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ORIGINAL ARTICLE

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

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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 $\sim -19^{\circ}\text{C}$ (Doran et al., 2002) and annual precipitation of only 3–50 mm (Fountain, Nylen, Andrew, Basagic, & David, 2010). All the light in the McMurdo

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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 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (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 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ at a depth of 13 m, tapering to <1–14 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ 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 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ during the austral summer, with an annual mean of 188 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ (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 micro-scale (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, Pockock, Gudynaite-Savitch, & Huner, 2006; Morgan-Kiss et al., 2008). In particular, 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 (Pockock, 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, Hindiye, 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 ($A_{\text{max}} = 620 \text{ nm}$) and phycoerythrin ($A_{\text{max}} = 560 \text{ nm}$) 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 β -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 β -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 β -carotene is *cruA*, except in picocyanobacteria which use *crtL*. Canthaxanthin, echinenone and zeaxanthin are formed from β -carotene by *crtO*, *crtW* and *crtR*, respectively, and myxoxanthophyll from a β -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, β -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 μ L 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 Christmas 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 Christmas 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 Christmas 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 (α) 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 $F_m' > F_m$ during RLCs, NPQ was calculated after Serodio, Cruz, Vieira, and Brotas (2005) using the maximal F_m' achieved. Remaining cultures were filtered onto pre-weighed 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					
<i>ocp</i>	Orange carotenoid protein (OCP)	slr1963	Ga0078185_100888	508	0
<i>frp</i>	Fluorescence recovery protein	slr1964	Ga0078185_100887	106	4.00E-32
Carotenoid biosynthesis					
<i>crtE</i>	Geranylgeranyl diphosphate synthase	slr0739	Ga0078185_100722	379	8.00E-134
<i>crtB</i>	Phytoene synthase	slr1255	Ga0078185_100364	436	6.00E-156
<i>crtP</i>	Phytoene desaturase	slr1254	N/A	N/A	N/A
<i>crtQ</i>	Zeta-carotene desaturase	slr0940	N/A	N/A	N/A
<i>crtH</i>	Cis-trans Carotene isomerase	slr0033	Ga0078185_1004105	262	1.00E-82
<i>crtI</i>	Phytoene desaturase	gvip113	Ga0078185_1006103	806	0
<i>cruA</i>	Lycoprene cyclase	SynPCC7002_A2153	N/A	N/A	N/A
<i>crtL</i>	Lycoprene beta cyclase	SynPCC7942_2062	Ga0078185_102157	489	9.00E-174
<i>cruP</i>	Lycoprene cyclase	slr0659	Ga0078185_103223	553	0
<i>crtR</i>	Beta-carotene hydroxylase	slr1468	Ga0078185_100571	430	8.00E-154
<i>crtW</i>	Beta-carotene ketolase	SYNPCC7002_A2809	Ga0078185_10409	150	6.00E-46
			Ga0078185_10703	143	6.00E-43
<i>crtO</i>	B-carotene ketolase	slr0088	Ga0078185_10258	744	0
<i>crtD</i>	Methoxyneurosp-orene desaturase	slr1293	Ga0078185_101743	655	0
<i>cruF</i>	Gamma-carotene 1' hydroxylase myxoxanthophyll biosynthesis protein	SynPCC7002_A2032	Ga0078185_101870	305	8.00E-105
<i>cruG</i>	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 *cpeCDEST* (Cobley et al., 2002).

