Extremophiles (2013) 17:711–722
DOI 10.1007/s00792-013-0571-3

REVIEW

Review: the Antarctic *Chlamydomonas raudensis*: an emerging model for cold adaptation of photosynthesis

Jenna M. Dolhi · Denis P. Maxwell · Rachael M. Morgan-Kiss

Received: 15 April 2013 / Accepted: 18 July 2013 / Published online: 1 August 2013

Abstract Permanently cold habitats dominate our planet and psychrophilic microorganisms thrive in cold environments. Environmental adaptations unique to psychrophilic microorganisms have been thoroughly described; however, the vast majority of studies to date have focused on cold-adapted bacteria. The combination of low temperatures in the presence of light is one of the most damaging environmental stresses for a photosynthetic organism: in order to survive, photopsychrophiles (i.e. photosynthetic organisms adapted to low temperatures) balance temperature-independent reactions of light energy capture/transduction with downstream temperature-dependent metabolic processes such as carbon fixation. Here, we review research on photopsychrophiles with a focus on an emerging model organism, *Chlamydomonas raudensis* UWO241 (UWO241). UWO241 is a psychrophilic green algal species and is a member of the photosynthetic microbial eukaryote community that provides the majority of fixed carbon for ice-covered lake ecosystems located in the McMurdo Dry Valleys, Antarctica. The water column exerts a range of environmental stressors on the phytoplankton community that inhabits this aquatic ecosystem, including low temperatures, extreme shade of an unusual spectral range (blue-green), high salinity, nutrient deprivation and extremes in seasonal photoperiod. More than two decades of work on UWO241 have produced one of our most comprehensive views of environmental adaptation in a cold-adapted, photosynthetic microbial eukaryote.

Keywords Antarctica · Microbial eukaryote · Psychrophile · Photosynthesis

Abbreviations

cDNA	Complementary DNA
Chl	Chlorophyll
Ea	Activation energy
ELB	East lobe Bonney
HSP	Heat shock proteins
IBP	Ice-binding proteins
k_{cat}	Catalytic constant
KEGG	Kyoto Encyclopedia of Genes and Genomes
LHC	Light-harvesting complex
MGDG	Monogalactosyldiacylglycerol
PQ	Plastoquinone
PSI	Photosystem I
PSII	Photosystem II
NR	Nitrate reductase
Q_A	Quinone A
$Q_{Ared,ox}$	Reduced or oxidized quinone A
qE	Energy-dependent quenching
qPCR	Quantitative PCR
RubisCO	Ribulose-1,5-bisphosphate carboxylase/oxygenase
T_{max}	Maximum growth temperature
WLB	West lobe Bonney

Introduction

Microorganisms dominate low temperature ecosystems at the level of biodiversity and abundance (Morgan-Kiss et al.

Communicated by S. Albers.

J. M. Dolhi · R. M. Morgan-Kiss (✉)
Department of Microbiology, Miami University,
700 E High St., 32 Pearson Hall, Oxford, OH 45056, USA
e-mail: morganr2@miamioh.edu

D. P. Maxwell
Department of Biology, Western University,
London, ON, Canada

2006). Research on cold-adapted microorganisms has resulted in a considerable breadth of knowledge on elucidating the adaptations to low temperature in laboratory isolates and natural communities (D'amico et al. 2006; Margesin and Miteva 2011; Morgan-Kiss et al. 2006). A phylogenetically diverse group of microbial eukaryotes (protozoa, unicellular algae, fungi, chytrids, yeasts) have been detected in a variety of cold habitats (Alexander et al. 2009; Bielewicz et al. 2011; Jungblut et al. 2012; Lopez-Garcia et al. 2001; Lovejoy et al. 2006). Yet the study of psychrophilic microbial eukaryotes lags far behind their bacterial counterparts. The focus of this review is psychrophilic organisms that rely on photosynthesis for energy production. Our aim is to present recent findings on cold adaption with particular emphasis on the eukaryotic green alga *Chlamydomonas raudensis* UWO241 (UWO241). Originally isolated from a permanently ice-covered lake in the dry valleys of Antarctica (Neale and Priscu 1995), this alga is currently maintained in a number of laboratories as well as the National Center for Marine Algae and Microbiota culture collection (https://ncma.bigelow.org/; strain CCMP 1619). UWO241 is not capable of photoautotrophic growth at temperatures above 16 °C and is, therefore, a photopsychrophile (Morgan et al. 1998). After nearly two decades of research, UWO241 is a model for adaptation of photosynthetic processes to permanent cold.

Natural habitat and identity of *C. raudensis* UWO241

UWO241 was isolated from the water column of an ice-covered lake (Lake Bonney) located in the McMurdo Dry Valleys, Antarctica (Fig. 1a). UWO241 was originally classified by morphology as *Chlamydomonas subcaudata* (Neale and Priscu 1995). However, more recently it was discovered that the internal transcribed spacer (ITS) sequences of UWO241 are identical to those of the type strain, *C. raudensis* SAG49.72 (SAG49.72), while the ITS sequences of both *C. raudensis* strains were distantly related to *C. subcaudata* and the model green alga *C. reinhardtii* (Pocock et al. 2004). Despite identical ITS sequences, *C. raudensis* SAG49.72 was isolated from a

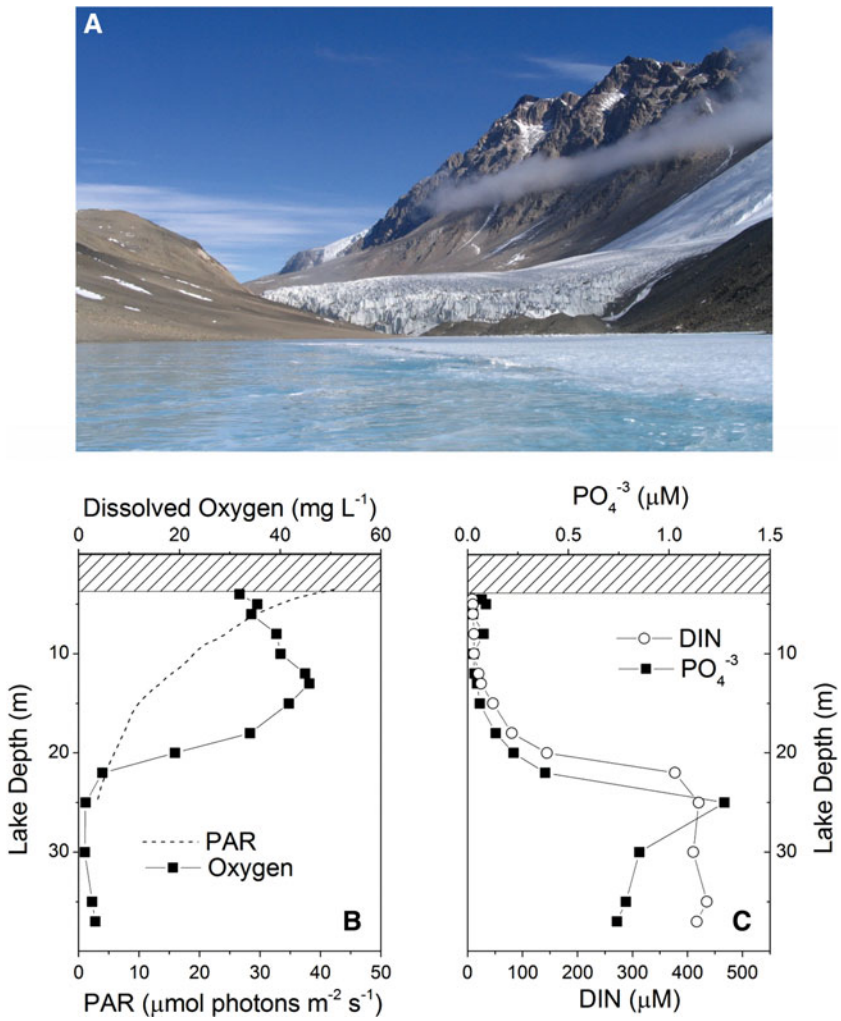

Fig. 1 **a** Site of isolation of *C. raudensis* UWO241, Lake Bonney in Taylor Valley, Antarctica. **b** and **c** General physicochemical characteristics of the east lobe of Lake Bonney. *C. raudensis* was isolated from a lake sample collected at 17 m. *Hatched square* shows permanent ice cover. *PAR* photosynthetically available radiation, *DIN* dissolved inorganic nitrogen. Nutrient data kindly provided by McMurdo Long Term Ecological Research Program (http://www.mcmlter.org)

pond in the Czech Republic and has been shown to be mesophilic as it has an optimum temperature for growth of 29 °C (Szyszka et al. 2007). The sister strains of *C. raudensis* represent a unique comparative system for understanding environmental adaptation in permanent low temperature habitats, whereby differences that may have arisen due to the evolution of psychrophily versus speciation can be distinguished.

