Algae drive enhanced darkening of bare ice on the Greenland ice sheet

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Key Points:
- we present the first quantitative assessment of the algal contribution to the Greenland ice sheet surface darkening
- we found that the effect of algae on bare ice darkening in the study area is greater than that of non-algal impurities
- incorporating the darkening effect of ice algal growth will improve mass balance and sea level projections of the Greenland ice sheet

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Abstract
Surface ablation of the Greenland ice sheet is amplified by surface darkening caused by light-absorbing impurities such as mineral dust, black carbon, and pigmented microbial cells. We present the first quantitative assessment of the microbial contribution to the ice sheet surface darkening, based on field measurements of surface reflectance and concentrations of light-absorbing impurities, including pigmented algae, during the 2014 melt season in the southwestern part of the ice sheet. The impact of algae on bare ice darkening in the study area was greater than that of non-algal impurities and yielded a net albedo reduction of 0.038 ± 0.0035 for each algal population doubling. We argue that algal growth is a crucial control of bare ice darkening, and incorporating the algal darkening effect will improve mass balance and sea level projections of the Greenland ice sheet and ice masses elsewhere.

Plain Language Summary
Melting of the Greenland ice sheet is enhanced by surface darkening caused by various impurities. We quantified the contribution of dark pigment-producing algae to the ice sheet surface darkening, based on field measurements in the southwestern part of the ice sheet during the 2014 melt season. Our analysis reveals that the impact of algae on bare (snow-free) ice darkening was greater than that of other impurities and, therefore, that algal growth was a crucial control of bare ice darkening in the study area. Incorporating the darkening effect of algal growth is expected to improve future projections of the Greenland ice sheet melting.

1 Introduction
Surface melting of the Greenland ice sheet is enhanced by darkening due to liquid water, snow grain metamorphism, and light-absorbing impurities (LAI) [Fettweis et al., 2011; Tedesco et al., 2016]. LAI include mineral dust [Bøggild et al., 2010; Doherty et al., 2010; Wientjes et al., 2011], black carbon [Doherty et al., 2010; 2013; Keegan et al., 2014], and pigmented microbial cells [Yallop et al., 2012]. Microbes that colonise glacier surfaces have the potential to increase in biomass and thus darkening impact given liquid water, sunlight and nutrients [Stibal et al., 2012]. By contrast, the potential of other LAI to increase their darkening impact once accumulated on the ice surface is limited.

Algae from the group Zygnematophyceae (‘surface ice algae’) are abundant on the surface of the ice sheet [Yallop et al., 2012]. Surface ice algae produce dark pigments as a screening mechanism when exposed to the high intensity radiation typical of glacier environments [Remias et al., 2012a; 2012b]. Humic by-products of microbial metabolism absorb in the same optical wavelengths and may further contribute to the darkening [Takeuchi, 2002; Takeuchi et al., 2015]. The impact of microbes on ice surface albedo is the least understood and quantified melt-enhancing factor on the ice sheet [Stibal et al., 2012; Benning et al., 2014].

Every summer, a dark area appears along the western margin of the ice sheet between 65 and 70 °N [Wientjes and Oerlemans, 2010; Shimada et al., 2016]. Previously, the low bare ice albedo has been attributed to outcropping dust and black carbon [Wientjes et al., 2011; Goelles et al., 2015]. However, high abundances of surface ice algae have also been observed in this area [Yallop et al., 2012]. To quantify the algal contribution to the ice surface darkening, we chose a study site at the edge of this dark area and, over ~2 months in the
summer 2014, we determined the changing surface albedo, measured the abundance of surface ice algae and other LAI, and obtained simultaneous reflectance spectra in the study site. We also gathered surface ice samples from outside the dark area to demonstrate the ubiquitous presence of surface ice algae and assess the environmental factors controlling their abundance. We then quantified the relationship between algae and non-algal LAI and bare ice darkening.

