CORE
Metadata, citation and similar papers at core.ac.uk
Provided by Plymouth Marine Science Electronic Archive (PlyMSEA)

Received: 24 April 2018 | Accepted: 11 October 2018
DOI: 10.1111/mec.14953

ORIGINAL ARTICLE

WILEY MOLECULAR ECOLOGY

# Photoecology of the Antarctic cyanobacterium *Leptolyngbya* sp. BC1307 brought to light through community analysis, comparative genomics and in vitro photophysiology

Nathan A. M. Chrismas[1,2] | Christopher J. Williamson[2,3] | Marian L. Yallop[3] | Alexandre M. Anesio[2,4] | Patricia Sánchez-Baracaldo[2]

[1]Marine Biological Association of the United Kingdom, The Laboratory, Citadel Hill, Plymouth, UK
[2]School of Geographical Sciences, University of Bristol, Bristol, UK
[3]School of Biological Sciences, Life Sciences Building, University of Bristol, Bristol, UK
[4]Department of Environmental Sciences, Aarhus University, Roskilde, Denmark

**Correspondence**
Nathan A. M. Chrismas, Marine Biological Association of the United Kingdom, The Laboratory, Citadel Hill, Plymouth, PL1 2PB, UK; School of Geographical Sciences, University of Bristol, BS8 1SS, UK
Email: natchr@mba.ac.uk

**Funding information**
Natural Environment Research Council, Grant/Award Number: GW4+ Doctoral Training Grant, NE/J02399X/1 and NE/M021025/1; Royal Society; Dorothy Hodgkin Fellowship; University Research Fellowship; National Science Foundation, Grant/Award Number: ANT-0423595

## Abstract

Cyanobacteria are important photoautotrophs in extreme environments such as the McMurdo Dry Valleys, Antarctica. Terrestrial Antarctic cyanobacteria experience constant darkness during the winter and constant light during the summer which influences the ability of these organisms to fix carbon over the course of an annual cycle. Here, we present a unique approach combining community structure, genomic and photophysiological analyses to understand adaptation to Antarctic light regimes in the cyanobacterium *Leptolyngbya* sp. BC1307. We show that *Leptolyngbya* sp. BC1307 belongs to a clade of cyanobacteria that inhabits near-surface environments in the McMurdo Dry Valleys. Genomic analyses reveal that, unlike close relatives, *Leptolyngbya* sp. BC1307 lacks the genes necessary for production of the pigment phycoerythrin and is incapable of complimentary chromatic acclimation, while containing several genes responsible for known photoprotective pigments. Photophysiology experiments confirmed *Leptolyngbya* sp. BC1307 to be tolerant of short-term exposure to high levels of photosynthetically active radiation, while sustained exposure reduced its capacity for photoprotection. As such, *Leptolyngbya* sp. BC1307 likely exploits low-light microenvironments within cyanobacterial mats in the McMurdo Dry Valleys.

KEYWORDS
Antarctica, cyanobacteria, genomics, photoecology, photophysiology

## 1 | INTRODUCTION

Inland polar regions are harsh environments, providing a challenge to even the most resilient microorganisms. Rather than homogeneous ice, they are diverse environments. In Antarctica, deep stratified lakes remain permanently wet, shallow pools are subject to periodic freezing, and inland habitats can receive little precipitation making surface environments exceptionally dry. Microbes must be able to tolerate these conditions, with freezing and desiccation posing similar challenges to survival. Furthermore, bright summers with constant sunlight and long winter nights of 24-hr darkness make light a major influence on Arctic and Antarctic environments. In the McMurdo Dry Valleys, Antarctica, temperatures can drop to −60°C during the winter with an annual mean of ~ −19°C (Doran et al., 2002) and annual precipitation of only 3–50 mm (Fountain, Nylen, Andrew, Basagic, & David, 2010). All the light in the McMurdo

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.
© 2018 The Authors. *Molecular Ecology* Published by John Wiley & Sons Ltd.

Dry Valleys occurs between August and April (Dana, Wharton, & Dubayah, 1998), when peak photosynthetically active radiation (PAR) in the McMurdo Dry Valleys reaches 1,200 µmol–1,400 µmol $m^{-2}$ $s^{-1}$ (PAR, 400–700 nm) (Bagshaw et al., 2016; Hawes & Schwarz, 1999), while the sun is below the horizon for the remaining 125 days a year (Clow, McKay, Simmons, & Wharton, 1988).

Despite the challenging conditions, many prokaryotic and eukaryotic microorganisms thrive in the McMurdo Dry Valleys. Amongst these are the cyanobacteria, which represent an important component of Antarctic photoautotrophic assemblages. Cyanobacteria are common in many habitats of the McMurdo Dry Valleys, including cryoconite sediment (Porazinska et al., 2004), rocks (Pointing et al., 2009) and deep lakes that remain permanently wet throughout the annual cycle (Laybourn-Parry & Wadham, 2014; Zhang et al., 2015). The lakes of the McMurdo Dry Valleys are a collection of stratified, perennially ice-covered closed basin lakes that have long been studied in terms of their biological, chemical and physical properties (Laybourn-Parry & Wadham, 2014). They range from freshwater to saline (Green & Lyons, 2009) and exhibit a variety of geochemical properties. Within them, cyanobacteria constitute the major primary producers (Taton, Grubisic, Brambilla, Wit, & Wilmotte, 2003; Zhang et al., 2015), with community dynamics significantly influenced by light availability (Dolhi, Teufel, Kong, & Morgan-Kiss, 2015). In Lake Hoare, a freshwater lake located next to Canada glacier (Wharton et al., 1989), irradiance is 1–40 µmol photons $m^{-2}$ $s^{-1}$ at a depth of 13 m, tapering to <1–14 µmol photons $m^{-2}$ $s^{-1}$ between 13 and 23 m (Hawes & Schwarz, 1999), making the ability to effectively photosynthesize in low-light essential for cyanobacteria surviving at depths. Conversely, the ice-free moat formed by seasonal melting that surrounds the surface of Lake Hoare experiences irradiances in the range of 140–1,400 µmol photons $m^{-2}$ $s^{-1}$ during the austral summer, with an annual mean of 188 µmol photons $m^{-2}$ $s^{-1}$ (Hawes & Schwarz, 1999).

Cyanobacterial mats are found in both the depths of lakes and their shallow moats (Jungblut et al., 2016; Mohit, Culley, Lovejoy, Bouchard, & Vincent, 2017; Zhang et al., 2015). Deep mats are distinctly laminated, sometimes forming large pinnacles, while those at lake margins and in shallow pools are less structurally complex. Microbial mats are heterogeneous at both a macro- and a microscale (Bolhuis, Cretoiu, & Stal, 2014) and generate steep irradiance gradients, with light attenuation of at least 90% occurring 1 mm below the mat surface (Jørgensen & Marais, 1988). As such, the structure of cyanobacterial mats encourages the formation of distinct light microenvironments.

Eukaryotic algae are the dominant planktonic autotrophs in Antarctic lakes and much work has been done on their photophysiology (Kong, Li, Romancova, Prasil, & Morgan-Kiss, 2014; Kong, Ream, Priscu, & Morgan-Kiss, 2012; Morgan-Kiss, Priscu, Pocock, Gudynaite-Savitch, & Huner, 2006; Morgan-Kiss et al., 2008). In particular, the photophysiology of the psychrophilic alga *Chlamydomonas raudensis* has undergone in-depth characterization (Gudynaite-Savitch et al., 2006; Morgan-Kiss, Ivanov, & Huner, 2002b; Morgan-Kiss, Ivanov, Williams, Khan, & Huner, 2002a; Morgan-Kiss et al., 2006) revealing that it is photosynthetically adapted to low-temperature growth (Pocock, Koziak, Rosso, Falk, & Huener, 2007; Szyszka-Mroz, Pittock, Ivanov, Lajoie, & Huener, 2015) under blue-green light (Morgan-Kiss et al., 2005) and exhibits a reduction of photosystem I (PSI) complexes (Morgan, Ivanov, Priscu, Maxwell, & Huner, 1998). There is some co-occurrence of algae and cyanobacteria in microbial mats (Jungblut, Vincent, & Lovejoy, 2012; Novis, Aislabie, Turner, & McLeod, 2015). However, despite being the dominant organisms in relation to their eukaryotic counterparts in mat communities, detailed information on polar cyanobacteria from a joint genomic and photophysiological perspective is currently lacking (Chrismas, Anesio, & Sánchez-Baracaldo, 2018).

The present study focuses on *Leptolyngbya* sp. BC1307, a new strain of *Leptolyngbya* isolated from the moat surrounding Lake Hoare in the McMurdo Dry Valleys. *Leptolyngbya* are a group of filamentous cyanobacteria with a global distribution across a range of diverse environments, including hot springs (Ionescu, Hindiyeh, Malkawi, & Oren, 2010), soda lakes (Lanzen et al., 2013), rock seeps (Johansen, Olsen, Lowe, Fučíková, & Casamatta, 2008), marine habitats (Li & Brand, 2007), and soil crusts (Richter & Matuła, 2013). *Leptolyngbya* sensu *lato* is polyphyletic, containing two distinct clades (Chrismas, Anesio, & Sanchez-Baracaldo, 2015): Groups I and II. Group I, including *Leptolyngbya* sp. PCC 7335 (previously incorrectly classified as *Synechococcus*), and *Leptolyngbya* sp. PCC 7375, forms a sister clade to the unicellular picocyanobacteria, and members are commonly found in Antarctic environments (Chrismas et al., 2015). In contrast, Group II, including *Leptolyngbya boryana* PCC 6306, is a separate clade that includes *Phormidesmis priestleyi* BC1401, which can be found in Arctic cryoconite holes (Chrismas, Barker, Anesio, & Sanchez-Baracaldo, 2016). While some Group II *Leptolyngbya* are predicted to have had a cold tolerant ancestor, there is no indication that any Group I lineages originated in the cryosphere (Chrismas et al., 2015).

Polar cyanobacteria such as *Leptolyngbya* sp. BC1307 are resilient photoautotrophs able to cope with the light conditions found in the McMurdo Dry Valleys. Cyanobacteria possess diverse photoacclimation mechanisms that enable them to balance excess excitation energy within their photosystems, including (i) complementary chromatic acclimation (CCA) (Kehoe & Gutu, 2006), (ii) redistribution and/or dissipation of excess excitation energy via state transitions and/or the orange carotenoid protein (OCP) (Campbell, Hurry, Clarke, Gustafsson, & Oquist, 1998; Kirilovsky & Kerfeld, 2012; Wilson et al., 2006, 2008) and (iii) photoprotection afforded by a suite of carotenoid pigments (Falkowski & Raven, 2007; Zhu et al., 2010).

### 1.1 | Complementary chromatic acclimation

In cyanobacteria, CCA involves light-induced variations in the proportions of the pigments phycocyanin ($A_{max}$ = 620 nm) and phycoerythrin ($A_{max}$ = 560 nm) within light-harvesting phycobilisomes, allowing them to adjust light-harvesting capabilities to the prevailing irradiance (Kehoe & Gutu, 2006; Stomp et al., 2004). The CCA mechanism, which has been studied in depth in *Fremyella diplosiphon* (Cobley et al., 2002; Cobley & Miranda, 1983; Conley, Lemaux,

Lomax, & Grossman, 1986; Li, Alvey, Bezy, & Kehoe, 2008; Rosinski, Hainfeld, Rigbi, & Siegelman, 1981), consists of the photoreceptor *rcaE* and the response regulators *rcaF* and *rcaC*, which together govern transcriptional regulation of inducible phycocyanin and phycoerythrin (Li, Alvey, Bezy, & Kehoe, 2008).

