven genera were cultured from material that had been frozen (-20°C) for >1 year, indicating their long-term cryotolerance. The diatom flora composition was similar to that recorded in relatively acidic arctic lakes of low conductivity, and bore similarities at the generic level to those from terrestrial/semi-terrestrial moss communities from both the Arctic and Antarctic. As glaciers retreat, the diatom cells residing in cryoconite have the potential to act as seeding agents for a variety of terrestrial and aquatic habitats in proglacial regions and beyond.

INTRODUCTION

In the 1930s, cryoconite holes were identified as sites of biological activity (Steinböck, 1936), and they are now recognized as important 'hot spots' for biogeochemical cycling on the surface of glaciers worldwide (Säwström and others, 2002; Anesio and others, 2009). They support a range of organisms including heterotrophic and phototrophic bacteria, cyanobacteria, algae, heterotrophic protists, nematodes, rotifers and tardigrades (De Smet and Van Rompu, 1994; Mueller and others, 2001; Christner and others, 2003; Porazinska and others, 2004). Microbial propagules are transported to glacial surfaces by various agents including wind, biovectors and water. Local water bodies and soils are often considered to act as a major source of colonizing material (Wharton and others, 1985; Kaštovská and others 2005; Stibal and others, 2006). Microbes dominate the relatively simple truncated food webs of cryoconite ecosystems and share similarities with those communities found in polar lakes (Laybourn-Parry, 2009).

Compared to studies on polar lakes and streams, detailed investigations of the microbial communities from cryoconite holes are relatively limited (e.g. Mueller and others, 2001; Säwström and others, 2002; Christner and others, 2003; Stibal and others, 2006). Species of cyanobacteria and, occasionally, chlorophytes are the most commonly recorded primary producers in these habitats (Vincent, 2000; Mueller and others, 2001; Stibal and others, 2006). The dominance of cyanobacteria in cryoconite holes is explained by their high tolerance to adverse environmental conditions including low nutrient levels, high irradiance, ultraviolet radiation and low temperatures (Mueller and others, 2001). Bipolar differences have been identified in the cyanobacterial and green algal communities of cryoconite holes, which could be related to differences in their abiotic regimes (Mueller and others, 2001). Diatoms are seldom reported in cryoconite material, despite their prevalence in polar lakes and streams where they might experience a similar suite of environmental pressures (Jones, 1996; Spaulding and McKnight, 1999; Mueller and others, 2001; Mueller and Pollard, 2004; Sabbe and others, 2004; Antoniades and others, 2005).

It is commonly thought that freshwater diatom species are widespread, and are capable of growth in a wide variety of environmental conditions. In the microbial world, the much quoted phrases that 'everything is everywhere' and 'the environment selects', put forward by Baas-Becking (1934), have been reviewed more recently, in the context of diatoms, by a number of researchers. Finlay and others (2002) proposed, for instance, that the rate of scale of dispersal of freshwater diatom species is a function of their global abundance. They predict that rare species will be found with additional sampling effort. Therefore, they oppose the view that many diatom species are endemic (Mann and Droop, 1996; Kociolek and Spaulding, 2001; Van de Vijver and others, 2005; Vanormelingen and others, 2008; Vyverman and others, 2010), because it is impossible to prove that they do not occur elsewhere. In this paper, we hypothesize that given their proximity to sources of local propagules, diatoms should be able to settle in cryoconite holes and their composition should reflect that of other local habitats. We hypothesize that the paucity of records of diatom species inhabiting cryoconite holes relates to undersampling. As cyanobacteria or chlorophytes are numerically dominant, diatom frustules may be harder to find in the debris. Given the strong environmental signal provided by diatoms, differences in their assemblages between cryoconite holes may indicate differences in the hydrology and physico-chemical regimes, pertaining to their catchments. A number of investigations have been undertaken on the diatom species assemblages and environmental drivers in

both lentic and lotic water bodies and terrestrial habitats in polar regions over the past few years (e.g. Elster and Komarek, 2003; Sabbe and others, 2003; Bouchard and others, 2004; Jones and Birks, 2004; Vinocur and Maidana, 2010; Vyverman and others, 2010). A number of these studies highlight the problems associated with obtaining comparable taxonomic records due to nomenclatural difficulties and the presence of cryptic and semicryptic diatom species (Mann and Evans, 2007). An alternative approach taken to overcome such difficulties is to analyse assemblages at the level of genus (Verleyen and others, 2009; Vyverman and others, 2010). Recent revisions in the diatom flora have led to splitting of larger genera into a small number of new genera which may provide improved resolution at this level. Here we adopt a generic-level approach to examine the diatom flora in cryoconite from supraglacial habitats in Svalbard and Greenland and draw upon historical diatom records from selected polar habitats to examine spatial relationships.