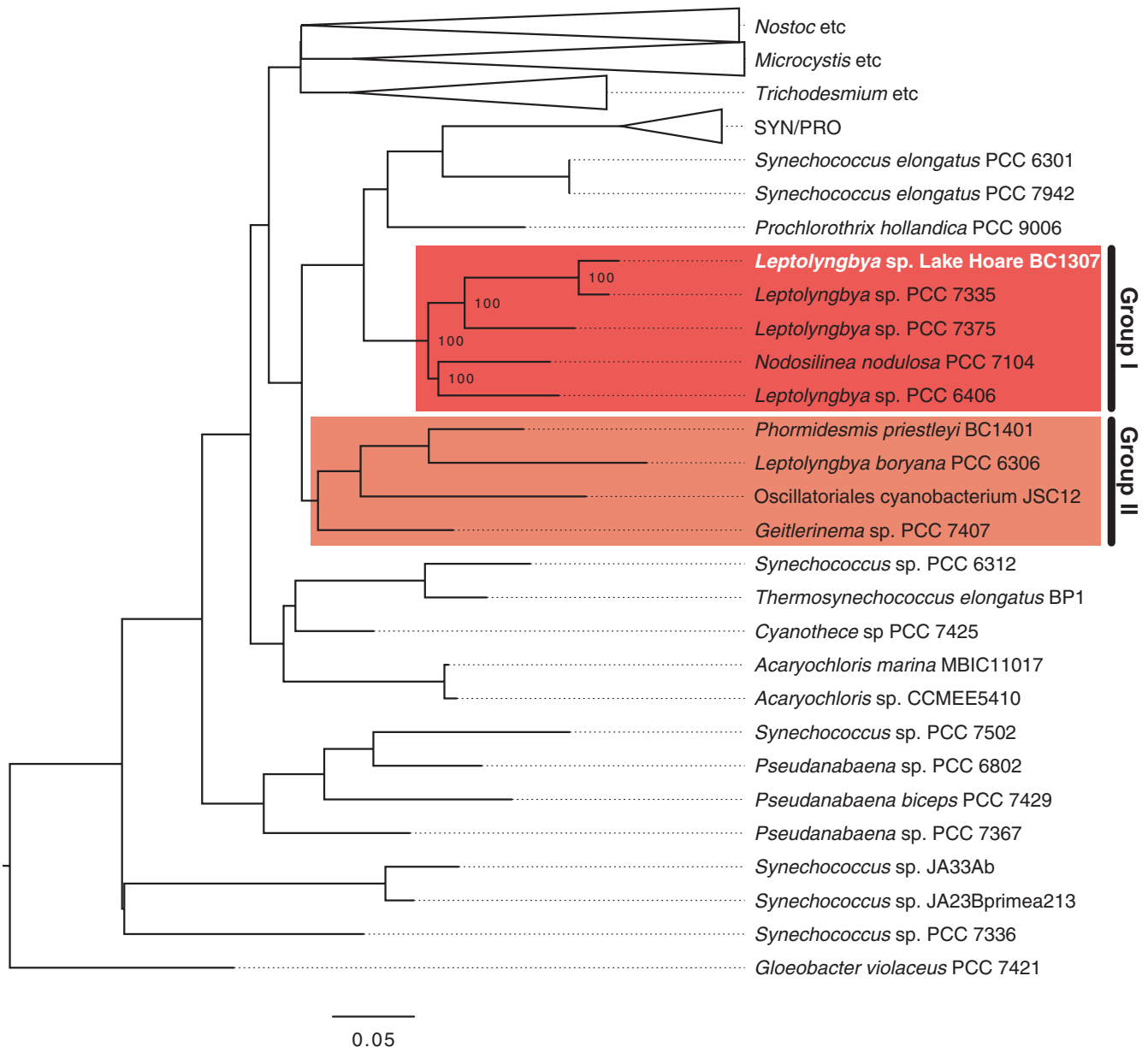


FIGURE 1 Maximum-likelihood SSU rRNA phylogeny depicting Group I (red) and Group II (orange) *Leptolyngbya* in relation to the rest of the cyanobacterial phylum. The newly sequenced *Leptolyngbya* sp. BC1307 is highlighted in white. The tree topology was constrained using a 130 taxa phylogenomic tree (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 (α) 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 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ 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 $\sim E_k$, were consistent with re-direction 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 $\text{PAR} > E_k$, driven by a quenching of maximum fluorescence in actinic light (F_m' , 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]