### 1.2 | Nonphotochemical quenching

Nonphotochemical quenching (NPQ) of excess excitation pressure within cyanobacterial photosystems involves energy exchange between photosystems (state transitions), and/or energy dissipation away from photosystems (OCP-driven NPQ). State transitions control the relative proportion of energy transfer between photosystem I (PSI) and II (PSII) (Campbell et al., 1998; Mullineaux, 2014). In the dark/low light, cyanobacteria are in state II, whereby captured excitation is directed largely towards PSI. As light is applied, cells shift towards state I, in which captured energy is redirected to PSII (Campbell et al., 1998; Mullineaux & Emlyn-Jones, 2005). In contrast, OCP-driven NPQ functions as a mechanism analogous to xanthophyll cycling in eukaryotic microalgae (Demmig-Adams, 1990; Goss & Jakob, 2010; Punginelli, Wilson, Routaboul, & Kirilovsky, 2009), interacting with the phycobilisome upon light activation to dissipate excess excitation as heat, away from photosystems (Kirilovsky & Kerfeld, 2012; Wilson et al., 2006, 2008). The OCP is encoded by a single gene first identified in *Synechocystis* sp. PCC 6803 (*slr1963*) (Wu & Krogman, 1997). This gene is present in numerous cyanobacteria (Kirilovsky & Kerfeld, 2016) and is flanked by *frp*, encoding the fluorescence recovery protein, responsible for recovery of the phycobilisome complex after NPQ (Boulay, Wilson, D'Haene, & Kirilovsky, 2010).

### 1.3 | Carotenoids

In addition to the above mechanisms, cyanobacteria produce a suite of carotenoid pigments that act as light-harvesting pigments, contribute to the structure of thylakoid membranes and play important roles in photoprotection by screening out harmful radiation and protecting against oxidative stress (Falkowski & Raven 2007; Zhu et al., 2010). Predominant cyanobacterial carotenoids include ß-carotene, zeaxanthin, the keto-carotenoids echinenone and canthaxanthin, and the carotenoid-glycoside myxoxanthophyll (Schagerl & Muller, 2006). The genes for first two steps of carotenoid biosynthesis, *crtE* and *crtB*, are found in all cyanobacteria. Typically, conversion of the carotenoid precursor phytoene to the ß-carotene precursor lycopene is carried out by proteins encoded by *crtP*, *crtQ* and *crtH*, except for *Gloeobacter violaceus* which uses *crtI* (Steiger, Jackisch, & Sandmann, 2005; Tsuchiya et al., 2005). The gene for the conversion of lycopene to ß-carotene is *cruA*, except in picocyanobacteria which use *crtL*. Canthaxanthin, echinenone and zeaxanthin are formed from ß-carotene by *crtO*, *crtW* and *crtR*, respectively, and myxoxanthophyll from a ß-carotene precursor by *crtD*, *cruF* and *cruG* (Hirschberg & Chamovitz, 1994; Liang, Zhao, Wei, Wen, & Qin, 2006; Mohamed & Vermaas, 2004; Punginelli et al., 2009; Sandmann, 1994; Zhu et al., 2010). Under high-light conditions, ß-carotene tends to decrease with chlorophyll *a* (Chl*a*) and phycobiliprotein concentrations (Schagerl & Müller, 2006), while keto-carotenoids and zeaxanthin tend to accumulate (MacIntyre, Kana, Anning, & Geider, 2002; Schagerl & Müller, 2006; Zhu et al., 2010).

In this study, we investigated the light tolerance of *Leptolyngbya* sp. BC1307 from the McMurdo Dry Valleys by combining community structure analysis, comparative genomics and photophysiological assessments. We sequenced the genome of *Leptolyngbya* sp. BC1307 and examined it within the context of known Antarctic cyanobacterial diversity from deep perennially ice-covered lakes and terrestrial and shallow, ice-free environments. To assess light tolerance inferred from genomic analysis, *Leptolyngbya* sp. BC1307 photophysiology and carotenoid pigment regulation under different irradiance regimes were constrained using a combination of pulse amplitude modulated (PAM) fluorimetry and high-performance liquid chromatography (HPLC). Findings provide first insight into the photoecology of this Antarctic photoautotroph.

## 2 | MATERIALS AND METHODS

### 2.1 | Sampling and cultivation

*Leptolyngbya* sp. BC1307 was isolated from a 50-mL water sample obtained on 7/12/2011 from under the thin surface ice layer of the moat surrounding Lake Hoare, a permanently ice-covered meromictic lake in the McMurdo Dry Valleys, Antarctica (S: 77°37.521′, E: 162°54.036′) and subsequently stored at −20°C. Frozen water was first defrosted, and while at room temperature, 10–20 µL was plated onto 1% agar BG11 (Rippka, Deruelles, Waterbury, Herdman, & Stanier, 1979) Petri dishes and incubated at 4°C under constant light conditions. Resulting colonies were picked and used to inoculate 100-mL flasks of BG-11 and maintained aerobically at 4°C under constant light conditions with subsampling occurring every 4 weeks. Optimal growth temperatures were determined using methods adapted from Nadeau and Castenholz (2000) (Supplementary Information).

### 2.2 | DNA extraction, genome assembly and annotation

Full methods for DNA extraction and genome assembly are described in Chrismas et al. (2016). Briefly, cells from stationary phase cultures of *Leptolyngbya* sp. BC1307 were harvested and lysed using Solulyse (Genlantis) and bead beating using MO BIO (MO BIO Laboratories) bead tubes. Genomic DNA was extracted using AXG 200 gravity flow columns (Machery-Nagel), checked for integrity using 1% agarose gel electrophoresis and quantified using a QUBIT (Invitrogen) assay. Sequencing was performed at the Bristol Genomics Facility. Libraries were constructed using the Illumina Truseq Stranded RNA kit (Illumina) according to the manufacturer's instructions with an average library size of 750 bp (including adapters). Sequencing was performed using Illumina HiSeq 2500 (Illumina) technology (one lane) (100 bp paired-end reads, insert size =400 bp). Assembly was carried out using SPades v3.5

(Bankevich et al., 2012) and noncyanobacterial sequences identified and removed using BLAST and Bandage (Wick, Schultz, Zobel, & Holt, 2015) according to the methods described in Chrismas et al. (2016). Original reads were mapped to the final draft assembly using BBmap revealing an overall coverage of 181.23 ×. The draft assembly of *Leptolyngbya* sp. BC1307 was annotated using the JGI IMG/ER pipeline (GOLD Analysis Project ID: Ga0078185) (Markowitz et al., 2012). This Whole Genome Shotgun project is available on GenBank (Accession no. PRJNA399838). Genome sequence and annotation data are publicly available on the JGI IMG/ER database.

### 2.3 | Phylogenetics

To determine the phylogenetic position of *Leptolyngbya* sp. BC1307 within the cyanobacterial phylum, an SSU rRNA gene database was constructed with SSU rRNA genes from 131 cyanobacteria with available genomes (130 used in Sánchez-Baracaldo (2015) plus *P. priestleyi* BC1401. SSU genes were aligned with SATé 2.2.7 (Liu, Raghavan, Nelesen, Linder, & Warnow, 2009) (implementing MAFFT v6.717 (Katoh & Standley, 2013), MUSCLE v3.7 (Edgar, 2004), FASTTREE v2.1.4 (Price, Dehal, & Arkin, 2010), CAT approximation, decomposition strategy = "longest") resulting in an alignment of 1561 characters. Tree reconstruction was done using RaxML v8.1.11 (Stamatakis, 2014) (GTR+G model) and constrained with a 130 taxa phylogenomic tree (136 proteins and two rRNA genes: LSU and SSU) (Sánchez-Baracaldo, 2015).

### 2.4 | Community analysis

Cyanobacterial community composition of Antarctic deep lakes and shallow/terrestrial habitats was compared by analysing a combination of previously published SSU rRNA gene clone library data sets. The following locations were covered: Lake Joyce, Lake Vanda, Lake Hoare (Zhang et al., 2015); Reid lake, Heart Lake (Taton et al., 2006); Lake Fryxell (Taton et al., 2003); Alexander Island (Chong, Convey, Pearce, & Tan, 2012); Transantarctic Mountains (Fernandez-Carazo, Hodgson, Convey, & Wilmotte, 2011). Samples from Ace Lake and Rauer8 Lake from Taton et al. (2006) were excluded due to small sequence numbers. See Supplementary File 1 for a complete list of sequences used. To identify sequences and ensure that *Leptolyngbya* Group I and Group II were classified separately, clone library SSU rRNA gene sequences were combined with a reduced data set (270 sequences) from Chrismas et al. (2015). All sequences (461 in total with sequence lengths of 323–1,498 bp) were aligned using SATé 2.2.7 (Liu et al., 2009) as described above. Sequences were identified based on their phylogenetic position and closest named relative previously identified in Antarctica (Figure S1). Five sequences that could not be classified in this way were excluded from further analysis.

### 2.5 | Comparative genomics

Genomes were investigated using online tools as part of the JGI IMG/ER pipeline. Phycobiliprotein gene clusters were located using sll1578 (CpcA) and SynWH7803_0486 (CpeA) as search queries and compared with those from genomes of closely related organisms isolated from marine pelagic (*Leptolyngbya* sp. PCC 7375) and intertidal (*Leptolyngbya* sp. PCC 7335) environments. Carotenoid biosynthesis and photoprotective genes were searched for using queries shown in Table 1. All searches were performed using BLASTp with an e-value threshold of 1e-10. Gene diagrams were generated using genoPlotR (Guy, Roat Kultima, & Andersson, 2010) and manually edited in Inkscape http://inkscape.org/en/.

### 2.6 | Photophysiology and carotenoid regulation

Cultures were established in BG-11 at 15°C (according to optimum growth temperature, Figure S2) in both low light (25 µmol photons $m^{-2}$ $s^{-1}$) and high light (170 µmol photons $m^{-2}$ $s^{-1}$) and incubated for a minimum period of three weeks. Cultures in exponential growth phase were examined using a combination of variable chlorophyll fluorescence measurements and HPLC. Rapid light-response curves (Perkins, 2006) were performed using a Walz Water PAM fluorometer on five replicate low- and high-light cultured samples. Given clumping of filaments, samples were gently filtered onto moist (saturated with culture water) GF/F filters prior to rapid light-response curve (RLC) assessment with a red-light fibre-optic emitter/detector unit. Following five minutes of dark adaptation, RLCs were performed using a saturating pulse of ca. 8,600 µmol photons $m^{-2}$ $s^{-1}$, for 600-ms duration, with nine 20 s incrementally increasing light steps from 0 to 1,944 µmol photons $m^{-2}$ $s^{-1}$. Analysis of RLCs followed Perkins, Mouget, Lefebvre, and Lavaud (2006) with iterative curve fitting and calculation of the relative maximum electron transport rate ($rETR_{max}$), the theoretical maximum light utilization coefficient ($\alpha$) and the light saturation coefficient ($E_k$) following Eilers and Peeters (1988). Additionally, the maximum light utilization efficiency in the dark-adapted state ($F_v/F_m$, Genty, Briantais, & Baker, 1989) and Stern-Volmer NPQ were calculated from RLC fluorescence yields. Given $Fm'$>$Fm$ during RLCs, NPQ was calculated after Serodio, Cruz, Vieira, and Brotas (2005) using the maximal $Fm'$ achieved. Remaining cultures were filtered onto preweighed GF/F filters and frozen immediately at −80°C for subsequent pigment profiling. Filters were freeze-dried for 48 hr, weighed, and pigments extracted in 100% acetone containing vitamin E as an internal standard. A modified version of Van Heukelem and Thomas (2001) HPLC protocol was applied using a c8 column in an Agilent 1,100 HPLC equipped with a diode-array detector. Pigments were identified and quantified against analytical standards from DHI and Sigma using both retention time and spectral analysis.

