

**Extant mat world analog microbes synchronize migration to a diurnal tempo**

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**Key Points:**

- Microbes in modern-day hypoxic, sulfidic mat ecosystems indulge in active diurnal vertical migration (DVM).
- Alternating waves of photosynthetic and chemosynthetic microbes surface at day and night, respectively – optimizing mat ecosystem function.
- DVM in the Precambrian mat world may have played a key role in oxygenation of early Earth – setting the stage for the modern-day biosphere.

**Abstract**

Animal migrations mark the largest daily movement of biomass on Earth today, but who performed the first diurnal migration? Extant benthic microbial mats inhabiting Lake Huron's low-oxygen, high-sulfur submerged sinkholes that resemble life on early Earth, may offer some answers. Herein, mats are dominated by motile filaments of purple-pigmented cyanobacteria capable of oxygenic and anoxygenic photosynthesis, and pigment-free chemosynthetic sulfur-oxidizing bacteria. We captured time-lapse images of diurnal vertical migration between phototactic cyanobacteria and chemotactic sulfur-oxidizing bacteria – dramatically turning the mat surface purple at dawn and white at dusk. Alternating waves of vertically migrating photosynthetic and chemosynthetic filaments rapidly tracked diurnally fluctuating light; observations corroborated with intact mats under simulated day-night conditions. Both types of filaments increased in surface coverage non-linearly, albeit at different rates. During their respective surface takeovers, maximum nightly rate of movement for white chemosynthetic filaments occurred an hour before that of purple cyanobacteria during the day. However, though slow to start at dawn, the cyanobacteria's maximum rate of movement was double that of the chemosynthetic bacteria, leading to greater total coverage over the span of the day. Such synchronized diurnal “tango” might have been the largest daily mass movement of life during the long Archean and Proterozoic eras, when the biosphere was mostly benthic, and played a critical role in optimizing photosynthesis, chemosynthesis, carbon burial, and oxygenation. Further studies of extant microbial “mat worlds” will add to the expanding knowledge of Earth's biodiversity and physiologies, and may aid our ongoing search for life in extraterrestrial waters.

**Plain Language Summary**

Animal migrations mark the largest daily movement of biomass on Earth today. Not to be discounted are the daily movements of microbes that occur in synchrony with diurnally (daily)

changing environmental stimuli such as light and chemicals. Microbial mats resembling those that once prevailed on early Earth inhabit the bottom of Lake Huron's low-oxygen, high-sulfur submerged sinkholes. Mats here are dominated by motile filaments of purple-pigmented photosynthetic cyanobacteria and pigment-free (white) chemosynthetic sulfur-oxidizing bacteria. These mats may help answer the question of who performed the first diurnal vertical migration (DVM) on the Precambrian seafloor billions of years ago. We captured time-lapse images of DVM between light-attracted (purple) cyanobacteria and chemical-attracted (white) sulfur-oxidizing bacteria – dramatically turning the mat purple at dawn and white at dusk; observations corroborated with intact mats under simulated day-night conditions in the lab. Such synchronized diurnal “tango”, might have been the largest daily mass movement of life during Archean and Proterozoic eras. Back then, when the biosphere was mostly a “mat world”, DVM may have been critical for optimizing photosynthesis and oxygenation. The biodiversity and physiologies in modern-day microbial mat ecosystems may also serve as useful models in our ongoing search for life in extraterrestrial waters.

## **1 Introduction**

### **1.1 Motility and migration of microbial life**

Diurnal vertical migration (DVM) of zooplankton in lakes and the oceans constitutes the largest daily mass movement of life on the planet today (Behrenfeld et al. 2019). Similarly, the seasonal migration of mammals, fishes, birds and insects accounts for the largest annual mass movement of biomass on Earth (Bauer & Hoyle, 2014). But what was the largest movement of life in the early biosphere when all of life was microbial and microbes dominated a benthic “mat world” on the Precambrian seafloor? Fortunately, even today, cyanobacteria similar to life in the shallow, euxinic seas of the early biosphere thrive in several globally distributed extreme

environments (Jørgensen et al. 1986; Stal 1995; Biddanda et al. 2009; Bühring et al. 2011; Anderson et al. 2011; Gischler et al. 2010; Klatt et al. 2016a). These extant mat ecosystems resemble the Precambrian mat world when the biosphere was mostly microbial and benthic (Allwood et al., 2006; Falkowski et al. 2008; Biddanda et al. 2012; Dick et al. 2018).

Microorganisms like cyanobacteria have evolved numerous structural and physiological adaptations, which help them survive in extreme environments (Falkowski et al. 2008). For example, microbes within a mat operate in a 3-dimensional world, using motility to adjust to changing environmental gradients such as oxygen and sulfide on a diel basis (Ramsing et al. 2000; Tamulonis et al. 2011; Kruschel & Castenholz, 1998; Nold et al. 2010; Biddanda et al. 2015). In earlier laboratory studies with microbial mats, we observed rapid phototactic motility of cyanobacterial filaments (both horizontal and vertical) at rates of 50-200  $\mu\text{m minute}^{-1}$  and have suggested - without direct evidence for DVM - that such coordinated motility may serve to optimize mat formation, photosynthesis and carbon burial (Nold et al. 2013; Biddanda et al. 2015; Snider et al. 2017).

## 1.2 Metabolic processes and environmental characteristics of mat ecosystems

Several studies suggest that not only cyanobacteria but also motile sulfur-oxidizing bacteria (SOB) take advantage of varying  $\text{H}_2\text{S}$  and  $\text{O}_2$  levels within the upper  $\mu\text{m-mm}$  of the mat-sediment complex (Jørgensen et al. 1986; Castenholz et al. 1991; Nold et al 2010, Kinsman-Costello et al 2017, Klatt et al 2016 a). Indeed, if production processes such as anoxygenic photosynthesis (AP), oxygenic photosynthesis (OP), and chemosynthesis (CS), were to occur at the mat-water interface where light, sulfur and oxygen variably interact, it would require active diurnal migration of photosynthetic and CS filaments in response to diurnally fluctuating redox (Klatt et al. 2016b; Dick et al. 2018). Most cyanobacteria are highly sensitive to sulfide, yet some

are tolerant and others can “use” sulfide as the preferred electron donor over water, switching from OP to AP (Jørgensen et al. 1986; Buhring et al 2011; Klatt et al. 2016b; Dick et al. 2018). Indeed, cyanobacteria and SOB that move in synchrony with fluctuating redox gradients may have competitive advantages over sessile lifestyles (Richardson & Castenholz, 1987a; Mitchell & Kogure 2006).

Sulfidic environments inhabited by cyanobacteria, like those that were present long ago in Earth’s history, are found in the coastal waters of NW Lake Huron – a region underlain by karstic limestone wherein groundwater seeps through Paleozoic marine evaporites (Supplemental Figs 1 and 2 Biddanda et al., 2009, 2012). Here, dissolution of Silurian-Devonian bedrock has produced karstic sinkhole formations, through which anoxic sulfurous groundwater emerges onto the lake floor fueling the growth of microbial mats. The venting groundwater here is characterized by low oxygen (0-2 mg l<sup>-1</sup>) and high sulfate (>1000 mg l<sup>-1</sup>) compared to overlying Lake Huron water (Ruberg et al., 2008).

