



Letter

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Authors for correspondence:

Laura Halbach, E-mail: lh@envs.au.dk;

Lou-Anne Chevrollier,

E-mail: lou.chevrollier@envs.au.dk

Dark ice in a warming world: advances and challenges in the study of Greenland Ice Sheet's biological darkening

Laura Halbach¹ , Lou-Anne Chevrollier¹, Joseph M. Cook¹ , Ian T. Stevens¹ ,
Martin Hansen¹ , Alexandre M. Anesio¹ , Liane G. Benning^{2,3} 
and Martyn Tranter¹ 

¹Aarhus University, Environmental Science, iClimate, Roskilde, Denmark; ²GFZ German Research Centre for Geosciences, Potsdam, Germany and ³Department of Earth Sciences, Freie Universität Berlin, Berlin, Germany

Abstract

The surface of the Greenland Ice Sheet is darkening, which accelerates its surface melt. The role of glacier ice algae in reducing surface albedo is widely recognised but not well quantified and the feedbacks between the algae and the weathering crust remain poorly understood. In this letter, we summarise recent advances in the study of the biological darkening of the Greenland Ice Sheet and highlight three key research priorities that are required to better understand and forecast algal-driven melt: (i) identifying the controls on glacier ice algal growth and mortality, (ii) quantifying the spatio-temporal variability in glacier ice algal biomass and processes involved in cell redistribution and (iii) determining the albedo feedbacks between algal biomass and weathering crust characteristics. Addressing these key research priorities will allow us to better understand the supraglacial ice-algal system and to develop an integrated model incorporating the algal and physical controls on ice surface albedo.

Introduction

The surface of the Greenland Ice Sheet is darkening (He and others, 2013; Tedesco and others, 2016; Tedstone and others, 2017), which accelerates its surface melt during the summer. The surface darkening is attributed to changes in the physical properties of snow and ice during the melt season, as well as the presence of light-absorbing particulates (LAPs; Dumont and others, 2014, Tedesco and others, 2016, Tedstone and others, 2020). The physical changes in ice structure and variability in the concentration of LAPs in bare ice areas are not well represented in regional climate models (RCMs; Tedesco and others 2016), leading to underestimations of predicted melt rates, particularly in the southwestern margin of the ice sheet (Alexander and others, 2014; Tedesco and others, 2016; Antwerpen and others, 2022). In this region, part of the discrepancy between observed and modelled albedo is explained by the presence of biological LAPs, in particular blooms of pigmented microalgae, which darken large areas of the ice surface (Wang and others, 2020; Tedstone and others, 2020; Cook and others, 2020; Williamson and others 2021). The prolonged exposure of bare ice areas, due to the accelerated snowline retreat induced by climate warming (Ryan and others, 2018), is thought to extend the growth season of these microalgae. This could lead to larger, darker and more prolonged algal blooms in future (Benning and others, 2014). At the same time, changes in precipitation and intensified run-off may alter the physical and chemical conditions on the ice surface, with unknown consequences for algal bloom development and, thus, biological albedo reduction.

The main algal species darkening the ice surface are *Ancylonema alaskana* and *A. nordenskiöldii* (Lutz and others 2018), hereafter referred to as glacier ice algae (Fig. 1a). The strong light absorption and albedo-reducing effect of glacier ice algae is due to their intracellular accumulation of the pigment purpurogallin carboxylic acid-6-O-β-D-glucopyranoside (Remias and others, 2012a, 2012b; Williamson and others, 2020; Halbach and others, 2022; Fig. 1a, b). The optical properties of glacier ice algae have recently been measured (Chevrollier and others, 2022; Fig. 1d) and incorporated into the radiative transfer model, BioSNICAR (Flanner and others 2007; Cook and others, 2020), along with an adding-doubling solver (Briegleb and Light, 2007) that was shown to accurately predict glacier ice albedo (Whicker and others, 2022). BioSNICAR predicts algal-driven albedo reduction from the surface concentration of algal cells, illumination conditions, as well as vertical profiles of ice density and bubble/pore size (<https://github.com/jmcook1186/biosnicar-py>). Chevrollier and others (2022) showed this model could be used to accurately recreate the spectral reflectance of ice surfaces populated by algal blooms (Fig. 1e), suggesting that it can be used to study the algal impact on bare ice albedo, including an integration into remote sensing and predictive modelling systems. In particular, Chevrollier and others's (2022) model validations imply that synthetic albedo datasets covering wide ranges of possible ice column, impurity and illumination conditions can be used to derive algal detection algorithms. So far, these algorithms had been derived from relatively small empirical datasets because radiative transfer models did not have access to reliable algal optical properties or validation data.

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BioSNICAR could eventually be refactored for coupling to RCMs to forecast algal-driven melt, but this will require models for algal biomass accumulation and surface crust development to be built. However, the controls on surface algal biomass distribution and weathering crust state as well as the feedback between them are not yet sufficiently well understood (Fig. 2). Here we outline the knowledge and process-level understanding needed for these modelling developments, using a combination of field measurements, laboratory experiments, remote sensing and modelling.

Controls on algal growth and mortality

The availability of liquid water, light and nutrients could limit glacier ice algal growth (Fig. 2). As CO₂ is constantly supplied from the atmosphere to the ice surface, where it easily dissolves, it is unlikely to be a limiting factor at the ice surface that the algae inhibit. To date, algal growth has been modelled as a function of the cumulative growth period where environmental conditions allow for algal growth (Williamson and others, 2018, 2020; Onuma and others, 2022). The thresholds of these environmental conditions were defined by Williamson and others (2020) as a snow-free ice surface (snow cover <2 cm), sufficient solar irradiance to drive photochemistry (shortwave radiation >10 W m⁻²) and the availability of liquid water (air temperature >0.5°C). In contrast, Onuma and others (2022) used an ice temperature >0°C as a threshold for liquid water availability and did not define a solar irradiance threshold. However, there remains a lack of data to support the environmental conditions and values used as thresholds.