SAMPLING SITES

Cryoconite holes were sampled in two glaciers in the Kongsfjord region of northwest Spitsbergen (78°53′ N, 12°04′ E), Austre Brøggerbreen and Vestre Brøggerbreen, and two glaciers in Greenland, Frøya Glacier (74°24′ N, 20°50′ W) and the terminus of a small cirque glacier near Zackenberg station (74°30′ N, 20°46′ W). Cryoconite material was placed in sterile Whirl-Pak bags (Nasco, Fort Atkinson, WI, USA) and frozen at –20°C. Prior to analysis, samples of frozen cryoconite from Greenland and Svalbard were removed and gently thawed. All samples were processed using aseptic techniques. Subsamples of untreated material were strewn on microscope slides and examined for diatom cells using light microscopy (Leica DM LB2) at $1000\times$ magnification. The large volume of inorganic debris relative to diatom frustules made direct observations unfeasible. Subsequently, cultures were set up to promote the growth of viable propagules within the debris. Three types of media were prepared to promote the growth of algae and cyanobacteria: Bold's Basal media (Nichols, 1973), Diatom media (Beakes and others, 1988) and BG-11 (Stanier and others, 1971). Slurries of debris in $10\,\mu L$ aliquots were introduced to sterile $40\,mL$ Nunc polystyrene tissue culture flasks (Cole-Palmer, UK) containing $25\,mL$ of selected media. Samples were incubated at $4.0\pm0.2°C$, with light intensity of 20–$60\,\mu mol\,m^{-2}\,s^{-1}$ for a period of 12 weeks. Incubating samples in different media allowed for any potential symbiotic or mutualistic relationships to be supported within the developing microbial community.

Samples were harvested and digested to remove organic material using a saturated potassium permanganate solution and concentrated HCl (Kelly and others, 2007). Subsamples of cleaned material were mounted in Naphrax (Brunel Microscopes Ltd, UK) and examined by light microscopy. Permanent slides were prepared and observed using $100\times$ oil-immersion objective (numerical aperture 1.4) (CEN, 2004). Identification was carried out to the highest possible taxonomic resolution. Images were taken using an Olympus DP70 camera. Undigested samples were used to check cell viability. The primary floras used in this study were Krammer and Lange-Bertalot (1986, 1991, 1997, 2000). Reference was also made to other literature specific to polar regions (Sabbe and others, 2003; Esposito and others, 2008; Van de

Vijver and Mataloni, 2008; Van de Vijver and others, 2010). Comparisons were made between the data obtained in the present study and other datasets of diatom assemblages from selected polar environments. Datasets of benthic diatom assemblages comprised: (1) diatom assemblages of sediment samples from lakes from Svalbard, obtained from the European Diatom Database (http://craticula.ncl.ac.uk/Eddi/); (2) epiphytic terrestrial diatom assemblages from moss samples in Edgeøya, Svalbard (Beyens, 1989); (3) epiphytic diatom assemblages from ponds in Potter Peninsula, King George Island, Antarctica (Vinocur and Maidana, 2010); and (4) diatom assemblages of microbial mats in the Larsemann Hills and Rauer Islands, East Antarctica (Sabbe and others, 2003). The different diatom assemblages were reduced to genus level to examine spatial relationships between the sample sets. Taxonomic revisions followed the recent DARLEQ (Diatoms for Assessing River and Lake Ecological Quality) nomenclature (http://craticula.ncl.ac.uk/DARES/), and generic names were revised where necessary. We are aware that the culturing approach may have promoted the growth of some diatom species relative to others and any analyses based on the relative abundance of the diatoms could be misleading. To offset this problem, we adopted a presence–absence approach to compare samples and for the subsequent application of ordination techniques for the larger datasets. The divisive clustering method of two-way indicator species analysis (TWINSPAN; Hill, 1979) was used to investigate taxonomic structural similarities between the diatom floras of the samples using the Community Analysis Package (CAP version 4.1, Pisces Conservation). A detrended correspondence analysis (DCA; Hill and Gauch, 1980; ter Braak, 1986) was used to examine spatial patterns using the computer program CANOCO version 4.5 (ter Braak and Šmilauer, 2002). Genera recorded in two or fewer samples were removed prior to analysis.

