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Antarctic microbial mats: A modern analog for Archean lacustrine oxygen oases

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ABSTRACT

The evolution of oxygenic photosynthesis was the most important geochemical event in Earth history, causing the Great Oxidation Event (GOE) ~2.4 b.y. ago. However, evidence is mixed as to whether O_2 production occurred locally as much as 2.8 b.y. ago, creating O_2 oases, or initiated just prior to the GOE. The biogeochemical dynamics of possible O_2 oases have been poorly constrained due to the absence of modern analogs. However, cyanobacteria in microbial mats in a perennially anoxic region of Lake Fryxell, Antarctica, create a 1–2 mm O_2-containing layer in the upper mat during summer, providing the first known modern analog for formation of benthic O_2 oases. In Lake Fryxell, benthic cyanobacteria are present below the oxycline in the lake. Mat photosynthesis rates were slow due to low photon flux rate (1–2 µmol m^{-2} s^{-1}) under thick ice cover, but photosynthetic O_2 production was sufficient to sustain up to 50 µmol O_2 L^{-1}, sandwiched between anoxic overlying water and anoxic sediments. We hypothesize that Archean cyanobacteria could have similarly created O_2 oases in benthic mats prior to the GOE. Analogous mats may have been at least partly responsible for geological evidence of oxidative weathering prior to the GOE, and habitats such as Lake Fryxell provide natural laboratories where the impact of benthic O_2 oases on biogeochemical signatures can be investigated.

INTRODUCTION

The most significant geochemical change in Earth's history was caused by oxygenic photosynthesis in cyanobacteria (Farquhar et al., 2011; Kasting, 2013; Kump et al., 2013; Lyons et al., 2014). Prior to ~2.5 b.y. ago, most environments on Earth's surface were anoxic. However, between 2.45 and 2.32 b.y. ago, the Great Oxidation Event (GOE) led to substantial changes in atmospheric and oceanic chemistry, including the accumulation of free molecular oxygen in the atmosphere and shallow oceans, the loss of reduced ions such as Fe(II) and Mn(II) from shallow seawater, and more robust sulfur cycling through multiple oxidation states (Farquhar et al., 2011; Kasting, 2013; Kump et al., 2013; Lyons et al., 2014). Prior to 2.45 Ga, abundant evidence suggests the presence of either local or temporally short oxidative environments, possibly including O_2 (e.g., Kasting, 1992; Eigenbrode and Freeman, 2006; Anbar et al., 2007; Bosak et al., 2009; Duan et al., 2010; Kendall et al., 2010; Czaja et al., 2012). Evidence for local O_2 accumulation before the GOE can be reconciled with an anoxic atmosphere if "oxygen oases" emerged with sufficient oxygenic photosynthetic activity to produce local oxygenated environments, but insufficient O_2 production to cause a global change in oxidation state (e.g., Kasting, 1992; Eigenbrode and Freeman, 2006; Kendall et al., 2010; Olson et al., 2013; Reinhard et al., 2013; Lalonde and Konhauser, 2015).

Oxygen oases have been proposed for open oceans and coastal waters (Fischer, 1965; Kasting, 1992; Olson et al., 2013; Reinhard et al., 2013) and more recently for terrestrial environments (Lalonde and Konhauser, 2015). In the pelagic oceans, rapid mixing and gas exchange with the atmosphere would have made it difficult for more than a few micromoles of O_2 per liter to accumulate in Archean seawater (Olson et al., 2013; Reinhard et al., 2013). In contrast, benthic microbial mats have relatively low exchange rates, and solute fluxes are limited to diffusion through the boundary layer separating mats from the bulk water column. Thus, it is more likely that the first O_2 oases, and those with the highest O_2 concentrations, formed in benthic mats rather than in pelagic environments (e.g., Herman and Kump, 2005; Lalonde and Konhauser, 2015). Terrestrial O_2 oases are of particular interest for understanding geochemical indications of oxidative weathering prior to 2.5 Ga; sulfide minerals might have oxidized within Archean soil and freshwater cyanobacterial mats without O_2 accumulating in the atmosphere (Reinhard et al., 2013; Lalonde and Konhauser, 2015).

