Dear Tom Battin,

Thank you for handling this manuscript and for your positive feedback. Please see our responses to the reviewer comments and a revised copy of the manuscript identifying the changes below.

Regards,

Ashley Dubnick

Reviewer 1 (Marek Stibal)

First, the results of microbiological analysis should be showed and discussed in more detail (e.g. how many raw sequences were obtained and how did that change after rarefaction; how many OTUs were identified and were the dominant OTUs similar to those of other glacial environments; was microbial abundance in the samples quantified in any way?).

Response: Microbial abundance in the samples were not quantified. We have included a sentence in Methods/Data Processing and Statistical Analyses to include the min (7,608) and max (188,117) number of raw reads per sample and the number of reads after rarefaction (7,608). We also added to the Results/Microbial assemblage the total number of OTUs identified across the rarefied dataset (3,555 OTUs) and material was added to the Discussion/Microbial assemblage to relate dominant OTUs to those identified in other glacial environments and prior literature: "Like glacier ice, the microbial assemblages observed in cold basal ice included Proteobacteria ($\bar{x}$ = 42%), Bacteroidetes ($\bar{x}$ =16%), Actinobacteria ($\bar{x}$ =15%) and Cyanobacteria ($\bar{x}$ = 7.8%) (Table 1). Proteobacteria, Bacteroidetes, Actinobacteria, and Cyanobacteria commonly dominate the microbiome of surface environments such as cryoconite holes (e.g. Cameron et al., 2012), glacier ice (e.g. Christner et al., 2005) and snow (e.g. Harding et al., 2011), and Cyanobacteria, Proteobacteria, and Actinobacteria contain organisms with the potential to photosynthesise (Cameron et al., 2012)." […] "The microbial assemblages observed in warm basal ice were dominated by Proteobacteria ($\bar{x}$ =30%) and Actinobacteria ($\bar{x}$=30%) which are commonly observed in cold ecosystems (Amato et al. 2007; Møller et al. 2013) including those in glacier ice (this study), basal ice (Stibal et al., 2012b; Yde et al., 2010), and subglacial waters (Christner et al., 2006; Rondón et al., 2016). Additionally, the warm basal ice contained a large proportion of Chloroflexi ($\bar{x}$ =8.1%) and Gemmatimonadetes ($\bar{x}$ =3.9%), which are common and active in permafrost soils (Tuorto et al., 2014) and other basal ice environments (Yde et al., 2010) but were significantly less dominant in glacier ice samples in this study (Table 1; T-test, $p<0.05$). Warm basal ice also contained relatively few Bacteroidetes ($\bar{x}$ =9.2%) and Cyanobacteria ($\bar{x}$ =0.07%) which were more abundant in glacier ice (Table 1) and in other surface environments (Cameron et al., 2012; Harding et al., 2011)."

Second, it is a bit unfortunate that the only cold-based glacier sampled had a different bedrock type than the three polythermal glaciers, as it makes the differences between the sites more difficult to explain (bedrock vs. thermal regime effect). This should be acknowledged in the relevant sections of the discussion.

Response: Agreed that this is unfortunate and a significant limitation to the study, which is why we attempted to frame the discussion of the warm and cold basal ice by comparing them to meteoric glacier ice rather than directly to each other. Conveniently, the cold basal ice remained remarkably similar to meteoric glacier ice even though it was surrounded by/overlying a more reactive substrate (sandstone, dolomite and limestone) than the warm-based systems (metasedimentary rocks and gneiss). Thus, the warm basal ice acquired more material from a relatively unreactive substrate while the cold basal ice acquired little material from a reactive substrate. Material on this topic was already integrated in the discussions of

"Inorganic nutrients", "DOM" and "Microbial Assemblages" but additional text was added to the Discussion under 'Chemistry' : "The cold basal ice therefore contained solute concentrations and compositions more similar to those in meteoric glacier ice than warm basal ice, even though the substrate beneath the cold-based ice (local sandstone, dolomite, limestone and conglomerate substrate) is likely far more reactive than the substrate beneath the warm-based glaciers (metasedimentary rocks and gneiss). Therefore, the differences in chemistry between these basal environments cannot be explained by differences in substrate alone."

The text regarding cold basal ice in the conclusion was rewritten to better highlight that the differences in biogeochem can not be fully explained by differences in substrate composition alone: "While basal ice in warm subglacial systems appear to have acquired abundant solutes, microbes and nutrients from the underlying substrate, basal ice produced in cold-based systems acquired few biogeochemical characteristics from the underlying substrate. The cold basal ice explored in this study may have acquired some inorganic and organic nutrients from the substrate, but acquisition of other solutes or microbes appear to be limited. This cold basal ice acquired few solutes and microbes even though the local substrate, composed of sandstone, dolomite and limestone, and relatively well developed soils, would have been more reactive than the metasedimentary and gneiss substrate beneath the warm-based systems."

Last, there is a discrepancy between DOC (both warm and cold basal ice contained more DOC, including proteinaceous material, compared with meteoric ice) and microbial communities (warm basal ice vs. cold basal ice and meteoric ice). This is in my opinion not sufficiently explained in the ms. Is it because solutes are entrained even by cold-based glaciers but particulates are not? Or may it be an effect of bedrock (see above)?

Response: This research indicates that basal processes in warm-based glaciers result in the acquisition of abundant solutes, microbes and nutrients from the substrate (and possibly from in situ processes), but that cold basal ice appeared to have only acquired specific nutrients from the substrate and not microbes or bulk solutes (even though the substrate was more reactive). We can therefore argue that basal temperature likely plays an important role in controlling subglacial biogeochem. However, identifying the detailed processes that result in the biogeochemical intricacies (and contradictions) of cold-basal ice (ie DOC vs microbes) is beyond the scope of this study - we do not have sufficient information to identify detailed substrate characteristics, mechanism(s) of basal ice formation, or in situ processes that may occur so even speculating in any detail would be unconstrained, and as far as we are concerned, there is no obvious explanation. Instead, we have tweaked the last two sentences of the conclusion to explicitly highlight this the gap in our collective understanding of cold-basal ice biogeochem (and that at this field site) and suggest further research be conducted to help answer these pending and fundamental questions that this research has highlighted: "It remains unknown whether the intricacies of the biogeochemical characteristics that were observed in the cold basal ice in this study result from (i) specific characteristics of the underlying/surrounding substrate, (ii) specific glaciological/hydrological processes that occurred during the formation of the cold basal ice, or (iii) the effects of biogeochemical processes that occur *in situ* in cold basal ice. Further research is required to define how the cold basal ice at the Western Margin of the DIC developed, and to better characterize the biogeochemical processes that occur in subglacial environments where liquid water is limited."

Minor comments

260-264 As you didn't specifically look at any microbial functions, the discussion of potential N2 fixation feels a bit out of place here and could be deleted.

Response: Agreed, so this discussion regarding potential N2 fixation was deleted

266-289 Emily O'Donnell (Lawson)'s 2016 in BG was the first detailed study on DOM in basal ice and showed e.g. the importance of bedrock and leaching of DOM in wet conditions at the glacier bed. I think it would be a useful reference for this section.

Response: Agreed. The paragraph regarding DOM substrate and microbial DOM sources was revised/expanded to integrate Lawson et al's (2016) findings "Both warm and cold basal ice contained higher average DOC concentrations (0.49 ppm and 0.40 ppm, respectively) than glacier ice (0.15 ppm) (Table 1) suggesting a potential source of DOC in subglacial systems, as observed in Greenland (Lawson et al., 2016) and Antarctica (Wadham et al., 2012)" and "Humic DOM, and humic-like C3 and C5 fluorescence are commonly associated with soils and vegetation (Cory and McKnight, 2005; Osburn et al., 2016; Stedmon et al., 2003) so it is possible that both the fast and slow-flowing glaciers acquired these compounds by direct (via abiotic leaching) and indirect (via microbial cycling) of material from the substrate. Similar observations were made for low molecular weight DOC compounds in previous studies of basal ice from Greenland (Lawson et al., 2016)."

305 Here, the 2012 Global Change Biology paper would be a more appropriate reference, as the experimental data in Wadham et al. come from it (as the first author of this ms surely remembers: : :).

Response: Sincere apologies to the author of this ms – it has been included instead!

323 There already exist spatially explicit studies of microbial communities in glacial environments, mostly the surface – e.g. Cameron et al. 2016 FEMS, Darcy et al. 2017 FEMS. We also found spatial differences in Disko Island glacier stream assemblages (Zarsky et al. 2018 FEMS). These studies might be worth mentioning here.

Response: Thanks for the suggestion – the paragraph was revised to include reference to these studies: "Geographic location has previously been identified as an important determinant of microbial assemblages across various spatial scales, from meters (Lear et al., 2014) to global (Fuhrman et al., 2008), and within other polar environments including Antarctic and Arctic terrestrial and aquatic habitats (Comte et al., 2016; Yergeau et al., 2007) as well as on glacier surfaces (Cameron et al., 2016) and in subglacial discharge (Zarsky et al., 2018)."

Figure 3 seems to show data already shown in Table 1. If this is the case it may be redundant.

Response: Table 1 contains a summary of important and necessary statistical results that are heavily referenced throughout the text. However, it contains a lot of condensed information so is perhaps difficult for some readers to navigate and discern trends (see comment #7 from Reviewer #2). Therefore Figure 3 was included to provide a visual summary (of scaled results) from which trends can be more easily discerned for the average reader.

Reviewer 2

Methods:

1) The analytical methods, as presented, are relatively sparse, especially in relation to the analytical procedure for SRP, TDN and TDP. It would be useful to include a description of the digests performed and the recovery. It would also be useful to understand if any reference material or standards were used and the outcome of this.

Response: SRP was measured directly as PO_4^{3-} while TDP was digested with potassium persulfate to convert all dissolved P to PO_4^{3-}.TDN was digested with potassium persulfate and sodium hydroxide to convert all dissolved N to NO_3^-/NO_2^-. Analyses were conducted in an ISO17025 accredited laboratory and reference material and standards were applied according to those standards. These details have been added to Methods/Analytical Methods.

Findings:
2) The concentrations reported for DOC in Table 1 appear to be less than the LoD, in numerous cases. Additionally, there is a discrepancy between the LoD cited in text and in the table. Naturally, it is highly problematic if the concentrations reported are lower than the LoD. The statistical differences and comparison between basal and overlying ice, referred to in the results and discussion, would have to be amended. If authors wish to keep DOC data included in this exercise, they need to make it clear to the reader that their DOC data is of good quality, by providing transparent details on the methodology, as well as appropriate use of CRMs.
Response: DOC detection limits were incorrectly reported and have been revised to 0.06 ppm throughout. Five standards between 0 ppm and 2 ppm were used for calibration (R^2=1.0) and the LoD was calculated based on instrument blanks according to methods outlined by Shrivastava and Gupta (2011). These details were added to the Analytical Methods/DOC concentrations.