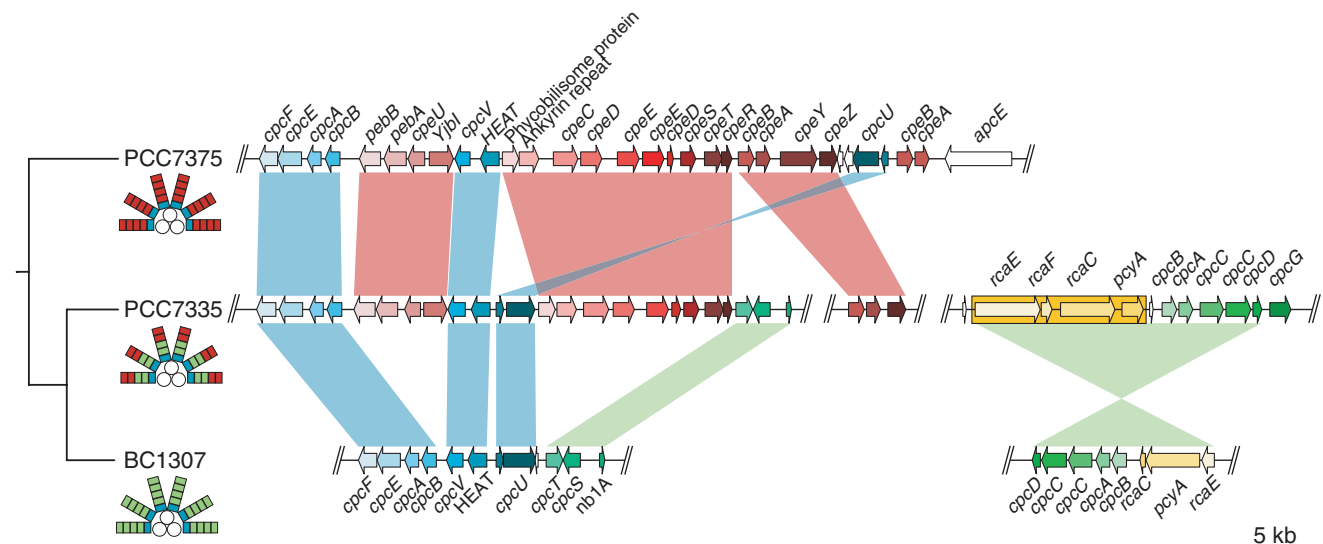
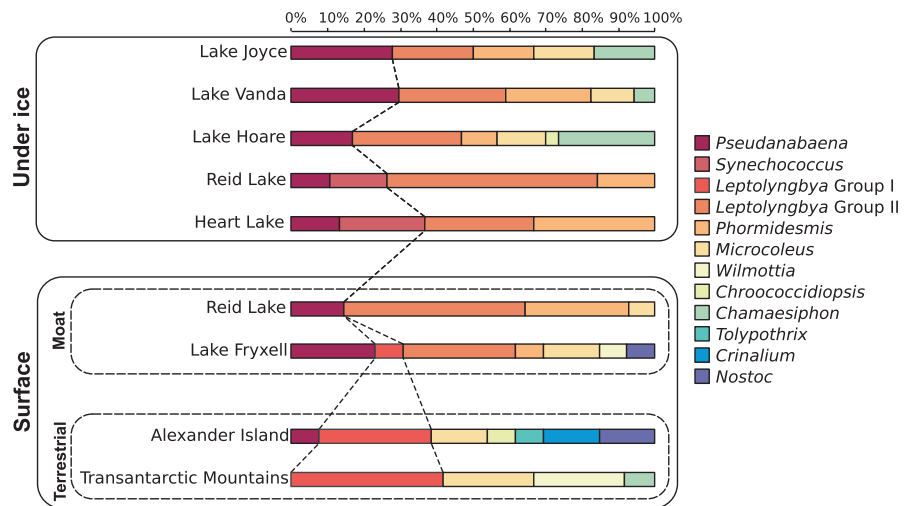


FIGURE 3 Gene order plot showing arrangement of phycobiliprotein gene clusters in *Leptolyngbya* sp. PCC 7375, *Leptolyngbya* sp. PCC 7335 and *Leptolyngbya* sp. BC1307. Genes shared by all three genomes (predominantly related to core phycocyanin structure and biosynthesis) are shown in shades of blue. 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]