For example, the environmental conditions under which liquid water limits algal growth remain unknown. It has been estimated that glacier ice algae direct 48 to 65% of the incident irradiance to ice melting (Williamson and others, 2020), and thereby create their own liquid micro-environment, which would need to be considered for assessing a potential lack of liquid water for the algae (Fig. 2). Light availability may restrict photochemistry and subsequently growth during the beginning of the melt season when glacier ice algae are buried under a thick snow cover and, therefore, growth onset also depends on the timing of winter

snowpack retreat (Williamson and others, 2018). Yet, algal activity measurements from below the snow cover are currently not available. Light availability is unlikely to be growth-limiting later in the season due to typically high incident solar irradiance and long day length duration, increasing with decreasing longitude. On the other hand, high incident irradiances in the middle of the season may potentially suppress glacier ice algal productivity, as demonstrated by in situ incubations that show the suppression of photochemistry at 100% ambient light during a mid-ablation season (Williamson and others, 2020). To define the thresholds for algal light requirements, incubation experiments or field measurements of glacier ice algal activity pre- and during snowline retreat, together with the light transmission through the snow are required. Sampling glacier ice algal populations from beneath the snow or the analysis of regression fits of their biomass progression throughout the season could additionally provide estimates of their initial population size, which is required to model algal bloom progression throughout the season (Williamson and others, 2020; Onuma and others, 2022).

So far, nutrient availability has not been incorporated into glacier ice algal growth models for the Greenland Ice Sheet (Fig. 2). McCutcheon and others (2021) found that glacier ice algal growth is limited by phosphorous after long incubations (120 h) and suggested that the delayed response could be due to an internal phosphorus storage by the cells. No indication of nutrient limitation was found for short incubation times, suggesting that in situ nutrients can support algal nutrient requirements (Halbach, 2022). Moreover, the low intracellular carbon:nitrate:phosphorous ratios of algal dominated particulate organic matter (Williamson and others 2021) and single glacier ice algal cells (Halbach, 2022) suggest that they are well adapted to their oligotrophic environment. To fully comprehend the role of nutrients in glacier ice algal growth and their potential relevance for models, future studies should quantify algal nutrient uptake and storage (e.g. by using stable isotope tracers), as well as the competition and recycling of nutrients by other organisms of the community (e.g. by following examples from other aquatic systems in Klawonn and others, 2019 or Adam and others, 2016) (Fig. 2).

Controls on cell mortality are also currently understudied (Fig. 2). It has been shown that Chytridiomycota, a group of

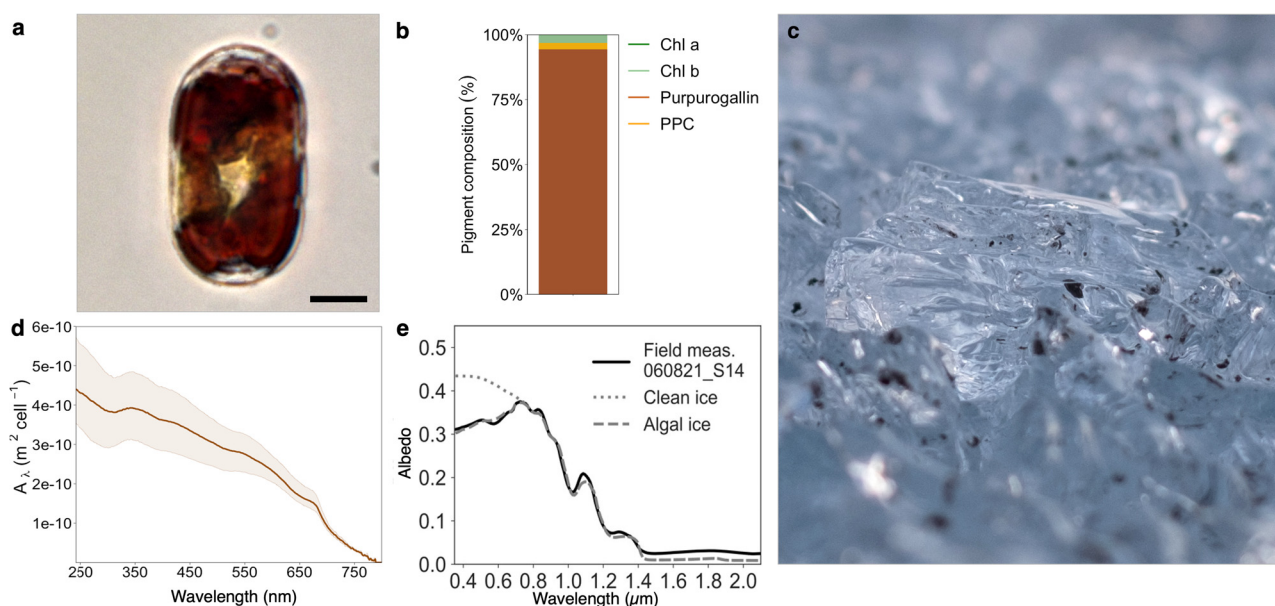


Fig. 1. Pigments, light absorption and albedo reduction by glacier ice algae. (a) Microscope picture of *Ancydonema alaskana*, scale bar = 5 μm (b) average pigment composition of glacier ice algae, (c) picture of the weathering crust surface, (d) average absorption cross-section of glacier ice algae and (e) measured and modelled spectra of an ice surface colonised by glacier ice algae. Figures adapted from Halbach and others (2022) and Chevrollier and others (2022).