2 Materials and Methods

2.1 Field site

The study site was located in the southwestern sector of the Greenland ice sheet near the automated climate station S6 at 67° 04.779’ N, 49° 24.077’ W and 1011 m a.s.l. [van den Broeke et al., 2011; Supplementary Fig. 1]. Field measurements and sampling were conducted over 56 days from 17 June to 11 August 2014 (doy 168 – 223). At the start of the survey (17 June), the ice surface was covered in 10-30 cm deep snow, and our first LAI concentration and spectral reflectance measurements were therefore made for melting snow. On 19 June, the first bare ice was exposed and in the first week we performed surface reflectance and albedo measurements and collected samples of snow, surface streams and pools, and clean, medium, and dark ice to quantify the full variability of surface types in the study area. From 1 July until 11 August a 20 × 20 m study site was established, and on each sampling day 10 randomly selected 1 × 1 m sampling plots were targeted to capture average changes in surface reflectance over time while avoiding sample location bias and/or disturbance. Digital images of the study area were acquired by a Sony NEX-5N camera mounted on fixed-wing UAV [Ryan et al., 2015]. Each image was georeferenced with the GPS and attitude data. A total of 780 overlapping images at an altitude of 300 m above the ice surface were obtained.

Additional samples to determine algal abundance and biovolume in surface ice were collected at other locations on the ice sheet during the summer 2013 (Supplementary Fig. 2). Most sites were in the vicinity of an automated climate station of the Programme for the Monitoring of the Greenland Ice sheet (PROMICE) network [Ahlstrøm et al., 2008; van As et al., 2016]. Samples were also taken at the ‘Dark Site’ (DS), one of the darkest 5 km pixels from optical satellite imagery [Box et al., 2012]. Details of the sites can be found in Stibal et al. [2015].

2.2 Surface reflectance and albedo measurements
Spectral reflectance in the range of 350-2500 nm was acquired using an Analytical Spectral Devices (ASD) Field Spectrometer 2 with a hemispheric cosine receptor. The instrument was levelled sighting a bubble in a fluid chamber to an accuracy of 1 degree. The effective footprint of the sensor held at hip height was ~80 cm in diameter, with a 120 degree cone giving ~80% of the incident energy. The measurements were based on a ratio of upward to downward facing measurements made within 2 h of local solar noon. A variety of surfaces were sampled, spanning 0.4 m deep melt water stream at the low albedo limit to 1 mm grain ~10 day old snow at the high limit. To estimate broadband albedo, the spectral reflectance values were weighted by downward solar spectrum values calculated using SBDART [Richiazzi et al., 1998] with inputs of observed cloud fraction and climatological values for ozone, water vapour, and aerosol optical depth after Box [1997].

2.3 Sample collection and analysis

Samples of surface (2-3 cm) snow and ice were collected from a 0.4 × 0.4 m area using a chisel, pre-cleaned with 10% HCl and 70% ethanol, from the area over which reflectance measurements were acquired. The samples were allowed to thaw at < 15 °C and between 0.5 and 30 ml of the sample was filtered through a 0.22 μm Whatman Nucleopore polycarbonate membrane filter, depending on sample turbidity. Algal cells were counted in 5-20 fields of view at a 160× magnification using a Bresser Biolux NV field microscope. Unfiltered sample (40 ml) was fixed with formaldehyde (final concentration 2% v/v) and stored at < 5 °C for further analysis. The rest of each sample was filtered through a pre-weighed 0.45 μm Whatman cellulose nitrate membrane filter for total suspended solids (TSS) analysis. HCl- and ethanol-sterilised gloves were worn throughout all sample handling.

Separate samples were collected in pre-cleaned and combusted amber glass bottles for black carbon (BC) analysis just prior to scheduled helicopter flights to minimise sample melting prior to processing. The samples were melted upon arrival in the laboratory and immediately aerosolised with a calibrated CETAC U5000 nebuliser. Refractory BC (rBC) concentrations in the samples were determined using a single particle soot photometer (SP2), which measures single-particle incandescence of rBC at 1064 nm. The SP2 was calibrated with fullerene soot (Lot F12S011; Alfa Aesar) and applied over masses of 1 – 20 fg [Baumgardner et al., 2012]. The resulting linear calibration was extrapolated to large rBC masses using a power law dependence of 1/(0.9) [Schwarz et al., 2012].

