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Research article

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Antarctic snow algal responses to temperature - potential implications of climate change

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Abstract

Snow algae are important primary producers in Antarctic terrestrial ecosystems. As short-term Antarctic summer temperatures approach 20°C, parameterising temperature tolerance for snow algal species is key to determining how climate change may affect community composition and primary productivity. We studied three Antarctic snow algae strains isolated from Ryder Bay, Adelaide Island (Antarctic Peninsula). The strains were exposed to 4, 8, 10, 12, 16, and 20°C across four laboratory experiments to assess the effects of temperature on growth, metabolite composition, and photochemistry. Growth of *Limnomonas* sp. and *Chlorominima* sp. was negatively affected at 8°C, and they did not survive at 20°C. *Micractinium* sp., conversely, grew well at all temperatures and displayed metabolic profiles similar to those of the temperate alga, *Chlorella vulgaris*. Photosynthetic parameters, measured by quantum yield (QY) curves, O_2 production and pigment content, were minimally affected by temperature in *Micractinium* sp., whereas *Limnomonas* sp. showed reduced QY at temperatures of 8°C and above. *Chlorominima* sp. exhibited the greatest variation in QY and O_2 production across temperature treatments. Our findings suggest that increased temperatures are likely to lead to changes in cryomicrobial community composition, with the psychrotolerant *Micractinium* sp. being more resilient to these changes.

Sustainability statement

Sustainability Statement (primary SDG 13: Climate Action)
This study primarily supports UN SDG 13 (Climate Action) by improving understanding of how Antarctic snow algal communities respond to realistic warming and heatwave conditions. By quantifying thermal tolerance, metabolic plasticity, and photophysiology, our results help constrain predictions of carbon cycling inputs. Evidence for shifts in community composition and potential establishment of psychrotolerant taxa also informs climate-risk monitoring and early biosecurity planning in a rapidly warming cryosphere. Additional relevant SDGs: SDG 15 (Life on Land), SDG 14 (Life Below Water).

Keywords algae, microbial physiology and metabolism, microbial physiology, phycology, polar

Introduction

In the limited terrestrial ecosystems of Antarctica, three groups of photosynthetic organisms predominate, lichens, mosses, and microalgae (Colesie et al. 2023). However, the substrate requirements for each group differ, with lichens and mosses requiring exposed and fixed stable rock or soil surfaces, while habitats and substrates for microalgae, such as seasonal snow, ice, or melt water, are more transient. Among the latter, snow algae are a prominent and widespread component of Antarctic cryospheric habitats. Despite the seasonal transient nature of these habitats, terrestrial snow algal blooms are common in Antarctica, especially in coastal areas, and contribute importantly to primary production and carbon capture in polar ecosystems (Hoham and Remais 2020, Luo et al. 2020, Soto et al. 2022, Walshaw et al. 2024). Surveys using both satellite imagery and field data in 2018–2019 de-

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tected over 1600 green snow algal blooms (~2.0 km^2 in a season) along the Antarctic Peninsula (Gray et al. 2020, 2021), and 3.3 km^2 of bloom area was identified across the whole continent (Walshaw et al. 2024). However, the warming Antarctic Peninsula (Robinson et al. 2020) is likely to affect the range and extent of its snow algal blooms. Warming may initially increase the overall area and southward range extent of these blooms as conditions (more biologically available water, i.e. slush) become more favourable further south and at higher altitudes (Gray et al. 2020, Thomson et al. 2025). Any increase in bloom areas on larger icecaps may lead to enhanced melting, as biological entities such as algae are implicated in reducing snow and ice albedo (Cook et al. 2017, Thomson et al. 2025). Conversely, since 54% of habitable area for snow algae blooms was located on small islands with no high ground for upward range expansion (Gray et al. 2025), these bloom areas are likely to be lost during warmer periods, which may impact the flow of fixed nutrients into adjacent terrestrial and nearshore marine ecosystems.

With a suitable acclimation period, some microalgae may be able to tolerate a temperature increase, however, heat shock events may pose a particular threat to psychrophilic microalgae whose growth optima typically range from 0 to 5°C. In February 2020, a record-breaking temperature of 18.4°C was recorded on the Antarctic Peninsula (Esperanza Station, long-term average February temperature 0.0°C), during a warm spell that persisted for 8 days (Robinson et al. 2020). Local heatwaves such as these in the Antarctic have increased 10-fold since 1950 (González-Herrero et al. 2022) and, as the climate continues to warm, these events are likely to become more frequent (Siegert et al. 2023). Determining the thermal tolerance of polar organisms is therefore key to understanding their long-term ecological response. It is likely that psychrotolerant microbes (which tolerate wider temperature ranges up to 20°C) will be able to withstand such events, whereas true psychrophiles may not. As a result, psychrophilic species would have a more restricted habitat range available than those that are psychrotolerant. In the field, snow algal cells are likely to encounter temperatures above 4°C, mainly under melting conditions such as thawing snow, slush, biofilms on exposed rock, or small puddles and streams, rather than within colder snowpack interiors (Kuklinski and Balazy 2014).

To understand how climate change will affect microbial snow communities, the phenotypic plasticity of these organisms needs to be determined (Morgan-Kiss et al. 2006, Davey et al. 2019). There is a diverse range of snow algal strains present in the blooms found in Antarctica, largely belonging to genera within the Chlamydomonadales and Trebouxiophyceae for green (e.g. *Chloromonas*, *Chlorominima*, *Raphidonema*) and red blooms (*Sanguina*, *Chlainomonas*), and Zygnematophyceae for the purple ice algae (*Ancylonema*) (Davey et al. 2019, Gray et al. 2020, Soto et al. 2022, Thomson et al. 2025). Therefore, with fewer but larger blooms in new locations predicted in the future, and the possibility that each species may have different adaptive and acclimatory capabilities, changes in community composition and diversity loss may occur. Recent studies have shown that algae isolated from Antarctica (King George Island, South Shetland Islands), such as the psychrophilic *Chlorominima collina* (Gálvez et al. 2021, Soto et al. 2022) and the psychrotolerant *Chloromonas* sp. and *Microglena* sp. (Broadwell et al. 2023), show distinct responses in growth traits when grown under varied abiotic conditions such as temperature (Bidigare et al. 1993, Hoham and Ling 2000, Rivas et al. 2016, Hoham and Remias 2020). However, thermal responses are not only expressed through growth. Changes in metabolism, pigment composition, and photosynthetic performance are also central components of microalgal acclimation to environmental stress (Soto et al. 2022). For example, some snow algae can enter a dormant, red encystment phase by increasing the internal content of astaxanthin esters, possibly to prevent extreme photodamage (Bidigare et al. 1993, Remias et al. 2010, Lutz et al. 2015, 2016,) while other species change their fatty acid composition (decrease in length and increase in unsaturation) in membranes to maintain membrane fluidity and avoid cell rupture (Feller and Gerday 2003, D'Amico et al. 2006, Dolhi et al. 2013).

Antarctic field environmental data confirm that snow algal cells can experience very high levels of photosynthetically active radiation (often above 1000 μmol m^{-2} s^{-1} PAR) at low temperatures (−3 to 3°C) (Davey et al. 2019). In addition, the increased summer day length at high latitudes may result in a potentially higher photon load per cell, compared to that experienced by temperate species. Nonetheless, significant rates of carbon accumulation (10 mg C m^{-2} d^{-1}) have been measured in blooms where snow contains approximately 5000 cells mL^{-1} (Hodson et al. 2017). We might, therefore, predict that the maximum capacity and efficiency of electron transfer in photosystem II, along with the production of oxygen, would be affected by temperature and other abiotic factors (Dolhi et al. 2013, Mlinarić et al. 2016) and that any plasticity in these traits will be crucial for range and habitat expansion of Antarctic snow algae. Intra- and interspecific variation in these photosynthetic traits have been measured in snow algal blooms *in situ* and in isolated strains from various latitudes (Remias et al. 2005, Soto et al. 2020, Gálvez et al. 2021, Broadwell et al. 2023). In addition, snow algal strains are more resilient in terms of maintained photosystem II capacity and efficiency at low temperature than related strains from more temperate regions (Peng et al. 2020, Zhang et al. 2020).

Here, we studied the physiology of three Antarctic terrestrial green snow algal strains isolated from the same coastal location. Although we recognize that there are limitations of using cultured strains to directly infer responses in nature, isolates are an important tool for assessing how cryospheric algal blooms may respond to warming and to understand the underlying physiology of the organisms that contribute to these changes. Our aim was to determine the thermal tolerance and the degree of plasticity of these strains to different temperatures. The strains were exposed to increasing temperatures from 4°C to 20°C across four laboratory experiments to measure the intra- and interspecific effects of temperature on their growth, metabolite composition, and photosynthetic parameters.

Materials and methods

Strain selection and growth

The snow algal isolates *Chlorominima* sp., *Micractinium* sp. (CCAP 248/21), and *Limnomonas* sp. (CCAP 6/3) were originally collected by Dr Matthew Davey from Ryder Bay (Adelaide Island, 68°S), off the west coast of the Antarctic Peninsula in 2015 and 2018, where the temperature at the snow surface and 5 cm depth at bloom sites ranged from −3.8°C ± 0.41 to 1.4°C ± 1.6 (Davey et al. 2019). They were isolated the year after collection using suc-

cessive streaking and colony selection on agar plates, identified and in 2023 deposited at the UK Culture Collection of Algae and Protozoa (CCAP; https://www.ccap.ac.uk) using 1N-Bold's Basal Medium (1N-BBM) at 4°C. The temperate control strain, *Chlorella vulgaris* (CCAP 211/11B), originally isolated from the Netherlands, was obtained from CCAP and grown in Jaworski's Medium (JM) (Jaworski et al. 1981) at 20°C.