Writing Style/ Formatting:
3) The abstract and introduction's wording should be tightened to maintain clarity and flow. There is a considerable number of lists. Often lists of factors, studies or processes are lengthy and the point can become lost. Amending this will help the research aim (in line 46) to be stated more clearly. Currently, the importance of this line is lost. The meaning is lost elsewhere, for example in lines 28 through to 31.
Response: The abstract and introduction have been revised and tightened and detailed lists were removed.

4) Additional reference to important literature, especially that relating to microbially mediated chemical weathering, could be made in the introduction. Similarly, the discussion is sparsely referenced, particularly in the first paragraph.
Response: We added Wadham et al (2004) as another example of microbial mediated redox reactions at the bed of glaciers in the Introduction. We also added Price and Sowers (2004) and Hubbard et al (2009) references to the first paragraph of the Discussion/Basal ice formation and a few other references throughout the Discussion including: O'Donnel et al (2016) in reference to subglacial DOM, Cameron et al (2012), Christner et al. (2005), Harding et al., (2001), Yde et al., (2010), Stibal et al (2012)., Rondon et al. (2016) and Tuorto et al. (2014) in reference to microbial assemblages, and Cameron et al (2016) and Zarsky et al (2018) in reference to geographic influence on microbial assemblages. An effort was made to reference review papers and initial seminal research throughout the presentation of high-level interdisciplinary concepts to maintain readability.

5) In the introduction, it would be useful to include a few additional lines on the importance of this study. Why should the broad readership of BG care about this study? I know that the majority of this study may be lost on the readership, due to the intricacy of the comparison specifically relating to glacial systems. As such, the importance of this work for the BG's audience needs to be clarified.
Response: The first and second paragraphs of the introduction were revised to more clearly articulate the importance of this study to the BG community:

"Glaciers form by the compression and metamorphism of snow and slowly deform and flow under their own weight. A considerable portion of a glacier's ice is of meteoric origin and receives chemical and biological inputs primarily from the atmosphere. However, subglacial processes, including melt-freeze events and erosion can result in the production of basal ice near the bed. This basal ice is typically characterized by relatively high concentrations of solutes that are dominated by Ca^{2+}, Mg^{2+}, HCO_3^- and SO_4^{2-} (Tranter, 2007). These solutes are often produced from reactions that involve carbonate and sulphide minerals (Tranter, 2007), which are trace components in most types of bedrock (Holland, 1978). Basal ice can also contain organic matter, nutrients (e.g. phosphorus, silica, potassium) and microbes from the underlying substrate (Montross et al., 2014; Sharp et al., 1999). Both basal ice and subglacial water are known to host populations of microbes that mediate redox reactions (e.g. Sharp et al., 1999; Wadham et al., 2004), play an active role in bedrock weathering (e.g. Tranter et al., 2002), and produce and/or consume ecologically important nutrients (e.g. Bottrell and Tranter, 2002; Boyd et al., 2011; Hodson, 2007; Statham et al., 2008; Tranter et al., 2002; Wadham et al., 2012)

Subglacial processes and the composition of basal ice can dramatically impact the biogeochemistry of meltwater and sediments exported from glaciers in a warming world. For example, in glaciers where surface-derived meltwater drains through the subglacial environment and comes into contact with basal ice, subglacial water and sediments, its geochemistry (Tranter et al., 2002), nutrient content (Hawkings et al., 2014; Wadham et al., 2016) and microbial community composition (Dubnick et al., 2017) are dramatically altered. Direct links have recently been established between subglacial biogeochemical signatures and impacts on downstream environments including downstream freshwater (Sheik et al., 2015) and fjord ecosystem (Gutiérrez et al., 2015). Similarly, during glacial retreat, the biogeochemical material contained in basal ice are released to the terrestrial landscape. These materials have been directly linked to the nutrient dynamics of glacier forefields (Kazemi et al., 2016; Mindl et al., 2007; Sattin et al., 2010) and form the basis of the soils from which many postglacial landscapes evolve (Kastovská et al., 2005)."

6) There is some repetition in the methodology and introduction– especially in relation to the field sampling and the definition of warm/cold basal ice.
Response: Agreed, so repetition regarding field sampling and the definition of warm/cold basal ice was removed from the methods section.

7) Table 1 is rather lengthy and unclear, it may be useful to split the table up into its component parts (chemistry, in/organic nutrients and microbes) or to reformat the table.
Response: The table has been split into its component parts (chemistry, inorganic nutrients, organic nutrients and microbial assemblages):

Table 1: Number, mean and standard deviation of measures of major ions, inorganic nutrients and DOM components in glacier ice, warm basal ice, and cold basal ice and sstatistical tests between warm basal ice/cold basal and glacier ice. P-values that represent significant differences (p<0.05) are red.

	Units	Detection limit	Number			Mean			Standard Deviation			p-value			
			Glacier ice	Warm Basal Ice	Cold Basal Ice	Glacier ice	Warm Basal Ice	Cold Basal Ice	Glacier ice	Warm Basal Ice	Cold Basal Ice	Warm BI vs glacier ice		Cold BI vs glacier ice	
												T-test	F-test	T-test	F-test
Chemistry															
Ionic strength	µeq/L	N/A	11	12	5	15.6	241	22.0	7.13	265	10.4	0.00	0.00	0.17	0.30
SiO_2	ppm	0.02	11	12	5	0.04	0.24	0.04	0.01	0.31	0.00	0.01	0.00	0.75	0.00
Cl^-	µeq/L	0.85	11	12	5	2.92	9.10	5.25	1.14	16.5	2.30	0.17	0.00	0.02	0.07
SO_4^{2-}	µeq/L	0.83	11	12	5	3.60	19.6	4.33	3.09	25.8	3.69	0.33	0.17	0.68	0.59
Na^+	µeq/L	0.87	11	12	5	2.97	45.9	3.57	1.94	101	1.72	0.01	0.37	0.56	0.88
K^+	µeq/L	0.26	11	12	5	0.34	9.04	0.50	0.24	7.60	0.45	0.00	0.00	0.81	0.39
Ca^{2+}	µeq/L	0.50	11	12	5	2.31	43.3	2.49	1.36	53.0	2.39	0.00	0.00	0.85	0.14
Mg^{2+}	µeq/L	0.82	11	12	5	1.43	22.3	2.97	0.83	18.3	2.57	0.00	0.00	0.09	0.00
HCO_3^-	µeq/L	0.87	11	12	5	0.52	91.8	-0.05	4.61	104	7.68	0.00	0.00	0.85	0.17
Inorganic Nutrients															
TDP	P µg/L	0.2	11	12	5	1.82	13.7	3.80	0.06	35.5	3.03	0.08	0.00	0.03	0.00
SRP	P µg/L	0.9	11	12	5	1.00	11.9	3.20	0.33	32.6	2.77	0.27	0.26	0.00	0.03
TDN	N µg/L	7	11	12	5	44.8	44.3	134	16.0	24.9	138	0.96	0.17	0.03	0.11
$NO_2^- + NO_3^-$	N µg/L	2	11	12	5	11.9	9.08	6.00	5.99	10.7	3.67	0.00	0.00	0.06	0.36

NH_4^+	N µg/L	3	11	12	5	24.6	23.6	90.2	8.81	17.4	110	0.86	0.04	0.03	0.04
Organic Nutrients															
DOC	ppm	0.06	11	12	5	0.15	0.49	0.40	0.06	0.59	0.25	0.12	0.61	0.00	0.68
DOM C1	FI	N/A	10	9	5	3.24	3.72	3.22	2.94	3.71	2.24	0.76	0.50	0.99	0.63
DOM C2	FI	N/A	10	9	5	5.27	6.40	3.28	4.27	4.41	1.25	0.58	0.91	0.33	0.03
DOM C3	FI	N/A	10	9	5	1.63	6.44	21.2	1.46	6.48	28.5	0.04	0.00	0.00	0.00
DOM C4	FI	N/A	10	9	5	2.96	4.69	2.74	2.39	3.49	0.94	0.22	0.28	0.85	0.09
DOM C5	FI	N/A	10	9	5	1.95	4.78	6.77	2.25	5.48	5.29	0.15	0.02	0.03	0.03
Microbial Assemblages															
Acidobacteria	%	N/A	5	11	3	1.1	3.2	1.5	0.84	3.6	1.2	0.73	0.70	0.54	0.53
Actinobacteria	%	N/A	5	11	3	17	30	15	6.4	22	21	0.81	0.75	0.86	0.05
Bacteroidetes	%	N/A	5	11	3	14	9.2	16	5.2	15	18	0.00	0.03	0.82	0.04
Chloroflexi	%	N/A	5	11	3	0.7	8.1	6.1	0.51	5.6	9.1	0.01	0.00	0.20	0.00
Cyanobacteria	%	N/A	5	11	3	16	0.07	7.8	17	0.11	7.5	0.04	0.00	0.47	0.34
Firmicutes	%	N/A	5	11	3	1.0	10	0.06	1.9	15	0.10	0.10	0.24	0.54	0.22
Gemmatimonadetes	%	N/A	5	11	3	0.39	3.9	0.02	0.23	4.9	0.02	0.01	0.01	0.04	0.01
Proteobacteria	%	N/A	5	11	3	43	30	42	16	17	9.1	0.17	0.99	0.92	0.52

Technical corrections/comments:

1) Is the use of ‘warm’ and ‘cold’ in quotations necessary throughout? I feel it is not, as long as you state early on that these are the terms you are going to use.

Response: Quotations on ‘warm’ and ‘cold’ basal ice were removed, except for the last paragraph of the introduction when they are first introduced and defined.

2) The definition of cold based and warm based glaciers is repeated throughout the paper – it is only really necessary to define these terms once.

Response: Definitions were removed after the initial description of these terms

3) Consider revising the word ‘parent’ in ‘parent ice’ - this could lead to inference that the basal ice is always of younger age, which is not necessarily true. As such, this phrase may be slightly misleading. Consider revising throughout. If you choose to use parent ice – this should be defined and used consistently.

Response: Changed ‘parent ice’ to ‘meteoric glacier ice’ throughout.

4) There are many sentences which are poorly constructed, with use of multiple ‘and/s’, ‘and/or’ and ‘also/s’. Often, this disrupts clarity and flow. Please consider revising.

Response: Several sentences were revised to remove ‘and/or’ (x8) and ‘also’ (x7). Lists were condensed where appropriate, for example: the last sentence of the first paragraph was changed to “Both basal ice and subglacial water are known to host populations of microbes that mediate redox reactions (e.g. Sharp et al., 1999; Wadham et al., 2004), play an active role in bedrock weathering (e.g. Tranter et al., 2002), and produce and/or consume ecologically important nutrients (e.g. Bottrell and Tranter, 2002; Boyd et al., 2011; Hodson, 2007; Statham et al., 2008; Tranter et al., 2002; Wadham et al., 2012)").