Lake Bonney is separated into two basins named East and West Lobe Bonney (ELB and WLB, respectively). Ice covers minimize wind-driven mixing as well as allochthonous inputs, resulting in permanently stratified water chemistry and isolated microbial communities. The vast majority of organic carbon is provided by photosynthetic microbial eukaryotes (Bielewicz et al. 2011; Kong et al. 2012). UWO241 was isolated from the deep photic zone in ELB at a depth of 17 m. The unusual light environment at this depth is extreme shade below the light compensation point for photosynthesis ($\sim$5 µmol photons m^{-2} s^{-1} during mid-day in the summer; Fig. 1b), a light spectral distribution that is heavily biased to short wavelengths (450–550 nm), and extreme seasonality in intensity (24 h summer daylight/24 h winter darkness) (Lizotte and Priscu 1992; Lizotte et al. 1996). There is minimal exchange of gases between the water column and the atmosphere, with dissolved oxygen levels being very high and peaks at >200 % saturation at the chemocline where primary productivity is at maximum levels ($\sim$15 m depth; Fig. 1b). Under-ice surface waters of Lake Bonney are ultra-oligotrophic and phosphorus-limited (Fig. 1c), while deeper layers of the lake are hypersaline (up to 10 times seawater) (Fritsen et al. 1988; Priscu 1995). Thus, UWO241 is a polyextremophile, possessing environmental adaptations to survive a range of extreme limits on growth.

Adaptation to permanent low temperatures

Membranes

Maintenance of proper membrane fluidity is paramount to membranes serving as selective barriers and also influences the embedded proteins that function in transport, receptor/recognition, and energy generation. The most common changes to lipids in response to low temperature include increases in fatty acid unsaturation and decreases in fatty acid length. Both of these responses are found in all major taxonomic groups and result in increased membrane fluidity and lower the temperature at which the transition from liquid-crystalline to gel phase takes place (Chintalapati et al. 2004; D'Amico et al. 2002; Hughes and Dunn 1996). The lipid class profile of UWO241 exhibits similarities with other *Chlamydomonas* species: over 75 % of the total lipid content of UWO241 was found to be associated with the chloroplast, which is common for single-celled photosynthetic eukaryotes (Morgan-Kiss et al. 2002a). A comparison of chloroplast lipids with *C. reinhardtii* showed that UWO241 has significantly higher levels of polyunsaturated fatty acids for the chloroplast galactolipids monogalactosyldiacylglycerol (MGDG), digalactosyldiacylglycerol and sulfoquinovosyldiacylglycerol. The major MGDG fatty acid species in UWO241 was found to be 18:4, whereas *C. reinhardtii* was enriched in 18:1 fatty acids. Additional work by Morgan-Kiss et al. (2002a) has shown that UWO241 possesses novel polyunsaturated fatty acids where the double bond is positioned closer to the head group. This alteration in the position of the double bond is likely to increase the cross-sectional area of the fatty acyl chains thereby increasing their fluidity. We have also recently identified multiple homologs for fatty acid desaturases in a cDNA sequence library from UWO241 (Morgan-Kiss, Kiss & Raymond, in prep.). However, highly unsaturated fatty acids are not essential for photopsychrophiles: an Antarctic algal mat isolate, *Chlorella* BI sp., exhibits unsaturated fatty acid levels that are more comparable with mesophilic algae (Morgan-Kiss et al. 2008). Unlike UWO241, photoautotrophy is dispensable in the mat alga, and it can grow in the dark on a suitable organic carbon source (Jaffri 2011; Morgan-Kiss et al. 2008). Thus, highly unsaturated fatty acids within the photosynthetic membranes could be essential in obligate photoautotrophic eukaryotes such as UWO241.

Enzymes

Organisms which live in permanently cold environments must cope with the exponential loss of reaction rates at low temperatures. Many fully characterized cold-adapted enzymes have been described which exhibit high catalytic rates at lower temperatures (k_{cat}), reduced thermostability and inactivation at even moderate temperatures, as well as low activation energy (E_a) requirements. These properties, which are typical of enzymes at low temperatures, are associated with increased plasticity or structural flexibility in comparison to homologous mesophilic counterparts (D'amico et al. 2006; Doyle et al. 2011; Siglioccolo et al. 2010). Several studies have reported polar algal species exhibiting cold active enzymes. The Antarctic chlorophyte *Koliella antarctica* exhibits maximum nitrate reductase (NR) activity in crude lysate at lower temperatures (15 °C), as well as an increase in thermal lability of the enzyme compared to the mesophile *Chlorella sorokiniana* (Rigano et al. 2006). A low temperature for maximum NR activity was also observed in the Antarctic *Chloromonas* sp. ANT1 (Loppes et al. 1996), in sea-ice cultures dominated by the diatoms, *Nitzschia stellata* Mangin and *Amphiprora*

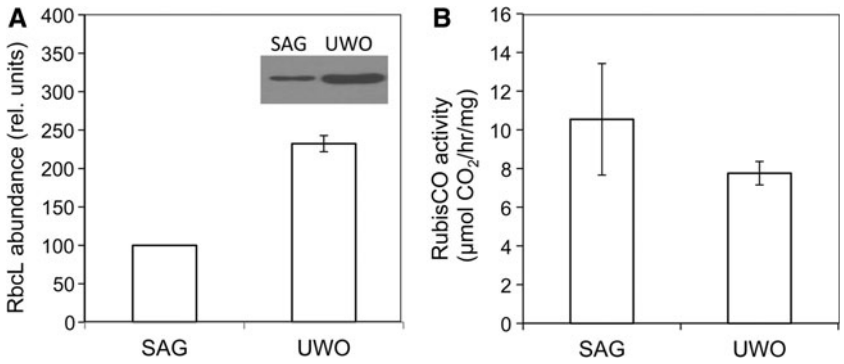

Fig. 2 **a** RubisCO abundance determined by immunoblotting against the large RubisCO subunit (RbcL) and quantified by densitometry in mesophilic and psychrophilic *C. raudensis* strains SAG49.72 (SAG) and UWO241 (UWO), respectively. Abundance is relative to that for *C. raudensis* SAG49.72. *Inset* a representative western blot. **b** RubisCO activity of soluble lysates extracted from psychrophilic and mesophilic *C. raudensis* strains grown under optimal conditions (8 °C and 20 µmol protons m^{-2} s^{-1}, 29 °C and 110 µmol protons m^{-2} s^{-1}, respectively) (mean ± SE; $N = 3$–4)

kufferathii Mangin (Priscu et al. 1989), as well as two psychrotrophic *Stichococcus* sp. (Chen et al. 2012). Glucose 6-phosphate dehydrogenase (G6PDH) catalyzes the first reaction in the oxidative pentose phosphate pathway, and has been implicated in cold hardening in plants and animals (Bredemeijer and Esselink 1995; Joanisse and Storey 1994). G6PDH from *K. antarctica* exhibits catalytic activity at low temperatures (10 °C) (Ferrara et al. 2013), and two different isoforms of G6PDH are thought to play a role in freezing tolerance in *Chlorella vulgaris* C-27 (Honjoh et al. 2003). Last, glutathione reductase purified from *Chlamydomonas* sp. ICE-L exhibits an increasing catalytic rate at temperatures ranging from 0 to 25 °C, as well as enhanced thermolability (Ding et al. 2007). Further characterization of cold-adapted enzymes and the comparison to their thermostable homologs will help to elucidate which structural modifications are important for catalytic activity at low temperature.