An initial experiment was set out to test if growth and metabolic differences were detectable between two strains, *Chlorominima* sp. and *Limnomonas* sp. (CCAP 6/3), at two different growth temperatures (4°C, 10°C). The wider experiment included more taxa by also including the snow algal isolate *Micractinium* sp. and *Chlorella vulgaris* (temperate control strain) and expanded the range of growth temperatures (4°C, 8°C, 20°C). Initial experiment: *Chlorominima* sp. and *Limnomonas* sp. were cultivated in 250 mL Erlenmeyer flasks containing 100 mL sterile 1N-BBM with a starting cell density of 1×10^5 cells mL^{-1} (day 0). Triplicate flasks were placed in two shaking incubators at 45 rpm and at 4°C or 10°C, 16:8 h (light: dark) cycle with photosynthetic active radiation (PAR) between 75–80 μmol m^{-2} s^{-1}. Every other day, a 1-mL subsample from each culture was taken to measure optical density (OD) at 600 nm (Implen NanoPhotometer) and cell counts (MultisizerTM 3 Beckman Coulter Counter, gated at 2–20 μm, Germany). Three experiments were undertaken lasting 13, 21, and 42 days. A 6 mL subsample of every replicate was taken every week and centrifuged (2 min at 2000 *g*, Eppendorf 5810 R centrifuge). The supernatant was discarded, and the pellets stored at −80°C for subsequent metabolite extraction. Wider experiment: Cultures of the three Antarctic snow algal strains, *Micractinium* sp., *Chlorominima* sp., and *Limnomonas* sp., and the model control strain, *Chlorella vulgaris*, were normalized to a starting cell count of 2.5×10^6 cells mL^{-1}. One millilitre of culture was added to 4 mL of growth medium (JM for *Chlorella vulgaris* and 1N-BBM for snow algae) to each well (5 mL per well) of clear 6-well plates (Corning Co-Star), with triplicate well-plates for each strain and growth temperature. Plates were sealed with parafilm to reduce evaporation and contamination. A 6-well plate of growth media (5 mL per well) was also prepared for each temperature to act as a blank control. Plates were stacked either within a 4°C Eppendorf Innova S44i incubator, 8°C or 20°C Polysec controlled temperature room at 12:12 hour (light: dark) cycle, PAR 22–86 μmol m^{-2} s^{-1} with plates rotated three times per week to ensure even light availability. OD of the cultures in each well was measured three times per week (POLARstar Omega plate reader). Cells were harvested on days 25 (lag phase), 33 (exponential phase), and 46 (stationary phase) by adding the contents of each well to separate 15-mL centrifuge tubes. The tubes were centrifuged (2 min, 2000 rpm, Eppendorf 5810 R), the supernatant discarded, and the pellets frozen at −80°C for metabolite analysis. Specific growth rates between the harvest points were calculated using the equation:

$$\mu = (L\,(D2) - Ln\,(D1)) \,/\, (T2 - T1)$$

where μ = specific growth rate, T1 and T2 represent two points in time, and D1 and D2 represent the optical density at these time points.

Metabolite profiling

Metabolites were extracted and analysed by gas chromatography–mass spectrometry (GC–MS) based on the methods of Davey et al. (2014, 2008, 2019). An untargeted metabolite profiling approach was used, meaning that detectable GC–MS features were analysed as a whole rather than restricting the analysis to a predefined set of target metabolites. For each frozen pellet inside the 15-mL sample tube, 2 mL of chilled methanol: chloroform: water mixture (2.5:1:1) were added and vortexed for 10 s, placed in ice and left on a rotating plate for 30 min. The tubes were again vortexed, centrifuged at 4°C for 2 min at 2000 rpm, with the supernatant added to new pre-chilled 15-mL tubes. The remaining pellet was re-extracted into 1 mL methanol: chloroform (1:1), vortexed and placed on the rotating plate for 30 min, after which the samples were vortexed and centrifuged at 4°C for 2 min at 2000 rpm. The supernatants were combined and 0.5 mL of chilled water was added to the combined supernatants, vortexed and centrifuged at 4°C for 2 min at 2000 rpm to separate the phases. The upper aqueous methanol phase was collected using a pipette and added to a 1.8-mL GC vial and stored at −80°C. On the day of analysis, to each extract, 5 μL of a 3 mg mL^{-1} phenyl beta-glucopyranoside (Sigma, 292710–5 g) spike was added to each sample and completely evaporated (EZ-2 plus Genevac). To the dried samples, 50 μL of a 20 mg mL^{-1} pyridine-O-methoxyamine solution [Sigma, 226904–5 g, (99.8%, Sigma, 270970–100 mL)] were added using a glass syringe and the sample vortexed until the crust was fully suspended in solution and placed in a heat block (37°C) for 90 min. Next, 50 μL of N-methyl-4 (trimethylsilyl) trifluoroacetamide (Sigma, 69479–10 × 1 mL) were added to each sample, vortexed and added to the heat block for a further 60 min. The samples were cooled to room temperature and transferred to a new GC glass vial with an insert. The metabolites were separated and analysed on a Shimadzu Nexis GCMS-QP2020 NX GC-MS (ZB-5MSi column (30 m, 0.25 mm ID, 0.25 μm film thickness), injection volume 1 μL, injection temperature 300°C, Carrier gas flow was constant at 1 mL^{-1}. Initial oven temperature was 70°C, increased to 130°C at 10°C min^{-1}, then to 230°C at 5°C min^{-1}, 310°C at 10°C min^{-1} and then held for 15 min, positive ionization, interface line 250°C, ion source 200°C, mass range 45–800 Da. The peaks in each chromatogram were putatively annotated using the top hit metabolite match in the Shimadzu-NIST library, meaning identification was at either level 3 or 4 according to the metabolomics standardized reporting structure (Salek et al. 2013). The output files for each sample containing the total ion count and peak area for each putatively annotated metabolite were aligned and merged using Metapolish (https://github.com/AndreHolzer/Metapolish). Variation in the metabolite profiles between strains and temperature treatments were analysed by partial least square-discriminant analysis (PLS-DA) using Simca-P (Umetrics V17) and sparse sPLS-DA in MetaboAnalyst v6.0 (Xia et al. 2009). PLS-DA plots provide insight on correlation among samples and allow assessment of the overall metabolomic similarity between the samples.

Photosynthetic parameters (pulse-amplitude-modulated fluorometry, oxygen evolution, and pigment content)

Cultures of *Chlorominima* sp., *Micractinium* sp. (CCAP 248/21), and *Limnomonas* sp. (CCAP 6/3) were added to either 3 × 50 mL clear vented tissue culture flasks for pulse-amplitude-modulated (PAM) fluorometer measurements or in clear 6-well plates (5 mL per well,

Corning Costar) for oxygen measurements. Samples were placed in a growth incubator (Polar Series G, Nisbets, Ireland) set at 4°C, 8°C, 12°C or 16°C for either 1 day (24 h, acute shock) or 7 days (chronic shock). The PAM experiment was performed twice for the 1-day (1 d) treatment and once for the 7-day (7 d) treatment. The samples were placed back in the 4°C incubator for 30–90 min for OD and cell count measurements and dark-adapted for 15 min at 4°C before PAM measurements were taken (Aquapen-C PAM, Photon Systems Instruments, Czech Republic). Total chlorophyll and carotenoid concentrations were determined after extraction of pigments from cell pellets (from 1 mL culture) with 1 mL dimethylformamide using the equations of Inskeep and Bloom (1985) and Wellburn (1994).

F_vF_m (maximum efficiency of PSII photochemistry in dark adapted material) and F_v'/F_m' (maximum efficiency of PSII photochemistry in the light) (Murchie and Lawson 2013) were measured using the OJIP and NPQ1 settings (actinic light 60 s, 5 pulses, 1st pulse 7 s at 12 s intervals; dark recovery 88 s of 3 pulses, 1st pulse 11 s at 26 s intervals). Super pulse (F_m) PAR intensity was optimized and set at 600 μmol m^{-2} s^{-1} (20%) for *Limnomonas* sp. and *Micractinium* sp. and 1200 μmol m^{-2} s^{-1} (40%) for *Chlorominima* sp. Flash pulse (F_o or F_t) PAR was optimized and set at 10% (0.009 μmol m^{-2} s^{-1}) for *Micractinium* sp. and *Chlorominima* sp. and 20% (0.018 μmol m^{-2} s^{-1}) for *Limnomonas* sp. Actinic level was set at a PAR of 50 μmol m^{-2} s^{-1} (5%) throughout. Light response curves of quantum yield (QY) F_v'/F_m' were achieved using setting (LC3) consisting of initial super pulse followed by increasing PAR actinic levels of 10, 20, 50, 100, 300, 500, 1000 μmol m^{-2} s^{-1} with phase duration of 60 s. Relative electron transport rates of PSII (rETR; μmol electrons m^{-2} s^{-1}) were calculated using equations from Remias et al. (2010) (QY × PAR from 10 to 1000) and the initial slope (α) and $rETR_{max}$ were calculated using the same two-stage exponential rise to maximum equation in SigmaPlot (Davey et al. 2007).