5) Line 32 - are you missing a reference related to subglacial microbial mediated chemical weathering?

Response: Tranter et al (2007) reference was added since the sentence is referring to weathering. Microbial mediated chemical weathering is discussed two sentences later and relevant references are included there.

6) Consider rephrasing line 39 for clarity – the first sentence is a little unclear, I think you may be missing a word.

Response: This sentence was rewritten: "Subglacial processes and the composition of basal ice can dramatically impact the biogeochemistry of meltwater and sediments exported from glaciers in a warming world. For example […]",

7) Line 44 274 - too many spaces.

Response: Removed space

8) Line 259, this would be an appropriate place to reference the Wadham (2016) study.

Response: The sentence was restructured to highlight and reference O'Donnell et al (2016) which we assume is the one you're referring to: "Excess NH_4^+ would be particularly prevalent during the degradation of nitrogen-rich organic matter as has been identified in basal ice from other sites (O'Donnell et al., 2016), and observed in this study (protein-like DOM described by PARAFAC C1 and C2)"

9) Line 274 - consider rephrasing the sentence starting with 'Because: : :'.

Response: Sentence was rephrased and split into two: "The sedimentary rocks near/underlying the Western Margin support well-developed soils and vegetation. Therefore, even limited interaction with the substrate could have resulted in the acquisition of significant humic-like DOM in this cold-based system if this material was abundant in the substrate."

10) Line 289, although production and consumption of autochthonous OM are mentioned in Wadham (2016), I think there are other more appropriate references for this point.

Response: That should have been O'Donnell et al (2016) rather than Wadham et al (2016) so has been revised accordingly.

11) The font size of the figure captions vary.

Response: Original figure files can be provided for publishing to ensure consistent formatting.

12) Please, standardized units throughout. For example, currently, there is a mixing of DOC units mg L-1 and ppm.

Response: revised to consistently use ppm throughout

Reviewer 3

Line 64: I am not sure what the “a” refers too in “> 20 m a-1” but perhaps this is a common unit from studies on glaciers that I am unfamiliar with

Response: a refers to annum and is a common unit for representing glacier velocity but has been changed to ‘yr’ for this biogeochemistry audience.

Line 199 - this seems like an odd way to report this. “less than half a percent of the OTUs” perhaps <0.5% would be clearer?

Response: Revised to say “<0.5%”

Basal thermal regime affects the biogeochemistry of subglacial systems

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Abstract

Ice formed in the subglacial environment can contain some of the highest concentrations of solutes, nutrients, and microbes found in glacier systems that can be ~~. Upon glacial melt, these materials are~~ released to downstream freshwater and marine ecosystems and glacier forefields. Despite the potential ecological importance of basal ice, our understanding of its ~~biogeochemical characteristics, and their~~ spatial and temporal biogeochemical variability, remains limited. We hypothesize that the basal thermal regime of glaciers is a dominant control on subglacial biogeochemistry because it influences the degree to which glaciers mobilize material from the underlying substrate and controls the nature and extent of biogeochemical activity that occurs at glacier beds. Here, we characterize the solutes, nutrients, and microbes found in the basal regions of a cold-based glacier and three polythermal glaciers and compare them to those found in overlying glacier ice of meteoric origin. Compared to ~~its parent~~ meteoric glacier ice, basal ice from polythermal glaciers was consistently enriched in major ions, dissolved organic matter (including a specific fraction of humic-like fluorescent material), and microbes, and was occasionally enriched in dissolved phosphorus and reduced nitrogen (NH_4^+) and in a second dissolved component of humic-like fluorescent material. In contrast, the biogeochemistry of basal ice from the cold-based glacier was remarkably similar to that of ~~its parent~~ meteoric glacier ice. ~~Although basal ice from the cold-based glacier may have acquired some inorganic and organic nutrients from the underlying substrate, it did not appear to contain significant amounts of either solutes or microbes derived from the glacier bed.~~ These findings suggest that a glacier's basal thermal regime can play an important role in determining the mix of solutes, nutrients, and microbes that are acquired from subglacial substrates ~~and/~~or produced *in situ*.

1 Introduction

Glaciers form by the compression and metamorphism of snow and slowly deform and flow under their own weight. ~~While a~~A considerable portion of a glacier's ice is of meteoric origin and ~~,~~ receives~~ing~~ chemical and biological inputs primarily from the atmosphere. However, subglacial processes, including melt-freeze events and erosion can result in the production of ~~, ice can~~

~~also form at or near the~~ basal ice near the bed. ~~bed as glaciers erode bedrock and/or subglacial sediments and entrain both particulate and dissolved materials.~~ This basal ice is typically characterized by relatively high concentrations of solutes that are dominated by ~~acquires solutes (often dominated by~~ Ca^{2+}, Mg^{2+}, HCO_3^- and SO_4^{2-} (Tranter, 2007). These solutes are often produced ~~),~~from ~~via~~ reactions that involve carbonate and sulphide minerals (Tranter, 2007), which are trace components in most types of bedrock (Holland, 1978). Basal ice can also contain ~~It may also incorporate~~ organic matter, ~~and~~ nutrients (e.g. phosphorus, silica, potassium) and microbes from the underlying substrate (Montross et al., 2014; Sharp et al., 1999). Both basal ice and subglacial water are known to ~~may also~~ host populations of microbes that mediate redox reactions ~~-~~(e.g. Sharp et al., 1999; Wadham et al., 2004)~~(e.g. Sharp et al., 1999)~~, play an active role in bedrock weathering (e.g. Tranter et al., 2002), and produce ~~and/~~or consume ecologically important nutrients ~~such as sediment-bound phosphorus~~ (e.g. Bottrell and Tranter, 2002; Boyd et al., 2011; Hodson, 2007; Statham et al., 2008; Tranter et al., 2002; Wadham et al., 2012)~~(e.g. Hodson, 2007), iron (e.g. Statham et al., 2008), sulphate (e.g. Bottrell and Tranter, 2002), silica (e.g. Tranter et al., 2002), nitrogen (e.g. Boyd et al., 2011), and organic carbon (e.g. Wadham et al., 2012).~~

Subglacial processes and the composition of basal ice can dramatically impact the biogeochemistry of meltwater and sediments exported from glaciers in a warming world. For example, ~~I~~in glaciers where surface-derived meltwater drains through the subglacial environment and comes into contact with basal ice, ~~and~~ subglacial water and sediments, its ~~it will mix meltwater produced at the bed. These processes can dramatically alter the~~ geochemistry (Tranter et al., 2002), nutrient content (Hawkings et al., 2014; Wadham et al., 2016) and microbial community composition (Dubnick et al., 2017) are dramatically altered. Direct links have recently been established between subglacial biogeochemical signatures and impacts on downstream environments including downstream freshwater (Sheik et al., 2015) and fjord ecosystem (Gutiérrez et al., 2015)~~of meltwater during its transit from the glacier surface to downstream proglacial environments.~~. Similarly, ~~D~~during glacial retreat, ~~melting of basal ice releases~~ the biogeochemical material ~~sediment, solutes, nutrients and microbes~~contained in basal ice are released to the terrestrial landscape.~~–~~ These materials have been directly linked to ~~contribute to~~ the nutrient dynamics of glacier forefields (Kazemi et al., 2016; Mindl et al., 2007; Sattin et al., 2010) and form the basis of the soils from which many postglacial landscapes evolve (Kastovská et al., 2005).

Despite the relatively high concentration and/or unique composition of solutes, nutrients, and microbes often found in subglacial systems, and their potential to impact glacier forefields and downstream ecosystems, our understanding of the controls on subglacial biogeochemical processes and products~~, and their spatio-temporal variability,~~ remains limited. ~~Basal temperature can vary considerably within and between glaciers and it controls rates of ice deformation and basal sliding, the amount of water near the bed and thus the extent to which glaciers mobilize material from the underlying substrate, and the extent and characteristics of *in situ* biogeochemical activity.~~ We ~~therefore~~ hypothesize that the basal thermal regime plays an important role in defining the physical and biogeochemical characteristics and variability of basal ice. Since warm ice deforms more easily than cold ice, and subglacial water promotes basal sliding (Iken, 1981; Iken and Bindschadler, 1986), we expect basal ice that forms and persists in fast-flowing glaciers to experience relatively ‘warm’ conditions and have distinct biogeochemistries from basal ice that forms and persists in the relatively ‘cold’ conditions of slow-flowing glaciers. To evaluate how basal thermal regime affects the biogeochemical materials that glaciers mobilize from the substrate or produce/cycle within subglacial environments, we explore the solutes, nutrients and microbes found in the basal regions of three fast-flowing, polythermal outlet glaciers and the slow-flowing Western Margin of the Devon Ice Cap (DIC, Devon Island, Nunavut, Canada).

2 Methods

2.1 Study Site

The Devon Ice Cap (DIC) covers an area of approximately 14,400 km^2 (Burgess and Sharp, 2004) and has been shrinking since 2005 (Sharp et al., 2011). The three ~~We collected and characterized basal ice from three fast-flowing outlet glaciers (Sverdrup Glacier, Belcher Glacier, and East 7 Glacier) and the slow-flowing Western Margin of the ice cap (Fig. 1). All three~~ fast-flowing glaciers from which warm basal ice was collected (Fig. 1) have surface velocities > 20 m ~~a~~yr^{-1} and a temporally varying component of flow which peaks in summer and has been attributed to seasonal variation in the rate of basal motion (Burgess et al., 2005; Van Wychen et al., 2017) (Fig. 1). The occurrence of time-varying basal motion in these glaciers suggests that geothermal and frictional heat keep ice near the glacier bed at temperatures that are at or near the pressure-melting point over a considerable portion of their beds (Burgess et al., 2005; Cuffey and Paterson, 2010). Further, field observations of hydrologically active moulins on the surfaces of these glaciers suggests that surface-derived meltwater likely reaches at least some areas of their beds during the melt season. The presence of large open subglacial meltwater channels beneath the lateral margins of Sverdrup and Belcher glaciers suggests channelized subglacial water drainage. In May, prior to the initiation of surface melt, air temperatures at distances of >500 m into these subglacial channels were near 0 ºC. We therefore assume that the basal ice in these fast-flowing glacier systems likely formed and persisted under relatively ~~‘warm’~~ warm subglacial conditions~~, and we refer to it as ‘warm’ basal ice~~. In contrast, ~~I~~ice at the Western Margin of the ice cap (Fig. 1) is relatively slow-flowing (with surface velocities generally <10 m a^{-1} (Burgess et al., 2005)) and is not constrained laterally by bedrock topography. We infer that glacier flow in this region occurs exclusively by internal deformation with ice frozen to the bed (Burgess et al., 2005). Therefore~~, unlike the ‘warm’ basal ice that forms and persists at the beds of the faster-flowing glaciers, the~~ basal ice at the Western Margin is likely below the pressure melting point and likely formed and persisted under relatively~~is referred to here as ‘cold’ basal ice~~ cold subglacial conditions. Although located up to ~100 km apart, the three fast-flowing glaciers explored in this study are all underlain by metasedimentary rocks and gneiss, while ice at the Western Margin is largely underlain by sandstone, dolomite and limestone bedrock (Harrison et al., 2016) (Fig. 1).

