Storage and export of microbial biomass across the western Greenland Ice Sheet

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The Greenland Ice Sheet harbours a wealth of microbial life, yet the total biomass stored or exported from its surface to downstream environments is unconstrained. Here, we quantify microbial abundance and cellular biomass flux within the near-surface weathering crust photic zone of the western sector of the ice sheet. Using groundwater techniques, we demonstrate that interstitial water flow is slow (~10⁻² m d⁻¹), while flow cytometry enumeration reveals this pathway delivers 5 × 10⁸ cells m⁻² d⁻¹ to supraglacial streams, equivalent to a carbon flux up to 250 g km⁻² d⁻¹. We infer that cellular carbon accumulation in the weathering crust exceeds fluvial export, promoting biomass sequestration, enhanced carbon cycling, and biological albedo reduction. We estimate that up to 37 kg km⁻² of cellular carbon is flushed from the weathering crust environment of the western Greenland Ice Sheet each summer, providing an appreciable flux to support heterotrophs and methanogenesis at the bed.
The Greenland Ice Sheet sequesters and exports organic carbon\(^1-4\), yet many of the associated biogeochemical processes and pathways remain largely undocumented. One important carbon source is the ice sheet surface\(^5-6\), which is host to diverse and active microbial assemblages\(^7-10\). Recent work has highlighted the global significance of these supraglacial microbial communities: they hold key roles in amplifying ice melt by lowering bare-ice albedo\(^9,11\) and driving biogeochemical cycling of carbon\(^1,12-14\), nitrogen\(^15,16\) and anthropogenic contaminants\(^18,19\).

During seasonal melt, across Greenland’s 220 × 10\(^3\) km\(^2\) bare-ice ablation area\(^20\), microbes, organic and inorganic debris and associated nutrients are washed downslope by the supraglacial meltwater drainage networks that develop\(^21\). These networks commonly terminate in moulins that provide meltwater pathways to the subglacial environment\(^22,23\). Such seasonal meltwater transfer affects the labile, bioavailable carbon exported from the ice sheet\(^3,4,24\), and ultimately influences the microbial community composition and nutrient supply to downstream aquatic and marine ecosystems\(^24,25\). However, supraglacial drainage networks comprising streams, rivers and lakes account for a small fraction of the total abating area of the ice sheet\(^26-28\) and the majority of summer-season runoff is generated over extensive bare-ice areas between supraglacial meltwater channels\(^29\). The hydrological functioning of this wide-spread interfluvial area is unconstrained\(^28,30\) and its role in modulating the delivery of microbes, organic and mineral dusts and debris, and associated nutrients to the subglacial environment remains unquantified.

The bare-ice interfluve area is characterised by the presence of an up to ~1 m thick, porous ice weathering crust, that forms due to subsurface shortwave radiation penetration, melting and percolation. In west Greenland, this weathered near-surface ice exhibits an effective porosity of up to 47% with a specific water storage potential of up to 0.18 m\(^2\) (ref.\(^{31}\)) and has an assumed meltwater throughflow velocity of ~1–10 m d\(^{-1}\) (ref.\(^{28}\)). Smith et al.\(^{32}\) demonstrate that the weathering crust has an important hydrological function and delays surface meltwater runoff, challenging the commonly held assumptions of efficient and rapid supraglacial drainage. Furthermore, the weathering crust photic zone is increasingly recognised as an important microbial habitat\(^33-35\), yet little is known about how, where and what quantities of microbial biomass are stored and produced within, or exported from, the weathering crust to downstream environments and ecosystems.

Here, we present the first quantitative assessment of microbe transport through the near-surface of the Greenland Ice Sheet and estimate the equivalent carbon fluxes exported from the weathering crust to the subglacial environment. In July 2014, at a site located on ice sheet’s western margin (\(67^\circ\) 04.78’N, \(49^\circ\) 24.08’W: Fig. 1a), we applied standard groundwater techniques to determine the conductivity of the near-surface ice\(^36\) and employed flow cytometry to quantify the abundance of microbes entrained in the meltwater within the weathering crust. A first-order, catchment-scale model of microbial cell transport was developed by applying our observations across a high-resolution digital elevation model (DEM) derived from unmanned aerial vehicle (UAV) surveys (Fig. 1b). Our analysis reveals that within the overlooked supraglacial habitat of the weathering crust, in situ cellular accumulation exceeds microbial export; a finding that has significant implications for surface biogeochemical dynamics, carbon sequestration and cycling, and regional albedo reduction.

### Results and discussion

#### Meteorology and meltwater production

The study period of July 23 to 29, 2014 was characterised by predominantly clear-sky conditions with a mean two-metre air temperature of 1.9\(^\circ\)C (Fig. 2) and consistent diurnal melt variability, typically peaking at between 3 and 4 mm h\(^{-1}\) at 13:00–14:00. Ninety local cryoconite holes and 57 shallow experimental auger holes indicated that the near-surface water table was located 7.5 (± 3.9) to 10.9 (± 5.4) cm below the ice surface, respectively. A total of 47 successful recharge experiments were conducted, yielding a mean hydraulic conductivity (\(K\)) of 0.28 (± 0.34) m d\(^{-1}\) (Fig. 2d). The \(K\)-values derived from 23–26 cm and 34–36 cm deep auger holes are from statistically similar populations (\(U = 522.5, p = 0.37\)). Comparison of \(K\) against melt rate (Fig. 3a) and daily melt cycle timing (Fig. 3b) indicates there is no strong interdependency, although water table height within the weathering crust correlates positively with \(K\) (\(p = 0.66, p < 0.001\)) it is not associated with the instantaneous melt rate (\(p = –0.12, p = 0.43\)).