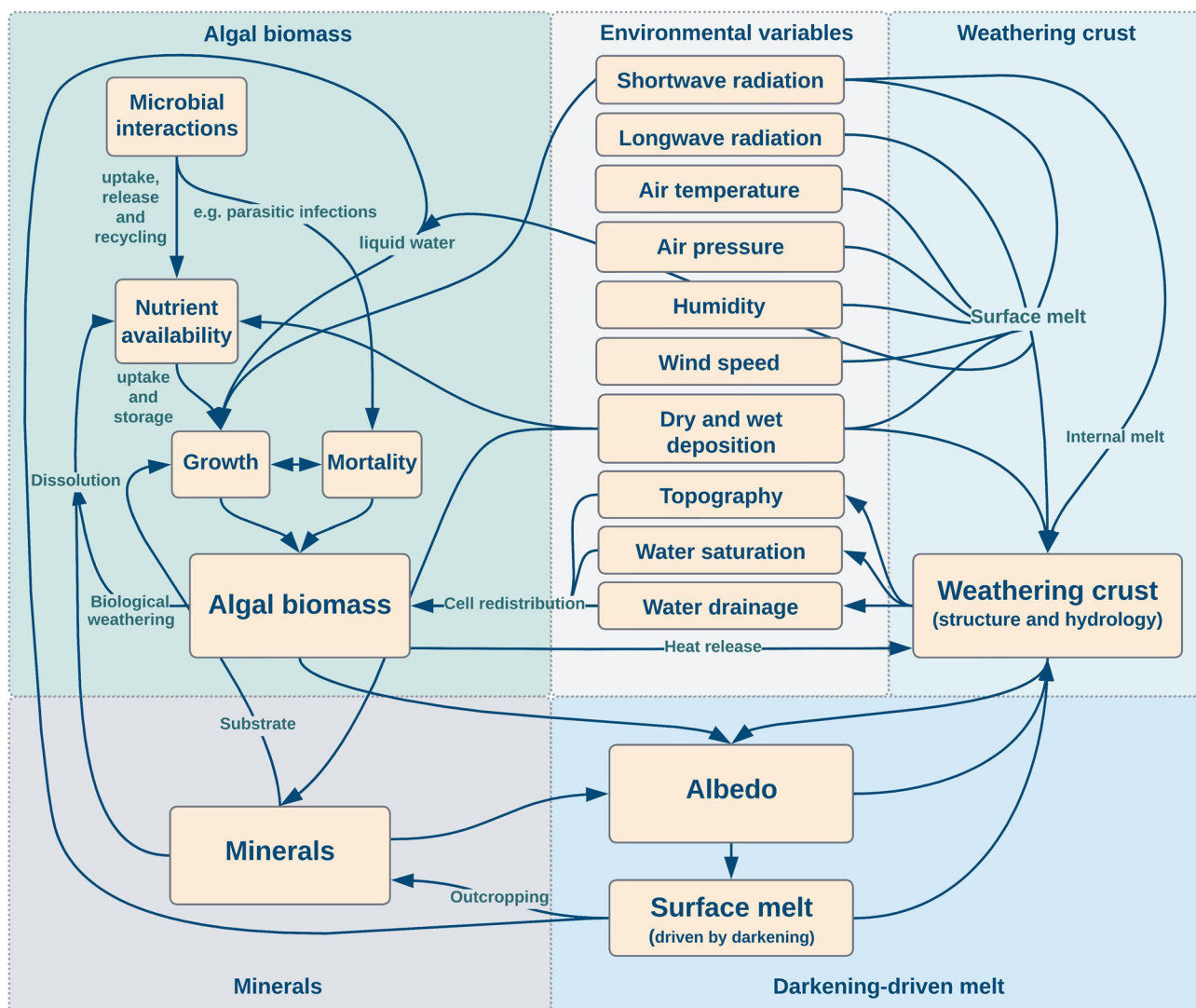


Fig. 2. Schematic overview of the ice-algal system and key feedbacks with environmental variables and surface albedo. Note that not all interactions are included, for example among environmental variables. The incoming shortwave radiation available for the algae will also indirectly depend on the presence and properties of a snow cover.

parasitic fungi, are widespread on the ice sheet and can infect algal cells (Perini and others, 2019, 2022; Fiolka and others, 2021). Recently, it has been found that the prevalence of infection with chytrids among glacier ice algal populations from Alaska is $3.9 \pm 5.6\%$ on the bare ice (Kobayashi and others, 2023). However, the relative proportions of uninfected and infected cells on the Greenland Ice Sheet and a potential variability of infection prevalence throughout the season remain unknown. Ratios of viable, dead, infected or uninfected cells could be estimated by microscopy techniques, multi-stain, flow-cytometry and cell-sorting (Davey and Kell, 1996; Klawonn and others, 2021a) as well as algal activity assessments (e.g. by Secondary-Ion-Mass-Spectrometry or BONCAT; Hatzepichler and others, 2016; Gao and others, 2021; Klawonn and others, 2021b, Grujic and others, 2022).