Rates of oxygen production were measured by adding 1.5 mL dark-adapted culture into an Oxytherm + P oxygen electrode chamber (Hansatech Instruments, Kings Lynn, UK) set at 4°C, 70 rpm stirring and after 3 min at 0 irradiance, increasing PAR through 0, 10, 20, 40, 50, 80, 100, 200, 300, 500, 1000 μmol m^{-2} s^{-1} at 2 min intervals. Rates of O_2 production were measured over 1 min during the 2-min interval and O_2 production rates normalized to a per cell basis (cells counted on a MultisizerTM 3 Beckman Coulter Counter, Germany). To determine whether differences in the photochemistry measurements between strains, temperatures and exposure duration (1 d or 7 d) were statistically significant, two-way ANOVAs and, where significant, *post hoc* Tukey's tests (SIGMAPLOT v.15.0.0.13, Systat Software Inc., Chicago, IL, USA) were performed.

Results

Temperature-dependent growth responses

The initial experiment growing isolated snow algae in 100 mL cultures indicated that an increase in incubator temperature from 4°C to 10°C reduced the growth of *Limnomonas* sp. (Δ1.9 ± 0.06 OD at day 41) more than that of *Chlorominima* sp. (Δ0.5 ± 0.05 OD at day 41) (Fig. 1). The wider experiment including the snow algal isolate *Micractinium* sp. and *Chlorella vulgaris* (temperate control strain) and expanding the range of growth temperatures (4°C, 8°C, 20°C) confirmed the finding that growth (using 5 mL cultures in 6-well plates) of *Limnomonas* sp. was reduced by an increase in temperature (Δ0.3 ± 0.1 OD between 4°C and 20°C day 46) (Fig. 2A). *Chlorominima* sp. tolerated an increase from 4°C to 8°C but did not grow at 20°C (Δ0.18 ± 0.05 OD between 4 and 20°C day 46) (Fig. 2B). *Micractinium* sp. was able to grow at all temperatures and was the only Antarctic strain to grow at 20°C, with growth at 8°C lower than that at 20°C (Δ0.3 ± 0.02 OD between 4 and 20°C day 46) (Fig. 2C). The growth of the temperate *C. vulgaris* was highest at 20°C, with lower growth at 8°C and 4°C (Δ0.12 ± 0.03 OD between 4°C and 20°C day 46) (Fig. 2D) (Table S1). The growth response was verified by visual assessment of cultures in the well-plates, showing the growth of *Micractinium* sp. and *C. vulgaris* compared to the lack of growth of *Chlorominima* sp. and *Limnomonas* sp. at 20°C. *Chlorominima* sp. at 4°C and 8°C also displayed cell aggregation and *Limnomonas* sp. at 8°C attached to the walls of the well (Fig. 3).

Metabolite profiling

In addition to the responses to growth temperature, we detected distinct metabolic profiles amongst strains and variation in the measurable metabolome in response to growth temperature. The untargeted GC–MS metabolic profiles obtained from the initial experiment showed significant metabolic variation between *Chlorominima* sp. and *Limnomonas* sp., as well as intraspecific variation in the metabolic profiles, at each growth temperature (4°C or 10°C). Metabolic variation in *Limnomonas* sp. between the two growth temperatures was greater than that in *Chlorominima* sp. (Fig. 4A). The top six putatively annotated metabolites contributing most strongly to separation in sPLS-DA (based on VIP scores for PC1, PC2, and PC3) were glutaric acid and malic acid (PC1, higher in *Chlorominima* sp.), uridine and L-proline (PC2, higher in cells grown at 4°C) and sucrose and L-leucine (higher in *Chlorominima* sp. at 10°C) (Fig. S1). Sucrose, uridine, glutaric acid, L-proline, malic acid, doconexent (Docosahexaenoic acid; DHA), and 2-butenedioic acid (maleic acid) were also among the top putatively annotated metabolites that differed significantly between strains and temperatures (ANOVA; Fig. S2).The untargeted GC–MS metabolic profiles obtained from the wider experiment showed significant interspecific metabolic variation between all four strains (Fig. 4B). *Chlorella vulgaris* and *Micractinium* sp. largely clustered together, as did *Chlorominima* sp. and *Limnomonas* sp. There was intraspecific variation in the overall metabolic profile of cells grown at the three temperature conditions (4°C, 8°C, 20°C) for *C. vulgaris*, *Micractinium* sp., and especially for *Limnomonas* sp. However, as in the initial experiment, there was relatively little overall variation in the metabolome of *Chlorominima* sp. in response to increased temperature. The top six putatively annotated metabolites contributing most strongly to separation in sPLS-DA space (based on VIP scores for PC1, PC2, and PC3) were docosahexaenoic acid (DHA) and allose (PC1, higher in *Limnomonas* sp. at 4°C), valine and butyric acid (PC2, higher in *C. vulgaris*) and L-lysine and erythrono-1–4-lactone (higher in *Micractinium* sp. at 4°C) (Fig. S3). DHA, L-serine, allose, L-tyrosine, uridine, butyric acid, L-valine, sucrose, D-xylose, putrescine, uracil, and homocitrulline were also among the putatively annotated metabo-

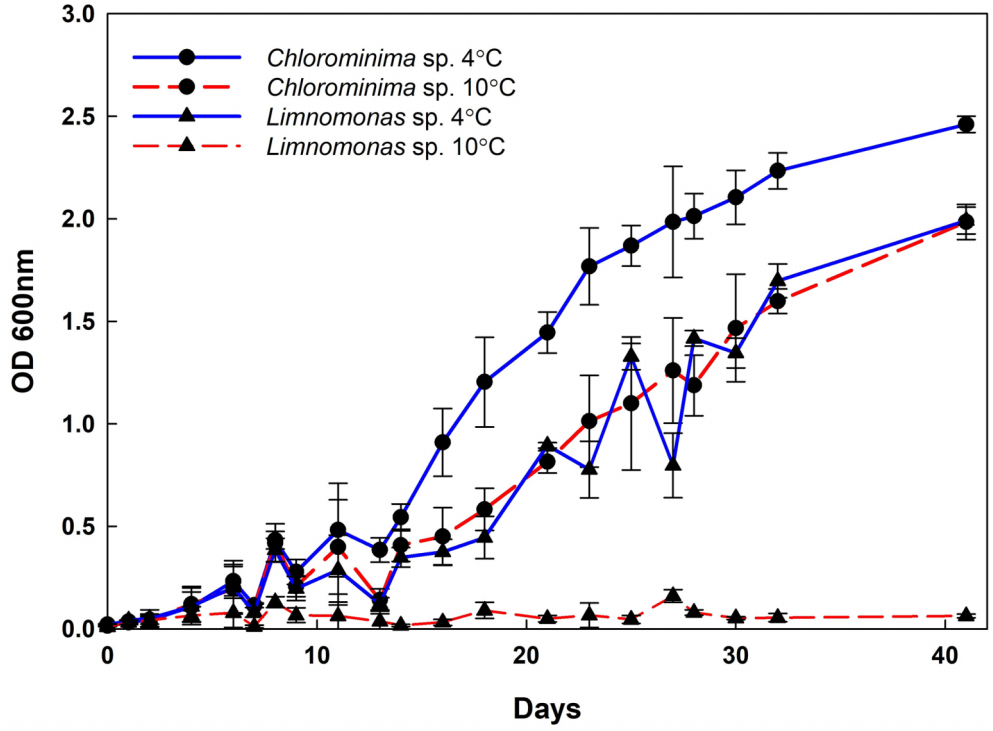

Figure 1 Initial experiment of growth of *Chlorominima* sp. and *Limnomonas* sp. snow algal isolates (OD 600 nm) over 42 d at 4°C or 10°C (16:8 light: dark, PAR 80 μmol m^{-2} s^{-1}). Mean ± SD ($n = 9$) from three separate growth experiments in 100 mL culture volumes. ODs were significantly different ($P \leq 0.05$) between temperatures on day 13 and onwards from day 16 for *Chlorominima* sp. and from day 7 for *Limnomonas* sp.

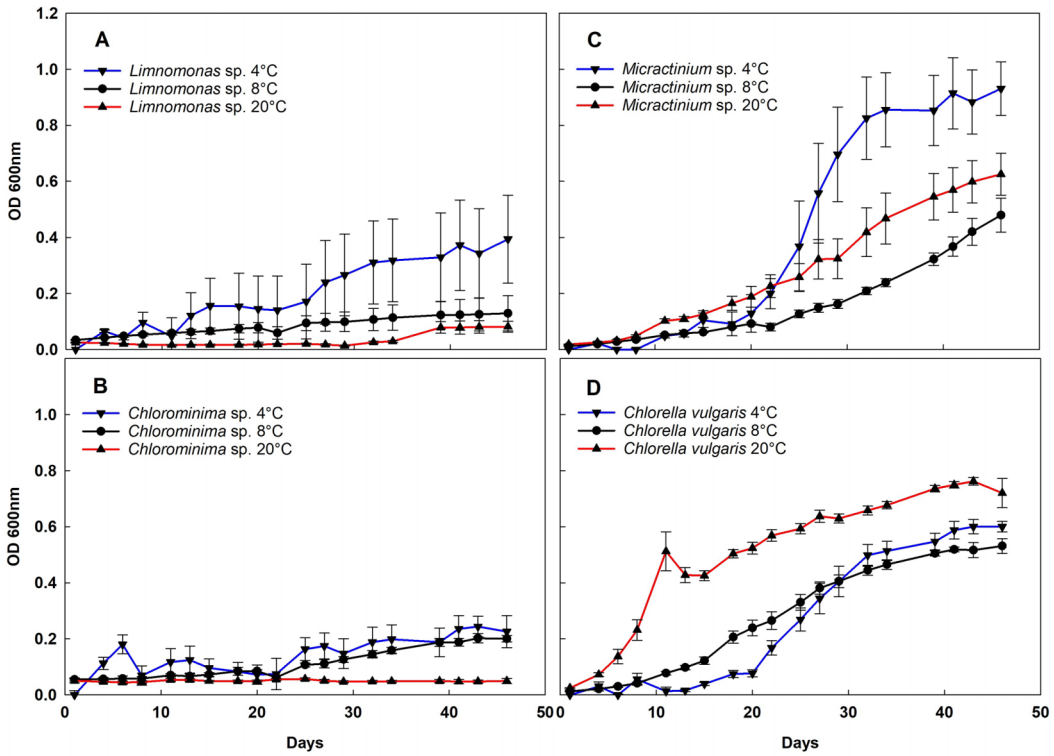

Figure 2 Wider experiment of the effects of temperature on the growth of *Limnomonas* sp. (A), *Chlorominima* sp. (B), *Micractinium* sp. (C) snow algae and the temperate *Chlorella vulgaris* (D) at OD 600 nm over 46 d at 4°C, 8°C, and 20°C in 5 mL cultures within 6-well plates. Mean ± SD ($n = 6$).