RESULTS

Species composition

Diatoms grew in all of the culture material but grew more abundantly in the Bold's Basal and BG-11 media, along with many species of green algae and cyanobacteria. Only the results for diatoms are presented in this study. Cultured material from each medium type was pooled for subsequent analysis. Diatom species from 27 genera were identified in the material sampled from the cryoconite holes and cirque glacier site (Table 1). The total number of genera ranged from 12 (Frøya Glacier) to 17 (cirque glacier). A number of genera were common to all sites, namely *Achnanthidium*, *Diadesmis*, *Mayamaea*, *Navicula*, *Nitzschia* and *Psammothidium*. Only two species of *Luticola* were identified: *L. nivalis* and *L. ventricosa* (Fig. 1). Three other distinct forms were identified, though they could not be reliably assigned to any species in the literature and could be new taxa for this genus (personal communication from B. van de Vijver, 2010). This genus was restricted to the Greenland cirque glacier. *Diadesmis contenta* (Fig. 1) grew particularly well in the cultured samples from this site but was also found in the material cultured from the three cryoconite hole samples. By contrast, *Psammothidium helveticum* dominated the cultured material from Frøya Glacier and Austre Brøggerbreen. Three species of *Gomphonema*, *G. parvulum*, *G. olivaceoides* and *G. angustatum*, were recorded from Austre

Brøggerbreen, and four species of *Nitzschia* were found: *N. amphibia*, *N. paleaeformis*, *N. paleacea* and *N. palea* var. *debilis* (Fig. 1). The latter species dominated the samples from Vestre Brøggerbreen.

Spatial comparisons

To examine associations between samples, comparisons were made, at the generic richness level, between the diatom assemblages collected from cryoconite material and those identified from previously published work in polar environments, totalling 73 sites. The first split of the TWINSPAN analysis separated the Antarctic lake samples from the rest of the samples, based on the more frequent co-occurrence of *Stauroforma* and *Psammothidium* in the benthic diatom samples taken from Antarctic lakes and more frequent co-occurrence of *Navicula*, *Staurosirella*, *Staurosira*, *Encyonema*, *Caloneis*, *Nitzschia* and *Achnanthidium* at the other sites. In the second quadrat division, all the Svalbard lake samples and the Frøya Glacier sample formed a group (*n* = 24; TWINSPAN group 1), though the glacier sample was borderline in terms of assignment. Genera preferring this group included *Achnanthidium*, *Diatoma*, *Fragilaria*, *Cymbella*, *Encyonema*, *Tabellaria* and *Staurosirella*. The Greenland cirque glacier diatom assemblage and other samples from cryoconite holes formed a second group (TWINSPAN group 2) together with the samples of diatom assemblages from terrestrial mosses in Svalbard and diatoms sampled from both submerged and emergent mosses in three shallow ponds on the Potter Peninsula. Genera preferring TWINSPAN group 2 included *Luticola* and *Muelleria*. The Antarctic lake samples formed two further groups. Samples assigned to TWINSPAN group 3 (*n* = 14) commonly supported *Luticola* and *Stauroneis*, while lakes in group 4 were more typically represented by *Amphora*, *Craticula* and *Planothidium*.

Spatial segregation of the sites is shown in the DCA samples plot (Fig. 2a). The eigenvalues of axes 1 and 2 were 0.551 and 0.152 respectively, and collectively explain 31% of the cumulative percentage variance in the species data. Symbols differentiate the four TWINSPAN groups on the DCA and indicate the clear separation of Antarctic lake sites (open diamonds and circles), to the right of the ordination, from the Arctic lakes to the left (closed diamonds), based on the composition of the diatom assemblages at the generic level. The samples from two of the cryoconite holes in Svalbard, the cirque glacier in Greenland and aquatic and terrestrial moss communities from both the Arctic (coded E1–3) and Antarctica (coded P1–3) occupy a central position on the ordination between the two sets of lake sites (Fig. 2).