## 3 | RESULTS

### 3.1 | Genome statistics and growth characteristics of *Leptolyngbya* sp. BC1307

Genome statistics for *Leptolyngbya* sp. BC1307 compared to *Leptolyngbya* sp. PCC 7335 and *Leptolyngbya* sp. PCC 7375 are shown in Table S1. Only small differences in % proline content (*Leptolyngbya*

**TABLE 1** BLAST matches for genes in *Leptolyngbya* sp. BC1307 involved in photoprotection and carotenoid biosynthesis

| Gene | Protein | Query | BBH | score | e-value |
|---|---|---|---|---|---|
| Photoprotection | | | | | |
| *ocp* | Orange carotenoid protein (OCP) | slr1963 | Ga0078185_100888 | 508 | 0 |
| *frp* | Fluorescence recovery protein | slr1964 | Ga0078185_100887 | 106 | 4.00E−32 |
| Carotenoid biosynthesis | | | | | |
| *crtE* | Geranylgeranyl diphosphate synthase | slr0739 | Ga0078185_100722 | 379 | 8.00E−134 |
| *crtB* | Phytoene synthase | slr1255 | Ga0078185_100364 | 436 | 6.00E−156 |
| *crtP* | Phytoene desaturase | slr1254 | N/A | N/A | N/A |
| *crtQ* | Zeta-carotene desaturase | slr0940 | N/A | N/A | N/A |
| *crtH* | Cis-trans Carotene isomerase | sll0033 | Ga0078185_1004105 | 262 | 1.00E−82 |
| *crtI* | Phytoene desaturase | gvip113 | Ga0078185_1006103 | 806 | 0 |
| *cruA* | Lycoprene cyclase | SynPCC7002_A2153 | N/A | N/A | N/A |
| *crtL* | Lycoprene beta cyclase | SynPCC7942_2062 | Ga0078185_102157 | 489 | 9.00E−174 |
| *cruP* | Lycoprene cyclase | sll0659 | Ga0078185_103223 | 553 | 0 |
| *crtR* | Beta-carotene hydroxylase | sll1468 | Ga0078185_100571 | 430 | 8.00E−154 |
| *crtW* | Beta-carotene ketolase | SYNPCC7002_A2809 | Ga0078185_10409 | 150 | 6.00E−46 |
| | | | Ga0078185_10703 | 143 | 6.00E−43 |
| *crtO* | B-carotene ketolase | slr0088 | Ga0078185_10258 | 744 | 0 |
| *crtD* | Methoxyneurosp-orene desaturase | slr1293 | Ga0078185_101743 | 655 | 0 |
| *cruF* | Gamma-carotene 1′ hydroxylase myxoxanthophyll biosynthesis protein | SynPCC7002_A2032 | Ga0078185_101870 | 305 | 8.00E−105 |
| *cruG* | Glycosyl transferase family protein myxoxanthophyll biosynthesis | SynPCC7002_A2031 | Ga0078185_101869 | 442 | 2.00E−155 |

sp. BC1307, Pro = 5.04%; *Leptolyngbya* sp. PCC 7375, Pro = 4.61%; *Leptolyngbya* sp. PCC 7335, Pro = 4.75%) and arginine:lysine ratios (*Leptolyngbya* sp. BC1307, Arg:Lys = 1.57; *Leptolyngbya* sp. PCC 7375, Arg:Lys = 1.39; *Leptolyngbya* sp. PCC 7335, Arg:Lys = 1.41) were found between genomes (Table S2). Copies of genes implicated in cold shock response (Barria, Malecki, & Arraiano, 2013; Varin, Lovejoy, Jungblut, Vincent, & Corbeil, 2012) were present in all three genomes at similar numbers (Table S2). Growth was detected as low as 4°C and as high as 24°C with maximum growth rates observed ~15°C–24°C in BG-11 cyanobacterial growth media at pH 7.1.

## 3.2 | Phylogenetics and composition of Antarctic cyanobacterial communities

Maximum-likelihood phylogenetic analysis found *Leptolyngbya* sp. BC1307 to be a derived strain placed close to *Leptolyngbya* sp. PCC 7335 with 100% bootstrap support (1,000 replicates) (Figure 1) with an SSU similarity of 97%. Cyanobacteria from surface and under ice environments were found to belong to twelve main lineages (Figure 2). Community composition was similar between perennially ice-covered lakes as reported by Zhang et al. (2015), while moat and terrestrial environments were more variable. *Leptolyngbya* (Group I) was found to be completely absent from below the ice and present in the moat and terrestrial samples with the exception of the Reid Lake moat. Similarly, the Nostocales *Tolypothrix* and *Nostoc*, and Oscillatoriales *Wilmottia* and *Crinalium* were found only in surface environments. Deep perennially ice-covered and shallow ice-free environments were dominated by the presence of *Leptolyngbya* (Group II) and *Phormidesmis*, which were both absent from purely terrestrial environments. *Pseudanabaena* was found in all locations apart from the Transantarctic Mountains. Overall, surface (terrestrial and moat) and under ice environments contained different communities (PERMANOVA, $p = <0.001$).

## 3.3 | Comparative genomics of phycobiliproteins and carotenoids

While both *Leptolyngbya* sp. BC1307 and *Leptolyngbya* sp. PCC 7335 included *cpcBA* of inducible phycocyanin and genes for associated linker proteins, in *Leptolyngbya* sp. BC1307 the genes for regulation of CCA (*rcaE*, *rcaF*, *rcaC* and *pcyA*) (Li et al., 2008) were either truncated or absent (Figure 3). Several core genes involved in phycobiliprotein structure and biosynthesis were shared by all three genomes (Figure 3), and all contained at least one copy of the phycocyanin genes *cpcBA* and associated structural genes. *Leptolyngbya* sp. BC1307 did not contain the phycoerythrin genes *cpeBA*, *pebBA* or the phycoerythrin linker-polypeptide operon *cpeCDESTR* (Cobley et al., 2002).

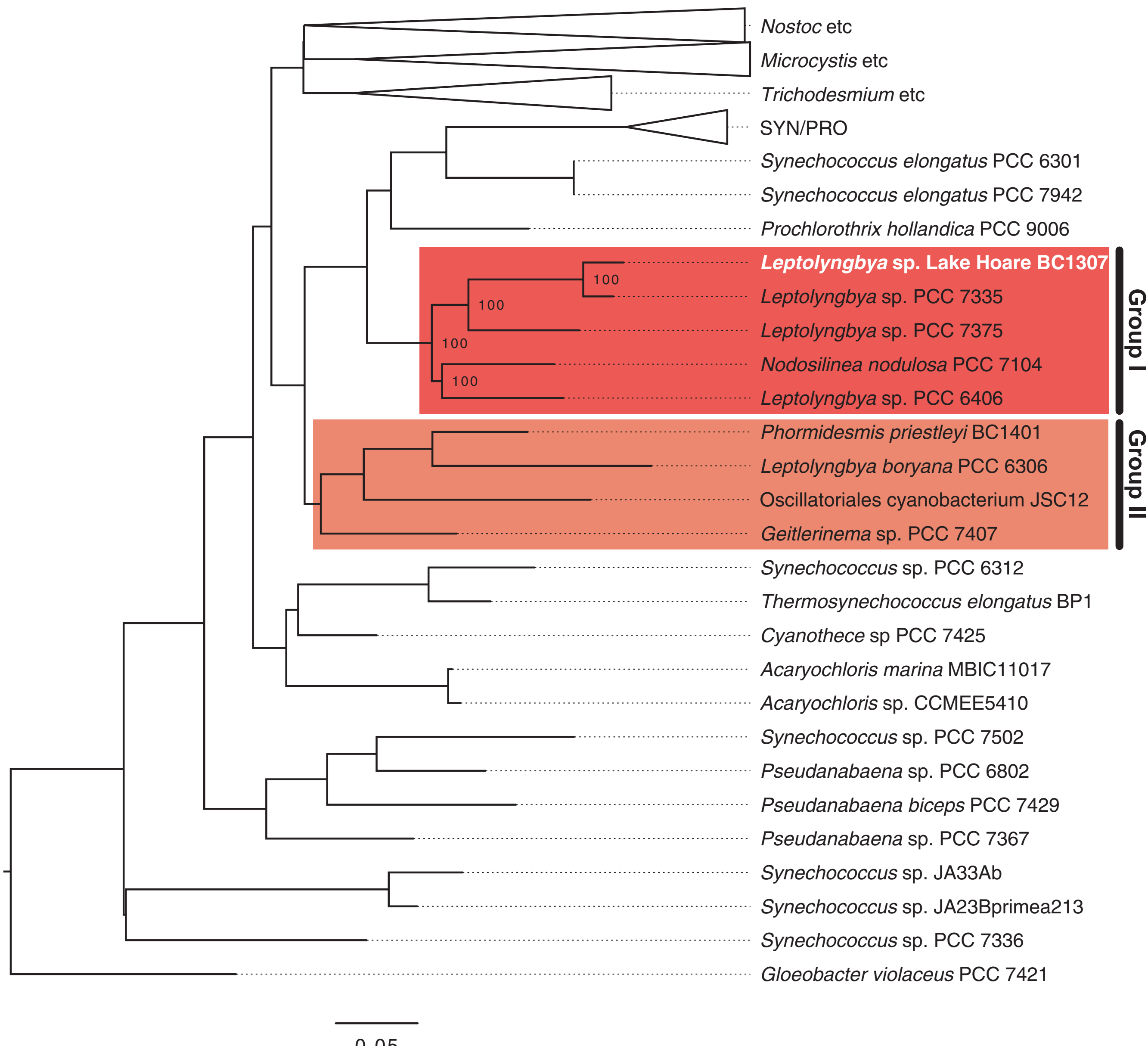


**FIGURE 1** Maximum-likelihood SSU rRNA phylogeny depicting Group I (red) and Group II (orange) *Leptolyngbya* in relation to the rest of the cyanobacterial phylum. The newly sequenced *Leptolyngbya* sp. BC1307 is highlighted in white. The tree topology was constrained using a 130 taxa phylogenomic tree (135 proteins, LSU and SSU rRNA) (Sánchez-Baracaldo, 2015) [Colour figure can be viewed at wileyonlinelibrary.com]

Matches for carotenoid biosynthesis and photoprotective genes within the genome of *Leptolyngbya* sp. BC1307 are shown in Table 1. Rather than organization within coherent clusters, carotenoid genes were distributed over the genome of *Leptolyngbya* sp. BC1307, a pattern seen throughout the cyanobacteria (Liang et al., 2006). Interestingly, *Leptolyngbya* sp. BC1307 appears to use the *crtL* pathway for conversion of phytoene to lycopene-like *Gloeobacter violaceus* and noncyanobacterial bacteria, as opposed to using *crtP* and *crtQ* as in most other cyanobacteria. Genes responsible for the biosynthesis of canthaxanthin (*crtO*), echinenone (*crtW*), zeaxanthin (*crtR*) and myxoxanthophyll (*cruF*, *cruG*) were all present, as were the OCP gene and *frp*. Additionally, the lycopene cyclase *cruP* was found which has a role in the prevention of accumulation of reactive oxygen species. All of these genes were present in the genomes of *Leptolyngbya* sp. PCC 7335 and *Leptolyngbya* sp. PCC 7375, except for the genes *crtO*, *cruF* and *cruG* which were absent from *Leptolyngbya* sp. PCC 7375. There was no evidence of scytonemin biosynthetic gene clusters in any of the genomes.

### 3.4 | Photophysiology and carotenoid pigment regulation

Rapid light-response curves revealed significant differences in *Leptolyngbya* sp. BC1307 photophysiology between low- and

high-light cultured samples (Figure 4a–b). Significantly decreased $F_v/F_m$ of high-light relative to low-light samples indicated increased stress in *Leptolyngbya* sp. BC1307 under high-light culture conditions (Figure 4c). Low-light samples demonstrated significantly increased theoretical maximum light utilization coefficient ($\alpha$) and rates of relative maximum electron transport rate ($rETR_{max}$) over RLCs compared to high-light samples (Figure 4d–f), consistent with increased capacity for light-harvesting, electron transport and ability to photoregulate to short-term high PAR exposures. In contrast, high-light samples achieved comparatively minimal levels of electron transport over RLCs, with significant down-turn in *rETR* at PARs > 580 μmol photons $m^{-2}$ $s^{-1}$ indicating significant photoinhibition (Figure 4a). Though patterns in the light saturation coefficient ($E_k$) reflected light treatment, *that is*, lower $E_k$ observed for low-light cultured samples, $E_k$ did not differ statistically between treatments.