#### Microbial abundance and mobility

The 73 water samples recovered from both fully and partially recharged auger holes in bare-ice show a mean microbial abundance of 2.28 × 10\(^4\) cells mL\(^{-1}\) (±1.91 × 10\(^4\) cells mL\(^{-1}\) standard deviation) (Fig. 2e). Abundance exhibits no significant correlation with contemporaneous melt rate (\(p = 0.07, p = 0.53\)), but at the 95% confidence level suggests a slight negative relationship with time since daily peak melt (\(p = –0.26, p = 0.03\)), where both melt variables provide proxies for diurnal energy receipt and weathering crust development (see Fig. 3c, d). The cell size distribution from recharge waters (Fig. 4) reveals that the dominant size of SYBR Gold stained cells was 1–2 \(\mu\)m, representing 50% (± 7.0% standard deviation) of the suspended microbial abundance. The <1 \(\mu\)m category represents a mean of 19% (± 5.5%) of the total microbial abundance, but may include large viruses, thereby overestimating the true cell count. The microbial abundance in each of the six size classes were moderately to highly correlated (0.28 < \(r < 0.93, p < 0.05\)).

To examine the association between microbial abundance and ice surface hydrology, 26 completed recharge experiments were paired with coincident enumerations and reveal an inverse relationship between the hydraulic conductivity and microbial abundance, described by an exponential decay function (coefficient of determination \(r^2 = 0.50, p < 0.001\): Fig. 5a). To differentiate between bacteria (and archaea) and larger algae, a 10 \(\mu\)m size classification threshold was applied\(^{37}\). Examination of the association between \(K\) and abundance independently for these nominal bacteria and algae classes highlights similar non-linear, inverse relationships (respectively, \(r^2 = 0.51, p < 0.001\) and \(r^2 = 0.34, p < 0.002\): Fig. 5b), but with a reduced rate of algal abundance decline as the hydraulic conductivity increases.

#### Microbial and carbon fluxes

To investigate the microbial fluxes within our supraglacial catchment, we assimilate our field-based measurements with a 1 m horizontal resolution DEM (Fig. 1b). Based on observations of the water table, we infer that porous ice extends to ~0.4 m depth with a hydrologically active, saturated weathering crust thickness of 0.29 m; by applying an effective porosity (\(\phi\)) of 22% (ref.\(^{31}\)), the cross-sectional water flow area can be determined. Considering saturated transport through the weathering crust under Darcian flow\(^{28,36}\), the throughflow velocity \(v_t\) is given by:

\[
v_t = K\Delta h / \phi
\]

where \(\Delta h\) is the average local surface slope (0.022 m m\(^{-1}\)). With a mean value for hydraulic conductivity (\(K\)) of 0.28 m d\(^{-1}\), we determine a spatially averaged weathering crust throughflow velocity of 0.028 m d\(^{-1}\) and a specific meltwater discharge of 0.0018 m\(^3\) d\(^{-1}\). Typically, at our study site located within the western sector of the Greenland Ice Sheet, ablating bare-ice and, by inference, its hydraulically active weathering crust is exposed, on average, for around 70 days (or 76%) of the summer melt season\(^{20,38}\). Accordingly, using our derived mean and maximum \(v_t\) values, respectively,
only 22 to 66% of the catchment’s weathering crust area delivers interstitial meltwater directly to the stream network seasonally (Fig. 1b).

From aerial photogrammetry of our study catchment, we calculate a bare-ice weathering crust area of \(6.84 \times 10^4\) m\(^2\) drained immediately (i.e., \(<1\) m) into the stream network. Coupling this stream bank area with our estimates of mean throughflow velocity and mean microbial abundance we derive a daily microbial cell flux of \(2.80 \times 10^{12}\), which equates to \(5.73 \times 10^{12}\) cells m\(^{-2}\) d\(^{-1}\) when scaled across the entire catchment. Using our uppermost observed K-value, the specific discharge, total and specific cell fluxes increase to 0.008 m\(^3\) d\(^{-1}\), 1.27 \(\times\) \(10^{13}\) cells d\(^{-1}\) and 2.61 \(\times\) \(10^{13}\) cells m\(^{-2}\) d\(^{-1}\).

To convert the daily cell fluxes to biomass estimates (see Methods), we apply a constant carbon content to derive a minimum, and a biovolume ratio to determine a maximum. Employing these approaches, for a conservative throughflow and fast rills and micro-channels\(^43\), yielding more rapid transit hydrological functions of the slow interstitial near-surface matrix, and karstic sandstone\(^39\), but are typically an order of magnitude lower than that reported for unconsolidated, saturated silt and karstic sandstone\(^39\), but are typically an order of magnitude lower than that reported for firn\(^40\). Our hydraulic conductivity compares well to other glacier surfaces across the northern hemisphere\(^36\), but is somewhat lower than assessments made using different methods\(^41,42\), and two orders of magnitude less than that theoretically estimated for Greenland by Yang et al.\(^28\).