Another strategy psychrophiles employ to overcome a low turnover rate of specific enzymes in crucial metabolic pathways is increase in the relative abundance of critical enzyme(s). UWO241 possesses higher levels of the large subunit of RubisCO than that of SAG49.72 (Fig. 2a). Despite possessing higher levels of RubisCO, in vivo activity was 30 % lower in the psychrophile compared with the mesophilic strain when grown at their respective optimal growth temperatures of 8 and 29 °C (Fig. 2b). This discrepancy may be due to the complex regulation of RubisCO activity which requires an additional enzyme, RubisCO activase, for full activation of the enzyme (Parry et al. 2008; Sage et al. 2008). A homolog for RubisCO activase was identified in a cDNA sequence library of UWO241 (Morgan-Kiss, Kiss & Raymond, in prep.), and efforts are currently underway to heterologously express the psychrophilic RubisCO activase and characterize its thermal properties.

Ice-binding proteins

Ice-binding proteins (IBPs) have diverse functional roles in cold-adapted organisms, including antifreezes, ice recrystallization inhibitors and ice nucleators, and have been described in taxonomically divergent organisms, including fish, insects, plants, fungi and bacteria (Griffith and Yaish 2004; Lee et al. 2010; Raymond and Kim 2012). Multiple IBP isoforms have been discovered in several polar algal isolates, suggesting that IBPs also play an essential role in survival of algae in icy environments (Janech et al. 2006; Raymond et al. 2009). A recent study found that UWO241 culture supernatant exhibits ice-binding activity (Raymond and Morgan-Kiss 2013). Moreover, UWO241 expresses multiple putative IBP isoforms when grown at its minimal growth temperature of 1 °C (Raymond and Morgan-Kiss 2013). To confirm the function of these putative IBPs, a type 1 IPB from UWO241 was heterologously expressed and purified. The resultant protein exhibited clear ice-binding activity, confirming that this protein is an IBP (Raymond and Morgan-Kiss 2013). In contrast, the mesophilic sister species SAG49.72 did not exhibit ice-binding activity and no IBP sequences were recovered from a transcriptome of the mesophile (Raymond and Morgan-Kiss 2013). Secreted IBPs in UWO241 and other algae from polar environments may confer increased freezing resistance by maintaining a liquid environment and the formation brine pockets as water freezes.

Energetics

A major trend that has been observed across many psychrophiles (including UWO241) is high intracellular adenosine 5′-triphosphate (ATP) concentrations (Napolitano and Shain 2004, 2005). In conjunction with high cellular levels of ATP, UWO241 exhibits higher levels of two

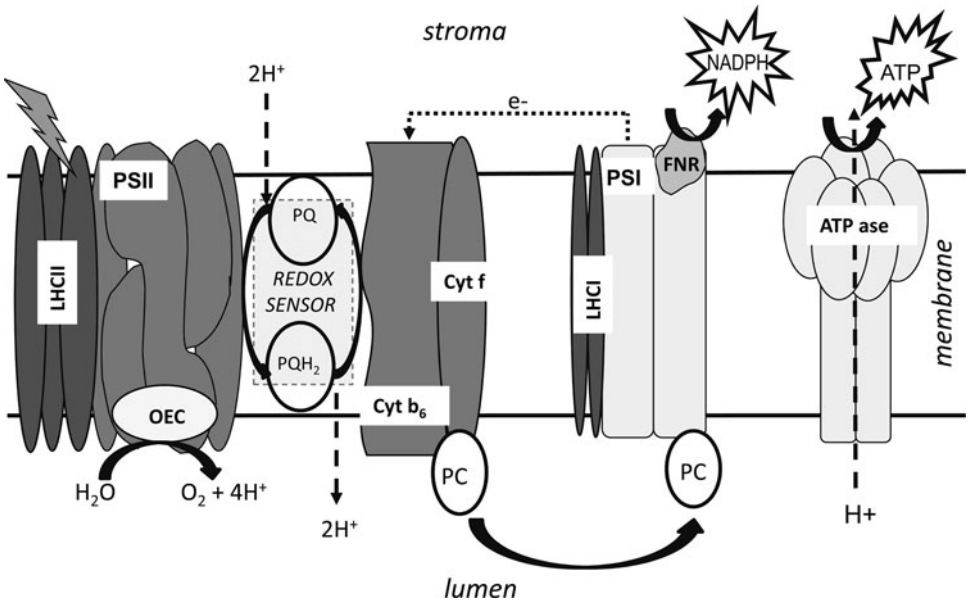

Fig. 3 Photosynthetic electron transport chain in green algae and plants. Light energy absorption occurs via light-harvesting complexes/antenna and is transferred to chlorophyll reaction centers in PSII and PSI. Oxidized PSII reaction centers drive electron separation from a water molecule by the oxygen evolving complex. Electrons pass through PSII to the mobile electron carrier plastoquinone which delivers electrons to Cyt b_6f. The lumenal protein plastocyanin carries electrons to oxidized PSI reaction centers where $NADP^+$ is reduced to NADPH via Ferredoxin-$NADP^+$ reductase. Lumenal protons are utilized by chloroplastic ATP synthase to generate ATP. The dotted line shows the alternative cyclic electron transport pathway. The redox state of the PQ pool is an early sensor of imbalances between turnover rates of PSII and PSI (*gray box*). *LHC* light harvesting complex, *OEC* oxygen evolution complex, *PS* photosystem, *PQ* plastoquinone, *Cyt* cytochrome, *PC* plastocyanin, *ATPase* ATP synthase

major subunits of the chloroplastic ATP synthase compared with the mesophilic *C. reinhardtii* (Morgan et al. 1998). Such an increase may offset the reduction in diffusion rates as temperature declines and allow for the maintenance of sufficiently high concentrations of ATP required for the activity of enzymes that catalyze endergonic (biosynthetic) reactions. Higher ATP levels may also be needed in natural communities of UWO241 residing in the hypersaline waters of the deep photic zone to actively pump Na^+ across the cell membrane, which is a common adaptive mechanism in salt-tolerant algae such as the model halophile, *Dunaliella salina* (Liska et al. 2004). In addition to higher ATP levels, a recent survey of the KEGG database shows that the genomes of many psychrophilic organisms are enriched in adenosine 5′-monophosphate (AMP) synthetic pathways, while mesophilic organisms tend to possess more AMP degradative enzymes (Parry and Shain 2011).

Photosynthesis at low temperatures

The photosynthetic apparatus of UWO241

UWO241 is a green alga and thus the organization of its photosynthetic apparatus is very similar to plants. The transformation of light energy into chemical energy occurs through photosynthetic electron transport, which is composed of a group of supramolecular pigment-binding protein complexes and related molecules associated with the thylakoid membrane of the chloroplast (Fig. 3). Photosynthetic electron transport is driven by absorption of light energy by the pigment/proteins that constitute the light-harvesting complexes (LHCs) of photosystem II (PSII) and photosystem I (PSI). Electron transport between PSII and PSI is facilitated by a pool of plastoquinone and the Cytochrome b_6f complex (Fig. 3). NADPH is the product of electron transport; ATP is generated by chloroplastic ATP synthase, which uses the proton gradient that is established across the thylakoid membrane during electron transport. As the demand for ATP and NADPH is not always constant, the photosynthetic apparatus can switch rapidly from linear electron transport that generates both molecules, to cyclic electron flow which generates additional ATP (Fig. 3; dotted line). Compared with *C. reinhardtii*, rates of cyclic electron transport are up to 2-fold greater in UWO241 which probably provides additional proton gradient to drive a higher demand for ATP in the photopsychrophile (Morgan-Kiss et al. 2002b).

Photoautotrophs inhabiting low light environments tend to have larger LHCs compared to organisms found in high light habitats (Falkowski and Owens 1980). LHC size can be inferred by the ratio of chlorophyll (Chl) *a* to Chl *b*: Chl *b* is found exclusively in LHCs, so a lower Chl *a*/*b* ratio reflects increased LHC size. UWO241 has been found to

have a very low Chl *a*/*b* of ~1.5 (Morgan et al. 1998; Pocock 2004), compared to a ratio >3 for most other species of green algae. This was accompanied by a relatively high oligomeric:monomeric LHC ratio in UWO241 (Morgan et al. 1998). Unlike the vast majority of other laboratory-studied algal species, LHC size in UWO241 is generally invariant regardless of growth regime. These data indicate that UWO241 is adapted for growth under low light conditions and has limited ability to acclimate to changes in light intensity by adjusting photosystem antenna size.