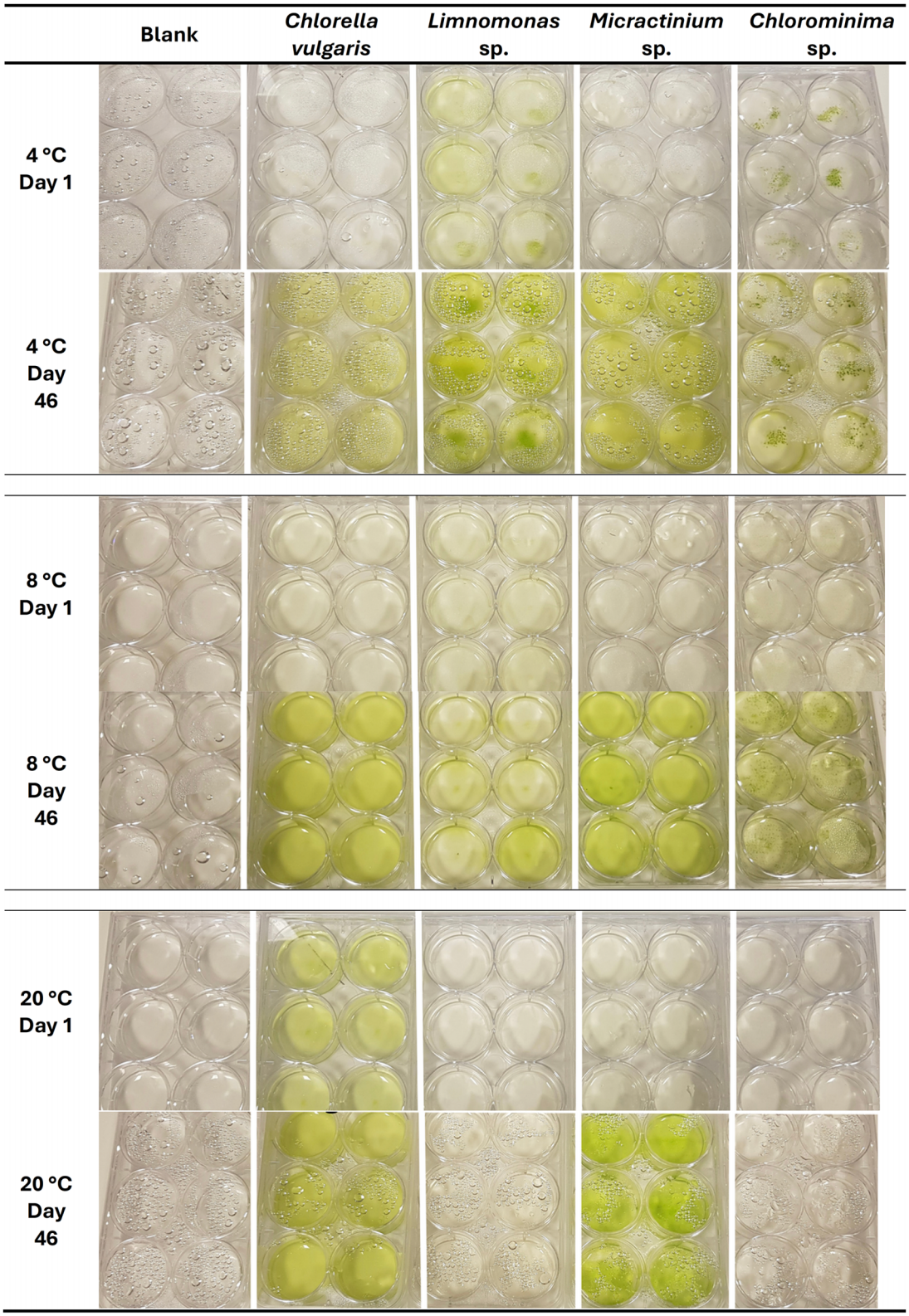

Figure 3 Effects of temperature on algal cell growth over 46 days. Standard well plates containing 5 mL algal cultures (blank growth media only; the temperate *Chlorella vulgaris*, and the snow algae *Limnomonas* sp., *Micractinium* sp., *Chlorominima* sp. at the start (day 1) (top row) and end point (day 46) (bottom row), at growth temperatures of 4°C, 8°C, and 20°C.

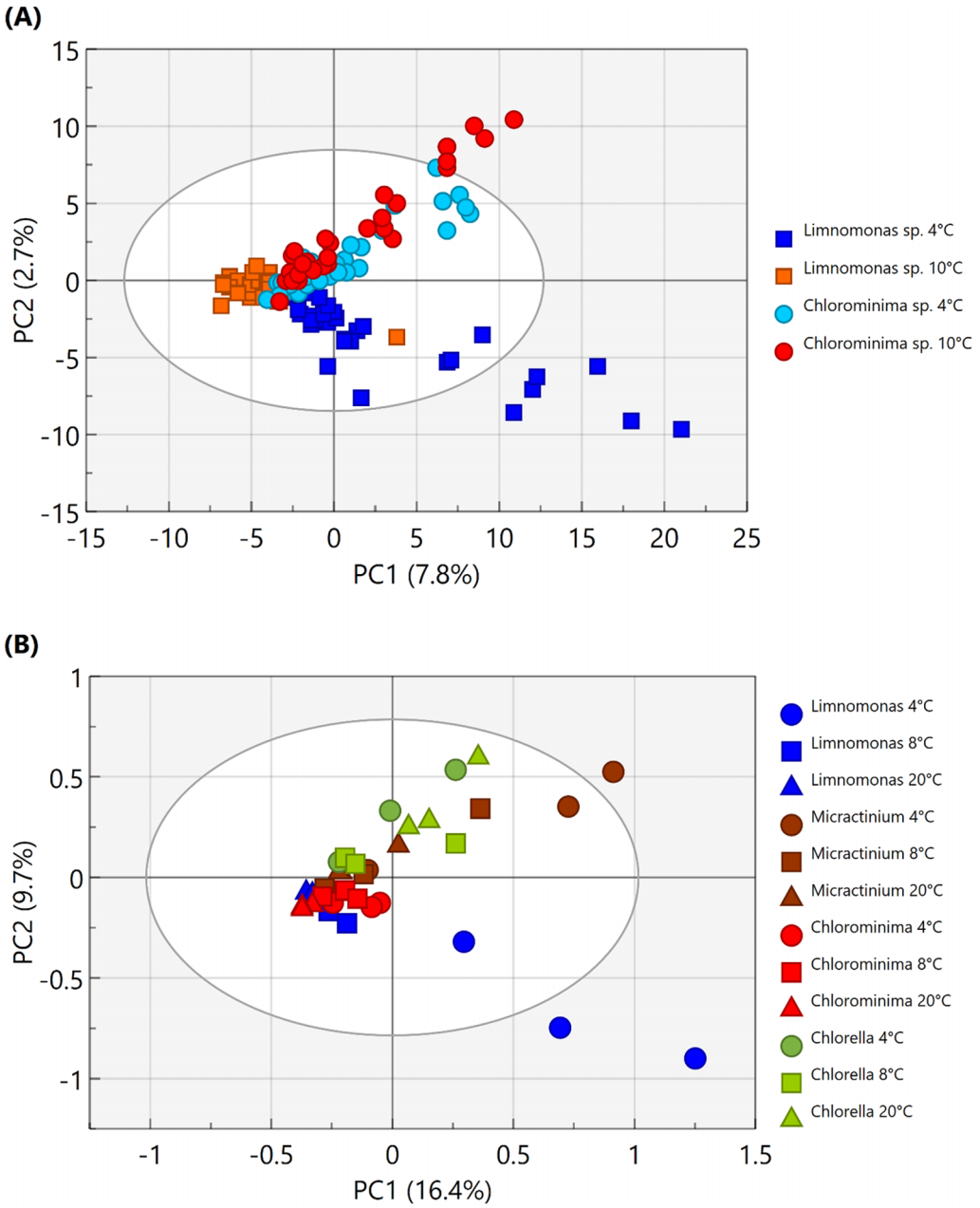

Figure 4 Effects of growth temperature on metabolite production shown by Partial Least Squares Discriminant Analysis (PLS-DA). Score scatter plots showing cluster differences of GC–MS peak intensities of (A, initial experiment): *Chlorominima* sp. and *Limnomonas* sp. snow algal isolates ($n = 33$) grown at 4°C or 10°C, with treatment groups indicated in the figure legend, and harvested for metabolite extraction on day 4, 6, 9, 11, 12, 15, 21, and 27 from three separate growth experiments; and (B, wider experiment): *Limnomonas* sp., *Micractinium* sp., *Chlorominima* sp. and *Chlorella vulgaris* (all $n = 3$) grown at 4°C, 8°C, or 20°C, with strain and temperature groups indicated in the figure legend, and harvested for metabolite extraction on day 46. Hotelling circle denotes 95% data inclusion.

lites that differed significantly between strains and temperatures (ANOVA; Fig. S4).