We propose that their coarse, 3 m resolution DEM and larger (>2000 m\(^2\)) stream-defining contributing area threshold aggregates the two hydrological functions of the slow interstitial near-surface matrix, and fast rills and micro-channels\(^43\), yielding more rapid transit times. The hydrological function of the weathering crust is further compounded by macro-spatial variations in hydrodynamics, the saturated and unsaturated zones, near-surface fracturing processes and ice structure and crystal sizes\(^31,32,36,44\). Given these intrinsic environmental controls, the derivation of a spatially and/or temporally consistent estimate of the hydraulic conductivity from coarse resolution topographic metrics without any ground measurements is problematic.

Unsurprisingly, our throughflow velocities of <0.13 m d\(^{-1}\) for the weathering crust are markedly lower than supraglacial stream and river velocities of \(10^4\)–\(10^6\) m d\(^{-1}\) (ref. 45,46), but are similar to those reported for low-gradient ablating sea ice surfaces\(^47\).

Though slow, the throughflow velocities could increase if the water table within the weather crust rose into the higher porosity uppermost unsaturated ice layer\(^31,44,48\). Our calculated meltwater efflux from the weathering crust to the stream network represents a relatively small proportion of the total discharge in the supraglacial channels, emphasising the potential importance of

Weathering crust hydrology. Our analysis demonstrates that an extensive saturated porous layer, with a water table extending from \(<0.1\) m below the surface, is hydraulically active in a study catchment located on the ablating western margin of the Greenland Ice

Sheet. Calculations of the weathering crust’s hydraulic conductivity of \(10^{-6}\)–\(10^{-5}\) m s\(^{-1}\) and throughflow velocity of \(10^{-7}\)–\(10^{-6}\) m s\(^{-1}\) are comparable to those reported for unconsolidated, saturated silt and karstic sandstone\(^39\), but are typically an order of magnitude lower than that reported for firn\(^40\). Our hydraulic conductivity compares well to other glacier surfaces across the northern hemisphere\(^36\), but is somewhat lower than assessments made using different methods\(^41,42\), and two orders of magnitude less than that theoretically estimated for Greenland by Yang et al.\(^28\). We propose that their coarse, 3 m resolution DEM and larger (>2000 m\(^2\)) stream-defining contributing area threshold aggregates the two hydrological functions of the slow interstitial near-surface matrix, and fast rills and micro-channels\(^43\), yielding more rapid transit times. The hydrological function of the weathering crust is further compounded by macro-spatial variations in hydrodynamics, the saturated and unsaturated zones, near-surface fracturing processes and ice structure and crystal sizes\(^31,32,36,44\). Given these intrinsic environmental controls, the derivation of a spatially and/or temporally consistent estimate of the hydraulic conductivity from coarse resolution topographic metrics without any ground measurements is problematic.

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Flow contributions from within the unsaturated layer and micro-channels, and which merits further investigation. Nonetheless, the slow transit of water through the saturated weathering crust hydraulically acts to delay surface meltwater runoff and impedes any associated microbe and nutrient transport.

Microbial abundance and mobility. Our estimates for microbial abundance in the recharge water compare well to other supraglacial enumerations using flow cytometry as well as alternative methods. We derive a microbial load of 1.46 × 10^9 cells m^{-2} for the hydraulically active weathering crust, with a minimum of 1.46 × 10^8 cells m^{-2} (Table 1) taken as the background load. The three standard methods applied to estimate net biomass stored in the near-surface yield a range of 0.02 to 4.3 kg C km^{-2} excluding the largest algae, or 0.03 to 14.0 kg C km^{-2} including these >15 µm cells. Assuming the allometric biomass method provides the most robust calculation, our best conservative estimate of the interfluval weathering crust carbon load is 3.6 kg C km^{-2}, or 12.6 kg C km^{-2} if algae are included. If we consider the inclusion of elevated microbial abundance related to discrete dust concentrations or

Fig. 2 Time-series plots of hydrometeorological variables at the S6 weather station location during the study period in 2014. a Record of incident shortwave radiation and daily mean surface albedo with associated temporal trends before and after the cloudy conditions on day of year (DOY) 209. b Air temperature over the 9-day study period. c Estimated ice melt according to a simple point-based energy balance model (see Methods). d The derived weathering crust hydraulic conductivity (K) values for 26 and 36 cm deep auger holes. e Microbial abundance in the recharge water samples associated with individual bail-recharge experiments; note the 10^5 cells mL^{-1} threshold (dashed line) used to define samples as outliers (see Methods).
algal blooms within our sample set (see Methods), the mean abundance is increased to $6.12 \times 10^4$ cells mL$^{-1}$, and our load rises to $3.9 \times 10^9$ cells m$^{-2}$ or 0.05 to 34.1 kg C km$^{-2}$.