2.2 Field Sampling

We sampled ~~‘warm’~~ basal ice ~~from the three fast-flowing glaciers, and ‘cold’ basal ice from the Western Margin of the ice cap,~~ as well as overlying meteoric glacier ice from the Devon Ice Cap~~each~~ (Fig. 1). We identified basal ice near the glacier bed as an ice facies with high debris content and an anisotropic structure that incorporated features such as discontinuous layers, lenses and pods of varying size (Hubbard and Sharp, 1989; Knight, 1997). In contrast, glacier ice is typically white, bubby and horizontally stratified.~~–~~ Ice samples were collected from marginal ice cliff faces, ice rubble at the base of cliff faces, and the walls of subglacial meltwater channels. All ice samples were collected using sterile (furnaced at 500 ºC for 8 hrs) carbide chisels that were ethanol-bathed and flame-sterilized in the field before each use. One chisel was used for debris-poor samples and another was used for debris-rich samples. At least 10 cm of material was removed from exposed surfaces in the field before samples were collected. Samples were stored in 5L Whirl-pak bags (Nasco, Fort Atkinson, USA) and kept frozen (~ -20ºC) until analysis.

2.3 Sample Processing

Prior to analysis, samples were removed from the freezer and melted at 4 ºC in Whirl-pak bags. For 16S rRNA gene sequencing, a glass filter tower and 0.2 µm Pall Supor® polysulfone 47 mm sterile filter papers were used to filter samples. Filter papers were collected in duplicate and stored in sterile petri dishes at -80ºC until further processing.~~–~~ For analyses of soluble reactive phosphorus (SRP), NO_3^- + NO_2, and NH_4^+ water analyses, a sterile syringe (60 ml) with a 0.45 µm cellulose acetate luer-lok filter was used to fill two sterile 15 ml centrifuge tubes. One 120 ml Nalgene® bottle was also filled (with no headspace) for major ion analyses and stored at 4 ºC for ~2 weeks until analysis. For dissolved organic carbon (DOC) quantification and characterization, a 0.7 µm GF/F luer-lok filter was used to fill two sterile 45 ml universal glass vials (leaving headspace) and a piece of foil was placed beneath the cap for closure before freezing.

All filtration equipment was rinsed 3 times with sample, and a minimum of 5 ml of sample was passed through each filter paper before the sample was filtered for analysis. Glassware was acid-washed (10% HCl for >48 hrs), and both glassware and foil were combusted (450ºC for 8 hrs) prior to use. All storage bottles, lids, and foil caps were rinsed 3 times with filtrate before a sample was collected for analysis.

2.4 Analytical Methods

Nutrient concentrations (SRP/TDP/NH_4^+/NO_3^-+NO_2^-/TDN/SiO_2): Determinations of soluble reactive phosphorus (SRP; PO_4^{3-}), ~~and~~ total dissolved phosphorus (TDP), ammonium (NH_4^+), nitrate (NO_3^-) + nitrite (NO_2^-), total dissolved nitrogen (TDN) and reactive silica (SiO_2) were made with a Lachat QuickChem QC 8500 FIA Automated Ion Analyzer (Lachat Instruments, Loveland, CO, USA) using methods outlined by Rice *et al.* (2012) and O'Dell (1993) for NO_3^- + NO_2^-. TDP was digested with $K_2S_2O_8$ to convert all dissolved P to PO_4^{3-}. TDN was digested with $K_2S_2O_8$ and NaOH to convert all dissolved N to NO_3^-/NO_2^-. Analyses were conducted in an ISO17025 accredited laboratory and reference material and standards were applied according to those standards. Detection limits were based on instrument blanks (Shrivastava and Gupta, 2011) as follows: TDP = 1.8 ppb, SRP = 0.9 ppb, NH_4^+ = 3 ppb, NO_3^- + NO_2^- = 2 ppb, TDN = 7 ppb, and SiO_2 = 0.02 ppm.

DOC concentrations: dissolved organic carbon was quantified using a Shimadzu TOC-5000A Total Organic Carbon Analyzer (Shimadzu, Japan) equipped with a high-sensitivity platinum catalyst using US EPA method # 415.1. Five standards between

0 ppm and 2 ppm were used for calibration (R^2=1.0). The detection limit for DOC was 0.06 ppm and was based on instrument blanks (Shrivastava and Gupta, 2011)~~0.2 mg L^{-1}.~~

***DOM characteristics**:* We used three-dimensional Excitation Emission Matrices (EEMs) derived from total fluorescence scans to broadly characterize dissolved organic matter (DOM) into humic-like and protein-like fractions and to correlate specific fluorophores with those previously identified in the literature. DOM fluorescence was measured in ratio mode (S/R) using an Agilent G1321B fluorescence detector (Agilent Technologies, Santa Clara, USA) and methods outlined by Cuss and Gueguen (2015). Prior to each analysis, the system was rinsed 3 times with deionized water and 3 times with sample at room temperature. EEMs were produced by measuring the fluorescence intensity every 1 nm at excitation wavelengths from 220-450 nm and every 5 nm at emission wavelengths from 280-545 nm.

Major Ions (Cl^-, SO_4^{2-}, Na^+, K^+, Mg^{2+}, Ca^{2+}): Anions were quantified using a Dionex DX-600 Ion Chromatograph (Dionex, USA) and methods outlined by US EPA method # 300.1. Cations were measured using Inductively Coupled Plasma - Optical Emission Spectroscopy (ICP-OES; Thermo Scientific iCAP 6300, Cambridge, UK) and US EPA method #200.7. Detection limits were Cl^- = 0.85 μeq L^{-1}, SO_4^{2-} = 0.83 μeq L^{-1}, Na^+=0.87 μeq L^{-1}, K^+=0.26 μeq L^{-1}, Mg^{2+}=0.82 μeq L^{-1}, and Ca^{2+}= 0.5 μeq L^{-1}.

Sediment concentration: 50 ml of unfiltered, melted ice was placed in a pre-weighed 50 ml dish and dried at 50 ºC. The dish was then reweighed and the sediment in 50 ml was calculated as the change in mass from before to after the sample was added/dried.

16S rRNA gene sequencing: DNA was extracted from filter papers using MO BIO's PowerSoil ® DNA Isolation kit following the manufacturer's protocol, but with several modifications to maximize the efficiency of the extraction, including: 1) at Step 14, solution C4 was added for a total of 4 ml instead of 1,200µl and vortexing was for 20 seconds instead of 5 seconds, 2) prior to step 15, the samples were incubated for 30 minutes, and 3) at step 20, the DNA was eluted in 50µl of solution C6 instead of 100µl. Primers 515F and 806R were used to amplify V4 region of the 16S rRNA gene. The Illumina libraries were prepared according to ~~denatured and diluted following~~ Illumina guidelines. An 8 pM library containing 7% PhiX each was sequenced on a MiSeq instrument (Department of Biology, University of Waterloo) using a 2 x 250 cycle Reagent Kit v2.

2.5 Data Processing and Statistical Analyses

Geochemistry and inorganic nutrients: The concentration of HCO_3^- (μeq L^{-1}) was calculated as the charge deficit between the sum of cations (μeq L^{-1}) and the sum of anions (μeq L^{-1}). To summarize the geochemical composition of the solute load in each sample, we (i) calculated the fractional contribution of each major ion to the total solute load by dividing the concentration of each major ion (μeq L^{-1}) by either the sum of cations or the sum of the anions in the respective sample, (ii) normalized the fractional contributions of each ion species by their respective mean and variance (Iwamori et al., 2017) and (iii) conducted a Principal Components Analysis (PCA) in Matlab R2018a using these data. To summarize the nutrient composition of each sample and evaluate the concentrations of TDP and TDN relative to the total solute load, the concentrations of TDP (μg P L^-

^{1}) and TDN (μg N L^{-1}) were divided by the solute concentration (μeq L^{-1}) of the corresponding sample. Spearman rank-order correlation coefficients (r_s) were used to evaluate the significance of dependency between geochemical/nutrient variables.

DOM Characterization: Parallel Factor Analysis (PARAFAC) was used to decompose the complex EEMs into discrete components using the drEEM toolbox in Matlab2018a and methods developed by Murphy et al. (2013). Corrections were applied for instrument spectral bias and for inner filter effects, and Raman scatter was normalized to daily Raman scans (Murphy et al., 2013). The scatter region for each EEM was excised and smoothed and EEMs were normalized to unit variance. PARAFAC was completed using non-negativity constraints and the EEM normalization was reversed after modelling. Although the modelled components cannot be identified as specific organic compounds, they were characterized using the OpenFluor database (Murphy et al., 2014) and comparisons with previous literature. To summarize the DOM composition of each sample, the fluorescent intensity of each component was normalized to its mean and variance across the dataset and a PCA was completed.

Microbial Assemblage: Paired-end reads were assembled using PANDAseq (Masella et al., 2012) and analysed using Quantitative Insights Into Microbial Ecology (QIIME, (Caporaso et al., 2010)), managed by the automated exploration of microbial diversity v. 1.5 (AXIOME, (Lynch et al., 2013)). Sequences were clustered with UPARSE (Edgar, 2013) ~~and compressed~~ into unique operational taxonomical units (OTUs) with 97% similarity. OTUs were assigned to taxonomy ~~, and classified by~~ via The Ribosomal Database Project (RDP) (Wang et al., 2007) with a confidence threshold of 0.8. The number of reads ranged from 7,608 to 188,117 per sample so reads were rarefied to the lowest read count (7,608)~~Rarefaction analysis was used to sub-sample the processed dataset to lower than the smallest library for subsequent analyses~~. The microbial assemblages in each sample were summarized by completing non-metric multidimensional scaling (NMDS) of Bray-Curtis distance measures, statistical significance between groups was determined using multi response permutation procedure (MRPP) and multiple linear regressions to fit environmental vectors onto the NMDS (using the Vegan toolbox in R).

3 Results

3.1 Major Ion Chemistry

Glacier ice and ~~‘cold’~~cold basal ice had relatively low solute concentrations ($\bar{x}$ = 15.6 μeq L^{-1} and 22 μeq L^{-1}, respectively) that were dominated by atmospherically-derived solutes, including Cl^-, SO_4^{2-}, and Na^+ (Table 1). ~~‘Warm’~~Warm basal ice samples contained significantly higher concentrations of solutes ($\bar{x}$ = 241 μeq L^{-1}), including common rock-derived solutes such as K^+, Ca^{2+}, Mg^{2+}, and HCO_3^-, than did glacier ice (T-test, $p<0.05$) (Table 1; Fig. 3). Therefore, while the composition and concentration of solutes in ~~‘cold’~~cold basal ice were very similar to those in glacier ice, it is likely that distinct solute sources exist in relatively ~~‘warm’~~warm subglacial systems (Fig. 2).