Formaldehyde-preserved samples were examined by light microscopy for algal species identification, quantification of cell abundance and determination of cell size and biovolume. A Leica DM LB2 light microscope was used at a magnification of 400× and 1000×. Biovolume was determined using an appropriate geometric model [Hillebrand et al., 1999]. At least 50 cells of each algal species were measured. The concentration of total suspended solids (TSS) was determined by filtering samples through pre-weighed 0.45 μm cellulose nitrate membrane filters and re-weighing them after oven drying at 90 °C for 5 hours. The non-algal LAI fraction (NA; μg ml⁻¹) of the TSS was estimated as NA = TSS – (B × C), where B is cell biomass in μg cell⁻¹ and C is cell abundance in cells ml⁻¹. Wet biomass of the algae was calculated from their biovolume, assuming neutral buoyancy of the algal cells; dry biomass was estimated as 50 % of wet biomass. We tested the sensitivity of the calculated non-algal fraction concentration, its proportion in TSS and the calculated correlations with albedo to the cell biomass estimates. This analysis suggested that a biomass between 1 and 5 ng dry weight per cell is a realistic estimate (Supplementary Fig. 3), which agrees with an estimate of 3 ng wet weight obtained from a laboratory analysis of preserved ice samples.
2.4 Data analysis

To quantitatively assess the relationship between the algal and non-algal LAI concentrations and ASD-derived surface reflectance measured at the study site in the summer 2014, a linear regression analysis was performed using all samples for which reflectance, algal abundance and non-algal LAI concentrations were available (n = 93). Binary logarithms of algal abundance and non-algal LAI concentrations were used as the absorption of solar radiation by particles, including algal cells, is directly proportional to their mass absorption cross-section. The resulting linear regression assumes the form \( \alpha = \alpha_0 + s \times C \), where \( \alpha \) is the reflectance (relative units), \( C \) the binary logarithm of cell abundance in \( 10^3 \) cells \( \text{ml}^{-1} \) or the non-algal fraction concentration in \( \mu \text{g} \text{ml}^{-1} \), \( \alpha_0 \) is the initial no-algae bare ice reflectance, and \( s \) is the function multiplier.

We applied redundancy analysis to explain the variation in the ASD-derived reflectance data collected at the study site in the summer 2014 and in the algal abundance and biovolume data from the far-field samples collected around the ice sheet in the summer 2013. For the former, ASD-derived reflectance data averaged over 10 nm increments were the response variables; day of year 2014, days since the last precipitation event, non-algal fraction concentration, and algal abundance were the explanatory variables. For the latter, algal abundance and biovolume were the response data; geographical position, altitude, distance from the margin of the ice sheet, surface type (firm, ice), positive screen-level air temperature (\( T_a \)) days and days of surface temperature (\( T_s \)) of 0 \( ^\circ \text{C} \) since the beginning of the year, days since the last precipitation event, dust and nitrate concentrations were the explanatory data; day of sampling (day of year 2013) was a covariate. All concentration, microbial abundance and biovolume data were log-transformed prior to analysis, and all data were standardised and centred. Data below detection limit (b.d.) were treated as zeroes. The \( p \) values were corrected for multiple testing using false discovery rate.