The contrast in the hydraulic conductivity and abundance relationships between bacterial and algal categories suggests size-selective mobilisation: either bacteria are more rapidly depleted or excluded from transport as throughflow increases, or microbe availability is controlled by processes delivering or releasing cells from the ice surface or englacial environment. We suggest that these controlling processes may include mechanical filtering within the weathering crust ice matrix$^{49,53}$; extrusion of exopolysaccharides (EPS) or other critical compounds$^{54-56}$; or hydrological elution (flushing) with increased melt, analogous to the ‘first flush effect’$^{57}$ at diurnal, synoptic and/or seasonal timescales as alluded to by the weak correlation between abundance and time since daily peak melt (Fig. 3d).

Microbial export from western Greenland’s weathering crust.

At our study catchment, we estimate that between $1.4 \times 10^{14}$ and $6.2 \times 10^{14}$ cells were liberated from the interfluvе area to supraglacial stream transport during the 2014 ablation season, which had a bare-ice duration of 68 days. These values equate to 0.3 and 1.2 kg C (or 9.2 and 21 kg C if large algae are included) using an allometric best-estimate of biomass. If we consider our study catchment to be representative of all the moulin terminating supraglacial catchments across the ice sheet’s western ablation zone$^{22}$, upscaling our catchment data suggests that between $1.8 \times 10^{18}$ and $8.3 \times 10^{18}$ microbial cells were delivered to the subglacial drainage system over the 2014 ablation season. Accounting for the different biomass estimation methods, this equates to a seasonal carbon delivery of 25 kg C to $3.0 \times 10^5$ kg C from western Greenland’s ablation zone under a mean throughflow velocity (or 42 kg C to $1.7 \times 10^4$ kg C if large algae are included). These biomass assessments increase to $10^2$ to $10^5$ kg C under the maximum observed throughput velocity.

Using the mean hydraulic conductivity and the allometric biomass conversion, we calculate that over the entire 2014 ablation season 0.3 to 1.1 kg C km$^{-2}$ of microbial cellular carbon was delivered from the supraglacial drainage network to the subglacial environment in western Greenland. However, weathering crust development and biomass transport are defined by the cumulative shortwave radiation receipt and the length of the bare-ice melt season. Therefore, to contextualise our observations in 2014, a typical or average melt year, we recalculate our biomass fluxes for 2006 and 2012: anomalously low and high melt years. Using the mean throughflow velocity and all the biomass estimates, we derive a flux of between $7.2 \times 10^{-4}$ kg C km$^{-2}$ and 0.5 kg C km$^{-2}$ for the 2006 low melt year. For 2012, which sustained high melt, these estimates increase fourfold to $3.1 \times 10^{-3}$ kg C km$^{-2}$ and 2.1 kg C km$^{-2}$. Refining these biomass export estimates on a by-catchment basis, we find a mean of 9.8 kg C km$^{-2}$ and a maximum of 21.8 kg C km$^{-2}$ in 2014, with

![Fig. 3 Scatter plots comparing melt conditions, near-surface hydraulic conductivity and microbial abundance.](https://example.com/fig3.png)

**Fig. 3** Scatter plots comparing melt conditions, near-surface hydraulic conductivity and microbial abundance. **a** Relationship between hydraulic conductivity ($K$) and coincident melt. **b** Association between $K$ and time relative to peak melt. **c** Scatter plot of microbial abundance and coincident melt. **d** Scatter plot of microbial abundance and time relative to peak melt. Sample points are grouped and shaded according to the day of year (DOY) collection date, and those assessed as outliers, with $>1 \times 10^5$ cells mL$^{-1}$ (see Methods), are shown with hollowed markers above a dashed line.
Microbial accumulation in the weathering crust. Our low observed throughflow velocity of 0.28 m d\(^{-1}\) coupled with a mean distance-to-stream index across our catchment of 7.24 ± 6.6 m (Fig. 1b), suggests microbes will experience extended transit times through the weathering crust photic zone. As this transit time exceeds typical 4 d doubling times determined for bacteria\(^{50}\) and algae\(^{58}\) in glacial meltwaters, we propose that the weathering crust is deems a locus for microbially-driven biogeochemical processes, carbon and nutrient transformations, and community growth. The ablation ice surface continually replenishes the weathering crust with emergent and deposited microbes, and there is an ongoing nutrient supply associated with both aeolian-derived and emergent mineral dusts. Solute-rich water films surrounding individual ice crystals are also actively replenished throughout the summer ablation season\(^{53}\).

A range of microbial biomass doubling times from 1 to 5.5 days\(^{12,34,50,58}\) have been derived for supraglacial habitats, with 11 days determined for the photic zone community sampled from an Alaskan glacier’s weathering crust\(^{35}\). Taking the lowest concentration of cells observed in recharge waters (2.3 × 10\(^3\) cells mL\(^{-1}\)) as a conservative estimate of antecedent near-surface microbial load, we calculate microbial abundance increases of

\[
\begin{align*}
\text{Range} & = 10^2 \text{ to } 10^6 \\
\text{Median} & = 10^3 \\
\text{Mean} & = 10^4 \\
\text{25th-75th percentile} & = (10^1, 10^5)
\end{align*}
\]

\[
\begin{align*}
\text{Cell size class (µm)} & = 0.25 - 2.0 \\
\text{Abundance (cells mL}^{-1}) & = 10^2 - 10^6
\end{align*}
\]

\[
\begin{align*}
\text{SYBR stained cell size class (µm)} & = 0.25 - 1.0 \\
\text{Abundance (cells mL}^{-1}) & = 10^2 - 10^6
\end{align*}
\]