3.2 Nutrients (N and P)

While ~~‘warm’~~warm basal ice did not contain significantly more dissolved inorganic nutrients than glacier ice, including nitrogen (TDN, NH_4^+ or NO_3^-) and phosphorus (SRP, TDP) (T-Test, $p>0.05$), it contained, on average, less NO_3^- (T-test, $p<0.05$) and had higher inter-sample variability in the concentrations of NO_3^-, and NH_4^+ and TDP (F-Test, $p<0.05$; Table 1, Fig. 3). Therefore, while the subglacial system of ~~‘warm’~~warm based glaciers may function as a sink of NO_3^-, the sources (and potentially ~~also~~ sinks) of other inorganic nutrients may be spatially heterogeneous. ~~‘Cold’~~Cold basal ice samples had significantly higher concentrations of NH_4^+, TDN, SRP, TDP than samples of meteoric ~~parent~~ glacier ice (T-test, $p<0.05$; Table 1), suggesting the existence of a relatively consistent subglacial source for these nutrients in this ~~‘cold’~~cold subglacial system.

3.3 Dissolved Organic Matter

A 5 component PARAFAC model explained 98.6% of the variability in the spectrofluorescence dataset. Two of these components were similar to protein-like fluorescence and three were similar to humic-like fluorescence as described in other studies (Table 2). DOC concentrations in ~~‘warm’~~warm basal ice were not significantly different from those in glacier ice (T-test, $p<0.05$) but DOC concentrations in ~~‘warm’~~warm basal ice were positively correlated with the tyrosine-like C1 fluorescence (r_s =0.61, p=0.01, n=9). ~~‘Warm’~~Warm basal ice also contained significantly more humic-like C3 fluorescence (T-test, $p<0.05$), and significantly more variable humic-like C3 and C5 fluorescence (*F*-test, $p<0.05$) than did glacier ice (Table 1). Thus, a relatively consistent fraction of the DOC derived from these subglacial systems was probably in the form of proteinaceous and humic organic matter.

~~‘Cold’~~Cold basal ice had significantly higher DOC concentrations ($\bar{x}$ = 0.40 ppm) than glacier ice ($\bar{x}$ = 0.15 ppm) (T-test, $p<0.05$; Table 1), suggesting that ice can acquire DOC in ~~‘cold’~~cold basal environments. Relative to glacier ice, ~~‘cold’~~cold basal ice also contained significantly higher and more variable fluorescence of humic-like DOM components C3 and C5 (T-test and F-Test, $p<0.05$) and exhibited significantly more variable fluorescence of protein-like DOM component C2 than did glacier ice (*F*-test, $p<0.05$; Table 1). Since C3 and C5 humic-like DOM is typically associated with terrestrial soils and vegetation (Table 2), this DOM may have been acquired during past glacial advances over soils and sediments.

3.4 Microbial Assemblages

A total of 3,555 OTUs were identified across the rarefied dataset. Microbial assemblages in ~~‘warm’~~warm basal ice and glacier ice formed two distinct groups (Fig. 2). 76% of the OTUs observed in ~~‘warm’~~warm basal ice were absent from glacier ice (Fig. 4), suggesting that a large portion of the microbial assemblage in ~~‘warm’~~warm basal ice was sourced from the subglacial environment. Microbial assemblages in ~~‘warm’~~warm basal ice were also highly variable - <0.5% ~~less than half a percent~~ of the OTUs found in ~~‘warm’~~warm basal ice were present in all ~~‘warm’~~warm basal ice samples. Geographic location influenced the structure of microbial assemblages in ~~‘warm’~~warm basal ice since ~~‘warm’~~warm basal ice samples from a given glacier had more OTUs in common with other basal ice samples from the same glacier (42% of their OTUs and 26% of their assemblages) than they did with basal ice samples from other ~~‘warm’~~warm based glaciers (32% of their OTUs and 15% of their assemblages) (T-test, $p<0.001$). Furthermore, although multiple linear regressions did not indicate any significant correlations between the major ion concentrations, major ion composition, nutrient concentrations or fluorescence index and the microbial assemblage structure of ~~‘warm’~~warm basal ice samples, sample location was significantly correlated with the structure of microbial assemblages in ~~‘warm’~~warm basal ice samples ($p=0.01$).

The microbial assemblages in ~~‘cold’~~cold basal ice were broadly similar to those in glacier ice (Fig. 2). ~~‘Cold’~~Cold basal ice shared most (73%) OTUs with glacier ice (Fig. 4). Of the shared OTUs between ~~‘cold’~~cold basal ice and glacier ice, many (37%) were absent from the ~~‘warm’~~warm basal ice samples. Thus, the microbial assemblages in ~~‘cold’~~cold basal ice remained remarkably similar to those in meteoric glacier ice~~its parent material~~, despite the potential for interactions with the substrate.

4 Discussion

4.1 Basal ice formation

Glacier ice originates as snow in the accumulation zones of glaciers/ice caps. This ice is of meteoric origin and receives chemical and biological inputs primarily from the atmosphere, experiences consistently sub-freezing temperatures and is likely to host ~~limited *in situ*~~ low rates of biogeochemical activity in the englacial system (Price and Sowers, 2004). Surface melt routed through the subglacial system ~~and/~~or subglacially-produced meltwater formed by geothermal and frictional heat sources may refreeze to form basal ice beneath temperate and polythermal glaciers. The interactions between ice/water and the overridden substrate can mobilize particulates and solutes ~~sediment, solutes, microbes, and nutrients~~ and incorporate them into the base of the glacier during the formation of ~~‘warm’~~warm basal ice (Hubbard et al., 2009). Relatively warm temperatures (ie: near the pressure melting point) beneath the glacier may also promote biogeochemical activity by increasing both the availability of liquid water, the rates of chemical weathering, and the metabolic rates of micro-organisms (Price and Sowers, 2004)~~, and rates of chemical weathering~~.

The subglacial conditions in cold-based glaciers ~~that are frozen to their beds~~ differ considerably from those in temperate and polythermal glaciers because temperatures are below the pressure melting point. The modes of formation of ~~‘cold’~~cold basal ice can vary between glaciers and are generally poorly understood. Thus, interpretations of the environments in, and processes by, which such ice is formed are often ambiguous, making our understanding of the biogeochemistry of ~~‘cold’~~cold basal ice even more limited. The formation of ~~‘cold’~~cold basal ice is often described by the ‘apron entrainment model’ that invokes the production of basal ice by the overriding and reworking of apron material (snow, ice blocks, refrozen melt water and debris) along an advancing margin (Shaw, 1977). However, the dark, largely bubble-free ice and absence of coarse-grained debris in the Western Margin basal ice facies suggests that the apron entrainment model may not describe its mode of formation. Case studies have demonstrated that basal ice in cold-based systems can also be produced by subglacial processes including the deformation and entrainment of subglacial permafrost (Fitzsimons et al., 2008), the overriding of ice marginal lakes (Lorrain et al., 1999), and the refreezing of water produced in warm thermal zones ~~and/~~or high pressure zones at the glacier bed that then flows into cold thermal zones ~~and/~~or low pressure zones downstream, where it refreezes (Knight, 1997; Wettlaufer et al., 1996) and entrains debris and excludes gases as it accretes to the glacier sole (Gilpin, 1979; Walder, 1986).

4.2 Chemistry

~~'Warm'~~Warm basal ice from fast-flowing glaciers was consistently enriched in rock-derived solutes, including SiO_2, SO_4^{2-}, K^+, Ca^{2+}, Mg^{2+}, and HCO_3^-, compared to overlying glacier ice (Table 1~~, Fig. 3~~). These solutes were likely derived from weathering of reactive minerals such as carbonates, sulphides and aluminosilicates in the underlying bedrock (Tranter et al., 1996) that are commonly present in trace amounts (Holland, 1978). Furthermore, the presence of water during the formation of ~~'warm'~~warm basal ice would support reactions involving acid hydrolysis, which are usually the most important subglacial weathering processes (Raiswell, 1984). In contrast, limited rock-water contact during the formation and persistence of ~~'cold'~~cold basal ice likely limited chemical weathering, resulting in low mean solute concentrations (22 μeq/L) similar to those in glacier ice (15.6 μeq/L). Also like glacier ice, the solutes in ~~'cold'~~cold basal ice were dominated by atmospherically-derived components (Cl^-, SO_4^{2-}, and Na^+), rather than by solutes likely to be derived from the local sandstone, dolomite, limestone and conglomerate rocks (Ca^{2+}, Mg^{2+}, HCO_3^-). The cold basal ice therefore contained solute concentrations and compositions more similar to those in meteoric glacier ice than warm basal ice, even though the substrate beneath the cold based ice (local sandstone, dolomite, limestone and conglomerate substrate) is likely far more reactive than the substrate beneath the warm-based glaciers (-metasedimentary rocks and gneiss). Therefore, the differences in chemistry between these basal environments cannot be explained by differences in substrate alone.

4.3 Inorganic nutrients

Both ~~'warm'~~warm and ~~'cold'~~cold basal ice showed some evidence of inorganic nutrient acquisition in the subglacial environment. The ~~'cold'~~cold basal ice ~~from the Western Margin~~ had relatively high concentrations of TDP, TDN (particularly NH_4^+) (Table 1~~, Fig. 3~~) while the ~~'warm'~~warm basal ice samples were only occasionally enriched in reduced nitrogen (NH_4^+) and dissolved phosphorus (TDP) (Table 2). The substrate surrounding the Western Margin sample sites is composed largely of Cambrian and Ordovician sandstone, dolomite, limestone, and conglomerate (Harrison et al., 2016), which likely contain higher phosphorus concentrations than do the metasedimentary rocks (Porder and Ramachandran, 2013) that underly the polythermal glaciers in this study. Phosphorus in rocks is almost exclusively found in apatite mineral groups (Taylor and McClennan, 1985) while nitrogen can occur in recalcitrant organic matter or NH_4^+ in silicate minerals (Honma, 1996; Honma and Schwarcz, 1979). The distribution of these components, and thus P and N, in shield rocks, volcaniclastics and the Canadian Shield can be spatially heterogeneous (Honma, 1996; Honma and Schwarcz, 1979). ~~'Warm'~~Warm basal ice may also have variable inorganic nutrient concentrations if the location of subglacial biogeochemical activity is temporally ~~and/~~or spatially heterogeneous. Subglacial microbial communities may function as a source of NH_4^+ via catabolic processes and the degradation of organic matter. Excess NH_4^+ would be particularly prevalent during the degradation of nitrogen-rich organic matter as has been identified in basal ice from other sites (O’Donnell et al., 2016), and observed in this study ~~such as the~~ (protein-like DOM ~~that was observed in basal ice (~~described by PARAFAC C1 and C2). ~~In subglacial environments where organic matter contains insufficient nitrogen to meet the requirements for anabolic metabolism, specific organisms may fix nitrogen *in situ*. Genes indicative of nitrogen fixation (nitrogenase iron protein (*nifH*) gene) have been found in subglacial microbial communities (Boyd et al., 2011). However, despite the presence of *nifH* genes (Boyd et al., 2011) and observations of N_2 fixation on glacier surfaces (Telling et al., 2011), N_2 fixation has yet to be documented in subglacial environments.~~