The DCA species biplot (Fig. 2b) displays the main variation in the diatom genera. The diatom genera *Craticula*, *Stauroforma*, *Amphora*, *Diadesmis* and *Psammothidium* situated more to the right of the ordination were commonly recorded in the benthic diatom samples in Antarctic lakes. *Craticula*, *Amphora* and *Stauroforma* were not recorded in any of the cryoconite samples analysed in the present investigation from the Arctic cryoconite. Some species common to all the cryoconite samples including *Achnanthidium*, *Nitzschia* and *Navicula* were positioned to the left of centre, along axis 1, and were more commonly found co-occurring in Arctic assemblages. Along axis 2, a number of genera positioned towards the positive and negative end, including *Eunotia*, *Brachysira*, *Surirella*, *Denticula*, *Neidium* and *Diploneis*, were commonly recorded for some of the

Table 1. Genera (with codes recorded in parentheses) from cryoconite in Austre Brøggerbreen (C1) and Vestre Brøggerbreen (C2), Svalbard, and Frøya Glacier (C3) and cirque glacier (RT1), Greenland

Genus	C1	C2	C3	RT1
Achnanthes (Ach)		✔	✔	✔
Achnanthidium (Achn)	✔	✔	✔	✔
Caloneis (Cal)	✔			✔
Cocconeis (Coc)		✔		✔
Diadesmis (Diad)	✔	✔	✔	✔
Diatoma (Diat)	✔			
Encyonema (Ency)	✔	✔		
Eunotia (Euno)			✔	
Fragilaria (Frag)		✔	✔	
Frustulia			✔	
Gomphonema (Gomp)	✔	✔		✔
Hantzschia (Hant)	✔			✔
Kolbesia	✔			✔
Luticola (Luti)				✔
Mayamaea (Maya)	✔	✔	✔	✔
Meridion (Mero)		✔		✔
Muelleria (Muel)				✔
Navicula (Navi)	✔	✔	✔	✔
Nitzschia (Nitz)	✔	✔	✔	✔
Pinnularia (Pinn)	✔		✔	✔
Planothidium (Plan)		✔		
Psammothidium (Psam)	✔	✔	✔	✔
Reimeria		✔		
Sellaphora (Sell)	✔		✔	✔
Stauroneis (Stan)	✔			
Staurosira (Stau)		✔		
Surirella (Suri)	✔			

Svalbard lakes. These genera were notably absent from the Antarctic lake samples, though recorded as occasional or rare in the moss samples in Potter Peninsula. *Surirella* was recorded in Austre Brøggerbreen, and *Eunotia* and *Frustulia* were recorded in the cryoconite from Frøya Glacier, though no records of the other four genera were recorded in other cryoconite material sampled during this study.