Fig. 4 Microbial abundance in weathering crust water samples according to cell size. Microbial size fractions and summary statistics for \(n = 73\) independent meltwater samples drawn from the saturated zone within the weathering crust; the nominal classes of bacteria and algae are shown in blue and red, respectively. Samples with total microbial abundance \(>10^5\) cells mL\(^{-1}\) were excluded (\(n = 10\)).

\[
\text{Bacterial size classes:} \\
\text{25th-75th percentile} \\
\text{Mean} \\
\text{Median} \\
\text{Range}
\]

\[
\text{Algal size classes:} \\
\text{25th-75th percentile} \\
\text{Mean} \\
\text{Median} \\
\text{Range}
\]

4.1 kg C km\(^{-2}\) and 16.6 kg C km\(^{-2}\) in 2006, and 15.9 kg C km\(^{-2}\) and 23.6 kg C km\(^{-2}\) in 2012; inclusion of large algae more than doubles these seasonal biomass flux values.

The wide range of values in our assessment of cellular carbon delivery from the weathering crust emphasises its dependence on the melt season duration and intensity, the near-surface hydraulic conductivity of glacier ice, the representative microbial abundance in transport, the biomass conversion utilised, and the treatment of larger algal size fractions. Moreover, the definition of the supraglacial stream network that transports the cells released from the weathering crust also influences these estimates; a simple linear relationship exists between the seasonal mass of delivery from the weathering crust emphasises its dependence on

\[
\begin{align*}
\text{Conductivity} & = (0.1 \pm 0.06) \times 10^{-3} \text{ m d}^{-1} \\
\text{Melt season duration} & = 60 \pm 10 \text{ days}
\end{align*}
\]

\[
\begin{align*}
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\[
\begin{align*}
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\end{align*}
\]

Fig. 5 Relationships between microbial abundance and hydraulic conductivity \((K)\). a Scatter plot of hydraulic conductivity \((K)\) and total microbial abundance for \(n = 29\) successful, independent recharge experiments showing ordinary least squares (OLS) exponential regression relationship and coefficient of determination \((r^2)\) excluding the outlying samples \((n = 3)\) with \(>1 \times 10^5\) cells mL\(^{-1}\) (see Methods) shown with hollowed markers above a dashed line. b Scatter plot, as in a, of \(K\) against abundance for the size-defined bacterial and algal classes, again indicating the non-linear OLS regression line and \(r^2\), and outlying samples indicated with hollow markers.

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1.5 × 10^2 to 2.3 × 10^3 cells mL\(^{-1}\) d\(^{-1}\) using published doubling times. This translates to between 1.4 × 10\(^{-4}\) and 1.4 kg km\(^{-2}\) d\(^{-1}\) of accumulated organic carbon (i.e., the increase in cell numbers) in the weathering crust: the minimum estimate assumes 11 fg per cell, and an 11 d doubling time (excluding large algae), while the maximum includes >15 μm algal cells, and assumes a 1 d doubling time with constant biovolume ratios (see Table 1).

### Table 1 Catchment-wide microbial abundance and carbon biomass estimated using bacterial and algal cell constants, allometric and constant ratios, and using published supraglacial community doubling times over a single day residence time.

| Weathering crust meltwater: | Minimum | Mean |
|-----------------------------|---------|------|
| Cells per unit area (m\(^{-2}\)) | 1.46 × 10^9 | 1.23 × 10^9 |
| Constant cell mass 11+153 fg | 2.14 (3.48) | 3.81 (6.1) |
| Constant cell mass 20+260 fg | 361 (1268) | 361 (1268) |
| Allometry\(^{12}\) | 423 (1405) | 423 (1405) |
| Constant biovolume ratio\(^{16,18}\) | 429 (1390) | 429 (1390) |

### Throughflow export:

| Throughflow export: | Minimum | Mean |
|---------------------|---------|------|
| Cells per unit area (m\(^{-2}\)) | 1.46 × 10^9 | 1.23 × 10^9 |
| Constant cell mass 11+153 fg | 2.14 (3.48) | 3.81 (6.1) |
| Constant cell mass 20+260 fg | 361 (1268) | 361 (1268) |
| Allometry\(^{12}\) | 423 (1405) | 423 (1405) |
| Constant biovolume ratio\(^{16,18}\) | 429 (1390) | 429 (1390) |

### In situ biomass accumulation, assuming published doubling times (d): 1 d\(^{84}\), 1+4 d\(^{34,58}\), 4 d\(^{50,58}\), 11+4 d\(^{35,58}\), 11 d\(^{35}\)

- Cells per unit area (m\(^{-2}\)) | 2.29 × 10^2 | 2.14 × 10^2 | 2.14 × 10^2 | 4.34 × 10^2 | 1.72 × 10^2 | 1.49 × 10^2 |
- Constant cell mass 11+153 fg | 1.38 (0.62) | 1.58 (1.84) | 2.85 (3.31) | 0.40 (0.66) | 0.19 (0.44) | 0.14 (0.23) |
- Constant cell mass 20+260 fg | 6.44 (226) | 7.14 (251) | 119 (312) | 68.5 (240) | 51.1 (214) | 23.5 (82.4) |
- Allometry\(^{12}\) | 432 (1405) | 432 (1405) | 432 (1405) | 81.8 (266) | 57.6 (232) | 28.1 (91.4) |
- Constant biovolume ratio\(^{16,18}\) | 76.9 (250) | 71.4 (251) | 119 (312) | 81.8 (266) | 57.6 (232) | 28.1 (91.4) |

Implications for the carbon cycle of the Greenland Ice Sheet.