### 1.3 Microbial mats of Lake Huron’s submerged sinkholes

Microbial mats composed primarily of communities of photosynthetic cyanobacteria and chemosynthetic SOB, cover the floor and walls of Lake Huron’s shallow submerged sinkholes (Biddanda et al. 2009; Voorhies et al. 2012). Mats are composed of a consortium of purple-pigmented cyanobacteria of *Planktothrix* (formerly *Oscillatoria*) and *Phormidium* genera, which are capable of OP and AP, and whitish filaments of SOB (*Beggiatoa*) (Biddanda et al., 2012; Voorhies et al., 2012; Kinsman-Costello et al. 2017). In the organic matter-rich sediments beneath these mats, thrive successive layers of sulfate-reducing bacteria (SRB) and methanogenic bacteria that, together with the producer communities at the top, establish a functioning redox tower (Nold et al. 2010; Biddanda et al. 2012). These mat ecosystems are

105 closely related to those inhabiting the bottom of hot springs and Antarctic lakes (Castenholz et al.  
106 1991; Andersen et al. 2011), and are analogous to the most ancient forms of life on Earth  
107 (Allwood et al., 2006; Falkowski et al. 2008), making them model systems for exploring the  
108 biosphere's evolution, biodiversity and physiology (Voorhies et al., 2012; Biddanda et al. 2012;  
109 Dick et al. 2018).

110 In studying Lake Huron's submerged sinkholes, we have made several in-field and  
111 onboard/laboratory observations of freshly collected purple mats that subsequently turned white  
112 within hours when stored in the dark. Similarly, some day-long dive/ROV observations in-field  
113 revealed tell-tale evidence of the mat surface turning increasingly purple as the day progressed.  
114 Both earlier experimental and field observations suggested large-scale shifts in mat color  
115 between day and night. The development of a field-deployable underwater camera system  
116 capable of long-term time-lapse photography provided the opportunity to perform field studies to  
117 test the notion of a day-night shift. Here, we chronicle the dramatic shift in mat surface color  
118 from purple during the day to white at night in-field and ascribe it to rapid upward and  
119 downward phototactic and chemotactic motility of cyanobacteria and SOB chasing sunlight and  
120 sulfur, respectively. We corroborated field observations with a laboratory study of intact mats  
121 under simulated day-night conditions, and consider the possible relevance of microbial DVM to  
122 the carbon and oxygen cycle during biosphere's early and prolonged "mat world" stage in the  
123 Precambrian seas.

## 124 **2 Materials and Methods**

### 125 **2.1 Study site**

126 Study location was the Middle Island Sinkhole (MIS), 17.3 km northeast of Alpena,  
127 Michigan in Thunder Bay National Marine Sanctuary, Lake Huron (Supplemental Figures 1 and

2). MIS is a result of karst geology containing marine evaporites, venting oxygen-poor, sulfur-rich groundwater (Biddanda et al. 2012). MIS is 23m deep, where only 5-10% of ambient surface light reaches the bottom topped by a mat of microbes.

## 2.2 Groundwater water quality

Main source of groundwater vented into the sinkhole comes out of the “Alcove” at 15m deep, and averages 9 C°, 7.1 pH, 2300  $\mu\text{S}/\text{cm}$ , 0 mg/L dissolved Oxygen (DO), 1250 mg/L Sulfate ( $\text{SO}_4^{2-}$ ). The groundwater then flows over a ledge out into the main “Arena”, the study area. During this study, the groundwater averaged 11 C° Temperature, 2000  $\mu\text{S}/\text{cm}$ , 1.7 mg/L DO, and 1250 mg/L  $\text{SO}_4^{2-}$ . Here, sediment pore water quickly goes anoxic, with the near-surface of the sediment being rich in  $\text{H}_2\text{S}$  (Biddanda et al. 2012).

### 2.3.1 Time-lapse imagery

Time-lapse imagery was captured using an underwater camera system. Images were captured by a GoPro Hero 4 camera with a CamDo Blink attachment to enable time-lapse image capture. The GoPro camera and Blink board were housed within a GP4c Underwater Housing (Marine Imaging Technologies). Night-time imagery was enabled by 4 LED lights (Blue Robotics) attached and synced to the camera system so that the lights only turned on for 5 seconds before and after the image was taken – minimizing exposure of mats to light during night-time when they would not normally experience it. Camera, Blink board, and light integration was performed by engineers at Marine Imaging Technologies ([www.marineimagingtechnologies.com](http://www.marineimagingtechnologies.com)).

The camera housing was attached to a PVC mount which angled the camera slightly downward. This camera system was deployed to the bottom of the sinkhole by NOAA divers from the Thunder Bay National Marine Sanctuary (Figure 1). Images were taken every 30

minutes from July 10, 2018 at 12:00 noon until July 12, 2018 at 10:00 A.M. EST. Concurrent PAR measurements were gathered by a HOBO Pendant Light/Temperature logger.



Figure 1. Time-lapse Imaging the sinkhole mat world: Diver image of the deployment position of the time-lapse submersible camera system mounted on top of a PVC frame on microbial mat at the bottom of Middle Island Sinkhole, Lake Huron at ~23 m depth. This diver image was taken around mid-day. Photo credit: Phil Hartmeyer, NOAA Thunder Bay National Marine Sanctuary.

### 2.3.2 Time-lapse image analyses

Time-lapse images were analyzed to estimate the percent coverage by purple photosynthetic cyanobacteria and white SOB. Images were overlaid by a 10 x 10 grid enclosing an area 1m x 1m (Figure 2). For each image, every individual square (100 total) was estimated to be covered mostly by purple cyanobacteria or white SOB by the binary method. All 100 squares



were totaled to calculate percent coverage of the mat surface by purple cyanobacteria or white SOB at each 30-minute time point in the time-lapse imagery spread over day-night cycle.

