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...
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·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 it difficult for effectively photosynthesizing 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 irradiance 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 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 photosynthesis (Kong, Li, Romanova, Prasil, & Morgan-Kiss, 2014; Kong, Ream, Priscu, & Morgan-Kiss, 2012; Morgan-Kiss, Priscu, Pocock, Gudynaitė-Savitch, & Huner, 2006; Morgan-Kiss et al., 2008). In particular, the photosynthesis of the psychrophilic alga *Chlamydomonas raudensis* has undergone in-depth characterization (Gudynaitė-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, Pittcock, 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 & Matula, 2013). *Leptolyngbya sensu lato* is polyphyletic, containing two distinct clades (Chrismas, Anesio, & Sanchez-Baracaldo, 2015): Group 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 *Phormidium minus* 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 portions of the pigments phycocyanin (*Aₘₐₓ* = 620 nm) and phycoerythrin (*Aₘₐₓ* = 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; Puginelli, 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 (slr1693) (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 & Müller, 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, crucF and crucG (Hirschberg & Chamovitz, 1994; Liang, Zhao, Wei, Wen, & Qin, 2006; Mohamed & Vermaas, 2004; Puginelli et al., 2009; Sandmann, 1994; Zhu et al., 2010). Under high-light conditions, β-carotene tends to decrease with chlorophyll a (Chla) 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 perennally 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 photautotroph.

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 Solylyse (Genlanlis) 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
sequences used. To identify sequences and ensure that available genomes (130 used in Sánchez-Baracaldo (2015) plus constructed with SSU rRNA genes from 131 cyanobacteria within the cyanobacterial phylum, an SSU rRNA gene database was created with 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, & Wilmutte, 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 Antarctic (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 (Gu, 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
an SSU similarity of 97%. Cyanobacteria from surface and under (Figure 2). Community composition was similar between perennially ice environments were found to belong to twelve main lineages in the moat and terrestrial samples with the exception of the Reid was found to be completely absent from below the ice and present (Group I) terrestrial environments were more variable. Leptolyngbya sp. BC1307 was not contained the phycoerythrin genes cpeBA, pebBA or the phycoerythrin linker-polypeptide operon cpeCDESTR (Coble et al., 2002).

3.3 | Comparative genomics of phycobiliproteins and carotenoids

While both Leptolyngbya sp. BC1307 and Leptolyngbya sp. PCC 7335 included cpeBA 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 (Coble et al., 2002).

Table 1: BLAST matches for genes in Leptolyngbya sp. BC1307 involved in photoprotection and carotenoid biosynthesis

| Gene | Protein | Query | BBH | score | e-value |
|------|---------|-------|-----|-------|---------|
| 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 | SYNPC7002_A2809 | Ga0078185_10409 | 150 | 6.00E–46 |
| crtO | B-carotene ketolase | slr0088 | Ga0078185_10258 | 744 | 0 |
| cruD | Methoxyneurop-orene desaturase | slr1293 | Ga0078185_101743 | 655 | 0 |
| cruF | Gamma-carotene 1 hydroxylase | 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, & Araiano, 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.

Leptolyngbya 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).

3.2 | 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
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 scyttonemin 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 (\( rETR_{\text{max}} \)) 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 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 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]
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 Chlα, several carotenoid pigments were isolated from *Leptolyngbya* sp. BC1307 (Figure 5), including antheraxanthin, β-carotene, canthaxanthin, echinenone, 3-hydroxylechinone, myxoxanthophyll and zeaxanthin. Chlα showed significant difference between high- and low-light cultures (Figure 5b); therefore, all other pigments are expressed as a ratio to Chlα concentrations (Table 2). While no significant difference in β-carotene, echinenone or myxoxanthophyll:Chlα ratios was apparent between

![Figure 4](https://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]
high- and low-light samples, antheraxanthin, canthaxanthin and zeaxanthin:Chl 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 Chl 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 psychrophyphil, similar to that found in the Arctic strain *Phormidiums preistleyei* 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 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 psychrophyphil (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 (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, thereby increasing 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, Spiller, & 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.
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 > Eₜ (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.

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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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**SUPPORTING INFORMATION**

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

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