To estimate the doubling time for the algal population a linear regression was performed using samples from the random plots where bare ice reflectance and algal abundance were available. Based on the assumption that algae are buried by snow or washed away by rain, we classified the days after precipitation events as the start-up dates for population growth. The resulting linear regression takes the form of \( C = C_0 + GR \times DSP \), where \( C \) is the binary logarithm of cell abundance in \( 10^3 \) cells \( \text{ml}^{-1} \), \( DSP \) the number of days since a precipitation event as simulated in the ERA-Interim driven regional climate model HIRHAM5 [Langen et al., 2015], \( C_0 \) is the calculated initial cell abundance, and \( GR \) is the growth rate calculated from the slope of the linear fit. Algal population doubling time was subsequently determined as \( 1/GR \).
3 Results

3.1 Bare ice albedo

After winter snowpack had completely ablated, surface albedo ($\alpha$) decreased from 0.50 to 0.42 ($\Delta\alpha = -0.08 \pm 0.04$) in the 35 days of observation at the S6 climate station (from 7 July to 11 August; day of year 188-223). Over the same time period, NASA Moderate Resolution Imaging Spectroradiometer (MODIS) MOD10A1 daily gridded albedo data indicate a mean albedo decline from 0.42 to 0.38 ($\Delta\alpha = -0.04 \pm 0.05$) at the nearest 500 m MOD10A1 pixel and from 0.43 to 0.37 ($\Delta\alpha = -0.06 \pm 0.05$) in a 10 km radius area of MOD10A1 pixels located 13.5 km northeast of the S6 climate station (Supplementary Fig. 1). UAV imagery indicates that snow cover was completely absent from the study area in early August and that surface meltwater covered a fractional area of only 4% (Supplementary Fig. 4).

3.2 Surface ice algae

At melt onset, we observed dead algal cells and other dark material being transported with slush and meltwater flow (Supplementary Fig. 5). After melting and runoff from winter snow and slush had completely ceased from the study site, we detected the first live algal cells in the surface ice (Figure 1). The distribution of surface ice algae in the principal study area was patchy, as demonstrated by the large spatial variation in abundance within the sampling area of $20 \times 20$ m (Figure 2). The abundance of algal cells ranged from <100 to 85,000 ml$^{-1}$ of melted ice in the sampling plots (Figure 2a) and up to 180,000 cells ml$^{-1}$ at sample sites selected for their dark appearance. Three species of algae were identified in the samples based on their morphology: Ancylonema nordenskiöldii, usually the dominant component of the community (40-100% of cells observed), Mesotaenium berggrenii reaching up to 50%, and Cylindrocystis sp. (Figure 1). By contrast, cyanobacterial filaments were only observed in low numbers. Observations of dividing cells (Figure 1c-g) confirm active growth of algae in surface ice occurred. Algal growth, as demonstrated by the increase in abundance through time (Figure 2a), appeared to be moderated by rainfall events. This is supported by the significant correlation between the number of days since the last precipitation event and algal abundance in the study area (Figure 2b). Redundancy analysis performed to explain the variation in algal abundance and biovolume data from around the ice sheet (Supplementary Table 1) identified the time since the last precipitation event as a significant factor (Supplementary Table 2). We attribute this effect to the flushing of algae into cryoconite holes and supraglacial stream channels during rainfall events. Assuming uninterrupted algal growth between the observed precipitation events in our study area, the mean time for doubling of the population size was estimated to be 5.5 ± 1.7 days (Figure 2b).

3.3 Reflectance spectra

The field spectrometer-obtained optical reflectance spectra (Figure 3a) indicate the surface ice in the principal study area contained a mixture of microbial pigments and humic substances. An absorption feature at ~680 nm (Figure 3b) is attributed to algal chlorophyll [Bidigare et al., 1990; Painter et al., 2001], while algal chlorophylls and carotenoids likely cause the absorption features between 370 and 680 nm [Bidigare et al., 1990]. The absorption peaking at 576 nm (Figure 3b) could be attributed to phycoerythrin produced by
cyanobacteria [Bryant, 1982], common microbes on the Greenland ice sheet surface [Stibal et al., 2010; Wientjes et al., 2011; Yallop et al., 2012]. However, cyanobacteria were only detected in low numbers, and the identity of this peak thus remains inconclusive. Distinct peaks of spectral absorption features are likely masked by humic substances [Takeuchi, 2002] and factors such as snow and ice grain size, solar angle, and liquid water [Hadley and Kirchstetter, 2012]. The brown-coloured protective pigments produced by surface ice algae have their main absorption peaks below 350 nm [Remias et al., 2012a; 2012b], and these peaks were not detectable with the ASD spectrometer used. BC, which absorbs across the visible spectrum with no discernible spectral absorption peaks [Bond and Bergstrom, 2006], was also detected in our samples at concentrations between 2.9 ng g\(^{-1}\) in fresh snow and clean ice and 32 ng g\(^{-1}\) in dark ice with high impurity contents (Supplementary Table 3). The role of dust in the reflectance spectra was likely small compared with biotic absorbers, as demonstrated by Yallop et al. [2012].