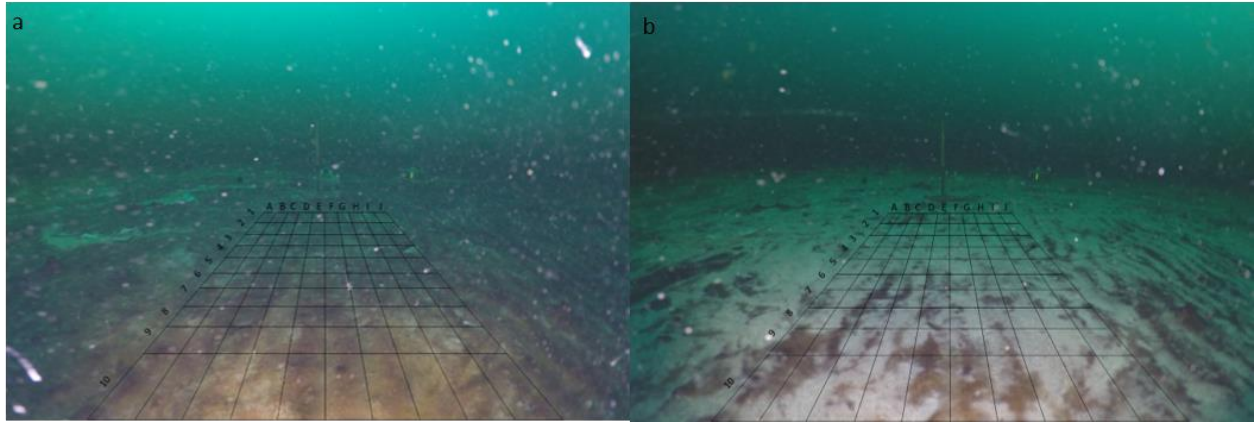


Figure 2. Quantifying the diurnal color change: Example 2018 dusk (a) and dawn (b) images overlain by 1m x 1m counting grid for quantification of the extent of surface color.

The increase on surface coverage by both purple cyanobacteria and white SOB was non-linear, slowly increasing at first, then quickly increasing, followed by slowly increasing or holding steady. This indicated that a non-linear growth model of percent coverage change was most appropriate to model this DVM phenomena. Non-linear growth models (equation 1) were applied to analyze the difference in coverage progression during the day/night for purple cyanobacteria and white SOB using R as described in Fox and Weisberg 2019.

$$(1) \text{ Purple or White Coverage} = \frac{\theta_1}{1 + e^{-(\theta_2 + \theta_3 * \text{Timepoint})}}$$

A single white SOB model was made from averaging the coverage progression of two nights, while the purple cyanobacteria model was only based on the one full day of coverage progression observed.  $\theta_1$  parameters for the white and purple models indicate an asymptote of maximum coverage potential.  $\theta_2$  and  $\theta_3$  adjust the model curve slope, making it more exponential in the beginning, or more logarithmic at the end, respectively. 95% confidence

intervals were calculated for the three  $\theta$  equation parameters (Table S1). Given the limited sample size, model curves were not evaluated intensely for statistical differences.

#### 2.4.1 In-lab validation

Using clear PVC tubing and rubber stoppers, divers, hand-collected 7-cm diameter, 20-cm long cores from MIS in the same area the camera system was taking time-lapse imagery. Cores contained intact 1-2mm thick discs of mat along with undisturbed sediment below them. They were sealed with tape on board the research vessel and kept vertically stable on ice in a dark cooler until return to the lab at Annis Water Resources Institute in Muskegon, Michigan. Cores were put into an incubator, kept at 10°C, on a 16-hour light/8-hour dark cycle (as they would experience in July). Cores were allowed 4 light/dark cycles to adjust to the new diurnal period before we began to take photos, and the groundwater over each core was gently replaced with fresh groundwater every day. Pictures were taken 30 minutes before each light and dark cycle would end.

#### 2.4.2 Repeat field observations

In June 10-11, 2019, we repeated the time-lapse study with images taken every 15 minutes over a 24-hour day-night cycle to confirm the 2018 results (Figure S3).

### **3 Results, or a descriptive heading about the results**

#### 3.1 Mat tricks: Chameleon-like diel color changes in the mat world

Time-lapse photography of the bottom of Lake Huron's Middle Island Sinkhole revealed dramatic footage of mat surface changes throughout the diel cycle in July 2018 (Figure 3). During daylight, purple cyanobacteria were the dominant surface dwellers, covering nearly the entire surface area of the mat ecosystem. During night, white SOB emerged upwards, covering

much of the mat surface. Soon after dawn, when sunlight became available, cyanobacteria rapidly covered the mat surface attaining 100% coverage 5-6 hours. Similarly, following nightfall, SOB covered the mat, attaining 90-93% coverage within 8-11 hours. These dramatic changes in mat surface color between day and night were tracked via time-lapse, spanning 2 days spread over 2 sunsets and 2 sunrises (93 images at 30 min intervals; Supplemental Movie S1). A shorter (24 hrs) but higher frequency time-lapse (15 min image intervals) deployment in June 2019 confirmed these field observations: during the day cyanobacteria surfaced, and at night SOB did the same (Supplemental Figure 3).