Photosynthetic organisms sense and respond to changes in the wavelength distribution of incoming light (i.e. light quality). Such adjustments are required because while PSII and PSI have distinctly different absorption characteristics (PSII preferentially blue-green light and PSI red light), light absorption by both photosystems needs to be balanced to maintain linear electron transport (Wilson et al. 2006). State transitions are a short-term mechanism used by plants and algae to redistribute absorbed energy between PSII and PSI (Wollman 2001). The ability to perform state transitions requires reversible phosphorylation of LHCII proteins and rearrangements within the thylakoid membranes (Bennett et al. 1980). Data from chlorophyll fluorescence spectroscopy indicate that UWO241 does not appear to perform state transitions, and biochemical data using antibodies against phosphorylated proteins provide evidence that LHCII proteins are not phosphorylated in UWO241 (Morgan-Kiss et al. 2002b; Szyszka et al. 2007; Takizawa et al. 2009). However, unidentified protein(s) within the PSI core complex of UWO241 are reversibly phosphorylated in response to high salinity, and may play a role in controlling rates of PSI-driven cyclic electron transport and ATP synthesis (Morgan et al. 1998; Szyszka et al. 2007). Last, a homolog of the LHCII kinase *stt7* was identified in the UWO241 cDNA sequence library (Morgan-Kiss, Kiss & Raymond, *in prep.*) which is essential for LHCII phosphorylation in *C. reinhardtii* (Depège et al. 2003), indicating that the lack of a state transition response in the psychrophile is not due to the absence of the kinase.

The limited ability of UWO241 to adjust its PSI/PSII stoichiometry is reflected, in part, by its surprising inability to grow under red light (Morgan-Kiss et al. 2005). This lack of plasticity has been explained by its constitutive down-regulation of PSI that includes the presence of a very small amount of LHCI; however, surprisingly, the transcriptome of UWO241 possesses multiple homologs of *lhcA* genes which encode for LHCI proteins (Morgan-Kiss, Kiss & Raymond, in prep.). That UWO241 has lost the ability to acclimate to red light is likely the result of long-term adaptation to a native habitat that is dominated by blue-green wavelengths as long-wavelength red light is attenuated by the water column. It has been postulated that the unusual light quality response observed under lab-controlled conditions mimics adaptation in natural UWO241 communities to the Antarctic winter (Morgan-Kiss et al. 2006). This model is based on the premise that the photochemical apparatus of this photopsychrophile remains intact during the Antarctic winter, but is shutdown during the polar winter. This strategy is similar to that used by overwintering evergreens which modulate photochemical efficiency on a seasonal level, exhibiting a prolonged state of lowered energy conversion efficiency for the entire winter season and quickly converting to efficient energy capture during the short growing season (Demmig-Adams et al. 2012). The winter adaptation model was recently tested in a series of experiments that monitored responses of UWO241 cultures transplanted back to the organism's original habitat (i.e. 17 m sampling depth in ELB) in a novel algal dialysis frame. In response to the loss of light availability during the seasonal transition between Antarctic summer and winter, transplanted cultures downregulated expression of genes essential for carbon fixation and photochemistry (*rbcL* and *psbA*, respectively), but maintained essential photochemical proteins during the polar night transition (Morgan-Kiss et al. in revision).

Photostasis

The balance between light absorption and its utilization is a combination of acclimatory responses termed photostasis (Hüner et al. 2003). Maintaining photostasis is essential to provide maximum amounts of usable energy to the cell, while preventing the absorption of excess light, which may be damaging. Low temperature presents unique challenges to maintaining photostasis because the primary photochemical events of photon capture and charge separation are largely temperature independent, but the rate of enzyme-catalyzed reactions of the Calvin cycle and other metabolic processes decrease as temperature decreases (Ensminger et al. 2006).

The redox state of the mobile electron acceptor, plastoquinone (PQ; Fig. 3), has been implicated in being central to the photostasis sensing mechanism. The redox state of PQ can be estimated by measuring the redox state of Q_A: $Q_{Ared}/(Q_{Ared} + Q_{Aox})$, the first stable quinone electron acceptor of PSII, using the non-invasive technique of Chl *a* fluorescence quenching analysis (Baker 2008). The redox state of Q_A is a measure of what is referred to as PSII excitation pressure; an excitation pressure of zero (Q_A fully oxidized) occurs in the dark, while an excitation pressure of 1 (Q_A fully reduced) is achieved under very high irradiance (Hüner et al. 1998). Although excitation pressure can increase as a consequence of high light, it has also been shown that a similar increase in excitation pressure can

occur, by lowering the temperature (Maxwell et al. 1995a). The explanation for this is that given a constant rate at which Q_A (or PQ) is reduced by electrons from PSII, a decrease in temperature has the effect of reducing the rate of oxidation as the cellular demand for reductant decreases. Evidence that photoautotrophs use the redox state of intersystem electron transport as a sensor for acclimation responses is provided by the finding that regardless of using high light or low temperature, similar changes in excitation pressure result in similar changes to the photosynthetic apparatus (Gray et al. 1997, 2005; Maxwell et al. 1994, 1995b; Miskiewicz et al. 2000, 2002). Data collected from a range of species suggest that photosynthetic organisms use one of the two major mechanisms to adjust to increased excitation pressure brought about by high light or low temperature. In most single-celled systems (cyanobacteria, algae), the response to high excitation pressure involves a decrease in the size of LHCII and increased synthesis of xanthophyll cycle pigments, which has the effect of reducing the redox state of PQ and regaining photostasis (Maxwell et al. 1994, 1995b; Miskiewicz et al. 2002). Plants, however, have the ability to utilize the excess light by upregulating carbon metabolism (Hüner et al. 1998).

UWO241 exhibits distinct acclimation strategies in comparison with mesophilic algae. In cultures grown at low temperature, an 8-fold increase in irradiance resulted in the predicted increase in PSII excitation pressure in both species, yet the value was always significantly lower in UWO241 than cultures of *Chlorella vulgaris*. As well, only *C. vulgaris* responded to the increase in irradiance by downsizing light-harvesting capacity and increasing xanthophyll cycle pigment content (Maxwell et al. 1994). That UWO241 failed to show these responses can be explained by the fact that, unlike *C. vulgaris*, UWO241 was able to increase its growth rate in response to the higher irradiance which is consistent with higher rates of carbon fixation potential (Morgan-Kiss et al. 2006). The increase in growth rate would require increased photosynthetic energy utilization, which has previously not been found in green algae acclimated to low temperature. In support of this hypothesis, UWO241 exhibits a linear increase in RubisCO carboxylation activity in response to higher growth irradiance which would be utilized to support higher growth rates (Morgan-Kiss and Dolhi 2011).

Response of UWO241 to environmental stress

High light

As discussed above, maintenance of photostasis reflects acclimation to long-term shifts (i.e. days to weeks) in the organism's environment, whereas responses to short-term environmental stress (i.e. minutes to hours) rely on rapid induction of stress avoidance mechanisms. Exposure to light in excess of photosynthetic capacity can result in a decrease in photosynthesis referred to as photoinhibition (Murata et al. 2007). Photoinhibition is often considered to occur when the rate of damage to the photosynthetic apparatus (most often the D1 polypeptide of PSII) exceeds the rate at which it can be repaired. Photoinhibition may also be the result of active quenching mechanisms that dissipate excess energy after it is absorbed. Such mechanisms include antenna quenching that involves the formation of the carotenoid zeaxanthin as part of the xanthophyll cycle (Demmig-Adams and Adams 1992) that contributes to the non-photochemical dissipation of excess light. Bonente et al. (2008) observed that several algal species isolated from low light environments lack PsbS, a protein that is essential for photoprotective thermal dissipation (qE). The transcriptome of UWO241 also revealed that this shade-adapted organism lacks a *psbS* homolog (Morgan-Kiss, Kiss & Raymond, in prep.). Moreover, UWO241 possesses a low capacity for induction of qE-dependent energy dissipation under excessive absorption of light energy (Pocock et al. 2007; Szyszka et al. 2007). Thus, *psbS* and qE-dependent energy quenching may be negatively selected in organisms residing in low light environments, such as UWO241.

Because low temperature decreases the rate of the enzyme-catalyzed reactions of the Calvin cycle as well as the mechanisms involved in repairing damaged PSII units, exposure to low temperature can result in photoinhibition even under moderate light intensities (Hüner et al. 1995). Research by Pocock et al. (2007) demonstrated that compared to *C. reinhardtii,* UWO241 is more susceptible to photoinhibition upon exposure to excessive light at either high or low temperatures. Yet surprisingly, this susceptibility is met with an exceptional capacity to rapidly recover photosynthetic efficiency that is not due to an enhanced capacity to repair damage (Pocock et al. 2007). Taken together, these data indicate that the ability of UWO241 to recover from photoinhibition is both novel and as yet unknown. Reaction centre quenching appears to be a major source of energy dissipation in UWO241 (Szyszka et al. 2007), and may also play a role in photoprotection in the photopsychrophile.