Experiments under controlled conditions are needed to quantify growth and mortality specifically, isolated from other physical and hydrological redistribution processes (Fig. 2). Available glacier ice algal population doubling times using this approach amounted to 3.75 ± 0.36 days (net primary productivity measurements in the field Williamson and others (2018)). It should be noted that any incubation of glacier ice algae in a liquid medium within bottles changes the growth conditions relative to in situ conditions (growth substrate, nutrient conditions, irradiance, temperature). Thus, in situ incubations in the field directly on

the ice or short incubation times should be generally preferred to avoid or minimise extensive bottle effects. Laboratory cultures of glacier ice algae may allow the design and implementation of future experiments to study the role of microbial interactions on cell mortality and nutrient recycling (Fig. 2).

Physical and hydrological controls on the spatio-temporal variability of algal blooms

In addition to growth and mortality, it is hypothesised that glacier ice algal biomass distribution is also affected by hydrological processes, which can transport algal cells within supraglacial melt-water flow of the near-surface 'weathering crust' (see Cooper and others, 2018; Stevens and others, 2018) and supraglacial channels. Subsequently, such hydrological controls are likely to have important implications for albedo reduction (Fig. 2) (Stibal and others, 2017; Christner and others, 2018; Tedstone and others, 2020; Irvine-Fynn and others, 2021; Stevens and others, 2022). However, the interplay between the retention of algae and their hydrological transport from the ice surface presents a key research avenue, with rates and controls upon biomass transport remaining poorly characterised.

Recent work has revealed the simultaneous advection of microbes and accumulation of microbial biomass throughout

the melt season on the western Greenland Ice Sheet, with estimated bare-ice advection rates of microbes ($<20\ \mu\text{m}$) for a typical melt season of 5.73×10^{12} cells $\text{km}^{-2}\ \text{d}^{-1}$ (Irvine-Fynn and others, 2021). However, the controls upon microbial abundance and, hence, transport mechanics of weathering crust meltwaters remain poorly defined, with no apparent link between depth-integrated hydraulic conductivity and microbial abundance (Stevens and others, 2022). Henceforth, more sophisticated approaches are required to fully understand and quantify the transport and retention dynamics of glacier ice algae (and by extension, all glacier microbes) from the ice surface, through the weathering crust and into the channelised glacial hydrological system. Ultimately, addressing this knowledge gap will help to elucidate the role of the supraglacial hydrological system in the spatio-temporal variability of algal blooms and their associated albedo reduction.

It has been suggested that the retention and transport of microbes from the surface to and within the saturated weathering crust system is size selective (Irvine-Fynn and others, 2021; Stevens and others, 2022), with hypothesised controls including mechanical filtration by the weathering crust matrix (Mader and others, 2006), extra-cellular polymeric substances (e.g. Langford and others, 2010; Holland and others, 2019) or so-called hydrological ‘flushing’ (Adrien, 2004) with large melt events and/or weathering crust removal events. Future investigations should aim to ascertain the role of more precise hydrological metrics in partnership with algal concentrations and size distributions, specifically examining the following variables in depth-integrated and/or depth-specific manner: effective porosity of the weathering crust, direct weathering crust meltwater velocities, water delivery and drainage (from surface melt, internal melt and rainfall) and water table height. In addition, the application of tracer studies and/or high resolution 4D models at the micro-catchment scale, using the variables outlined above will help to ascertain algal mobility and near-surface residence periods beyond the point scale. Moreover, these variables are hypothesised to be highly temporally variable on a sub-hourly scale (Stevens, 2018), in response to diurnal and synoptic scale meteorological cycles, and should be examined under the widest possible range of antecedent and ongoing meteorological conditions. Physical, topographic and meteorological data can be gathered at different times and spatial scales from field studies, digital elevation models, automatic weather station networks (e.g. PROMICE: Fausto and others, 2021) or outputs from RCMs (e.g. MAR, Fettweis and others, 2017; RACMO, Noël and others, 2018). Links between these environmental data and changes in algal biomass distribution should be explored to unravel potential correlations between them.

Algal biomass can be assessed by field sampling or remote detection. Field samples can be analysed to retrieve detailed information about cell concentrations and community composition but can only represent very small areas within the very heterogeneous ice surface, which limits upscaling. Furthermore, it is common to retrieve surface ice using the adze of an ice axe or a trowel which, due to the very heterogeneous structure of the upper surface, can lead to uncertainty in the actual dimensions of the sampled area. It is also challenging to measure the specific surface area and effective grain radius in the field to configure a radiative transfer model to accurately represent a given sample area. However, new techniques for resolving the near-surface ice structure are emerging (e.g. Allgaier and others, 2022).

Remote sensing enables us to study ice albedo and algal biomass over large spatial scales but changes in algal biomass can only be inferred indirectly using algorithms. Ground truthing these algorithms can be challenging due to the scale mismatch between satellite pixel size and field samples. Using hyperspectral images mounted on low-flying unmanned aerial vehicles might

help to bridge that gap because the ground resolution of the resulting imagery is fine enough to match precisely to field sampling areas and can also be coarsened to match the footprint of satellite sensors. Several algorithms have been used to detect algal biomass. The simplest is based on Chlorophyll-*a* absorption (e.g. Painter and others, 2001; Ganey and others, 2017), however, they rely on a high spectral resolution to identify ‘biologically unique’ reflectance patterns. There have also been several papers that used classification algorithms such as K-nearest neighbours (Ryan and others, 2018), random forest decision trees (Cook and others, 2020) and optimal estimation (Bohn and others, 2022). Further, algal growth has also been estimated using the ratio of reflectance at two red wavelengths as a proxy for algal concentration at the scale of the entire Greenland Ice Sheet ablation zone (Wang and others, 2018, 2020) and for Alpine glaciers (Di Mauro and others, 2020). To date, the main limitation of all these approaches has been the small training dataset sizes, but with empirical algal optical properties now incorporated into radiative transfer models (Chevrollier and others, 2022) there is potential to train these algorithms on very large synthetic datasets that cover the complete range of weathering crust conditions and biomass concentrations. By informing algal detection algorithm development and validation, improvements to both radiative transfer models and field sampling techniques will lead to more accurate quantification of glacier algal spatio-temporal dynamics and albedo impacts at the ice-sheet scale.