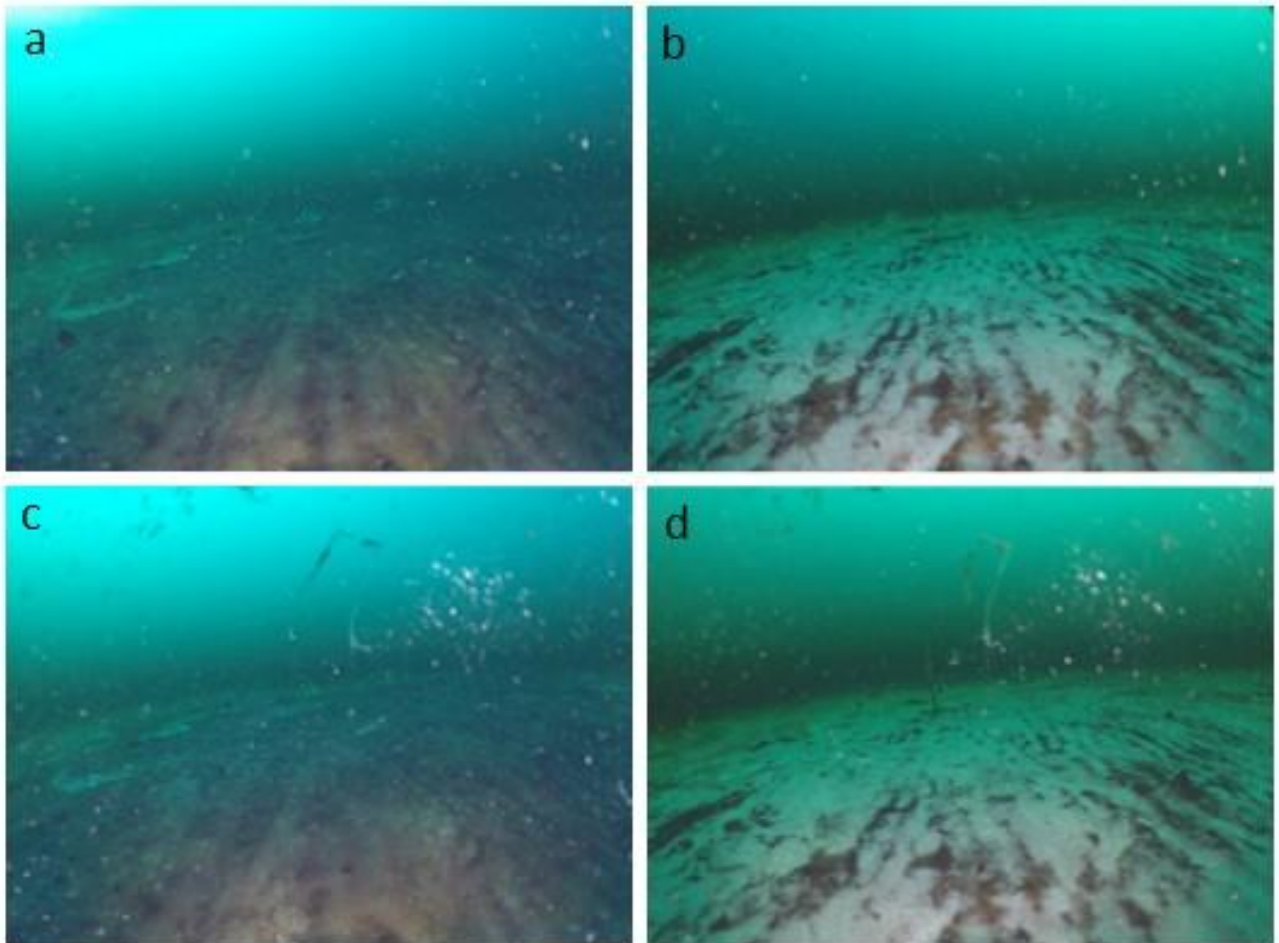


Figure 3. Chameleon-like day and night shifts: Images at dusk (20:00 hrs) and dawn (7:00 hrs) of microbial mats on the sinkhole bottom during July 10 to 12, 2018. Day 1 dusk (a), day 2 dawn

(b), day 2 dusk (c), and day 3 dawn (d). Note: Planktonic debris has settled on the top of the camera dome on days 2 and 3.

### 3.2.1 Takes two to tango: Microbes involved in the day-night shifts of DVM

Macroscopically, mats composed primarily of cyanobacteria and SOB at the surface, appear purple and white, respectively (Figure 4a; Voorhies et al. 2012; Biddanda et al. 2015). However, mat coloration was never evenly distributed – with surface patches of white SOB filaments visible no matter the time of the day. This suggests the redox environment below the mats may be quite patchy. Indeed, random patches of mat are often lifted into finger like projections 10-30 cm high – buoyed up by gasses such as  $H_2S$  and  $CH_4$  produced by SRB and methanogens in the sediments below, as well as by cyanobacteria themselves (Teske et al. 1998; Nold et al. 2013; Bizic et al. 2020).

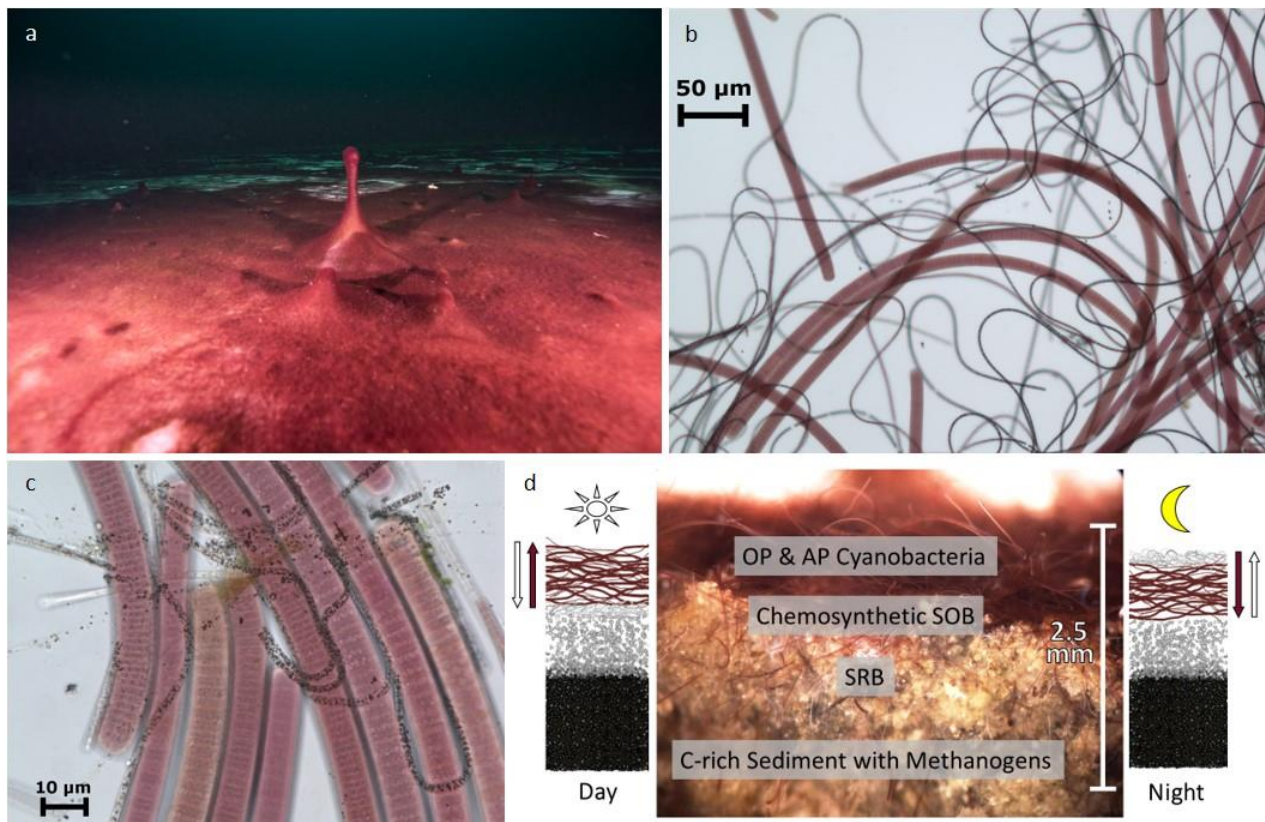


Figure 4. DVM microbes in the mat world: Underwater diver photo during daytime showing the predominantly cyanobacteria-dominated purple coloration at the surface along with a minority of white patches where sulfur oxidizing bacteria (SOB) continue to prevail (a; Photo credit: Phil Hartmeyer, NOAA Thunder Bay National Marine Sanctuary). Finger-like mat projections (10-30cm tall) are buoyed by excess  $H_2S$  and  $CH_4$  gasses trapped beneath them. Bright-field microscopy of microbes in the upper mms of mat reveals the presence of purple cyanobacteria and white/dark chemosynthetic bacteria (b, low magnification image; c, high magnification image). A cross-sectional stereo microscopic image of mat with intact sediment below reveals successive layers of motile purple cyanobacterial filaments followed by filamentous white SOBs, a zone of semi-permanent white carbonate crystals, and a larger zone of dark carbon-rich sediment at the bottom colonized by sulfur reducing bacteria and methanogens<sup>9,10,23</sup> (d). Schematic diagrams beside the mat cross section depict scenarios of day and night-time status at mat surface following vertical migration of alternating waves of photosynthetic and chemosynthetic filaments. (Stereo microscope image credit: S. Kendall and B. Biddanda, GVSU).