Evaluating the possible extent and weathering potential of Archean freshwater O_2 oases is difficult due to a paucity of modern analogs; none have been previously identified in anoxic environments. Although O_2 concentrations in cyanobacterial mats are commonly higher than in their environment during the day, their biogeochemical dynamics are likely different than in O_2 oases on a reducing Earth due to the prevalence of O_2 rather than reduced ions in the overlying water column. In contrast, benthic mats in Lake Fryxell, McMurdo Dry Valleys, Antarctica, accumulate O_2 during the summer below a poorly mixed, anoxic water column. Here, we describe the conditions under which this localized O_2 oasis forms and consider implications for Archean lacustrine O_2 oases.

LAKE FRYXELL

Lake Fryxell (75°35′S, 163°35′E; Fig. 1) is a perennially ice-covered lake in the McMurdo Dry Valleys, Antarctica. The lake occupies a closed basin; meltwater streams flow into the lake during summer, but water is lost only through ablation of ice from the surface and water evaporation from a summer "moat" of melt water around the margins of the lake (Lawrence and Hendy, 1985). Historical imbalances in water supply and loss resulted in evaporation and refilling events, creating density stratification of the lake due to increasing salinity with depth (Lyons et al., 2005). This stratification inhibits

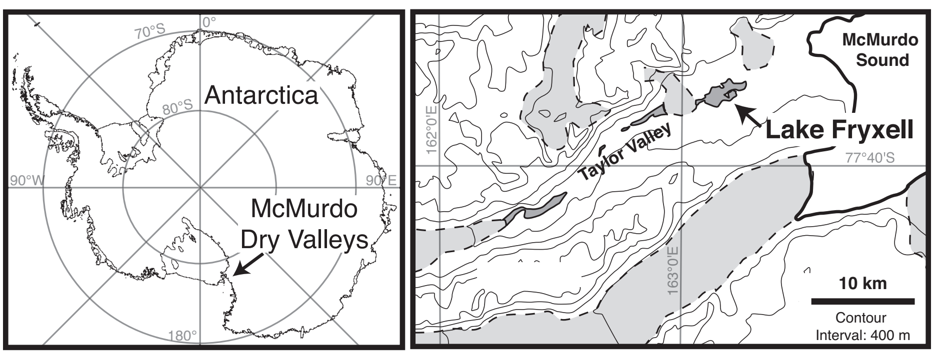

Figure 1. Location of Lake Fryxell in Taylor Valley, one of the McMurdo Dry Valleys, Antarctica.

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mixing, as does the permanent ice cover; solute transport below 5 m is dominated by diffusion. The perennial ice cover, which was 4–5 m thick in A.D. 2012, affects gas equilibration with the atmosphere. Dissolved gases enter the lake through stream inflow and are excluded from ice as water freezes, leading to gas accumulation in the upper water column over time. Atmospheric gases such as N_2, O_2, and noble gases are present at concentrations well above atmospheric saturation and are prevented from ebullition by hydrostatic pressure (Craig et al., 1992). Vertical gas transport is, however, limited to diffusion, and, while O_2 is present at high concentrations near the surface of the lake, microbial metabolic process produce an oxycline within the lake at 9–10 m depth (Vincent, 1981). The water column is euxinic immediately below the oxycline (Green et al., 1989).

Irradiance in Lake Fryxell is highly seasonal with about four months of complete winter darkness. During the summer, 0.5% to 3% of incident light penetrates the ice cover, and illumination declines with depth with an extinction coefficient of 0.5–0.6 m^{-1} (Howard-Williams et al., 1998). There is a sharp chlorophyll maximum in the planktonic community at ~8 m, just above the depth at which O_2 concentration and planktonic net photosynthesis fall to zero (e.g., Vincent, 1981; McKnight et al., 2000; Burnett et al., 2006; Vick-Majors et al., 2014). There are extensive benthic mat communities extending from the moat around the margin of the lake to ~11 m depth that are dominated by cyanobacteria, diatoms, and heterotrophic bacteria (e.g., Wharton et al., 1983; Taton et al., 2003).

METHODS

All measurements were obtained in November 2012. Observations of water column O_2 were made using an O_2 microelectrode (Unisense, www.unisense.com) with an outside tip diameter of 50 µm and a 90% response time of <1 s, connected to a Unisense UW-M underwater logging picoammeter. This was mounted alongside a Brancker Instruments Concerto conductivity-temperature depth (CTD) profiler, so that the tip of the O_2 electrode and the sensing element of the CTD were aligned in similar horizontal planes during deployment. These instruments were deployed by a diver along a fixed transit line at regular intervals to obtain dissolved oxygen, temperature, conductivity, and water depth 50 mm above the mat surface.