Photosynthetic parameters—acute 1-day and chronic 7-day heat shock

The maximum efficiency of PSII photochemistry in dark (F_v/F_m) and light (F_v'/F_m') adapted cultures was largely unaffected by increased temperatures over 24 h and 7 d in *Micractinium* sp. cells (Fig. 5A–D). In contrast, F_v/F_m of *Limnomonas* sp. reduced by 49% to 0.35 (Fig. 5A) when exposed to 16°C for 24 h ($P \leq 0.001$) compared to 4°C. After 7 d F_v/F_m reduced by 61% to 0.18 at 12°C ($P \leq 0.001$), and by 98% to 0.01 at 16°C ($P \leq 0.001$) compared to 4°C (Fig. 5B). A similar trend was measured for the maximum efficiency of PSII photochemistry measured at an actinic light level of 50 μmol m^{-2} s^{-1} (F_v'/F_m') where, after 24 h, F_v'/F_m' reduced by 62% at 16°C ($F_v'/F_m' = 0.12$; $P \leq 0.001$) (Fig. 5C) and, after 7 d, F_v'/F_m' by 55% to 0.18 at

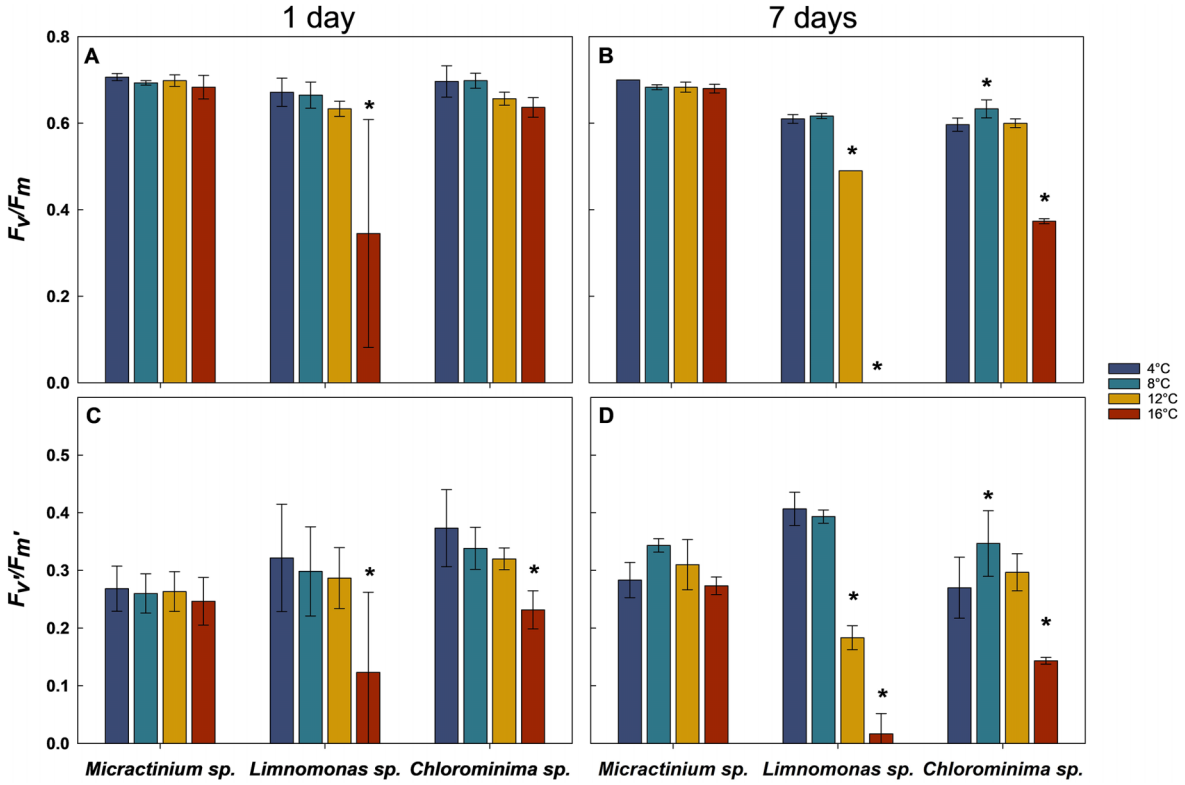

Figure 5 Effects of growth temperature on the maximum efficiency of PSII photochemistry in snow algae. Maximum efficiency of PSII photochemistry in the dark-adapted (F_v/F_m) (A, B) and in the light-adapted state (F_v'/F_m') (C, D) of *Micractinium* sp., *Limnomonas* sp., and *Chlorominima* sp. after exposure to 4°C, 8°C, 12°C, or 16°C for 1 or 7 d. Measurements made at 4°C. Mean ± SD, $n = 6$ (1 day) and 3 (7 days). Asterisk (∗) denotes a significantly different response ($P \leq 0.01$) at that temperature compared to the 4°C control within the species.

12°C ($P \leq 0.001$) and by 96% to 0.02 at 16°C ($P \leq 0.001$) (Fig. 5D).

Chlorominima sp. was less affected by increasing temperature and exposure time as, after 24 h, there was no significant change in F_v/F_m (Fig. 5A) and a more staged decrease in F_v'/F_m' resulting in a significant drop in F_v'/F_m' to 0.23 (38% reduction; $P \leq 0.001$) in cells exposed to 16°C (Fig. 5C). However, after 7 d at 16°C, there was a 37% reduction in F_v/F_m to 0.37 ($P \leq 0.001$) (Fig. 5B) and a 47% reduction of F_v'/F_m' to 0.14 ($P \leq 0.001$) (Fig. 5D), compared to 4°C.

The data for relative electron transport rates (rETR; μmol electrons m^{-2} s^{-1}) showed similar interspecific responses to temperature. Maximum rETR was obtained at 300 μmol m^{-2} s^{-1} for all strains. There was minimal variation in the rETR curves of *Micractinium* sp. after 1 d and rETR reduced from 33 at 4°C to 25 at 16°C when exposed for 7 d (300 μmol m^{-2} s^{-1}; $P \leq 0.001$) (Fig. 6A, D). In contrast, in *Limnomonas* sp., there was a near complete loss of photosynthetic efficiency after exposure to 16°C, where rETR reduced by 75% after 1 d and 100% after 7 d at 300 μmol m^{-2} s^{-1}, compared to 4°C (300 μmol m^{-2} s^{-1}; $P \leq 0.001$) (Fig. 6B, E). *Chlorominima* sp. showed more sequentially reduced photosynthetic efficiencies after exposure to 4°C, 8°C, 12°C, or 16°C for 24 h, but greater efficiencies were maintained at a higher light level (300–500 μmol m^{-2} s^{-1}) compared to the other strains. There were 50% and 62% reductions in rETR after exposure to 16°C after 1 and 7 d at 300 μmol m^{-2} s^{-1}, compared to 4°C (300 μmol m^{-2} s^{-1}; $P \leq 0.001$) (Fig. 6C, F).

Oxygen production was measured under increasing PAR (0–1000 μmol m^{-2} s^{-1}). The light compensation point (where the rate of photosynthesis equals that of respiration) was on average 4.9 ± 1.5 μmol m^{-2} s^{-1} for samples exposed to temperature treatments for 1 d and 3.5 μmol m^{-2} s^{-1} ± 0.8 for those exposed for 7 d and did not significantly differ between strains or treatments. Similarly, the PAR intensity at which the maximum O_2 evolution rate was obtained did not significantly vary between strains and treatments (median PAR at 20 μmol m^2 s^{-1} for all day 1 and 30 μmol m^2 s^{-1} for all day 7 samples).

The maximum rate of oxygen evolution per cell was not affected by increased temperature over 1 d for all strains (Fig. 7A, C, E). However, there was variation between strains in that the maximum oxygen production rate was significantly higher in *Limnomonas* sp. (0.013 ± 0.003 μmol O_2 $cell^{-1}$ min^{-1}) compared to *Micractinium* sp. (0.0003 ± 2.18^{-05} μmol O_2 $cell^{-1}$ min^{-1}) and *Chlorominima* sp. (0.0026 ± 0.0003 μmol O_2 $cell^{-1}$ min^{-1}) ($P \leq 0.001$). Over 7 d (Fig. 7B, D, F) the maximum oxygen production rate was significantly higher in *Limnomonas* sp. (0.012 ± 0.003 μmol O_2 $cell^{-1}$ min^{-1}) compared to *Micractinium* sp. (0.0004 ± 3.93^{-05} μmol O_2 $cell^{-1}$ min^{-1}) and *Chlorominima* sp. (0.0035 ± 0.0007 μmol O_2 $cell^{-1}$ min^{-1}) ($P \leq 0.001$). There was some support for a decrease in oxygen production per cell with increasing temperature treatment for 7 d for all strains. However, production differed significantly in only *Limnomonas* sp., where the maximum rate decreased from 0.03 μmol O_2 $cell^{-1}$ min^{-1} at 4°C to 0.009 (8°C), 0.007 (12°C), and 0.005 (16°C) ($P \leq 0.001$).