Salinity

A number of psychrophilic microbes found in polar regions are adapted to conditions of high salt (Krembs et al. 2000), including *Chlamydomonas* sp. (Morgan-Kiss and Dolhi 2011). Lake Bonney is characterized as hypersaline with the natural habitat of UWO241 having a NaCl concentration of approximately 700 mM (Priscu et al. 1998);

however, it has been shown that UWO241 is not a true halophile as originally assumed but rather is classified as halotolerant (Pocock et al. 2011; Takizawa et al. 2009). While UWO241 can grow well in a medium containing 700 mM NaCl, SAG49.72 is unable to grow at this salinity (Pocock et al. 2004). This sets up an experimental system for comparative genomics of the two strains to identify novel genes that have evolved in UWO241 to confer salt tolerance. Such a study would complement the work of Krell et al. (2007) who generated a cDNA library of the psychrophilic diatom *Fragilariopsis cylindrus.* This work led to the identification of a number of sequences related to osmolyte synthesis and ion transport in addition to a new class of ice-binding proteins (IBP) that seems to lack homologs in animals, plants as well as mesophilic species of diatoms (Krell et al. 2007). As mentioned above, several IBP homologs have been identified in the transcriptome of UWO241 grown in 0.7 M NaCl exhibiting ice-binding activity in its spent medium (Raymond and Morgan-Kiss 2013).

Consistent with salt stress affecting photosynthesis, UWO241 grown in high salt (850 mM) conditions had an increased excitation pressure compared to high salt conditions for SAG49.72 (100 mM). This supports the idea that UWO241 responds to this stress by modulating the redox signal (PQ pool redox state) which may subsequently affect gene expression to allow the organism to acclimate to high salinity (Pocock et al. 2011). Last, PSI-driven cyclic electron transport is enhanced in high salinity-grown UWO241 cultures (Morgan-Kiss et al. 2002b; Szyszka et al. 2007), which would support higher rates of ATP synthesis.

High temperatures

In order to deal with high temperature stress, psychrophiles induce the expression of a set of proteins upon temperature increase, collectively referred to as heat shock proteins (HSP). These can be involved in a variety of functions including transcription, translation, protein folding, or cell membrane modulation; however, heat shock responses have not been extensively studied in psychrophiles. Likewise, rapid temperature change to low temperatures can induce differential expression in cold shock proteins (D'amico et al. 2006). In addition to HSPs, cellular membrane structure, protein stability, antioxidants, and solute production are important for surviving high temperature stress (Allakhverdiev et al. 2008).

The ability to grow at low temperature is not restricted to psychrophiles (Maxwell et al. 1994; Morgan-Kiss et al. 2006). It is the inability to grow at relatively moderate temperatures (20–30 °C) that is definitive of psychrophiles, yet little is known about the underlying biochemistry that limits the growth of psychrophiles at supraoptimal temperatures. The most detailed study of supraoptimal temperatures on molecular and physiological aspects of UWO241 has recently been completed (Possmayer et al. 2011). Using the SYTOX green assay, Possmayer showed that cells grown at 10 °C and 120 µmol photons m^{-2} s^{-1} die when incubated at 24 °C with a half-time of 34.9 h. Surprisingly, the role of light in cell death was found to be relatively minor as incubation in total darkness delayed cell death by about 25 %. This finding suggests that the primary cause of cell death is not aberrant photosynthesis or excessive ROS production generated within the chloroplast. To examine the plasticity of UWO241 to temperature stress, 10 °C-grown cells were shifted to 24 °C for 12 h then returned to 10 °C to recover. The 12 h incubation at 24 °C, which resulted in less than 10 % cell death, led to declines in both light saturated rates of photosynthesis and respiration, PSII photochemistry and energy partitioning. In addition, changes to the abundance of specific gene transcripts were also detected. For example, the transcripts associated with the light-harvesting protein of PSII and ferredoxin declined by 60 and 90 %, respectively. That this was not a general cell response to supraoptimal temperatures was reflected by the finding that other transcripts remained unchanged or increased. The transcript abundance of the small subunit of RubisCO (*RBCS1*) remained largely unchanged during the 12-h shift-recovery regime while the transcript abundance of mRNAs *HSP90A* and *HSP22A,* encoding cytosolic heat shock proteins, increased rapidly in abundance during exposure to 24 °C. Within 24–48 h of being transferred back to 10 °C, all parameters including transcript abundances returned to levels found in 10 °C-grown cells. This research shows that while 24 °C is a temperature that is lethal to UWO241 this organism displays considerable physiological and molecular plasticity under high temperature stress.

Microbial eukaryote diversity and the impacts of climate change in the dry valley lakes

UWO241 is a member of a diverse community of microbial eukaryotes residing within Lake Bonney. A recent paper reported on the phylogenetic diversity and distribution of microbial eukaryotes residing in both basins of Lake Bonney using 18S rRNA sequencing libraries coupled with real time quantitative PCR (qPCR) (Bielewicz et al. 2011). Both lobes are dominated by photosynthetic protists including a cryptophyte species related to *Geminigera cryophila*, a haptophyte (*Isochrysis* sp.) and a stramenopile (*Nannochloropsis* sp.), which represent the major primary producers in this closed-basin aquatic ecosystem. Analyses of environmental gene expression using the major gene of

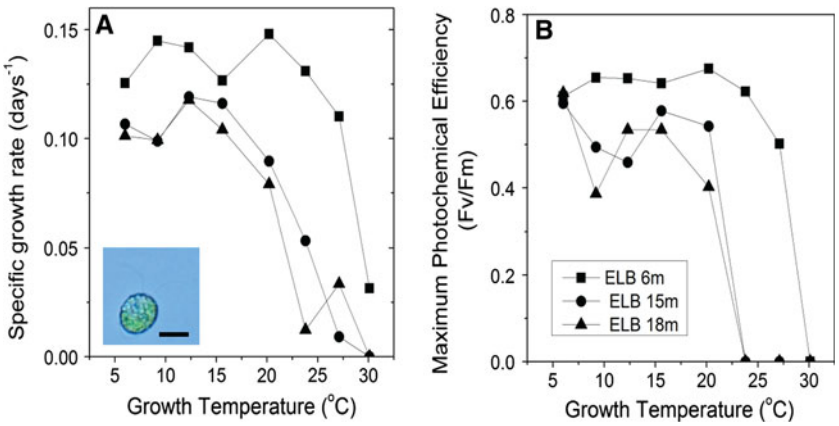

Fig. 4 Response of dry valley protist enrichments to temperature. Cultures from Lake Bonney enriched from sampling depths of 6, 15 or 18 m were grown under a range of temperatures and their physiology was monitored as specific growth rate (**a**) or maximum photosynthetic efficiency (**b**). *Inset* Bright field image of the dominant algal species in the cultures (related to *Chlamydomonas* ICE sp.) (*bar* 10 μm)

RubisCO (*rbcL*) as an indicator of carbon fixation support the finding that these organisms are the major primary producers (Kong et al. 2012).The deepest photic zone (18 m) harbors a variety of chlorophyte species including UWO241 (Bielewicz et al. 2011). While UWO241 is one of the few phototrophic isolates from the dry valley lakes, these new phylogenetic studies indicate that UWO241 is actually a minor player in the Antarctic lake phytoplankton community. Thus, it is important to increase attempts to cultivate new phototrophic protists which could be more critical in the primary production.