Incident irradiance to the lake surface was measured at 15 min intervals at a lakeside weather station (Long Term Ecological Research, www.mcmlter.org). Downwelling irradiance at the lake floor was determined by a diver carrying a LiCor Li192 photosynthetically available radiation (PAR) sensor along the transect line and recording irradiance at depths from 8.9 m to 11 m. Simultaneous measurements on the lake surface allowed the percent of incident irradiance to be calculated for each depth.

The dominant cyanobacterial and diatom morphotypes in different microbial mat sections were identified on site using an Olympus light microscope (BX51) at 400×–1000× magnification. Cyanobacteria were assigned to genera based on Komárek and Anagnostidis (1989, 2000, 2005; Table DR1 in the GSA Data Repository[1]) and diatoms identified as completely as possible based on Spaulding et al. (2008).

Profiles of O_2 in mats were measured by divers using the same Clark-type underwater O_2 microelectrode and picoammeter described above. The electrode was mounted in a manually operated micromanipulator on an aluminum post driven into the sediment (Vopel and Hawes, 2006). After a 24 h stabilization period, the diver returned to the stake and used the micromanipulator to move the electrode normal to the mat surface from a position above the boundary layer to a depth of up to 17 mm into the mat in 1.0 mm increments. The position of the mat surface was estimated by the diver and confirmed by a break in the dissolved O_2 versus depth profile. The diffusive flux of O_2 from the microbial mat into the overlying bottom water and the underlying sediments was calculated from the measured steady-state O_2 gradients according to methods described by Vopel and Hawes (2006) and Hawes et al. (2014).

RESULTS

Conductivity, Temperature, Oxygen, and Irradiance

Conductivity increased steadily between 6 m and 11 m depth, from <1 to 5 mS cm^{-1}, while water temperature ranged from slightly above 2.5 °C to slightly less than 2.75 °C, demonstrating that increasing salt content caused density stabilization of the water column. The water column was supersaturated with O_2 to a depth of 9.1 m (1 atm saturation at ambient temperature is ~450 µmol L^{-1}), transitioning to complete anoxia below ~9.8 m (Fig. 2). We refer to the depth at which O_2 is unmeasurable as the "O_2 limit".

During November 2012, the average daily PAR flux incident to the Lake Fryxell weather station ranged from 277 to 783 (average = 600) µmol photons m^{-2} s^{-1}. Average daily maxima and minima were 1186 and 96 µmol photons m^{-2} s^{-1}, respectively. The percent surface incident PAR

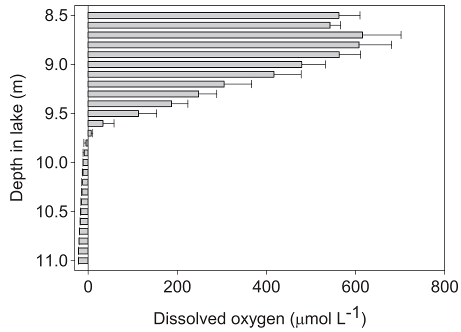

Figure 2. Depth profile of dissolved O_2 in water column of Lake Fryxell, Antarctica. Error bars represent mean and standard deviation of all measurements within a 10 cm depth bin.

reaching the lake floor fell from 0.74% at 8.9 m to 0.27% at the O_2 limit (9.8 m), 0.20% at 10.4 m, and 0.12% at 11.0 m. Combined surface incident and underwater measurements suggest that at the O_2 limit, monthly average PAR was ~1.6 µmol photons m^{-2} s^{-1}, which is above the minimum required light flux of ~1 µmol photons m^{-2} s^{-1} for oxygenic photosynthesis estimated for nearby Lake Hoare (Hawes et al., 2001, 2014; Vopel and Hawes, 2006), while average maximum daily values exceeded 3 µmol photons m^{-2} s^{-1}. The daily average 1 µmol photons m^{-2} s^{-1} threshold was reached at 10.4 m depth, well into the anoxic zone of Lake Fryxell.

Mat Composition

Laminated cohesive microbial mats coated the sediment-water interface to a water depth of more than 10.2 m. Deeper surfaces were still mat covered, but the mat surface was not cohesive. Based on field microscopy, the bulk of the mats at 9.0 m and 9.8 m consisted of cyanobacteria of the *Leptolynbya*, *Pseudanabaena,* and *Phormidium* morphotypes (Table DR1). Mats under O_2 supersaturated water at 9.0 m had pinnacles and were dominated by *Leptolynbya* morphotypes (<2 µm filament width), whereas the 9.8 m mats at the O_2 limit were flat and dominated by a conspicuous green film of a *Phormidium* morphotype with filament diameter of >6 µm (Fig. DR1 in the Data Repository; Table DR1), with the diatom *Diadesmis contenta* also present in some samples.