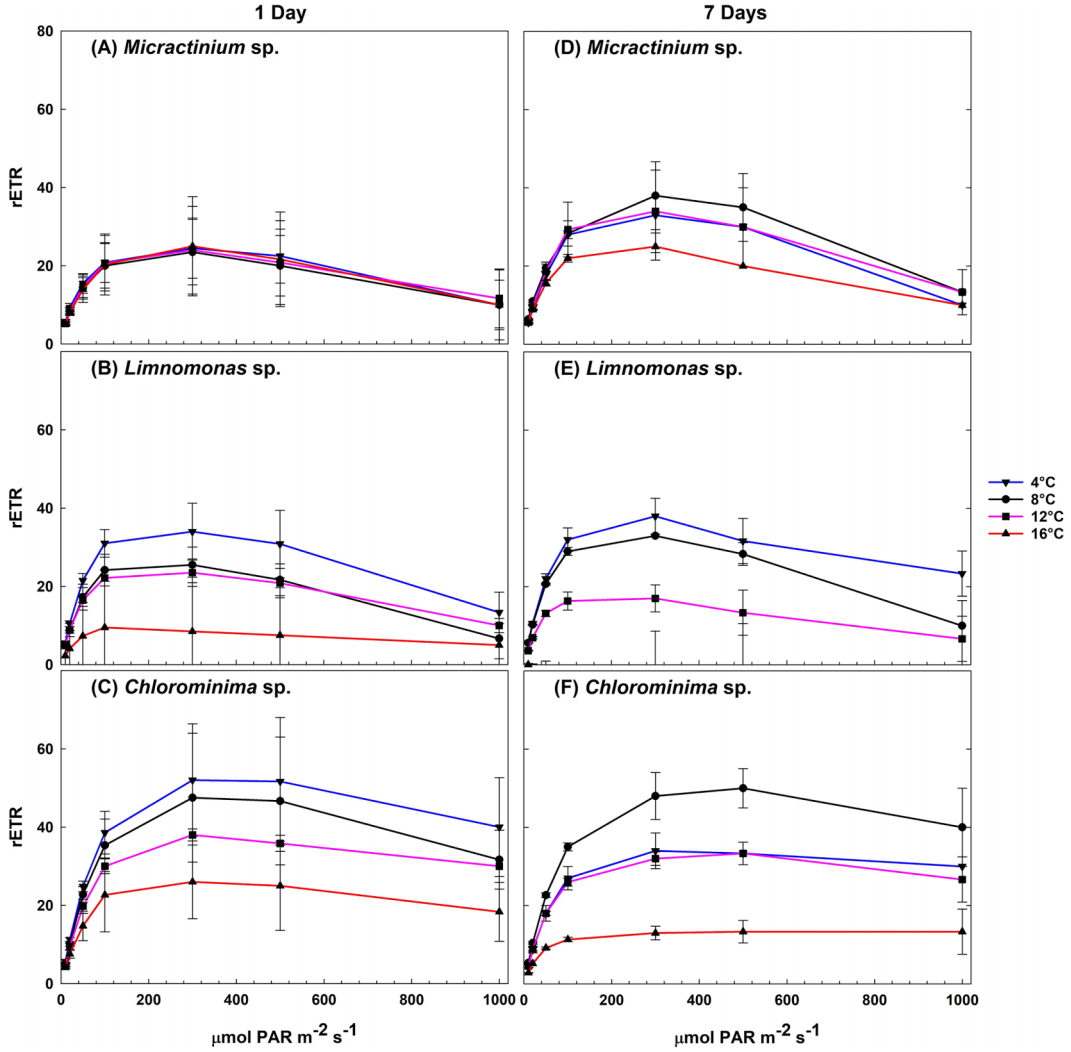

Figure 6 Effects of growth temperature on the relative electron transfer rate (rETR μmol electrons m^{-2} s^{-1}) of PSII photochemistry in snow algae. Light response curves of (A, D) *Micractinium* sp., (B, E) *Limnomonas* sp., and (C, F) *Chlorominima* sp. after exposure to 4°C, 8°C, 12°C, or 16°C for 1 or 7 d. Measurements made at 4°C at PAR from 10–1000 μmol m^{-2} s^{-1}. Mean ± SD, $n = 6$ (1 d) and 3 (7 d).

There was significant interspecific variation in the pigment content per cell. Across the four temperatures, total chlorophyll content was higher in *Limnomonas* sp. (9.4 ± 1.3 pg chlorophyll and 1.2 ± 0.2 pg carotenoid $cell^{-1}$) compared to *Chlorominima* sp. (3.1 ± 0.3 pg chlorophyll and 0.3 ± 0.02 pg carotenoid $cell^{-1}$) and *Micractinium* sp. (0.4 ± 0.04 pg chlorophyll and 0.03 ± 0.00 pg carotenoid $cell^{-1}$) (all $P \leq 0.05$) (Fig. 8A, C). Pigment content was not affected by increased temperatures over 1 d or 7 d in *Micractinium* sp. (Fig. 8A–D). Total chlorophyll and carotenoid contents of *Limnomonas* sp. were reduced when exposed to 16°C for 1 d ($P \leq 0.01$) (Fig. 8A, C) compared to 4°C. After 7 d there was a staged decrease, with chlorophyll and carotenoid contents per cell being reduced by 85% and 91%, respectively, at 16°C ($P \leq 0.001$) compared to values at 4°C (Fig. 8B, D). *Chlorominima* sp. pigment content was not affected by increasing temperature after 1 d (Fig. 8A, C) but, after 7 d, pigment content gradually increased in cells exposed to 8°C and 12°C. At 16°C there were 37% and 30% reductions in chlorophyll and carotenoid contents respectively ($P \leq 0.05$), compared to 12°C (Fig. 8B, D).

Discussion

Snow algal community contains taxa with both psychrophilic and psychrotolerant physiological traits

The aim of this study was to assess the intraspecific and interspecific effects of temperature on growth, metabolite composition and photochemistry of three Antarctic terrestrial snow algal strains isolated from the same location (Ryder Bay, Antarctic Peninsula). Of these strains, *Limnomonas* sp. and *Chlorominima* sp. did not grow in the 20°C treatment and demonstrated limited metabolic plasticity between the lower temperature treatments. *Micractinium* sp., however, grew well at all temperatures and displayed metabolomic parallels to the temperate alga, *Chlorella vulgaris*. Photosynthetic parameters (quantum yield, O_2 production, pigment content) of *Micractinium* sp. were also minimally affected by temperature, unlike *Limnomonas* sp. that had reduced

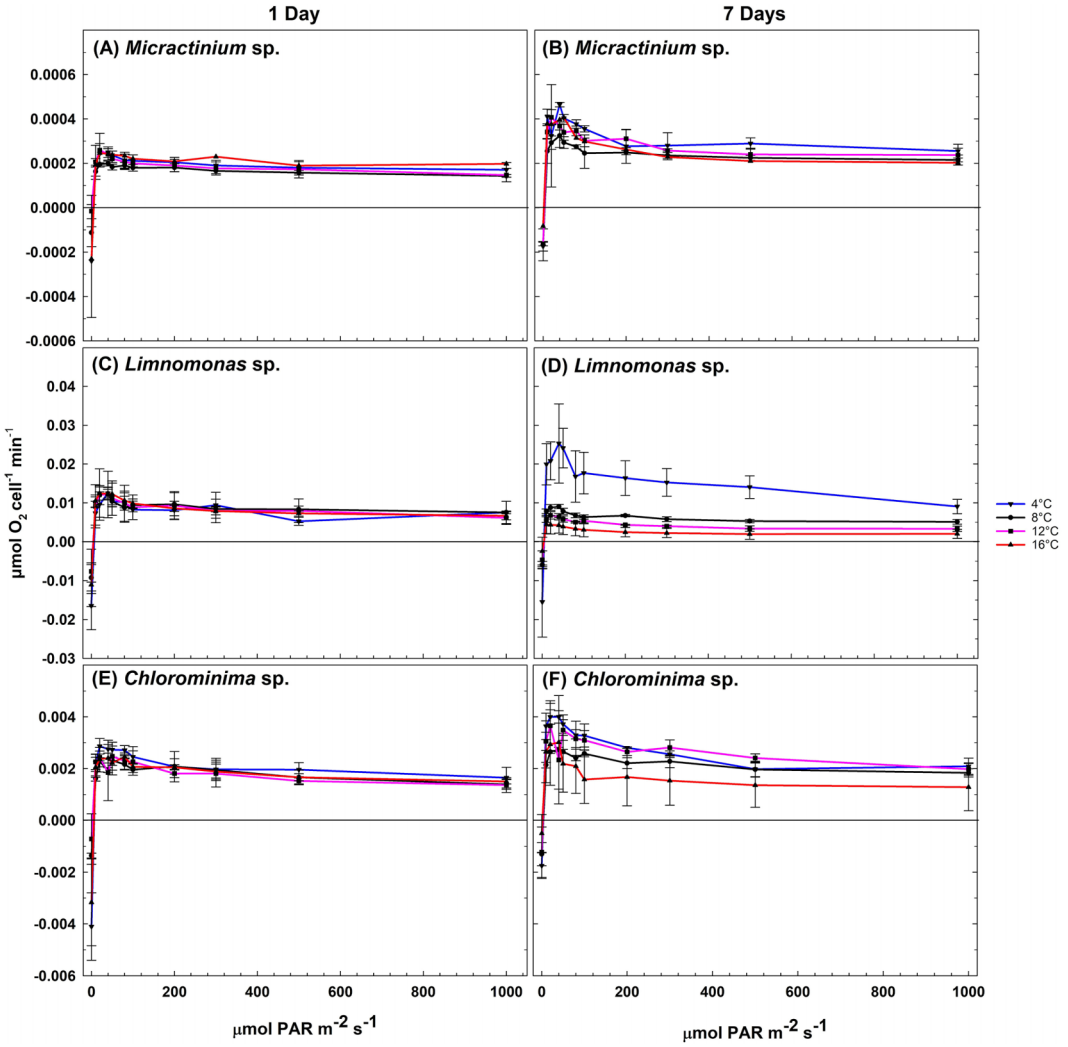

Figure 7 Effects of growth temperature on the rate of oxygen production per cell in snow algae. Light response curves showing rate of O_2 evolution of (A, B) *Micractinium* sp., (C, D) *Limnomonas* sp., and (E, F) *Chlorominima* sp. after exposure to 4°C, 8°C, 12°C, or 16°C for 1 or 7 d. Oxygen production normalized to per algal cell. Measurements made at 4°C at PAR from 0–1000 μmol m^{-2} s^{-1}. Note differing *y*-axis scales. Line at 0.0 μmol O_2 $cell^{-1}$ min^{-1} denotes compensation point between photosynthesis and respiration. Mean ± SD, $n = 3$.