DISCUSSION

Generic richness

The number of diatom cells in the raw cryoconite debris was relatively low, necessitating culturing to obtain a sufficient sample size. In studies of diatom species composition, the organic matter usually has to be removed to expose the frustules to obtain the required taxonomic resolution. One of the criticisms of these currently employed methods is that it is impossible to distinguish between living and dead cells. Empty frustules could therefore be included in cell counts. Between 12 and 15 live diatom genera were recorded in the cryoconite holes, and 17 genera were recorded for the cirque glacier. Although some genera were common to all samples, there were differences and, in total, 27 live genera were recorded. These numbers are comparable with mean local and regional numbers of diatom genera recorded from large-scale analyses of lakes in similar latitudes in the Northern Hemisphere (Vyverman and others, 2010), which suggests that cryoconite may support a similar diatom richness to that of surrounding lacustrine environments.
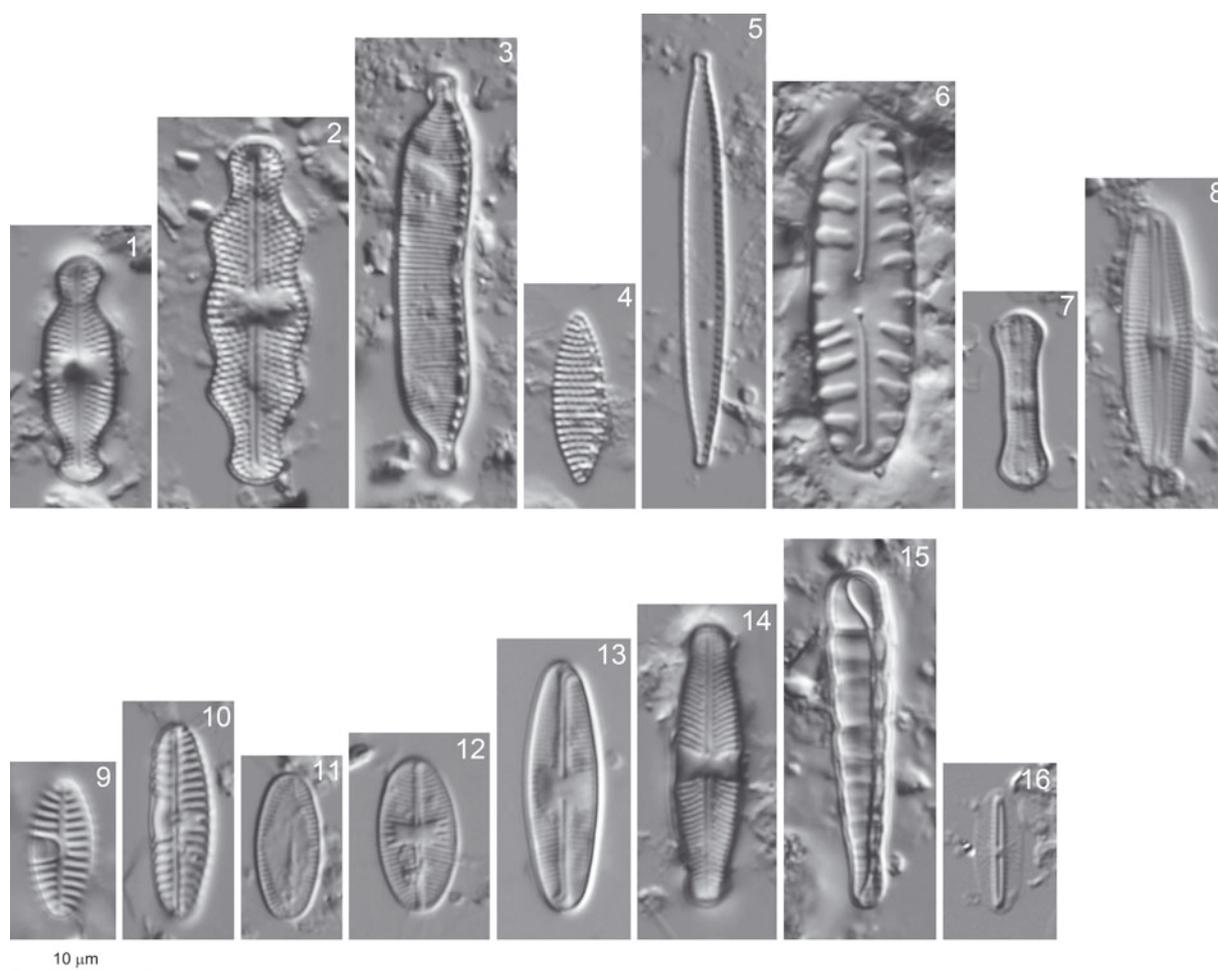
Fig. 1. Selected diatom species isolated from Arctic cryoconite. 1. *Luticola ventricosa*. 2. *Luticola nivalis*. 3. *Hantzschia amphioxys*. 4. *Nitzschia amphibia*. 5. *Nitzschia palea* var. *debilis*. 6. *Pinnularia borealis*. 7. *Diadesmis contenta*. 8. *Muelleria* cf. *terrestris*. 9. *Planothidium frequentissimum*. 10. *Reimeria sinuata*. 11. *Psammothidium marginulata*. 12. *Psammothidium subatomoides*. 13. *Caloneis molaris*. 14. *Stauroneis* (?) sp. 1. 15. *Meridion circulare*. 16. *Mayamaea atomus* var. *permitis*.

The number of live genera recorded was higher than has previously been recorded in cryoconite holes. Mueller and others (2001) found many different diatom frustules in Canada Glacier, McMurdo Dry Valleys, Antarctica, though only species in the genus *Muelleria* were regularly recorded as living. In agreement with this study, a number of species of *Luticola* were noted, though their relative abundance, compared to other algae and cyanobacteria, was low. Seven species of diatom belonging to three genera, *Achnanthes*, *Synedra* and *Gomphonema*, were found in cryoconite holes on North Glacier, Mount Athabasca, Alberta, Canada (Wharton and Vinyard, 1983). In other studies, no diatoms were found (Broady, 1989; Säwström and others, 2002). Pennate diatoms have previously been recorded in cryoconite from the glacial surfaces in Svalbard, but cyanobacteria were found to be numerically dominant compared to microalgae (Stibal and others, 2006), a finding corroborated in other studies (e.g. Mueller and others, 2001). Evidence obtained during this study indicates that cryoconite in Svalbard and Greenland can support a relatively high number of viable diatom genera.