Dissolved Oxygen Microprofiles and Oxygen Dynamics

Microelectrode O_2 profiles of benthic mats in the oxic part of the lake were similar to those previously seen in the photic zones of similar Antarctic lakes (Fig. 3A; Table DR2; e.g., Hawes et al., 2014). They show an increase in O_2 through the diffusive boundary layer separating the bulk water from the mat, a substantial O_2 subsurface peak of >800 µmol O_2 L^{-1} at ~2 mm below the surface of the mat, then a gradual decline in O_2 with depth, and remaining oxic to >17 mm. In contrast, profiles at 9.8 m showed

[1]GSA Data Repository item 2015298, Table DR1 (macroscopic characteristics of cyanobacteria morphotypes); Table DR2 (microelectrode profiles of dissolved O_2 in microbial mats from 9.0 m depth); Table DR3 (microelectrode profiles of dissolved O_2 in microbial mats from 9.8 m depth); and Figure DR1 (image of *Phormidium* from 9.8 m depth), is available online at www.geosociety.org/pubs/ft2015.htm, or on request from editing@geosociety.org or Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301, USA.

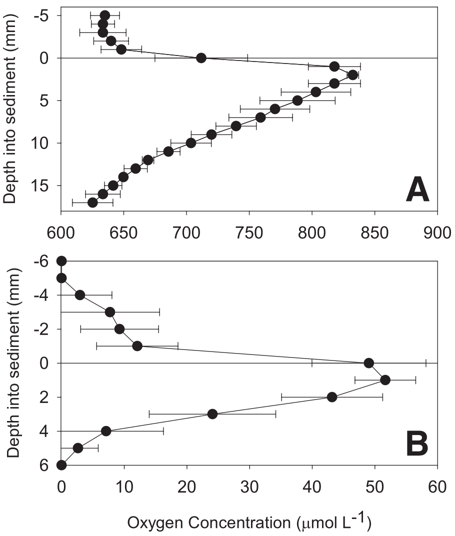

Figure 3. Profiles of dissolved oxygen through mat-water interfaces in Lake Fryxell, Antarctica. A: Mean and range of two replicate profiles through a mat in oxic part of water column (9.0 m depth). B: Mean and one standard deviation of five replicate profiles in anoxic part of water column (9.8 m depth).

no O_2 in the bulk water column, an increase in O_2 through the few millimeters of water above the mat, and an O_2 peak at ~1 mm depth below the mat surface of 50 μmol O_2 L^{-1} (10% atmospheric saturation), becoming anoxic again at a mat depth of ~6 mm (Fig. 3B; Table DR3).

The spatial distribution of O_2 within the mats allows calculation of net fluxes associated with the O_2 oasis. Diffusion of O_2 away from the O_2 maxima in microbial mats is an indicator of the net rate of photosynthetic O_2 production (Berg et al., 1998; Hawes et al., 2014), and fluxes of O_2 can be calculated using the slopes of O_2 gradients and appropriate diffusion constants. Using a diffusion coefficient (D_o) at 0 °C of 9.13×10^{-6} cm^2 s^{-1} (Broecker and Peng, 1974; modified for temperature according to Li and Gregory, 1974), the flux of O_2 from the 9.8 m mat to the water column was ~0.04 μmol O_2 m^{-2} s^{-1}. A similar calculation of downward flux suggests that 0.013 μmol O_2 m^{-2} s^{-1} was diffusing downward into the mat (calculated using a 20% reduction in D_o within the mat matrix; Vopel and Hawes, 2006). The total export of O_2 from the photic zone was 0.05 μmol O_2 m^{-2} s^{-1}.

This result is consistent with the expected rate of photosynthesis at the time of O_2 profiling, when irradiance was ~2.3 μmol photons m^{-2} s^{-1}. For nearby Lake Hoare, Hawes et al. (2014) presented evidence that microbial mats absorb 50% of incident irradiance into photosynthetic systems, and that the quantum yield of photosynthesis of shade-adapted mats is 0.06 mol O_2 mol^{-1} photons. If the Lake Fryxell mats behave similarly, photosynthetic production by mats at 9.8 m would be 0.07 μmol O_2 m^{-2} s^{-1}, slightly in excess of the calculated net flux out of the mat based on the diffusion profile. The excess of 0.02 μmol O_2 m^{-2} s^{-1} could have been consumed by respiration and sulfide oxidation within the mat.