QY at higher temperatures and *Chlorominima* sp. that had the most varied QY and O_2 production between temperature treatments. Therefore, of these three snow algal taxa, *Limnomonas* sp. and *Chlorominima* sp. are true psychrophiles (optimal growth below 10–15°C) whereas *Micractinium* sp. is psychrotolerant, capable of growing over a wider temperature range (4 to 20°C). This is consistent with growth limits reported in other *Chlorominima* strains from Antarctica, with reduced growth rates of *C. collina* at 10 and 20°C (Gálvez et al. 2021). Our data also build on the suggestion of Hoham and Remias (2020), namely that snow algae span a wide range of physiological strategies linked to habitat and acclimatory history, including substantial variation in temperature responses among taxa. More recently, Broadwell et al. (2023) showed that four isolated polar strains of *Chloromonas* sp. and *Microglena* sp. presented psychrophilic traits when assessed by final cell abundance, but that growth rate was greater at 15°C than 5°C. This contrasts with our strains, in which growth was reduced at 8°C and 20°C relative to 4°C, emphasising that snow algae differ markedly in the thermal metrics used to define their apparent optima.

In interpreting these responses, it is important to clarify that 4°C was used as the experimental baseline temperature value. We do not suggest that 4°C represents the full thermal niche, or the coldest temperatures experienced by Antarctic snow algae in nature. Rather, it was selected as a practical cold baseline for laboratory culture work and as an approximation of active melting conditions given that snow algal blooms are most closely associated with thawing snow, late-season melt and coastal snowfields rather than the colder interior of intact frozen snowpacks (Hoham and Remias 2020, Gray et al. 2020, 2021, Roman et al. 2026). This framing is also consistent with previous laboratory studies on isolated snow algae which have commonly examined growth and physiology across low-temperature gradients beginning at 4 to 5°C, rather than attempting to define a universal *in situ* baseline (Galvez et al. 2021, Broadwell et al. 2023). Once active melt conditions are established, however, cells at the snow surface, in slush, or in shallow meltwater may experience substantially warmer short-term conditions. This is particularly relevant on the Antarctic Peninsula, where recent heatwaves have produced exceptional regional tem-

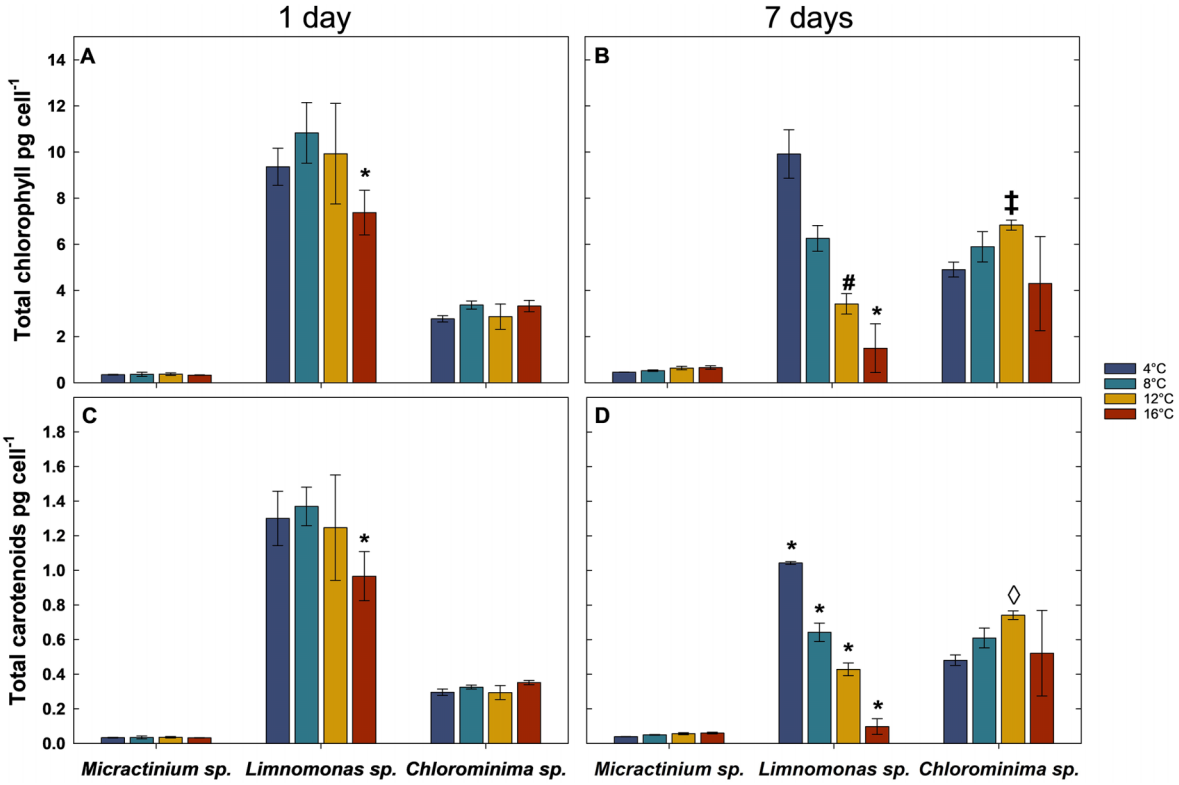

Figure 8 Effects of growth temperature on photosynthetic pigment content in snow algae. Total chlorophyll (A, B) and total carotenoid (C, D) content per cell of *Micractinium* sp., *Limnomonas* sp., and *Chlorominima* sp. after exposure to 4°C, 8°C, 12°C, or 16°C for 1 or 7 d. Mean ± SD, $n = 3$. Asterisk (∗) denotes significantly different response ($P \leq 0.05$) at that temperature compared to the other three temperature treatments within the group; # to 4°C and 8°C; ‡ to 16°C and ◇ to 4°C and 16°C.

perature anomalies over several consecutive days (Robinson et al. 2020, Gonzalez-Herrero et al. 2022, Siegert et al. 2023) and even warmer temperatures (34°C) in heat-dome events in snow algal blooms in North America (van Hees et al. 2023). We therefore interpret 4°C as a pragmatic lower experimental baseline for active growth and physiology in these coastal blooms, while acknowledging that additional biologically important shifts may also occur over smaller temperature increments closer to 0 and 2°C that were not tested here. Differences across life-cycle stages may also influence thermal responses in nature, although this was also not tested directly here (Broadwell et al. 2023 and Hoham and Ling 2000).

Chlorella vulgaris was used in this experiment to provide a temperate comparison. It grew exceptionally well at all three temperatures, only surpassed in increased cell count and change in OD by *Micractinium* sp. at 4°C. *Chlorella vulgaris* should therefore also be considered a psychrotolerant strain (Mayo et al. 1997). Such strains could present an invasion or biosecurity risk in cold climates, impacting ecosystem dynamics (Pereira et al. 2021). If psychrotolerant taxa with wide thermal tolerances establish more readily under future warming, they could alter bloom composition, competitive interactions and the timing or magnitude of primary production in coastal snow ecosystems. As events such as Antarctic heatwaves (Thomson et al. 2025) are expected to increase in frequency (González-Herrero et al. 2022), information on the growth response of these microbial communities to temperature is vitally important to understand and predict how these snow-influenced ecosystems and their carbon budgets will change. In this context, the 1 to 7 day temperature exposures used here are relevant to the duration of documented Antarctic Peninsula warm events, including the 6-day regional heatwave in February 2020, and suggest that short-term warming may increasingly favour psychrotolerant taxa such as *Micractinium* sp. over temperature sensitive strains (Gonzalez-Herrero et al. 2022).

Metabolic phenotypes of snow algal isolates vary between strains and temperature treatments

Organisms with a plastic metabolome can alter metabolite production in response to environmental change, including temperature, and may therefore have greater adaptive capacity as climate warming and heatwaves become more frequent (Casanueva et al. 2010). Our data show that metabolic phenotype varied both between species and within species across temperature treatments. However, variation among strains, particularly among *Limnomonas* sp., *Chlorominima* sp., *Micractinium* sp., and *Chlorella vulgaris*, was greater than variation between temperatures, indicating that strain identity was a major driver of metabolic phenotype.