Our observations of microbial abundance at the S6 site resonates with those previously reported elsewhere for supraglacial meltwaters\(^{34,55,49,30}\) confirming that the ice sheet’s weathering crust is a biologically-active habitat. Our study catchment suggests that the near-surface weathering crust in western Greenland exhibits an in situ storage of 1.5 × 10^15 cells km\(^{-2}\), equivalent to between 0.02 and 14.0 kg km\(^{-2}\), depending on the biomass conversion applied. This near-surface habitat is hydrologically active and characterised by protracted residence times owing to slow transport of meltwater through the spatially extensive porous interfluve area. To improve models of near-surface microbial transport, it is essential to explore the microbe entrainment and transport-controlling environmental characteristics (such as local ionic strength, water pH, pore space configuration and roughness, as seen in other porous media\(^{60}\)) and biophysical responses\(^{54-56}\). For example, the crystal size and dust content of Greenland’s ablation area is known to vary, in part due to the era when the emergent ice was formed\(^{61}\); such properties will influence spatial patterns in surface hydraulic conductivity and microbe entrainment. Nonetheless, the mean near-surface weathering crust hydraulic conductivity measured across the study catchment, during a typical Greenland melt season\(^{62}\), compares well to other supraglacial evaluations\(^{36}\), and yields a specific daily microbial flux of only 4.1 × 10^7 cells. Here, we expand on three core implications of this low rate of near-surface cellular biomass transport: the fluvial export of biomass from the ice sheet surface, the accumulation of biomass in the weathering crust, and the associated supraglacial carbon cycling.

Across an area of ~14 × 10^3 km\(^2\) in western Greenland during 2014, our allometric best-estimate of the ablation season biomass export from the surface weathering crust to moulins descending into the ice sheet interior is 3.8 to 15.5 tonnes of cellular carbon. This highlights the importance of the flushing of organic matter from the ice sheet’s surface to the subglacial environment. In low-melt years, these biomass estimates can decrease by an order of magnitude, while in high-melt years the values can double. However, current understanding of the nature of meltwater routing, transit times and the redox conditions in Greenland’s subglacial environment is incomplete. Therefore, we propose that the transport and potential subglacial deposition and storage of cellular organic carbon and associated compounds by inefficient basal drainage networks enhances microbe-water-rock interaction times and ratios, and provides a viable and contributory source of carbon for the support of heterotrophs\(^{25}\) and for methanogenesis\(^{63}\) at the ice sheet bed. Moreover, with knowledge that at least a portion of the weathering crust communities are active\(^{34,56,58}\), through their export from the supraglacial environment, they may deliver functionality to, and inoculate downstream sub- and pro-glacial aquatic systems. It is also established that the weathering crust evolves and decays, respectively, under clear-sky and cloudy or rainfall-dominated conditions\(^{48}\), consequently, the synoptic and seasonal patterns, and future of
supraglacial cellular biomass export warrant further investigation given the increasing clear-sky ablation season phases, expanding bare-ice area and/or more frequent rainfall events forecast for Greenland under future atmospheric warming. The abundance and proliferation of microbial cells across the bare-ice ablation zone is dependent on the duration of the melt season and cumulative shortwave irradiance. Our findings highlight how cell export from the ice surface is also conditioned by these environmental variables indicating that, during high melt years, two competing amplification mechanisms interact at seasonal time-scales: in situ microbial biomass accumulation and hydrological export both increase. Nonetheless, our assertion that cellular biomass export lies below the equivalent cellular load or estimated accumulation is of particular significance given the biological-darkening of the ice sheet (bio-albedo), where microbial abundance strongly influences the bare-ice reflectivity, darkens surface ice and enhances surface melt cycles. The disparity between the accumulation and export of cellular biomass across the western sector of the ice sheet also imparts a number of biogeochemical cycling processes. For example, with cryoconite holes and hydraulically linked to the porous weathering crust, it is unknown whether these features represent biomass sinks where a proportion of the entrained microbes within the near-surface become bound to cryoconite granules and are removed from the water column. Carbon cycling within the weathering crust itself is also promoted through cell mortality, from grazing by protists, viral lysis and photolysis. Indeed, the cycling of organic carbon and exudation or release of dissolved organic carbon (DOC) by microbes is commonly reported in supraglacial meltwaters and is evidenced by elevated DOC in near-surface ice. There will likely be a preference for the cycling of new, labile, rather than older, recalcitrant, ‘fossil’ carbon. Moreover, the extended residence time of microbes within the weathering crust can also account for DOC consumption. Combined, these processes will modulate the organic carbon and associated compounds supplied to subglacial and downstream environments. Given geophysical evidence of saturated sediments at least 1 m thick beneath the western Greenland Ice Sheet, coupled with indications of subglacial methane cycling and the emergence of methane-saturated proglacial waters, our findings confirm a considerable organic carbon flux enters and is likely sequestered and/or transformed within the subglacial environment. Consequently, there remains a need to better constrain microbial carbon cycling pathways and their controls across supraglacial, subglacial and proglacial environments in Greenland.