Indirect darkening effect of algal blooms

The state of the weathering crust is further an important control of surface albedo (Tedstone and others, 2020; Fig. 2). Glacier ice algae can indirectly impact surface albedo by modifying the weathering crust surface (stimulating ice melting), in addition to their direct impact on albedo through shortwave radiation absorption (Cook and others, 2017; Williamson and others, 2019). Thereby, glacier ice algae influence weathering crust decay by enhancing surface lowering relative to subsurface melting (Fig. 2), which creates a denser, less porous crust (Schuster, 2001; Cook and others, 2020; Tedstone and others, 2020), reducing the albedo. The indirect effect of algal blooms on weathering crust decay may be one of the reasons why algal abundance alone does not explain the discrepancy between MAR and MODIS albedo for the southwestern margin of the ice sheet in the study by Wang and others (2020). However, our understanding of the indirect albedo-reducing effect of algal blooms through weathering crust densification is currently limited by a lack of empirical data and validated weathering crust development models.

Simultaneous monitoring of algal abundance and weathering crust physical properties through field samplings, experiments or remote sensing could help to elucidate these feedbacks. These physical properties include for example the density of near-surface ice (defined as ice to a 2 m depth), which describes the weathering crust growth and decay (Schuster, 2001). The development of algorithms for predicting weathering crust physical properties from remote sensing data has so far been restricted. This is due to a ‘many-to-one’ problem, where the same spectral albedo can be generated with different combinations of ice density and effective bubble sizes, and it is impossible to assess the correct combination. For snow, effective grain sizes can be inferred from spectral measurements (Nolin and Dozier, 2000), but it is not clear that this method transfers to glacier ice. To address this, model inversions could be performed on many field spectra that have associated density profile measurements to establish a relationship between ice density and effective bubble size. This could enable remote quantification of weathering crust physical properties simultaneously with detecting algal cells.

To validate and improve weathering crust development models (Schuster, 2001; Woods and Hewitt, 2022), empirical datasets are needed combining simultaneous measurements of weathering crust physical properties, meteorological parameters and surface albedo through time (Fig. 2). Eventually, weathering crust models could be coupled to BioSNICAR or other radiative transfer models to predict the indirect darkening role of algal blooms, as other studies have done for LAPs in snow (Tuzet and others, 2017; Huang and others, 2022).

Conclusions

The presented comprehension of research priorities demonstrates the need for an interdisciplinary approach combining biological, hydrological and geophysical tools to understand the supraglacial algal system and its implications for albedo reduction. Key research questions that should be addressed in future studies are:

- (i) under which conditions does liquid water limit glacier ice algal growth at the micro-scale?
- (ii) what is the viable and dead fraction of glacier ice algal populations throughout the season and how do environmental factors and microbial interactions (e.g. parasitic infections by fungi) impact those?
- (iii) what controls the rate of advection of algal cells from the ice surface to and through the hydrological system in the near-surface weathering crust?
- (iv) what is the impact of algal blooms on the state of the weathering crust?

Addressing these questions about the biological darkening of the Greenland Ice Sheet requires the combination of mechanistic and descriptive study approaches. The mechanistic approaches are essential to isolate the controls on algal growth and mortality and may include laboratory and/or field experiments (e.g. bottle incubations or in situ experiments as done on large scales by Ganey and others, 2017). These need to be complemented with observations in the field to validate the interactions under 'true' in situ conditions during complex feedbacks with the weathering crust and other environmental processes of the algal habitat (Fig. 2). In addition, net algal biomass assessments by remote sensing must be combined with environmental data to identify the interaction between the algal-driven darkening and environmental variables at a larger scale. The assessments of the supraglacial algal system from a micro-to-macro-scale will improve its parametrisation within models and enable a better understanding and prediction of algal bloom development and associated albedo decline over space and time.

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References

Adam B and 7 others (2016) N₂-fixation, ammonium release and N-transfer to the microbial and classical food web within a plankton community. *ISME Journal* **10**(2), 450–459. doi: [10.1038/ismej.2015.126](https://doi.org/10.1038/ismej.2015.126)