3.4 Light-absorbing impurities and surface reflectance

We divided the LAI in the surface ice samples into algal and non-algal fractions to examine their respective roles in the observed surface darkening. Bare ice albedo was then correlated to the binary logarithms of algal abundance and the non-algal fraction concentration. Using samples from the random plots, we found a significant negative correlation between algal abundance and albedo, that was strongest in the visible wavelengths (Pearson’s \(r = -0.78, p < 0.0001\) for 350-750 nm). The broadband albedo sensitivity (Pearson’s \(r = -0.75, p < 0.0001\) for 350-2500 nm) was stronger than that of the non-algal fraction (Pearson’s \(r = -0.47, p < 0.0001\) for 350-750 nm; Pearson’s \(r = -0.45, p < 0.0001\) for 350-2500 nm; Figure 4; Supplementary Table 4). Algal abundance correlated best with surface reflectance between 350 and 600 nm, where the majority of algal pigments and humic substances have their absorption peaks [Bidigare et al., 1990; Takeuchi, 2002] and where incident solar energy peaks. Algal abundance contributed some 70% to the explained variation in the bare ice reflectance data, whereas non-algal impurities were not found to be a significant explanatory factor (Supplementary Table 5). Based on the correlation results we estimate a net reflectance reduction of 0.0380 ± 0.0035 for each algal population doubling (Figure 4; Supplementary Table 4).

4 Discussion

Our analysis shows that surface ice algae have a more significant impact than non-algal impurities on bare ice albedo across the study area of the Greenland ice sheet. The dominance of algae in the albedo signal is demonstrated by the stronger correlation between the algal fraction and albedo compared with the non-algal fraction and by the fact that algal abundance explained ~70% of variation in the bare ice reflectance data, whereas non-algal impurities were not a significant explanatory factor. The non-algal fraction consists mostly of mineral particles, but also contains black carbon and other organic material, such as small microbial cells and products of cell metabolism and decay. Hence, the absorption attributed to non-algal impurities may still contain a small biotic element. Direct microscopic observation from melted ice samples supports the important role of surface ice algae on bare ice albedo as they demonstrate dark algal cells contrasting with translucent mineral particles (Figure 1e-g). These observations agree with independent spectroscopy measurements of single algal cells and mineral particles [Yallop et al., 2012].
BC is an effective LAI and has been proposed as an important factor affecting albedo [Keegan et al., 2014]. In our analysis, BC is attributed to the non-algal fraction which does not appear to significantly impact on bare ice reflectance variance (Supplementary Table 5). This might be due to the way the non-algal LAI fraction is determined in our study, as the potential effect of BC could be masked by other non-absorbing impurities in the fraction. However, given the low BC concentrations in our samples and elsewhere on the Greenland ice sheet [Doherty et al., 2010] and the recent analysis suggesting the role of BC deposition in albedo change on the ice sheet is not significant [Tedesco et al., 2016], we propose that the effect of BC on bare ice albedo across the study area is subtle and secondary to that of algal biomass.