4.4 DOM

Both ~~‘warm’~~warm and ~~‘cold’~~cold basal ice contained higher average DOC concentrations (0.49 ppm and 0.40 ppm, respectively) than glacier ice (0.15 ppm) (Table 1) suggesting a potential source of DOC in subglacial systems, as observed in Greenland (O’Donnell et al., 2016) and Antarctica (Wadham et al., 2012). Compared to glacier ice, the DOM in ~~‘warm’~~warm and ~~‘cold’~~cold basal ice had higher and more variable proportions of humic-like fluorescent material (C3 and C5) but no significant differences in the presence of C1, C2 or C4 protein-like fluorescent material (Table 1, Table 2, Fig. 3). Humic DOM, and humic-like C3 and C5 fluorescence are commonly associated with soils and vegetation (Cory and McKnight, 2005; Osburn et al., 2016; Stedmon et al., 2003) so it is possible that both the fast and slow-flowing glaciers acquired these compounds by direct (via abiotic leaching) and indirect (via microbial cycling) of material from the ~~overridden~~ substrate. Similar observations were made ~~during past glacial advances~~ for low molecular weight DOC compounds in previous studies of basal ice from Greenland (O’Donnell et al., 2016). In polythermal glaciers, high rates of mechanical weathering and meltwater contact with the underlying substrate could ~~have~~ facilitate~~d~~ the acquisition of humic-like DOM from the substrate. While this is unlikely the case for cold basal ice where mechanical weathering and meltwater is limited, ~~Because t~~The sedimentary rocks near/underlying the Western Margin support ~~more~~ well-developed soils and vegetation. ~~than the metasedimentary rocks surrounding the fast-flowing polythermal glaciers in this study,~~ Therefore, even limited interaction with the substrate could have resulted in the acquisition of significant humic-like DOM in this cold-based system if this material was abundant in the substrate. Previous studies have also associated humic-like C3 and C5 fluorescence with microbial processing of organic matter (Table 2), suggesting basal ice may ~~also~~ have acquired these components via heterotrophic microbial activity in subglacial environments or in supraglacial or ice marginal material that was transported into the subglacial system by meltwater. The positive correlation between DOC concentrations in ~~‘warm’~~warm basal ice and tyrosine-like C1 fluorescence ($r_s = 0.61$, p=0.02, n=9) indicates that a relatively consistent fraction of the DOC derived from these subglacial systems was proteinaceous in character and ~~also~~ suggests the presence of *in situ* subglacial microbial activity. The production of tyrosine-like fluorescence has been widely linked to the degradation of terrestrially-derived humic-like DOM and microbial exudates (Table 2). Since tyrosine-like fluorophores are considered to be highly biodegradable (Yamashita and Tanoue, 2003), it is likely that tyrosine-like fluorescence was produced *in situ* within the subglacial environment from the degradation of allochthonous organic matter ~~and/~~or the production of autochthonous organic matter. This is consistent with other studies that suggest subglacial environments contain both allochthonous organic matter (i.e. from bedrock/paleosols/overridden soils and vegetation) and autochthonous organic matter that may be produced *in situ* from microbial metabolism (e.g. Hodson, 2006; O'Donnell et al., 2016).

4.5 Microbial assemblages

The microbial assemblages contained in the ~~'cold'~~cold basal ice was remarkably similar to those in meteoric glacier ice; ~~'cold'~~cold basal ice shared most (i.e. 73%) OTUs with glacier ice, of which many (37%) were unique to only ~~'cold'~~cold basal ice and meteoric glacier ice (Fig. 4). Like glacier ice, the microbial assemblages observed in ~~'cold'~~cold basal ice included Proteobacteria ($\bar{x}$ = 42%), Bacteroidetes ($\bar{x}$ =16%), Actinobacteria ($\bar{x}$ =15%) and Cyanobacteria ($\bar{x}$ = 7.8%) (Table 1). Proteobacteria, Bacteroidetes, Actinobacteria, and Cyanobacteria commonly dominate the microbiome of surface environments such as cryoconite holes (e.g. Cameron et al., 2012), glacier ice (e.g. Christner et al., 2005) and snow (e.g. Harding et al., 2011), and Cyanobacteria, Proteobacteria, and Actinobacteria contain organisms with the potential to photosynthesise (Cameron et al., 2012). Since microbial assemblages in soils and sediment typically differ considerably from those in the atmosphere and ~~meteroric~~meteoric glacier ice, it is very unlikely that the substrate surrounding the Western Margin, composed of sandstone, dolomite, limestone and conglomerate rocks and relatively well-developed soils, is characterized by the same microbial assemblages as were observed in glacier ice. Therefore, the remarkable similarity between the microbial assemblages in ~~'cold'~~cold basal ice and glacier ice suggest that either the ~~'cold'~~cold basal ice acquired few microbes from the underlying substrate during its formation or that most microbes acquired from the underlying substrate during its formation did not remain active *in situ* (and their DNA not preserved).

In contrast, the microbial assemblages in ~~'warm'~~warm basal ice ~~from fast-flowing glaciers~~ were distinct from those in glacier ice (Fig. 2, Fig. 4, MRPP, p<0.05). The ~~'warm'~~warm basal ice therefore probably acquired distinct microbes from the underlying substrate during its formation and may have ~~also~~ sustained *in situ* microbial activity, as has been reported in laboratory incubation experiments of basal material (e.g. (Stibal et al., 2012) ~~(e.g. Boyd et al., 2011; Wadham et al., 2012~~). ~~Like glacier ice, t~~The microbial assemblages observed in ~~'warm'~~warm basal ice were dominated by ~~p~~Proteobacteria ($\bar{x}$ =30%) and Actinobacteria ($\bar{x}$=30%) which are commonly observed in cold ecosystems (Amato et al., 2007; Møller et al., 2013) including those in glacier ice (this study), basal ice (Stibal et al., 2012b; Yde et al., 2010), and subglacial waters (Christner et al., 2006; Rondón et al., 2016). Additionally, ~~,~~the warm basal ice ~~but they~~ contained a ~~significantly~~ large~~r~~ proportion of Chloroflexi ($\bar{x}$ =8.1%) and Gemmatimonadetes ($\bar{x}$ =3.9%), which are common and active in permafrost soils ~~-~~(Tuorto et al., 2014) and other basal ice environments (Yde et al., 2010) but were significantly less dominant in glacier ice samples in this study (Table 1; T-test, p<0.05). Warm basal ice also contained relatively few ~~and a significantly smaller proportion of~~ Bacteroidetes ($\bar{x}$ =9.2%) and Cyanobacteria ($\bar{x}$ =0.07%) which were more abundant in glacier ice (stat) ~~than did glacier ice~~(Table 1) and~~.~~ other surface environments (Cameron et al., 2012; Harding et al., 2011). The ~~'warm'~~warm basal ice yielded a very small portion of 'ubiquitous' OTUs with less than 1% of the OTUs found in all ~~'warm'~~warm basal ice samples. The abundances of these 'ubiquitous' subglacial organisms were also highly variable between samples, ranging between a minimum of <0.01% of the assemblage, to a maximum of 2-40% of the assemblages, suggesting that the distributions of either the source(s) of these microbes and/or their *in situ* activity (i.e. reproduction) are spatially heterogeneous. Thus, even though there is evidence for globally-distributed microbial species that are capable of survival across the range of extreme subglacial environments (Bhatia et al., 2006; Lanoil et al., 2009; Skidmore et al., 2005), these species appear to be few and their local abundance may be highly dependent on site-specific conditions.

Although sample location did not affect the major ion chemistry, nutrient, or organic composition of basal ice, it was an important influence on the composition of the microbial assemblages in ~~'warm'~~warm basal ice. We observed that microbial assemblages in basal ice samples from the same glacier were more similar to each other than were assemblages in basal ice from different glaciers. Inter-glacier differences in basal microbial assemblages were resolved over relatively small distances (less than 100 km), and between glaciers with similar basal thermal regimes and underlying substrates (Fig. 1). Geographic location has previously been identified as an important determinant of microbial assemblages across various spatial scales, from meters (Lear et al., 2014) to global (Fuhrman et al., 2008), and within other polar environments including Antarctic and Arctic terrestrial and aquatic habitats (Comte et al., 2016; Yergeau et al., 2007) as well as on glacier surfaces (Cameron et al., 2016) and in subglacial discharge (Zarsky et al., 2018). Basal ice in different glaciers can be particularly isolated from each other, so microbial dispersal between systems is probably very limited. Furthermore, although residence times of ~~'warm'~~warm basal ice within a system are difficult to estimate, they may be sufficiently long to allow stochastic processes, such as random extinction, chance colonization, drift, and priority effects (Chase and Myers, 2011; Vellend and Agrawal, 2010) to play important roles in shaping the structure of microbial assemblages in basal ice. In contrast, basal processes within a system, including ice deformation and melt-freeze effects, would provide some degree of intra-glacial mixing of microbial assemblages and may explain the higher degree of similarity between assemblages in basal ice from the same system.

5 Conclusions

We investigated the biogeochemical properties of ~~'warm'~~warm basal ice from three polythermal glaciers that drain a region of the Devon Ice Cap that is underlain by metasedimentary rocks and gneiss. We found samples of basal ice from their subglacial environments to be consistently enriched in solutes (i.e. SiO_2, Na^+, K^+, Ca^{2+}, Mg^{2+}, and HCO_3^-), a specific fraction of humic-like fluorescent DOM (C3), and microbes compared to glacier ice of meteoric origin. Although these basal ice samples were not enriched in nitrate, they were occasionally enriched in dissolved phosphorus (TDP), reduced nitrogen (NH_4^+) and a second component of humic-like fluorescent DOM (C5), compared to meteoric glacier ice. The sources and/or sinks of these nutrients can therefore be spatially heterogeneous in the relatively warm subglacial systems of polythermal glaciers. Large fractions of the solutes, microbes, and nutrients derived from these subglacial systems were probably acquired directly from the underlying substrate.