Quenching analysis revealed the mechanisms underlying the ability of low-light samples to rapidly photoacclimate to increasing PAR (Figure 4b). Declines in low-light sample NPQ at the onset of RLCs, which reached a minimum at ~ $E_K$, were consistent with redirection of excitation pressure from PSI to PSII (state II to state I transition) (Campbell et al., 1998). Subsequent steady increase in low-light sample NPQ at PAR>$E_K$, driven by a quenching of maximum fluorescence in actinic light (*Fm′*, data not shown), was further indicative of induction of OCP-driven NPQ (Kirilovsky & Kerfeld, 2012). Decreases in NPQ across high-light sample RLCs also indicated the

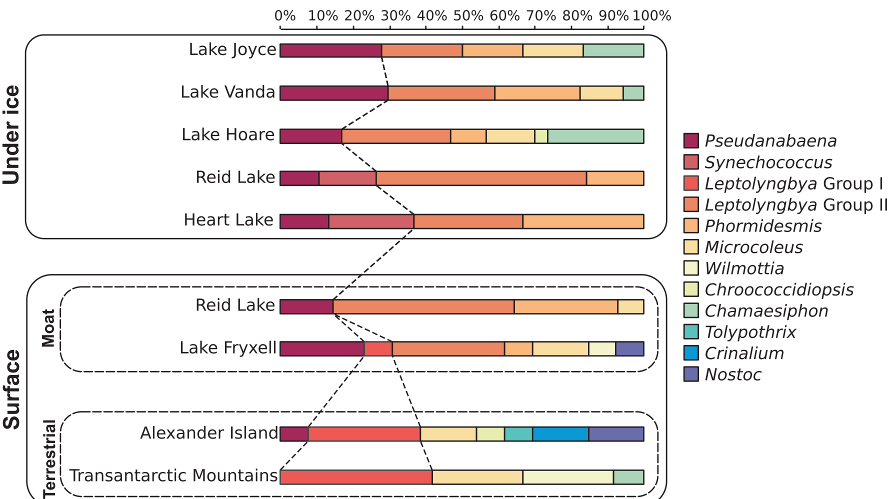


**FIGURE 2** Community structure of cyanobacteria in Antarctic terrestrial and lacustrine environments based on existing clone libraries. Environments are classified into two main groups; under ice (samples taken from meromictic lake beds below thick permanent ice) and surface (subdivided into littoral environments at lake edges not covered by thick ice and true terrestrial environments). *Leptolyngbya* (Group I) are shown in red [Colour figure can be viewed at wileyonlinelibrary.com]

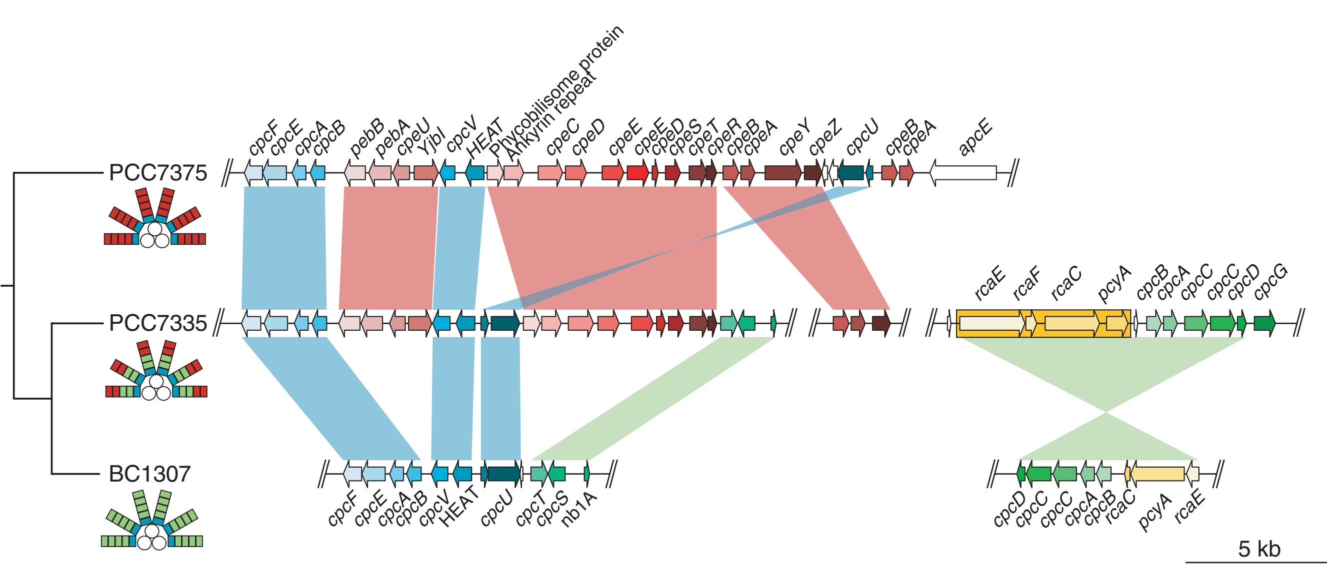


**FIGURE 3** Gene order plot showing arrangement of phycobiliprotein gene clusters in *Leptolyngbya* sp. PCC 7375, *Leptolyngbya* sp. PCC 7335 and *Leptolyngbya* sp. BC1307. Genes shared by all three genomes (predominantly related to core phycocyanin structure and biosynthesis) are shown in shades of blue. Genes shared by *Leptolyngbya* sp. PCC 7375 and *Leptolyngbya* sp. PCC 7335 (predominantly related to phycoerythrin structure and biosynthesis) are shown in shades of red. Genes shared between *Leptolyngbya* sp. PCC 7335 and *Leptolyngbya* sp. BC1307 (predominantly involved in inducible phycocyanin structure and biosynthesis) are shown in green. Genes necessary for CCA are shown in yellow; the complete CCA regulon in *Leptolyngbya* sp. PCC 7335 is highlighted with a yellow box. Putative arrangements of the PBS structures in each lineage are shown beneath the strain names [Colour figure can be viewed at wileyonlinelibrary.com]

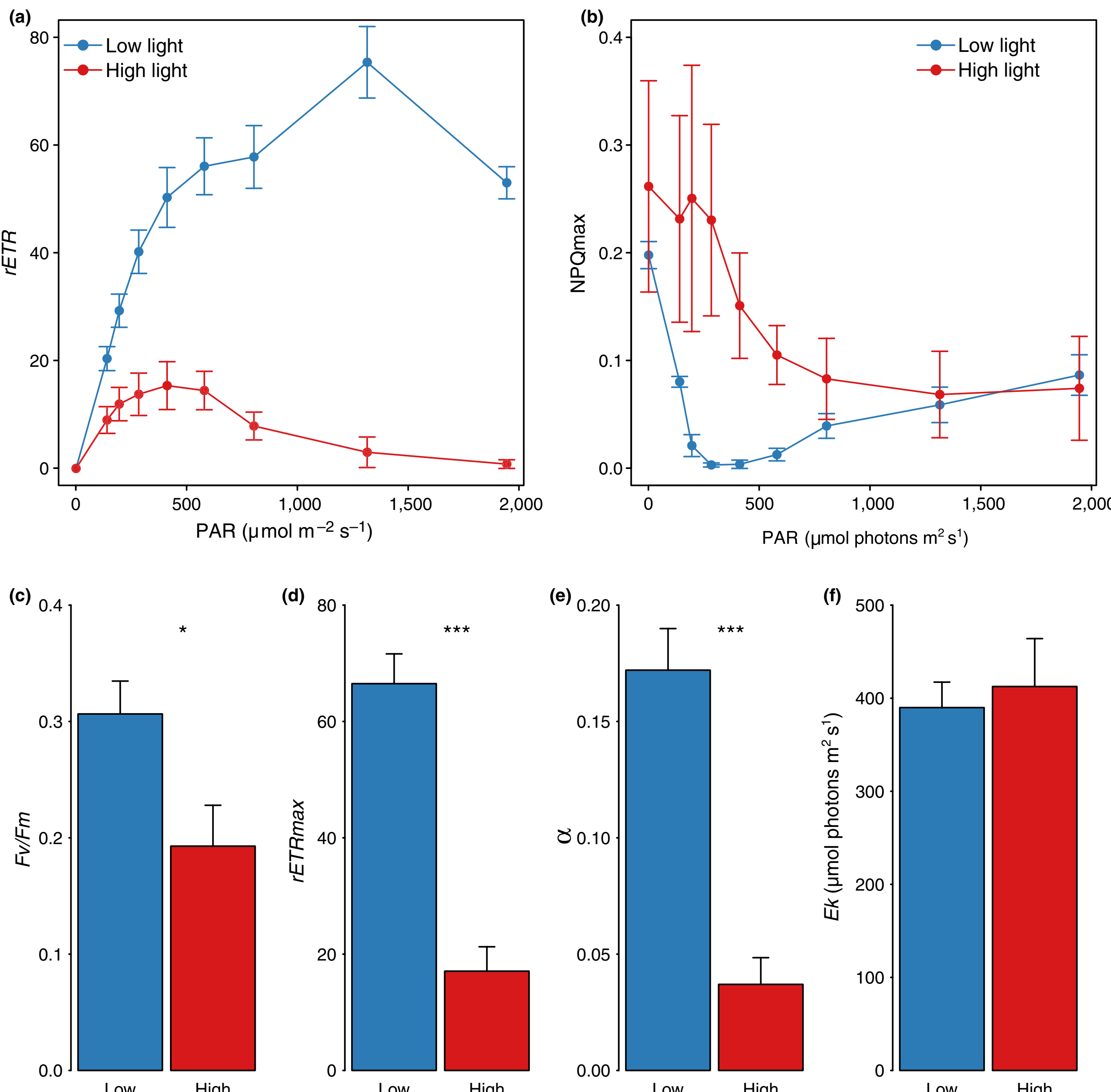


**FIGURE 4** Photophysiology of *Leptolyngbya* sp. BC1307 cultured under low- and high-light conditions. Showing (a) relative electron transport rates (*rETR*) and (b) nonphotochemical quenching (NPQmax) determined over rapid light-response curves (RLCs), and parameters derived from RLCs, including (c) the maximal quantum efficiency in the dark-adapted state, (d) the maximum relative electron transport rate ($rETR_{max}$), (e) the maximum light utilization coefficient (a), and (f) the light saturation coefficient (*Ek*) (mean ± SE, $n = 5$). Asterisks denote significant differences in parameters between low- and high-light cultured samples as determined from *t* tests (see Table 2) (***$p < 0.001$) [Colour figure can be viewed at wileyonlinelibrary.com]

use of state transitions in photoacclimation (Figure 4b). However, this was not sufficient to maintain *rETR* above 580 μmol photons $m^{-2}$ $s^{-1}$ (Figure 4a). Given the gradual plateau in high-light NPQ above this PAR, the capacity of state transitions to balance excess excitation between photosystems was likely exhausted, resulting in photoinhibition. No increase in NPQ (or decrease in *Fm′*) over RLCs for high-light samples further suggested the absence of OCP-driven NPQ.

In addition to Chl*a*, several carotenoid pigments were isolated from *Leptolyngbya* sp. BC1307 (Figure 5), including antheraxanthin, ß-carotene, canthaxanthin, echinenone, 3-hydroxylechinenone, myxoxanthophyll and zeaxanthin. Chl*a* showed significant difference between high- and low-light cultures (Figure 5b); therefore, all other pigments are expressed as a ratio to Chl*a* concentrations (Table 2). While no significant difference in ß-carotene, echinenone or myxoxanthophyll:Chl*a* ratios was apparent between

**TABLE 2** *T* test analysis of *Leptolyngbya* sp. BC1307 photophysiological parameters and pigment concentrations/ratios between low- and high-light cultured samples ($n = 5$ in all cases). Table shows *t*-value, associated degrees of freedom (*td.f*) and significance (***$p < 0.001$, **$p < 0.01$, *$p < 0.05$), including antheraxanthin (ANT), ß-carotene (CART), canthaxanthin (CANT), echinenone (ECHI), 3-hydroxylechinenone (H-ECHIN), myxoxanthophyll (MYXO) and zeaxanthin (ZEA)

| RLC parameters | | | |
|---|---|---|---|
| *Fv/Fm* | $t_8 = -3.07$* | $\alpha$ | $t_8 = -5.79$*** |
| $rETR_{max}$ | $t_8 = -4.44$*** | *Ek* | $t_8 = 0.91$ |
| Carotenoid pigment concentrations/Ratios | | | |
| Chl*a* | $t_8 = -3.78$** | ECHIN:Chl*a* | $t_8 = -1.97$ |
| B-carot:Chl*a* | $t_8 = 0.138$ | MYXO:Chl*a* | $t_8 = -1.93$ |
| CANT:Chl*a* | $t_8 = 8.68$*** | ANT:Chl*a* | $t_8 = 1.16$ |
| ZEA:Chl*a* | $t_8 = 4.92$** | H-ECHIN:Chl*a* | NA |

high- and low-light samples, antheraxanthin, canthaxanthin and zeaxanthin:Chl*a* ratios were significantly increased in high-light samples (Figure 5d–h). 3-hydroxylechinenone was absent from all but one high-light sample, precluding statistical comparisons between light treatments. Scytonemin was not recovered from any sample. Two un-assignable peaks (21.4 and 23.3 min retention time) (Figure 5a) were recovered at comparable ratios to Chl*a* across both high- and low-light cultured samples that could not be assigned to known pigments based on spectral analyses and/or comparisons of retention times.