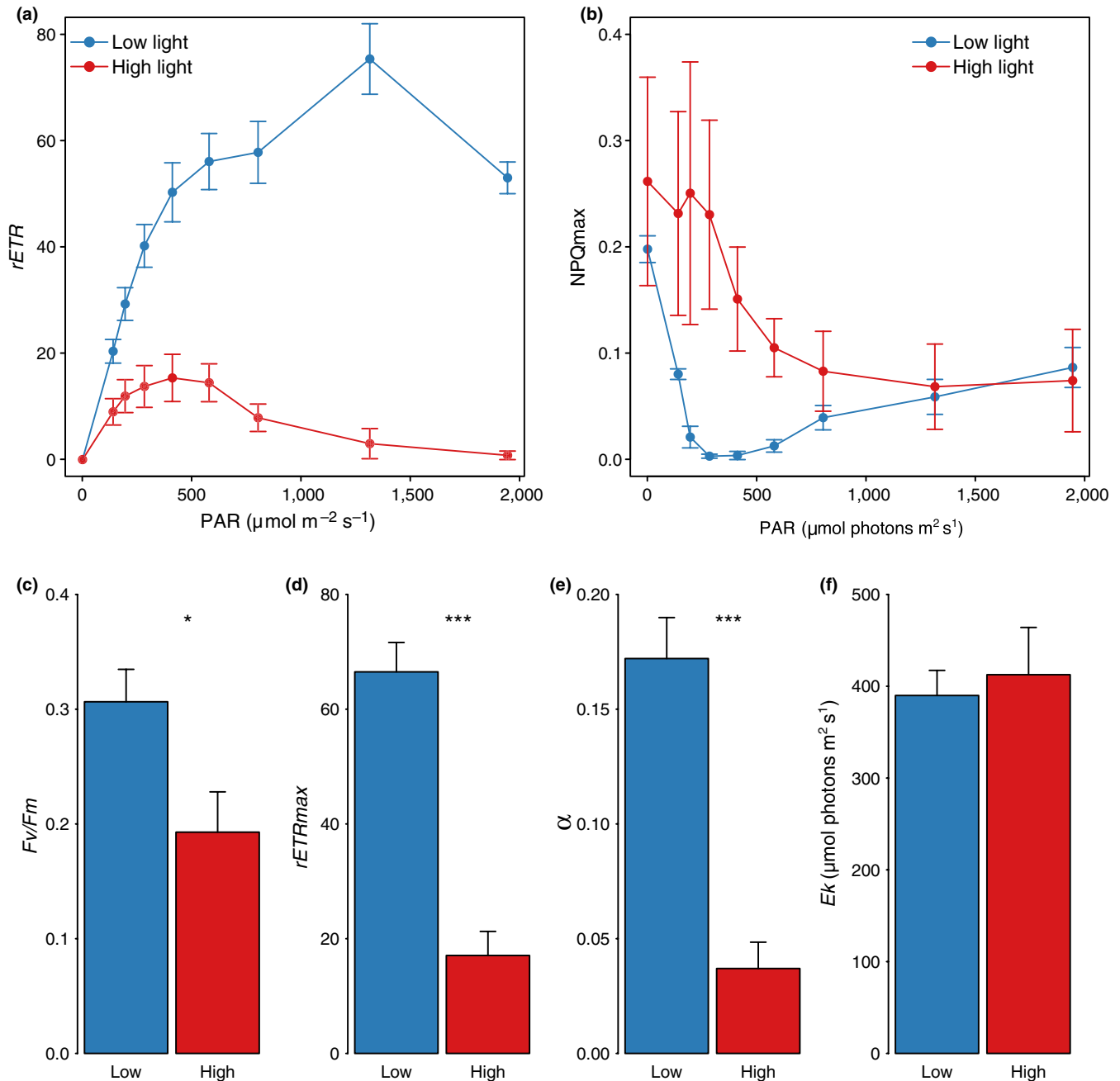


FIGURE 4 Photophysiology of *Leptolyngbya* sp. BC1307 cultured under low- and high-light conditions. Showing (a) relative electron transport rates ($rETR$) and (b) nonphotochemical quenching (NPQ_{max}) determined over rapid light-response curves (RLCs), and parameters derived from RLCs, including (c) the maximal quantum efficiency in the dark-adapted state, (d) the maximum relative electron transport rate ($rETR_{max}$), (e) the maximum light utilization coefficient (α), and (f) the light saturation coefficient (E_k) (mean \pm 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 $580 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ (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 F_m') 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, β -carotene, canthaxanthin, echinenone, 3-hydroxyechinenone, 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 β -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), β -carotene (CART), canthaxanthin (CANT), echinenone (ECHI), 3-hydroxyechinenone (H-ECHIN), myxoxanthophyll (MYXO) and zeaxanthin (ZEA)

RLC parameters			
<i>Fv/Fm</i>	$t_8 = -3.07^*$	α	$t_8 = -5.79^{***}$
<i>rETR</i> _{max}	$t_8 = -4.44^{***}$	<i>Ek</i>	$t_8 = 0.91$
Carotenoid pigment concentrations/Ratios			
Chla	$t_8 = -3.78^{**}$	ECHIN:Chla	$t_8 = -1.97$
B-carot:Chla	$t_8 = 0.138$	MYXO:Chla	$t_8 = -1.93$
CANT:Chla	$t_8 = 8.68^{***}$	ANT:Chla	$t_8 = 1.16$
ZEA:Chla	$t_8 = 4.92^{**}$	H-ECHIN:Chla	NA

high- and low-light samples, antheraxanthin, canthaxanthin and zeaxanthin:Chla ratios were significantly increased in high-light samples (Figure 5d–h). 3-hydroxyechinenone 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 Chla 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 prestleyi* BC1401 (Christmas 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 β -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 *Leptolyngbya*

sp. BC1307 is not a true psychrophile, in line with the majority of other polar cyanobacteria that have previously been investigated (Christmas 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 channeling 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.