Under the light microscope, the predominant composition of the mat community consisted of cyanobacterial filaments (*Planktothrix* and *Phormidium* genera), and colorless SOB filaments (*Beggiatoa* genus) with dark inclusions inside – presumably reduced sulfur granules stored within their cells (Figure 4b, 4c). A low-magnification image shows large purple-pigmented cyanobacterial filaments and much smaller SOB filaments that appear as colorless, whitish or dark due to intracellular sulfur granules (Figure 4b). A high magnification image shows details of cyanobacterial and SOB filaments (Figure 4d). Both these 2 functional guilds of



microbes (photosynthetic cyanobacteria and chemosynthetic SOB) play an active role in DVM (Figure 4d).

### 3.2.2. Rabbits and tortoises: Non-linear movements by microbes during day and night.

Estimates of predominant mat surface color within a 1m x 1m grid overlay in successive time-lapse images through day-night cycles indicated remarkable changes in coloration from day to night (Supplemental Movie S1). By this measure, purple cyanobacteria achieved 100% coverage during days 1 and 2, while white SOB achieved 90 and 93% coverage during nights 1 and 2 respectively (Figure 5, Table 1). During night, only the darkest purple mat sections remained covered by cyanobacteria. These specific areas consistently remained lightly purple during both nights. Such patchiness could be driven by variable ground water flow above the mat contours, and variable chemical and microbial composition of the sediment below (Nold et al. 2013; Kinsman-Costello et al. 2017).

Table 1. Diurnal color coverage over the mat surface: Time it took for white and purple filaments to cover a given % of the camera viewing area on the mat surface during night and day periods, based on counts from the image analysis of a grid overlay (1m x 1m square cells) on each of the time-series images.

Time to Cover Mat Surface (hrs)

Mat Coverage (%)	White Night #1		Purple Day #1		White Night #2	
Daily Minimum	0	0%	0	10%	0	0%
25	1.75		3		2	
50	3		3.5		3.5	
75	5		4		5	
Daily Maximum	8.5	90%	5.5	100%	10.5	93%

Just before sunset, white SOB started to rapidly cover the surface, gaining 25% coverage within about an hour after dark (Table 1). In the morning, purple cyanobacteria were slower, only attaining 25% mat surface coverage 3 hours after sunrise. Cyanobacteria, by contrast, only took 5.5 hours to reach 100% coverage; however, SOB slowly reached maximum coverage, taking over 8 hours to do so and never reaching 100%.

Modeled surface coverage progression during the day and night lends support to the differing rates of change in coverage by purple cyanobacteria and white SOB, as well as maximum coverage. The purple model confirms the obvious in that the maximum coverage potential ( $\theta_1$ ) is indeed higher (94.20 – 115.39 95% CI) than that of the white (86.87 – 93.11 95% CI) according to the limited dataset at hand (Table S1). Similarly, 95% confidence intervals of  $\theta_2$  and  $\theta_3$  model parameters indicate significant differences in model curve or coverage progression by white SOB and purple cyanobacteria.

When the logistic growth curves of coverage progressions by white SOB and purple cyanobacteria are graphed together starting at approximately sunset and sunrise respectively, the differences become visually clear (Figure S4). SOB appear to increase in coverage more quickly soon after sunset, while cyanobacteria increase initially at a slower rate after sunrise; however, within a few hours after sunrise the rate of increase in coverage by cyanobacteria is markedly higher than that of the SOB following a comparable time after sunset. The maximum rate of change in coverage percent for white SOB's is 19% per hour at 2.5 hours after sunset, quickly increasing early on. For purple cyanobacteria, their maximum rate of change occurs later at almost 3.5 hours after sunset, but the rate is 40% per hour – double that of the white SOB's. This leads to a quicker increase in overall mat coverage by cyanobacteria, while the extremely slow

increase in coverage by SOB after 6-7 hours limits their coverage potential of the mat surface within the slim 9-hour night period of summer at  $\sim 45^\circ$  N.

SOB filaments appear to function like rapid but soon to tire “Rabbits”, whereas cyanobacteria function as slower but steady “Tortoises” in the diurnal race. However, it is possible that cyanobacteria are not slow but the chemical gradients are slow to equilibrate after dusk, or cyanobacteria indulge in a form of sulfur metabolism that sustains them in the dark (Richardson & Castenholz 1987a,b). It is also conceivable that most motile microbes respond to keep up with the diurnally moving redox chemocline. Movement, however, is energy intensive. Motile microbes may seek better conditions, escape worse conditions, or move slowly to gather scarce metabolic resources nearby. Future studies should address these gaps in our knowledge.