# 4 | DISCUSSION

Genome analysis of *Leptolyngbya* sp. BC1307 revealed an absence of clear signals of psychrophily, similar to that found in the Arctic strain *Phormidesmis preistleyi* BC1401 (Chrismas et al., 2016). At 4.92 Mb, it had the smallest genome of the strains included here (Table S2), although since the genome is currently in draft format this size may be an underestimation. The G–C content of 52.93% was the highest G–C content of all three genomes included in this study. There was no clear distinction in amino acid-related indicators of genomic adaptation to the cold that allow protein flexibility at low temperatures (Table S2) (Feller, Arpigny, Narinx, & Gerday, 1997). However, the carotenoid biosynthesis gene *cruP* was identified, which has been shown to be upregulated in cold temperatures and has only been found in cyanobacteria in habitats characterized by large temperature fluctuations (Maresca, Graham, Wu, Eisen, & Bryant, 2007). The absence of *cruA* and presence of *crtL* suggests that *Leptolyngbya* sp. BC1307 uses the same pathway for the conversion of lycopene to ß-carotene as picocyanobacteria. Laboratory growth experiments revealed that *Leptolyngbya* sp. BC1307 is tolerant of a broad range of temperatures (Figure S2), well above the maximum threshold for psychrophily (15°C). Together, these findings suggest that *Leptolyngya* sp. BC1307 is not a true psychrophile, in line with the majority of other polar cyanobacteria that have previously been investigated (Chrismas et al., 2016; Tang, Tremblay, & Vincent, 1997). However, other factors remain important in determining the ecology of polar cyanobacteria, with light being key to driving niche differentiation.

## 4.1 | Differences in community composition

Our comparison of clone library data sets (Figure 2) revealed that different lineages of cyanobacteria do not exhibit a uniform distribution between near-surface and deep lake environments. We found a clear switch in dominance between Group I and Group II *Leptolyngbya* in habitats exposed to the surface and deep perennially ice-covered lakes, respectively (Figure 2). Group I was completely absent from the surface and Group II was completely absent from below the ice, with some co-occurrence of these two groups in shallow seasonally ice-free habitats. Variation in community structure between moat and perennially ice-covered environments has also been identified in Arctic cyanobacterial lakes (Mohit et al., 2017), and these differences are likely driven at least in part by the different irradiance regimes in each habitat, with above and below the ice representing distinct ecological niches.

## 4.2 | Phycobilisome genes

Some insight into the photoecology of *Leptolyngbya* sp. BC1307 was revealed through comparative genomics of the phycobilisome gene cluster. Given the presence of CCA in *Leptolyngbya* sp. PCC 7335, the absence of a functional CCA mechanism in *Leptolyngbya* sp. BC1307 is likely the result of loss/truncation of phycoerythrin (*cpeBA*) and the key CCA genes (*rcaE*, *rcaF*, *rcaC* and *pcyA*) from the genome. While there is no evidence that CCA in *Leptolyngbya* sp. BC1307 was lost subsequent to its establishment in the McMurdo Dry Valleys, its absence may have a metabolic benefit by allowing for redistribution of resources away from the phycobilisome complex, thereby assisting survival in the cold. Tang and Vincent (1999) proposed that, like in eukaryotic algae, changes in resource allocation within the photosynthetic apparatus could be a potential adaptive strategy in polar cyanobacteria; by decreasing the size of the phycobilisome complex (Davison, 1991; Geider, 1987) and channelling saved resources to RubisCO (Li & Morris, 1982), cyanobacteria could help to increase RubisCO activity at low temperatures. Lack of phycoerythrin may also have a photophysiological benefit. In the red alga *Rhodella violacea*, high irradiance leads to a reduction in the phycobilisome through loss of the terminal phycoerythrin hexamer (Bernard, Etienne, & Thomas, 1996; Ritz, Thomas, Spilar, & Etienne, 2000). Therefore, the absence of phycoerythrin from *Leptolyngbya* sp. BC1307 could help to reduce the potential for photoinhibition by limiting the wavelengths absorbed, thus reducing the potential excitation energy. Future studies examining the down-stream utilization of photochemically derived energy products are required to determine the mechanisms by which *Leptolyngbya* sp. BC1307 balances light capture with temperature-dependent metabolic processes.

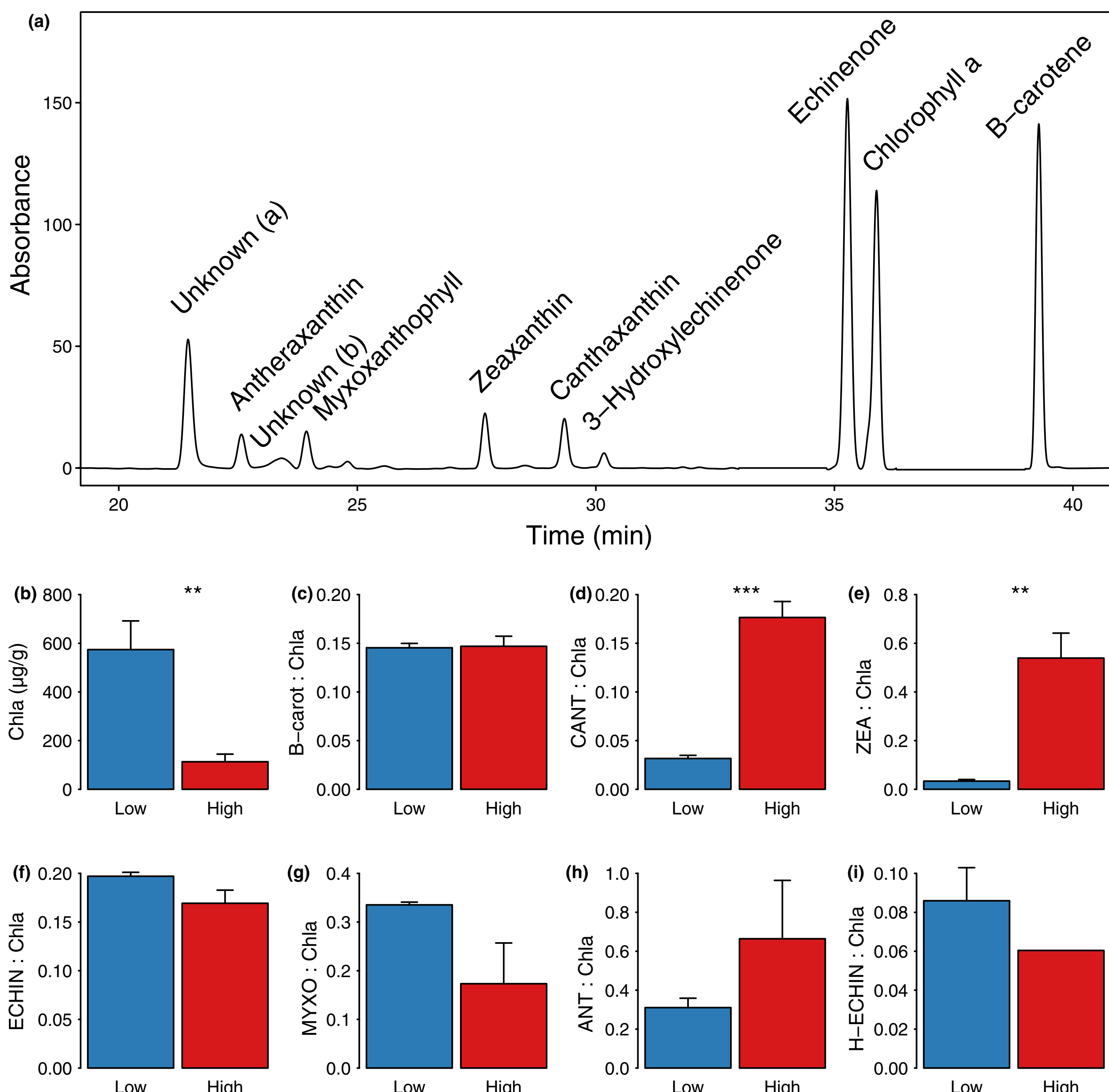


**FIGURE 5** Carotenoid pigment analysis of *Leptolyngbya* sp. BC1307 cultured under low- and high-light conditions. Showing (a) HPLC chromatogram of the carotenoids extracted from a typical low-light cultured sample, (b) the average concentration of Chlorophyll a (Chl*a*) in low- and high-light cultured samples, and the average ratios of (c) B-carotene (B-carot), (d) canthaxanthin (CANT), (e) zeaxanthin (ZEA), (f) echinenone (ECHIN), (g) myxoxanthophyll (MYXO), (h) antheraxanthin (ANT) and (i) 3-hydroxyechinenone (H-ECHIN), to chlorophyll a (Chl*a*) for low- and high-light cultured samples (mean ± SE, $n = 5$). Asterisks denote significant differences in parameters between low- and high-light cultured samples as determined from *t* tests (see Table 2) (***$p < 0.001$, **$p < 0.005$) [Colour figure can be viewed at wileyonlinelibrary.com]

### 4.3 | Photophysiology and carotenoid regulation

The photoecology of *Leptolyngbya* sp. BC1307 inferred from genomic analysis was further confirmed here through in vitro photophysiological assessment. Typical responses to ambient light intensity were manifest through differential regulation of i) Chl*a*, maximizing light harvesting under low light (increased Chl*a*) and minimizing light-capture under high light (decreased Chl*a*), and ii) carotenoids, maximizing photoprotection under high light (increased antheraxanthin, canthaxanthin and zeaxanthin). Consistent with the presence of OCP and *frp* genes within the *Leptolyngbya* sp. BC1307 genome (Table 1), we further identified the activation of a photoprotective mechanism additional to state transitions at PAR>$E_k$ (Figure 4b), demonstrating the capacity for OCP-driven NPQ in *Leptolyngbya* sp.

BC1307. *Leptolyngbya* sp. BC1307 therefore has considerable capacity to photoregulate under varying light conditions.

Overall, our photophysiology data suggested *Leptolyngbya* sp. BC1307 to be adapted to a low, variable light regime, rather than a sustained, high irradiance environment such as that experienced in the McMurdo Dry Valleys during the Austral summer. Under low-light conditions (25 µmol $m^{-2}$ $s^{-1}$), *Leptolyngbya* sp. BC1307 was found to harvest light efficiently, and typical photoregulatory mechanisms (i.e., state transitions, OCP-driven NPQ and regulation of light-harvesting and photoprotective pigments) were capable of preventing photoinhibition upon exposure to high irradiances (up to 1922 µmol $m^{-2}$ $s^{-1}$) for short periods of time. In contrast, when *Leptolyngbya* sp. BC1307 was cultured at 170 µmol $m^{-2}$ $s^{-1}$, it could not maintain effective electron transport when exposed to irradiances>580 µmols, with significant photoinhibition occurring above this threshold. This inability to photoregulate after exposure to higher irradiances for extended periods of time is likely due to exhaustion of key carotenoid pigment pools. The carotenoid 3-hydroxyechinenone, which is essential for OCP-driven NPQ (Wilson et al., 2008), was almost entirely absent from high-light cultured samples, resulting in a significant reduction in the photoregulatory capacity of *Leptolyngbya* sp. BC1307 during sustained periods of high light. In contrast, 3-hydroxyechinenone was found in all low-light cultured samples. Similarly, other key carotenoids known to be upregulated in cyanobacteria in response to high light, for example, myxoxanthophyll (Millie, Ingram, & Dionigi, 1990), were decreased in high- compared to low-light cultures, indicating potential exhaustion of these important pigment pools with sustained high-light conditions.