Methods

Study location. Our study site was located proximate to the S6 automatic weather station (AWS) on the Kangerlussuaq Transect in western Greenland (67°04′78″N, 49°24′08″W), 38 km from the ice margin at an elevation of approximately 1020 m a.s.l. within the well-reported Dark Zone (Fig. 1a). The location has a mean annual air temperature (2003-2016) of −10.2 °C, which has shown a rising trend over the last decade. Observations over the last two decades suggest an annual ablation at the site of 1.96 m w.e. Situated on the western edge of the Dark Zone, a combination of enhanced dust content, black carbon and microbial community loading reduce the local bare-ice albedo at the site. Neighbouring ice temperature observations show that at ~1000 m a.s.l. only the uppermost 1–2 m of the western sector of the ice sheet’s ablation zone reaches 0 °C during the summer ablation season. This shallow, seasonally transient, temperate ice layer is likely to develop as a porous and hydrologically active weathering crust during summer.

Meteoroology and meltwater production. Hourly meteorological data from the S6 AWS were used as input to a point-based energy balance model to estimate local melt conditions across the low elevation range supraglacial catchment during the observational period. We estimated ice surface albedo for the catchment simplistically using a 12-hour running mean of the ratio of incoming and outgoing shortwave radiation at the S6 AWS, filtered for erroneous values, and which ranged between 0.37 and 0.50. The surface aerodynamic roughness parameter (z0) was kept constant, and taken as an average derived from a set of ten random 10 m transects. Oriented perpendicular to the domes, the southerly wind (true orientation: 116°) during the field campaign with elevation data extracted from the 0.25 m resolution DEM (see below, and Supplementary Method S1) within the supraglacial catchment of interest: z0 = 1.142 mm compared well to the 10−3 m−1 range quoted for bare-ice in the locality. The 2014 summer season was unexceptional in surface mass balance terms, suggesting our study period provides a representative baseline.

Near-surface hydrological functioning. Observations of the weathering crust and its hydrological functioning were made following Stevens et al. Briefly, shallow (0.26 or 0.36 m) holes were made using a 50 mm diameter Kovacs ice auger, and bespoke capacitance piezometers were used to record bail-recharge experiments, yielding water level recovery records at 2 s time intervals. Hydraulic conductivity (K) was assessed from these recharge curves following standard groundwater techniques (see Supplementary Method S2). A total of 9 experimental auger holes sites, separated by distances of ~9 m, were located in a quasi-random grid aligned perpendicular to the primary characteristic flow direction. The auger holes were evacuated manually using a DiORe SM syphon after the syphon was rinsed and flushed three times with supraglacial stream water; similarly, the piezometers were rinsed three times prior to installation and onset of recharge. Variance in recharge rates made systematic timing of experiments across the experimental grid feasible. A portion (c. 40%) of all the recharge experiments undertaken bore incomplete recharge, which precluded confident estimation of K-values.

Microbial enumeration. Following auger hole recharge experiments, using a polyethylene syringe and 30 cm polypolyethylene tube rinsed three times with a supraglacial stream water prior to sampling, a 15 mL depth-integrated sample of recharge water was abstracted. Of this, 10 mL was decanted into a 15 mL sterile polyethylene centrifuge tube, and fixed using 50 µL gluteraldehyde (2% w/v final concentration). The preserved samples were kept dark and cool (−4 °C) for up to 8 days while in the field and in transit, and subsequently fast frozen and stored at −80 °C until analysis.

We used flow cytometry to enumerate the microbes in the recharge water samples, employing the following protocol: samples were thawed at ambient laboratory room temperature, gently agitated, and stained with SYBR Gold (Molecular Probes, UK) at a final concentration of 1x and stored in the dark at 20 °C. Staining was undertaken bore complete recharge, which precluded confident estimation of K-values.

Microbial abundance and composition. Cell concentrations were determined using a Sony SH-800EC Cell-Sorter (Sony Biotechnology, Japan), using gates set within the Sony Cell Sorter v.2.1.3 software package to describe stained and non-stained cells, with a threshold applied to eliminate detection noise. To remain conservative in our assessment of the weathering crust hydrology, recharge water samples yielding microbial abundance of >10x 10 cm−3 were treated as outliers. These ten samples, we found, were proximate to highly localised microbial blooms and/or anomalously high particle concentrations, as reported by other authors. We justify our approach here based on cell abundances of <105 mL−1 being distinctive of supraglacial meltwaters and weathering crust water, and glacier ice. Further, eighteen ancillary water samples taken from exploratory auger and cryoconite holes in bare-ice areas at the S6 site demonstrated no cell concentrations >105 mL−1.