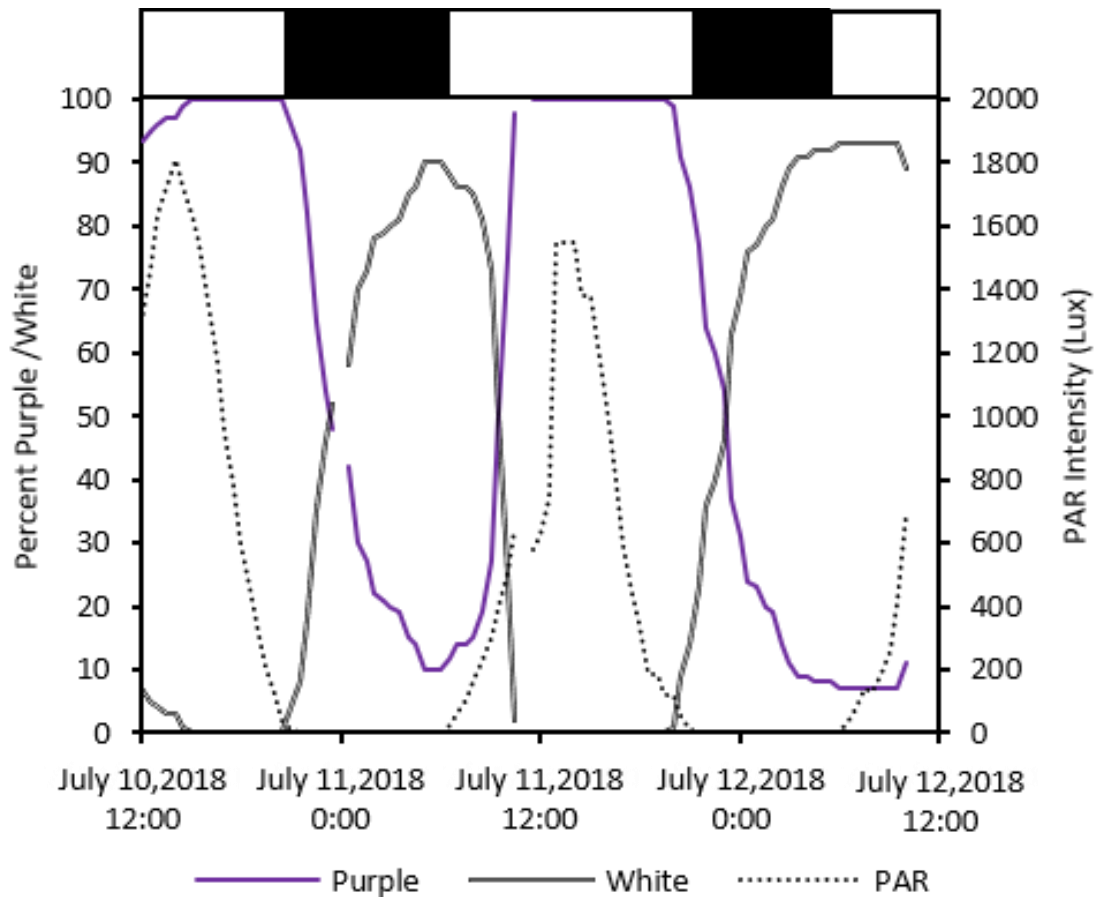




Figure 5. Following the Sun: Percent coverage of purple photosynthetic cyanobacteria (purple line) and white chemosynthetic bacteria (black and white line) on the surface of the mat in relation to ambient photosynthetically active radiation (PAR, dotted line) from July 10 to July 12, 2018. Missing values for 0:00 on July 11, 2018 due to technical error in time-series camera scheduling, and 11:00 on July 11, 2018 represents a cloudy image caused by sediment kicked up by divers during mid-day operations nearby. Note: The bars at the top represent times when daylight is available (white) or unavailable (black).

### 3.3 In-Lab validation of microbial DVM

In-lab simulations of day and night conditions with intact sediment cores collected from the sinkhole in 2018, produced similar results as in the field (Figure 6). Photographs taken just before “nightfall” and “daybreak” showed mat surfaces to be mostly covered by purple cyanobacteria during day and by white SOB at night. We followed 2 separate cores over several diurnal cycles (~14 days) and consistently recorded day-night shifts in mat appearance confirming active DVM and corroborating field observations. Indeed, the study confirmed the central role of daylight in DVM control.

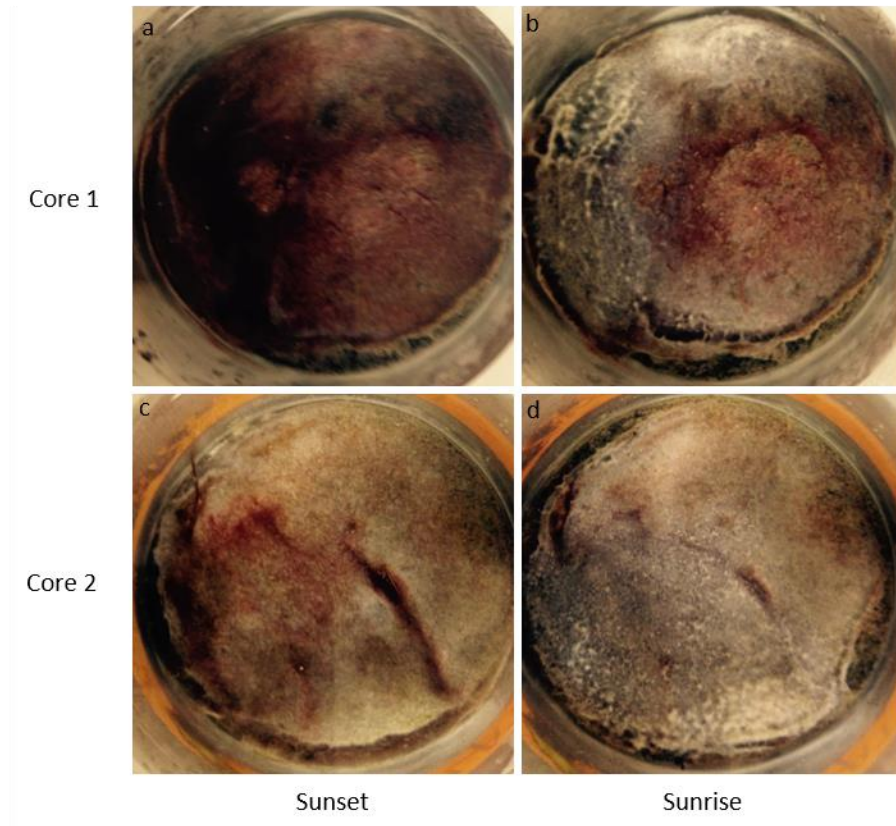


Figure 6. Day-night shifts in mats over intact sediment cores in the laboratory: Two separate sediment cores were incubated in the lab under simulated day and night light cycles. Core 1 shows a more dramatic surface color change from purple to white (a, dusk; b, dawn), while Core 2 (which started out with fewer purple filaments) shows a minor change in surface color (c, dusk; d, dawn).

### 3.4 Up and down: Chasing sunlight, sulfur, and oxygen

So – why and how do the 2 key partners of the mat community indulge in this diurnal dance? Starting at sunset, purple cyanobacteria migrate downwards into the reducing environment of the sediment (Figure 7). This may be a night-time survival mechanism for when they cannot perform photosynthesis (Richardson & Castenholz 1987b). Concurrently, white SOB line-up at the junction between the surface of the mat, relatively rich in oxygen due to

330 cyanobacterial OP, and the sediment, where SRB enriched it with H<sub>2</sub>S (Teske et al. 1998; Nelson  
331 & Castenholz 1982; Møller et al. 1985). This O<sub>2</sub>/H<sub>2</sub>S interface presents SOB filaments with the  
332 necessities for CS, with ongoing sulfate reduction by SRB given the ready source of sulfate in  
333 groundwater and porewater (Kinsman-Costello et al. 2017). Following sunset and cessation of  
334 OP, heterotrophic bacteria and SOB consume the oxygen, forcing the O<sub>2</sub>/H<sub>2</sub>S boundary to move  
335 up vertically within the mat. SOB filaments follow this boundary, until eventually they cover the  
336 mat surface, where the water contains some O<sub>2</sub> and H<sub>2</sub>S diffuses upwards from SRB activity in  
337 the sediment below (Castenholz et al. 1991; Gray & Head 1999). During the night, we would see  
338 the decline of O<sub>2</sub> concentration and the rise of H<sub>2</sub>S within the mat (Klatt et al. 2016a; Kinsman-  
339 Costello et al. 2017).