### 4.4 | Ecological implications

Genome and photophysiological investigations of the present study indicated high-light conditions to be detrimental to *Leptolyngbya* sp. BC1307. Given the sustained high-light regime apparent during the austral summer in the McMurdo Dry Valleys, *Leptolyngbya* sp. BC1307 must therefore occupy a low-light microhabitat in the ice-free moat surrounding Lake Hoare. Cyanobacterial mats in these environments are known to provide microhabitats for microbial eukaryotes shielded from their environment (Jungblut et al., 2012) with self-shading an important characteristic of these mats. Antarctic cyanobacterial mats often consist of a carotenoid pigmented surface layer and a deeper phycocyanin rich layer in which most production occurs (Hawes & Schwarz, 1999; Vincent, Downes, Castenholz, & Howard-Williams, 1993). *Leptolyngbya* sp. BC1307 may be capable of contributing to both of these layers; organisms at the surface could take on a photoprotective role by producing carotenoids, allowing those in lower layers to retain optimum capacity for photosynthesis with phycocyanin utilizing the red-orange light that remains after shorter wavelengths have been screened. Movement within the mat itself may also be important, and while no motility was observed in culture, it may be possible for *Leptolyngbya* sp. BC1307 to migrate deeper into the mat, thus selecting for dark conditions. Alternatively, shading may be provided by other members of the community. *Microcoleus*, which are also present in the type of environment from which *Leptolyngbya* sp. BC1307 was isolated, have been shown to be capable of migrating within microbial mats (Yallop, Winder, Paterson, & Stal, 1994). The potential therefore exists for these organisms to move to the surface of the mat where they are exposed to most of the light, thus providing shading for more light-sensitive organisms such as *Leptolyngbya* deeper in the mat. Further investigation of *Leptolyngbya* and their associated community within active mats is therefore required to fully examine these community effects.

## 5 | CONCLUSION

In this study, we show that genomic information from an organism can be used to infer their information about their ecological niche; by linking comparative genomics, photophysiology and microbial community analysis, ecological insights can be obtained. While *Leptolyngbya* sp. BC1307 may not be truly cold adapted, it occupies a distinct niche within broader Antarctic environments, being found in shallow and surface environments while absent from the deep perennially ice-covered lakes of the McMurdo Dry Valleys. It possesses many photoprotective mechanisms yet is not a high-light adapted organism. Rather, it occupies an ecological niche where it experiences moderate (or low) PAR and, while capable of withstanding short-term exposure to high-light, long-term exposure exhausts its photoprotective capacity. Cyanobacterial mats themselves represent a refuge from high-light conditions, and future studies should focus on the positioning of organisms such as *Leptolyngbya* sp. BC1307 within the mats of which they are a component. A huge diversity of Antarctic and Arctic cyanobacteria remains to be explored in this manner, and further investigation of other organisms using the integrated approach applied here will of great benefit to our overall understanding of polar ecology and the evolution of polar cyanobacteria in a changing world.

### ACKNOWLEDGEMENTS

This work was supported by the Natural Environment Research Council (GW4+ to N.A.M.C., NE/J02399X/1 to A.M.A., NE/M021025/1 to C.J.W. and M.L.Y.), and the Royal Society (Royal Society Research Grant: “The evolution of cyanobacteria from glacial ecosystems,” and a Royal Society Dorothy Hodgkin Fellowship to P.S-B.). Samples from the McMurdo Dry Valleys were collected by Jon Telling, with additional funding and logistics in Antarctica being provided by Andrew Fountain (NSF grant ANT-0423595). Thanks to Jane Coghill and Christy Waterfall at the Bristol Genomics facility and Annette Richer for assistance in strain isolation.

### AUTHOR CONTRIBUTIONS

The paper was devised by N.A.M.C., C.J.W., A.M.A. and P.S-B. N.A.M.C. isolated the strain (with assistance from Annette Richer),

performed growth experiments, and assembled and analysed the genome. C.J.W. performed photophysiology experiments and analysed the photophysiology data. N.A.M.C. and C.J.W. wrote the manuscript with additional comments provided by A.M.A., M.L.Y. and P.S-B.

## DATA ACCESSIBILITY

The genome of *Leptolyngbya* sp. BC1307 is available on GOLD (GOLD Analysis Project ID: Ga0078185) and GenBank (Accession no. PRJNA399838).

## ORCID

*Nathan A. M. Chrismas* https://orcid.org/0000-0002-2165-3102
*Christopher J. Williamson* https://orcid.org/0000-0002-8239-7368
*Marian L. Yallop* https://orcid.org/0000-0001-9556-6389
*Alexandre M. Anesio* https://orcid.org/0000-0003-2990-4014
*Patricia Sánchez-Baracaldo* https://orcid.org/0000-0002-5216-2664

## REFERENCES

Bagshaw, E. A., Wadham, J. L., Tranter, M., Perkins, R., Morgan, A., Williamson, C. J., ... Dubnick, A. (2016). Response of Antarctic cryoconite microbial communities to light. *Fems Microbiology Ecology*, *92*(6), UNSP fiw076. https://doi.org/10.1093/femsec/fiw076.

Bankevich, A., Nurk, S., Antipov, D., Gurevich, A. A., Dvorkin, M., Kulikov, A. S., ... Pevzner, P. A. (2012). SPAdes: A new genome assembly algorithm and it's applications to single-cell sequencing. *Journal of Computational Biology*, *19*(5), 455–477. https://doi.org/10.1089/cmb.2012.0021.

Barria, C., Malecki, M., & Arraiano, C. M. (2013). Bacterial adaptation to cold. *Microbiology-sgm*, *159*, 2437–2443. https://doi.org/10.1099/mic.0.052209-0.

Bernard, C., Etienne, A. L., & Thomas, J. C. (1996). Synthesis and binding of phycoerythrin and its associated linkers to the phycobilisome in *Rhodella violacea* (Rhodophyta): Compared effects of high light and translation inhibitors. *Journal of Phycology*, *32*(2), 265–271. https://doi.org/10.1111/j.0022-3646.1996.00265.x.

. Bolhuis, H., Cretoiu, M. S., & Stal, L. J. (2014). Molecular ecology of microbial mats. *FEMS Microbiology Ecology*, *90*(2), 335–350. https://doi.org/10.1111/1574-6941.12408.

Boulay, C., Wilson, A., D'Haene, S., & Kirilovsky, D. (2010). Identification of a protein required for recovery of full antenna capacity in OCP-related photoprotective mechanism in cyanobacteria. *Proceedings of the National Academy of Sciences of the United States of America*, *107*(25), 11620–11625. https://doi.org/10.1073/pnas.1002912107.

Campbell, D., Hurry, V., Clarke, A. K., Gustafsson, P., & Oquist, G. (1998). Chlorophyll fluorescence analysis of cyanobacterial photosynthesis and acclimation. *Microbiology and Molecular Biology Reviews*, *62*(3), 667–683.

Chong, C. W., Convey, P., Pearce, D. A., & Tan, I. K. P. (2012). Assessment of soil bacterial communities on Alexander Island (in the maritime and continental Antarctic transitional zone). *Polar Biology*, *35*(3), 387–399. https://doi.org/10.1007/s00300-011-1084-0.

Chrismas, N. A. M., Anesio, A. M., & Sanchez-Baracaldo, P. (2015). Multiple adaptations to polar and alpine environments within cyanobacteria: A phylogenomic and Bayesian approach. *Frontiers in Microbiology*, *6*, 1070. https://doi.org/10.3389/fmicb.2015.01070.

Chrismas, N. A. M., Anesio, A. M., & Sánchez-Baracaldo, P. (2018). The future of genomics in polar and alpine cyanobacteria. *FEMS Microbiology Ecology*, *94*(4), https://doi.org/10.1093/femsec/fiy032.

Chrismas, N. A. M., Barker, G., Anesio, A. M., & Sanchez-Baracaldo, P. (2016). Genomic mechanisms for cold tolerance and production of exopolysaccharides in the Arctic cyanobacterium *Phormidesmis priestleyi* BC1401. *Bmc Genomics*, *17*, 533. https://doi.org/10.1186/s12864-016-2846-4.

Clow, G. D., McKay, C. P., Simmons, G. M., & Wharton, R. A. (1988). Climatological observations and predicted sublimation rates at Lake Hoare, Antarctica. *Journal of Climate*, *1*(7), 715–728. https://doi.org/10.1175/1520-0442(1988) 001<0715:COAPSR>2.0.CO;2.

Cobley, J. G., & Miranda, R. D. (1983). Mutations affecting chromatic adaptation in the cyanobacterium *Fremyella diplosiphon*. *Journal of Bacteriology*, *153*(3), 1486–1492. Retrieved from http://jb.asm.org/content/153/3/1486.

Cobley, J. G., Clark, A. C., Weerasurya, S., Queseda, F. A., Xiao, J. Y., Bandrapali, N., ... Chu, M. H. (2002). CpeR is an activator required for expression of the phycoerythrin operon (cpeBA) in the cyanobacterium *Fremyella diplosiphon* and is encoded in the phycoerythrin linker-polypeptide operon (*cpeCDESTR*). *Molecular Microbiology*, *44*(6), 1517–1531. https://doi.org/10.1046/j.1365-2958.2002.02966.x.

Conley, P. B., Lemaux, P. G., Lomax, T. L., & Grossman, A. R. (1986). Genes encoding major light-harvesting polypeptides are clustered on the genome of the cyanobacterium *Fremyella diplosiphon*. *Proceedings of the National Academy of Sciences*, *83*(11), 3924–3928. Retrieved from http://www.pnas.org/content/83/11/3924.

Dana, G. L., Wharton, R. A., & Dubayah, R. A. (1998). Solar radiation in the Mcmurdo Dry Valleys, Antarctica. In: *Ecosystem Dynamics in a Polar Desert: The Mcmurdo Dry Valleys, Antarctica*, 39–64. https://doi.org/10.1029/AR072p0039.

Davison, I. (1991). Environmental effects on algal photosynthesis - Temperature. *Journal of Phycology*, *27*(1), 2–8. https://doi.org/10.1111/j.0022-3646.1991.00002.x.

Demmigadams, B. (1990). Carotenoids and photoprotection in plants - A role for the xanthophyll zeaxanthin. *Biochimica Et Biophysica Acta*, *1020*(1), 1–24. https://doi.org/10.1016/0005-2728(90)90088-L.

Dolhi, J. M., Teufel, A. G., Kong, W., & Morgan-Kiss, R. M. (2015). Diversity and spatial distribution of autotrophic communities within and between ice-covered Antarctic lakes (McMurdo Dry Valleys). *Limnology and Oceanography*, *60*(3), 977–991. https://doi.org/10.1002/lno.10071.

Doran, P. T., McKay, C. P., Clow, G. D., Dana, G. L., Fountain, A. G., Nylen, T., & Lyons, W. B. (2002). Valley floor climate observations from the McMurdo Dry Valleys, Antarctica, 1986–2000. *Journal of Geophysical Research: Atmospheres*, *107*(D24), ACL 13-1–ACL 13-12. https://doi.org/10.1029/2001JD002045.

Edgar, R. C. (2004). MUSCLE: Multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research*, *32*(5), 1792–1797. https://doi.org/10.1093/nar/gkh340.

Eilers, P., & Peeters, J. (1988). A model for the relationship between light-intensity and the rate of photosynthesis in phytoplankton. *Ecological Modelling*, *42*(3–4), 199–215. https://doi.org/10.1016/0304-3800(88)90057-9.

Falkowski, P. G., & Raven, J. A. (2007). *Aquatic photosynthesis*. Princeton: Princeton University Press.

Feller, G., Arpigny, J. L., Narinx, E., & Gerday, C. (1997). Molecular adaptations of enzymes from psychrophilic organisms. *Comparative Biochemistry and Physiology A-Physiology*, *118*(3), 495–499. https://doi.org/10.1016/S0300-9629(97)00011-X.

Fernandez-Carazo, R., Hodgson, D. A., Convey, P., & Wilmotte, A. (2011). Low cyanobacterial diversity in biotopes of the Transantarctic Mountains and Shackleton Range (80–82°S). *Antarctica. FEMS Microbiology Ecology*, *77*(3), 503–517. https://doi.org/10.1111/j.1574-6941.2011.01132.x.