Cultivation attempts to increase the number of microbial eukaryote isolates from the dry valley lake ecosystems have been underway (Dolhi et al. 2012), and more recently there are enrichment cultures from Lake Bonney which exhibit a diversity of new protist species. Several cultures are dominated by a large chlorophyte related to the Antarctic sea-ice green alga, *Chlamydomonas* ICE sp. (Fig. 4a, inset), which was a dominant chlorophyte in sequencing libraries from Lake Bonney (Bielewicz et al. 2011; Kong et al. 2012). In a preliminary experiment, we explored whether microbial eukaryotes enriched from various depths in Lake Bonney exhibit comparable adaptation to low temperatures (Fig. 4a). Remarkably, despite isolation under permanent low temperatures for hundreds of years, the new dry valley lake protist cultures exhibited distinct responses to temperature that were dependent upon the original sampling depth. Shallow populations (6 m) exhibited a broad tolerance to growth temperature ($T_{opt} \sim$ 8–20 °C), while deeper populations (15 and 18 m) were restricted to lower growth temperatures ($T_{opt} \sim$ 12–15 °C). This differential temperature response appears to be due in part to differences in thermal lability of the photosynthetic apparatus: photochemical efficiency (F_V/F_M) in deeper populations was thermally labile at lower temperatures ($T_{max} = 20$ °C) as compared with shallow populations ($T_{max} = 25$ °C; Fig. 4b). These preliminary experiments challenge our assumptions that all microbial consortia residing in the dry valley lakes are psychrophilic. These protist enrichment cultures will be powerful tools to examine many outstanding questions regarding low temperature adaptation.

Polar and alpine environments are highly susceptible to small changes in temperature, and are, therefore, acutely sensitive to climate change (Williamson et al. 2009). As a consequence of a warming climate, episodic events, or "pulses", causing short duration variations in major environmental drivers of microbial carbon cycling (i.e. light, temperature, and nutrients) are intensifying in frequency and magnitude (Alley et al. 2003; Bernstein et al. 2007; Jentsch et al. 2007). In the dry valleys region, increases in episodic events associated with high summer flows will increase nutrient loading to the lakes (Doran et al. 2008). Current climate change models predict warmer, wetter summers in the dry valleys that will result in higher stream flow, larger perimeter moats and thinner ice covers resulting in increased nutrients and dissolved inorganic carbon into the water column (Fig. 5). Under current climatic conditions, interactions between the streams and water column are usually restricted to the upper 1–5 m of the water column (Fig. 5a); however, as the moat size increases we predict that the mixing layer will extend deeper into the lake, causing a displacement of the permanent chemocline (Fig. 5b). It is largely unknown how these climate-induced changes in lake chemistry will impact the microbial eukaryote populations, but at a minimum thinner ice covers in combination with alleviation of nutrient deprivation could stimulate photosynthesis and may favor "aquatic weeds" such as *Chlamydomonas* sp. that exhibit acclimatory plasticity over a range of environmental stresses.

Concluding remarks

Research in polar microbial physiology is critical as a dynamic interplay between microbes and climate exists. For example, atmospheric CO_2 content which impacts climate change is dependent on photosynthesis and respiration by primary producers. Due to this vital role in carbon

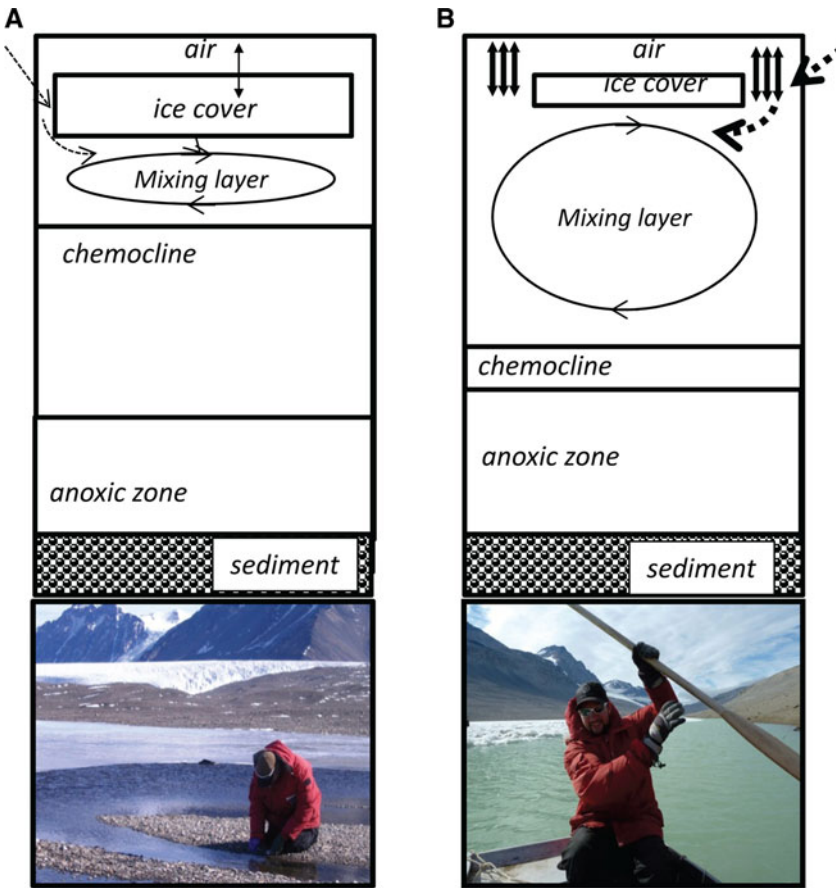

Fig. 5 Predicted climate effects in Antarctic lakes. **a** Dry valley lakes are permanently ice-capped for most of the year, with the exception of narrow open water moats which form around the perimeter of the lake during the short austral summer (mid-November to late-February). The moat allows input from glacial-fed streams into the lake (*dotted lines*) and limited mixing occurs between the moat and layers of the water column directly under the ice. Interactions between the water column and the atmosphere are minimal (*double arrows*). **b** As the dry valleys slowly warm, it is predicted that seasonal "pulse" events will lead to warmer, wetter summers, resulting in more stream input, larger moats and reduced ice covers. Images show examples of a typical summer moat (**a**) and an unusual large moat on the east lobe of Lake Bonney during the summer of 2010 (**b**). Larger moats are anticipated to be a more common occurrence as the dry valleys slowly warm

cycling and their position at the base of the aquatic food chain, it is important to understand how primary producers and subsequently the aquatic ecosystem will respond to climate change. Achieving this depth of knowledge will require studies of photopsychrophiles not only in the laboratory, but also in their native habitats relative to the natural communities. Research conducted across a range of laboratory and field-based studies on UWO241 has resulted in a broad picture of physiological function and ecological relevance of this organism. However, to build upon our current knowledge of this model photopsychrophile more studies on the level of genomics are required. Recently, the transciptome of UWO241 was sequenced and preliminary results have revealed many homologs for proteins and enzymes that play important roles in survival under a variety of stresses. Genomic, transcriptomic, and proteomic studies of UWO241 exposed to various environmental conditions will provide critical insights into how this organism not only survives, but also thrives in its harsh environment. Additionally, these studies will help predict how sensitive, low temperature, photosynthetic communities will respond to climate change.

Acknowledgments The authors thank John C. Priscu and Patrick J. Neale for original isolation and donation of *Chlamydomonas raudensis* UWO241 strain. RMK and JMD were supported by the National Science Foundation Faculty Early Career Development (CAREER) Program and Office of Polar Programs (Grant Nos. ANT0631659 and ANT1056396).

References

Alexander E, Stock A, Breiner HW, Behnke A, Bunge J, Yakimov MM, Stoeck T (2009) Microbial eukaryotes in the hypersaline anoxic L'Atalante deep-sea basin. Environ Microbiol 11:360–381

Allakhverdiev SI, Kreslavski VD, Klimov VV, Los DA, Carpentier R, Mohanty P (2008) Heat stress: an overview of molecular responses in photosynthesis. Photosynth Res 98:541–550

Alley RB, Marotzke J, Nordhaus WD, Overpeck JT, Peteet DM, Pielke RA Jr et al (2003) Abrupt climate change. Science 299:2005–2010

Baker NR (2008) Chlorophyll fluorescence: a probe of photosynthesis in vivo. Ann Rev Plant Biol 59:89–113

Bennett J, Steinback KE, Arntzen CJ (1980) Chloroplast phosphoproteins: regulation of excitation energy transfer by phosphorylation of thylakoid membrane polypeptides. Proc Nat Acad Sci USA 77:5253–5257

Bernstein, L, Bosch, P, Canziani, O, Chen, Z, Christ, R, Davidson, O et al (2007) Intergovernmental panel on climate change fourth assessment report. In: Jallow BP, Kajfež-Bogataj L, Bojariu R, Hawkins D, Diaz S, Lee H et al (eds) Climate change 2007 synthesis report. Cambridge University Press, Cambridge

Bielewicz S, Bell EM, Kong W, Friedberg I, Priscu JC, Morgan-Kiss RM (2011) Protist diversity in a permanently ice-covered