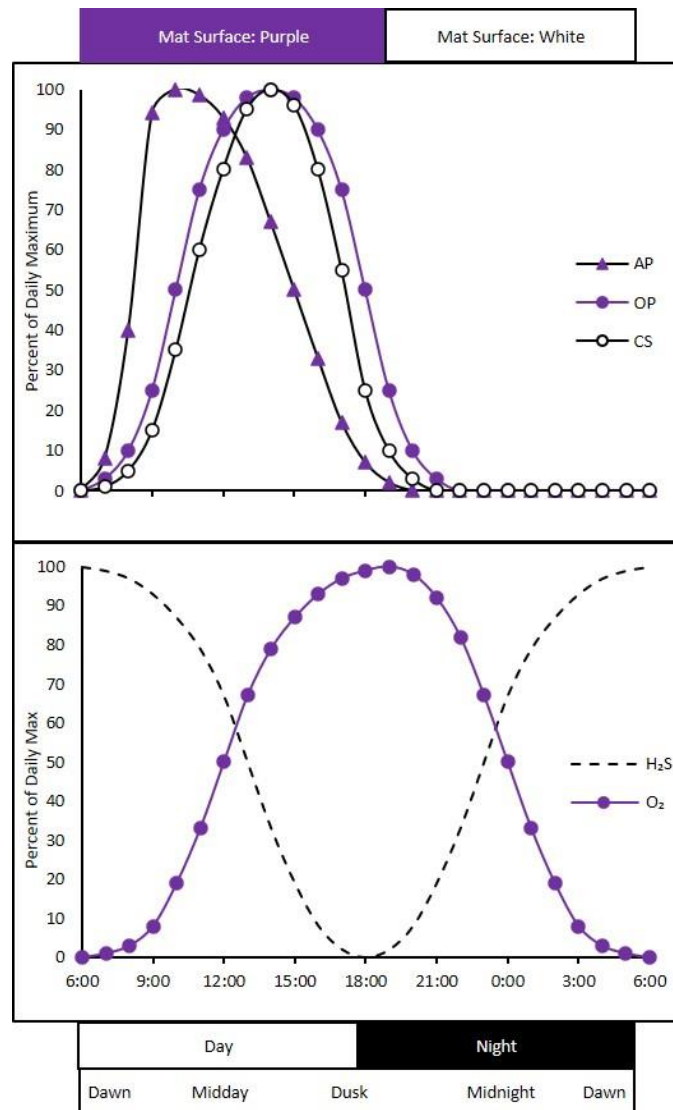


Figure 7. A day in the life of a mat: Schematic diagram of the scenarios of the diurnally varying production processes (top) and substrate-products (bottom) in extinct and extant microbial mats. Rates and concentrations are expressed relative to daily minimum and maximum. Sequential and coordinated vertical motility of anoxygenic and oxygenic cyanobacteria (AP and OP, respectively) and chemosynthetic microbes (CS) across rapidly fluctuating redox may have favored the survival and success of the mat world through time. Although most daily cycles end up in near balance, slight imbalance in daily production-consumption spread over years, millennia and ages in the mat world would have been of cumulative significance to the evolution

of the composition the biosphere over deep time. Composed with source information<sup>3,8,18,24</sup> and the present study.

At daybreak, the SOB filaments begin a photophobic response and migrate downwards into the mat (Nelson & Castenholz 1982). During night-time CS has been sole use of H<sub>2</sub>S, so H<sub>2</sub>S is probably at its maximum daily concentration at daybreak. With minimal light available and light-scattering white filaments still above, cyanobacteria slowly start meander to the mat surface and begin consuming H<sub>2</sub>S to simultaneously perform AP vigorously and OP slowly (Biddanda et al. 2015; Klatt et al. 2016a). Now, with O<sub>2</sub> possibly being generated below and around them, SOB chemotactically migrate downwards toward the H<sub>2</sub>S being generated below by SRB (Gray & Head 1999).

As morning progresses, cyanobacteria rise to the mat surface (Biddanda et al. 2015). They preferentially used H<sub>2</sub>S for AP and the SOB filaments have also used H<sub>2</sub>S for CS (Klatt et al. 2016a). As H<sub>2</sub>S gets depleted and purple filaments migrate towards light, they get further from the sediment sulfide source, and OP becomes favorable over AP (Castenholz et al. 1991; Klatt et al. 2016b). This causes net O<sub>2</sub> generation within the mat surface, but O<sub>2</sub> concentrations become cumulatively significant only later in the day (Dick et al. 2018). Only during the late-afternoon/early-evening does peak O<sub>2</sub> production occur and peak CS by the SOB takes place with access to H<sub>2</sub>S from below. Over the diel cycle, cyanobacteria and SOB deal with competing signals of light, O<sub>2</sub>, and H<sub>2</sub>S, to optimize their locations within the mat ecosystem.

The spatial range of DVM of filaments seeking sunlight and sulfide extend only  $\mu$ ms to mms in microbial mats. However, filamentous bacteria may individually and collectively transport electrons over far greater distances as shown for sulfidic marine sediments (Gray &

Head 1999; Pfeffer et al. 2012). Another consequence of microbial DVM in benthic mats is that settling planktonic material gets buried by filaments that climb over them seeking sunlight, O<sub>2</sub> or H<sub>2</sub>S, subducting deposited organic matter into the anaerobic sedimentary zone below – preserving organic carbon and supplying fuel for AP and CS (Nold et al. 2010; Biddanda et al. 2015).

## 4 Conclusions

### 4.1 Circadian rhythms and motility optimization of mat ecosystem function

Circadian rhythms, organismal behaviors that regularly repeat once a day, have fascinated naturalists through the ages. Whereas it is quite common for us to grasp the idea that the daily lives of larger animals and plants are synchronized to circadian rhythms, it is also true that the literature is replete with examples of microbial prokaryotes – including cyanobacteria - that reveal strong circadian rhythms and related movements (Kondo et al. 1993; Rust 2012). Arguably, such diurnal movements of multitudes of microbes (individually and in consortia such as mats) throughout the biosphere collectively contribute to daily, seasonal, annual and multi-year ecosystem effects.

Throughout Earth's history, massive colonial mats composed of tiny microorganisms have left big footprints in the geological record and in the composition of the air and water (Falkowski et al., 2008; Kemp et al., 2008). While it is generally accepted that cyanobacterial OP mediated Earth's oxygenation, cyanobacteria might have also prolonged the low-oxygen period by simultaneously practicing AP (Voorhies et al., 2012; Dick et al. 2018). However, despite the long period of cyanobacteria and Earth's co-evolution when oxygen was low (>2 billion years) and the critical geobiological turning points under those conditions, little is known about the physiology of cyanobacteria that thrived then (Lyons et al., 2014).