Cell viability and sources of colonizing diatoms

The diatoms and other photosynthetic microbes in the cryoconite samples cultured in this study had previously been frozen (~1–2 years), yet retained their viability.

Freshwater pennate benthic diatoms are frequently recorded to form resting cells that can survive adverse conditions (Sicko-Goad, 1986). In particular, subaerial or aerophytic diatom species that commonly inhabit rock or soil can survive desiccation for long periods of time (Round and others, 1990). A number of diatoms found in the cryoconite during this investigation including species of *Diadesmis*, *Pinnularia*, *Hantzschia and Luticola* are aerophytic. Aerophytic diatoms are less tolerant to desiccation than cyanobacteria (Poulíčková and Hašler, 2007), and moisture content may be crucial to their survival (Van de Vijver and Beyens, 1997). Some species within the genus *Luticola* (e.g. *L. nivalis*) are halophilous and can tolerate more saline conditions which may be experienced in areas of high evaporation. A number of representatives of this genus were recorded on the Greenland cirque glacier, where evaporative losses may be elevated, though they were not recorded elsewhere. Some of the diatom taxa recorded in the cryoconite are commonly recorded on mosses (e.g. *Nitzschia palea* var. *debilis*; *Hantzschia amphioxys*; *Pinnularia borealis*) or are truly epiphytic (e.g. *Planothidium* and *Gomphonema* species (Vinocur and Maidana, 2010)), and cryoconite samples containing these shared a similar location on the ordination plot to those diatom assemblages sampled from aquatic, terrestrial or semi-terrestrial mosses from both the Arctic and Antarctica (Fig. 2a). Other motile,
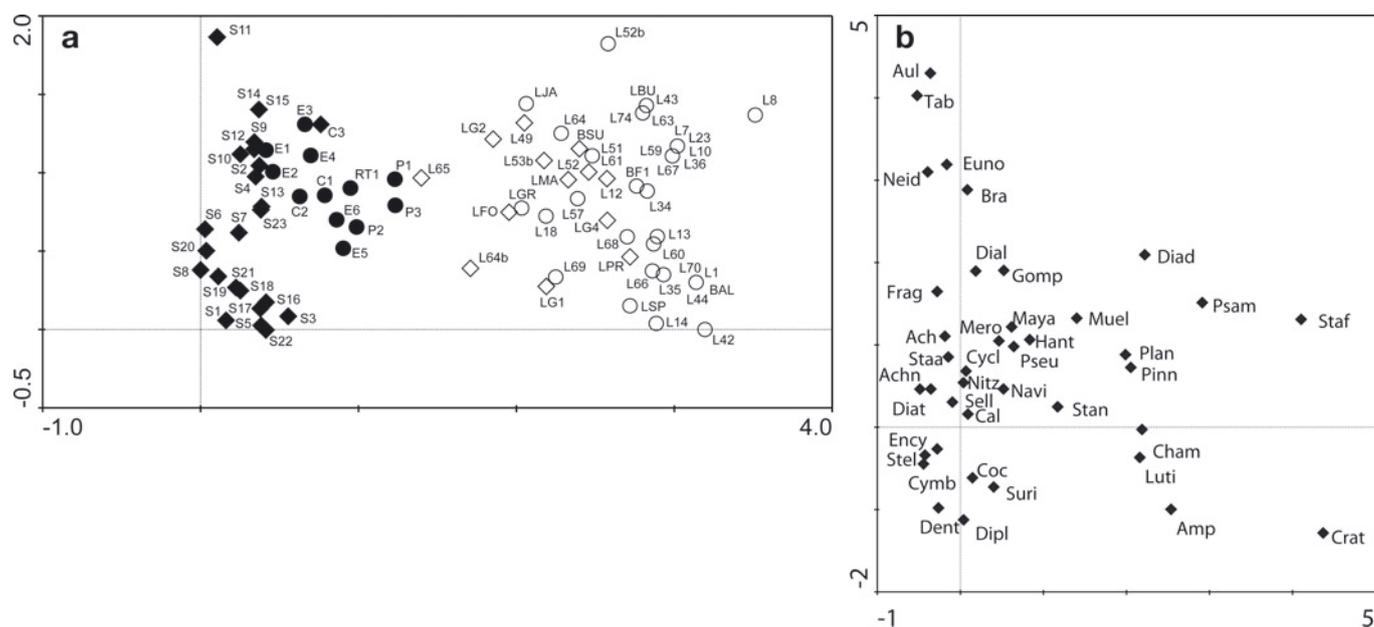
Fig. 2. Detrended correspondence analysis (DCA) of diatom assemblages, analysed at the genus level, showing the first two axes of (a) sample plot and (b) species plot based on their diatom composition. Site codes for the Arctic are: S = Svalbard lakes; E = Edgeøya (Svalbard) terrestrial moss; C and RT1 = cryoconite. Site codes for the Antarctic are: P = Potter Peninusula ponds and L = lakes from Larsemann Hills and Rauer Islands. Symbols reflect four groupings from TWINSPAN analysis: closed diamonds are TWINSPAN group 1; closed circles are TWINSPAN group 2; open diamonds are TWINSPAN group 3; and open circles are TWINSPAN group 4. Taxa codes for diatoms found in cryoconite (see Table 1), with additional codes: Dent = *Denticula*, Crat = *Craticula*, Amp = *Amphora*, Cham = *Chamaepinnularia*, Staf = *Stauroforma*, Aul = *Aulacoseira*, Neid = *Neidium*, Pseu= *Pseudostaurosira*, Bra = *Brachysira*, Staa = *Staurosira*, Cycl = *Cyclotella*, Stel = *Staurosirella*, Cymb = *Cymbella*, Dipl = *Diploneis*, Tab = *Tabellaria*.