DYNAMICS OF OXYGEN OASES

The two key factors required for development of mat O_2 oases are (1) O_2 production that exceeds local consumption, and (2) relatively slow O_2 transport out of the mat. As soon as O_2 production exceeds local consumption, O_2 transiently accumulates. When the export of O_2 to the surrounding environment is sufficiently slow, a stable O_2 oasis develops. One does develop at 9.8 m in Lake Fryxell even at very low photosynthetic rates. In addition, the net annual export of O_2 from mats at 9.8 m and deeper in Lake Fryxell is not sufficient to even seasonally oxidize the local water column, even though photosynthetic O_2 production is sufficient to create the O_2 oasis. The size and temporal persistence of the oasis depends on the spatial distribution and rates of O_2 production and consumption. These rates will change as irradiance fluctuates daily and seasonally. At higher irradiance, a larger O_2 peak and enhanced export to overlying waters and underlying sediments are likely, potentially facilitating oxidation of reduced species such as HS^-, Fe(II), and Mn(II) at the boundary between the oasis and anoxic waters. Conversely, at lower irradiance, the mats will contain a smaller O_2 peak, export less O_2, and support less oxidation of reduced species. During the winter when there is no light, the O_2 oasis is predicted to disappear entirely.

Implications for Archean Oxygen Oases

We propose that variations in the balance of net O_2 production and flux of reduced species in Lake Fryxell provide a modern analog for development of O_2 oases prior to the GOE. Archean terrestrial aquatic environments as old as 2.7 b.y. commonly contained benthic mats (e.g., Buck, 1980; Buick, 1992; Rye and Holland, 2000). Once these mats contained cyanobacteria, they likely developed O_2 oases even at very low net photosynthetic rates, such as the 0.05 μmol O_2 m^{-2} s^{-1} observed at 9.8 m in Lake Fryxell. At such low fluxes, all of the O_2 exported from the mat would have been consumed by oxidation of reduced species in the surrounding environment (e.g., Lalonde and Konhauser, 2015). Thus, O_2 oases with tens of micromoles O_2 per liter could have persisted for a long time without oxidizing large habitats. The size, productivity, and frequency of O_2 oases would have gradually increased with the ecological expansion of cyanobacteria and the evolution of more robust oxygenic photosynthesis. Eventually, O_2 oases may have expanded to the open oceans, although O_2 concentrations were likely an order of magnitude lower (Olson et al., 2013; Reinhard et al., 2013). Gradual declines in the concentrations of reduced species in seawater would have accompanied the spread of oxygenic photosynthesis and decreased the flux of reduced gases to the atmosphere from the oceans. With this expansion, Earth was primed for the GOE.

An accumulation of O_2 in benthic mats can explain some of the geochemical signatures of early weathering. Specifically, the ~50 μmol O_2 L^{-1} observed in Lake Fryxell O_2 oases is sufficiently high to allow some pyrite oxidation at reasonable sediment fluxes (Reinhard et al., 2013; Lalonde and Konhauser, 2015). Evidence for oxidative pyrite weathering on land extends back as far as 2.8 b.y. based on models of sulfur fluxes to the oceans (Stüeken et al., 2012) as well as intervals of enhanced molybdenum influx prior to the GOE (Anbar et al., 2007; Duan et al., 2010; Czaja et al., 2012). The "whiffs of oxygen" proposed for these intervals (e.g., Anbar et al., 2007) may record enhanced terrestrial O_2 oasis development rather than changes in the oxidation state of the atmosphere. Using Lake Fryxell O_2 oases as a model, the search for evidence for Archean O_2 can be more precisely targeted at environments where O_2 oases may have had a substantial impact on biogeochemical cycles as well as those environments where the first, small, transient oases may have formed.

CONCLUSIONS

The presence of transient O_2 oases in Lake Fryxell benthic mats demonstrates that cyanobacteria are capable of producing O_2 oases with sustained concentrations of ~50 μmol O_2 L^{-1} s^{-1} without oxidizing their environment. These oases provide a model for Archean O_2 oases, which may have formed prior to the oxidation of Earth's oceans and atmosphere. Similar benthic O_2 oases could have provided environments for oxidative weathering of continental minerals such as pyrite, creating the geochemical signatures indicating "whiffs of oxygen" prior to the GOE.

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