Fountain, A. G., Nylen, T. H., Andrew, M., Basagic, H. J., & David, B. (2010). Snow in the McMurdo Dry Valleys, Antarctica. *International Journal of Climatology*, *30*(5), 633–642. https://doi.org/10.1002/joc.1933.

Geider, R. (1987). Light and temperature dependence of the carbon to chlorophyll-a ratio in microalgae and cyanobacteria - Implications for physiology and growth of phytoplankton. *New Phytologist*, *106*(1), 1–34. https://doi.org/10.1111/j.1469-8137.1987.tb04788.x.

Genty, B., Briantais, J., & Baker, N. (1989). The relationship between the quantum yield of photosynthetic electron transport and quenching of chlorophyll fluorescence. *Biochimica Et Biophysica Acta*, *990*(1), 87–92. https://doi.org/10.1016/S0304-4165(89)80016-9.

Goss, R., & Jakob, T. (2010). Regulation and function of xanthophyll cycle-dependent photoprotection in algae. *Photosynthesis Research*, *106*(1–2), 103–122. https://doi.org/10.1007/s11120-010-9536-x.

Green, W. J., & Lyons, W. B. (2009). The Saline Lakes of the McMurdo Dry Valleys, Antarctica. *Aquatic Geochemistry*, *15*(1–2), 321–348. https://doi.org/10.1007/s10498-008-9052-1.

Gudynaite-Savitch, L., Gretes, M., Morgan-Kiss, R. M., Savitch, L. V., Simmonds, J., Kohalmi, S. E., & Huner, N. P. A. (2006). Cytochrome f from the Antarctic psychrophile, *Chlamydomonas raudensis* UWO 241: Structure, sequence, and complementation in the mesophile, Chlamydomonas Reinhardtii. *Molecular Genetics and Genomics*, *275*(4), 387–398. https://doi.org/10.1007/s00438-005-0094-4.

Guy, L., Roat Kultima, J., & Andersson, S. G. E. (2010). genoPlotR: Comparative gene and genome visualization in R. *Bioinformatics*, *26*(18), 2334–2335. https://doi.org/10.1093/bioinformatics/btq413.

Hawes, I., & Schwarz, A. M. (1999). Photosynthesis in an extreme shade environment: Benthic microbial mats from Lake Hoare, a permanently ice-covered Antarctic lake. *Journal of Phycology*, *35*(3), 448–459. https://doi.org/10.1046/j.1529-8817.1999.3530448.x.

Hirschberg, J., & Chamovitz, D. (1994). Carotenoids in Cyanobacteria. In *The Molecular Biology of Cyanobacteria* (pp. 559–579). Dordrecht: Springer. https://doi.org/10.1007/978-94-011-0227-8_18.

Ionescu, D., Hindiyeh, M., Malkawi, H., & Oren, A. (2010). Biogeography of thermophilic cyanobacteria: Insights from the Zerka Ma'in hot springs (Jordan). *Fems Microbiology Ecology*, *72*(1), 103–113. https://doi.org/10.1111/j.1574-6941.2010.00835.x.

Johansen, J. R., Olsen, C. E., Lowe, R. L., Fučíková, K., & Casamatta, D. A. (2008). *Leptolyngbya* species from selected seep walls in the Great Smoky Mountains National Park. *Algological Studies*, *126*(1), 21–36. https://doi.org/10.1127/1864-1318/2008/0126-0021.

Jørgensen, B. B., & Marais, D. J. D. (1988). Optical properties of benthic photosynthetic communities: Fiber-optic studies of cyanobacterial mats. *Limnology and Oceanography*, *33*(1), 99–113. https://doi.org/10.4319/lo.1988.33.1.0099.

Jungblut, A. D., Hawes, I., Mackey, T. J., Krusor, M., Doran, P. T., Sumner, D. Y., & Goroncy, A. K. (2016). Microbial Mat Communities along an Oxygen Gradient in a Perennially Ice-Covered Antarctic Lake. *Applied and Environmental Microbiology*, *82*(2), 620–630. https://doi.org/10.1128/AEM.02699-15.

Jungblut, A. D., Vincent, W. F., & Lovejoy, C. (2012). Eukaryotes in Arctic and Antarctic cyanobacterial mats. *FEMS Microbiology Ecology*, *82*(2), 416–428. https://doi.org/10.1111/j.1574-6941.2012.01418.x.

Katoh, K., & Standley, D. M. (2013). MAFFT multiple sequence alignment software version 7: Improvements in performance and usability. *Molecular Biology and Evolution*, *30*(4), 772–780. https://doi.org/10.1093/molbev/mst010.

Kehoe, D. M., & Gutu, A.. (2006). Responding to color: The regulation of complementary chromatic adaptation. In *Annual Review of Plant Biology* (Vol. *57*, pp. 127–150). Palo Alto: Annual Reviews.

Kirilovsky, D., & Kerfeld, C. A. (2012). The orange carotenoid protein in photoprotection of photosystem II in cyanobacteria. *Biochimica Et Biophysica Acta-Bioenergetics*, *1817*(1), 158–166. https://doi.org/10.1016/j.bbabio.2011.04.013.

Kirilovsky, D., & Kerfeld, C. A. (2016). Cyanobacterial photoprotection by the orange carotenoid protein. *Nature Plants*, *2*(12), 16180. https://doi.org/10.1038/NPLANTS.2016.180.

Kong, W., Li, W., Romancova, I., Prasil, O., & Morgan-Kiss, R. M. (2014). An integrated study of photochemical function and expression of a key photochemical gene (*psbA*) in photosynthetic communities of Lake Bonney (McMurdo Dry Valleys, Antarctica). *Fems Microbiology Ecology*, *89*(2), 293–302. https://doi.org/10.1111/1574-6941.12296.

Kong, W., Ream, D. C., Priscu, J. C., & Morgan-Kiss, R. M. (2012). Diversity and expression of RubisCO genes in a perennially ice-covered Antarctic lake during the polar night transition. *Applied and Environmental Microbiology*, *78*(12), 4358–4366. https://doi.org/10.1128/AEM.00029-12.

Lanzen, A., Simachew, A., Gessesse, A., Chmolowska, D., Jonassen, I., & Ovreas, L. (2013). Surprising prokaryotic and eukaryotic diversity, community structure and biogeography of Ethiopian sSoda lakes. *PLoS ONE*, *8*(8), e72577. https://doi.org/10.1371/journal.pone.0072577.

Laybourn-Parry, J., & Wadham, J. L. (2014). *Antarctic Lakes*. Oxford: Oxford University Press.

Li, L., Alvey, R. M., Bezy, R. P., & Kehoe, D. M. (2008). Inverse transcriptional activities during complementary chromatic adaptation are controlled by the response regulator RcaC binding to red and green light-responsive promoters. *Molecular Microbiology*, *68*(2), 286–297. https://doi.org/10.1111/j.1365-2958.2008.06151.x.

Li, W., & Morris, I. (1982). Temperature adaptation in *Phaeodactylum tricornutum* Bohlin: Photosynthetic rate compensation and capacity. *Journal of Experimental Marine Biology and Ecology*, *58*(2–3), 135–150.

Li, Z., & Brand, J. (2007). *Leptolyngbya nodulosa* sp nov (Oscillatoriaceae), a subtropical marine cyanobacterium that produces a unique multicellular structure. *Phycologia*, *46*(4), 396–401. https://doi.org/10.2216/06-89.1.

Liang, C., Zhao, F., Wei, W., Wen, Z., & Qin, S. (2006). Carotenoid biosynthesis in cyanobacteria: Structural and evolutionary scenarios based on comparative genomics. *International Journal of Biological Sciences*, *2*(4), 197–207. https://doi.org/10.7150/ijbs.2.197

Liu, K., Raghavan, S., Nelesen, S., Linder, C. R., & Warnow, T. (2009). Rapid and accurate large-scale coestimation of sequence alignments and phylogenetic trees. *Science*, *324*(5934), 1561–1564. https://doi.org/10.1126/science.1171243.

MacIntyre, H. L., Kana, T. M., Anning, T., & Geider, R. J. (2002). Photoacclimation of photosynthesis irradiance response curves and photosynthetic pigments in microalgae and cyanobacteria. *Journal of Phycology*, *38*(1), 17–38. https://doi.org/10.1046/j.1529-8817.2002.00094.x.

Markowitz, V. M., Chen, I.-M. A., Palaniappan, K., Chu, K., Szeto, E., Grechkin, Y., & Kyrpides, N. C. (2012). IMG: the integrated microbial genomes database and comparative analysis system. *Nucleic Acids Research*, *40*(D1), D115–D122. https://doi.org/10.1093/nar/gkr1044.

Maresca, J. A., Graham, J. E., Wu, M., Eisen, J. A., & Bryant, D. A. (2007). Identification of a fourth family of lycopene cyclases in photosynthetic bacteria. *Proceedings of the National Academy of Sciences of the United States of America*, *104*(28), 11784–11789. https://doi.org/10.1073/pnas.0702984104.

Millie, D., Ingram, D., & Dionigi, C. (1990). Pigment and photosynthetic responses of *Oscillatoria agardhii* (cyanophyta) to photon flux density and spectral quality. *Journal of Phycology*, *26*(4), 660–666. https://doi.org/10.1111/j.0022-3646.1990.00660.x.

Mohamed, H. E., & Vermaas, W. (2004). Slr1293 in *Synechocystis* sp. strain PCC 6803 is the c-3′,4′ desaturase (CrtD) involved in myxoxanthophyll biosynthesis (vol 186, pg 5624, 2004). *Journal of Bacteriology*, *186*(22), 7827–7827. https://doi.org/10.1128/JB.186.22.7827.2004.

Mohit, V., Culley, A., Lovejoy, C., Bouchard, F., & Vincent, W. F. (2017). Hidden biofilms in a far northern lake and implications for the changing Arctic. *NPJ Biofilms and Microbiomes*, *3*. https://doi.org/10.1038/s41522-017-0024-3.

Morgan, R. M., Ivanov, A. G., Priscu, J. C., Maxwell, D. P., & Huner, N. P. A. (1998). Structure and composition of the photochemical apparatus of the Antarctic green alga, *Chlamydomonas subcaudata*. *Photosynthesis Research*, *56*(3), 303–314. https://doi.org/10.1023/A:1006048519302.

Morgan-Kiss, R. M., Ivanov, A. G., & Huner, N. P. A. (2002b). The Antarctic psychrophile, *Chlamydomonas subcaudata*, is deficient in state I state II transitions. *Planta*, *214*(3), 435–445. https://doi.org/10.1007/s004250100635.

Morgan-Kiss, R. M., Ivanov, A. G., Pocock, T., Krol, M., Gudynaite-Savitch, L., & Huner, N. P. A. (2005). The Antarctic psychrophile, *Chlamydomonas raudensis* Ettl (UWO241) (Chlorophyceae, Chlorophyta), exhibits a limited capacity to photoacclimate to red light. *Journal of Phycology*, *41*(4), 791–800. https://doi.org/10.1111/j.1529-8817.2005.00094.x.

Morgan-Kiss, R., Ivanov, A. G., Williams, J., Khan, M., & Huner, N. P. A. (2002a). Differential thermal effects on the energy distribution between photosystem II and photosystem I in thylakoid membranes of a psychrophilic and a mesophilic alga. *Biochimica Et Biophysica Acta-Biomembranes*, *1561*(2), 251–265. https://doi.org/10.1016/S0005-2736(02)00352-8.

Morgan-Kiss, R. M., Priscu, J. C., Pocock, T., Gudynaite-Savitch, L., & Huner, N. P. A. (2006). Adaptation and acclimation of photosynthetic microorganisms to permanently cold environments. *Microbiology and Molecular Biology Reviews*, *70*(1), 222–252. https://doi.org/10.1128/MMBR.70.1.222-252.2006.

Morgan-Kiss, R. M., Ivanov, A. G., Modla, S., Czymmek, K., Huener, N. P. A., Priscu, J. C., … Hanson, T. E. (2008). Identity and physiology of a new psychrophilic eukaryotic green alga, *Chlorella* sp., strain BI, isolated from a transitory pond near Bratina Island, Antarctica. *Extremophiles*, *12*(5), 701–711. https://doi.org/10.1007/s00792-008-0176-4.