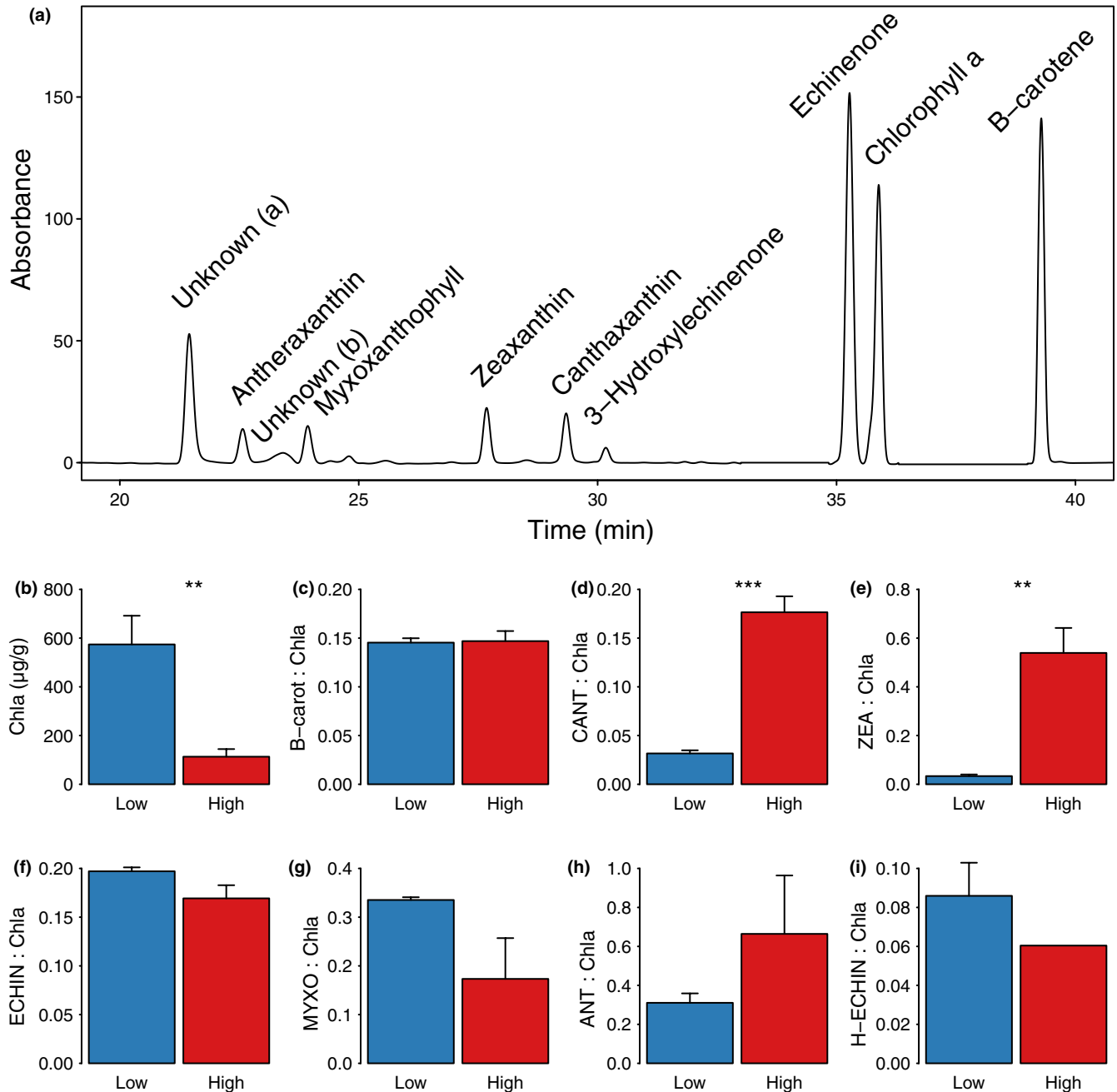


FIGURE 5 Carotenoid pigment analysis of *Leptolyngbya* sp. BC1307 cultured under low- and high-light conditions. Showing (a) HPLC chromatogram of the carotenoids extracted from a typical low-light cultured sample, (b) the average concentration of Chlorophyll a (Chla) in low- and high-light cultured samples, 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 (Chla) for low- and high-light cultured samples (mean \pm 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) Chla, maximizing light harvesting under low light (increased Chla) and minimizing

light-capture under high light (decreased Chla), 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 ($25 \mu\text{mol m}^{-2} \text{s}^{-1}$), *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 $1922 \mu\text{mol m}^{-2} \text{s}^{-1}$) for short periods of time. In contrast, when *Leptolyngbya* sp. BC1307 was cultured at $170 \mu\text{mol m}^{-2} \text{s}^{-1}$, it could not maintain effective electron transport when exposed to irradiances $>580 \mu\text{mol}$, 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.

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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).

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