We employed a 10 µm analytical limit, with a threshold applied to eliminate detection noise. To remain conservative in our assessment of the weathering crust hydrology, recharge water samples yielding microbial abundance of >10x 10 cm−3 were treated as outliers. These ten samples, we found, were proximate to highly localised microbial blooms and/or anomalously high particle concentrations, as reported by other authors. We justify our approach here based on cell abundances of <105 mL−1 being distinctive of supraglacial meltwaters and weathering crust water, and glacier ice. Further, eighteen ancillary water samples taken from exploratory auger and cryoconite holes in bare-ice areas at the S6 site demonstrated no cell concentrations >105 mL−1.

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**Biomass estimation.** Microbial abundance can be converted to carbon biomass using three established techniques: (i) constant carbon content, (ii) allometric, or (iii) constant carbon ratio approximations. Previous work has suggested constant values for bacteria and archaea (e.g., 11 fg C cell−1; ref. 20,34) and for fungi (c = 1.91; ref. 83) or equivalent estimates for cyanobacteria and algal cells (e.g., 153 fg C cell−1; ref. 84). However, these approaches may not fully reflect variations in microbe size. Consequently, biomass can also be approximated using either a size-dependent allometric model37, or a constant biomass ratio36.

Here, owing to the wide variety of unknown microbe geometries, biovolumes (V) were estimated by assuming bacteria <1 μm are spherical, with larger bacteria as rods (hemispherical-ended cylinders) exhibiting length:width ratios defined by typical allometric scaling factors (c and a): typical bacterial geometries37,85; algae were described as simple 10 μm diameter cylinders34,58,87. For each of these three geometries, the cell length was defined by the midpoint of the size fraction reported by the cytometric analysis. Allometric methods ascribe the mass of carbon (M, in fg C) as a function of V (in µm3) and detrended using 31 × 31 plane thin-planted spline warping was applied to the UAV-derived DEM. To correct the uncertainties associated with DEM registration and resolution, the threshold size used to define the supraglacial network and, here, the geometry of the saturated zone and subsurface flow that characterises the weathering crust, require further interrogation which is beyond the scope of this paper.

**Catchment upscaling.** Given the absence of a clear relationship between melt rate and K36, to reveal a regional picture we upsampled our observed data across 795 moulindemarcating supraglacial catchments in western Greenland defined by Yang and Smith2, employing the bare-ice duration maps from Ryan et al.20 for 2006, 2012, and the study year 2014. The mean summer season (June to August; JJA) bare-ice duration (b) for each catchment was used to account for latitudinal and elevational gradients, and annual variability. We presume that the depth of the hydraulically active weathering crust evolved over time: deepening from the onset of bare-ice, reaching a maximum depth (sill 29 m), and declining thereafter. We used a modified cosine function centred on July 15 (day of year (DOY) 196) and defined by our observation period to describe this growth and decay of the weathering crust: for short bare-ice durations (b <38 days), the hydraulically active layer did not reach the 0.29 m maximum but reached its greatest depth of 0.0076·b, while for longer bare-ice durations, the depth increased to 0.29 m and plateaued at that maximum prior to decaying (see Supplementary Method S5). From this simple evolving depth model and our mean microbial abundance, for each catchment within the 1.38 × 105 km2 region, we calculated a cell flux to supraglacial streams assuming a constant proportion (14%) for stream bank area over each of the internally drainage catchments, as found in our study catchment. We assumed that rapid (<1 d) in-stream transit capacity to export to the ocean results in minimal change in microbial abundance and biomass during transport.

**Reporting summary.** Further information on research design is available in the Nature Research Reporting Summary linked to this article.

**Data availability**

The datasets generated during and/or analysed in this study are available in the Zenodo repository (https://doi.org/10.5281/zenodo.4623697). Source imagery files from the UAV collected on 8 August 2014 are archived in the Pangaea repository (https://doi.org/10.1594/PANGAEA.885798) and available from the corresponding author on reasonable request. The energy balance model is available on Zenodo (https://doi.org/10.5281/zenodo.3228331). ArcTDM data is available via https://www.pgc.umn.edu/data/arcticdem/ and RSGISlib at https://www.rsgislib.org/; the S6 weather station data is available on request from the Institute for Marine and Atmospheric Research at Utrecht University.

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Author contributions
T.D.L.I.-F. conceived and designed the study, conducted the experimental fieldwork and analyses, and wrote the manuscript; A.E. contributed as lead of 2014 fieldwork phase, and to analytical development; I.T.S. established the flow cytometry protocol and derived data for K and microbial abundance in collaboration with T.D.L.I.-F., A.E. and A.C.M.; A.H. and J.R. led the collection and pre-processing of the flow cytometry datasets and contributed to the final version of the manuscript; K.N. and P.B. contributed to post-processing of the imagery and refinement of spatial datasets; J.M.C. contributed fieldwork assistance and input to biomass comparisons; C.J.W. and S.M.E.R. contributed to biomass calculations and comparisons; K.A.C. contributed logistical support for the field campaign led by J.E.B. and M.S.; A.H., A.E., I.T.S. and A.C.M., and all other authors contributed to substantive editing and finalisation of the manuscript.

Competing interests
The authors declare no competing interests.

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