Mullineaux, C. W. (2014). Electron transport and light-harvesting switches in cyanobacteria. *Frontiers in Plant Science*, *5*, 7. https://doi.org/10.3389/fpls.2014.00007.

Mullineaux, C. W., & Emlyn-Jones, D. (2005). State transitions: An example of acclimation to low-light stress. *Journal of Experimental Botany*, *56*(411), 389–393. https://doi.org/10.1093/jxb/eri064.

Nadeau, T. L., & Castenholz, R. W. (2000). Characterization of psychrophilic oscillatorians (cyanobacteria) from Antarctic meltwater ponds. *Journal of Phycology*, *36*(5), 914–923. https://doi.org/10.1046/j.1529-8817.2000.99201.x.

Novis, P. M., Aislabie, J., Turner, S., & McLeod, M. (2015). Chlorophyta, xanthophyceae and cyanobacteria in Wright Valley. *Antarctica. Antarctic Science*, *27*(5), 439–454. https://doi.org/10.1017/S0954102015000164.

Perkins, R. G., Mouget, J. L., Lefebvre, S., & Lavaud, J. (2006). Light response curve methodology and possible implications in the application of chlorophyll fluorescence to benthic diatoms. *Marine Biology*, *149*(4), 703–712. https://doi.org/10.1007/s00227-005-0222-z.

Pocock, T. H., Koziak, A., Rosso, D., Falk, S., & Huener, N. P. A. (2007). *Chlamydomonas raudensis* (UWO 241), Chlorophyceae, exhibits the capacity for rapid D1 repair in response to chronic photoinhibition at low temperature. *Journal of Phycology*, *43*(5), 924–936. https://doi.org/10.1111/j.1529-8817.2007.00380.x.

Pointing, S. B., Chan, Y., Lacap, D. C., Lau, M. C. Y., Jurgens, J. A., & Farrell, R. L. (2009). Highly specialized microbial diversity in hyper-arid polar desert. *Proceedings of the National Academy of Sciences of the United States of America*, *106*(47), 19964–19969. https://doi.org/10.1073/pnas.0908274106.

Porazinska, D. L., Fountain, A. G., Nylen, T. H., Tranter, M., Virginia, R. A., & Wall, D. H. (2004). The biodiversity and biogeochemistry of cryoconite holes from McMurdo Dry Valley glaciers, Antarctica. *Arctic Antarctic and Alpine Research*, *36*(1), 84–91. https://doi.org/10.1657/1523-0430(2004) 036[0084:TBABOC]2.0.CO;2.

Price, M. N., Dehal, P. S., & Arkin, A. P. (2010). FastTree 2 – Approximately maximum-likelihood trees for large alignments. *PLoS One*, *5*(3), e9490. https://doi.org/10.1371/journal.pone.0009490.

Punginelli, C., Wilson, A., Routaboul, J.-M., & Kirilovsky, D. (2009). Influence of zeaxanthin and echinenone binding on the activity of the orange carotenoid protein. *Biochimica Et Biophysica Acta-Bioenergetics*, *1787*(4), 280–288. https://doi.org/10.1016/j.bbabio.2009.01.011.

Richter, D., & Matula, J. (2013). *Leptolyngbya sieminskae* sp n. (Cyanobacteria) from Svalbard. *Polish Polar Research*, *34*(2), 151–168. https://doi.org/10.2478/popore-2013-0009.

Rippka, R., Deruelles, J., Waterbury, J. B., Herdman, M., & Stanier, R. Y. (1979). Generic assignments, strain histories and properties of pure cultures of cyanobacteria. *Microbiology*, *111*(1), 1–61. https://doi.org/10.1099/00221287-111-1-1.

Ritz, M., Thomas, J. C., Spilar, A., & Etienne, A. L. (2000). Kinetics of photoacclimation in response to a shift to high light of the red alga *Rhodella violacea* adapted to low irradiance. *Plant Physiology*, *123*(4), 1415–1425. https://doi.org/10.1104/pp.123.4.1415.

Rosinski, J., Hainfeld, J. F., Rigbi, M., & Siegelman, H. W. (1981). Phycobilisome Ultrastructure and Chromatic Adaptation in *Fremyella diplosiphon*. *Annals of Botany*, *47*(1), 1–12. Retrieved from http://www.jstor.org/stable/42764118.

Sánchez-Baracaldo, P. (2015). Origin of marine planktonic cyanobacteria. *Scientific Reports*, *5*. https://doi.org/10.1038/srep17418.

Sandmann, G. (1994). Carotenoid biosynthesis in microorganisms and plants. In *EJB Reviews 1994* (pp. 129–146). Berlin, Heidelberg: Springer. https://doi.org/10.1007/978-3-642-79502-2_10.

Schagerl, M., & Muller, B. (2006). Acclimation of chlorophyll a and carotenoid levels to different irradiances in four freshwater cyanobacteria. *Journal of Plant Physiology*, *163*(7), 709–716. https://doi.org/10.1016/j.jplph.2005.09.015.

Serodio, J., Cruz, S., Vieira, S., & Brotas, V. (2005). Non-photochemical quenching of chlorophyll fluorescence and operation of the xanthophyll cycle in estuarine microphytobenthos. *Journal of Experimental Marine Biology and Ecology*, *326*(2), 157–169. https://doi.org/10.1016/j.jembe.2005.05.011.

Stamatakis, A. (2014). RAxML version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics*, *30*(9), 1312–1313. https://doi.org/10.1093/bioinformatics/btu033.

Steiger, S., Jackisch, Y., & Sandmann, G. (2005). Carotenoid biosynthesis in *Gloeobacter violaceus* PCC 4721 involves a single *crtI*-type phytoene desaturase instead of typical cyanobacterial enzymes. *Archives of Microbiology*, *184*(4), 207–214. https://doi.org/10.1007/s00203-005-0004-5.

Stomp, M., Huisman, J., de Jongh, F., Veraart, A. J., Gerla, D., Rijkeboer, M., … Stal, L. J. (2004). Adaptive divergence in pigment composition promotes phytoplankton biodiversity. *Nature*, *432*(7013), 104–107. https://doi.org/10.1038/nature03044.

Szyszka-Mroz, B., Pittock, P., Ivanov, A. G., Lajoie, G., & Huener, N. P. A. (2015). The antarctic psychrophile *Chlamydomonas* sp UWO 241 preferentially phosphorylates a photosystem I-cytochrome b(6/f) supercomplex. *Plant Physiology*, *169*(1), 717. https://doi.org/10.1104/pp.15.00625.

Tang, E. P. Y., Tremblay, R., & Vincent, W. F. (1997). Cyanobacterial dominance of polar freshwater ecosystems: Are high-latitude mat-formers adapted to low temperature? *Journal of Phycology*, *33*(2), 171–181. https://doi.org/10.1111/j.0022-3646.1997.00171.x.

Tang, E. P. Y., & Vincent, W. F. (1999). Strategies of thermal adaptation by high-latitude cyanobacteria. *New Phytologist*, *142*(2), 315–323. https://doi.org/10.1046/j.1469-8137.1999.00385.x.

Taton, A., Grubisic, S., Balthasart, P., Hodgson, D. A., Laybourn-Parry, J., & Wilmotte, A. (2006). Biogeographical distribution and ecological ranges of benthic cyanobacteria in East Antarctic lakes. *FEMS Microbiology Ecology*, *57*(2), 272–289. https://doi.org/10.1111/j.1574-6941.2006.00110.x

Taton, A., Grubisic, S., Brambilla, E., De Wit, R., & Wilmotte, A. (2003). Cyanobacterial diversity in natural and artificial microbial mats of Lake Fryxell (McMurdo dry valleys, Antarctica): A morphological and molecular approach. *Applied and Environmental Microbiology*, *69*(9), 5157–5169. https://doi.org/10.1128/AEM.69.9.5157-5169.2003.

Tsuchiya, T., Takaichi, S., Misawa, N., Maoka, T., Miyashita, H., & Mimuro, M. (2005). The cyanobacterium *Gloeobacter violaceus* PCC 7421 uses bacterial-type phytoene desaturase in carotenoid biosynthesis. *Febs Letters*, *579*(10), 2125–2129. https://doi.org/10.1016/j.febslet.2005.02.066.

Van Heukelem, L., & Thomas, C. S. (2001). Computer-assisted high-performance liquid chromatography method development with applications to the isolation and analysis of phytoplankton pigments. *Journal of Chromatography A*, *910*(1), 31–49. https://doi.org/10.1016/S0378-4347(00)00603-4.

Varin, T., Lovejoy, C., Jungblut, A. D., Vincent, W. F., & Corbeil, J. (2012). Metagenomic analysis of stress genes in microbial mat communities from Antarctica and the High Arctic. *Applied and Environmental Microbiology*, *78*(2), 549–559. https://doi.org/10.1128/AEM.06354-11.

Vincent, W. F., Downes, M. T., Castenholz, R. W., & Howard-Williams, C. (1993). Community structure and pigment organisation of cyanobacteria-dominated microbial mats in Antarctica. *European Journal of Phycology*, *28*(4), 213–221. https://doi.org/10.1080/09670269300650321.

Wharton, R. A., Simmons, G. M., & McKay, C. P. (1989). Perennially ice-covered Lake Hoare, Antarctica: physical environment, biology and sedimentation. *Hydrobiologia*, *172*(1), 305–320. https://doi.org/10.1007/BF00031629

Wick, R. R., Schultz, M. B., Zobel, J., & Holt, K. E. (2015). Bandage: Interactive visualization of de novo genome assemblies. *Bioinformatics*, *31*(20), 3350–3352. https://doi.org/10.1093/bioinformatics/btv383.

Wilson, A., Ajlani, G., Verbavatz, J. M., Vass, I., Kerfeld, C. A., & Kirilovsky, D. (2006). A soluble carotenoid protein involved in phycobilisome-related energy dissipation in cyanobacteria. *The Plant Cell*, *18*(4), 992–1007. https://doi.org/10.1105/tpc.105.040121.

Wilson, A., Punginelli, C., Gall, A., Bonetti, C., Alexandre, M., Routaboul, J.-M., … Kirilovsky, D. (2008). A photoactive carotenoid protein acting as light intensity sensor. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(33), 12075–12080. https://doi.org/10.1073/pnas.0804636105.

Wu, Y. P., & Krogmann, D. W. (1997). The orange carotenoid protein of *Synechocystis* PCC 6803. *Biochimica Et Biophysica Acta-Bioenergetics*, *1322*(1), 1–7. https://doi.org/10.1016/S0005-2728(97)00067-4.

Yallop, M. L., de Winder, B., Paterson, D. M., & Stal, L. J. (1994). Comparative structure, primary production and biogenic stabilization of cohesive and non-cohesive marine sediments inhabited by microphytobenthos. *Estuarine, Coastal and Shelf Science*, *39*(6), 565–582. https://doi.org/10.1016/S0272-7714(06)80010-7.

Zhang, L., Jungblut, A. D., Hawes, I., Andersen, D. T., Sumner, D. Y., & Mackey, T. J. (2015). Cyanobacterial diversity in benthic mats of the McMurdo Dry Valley lakes, Antarctica. *Polar Biology*, *38*(8), 1097–1110. https://doi.org/10.1007/s00300-015-1669-0.

Zhu, Y., Graham, J. E., Ludwig, M., Xiong, W., Alvey, R. M., Shen, G., & Bryant, D. A. (2010). Roles of xanthophyll carotenoids in protection against photoinhibition and oxidative stress in the cyanobacterium *Synechococcus* sp. strain PCC 7002. *Archives of Biochemistry and Biophysics*, *504*(1), 86–99. https://doi.org/10.1016/j.abb.2010.07.007.

## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**How to cite this article:** Chrismas NAM, Williamson CJ, Yallop ML, Anesio AM, Sánchez-Baracaldo P. Photoecology of the Antarctic cyanobacterium *Leptolyngbya* sp. BC1307 brought to light through community analysis, comparative genomics and in vitro photophysiology. *Mol Ecol*. 2018;27:5279–5293. https://doi.org/10.1111/mec.14953