- Adrien NG** (2004) *Computational Hydraulics and Hydrology: An Introductory Guide for Field Biologists*. Boca Raton, FL: CRC Press.
- Alexander PM and 5 others** (2014) Assessing bare-ice albedo simulated by MAR over the Greenland ice sheet (2000–2021) and implications for meltwater production estimates. *The Cryosphere* **16**, 4185–4199. doi: [10.5194/tc-16-4185-2022](https://doi.org/10.5194/tc-16-4185-2022)
- Allgaier M and 5 others** (2022) Direct measurement of optical properties of glacier ice using a photon-counting diffuse LiDAR. *J. Glaciol* **68**, 1210–1220. doi: [10.1017/jog.2022.34](https://doi.org/10.1017/jog.2022.34)
- Antwerpen R, Tedesco M, Fettweis X, Alexander P and van de Berg WJ** (2022) Assessing bare Ice albedo simulated by MAR over the Greenland Ice Sheet (2000–2021) and implications for meltwater production estimates. *The Cryosphere* **16**, 4185–4199.
- Benning LG, Anesio AM, Lutz S and Tranter M** (2014) Biological impact on Greenland's albedo. *Nature Geoscience* **7**(10), 691–691. doi: [10.1038/ngeo2260](https://doi.org/10.1038/ngeo2260)
- Bohn N and 7 others** (2022) Glacier ice surface properties in south-west Greenland ice sheet: first estimates from PRISMA imaging spectroscopy data. *Journal of Geophysical Research Biogeosciences* **127**, e2021JG006718. doi: [10.1029/2021JG006718](https://doi.org/10.1029/2021JG006718)
- Briegleb P and Light B** (2007) A Delta-Eddington Multiple Scattering Parameterization for Solar Radiation in the Sea Ice Component of the Community Climate System Model, University Corporation for Atmospheric Research, technical note, 1–108. doi: [10.5065/D6B27S71](https://doi.org/10.5065/D6B27S71)
- Chevrollier L-A and 6 others** (2022) Light absorption and albedo reduction by pigmented microalgae on snow and ice. *Journal of Glaciology* **69**(274), 1–9. doi: [10.1017/jog.2022.64](https://doi.org/10.1017/jog.2022.64)
- Christner BC and 9 others** (2018) Microbial processes in the weathering crust aquifer of a temperate glacier. *The Cryosphere* **12**(11), 3653–3669. doi: [10.5194/tc-12-3653-2018](https://doi.org/10.5194/tc-12-3653-2018)
- Cook JM and 9 others** (2017) Quantifying bioalbedo: a new physically based model and discussion of empirical methods for characterising biological influence on ice and snow albedo. *The Cryosphere* **11**(6), 2611–2632. doi: [10.5194/tc-11-2611-2017](https://doi.org/10.5194/tc-11-2611-2017)
- Cook JM and 23 others** (2020) Glacier algae accelerate melt rates on the south-western Greenland Ice Sheet. *The Cryosphere* **14**(1), 309–330. doi: [10.5194/tc-14-309-2020](https://doi.org/10.5194/tc-14-309-2020)
- Cooper MG and 7 others** (2018) Meltwater storage in low-density near-surface bare ice in the Greenland ice sheet ablation zone. *The Cryosphere* **12**, 955–970. doi: [10.5194/tc-12-955-2018](https://doi.org/10.5194/tc-12-955-2018)
- Davey HM and Kell DB** (1996) Flow cytometry and cell sorting of heterogeneous microbial populations: the importance of single-cell analyses. *Microbiological Reviews* **60**(4), 641–696. doi: [10.1128/mr.60.4.641-696.1996](https://doi.org/10.1128/mr.60.4.641-696.1996)
- Di Mauro B and 8 others** (2020) Glacier algae foster ice-albedo feedback in the European Alps. *Scientific Reports* **10**, 1–9. doi: [10.1038/s41598-020-61762-0](https://doi.org/10.1038/s41598-020-61762-0)
- Dumont M and 8 others** (2014) Contribution of light-absorbing impurities in snow to Greenland's darkening since 2009. *Nature Geoscience* **7**(7), 509–512. doi: [10.1038/ngeo2180](https://doi.org/10.1038/ngeo2180)
- Fausto RS and 16 others** (2021) Programme for monitoring of the Greenland Ice Sheet (PROMICE) automatic weather station data. *Earth System Science Data* **13**, 3819–3845. doi: [10.5194/essd-13-3819-2021](https://doi.org/10.5194/essd-13-3819-2021)
- Fettweis X and 8 others** (2017) Reconstructions of the 1900–2015 Greenland ice sheet surface mass balance using the regional climate MAR model. *The Cryosphere* **11**(2), 1015–1033. doi: [10.5194/tc-11-1015-2017](https://doi.org/10.5194/tc-11-1015-2017)
- Fiołka MJ and 5 others** (2021) Morphological and spectroscopic analysis of snow and glacier algae and their parasitic fungi on different glaciers of Svalbard. *Scientific Reports* **11**(1), 1–18. doi: [10.1038/s41598-021-01211-8](https://doi.org/10.1038/s41598-021-01211-8)
- Flanner MG, Zender CS, Randerson JT and Rasch PJ** (2007) Present-day climate forcing and response from black carbon in snow. *Journal of Geophysical Research: Atmospheres* **112**, 11202. doi: [10.1029/2006JD008003](https://doi.org/10.1029/2006JD008003)
- Ganey GQ, Loso MG, Burgess AB and Dial RJ** (2017) The role of microbes in snowmelt and radiative forcing on an Alaskan icefield. *Nature Geoscience* **10**, 754–759. doi: [10.1038/NGEO3027](https://doi.org/10.1038/NGEO3027)
- Gao K, Hutchins DA and Beardall J** (2021) Research Methods of Environmental Physiology in Aquatic Sciences. doi: [10.1007/978-981-15-5354-7](https://doi.org/10.1007/978-981-15-5354-7)
- Grujic V, Taylor GT and Foster RA** (2022) One cell at a time: advances in single-cell methods and instrumentation for discovery in aquatic microbiology. *Frontiers in Microbiology* **13**(May). doi: [10.3389/fmicb.2022.881018](https://doi.org/10.3389/fmicb.2022.881018)
- Halbach L** (2022) Nutrient requirements and pigment signatures of glacial algae on the Greenland Ice Sheet (Doctoral dissertation). Aarhus University.