Antarctic lake during the polar night transition. ISME J 5:1559–1564
Bonente G, Passarini F, Cazzaniga S, Mancone C, Buia MC, Tripodi M et al (2008) The occurrence of the *psbS* gene product in *Chlamydomonas reinhardtii* and in other photosynthetic organisms and its correlation with energy quenching. Photochem Photobiol 84:1359–1370
Bredemeijer G, Esselink G (1995) Glucose 6-phosphate dehydrogenase during cold-hardening in *Lolium perenne*. J Plant Physiol 145:565–569
Chen Z, He C, Hu H (2012) Temperature responses of growth, photosynthesis, fatty acid and nitrate reductase in Antarctic and temperate *Stichococcus*. Extremophiles 16:127–133
Chintalapati S, Kiran M, Shivaji S (2004) Role of membrane lipid fatty acids in cold adaptation. Cell Mol Biol 50:631
D'Amico S, Claverie P, Collins T, Georlette D, Gratia E, Hoyoux A et al (2002) Molecular basis of cold adaptation. Philos Trans R Soc Lond B Biol Sci 357:917–925
D'amico S, Collins T, Marx JC, Feller G, Gerday C (2006) Psychrophilic microorganisms: challenges for life. EMBO Rep 7:385–389
Demmig-Adams B, Adams WW III (1992) Photoprotection and other responses of plants to high light stress. Ann Rev Plant Physiol Plant Mol Biol 43:599–626
Demmig-Adams B, Cohu C, Muller O, Adams W (2012) Modulation of photosynthetic energy conversion efficiency in nature: from seconds to seasons. Photosynth Res 113:75–88
Depège N, Bellafiore S, Rochaix J-D (2003) Role of chloroplast protein kinase Stt7 in LHCII phosphorylation and state transition in *Chlamydomonas*. Science 299:1572–1575
Ding Y, Miao J-L, Wang Q-F, Zheng Z, Li G-Y, Jian J-C, Wu Z-H (2007) Purification and characterization of a psychrophilic glutathione reductase from Antarctic ice microalgae *Chlamydomonas* sp. Strain ICE-L. Polar Biol 31:23–30
Dolhi JM, Ketchum N, Morgan-Kiss RM (2012) Establishment of microbial eukaryotic enrichment cultures from a chemically stratified antarctic lake and assessment of carbon fixation potential. J Vis Exp 62:e3992
Doran PT, McKay CP, Fountain AG, Nylen T, McKnight DM, Jaros C, Barrett JE (2008) Hydrologic response to extreme warm and cold summers in the McMurdo Dry Valleys, East Antarctica. Ant Sci 20:499–509
Doyle S, Dieser M, Broemsen E, Christner BC (2011) General characteristics of cold-adapted microorganisms. In: Miller RV, Whyte L (eds) Polar microbiology: life in a deep freeze. ASM Press, Washington, DC, pp 103–125
Ensminger I, Busch F, Huner NPA (2006) Photostasis and cold acclimation: sensing low temperature through photosynthesis. Physiol Plant 126:28–44
Falkowski PG, Owens TG (1980) Light–shade adaptation. Plant Physiol 66:592–595
Ferrara M, Guerriero G, Cardi M, Esposito S (2013) Purification and biochemical characterisation of a glucose-6-phosphate dehydrogenase from the psychrophilic green alga *Koliella antarctica*. Extremophiles 17:53–62
Fritsen CH, Adams EE, McKay CP, Priscu JC (1988) Permanent ice covers of the McMurdo Dry Valley Lakes, Antarctica: liquid water content. In: Priscu JC (ed) Ecosystem Dynamics in a Polar Desert: The McMurdo Dry Valleys, Antarctica. American Geophysical Union, Washington, DC
Gray GR, Chauvin LP, Sarhan F, Huner N (1997) Cold acclimation and freezing tolerance (a complex interaction of light and temperature). Plant Physiol 114:467–474
Gray GR, Ivanov AG, Krol M, Williams JP, Kahn MU, Myscich EG, Huner NP (2005) Temperature and light modulate the trans-Δ3-hexadecenoic acid content of phosphatidylglycerol: light-harvesting complex II organization and non-photochemical quenching. Plant Cell Physiol 46:1272–1282
Griffith M, Yaish MW (2004) Antifreeze proteins in overwintering plants: a tale of two activities. Trends Plant Sci 9:399–405
Honjoh K-I, Mimura A, Kuroiwa E, Hagisako T, Suga K, Shimizu H et al (2003) Purification and characterization of two isoforms of glucose 6-phosphate dehydrogenase (G6PDH) from *Chlorella vulgaris* C-27. Biosci Biotechnol Biochem 67:1888–1896
Hughes MA, Dunn MA (1996) The molecular biology of plant acclimation to low temperature. J Exp Bot 47:291–305
Hüner NPA, Maxwell DP, Gray GR, Savitch LV, Laudenbach DE, Falk S (1995) Photosynthetic response to light and temperature: PSII excitation pressure and redox signalling. Physiol Plant 17:167–176
Hüner NPA, Öquist G, Sarhan F (1998) Energy balance and acclimation to light and cold. Trends Plant Sci 3:224–230
Hüner NPA, Öquist G, Melis A (2003) Photostasis in plants, green algae and cyanobacteria: the role of light harvesting antenna complexes. In: Green BR, Parson WW (eds) Advances in photosynthesis and respiration light harvesting antennas in photosynthesis. Kluwer Academic Publishers, Dordrecht, pp 401–421
Jaffri S (2011) Characterization of the photosynthetic apparatus of *Chlorella* BI sp., an Antarctic mat alga under varying trophic growth states. In: Microbiol. Miami University, Oxford
Janech MG, Krell A, Mock T, Kang JS, Raymond JA (2006) Ice-binding proteins from sea ice diatoms (Bacillariophyceae). J Phycol 42:410–416
Jentsch A, Kreyling J, Beierkuhnlein C (2007) A new generation of climate-change experiments: events, not trends. Front Ecol Environ 5:365–374
Joanisse D, Storey K (1994) Enzyme activity profiles in an overwintering population of freeze-tolerant larvae of the gall fly, *Eurosta solidaginis*. J Comp Physiol B 164:247–255
Jungblut AD, Vincent WF, Lovejoy C (2012) Eukaryotes in Arctic and Antarctic cyanobacterial mats. FEMS Microbiol Ecol 82:416–428
Kong W, Ream DC, Priscu JC, Morgan-Kiss RM (2012) Diversity and expression of RubisCO genes in a perennially ice-covered lake during the polar night transition. Appl Environ Microbiol 78:4358–4366
Krell A, Funck D, Plettner I, John U, Dieckmann G (2007) Regulation of proline metabolism under salt stress in the psychrophilic diatom *Fragilariopsis cylindrus* (Bacillariophyceae). J Phycol 43:753–762
Krembs C, Gradinger R, Spindler M (2000) Implications of brine channel geometry and surface area for the interaction of sympagic organisms in Arctic sea ice. J Exp Mar Biol Ecol 243:55–80
Lee JK, Park KS, Park S, Park H, Song YH, Kang S-H, Kim HJ (2010) An extracellular ice-binding glycoprotein from an Arctic psychrophilic yeast. Cryobiol 60:222–228
Liska AJ, Shevchenko A, Pick U, Katz A (2004) Enhanced photosynthesis and redox energy production contribute to salinity tolerance in *Dunaliella* as revealed by homology-based proteomics. Plant Physiol 136:2806–2817
Lizotte MP, Priscu JC (1992) Photosynthesis-irradiance relationships in phytoplankton from the physically stable water column of a perennially ice-covered lake (Lake Bonney, Antarctica). J Phycol 28:179–185
Lizotte MP, Sharp TR, Priscu JC (1996) Phytoplankton dynamics in the stratified water column of Lake Bonney, Antarctica. I. Biomass and productivity during the winter-spring transition. Polar Biol 16:155–162
Lopez-Garcia P, Rodriguez-Valera F, Pedros-Alio C, Moreira D (2001) Unexpected diversity of small eukaryotes in deep-sea Antarctic plankton. Lett Nat 409:603–607
Loppes R, Devos N, Willem S, Barthelemy P, Matagne RF (1996) Effect of temperature on two enzymes from a psychrophilic *Chloromonas* (Chlorophyta). J Phycol 32:276–278