epipelic species in the genera *Navicula*, typically associated with lake or stream sediments, were also common in the cryoconite material. The presence of diatoms from a wide range of terrestrial, semi-terrestrial and aquatic sources indicates that cryoconites may act as a reservoir, accumulating a number of diatom species from a variety of local sources. Many of these diatom cells may be growing in conditions that fall outside their optima in terms of environmental preference, which would explain their relatively low abundance compared to other major autotrophic groups. However, their proven viability from the culturing techniques adopted in this study indicates that while diatoms may not be numerically dominant in cryoconite, the debris may contain a number of viable diatom cells. Given the tolerance of many of the diatom genera recorded in the cryoconite to desiccation and/or freezing, these cells could also serve to propagate other areas following ablation.

Comparisons between microbial assemblages in different types of supraglacial habitats indicate variation in the composition and relative abundance of species. Cyanobacteria-dominated cryoconite material and algae (mainly greens) were considered as 'accessory' organisms (Kaštovská and others 2005). Chemical and physical properties were found to be overriding factors determining the fate of microbial cells deposited on the glacial surface (Stibal and others, 2006). It is likely that only those diatom genera capable of tolerating low moisture content, or relatively higher salinity or conductivity (e.g. some species in the genera *Pinnularia* and *Luticola*), may proliferate in soil habitats including vegetated soils (Van de Vijver and Beyens, 1997).

A number of the benthic diatom species recorded in this study (e.g. *Achnanthidium minutissimum, Planothidium lanceolatum, Stauroneis anceps, Encyonema minutum,*

Nitzschia palea), commonly recorded in periphytic communities of lakes and rivers in European waters (King and others, 2006; Kelly and others, 2008), are psychrotolerant rather than obligately cold-tolerant (Seaburg and Parker, 1983), so they should be able to grow well in higher temperatures at lower altitudes and latitudes.

We recorded a number of 'pioneer' species in the cryoconite material belonging to three genera, *Gomphonema* spp., *Achnanthidium* spp. and *Cocconeis* spp., and these species typically represent the starting point in successional processes leading potentially to mature biofilms in lentic and lotic environments (Yallop and Kelly, 2006). Diatom assemblages supporting the latter two of these taxa typify relatively 'pristine' waters indicating a 'reference state', defined by European legislation as sites relatively unimpacted by human activity (Water Framework Directive (WFD; EU, 2000). These pioneer cells are fast colonizers with rapid growth rates and adopt the R-selected life-history strategy (i.e. opportunistic species with high intrinsic growth rates) within a habitat matrix of disturbance frequency and nutrient resource supply (Biggs and others, 1998; Yallop and Kelly, 2006). Typically, in relatively undisturbed habitats, S-selected (i.e. stress-tolerant) species, including more green algae, and cyanobacteria as well as other diatoms, would join the pioneer species once the biomass increased and competition for resources became more intense. Many of these species may be nitrogen fixers (Biggs and others, 1998). An isolated empty frustule of an S-selected diatom, *Rhopalodia gibba*, which contains nitrogen-fixing endosymbionts, was recorded in the material from cryoconite on Vestre Brøggerbreen (Yallop, unpublished data). The window of opportunity for further colonization of the cryoconite holes in the Arctic is limited to a period of weeks during the summer when the cryoconite holes are