- Halbach L and 14 others** (2022) Pigment signatures of algal communities and their implications for glacier surface darkening. *Scientific Reports* (0123456789), 1–14. doi: [10.1038/s41598-022-22271-4](https://doi.org/10.1038/s41598-022-22271-4)
- Hatzepichler R and 5 others** (2016) Visualizing in situ translational activity for identifying and sorting slow-growing archaeal – bacterial consortia. *Proceedings of the National Academy of Sciences* **113**(28), E4069–E4078. doi: [10.1073/pnas.1603757113](https://doi.org/10.1073/pnas.1603757113)
- He T and 5 others** (2013) Greenland surface albedo changes in July 1981–2012 from satellite observations. *Environmental Research Letters* **8**(4). doi: [10.1088/1748-9326/8/4/044043](https://doi.org/10.1088/1748-9326/8/4/044043)
- Holland AT and 10 others** (2019) Dissolved organic nutrients dominate melting surface ice of the Dark Zone (Greenland ice sheet). *Biogeosciences* **16**, 3283–3296. doi: [10.5194/bg-16-3283-2019](https://doi.org/10.5194/bg-16-3283-2019)
- Huang H, Qian Y, He C, Bair EH and Rittger K** (2022) Snow albedo feedbacks enhance snow impurity-induced radiative forcing in the Sierra Nevada. *Geophysical Research Letters* **49**(11), e2022GL098102.
- Irvine-Fynn TDL and 13 others** (2021) Storage and export of microbial biomass across the western Greenland Ice Sheet. *Nature Communications* **12** (1), 1–11. doi: [10.1038/s41467-021-24040-9](https://doi.org/10.1038/s41467-021-24040-9)
- Klawonn I and 10 others** (2019) Untangling hidden nutrient dynamics: rapid ammonium cycling and single-cell ammonium assimilation in marine plankton communities. *ISME Journal* **13**(8), 1960–1974. doi: [10.1038/s41396-019-0386-z](https://doi.org/10.1038/s41396-019-0386-z)
- Klawonn I and 6 others** (2021b) Characterizing the “fungal shunt”: parasitic fungi on diatoms affect carbon flow and bacterial communities in aquatic microbial food webs. *PNAS* **118**(23). doi: [10.1073/pnas.2102251118](https://doi.org/10.1073/pnas.2102251118)
- Klawonn I, Dunker S, Kagami M, Grossart HP and Van den Wyngaert S** (2021a) Intercomparison of Two fluorescent dyes to visualize parasitic fungi (Chytridiomycota) on phytoplankton. *Microbial Ecology* **85**, 9–23. doi: [10.1007/s00248-021-01893-7](https://doi.org/10.1007/s00248-021-01893-7)
- Kobayashi K, Takeuchi N and Kagami M** (2023) Distribution of parasitic chytrids of glacier algae in Alaska; cryoconite holes as a hotspot of chytrid infection. *Scientific Reports* **13**. doi: [10.21203/RS.3.RS-2189377/V1](https://doi.org/10.21203/RS.3.RS-2189377/V1).
- Langford H, Hodson A, Banwart S and Bøggild C** (2010) The microstructure and biogeochemistry of Arctic cryoconite granules. *Annals of Glaciology* **51**(56), 87–94. doi: [10.3189/172756411795932083](https://doi.org/10.3189/172756411795932083)
- Lutz S, McCutcheon J, McQuaid J B and Benning LG** (2018) The diversity of ice algal communities on the Greenland Ice Sheet as revealed by oligotyping. *Microbial Genomics* **4**, 1–10. doi: [10.1099/mgen.0.000159](https://doi.org/10.1099/mgen.0.000159).
- Mader HM, Pettitt ME, Wadham JL, Wolff EW and Parkes RJ** (2006) Subsurface ice as a microbial habitat. *Geology* **34**, 169–172. doi: [10.1130/G22096.1](https://doi.org/10.1130/G22096.1)
- McCutcheon J and 13 others** (2021) Mineral phosphorus drives glacier algal blooms on the Greenland Ice Sheet. *Nature Communications* **12**, 570. doi: [10.1038/s41467-020-20627-w](https://doi.org/10.1038/s41467-020-20627-w)
- Noël B and 11 others** (2018) Modelling the climate and surface mass balance of polar ice sheets using RACMO2–Part 1: Greenland (1958–2016). *The Cryosphere* **12**(3), 811–831. doi: [10.5194/tc-12-811-2018](https://doi.org/10.5194/tc-12-811-2018)
- Nolin AW and Dozier J** (2000) A hyperspectral method for remotely sensing the grain size of snow. *Remote Sensing of Environment* **74**(2), 207–216. doi: [10.1016/S0034-4257\(00\)00111-5](https://doi.org/10.1016/S0034-4257(00)00111-5)
- Onuma Y and 6 others** (2022) Modeling seasonal growth of phototrophs on bare ice on the Qaanaaq Ice Cap, northwestern Greenland. *Journal of Glaciology*, 1–13. doi: [10.1017/jog.2022.76](https://doi.org/10.1017/jog.2022.76)
- Painter TH and 5 others** (2001) Detection and quantification of snow algae with an airborne imaging spectrometer. *Applied and Environmental Microbiology* **67**(11), 5267–5272. doi: [10.1128/AEM.67.11.5267-5272.2001](https://doi.org/10.1128/AEM.67.11.5267-5272.2001)
- Perini L and 5 others** (2019) Darkening of the Greenland Ice Sheet: fungal abundance and diversity are associated with algal bloom. *Frontiers in Microbiology* **10**(March), 557. doi: [10.3389/fmicb.2019.00557](https://doi.org/10.3389/fmicb.2019.00557)