Fortunately, modern cyanobacteria in sulfidic low-O<sub>2</sub> refugia exhibit a range of carbon and sulfur physiologies such as OP, AP, CS, SR and methanogenesis, and provide a window into paleomicrobial lifestyles in our biosphere's past (Falkowski et al., 2008; Bühring et al., 2011; Yang et al. 2011; Klatt et. 2016a; Dick et al. 2018; Bizic et al. 2020). Lake Huron's sinkhole ecosystems are examples of low-O<sub>2</sub> mats where OP driven by inorganic carbon is supplemented by AP driven by sulfide and augmented by concurrent CS; all three primary production processes each contributing roughly 1/3<sup>rd</sup> to the daily metabolic budget of the mat ecosystem (Voorhies et al., 2012). Evaluating AP, OP, and CS in the light of motility, illustrates the natural selective advantage motility provides for optimizing resource use in these diurnally fluctuating ecosystems (Bühring et al., 2011; Biddanda et al., 2012; Voorhies et al., 2012; Snider et al. 2017). —

#### 4.2 From the first tango to modern dance

What might the dance have looked like in the past? We posit that it probably would have looked and worked similarly to extant low-oxygen sulfidic mat ecosystems. The main environmental differences between Lake Huron sinkhole mats and those of Precambrian shallow seas is the availability of H<sub>2</sub>S (which was higher) and the lack of O<sub>2</sub> (which was lower). Concerning the mat ecosystem's light response, ample evidence exists for cyanobacterial phototaxis and SOB photophobia in extant mats (Nelson & Castenholz 1982; Biddanda et al. 2015). While SOB are chemotactic towards H<sub>2</sub>S, in a paleo world with readily available H<sub>2</sub>S, photophobia during the day would still be present. O<sub>2</sub> availability would also need to be considered for SOB positioning. In Archean and Proterozoic seas, O<sub>2</sub> would have been scarce and discontinuous, only supplied by OP cyanobacteria which would not be produced in great amounts unless cyanobacteria had ample access to light under limited H<sub>2</sub>S conditions (Klatt et al.

2016a). Thus, daytime cyanobacterial surface dominance for light access would have been necessary, relegating SOB to the lower and darker layers of the mat (Klatt et al. 2016a).

Light levels also need to be considered. The Middle Island Sinkhole in Lake Huron is deep enough (~23 m, only 10% surface photosynthetically active radiation penetrating to the bottom) that UV damage and photoinhibition for cyanobacteria is not concerning (Snider et al. 2017). Perhaps the diurnal microbial dance of the distant past would have looked similar in coastal mats where water was deep enough to filter UV but shallow enough for sufficient light to penetrate into the benthos. It's possible that, in very shallow regions, cyanobacteria and SOB fought to stay away from the surface (Castenholz et al. 1991; Nelson & Castenholz 1982), and in deeper waters, strived to stay at the mat surface. Over time, these adaptations might have resulted in a day-night shift system in a "goldilocks band" at mid-depth in coastal waters providing optimal conditions for key primary producer communities of the past. Indeed, such coastal life bands may have laid the foundation for stromatolite reefs of the past and extant microbialites.

#### 4.3 Beyond appearances: Significance of DVM in a mat world

Today, benthic microbial mats covering submerged sinkhole ecosystems of Lake Huron exhibit rapid motility of photosynthetic and chemosynthetic filaments in response to variable environmental cues. Motility in sync with changing redox, may play a critical role in mat formation and dynamics, photosynthesis and CS, and sedimentary carbon accrual. Thus, our motility-related findings have important implications for advancing our understanding of the evolution of early Earth's atmosphere, as influenced by similar microbial communities in Archaean and Proterozoic seas.

Interestingly, similar microbial mat communities that reduce carbon and oxidize sulfur are found in geographically disparate locations such as thermal springs, and other oxygen-poor,



sulfur-rich environments that resemble conditions on early Earth (Stal 1995). In modern-day low-oxygen, high-sulfur refugia like submerged sinkholes, motility may confer cyanobacteria the ability to thrive under low-light conditions by maximizing their metabolism across sharply varying gradients of redox and resources in benthic habitats. If such motile DVM traits prevailed among photosynthetic and chemosynthetic microbes during the Proterozoic (The First Tango), they would have represented the largest daily mass movement of life. Active microbial DVM might have been critical to filaments staying close to the sediment surface (The Goldilock's Zone) in the shallow ocean – optimizing photosynthesis and burying organic carbon production – leading to the eventual oxygenation of the seas (Allwood et al., 2006; Biddanda et al. 2012; Lyons et al., 2014).

In considering events and processes that occurred billions of years ago, it is helpful to recall that seemingly everyday events of today also happened then. As the sun “rose and set” each day, life had to adjust to alternating “day” and “night” conditions concurrent with physical and chemical conditions like light, oxygen, and sulfur over the course of mere minutes-hours across sharp physico-chemical interfaces. In the Precambrian seas,  $\mu\text{m}$ -sized cyanobacteria and other tiny microbes had to adjust to daily redox changes occurring within the upper few mms of the mat-sediment ecosystem – a thin and tenuous layered biosphere. A well-choreographed microbial DVM concert might have been an emergent feature of organism-environment coevolution. Seemingly small microbial events within a globally expansive mat world may have set the stage for the modern-day biosphere – one day at a time. In this context, it is critical we appreciate that although ecosystems more or less reset over every day-night cycle, they are rarely perfect – with seasonal imbalances being quite the norm than exception (e.g., modern-day seasonal and annual Keeling Curves of atmospheric  $\text{CO}_2$  and  $\text{O}_2$ ). Thus, even tiny imbalances in

daily production:respiration ratios, add up over time – especially over billions of years – with annual imbalances cumulatively impacting the composition the biosphere such as the Great Oxidation Event ~2.4 billion years ago (Lyons et al. 2014).

Could Lake Huron’s low-oxygen, high-sulfur mat ecosystems provide a “working window” for peering into our distant evolutionary past and enable us to ponder their continuing relevance in today’s world? Cyanobacteria-dominated microbial mats – prevailing in the shallow, oxygen-poor, sulfur-laden seas of the Proterozoic – may have oxygenated our planet during its protracted youth. Indeed, Earth’s extant extreme ecosystems like these not only may have helped shape the early biosphere by producing organic carbon and releasing oxygen, but they also contribute critically to Earth’s biodiversity and physiologic potential today. Furthermore, extant Earthly microbial mat communities may serve as useful models in our search for extraterrestrial life in waters such as the oceans of Europa.

In time, everything in the world around us cycles and recycles again. Thus, the notion of a mat world arising again in a future Earth scenario is not inconceivable. Similarly, not inconceivable is the possibility that we will encounter familiar or bizarre mat worlds in our ongoing search for life on habitable planets and exoplanets – and perhaps even witness therein life’s migrations synchronized to the tempo of their own planetary spins.

According to the American Academy of Microbiology (2001), “Living creatures and the inanimate worlds they inhabit dance an intimate tango”. The challenge will be to comprehend the “biogeochemical tango” taking place in the world’s extant microbial mats, and determine its significance to our biosphere’s past, present and future. Such understanding will be increasingly useful in a world undergoing rapid environmental change, and possibly aid in our search for life elsewhere.

## **5 Data, or a descriptive heading about data**

All data is observational, composed of time-lapse images in the field and in the laboratory, or grid counts calculated from said images. The complete data set that supports this study (In-Field and In-Lab images, and grid counts) can be accessed through the Center for Open Science's - Open Science Framework, available at: <https://osf.io/seuq5>.

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The complete archived data set that supports this study (In-Field and In-Lab images, and grid counts) can be accessed through the Center for Open Science's - Open Science Framework, available at: <https://osf.io/seuq5>.

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