Cryoconite (glacier surface debris) granules, formed by microbial aggregation [Takeuchi et al., 2001; Langford et al., 2010], may contain > 5 % of organic carbon [Stibal et al., 2010], and have been found to decrease reflectance in laboratory experiments [Musilova et al., 2016]. An association between cryoconite coverage and bare ice albedo has also been observed on the ice sheet [Chandler et al., 2015]. However, cryoconite holes are hidden from non-zenith solar illumination angles and aerial imagery indicates that they only occupy a very small fractional area of the ice surface, meaning that they are of secondary importance for bare ice albedo to distributed impurities [Ryan et al., 2016].

The main factors controlling algal growth in surface ice are the presence of liquid water, light, and nutrient availability [Stibal et al., 2012; Yallop et al., 2012; Lutz et al., 2014]. Dust melting out from old ice may play an important role as a source of nutrients for growing algae. Significant amounts of phosphorus, which is a limiting nutrient in supraglacial ecosystems [Stibal et al., 2009], have been detected in dust outcropping in the study area [Wientjes et al., 2011]. Moreover, our redundancy analysis identified dust as contributing 9.5% to the explained variation in algal abundance and biovolume data (Supplementary Table 2). Significant correlation was also found between dust content and the abundance of microbes in ice sheet surface ice [Stibal et al., 2015]. Hence, algal growth rates on the ice sheet are likely to be dependent on surface dust concentration, and consequently algal hot spots may be concentrated in areas with high dust concentrations. However, surface ice algae are also found outside the dark area and so these areas should not be excluded when estimating the algal contribution to the ice sheet surface darkening.

5 Conclusions

We conclude that actively growing pigmented algae have a significant impact on albedo reduction in the study area in the southwestern part of the Greenland ice sheet, and that this impact is more important than that of other light-absorbing impurities such as dust or black carbon. Upscaling ice darkening due to algal growth over the entire ice sheet and incorporating this effect into radiative forcing models is expected to improve mass balance, runoff and sea level projections from Greenland and other ice masses elsewhere.
Supporting information
Supplementary Fig. 1
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Figure 1. Observing surface ice algae on the Greenland ice sheet. a) The principal study site. b) The ice sheet surface showing highly pigmented surface blooms. c-g) Photomicrographs of cells of the filamentous alga Ancylonema nordenskiöldii in various stages of cell elongation and cell division (c), terminal cell of a filament of A. nordenskiöldii alongside a much larger cell of Cylindrocystis sp. (d), and translucent mineral particles contrasting in absorbance with pigmented algal cells (e-g). Scale bars represent 20 µm. All samples were preserved in 2% formaldehyde resulting in some loss of pigment and shrunken protoplasts.
Figure 2. Surface ice algal abundance dynamics on the Greenland ice sheet. a) Algal abundance at ten random plots in the study area sampled each day, ASD-derived albedo (350-2500 nm), and precipitation data from the HIRHAM5 regional climate model. All precipitation was rain during the measurement period. b) Algal doubling time estimated on the basis of the relationship between the binary logarithm of mean algal abundance and the time elapsed since the last precipitation event. 95% confidence and prediction bands marked in blue and red, respectively.
Figure 3. Reflectance spectra of Greenland surface ice. a) Spectra of representative surfaces. Surface melt water stream depth was 1 m. Snow depth was 24 cm with ~0.6 mm grain diameter, estimated from visual inspection. b) Spectral reflectance of surface ice with high algal abundance showing four apparent absorption features with peak absorption wavelength computed from continuum reflectance model [Painter et al., 2001]. The 409 and 678 nm absorption features match the typical chlorophyll and carotenoid absorption values [Bidigare et al., 1990]. The absorption peaking at 576 nm might be attributed to phycoerythrin [Bryant, 1982]. The 790 nm absorption feature is likely abiotic. Each curve represents single pairs of ratios of upward- and downward-measured spectra. A low pass Gaussian weighted smoothing filter was applied to the shown spectra.
Figure 4. The effect of the algal and non-algal fraction concentrations on bare ice albedo on the Greenland ice sheet according to our observations. 95% confidence and prediction bands marked in blue and red, respectively. $n = 93$. 