While basal ice in ~~Unlike the biogeochemistry of the basal ice produced in relatively~~ warm subglacial systems appear to have acquired abundant solutes, microbes and nutrients from the underlying substrate, basal ice produced in cold-based systems acquired few biogeochemical characteristics from the underlying substrate. The cold basal ice explored in this study may have acquired some inorganic and organic nutrients from the substrate, but acquisition of other solutes or microbes appear to be limited. This cold basal ice acquired few solutes and microbes- ~~retained characteristics remarkably similar to those of meteoric glacier ice~~even though the local substrate, composed of sandstone, dolomite and limestone, and relatively well developed soils, would have been more reactive than the metasedimentary and gneiss substrate beneath the warm-based systems. ~~Although the 'cold' basal ice samples analysed in this study may have acquired some inorganic and organic nutrients from the subglacial substrate, the substrate did not appear to contribute significant solutes or microbes to the basal ice.~~ It remains unknown whether ~~the~~ the intricacies of the biogeochemical characteristics that were observed in the ~~differences between 'cold'~~cold basal ice in this study ~~and 'warm' basal ice reflect~~ result from (i) ~~differences in the~~ specific characteristics of the underlying/surrounding substrate, (ii) specific glaciological/hydrological processes that occurred during the formation of the ~~'cold'~~cold basal ice, or (iii) the effects of biogeochemical processes that occur *in situ* in ~~'cold'~~cold basal ice. Further research is required to define how the ~~'cold'~~cold basal ice at the Western Margin of the DIC developed, and to better characterize the biogeochemical processes that occur in subglacial environments where liquid water is limited. Nevertheless, findings from this study suggest that basal temperature play important roles in controlling subglacial biogeochemistry and the suite of solutes, nutrients, and microbes that are either mobilized from the substrate or produced within subglacial systems.

5 Data availability

Sequences were submitted to the National Center for Biotechnology Information Sequence Read Archive. Other data from this paper are available upon request to the corresponding author.

6 Author Contributions

AD conceptualized the study, AD and BD designed and completed the fieldwork, AM completed the DNA extractions in the laboratory, AD completed formal analysis and wrote the manuscript with reviews and edits from all authors.

7 Competing interests

The authors declare that they have no conflict of interest.

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Table 1: Number, mean and standard deviation of measures of major ions, inorganic nutrients and DOM components in glacier ice, ~~‘warm’~~warm basal ice, and ~~‘cold’~~cold basal ice and sstatistical tests between ~~‘warm’~~warm basal ice/~~‘cold’~~cold basal and glacier ice. P-values that represent significant differences ($p<0.05$) are red.

	Units	**Detection~~–~~ limit**	**Number**			**Mean**			**Standard Deviation**			**p-value**			
			Glacier ice	**~~‘Warm’~~Warm Basal**	**~~‘Cold’~~Cold Basal Ice**	**Glacier ice**	**~~‘Warm’~~Warm Basal**	**~~‘Cold’~~Cold Basal Ice**	**Glacier ice**	**~~‘Warm’~~Warm Basal**	**~~‘Cold’~~Cold Basal Ice**	**~~‘Warm’~~Warm BI vs glacier ice**		**~~‘Cold’~~Cold BI vs glacier ice**	
												T-test	**F-test**	**T-test**	**F-test**
Chemistry															
Ionic strength	µeq/L	N/A	11	12	5	15.6	241	22.0	7.13	265	10.4	0.00	0.00	0.17	0.30
SiO_2	ppm	0.02	11	12	5	0.04	0.24	0.04	0.01	0.31	0.00	0.01	0.00	0.75	0.00

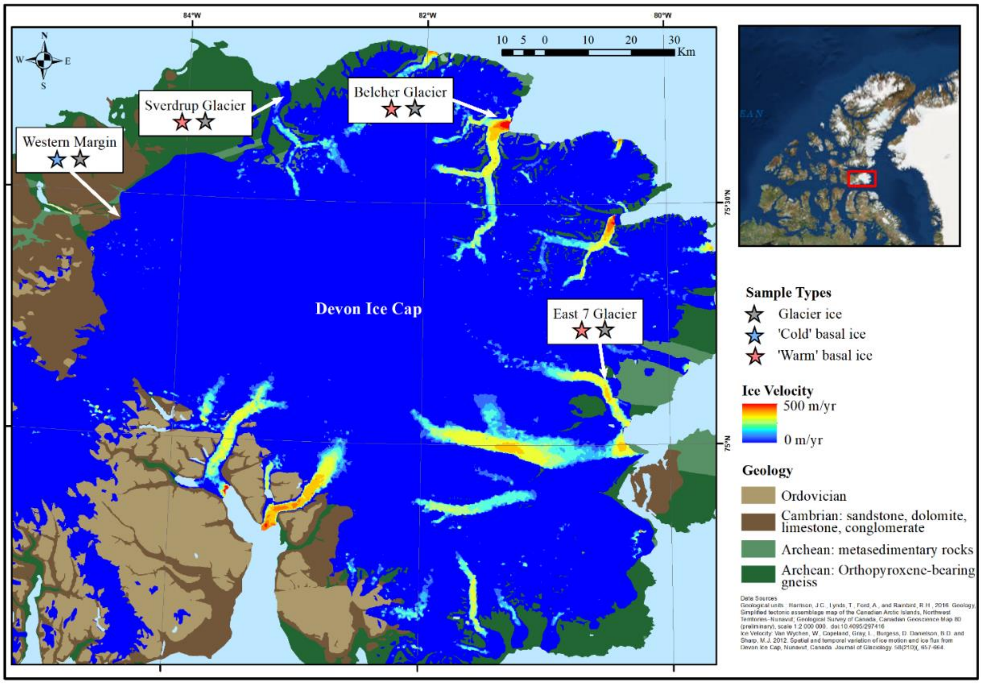
Cl^-	µeq/L	0.85	11	12	5	2.92	9.10	5.25	1.14	16.5	2.30	0.17	0.00	0.02	0.07
SO_4^{2-}	µeq/L	0.83	11	12	5	3.60	19.6	4.33	3.09	25.8	3.69	0.33	0.17	0.68	0.59
Na^+	µeq/L	0.87	11	12	5	2.97	45.9	3.57	1.94	101	1.72	0.01	0.37	0.56	0.88
K^+	µeq/L	0.26	11	12	5	0.34	9.04	0.50	0.24	7.60	0.45	0.00	0.00	0.81	0.39
Ca^{2+}	µeq/L	0.50	11	12	5	2.31	43.3	2.49	1.36	53.0	2.39	0.00	0.00	0.85	0.14
Mg^{2+}	µeq/L	0.82	11	12	5	1.43	22.3	2.97	0.83	18.3	2.57	0.00	0.00	0.09	0.00
HCO_3^-	µeq/L	0.87	11	12	5	0.52	91.8	-0.05	4.61	104	7.68	0.00	0.00	0.85	0.17
Inorganic Nutrients															
TDP	P µg/L	0.2	11	12	5	1.82	13.7	3.80	0.06	35.5	3.03	0.08	0.00	0.03	0.00
SRP	P µg/L	0.9	11	12	5	1.00	11.9	3.20	0.33	32.6	2.77	0.27	0.26	0.00	0.03
TDN	N µg/L	7	11	12	5	44.8	44.3	134	16.0	24.9	138	0.96	0.17	0.03	0.11
NO_2^-+ NO_3^-	N µg/L	2	11	12	5	11.9	9.08	6.00	5.99	10.7	3.67	0.00	0.00	0.06	0.36
NH_4^+	N µg/L	3	11	12	5	24.6	23.6	90.2	8.81	17.4	110	0.86	0.04	0.03	0.04
Organic Nutrients															
DOC	ppm	0.06	11	12	5	0.15	0.49	0.40	0.06	0.59	0.25	0.12	0.61	0.00	0.68
DOM C1	FI	N/A	10	9	5	3.24	3.72	3.22	2.94	3.71	2.24	0.76	0.50	0.99	0.63
DOM C2	FI	N/A	10	9	5	5.27	6.40	3.28	4.27	4.41	1.25	0.58	0.91	0.33	0.03
DOM C3	FI	N/A	10	9	5	1.63	6.44	21.2	1.46	6.48	28.5	0.04	0.00	0.00	0.00
DOM C4	FI	N/A	10	9	5	2.96	4.69	2.74	2.39	3.49	0.94	0.22	0.28	0.85	0.09
DOM C5	FI	N/A	10	9	5	1.95	4.78	6.77	2.25	5.48	5.29	0.15	0.02	0.03	0.03
Microbial Assemblages															
Acidobacteria	%	N/A	5	11	3	1.1	3.2	1.5	0.84	3.6	1.2	0.73	0.70	0.54	0.53
Actinobacteria	%	N/A	5	11	3	17	30	15	6.4	22	21	0.81	0.75	0.86	0.05
Bacteroidetes	%	N/A	5	11	3	14	9.2	16	5.2	15	18	0.00	0.03	0.82	0.04
Chloroflexi	%	N/A	5	11	3	0.7	8.1	6.1	0.51	5.6	9.1	0.01	0.00	0.20	0.00
Cyanobacteria	%	N/A	5	11	3	16	0.07	7.8	17	0.11	7.5	0.04	0.00	0.47	0.34
Firmicutes	%	N/A	5	11	3	1.0	10	0.06	1.9	15	0.10	0.10	0.24	0.54	0.22
Gemmatimonadetes	%	N/A	5	11	3	0.39	3.9	0.02	0.23	4.9	0.02	0.01	0.01	0.04	0.01
Proteobacteria	%	N/A	5	11	3	43	30	42	16	17	9.1	0.17	0.99	0.92	0.52

Table 2: Excitation and emission maxima for the 5 component PARAFAC model, including the identification of each component

	Ex (nm)	Em (nm)	Description	# of OpenFlour matches*
C1	276	300	**Protein (tyrosine)-like fluorescence** that may originate from the degradation of terrestrially-derived humic-like DOM (Coble, 2007; Coble et al., 1998; Mopper and Schultz, 1993; Stedmon and Markager, 2005) and microbial exudates (Smith et al., 2017).	0

C2	230 (286)	325	**Protein (tryptophan)-like fluorescence** (Coble et al., 1998; Lakowicz, 1999) that has been liked to microbial activity (Elliott et al., 2006) and is associated with the autochthonous production of DOM in various environments (Coble, 1996; Fellman et al., 2008; Mopper and Schultz, 1993; Yamashita and Tanoue, 2003)	3
C3	232 (336)	460	**Humic (fulvic acid)- like fluorescence** derived from higher plants (terrestrial) and/or organic matter with a certain degree of microbial processing (Cory and McKnight, 2005; Osburn et al., 2016)	10
C4	298 (231)	410	**Humic-like fluorescence** that can be highly processed terrestrial DOM with low biolability (Lapierre and Del Giorgio, 2014)	0 (4**)
C5	237 (317)	395	**Humic-like fluorescence** from marine (Coble, 1996) and terrestrial (Stedmon et al., 2003) environments and can be affiliated with microbial reprocessing of organic matter (Stedmon and Markager, 2005)	12

* >95% certainty
** 90-95% certainty



Data Sources
Geological units : Harrison, J.C., Lynds, T., Ford, A., and Rainbird, R.H., 2016. Geology, Simplified tectonic assemblage map of the Canadian Arctic Islands, Northwest Territories–Nunavut; Geological Survey of Canada, Canadian Geoscience Map 80 (preliminary), scale 1:2 000 000. doi:10.4095/297416
Ice Velocity: Van Wychen, W., Copeland, Gray, L., Burgess, D. Danielson, B.D. and Sharp, M.J. 2012. Spatial and temporal variation of ice motion and ice flux from Devon Ice Cap, Nunavut, Canada. Journal of Glaciology. 58(210)(, 657-664.