In the initial experiment, *Limnomonas* sp. and *Chlorominima* sp. showed distinct metabolic profiles across temperatures. *Limnomonas* sp. was characterized by strong signals for putatively annotated uridine, proline and DHA, all of which with known roles in cold tolerance, including osmoregulation, compatible solute

production and maintenance of membrane fluidity (Feller and Gerday 2003, Boelen et al. 2013, De Maayer et al. 2014, Meena et al. 2019, Patriarca et al. 2021, Yuan et al. 2024). Because *Limnomonas* sp. showed lower growth at 10°C than *Chlorominima* sp., our ANOVA results suggest that metabolites associated with comparatively greater tolerance of 10°C in *Chlorominima* sp. included sucrose, glutaric acid, malic acid and 2-butenedioic acid (maleic acid), which showed higher signals in *Chlorominima* sp. cultures at this temperature. These dicarboxylic acids and sugars are involved in central metabolism and energy storage (Sanz Smachetti et al. 2020). In microalgae and cyanobacteria, sucrose accumulation has been linked to salinity, desiccation, and heat stress (Sanz Smachetti et al. 2020), which is consistent with the possibility that our snow algae were approaching their upper temperature limit at 10°C. Although the role of sucrose in snow algae remains poorly resolved, sugars such as sucrose have also been suggested to contribute to freezing and desiccation tolerance (Leya 2013). Sucrose has been reported in some snow algal taxa, including *Mesotaenium berggrenii*, and sucrose-containing carbohydrate fractions have also been detected in Arctic snow algal metabolite studies, supporting its relevance in psychrophilic algal communities (Lutz et al. 2015, Hoham and Remias 2020). Proline and certain sugars are likewise recognized as contributors to osmotic regulation and, in some cases, protection against freezing and desiccation stress, supporting their likely ecological relevance in snow habitats (Welsh 2000).

The second experiment showed a similar pattern, with several metabolites differing between strains and temperature treatments, again including sucrose, uridine and DHA, together with other putatively annotated compatible solutes or stress-related compounds such as allose and xylose (Leya et al. 2013; Lutz et al. 2015). *Chlorella vulgaris* and *Micractinium* sp. also showed distinct clustering, indicating greater overall metabolic similarity between these two strains under the tested conditions. This pattern should, however, be interpreted cautiously. Although *C. vulgaris* and *Micractinium sp*. both belong to the Chlorellales, whereas *Limnomonas* sp. and *Chlorominima* sp. represent the Chlamydomonadales, our data do not allow us to distinguish clearly between effects of phylogenetic relatedness and those of shared physiology under the experimental conditions (Kuklinski and Balazy 2014, Lutz et al. 2015). We therefore interpret these groupings primarily as condition-dependent metabolic phenotypes, while recognizing that taxonomic proximity may also have contributed to the observed similarities.

Our findings are consistent with previous cryosphere studies showing that snow and ice algal metabolomes vary with bloom type, environmental conditions, and physiological state (Leya 2013, Lutz et al. 2015, Davey et al. 2019, Peter et al. 2024). Integrated metabolite analyses of Arctic snow algae have identified compounds associated with stress tolerance and acclimation (Lutz et al. 2015), while a community-level metabolome study of Antarctic snow algae from the same region as our strains highlighted many of the same metabolites putatively detected here (Davey et al. 2019). Because the strains analysed here were isolated from the same Ryder Bay bloom system previously studied at community level, they provide tractable strain-level models that can be interpreted alongside those broader observations. We do not suggest that these isolates capture the full metabolic diversity of the natural assemblage, but they are likely to represent physiologically relevant members of the bloom system from which the wider metabolome was described. Taken together, our results suggest that metabolites such as allose, uridine, xylose, putrescine, and uracil were associated with the cold-adapted physiological state of *Limnomonas* sp. and *Chlorominima* sp. under our culture conditions, whereas serine, sucrose and valine were more strongly associated with the metabolite profiles of *C. vulgaris* and *Micractinium* sp. under the same conditions. However, we avoid interpreting these compounds as universal biomarkers of psychrophily or psychrotolerance across snow algae more broadly. Instead, our results support the view that metabolic responses in snow algae are strongly strain dependent, with temperature effects expressed through distinct and context-dependent metabolic phenotypes.

Photosynthetic parameters

The photophysiology of the snow algae in the current study was remarkably resilient, with F_v/F_m and F_v'/F_m' remaining similar across most temperature treatments. This is consistent with the findings of Zhang et al. (2020) and Peng et al. (2020), who also reported that snow algal strains are more resilient in terms of maintained photosystem II capacity and efficiency at low temperature than are related strains from temperate regions. Our findings for *Chlorominima* sp. are also consistent with those of Gálvez et al. (2021), who reported a significant reduction of F_v/F_m in *Chlorominima collina* (isolated from King George Island, Antarctica) cultures when exposed to 20°C. In addition, the F_v/F_m of our *Limnomonas* sp. culture was close to zero when exposed to 16°C, implying that the electron transport system had largely collapsed as the cells were likely to be dead or dying. This may underpin the failure of *Limnomonas* sp. to grow well above 10°C or be a consequence of slow growth if some other part of cellular biochemistry is affected by low temperature. Similar significant reductions in F_v/F_m at warmer temperatures have also been measured in snow algal blooms in the field, implying that the data from the cultured laboratory experiments are comparable to field events. For example, the F_v/F_m of red snow algal blooms in Washington, USA dropped from 0.62 to 0.2 during a heat-dome event in 2021 (maximum day time temperature of 34°C) (van Hees et al. 2023).

The rETR values obtained here were similar to those reported for snow algal blooms in the field (~10–60 μmol electrons m^{-2} s^{-1}) (Soto et al. 2020), though higher rETR values (~150 μmol electrons m^{-2} s^{-1}) have recently been reported in ice algae (*Ancylonema* sp.) field studies with longer dark adaption periods (Williamson et al. 2025). The taxon-specific response to temperature was similar across all the photosynthetic parameters, in that there was a minimal response in *Micractinium* sp. compared to a wider range of responses in *Chlorominima* sp. and a deleterious response to temperatures above 12°C in *Limnomonas* sp.

We found that QY and rETR were lower in *Chlorominima* sp. cultures exposed to warmer temperatures, partially contrasting with the findings of Broadwell et al. (2023), who reported an increase in rETR with increased temperature (from 5°C to 10°C and 15°C) in Arctic and Antarctic isolated strains of *Microglena* sp. and *Chloromonas* sp. This indicates important interspecific variation in responses of isolated Antarctic snow algae when exposed to warming temperatures. The photophysiological resilience to temperature change demonstrated by *Micractinium* sp. could explain why this taxon had the greatest culture density (growth) compared to the other taxa examined (Fig. 2), with electron transport and carbon fixation maintained across all temperatures.

Conclusions

Our data demonstrated that, in the event of a sudden rise in temperature comparable to short-term heatwaves recently experienced in the polar regions, a shift in snow algal community composition might be expected, as only one of the three Antarctic taxa examined here survived the 20°C treatment. This is likely to impact the microbial community, as some species may no longer be capable of operating, potentially shifting community dynamics to favour taxa with more cosmopolitan temperature ranges. *Micractinium* sp. displayed metabolomic plasticity between temperature treatments and shared several metabolites with the temperate strain *Chlorella vulgaris*, consistent with its survival of the 20°C treatment. The psychrophilic strains (as suggested by the results of this study), *Limnomonas* sp. and *Chlorominima* sp., showed some metabolomic plasticity between 4°C and 8°C but did not grow well at 20°C.

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Author contributions

Carla Ruiz Gonzalez (Conceptualization [equal], Data curation [equal], Formal Analysis [equal], Investigation [equal], Methodology [equal], Project administration [equal], Validation [equal], Visualization [equal], Writing – original draft [equal], Writing – review & editing [equal]), Vaila Grigg (Formal Analysis [equal], Investigation [equal], Methodology [equal], Writing – original draft [equal], Writing – review & editing [equal]), Naomi Thomas (Formal Analysis [equal], Investigation [equal], Methodology [equal], Project administration [equal], Writing – review & editing [equal]), Alex Thomson (Investigation [equal], Supervision [equal], Writing – review & editing [equal]), Ewan MacPherson (Formal Analysis [equal], Investigation [equal], Methodology [equal], Visualization [equal], Writing – review & editing [equal]), Lara Dillon (Formal Analysis [equal], Investigation [equal], Methodology [equal], Writing – original draft [equal], Writing – review & editing [equal]), Emilie Gober (Formal Analysis [equal], Funding acquisition [equal], Investigation [equal], Methodology [equal], Visualization [equal], Writing – original draft [equal], Writing – review & editing [equal]), Alison Gail Smith (Funding acquisition [equal], Methodology [equal], Resources [equal], Supervision [equal], Writing – review & editing [equal]), Charles S Cockell (Methodology [equal], Supervision [equal], Writing – review & editing [equal]), Peter Convey (Funding acquisition [equal], Methodology [equal], Supervision [equal], Writing – original draft [equal], Writing – review & editing [equal]), Matthew P. Davey (Conceptualization [equal], Data curation [equal], Formal Analysis [equal], Funding acquisition [equal], Investigation [equal], Methodology [equal], Project administration [equal], Supervision [equal], Writing – original draft [equal], Writing – review & editing [equal])

Supplementary material

Supplementary material is available at *Sustainable Microbiology Journal* online.

Conflicts of interest

The authors declare no conflicts of interest.

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Data availability

The data underlying this article are available in the UKRI NERC Polar Data Centre https://data.bas.ac.uk/ and can be accessed with https://doi.org/10.5285/b16c9086-34e4-41c4-901f-d9223c522929, the metabolomic datasets are available at the European Molecular Biology Laboratory (EMBL-EBI) MetaboLights Data Repository https://www.ebi.ac.uk/metabolights/ and can be accessed with the accession number REQ20260421218900.

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