Lovejoy C, Massana R, Pedros-Alio C (2006) Diversity and distribution of marine microbial eukaryotes in the Arctic Ocean and adjacent seas. Appl Environ Microbiol 72:3085–3095

Margesin R, Miteva V (2011) Diversity and ecology of psychrophilic microorganisms. Res Microbiol 162:346–361

Maxwell DP, Falk S, Trick CG, Huner NPA (1994) Growth at low temperature mimics high-light acclimation in *Chlorella vulgaris*. Plant Physiol 105:535–543

Maxwell DP, Falk S, Huner N (1995a) Photosystem II excitation pressure and development of resistance to photoinhibition (I. light-harvesting complex II abundance and zeaxanthin content in *Chlorella vulgaris*). Plant Physiol 107:687–694

Maxwell DP, Laudenbach DE, Huner N (1995b) Redox regulation of light-harvesting complex II and *cab* mRNA abundance in *Dunaliella salina*. Plant Physiol 109:787–795

Miskiewicz E, Ivanov AG, Williams JP, Khan MU, Falk S, Huner NP (2000) Photosynthetic acclimation of the filamentous cyanobacterium, *Plectonema boryanum* UTEX 485, to temperature and light. Plant Cell Physiol 41:767–775

Miskiewicz E, Ivanov AG, Huner NP (2002) Stoichiometry of the photosynthetic apparatus and phycobilisome structure of the cyanobacterium *Plectonema boryanum* UTEX 485 are regulated by both light and temperature. Plant Physiol 130:1414–1425

Morgan RM, Ivanov AG, Priscu JC, Maxwell DP, Hüner NPA (1998) Structure and composition of the photochemical apparatus of the Antarctic green alga, *Chlamydomonas subcaudata*. Photosynth Res 56:303–314

Morgan-Kiss RM, Dolhi JM (2011) Microorganisms and plants: a photosynthetic perspective. In: Tanino K, Storey K (eds) Nature at risk: temperature adaptation in a changing climate. CABI, Wallingford, pp 24–44

Morgan-Kiss R, Ivanov AG, Williams J, Mobashsher K, Hüner NP (2002a) Differential thermal effects on the energy distribution between photosystem II and photosystem I in thylakoid membranes of a psychrophilic and a mesophilic alga. Biochim Biophys Acta 1561:251–265

Morgan-Kiss RM, Ivanov AG, Hüner NPA (2002b) The Antarctic psychrophile, *Chlamydomonas subcaudata,* is deficient in state I-state II transitions. Planta 214:435–445

Morgan-Kiss RM, Ivanov AG, Pocock T, Król M, Gudynaite-Savitch L, Hüner NPA (2005) The Antarctic psychrophile, *Chlamydomonas raudensis* Ettl (UWO241) (CHLOROPHYCEAE, CHLOROPHYTA) exhibits a limited capacity to photoacclimate to red light. J Phycol 41:791–800

Morgan-Kiss RM, Priscu JP, Pocock T, Gudynaite-Savitch L, Hüner NPA (2006) Adaptation and acclimation of photosynthetic microorganisms to permanently cold environments. Microbiol Mol Biol Rev 70:222–252

Morgan-Kiss RM, Ivanov A, Modla S, Cyzmmek K, Huner NPA, Priscu JC, Hanson TE (2008) Identity and phylogeny of a new psychrophilic eukaryotic green alga, *Chlorella* sp. strain BI isolated from a transitory pond near Bratina Island, Antarctica. Extremophiles 12:701–711

Murata N, Takahashi S, Nishiyama Y, Allakhverdiev SI (2007) Photoinhibition of photosystem II under environmental stress. Biochim Biophys Acta 1767:414–421

Napolitano MJ, Shain DH (2004) Four kingdoms on glacier ice: convergent energetic processes boost energy levels as temperatures fall. Proc R Soc Lond B 271:273–276

Napolitano MJ, Shain DH (2005) Distinctions in adenylate metabolism among organisms inhabiting temperature extremes. Extremophiles 9:93–98

Neale PJ, Priscu JC (1995) The photosynthetic apparatus of phytoplankton from a perennially ice-covered Antarctic lake: acclimation to an extreme shade environment. Plant Cell Physiol 36:253–263

Parry BR, Shain DH (2011) Manipulations of AMP metabolic genes increase growth rate and cold tolerance in *Escherichia coli*: implications for psychrophilic evolution. Mol Biol Evol 28:2139–2145

Parry MA, Keys AJ, Madgwick PJ, Carmo-Silva AE, Andralojc PJ (2008) Rubisco regulation: a role for inhibitors. J Exp Bot 59:1569–1580

Pocock T (2004) Phylogeny, photoinhibition and recovery of a new Antarctic psychrophile *Chlamydomonas raudensis* (UWO 241). In: Biology. University of Western Ontario, London

Pocock T, Lachance M-A, Proschold T, Priscu JC, Kim S, Huner NPA (2004) Identification of a psychrophilic green alga from Lake Bonney Antarctica: *Chlamydomonas raudensis* ETTL. (UWO 241) (*Chlorophyceae*). J Phycol 40:1138–1148

Pocock T, Koziak A, Rosso D, Falk S, Huner HPA (2007) *Chlamydomonas raudensis* ettl. (UWO241) exhibits the capacity for rapid D1 repair in response to chronic photoinhibition at low temperature. J Phycol 43:924–936

Pocock T, Vetterli A, Falk S (2011) Evidence for phenotypic plasticity in the Antarctic extremophile *Chlamydomonas raudensis* Ettl. UWO 241. J Exp Bot 62:1169–1177

Possmayer M, Berardi G, Beall BFN, Trick CG, Hüner NPA, Maxwell DP (2011) Plasticity of the psychrophilic green alga *Chlamydomonas raudensis* (UWO 241) (Chlorophyta) to supra-optimal temperature stress. J Phycol 47:1098–1109

Priscu JC (1995) Phytoplankton nutrient deficiency in lakes of the McMurdo Dry Valleys, Antarctica. Freshw Biol 34:215–227

Priscu JC, Palmisano AC, Priscu LR, Sullivan CW (1989) Temperature dependence of inorganic nitrogen uptake and assimilation in Antarctic sea-ice microalgae. Polar Biol 9:442–446

Priscu JC, Fritsen CH, Adams EE, Giovannoni SJ, Paerl HW, McKay CP et al (1998) Perennial Antarctic lake ice: an oasis for life in a polar desert. Science 280:2095–2098

Raymond JA, Kim HJ (2012) Possible role of horizontal gene transfer in the colonization of sea ice by algae. PLoS ONE 7:e35968

Raymond JA, Morgan-Kiss R (2013) Separate origins of ice-binding proteins in Antarctic *Chlamydomonas* species. PLoS ONE 8:e59186

Raymond JA, Janech MG, Fritsen CH (2009) Novel ice-binding proteins from a psychrophilic Antarctic alga (Chlamydomonadaceae, Chlorophyceae). J Phycol 45:130–136

Rigano M, Vona V, Lobosco O, Carillo P, Rigano C (2006) Temperature dependence of nitrate reductase in the psychrophilic unicellular alga *Koliella antarctica* and the mesophilic alga *Chlorella sorokiniana*. Plant Cell Environ 29:1400–1409

Sage RF, Way DA, Kubien DS (2008) Rubisco, Rubisco activase, and global climate change. J Exp Bot 59:1581–1595

Siglioccolo A, Gerace R, Pascarella S (2010) "Cold spots" in protein cold adaptation: insights from normalized atomic displacement parameters (B′-factors). Biophys Chem 153:104–114

Szyszka B, Ivanov AG, Huner NPA (2007) Psychrophily induces differential energy partitioning, photosystem stoichiometry and polypeptide phosphorylation in *Chlamydomonas raudensis*. Biochim Biophys Acta 1767:789–800

Takizawa K, Takahashi S, Huner NPA, Minagawa J (2009) Salinity effects the photoacclimation of *Chlamydomonas raudensis* Ettl UWO241. Photosynth Res 99:195–203

Williamson CE, Saros JE, Schindler DW (2009) Climate change: sentinels of change. Science 323:887–888

Wilson KE, Ivanov AG, Oquist G, Grodzinski B, Sarhan F, Huner NPA (2006) Energy balance, organellar redox status and acclimation to environmental stress. Can J Bot 84:1355–1370

Wollman FA (2001) State transitions reveal the dynamics and flexibility of the photosynthetic apparatus. EMBO J 20:3623–3630