- Perini L and 9 others** (2022) Interactions of fungi and Algae from the Greenland Ice Sheet. *Microbial Ecology* (0123456789). doi: [10.1007/s00248-022-02033-5](https://doi.org/10.1007/s00248-022-02033-5)
- Remias D and 5 others** (2012b) Characterization of an UV- and VIS-absorbing, purpurogallin-derived secondary pigment new to algae and highly abundant in *Mesotaenium berggrenii* (Zygnematophyceae, Chlorophyta), an extremophile living on glaciers. *FEMS Microbiology Ecology* **79**(3), 638–648. doi: [10.1111/j.1574-6941.2011.01245.x](https://doi.org/10.1111/j.1574-6941.2011.01245.x)
- Remias D, Holzinger A, Aigner S and Lu C** (2012a) Ecophysiology and ultrastructure of *Ancylonema nordenskiöldii* (Zygnematales, Streptophyta), causing brown ice on glaciers in Svalbard (high arctic), **35**, 899–908. doi: [10.1007/s00300-011-1135-6](https://doi.org/10.1007/s00300-011-1135-6).
- Ryan JC and 7 others** (2018) Dark zone of the Greenland Ice Sheet controlled by distributed biologically-active impurities. *Nature Communications* **9**(1), 1–10. doi: [10.1038/s41467-018-03353-2](https://doi.org/10.1038/s41467-018-03353-2)
- Schuster CJ** (2001) Weathering crust processes on melting glacier ice (Alberta, Canada) (PhD Thesis). Wilfrid Laurier University. doi: [10.1029/2006GL027819](https://doi.org/10.1029/2006GL027819)
- Stevens IT and 8 others** (2018) Near-surface hydraulic conductivity of northern hemisphere glaciers. *Hydrological Processes* **32**, 850–865. doi: [10.1002/hyp.11439](https://doi.org/10.1002/hyp.11439)
- Stevens IT and 11 others** (2022) Spatially consistent microbial biomass and future cellular carbon release from melting Northern Hemisphere glacier surfaces. *Communications Earth and Environment* **3**(1), 1–10. doi: [10.1038/s43247-022-00609-0](https://doi.org/10.1038/s43247-022-00609-0)
- Stibal M and 17 others** (2017) Algae drive enhanced darkening of bare ice on the Greenland Ice Sheet. *Geophysical Research Letters* **44**(22), 11,463–11,471. doi: [10.1002/2017GL075958](https://doi.org/10.1002/2017GL075958)
- Tedesco M and 5 others** (2016) The darkening of the Greenland ice sheet: trends, drivers, and projections (1981–2100). *The Cryosphere* **10**(2), 477–496. doi: [10.5194/TC-10-477-2016](https://doi.org/10.5194/TC-10-477-2016)
- Tedstone AJ and others** (2017) Dark ice dynamics of the south-west Greenland Ice Sheet. *The Cryosphere* **11**(6), 2491–2506. doi: [10.5194/tc-11-2491-2017](https://doi.org/10.5194/tc-11-2491-2017)
- Tedstone AJ and others** (2020) Algal growth and weathering crust state drive variability in western Greenland Ice Sheet ice albedo. *The Cryosphere* **14**(2), 521–538. doi: [10.5194/TC-14-521-2020](https://doi.org/10.5194/TC-14-521-2020)
- Tuzet F and 9 others** (2017) A multilayer physically based snowpack model simulating direct and indirect radiative impacts of light-absorbing impurities in snow. *The Cryosphere* **11**(6), 2633–2653. doi: [10.5194/tc-11-2633-2017](https://doi.org/10.5194/tc-11-2633-2017)
- Wang S, Tedesco M, Alexander P, Xu M and Fettweis X** (2020) Quantifying spatiotemporal variability of glacier algal blooms and the impact on surface albedo in southwestern Greenland. *The Cryosphere* **14**, 2687–2713. doi: [10.5194/tc-14-2687-2020](https://doi.org/10.5194/tc-14-2687-2020)
- Wang S, Tedesco M, Xu M and Alexander PM** (2018) Mapping ice algal blooms in southwest Greenland from space. *Geophysical Research Letters* **45**, 11,779–11,788. doi: [10.1029/2018GL080455](https://doi.org/10.1029/2018GL080455)
- Whicker CA and 5 others** (2022) SNICAR-ADv4: a physically based radiative transfer model to represent the spectral albedo of glacier ice. *The Cryosphere* **16**(4), 1197–1220. doi: [10.5194/tc-16-1197-2022](https://doi.org/10.5194/tc-16-1197-2022)
- Williamson CJ and 8 others** (2018) Ice algal bloom development on the surface of the Greenland Ice Sheet. *FEMS Microbiology Ecology* **94**(3), 1–10. doi: [10.1093/femsec/fiy025](https://doi.org/10.1093/femsec/fiy025)
- Williamson CJ and 5 others** (2019) Glacier Algae: a dark past and a darker future. *Frontiers in Microbiology* **10**(April). doi: [10.3389/fmicb.2019.00524](https://doi.org/10.3389/fmicb.2019.00524)
- Williamson CJ and 11 others** (2020) Algal photophysiology drives darkening and melt of the Greenland ice sheet. *Proceedings of the National Academy of Sciences* **117**, 201918412. doi: [10.1073/pnas.1918412117](https://doi.org/10.1073/pnas.1918412117).
- Williamson CJ and 5 others** (2021) Macro-nutrient stoichiometry of glacier algae from the southwestern margin of the Greenland Ice Sheet. *Frontiers in Plant Science* **12**, 1–8. doi: [10.3389/fpls.2021.673614](https://doi.org/10.3389/fpls.2021.673614).
- Woods T and Hewitt IJ** (2022) A model of the weathering crust and microbial activity on an ice-sheet surface. *EGU sphere*, [preprint]. doi: [10.5194/egusphere-2022-1086](https://doi.org/10.5194/egusphere-2022-1086)