Figure 1: Study Site indicating the geology of the surrounding substrate [*Harrison et al.*, 2016] and flow velocity of the Devon Ice Cap [*Van Wychen et al.*, 2012].—_Samples were collected from 3 polythermal glaciers with relatively fast flowing ice that are surrounded by Archean bedrock, and two locations along the relatively slow flowing cold-based section of the Western Margin.

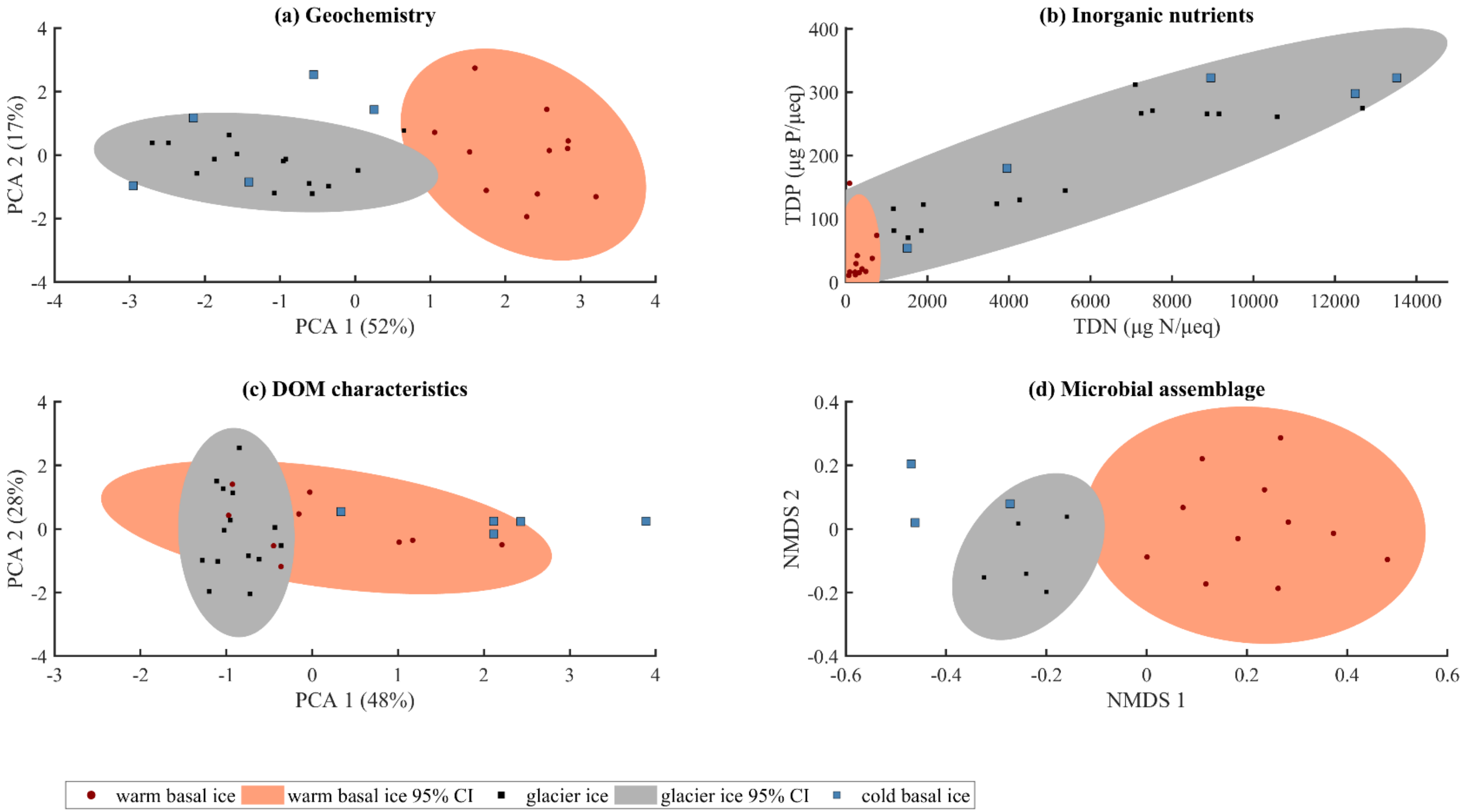


Figure 2: Summary of a) major ion composition, produced by PCA using the contribution of each major ion to the solute load, with each major ion normalized to its mean and variance b) inorganic nutrients relative to the solute load (TDP (µg P/µeq) and TDN (µgN/µeq)) (c) character of dissolved organic matter determined by principle component analysis using the relative contributions of the 5 modelled fluorescent components, with each component normalized to its mean and variance and d) microbial assemblage structure determined by nonmetric multidimensional scaling (NMDS) of Bray-Curtis distance measure using 16S rRNA gene sequencing (stress=0.12).

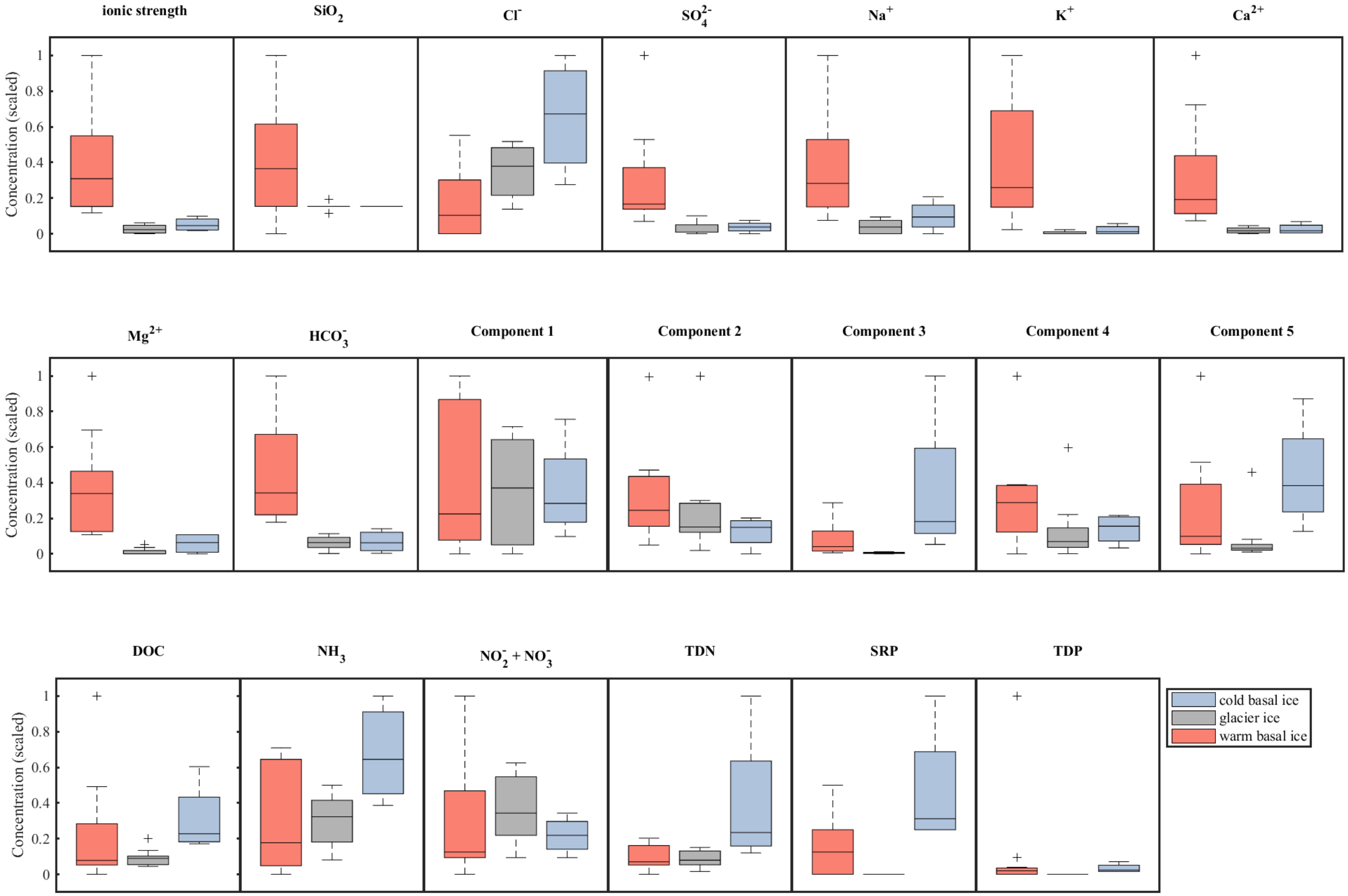


Figure 3: Relative abundance and range in concentrations of major ions (top), organic nutrients (middle) and inorganic nutrients (bottom) in basal ice and glacier ice. Data were scaled to the interval 0-1 and boxplots indicate the median, 25th and 75th percentiles, whiskers indicate the most extreme datapoints not considered outliers and outliers are indicated with a '+' symbol.

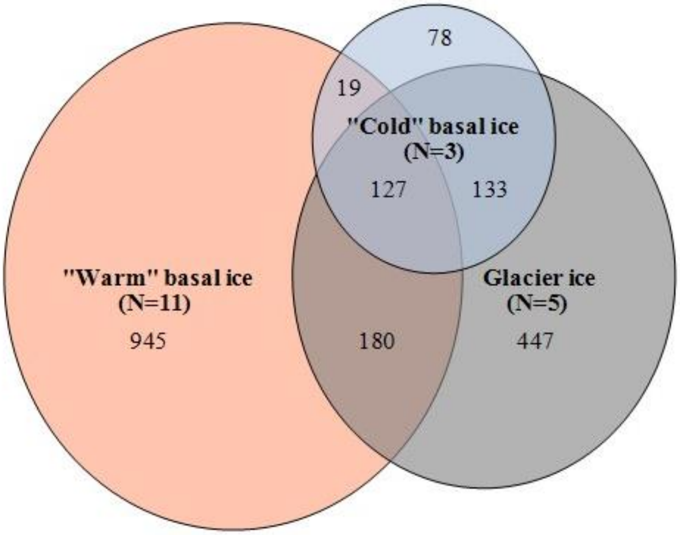


Figure 4: Venn Diagrams showing overlap in membership between the microbial assemblages observed in ~~‘warm’~~warm basal ice, glacier ice, and ~~‘cold’~~cold basal ice samples.~~–~~ Numbers represent the number of operational taxonomic units (OTUs) that are unique to each environment or shared between environments.