open. This period of time may be insufficient to allow for biofilms to reach a more mature stage. Repeated destabilization events and constant physical (e.g. flushing) and biological (e.g. grazing) stress may result in only the R-selected functional group surviving in the cryoconite holes. The unique habitat within the cryoconites may favour the growth of cyanobacteria and green algae, thereby accounting for the relatively low biomass of diatoms.

Origin of diatoms in cryoconite

The diatom assemblages from the cryoconite material bore many similarities, at the generic level, to the assemblages in some of the lakes from Svalbard, which could indicate they were a likely source of propagules for cryoconites. Jones and Birks (2004) found that these lakes were split into three groups, based on the relative abundance of diatoms, at the species level, separated along gradients of pH, alkalinity, concentrations of cations, and conductivity. The diatom assemblages in the cryoconite material shared more similarities with their TWINSPAN group 2 sites which were sites of relatively lower pH, low Ca and lower conductivity. Limnological measurements of meltwaters of glaciers in the Arctic generally indicate acidic conditions of very low conductivity (Remias and others, 2009). The lower pH of cryoconite holes may impose limitations on the growth of species with relatively higher pH optima. These variables have also been found to be important determinants in the spatial distribution of diatom assemblages in other polar habitats (Antoniades and others, 2005; Michelutti and others, 2006). Differences between the diatom assemblages from the cryoconite samples in Greenland and Svalbard may be due to differences in pH and associated correlates of the meltwaters at these sites. The presence of acid-loving genera *Eunotia* and *Frustulia* in the Greenland samples, and their absence from the Svalbard samples, lends further support to this argument. The lack of similarity between the diatom assemblages of the cryoconite material and most of the Antarctic lakes is not surprising given the relatively high chloride concentrations of Antarctic lakes which favoured species like *Craticula*, not recorded in the cryoconite samples taken in this study.

Analysis of debris from the cryoconite on the surface of snow on a Himalayan glacier indicated the presence of some fragments of plant origin (Takeuchi and others, 2001). Moss fragments could come from local aquatic and terrestrial sources and serve as vehicles for diatom transport to cryoconite holes. Additional propagules may arrive from geographically distant sources by aeolian transport. The observation that moss-derived diatom assemblages from Potter Peninsula bore a number of similarities to samples from the Arctic may be indicative of the taxonomic resolution of the study (i.e. generic rather than specific). Ongoing and recent advances in our understanding of the taxonomy and environmental preferences of some of the key taxa inhabiting these environments will help to address these questions (Van de Vijver and Mataloni, 2008; Van de Vijver and others, 2010). The degree of endemism in Antarctic diatom samples is considered to be relatively high, which may be explained by their relative isolation compared with Arctic communities. At the generic level, we identified broadly distinct patterns of site groupings. A generic-level analysis may not work in every situation (Chessman and others, 1999), as some genera (e.g. *Navicula*) contain species with a wide range of ecological tolerance (Lowe, 1974). However, using this higher level of taxonomy is still advantageous, given the degree of difficulty associated with identification of diatoms at the species level and the further complexities of cryptic and pseudo-cryptic species (Mann and Evans, 2007; Vanelslander and others, 2009). In situations where the genera are not particularly speciose, a generic level of analysis may be sufficient to pick up signals of environmental change, as found by Growns (1999), and this may be the case in polar environments. In accordance with Bouchard and others (2004), our findings lend support to the use of these more 'natural groupings' to understand patterns of biogeography and environmental inference.

As glaciers retreat, the diatom cells residing in cryoconite have the potential to act as seeding agents for a variety of terrestrial and aquatic habitats in proglacial sites, which, given the large surface area covered by cryoconite holes, may present a greater contribution than had previously been realized.

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