Geomicrobiology of a meromictic lake, Green Lake, Fayetteville, New York

Michael L. McCormick
Hamilton College, Clinton, NY 13323
mmccormi@hamilton.edu

INTRODUCTION

Meromictic lakes are composed of stratified non-mixing and geochemically distinct water bodies. The lack of annual turnover (*meromixis*) normally results in the depletion of oxygen in the bottom waters (*monimolimnium*) and a complementary limitation in nutrient return from sediments to surface waters (*mixolimnium*). Green Lake, located close to Fayetteville, New York, was the first meromictic lake described in North America (Eggleton, 1931). The earliest report of Green Lake (then named Lake Sodom) dates to 1839 in which the white marl that lines the shores and coats fallen trees was well described (Vanuxem, 1839). A decade later, the first qualitative geochemical assays of Green Lake confirmed the presence of hydrogen sulfide in the lake's bottom water (Clark, 1849). An excellent review of the early Green Lake literature, which spans 150 years, is provided by Thompson et al. (1990). This long record led Thompson to speculate that Green Lake may be the most well studied meromictic lake in the world. While this may be true with regard to the geology and limnology of Green Lake, much remains unknown about the lake's microbial ecology and biogeochemistry. Here I provide an overview of historic and recent work that addresses the relationship between Green Lake's microbial communities and its remarkable geochemical features. I also describe a low cost method developed for acquiring aseptic samples at high spatial resolution and present partial results from a survey of microbial community composition and geochemistry throughout the water column of Green Lake using this technique.

GEOLOGY AND LIMNOLOGY OF GREEN LAKE

Although the precise origins of Green Lake and its close neighbor Round Lake are debated, they are most commonly reported to have formed as waterfall plunge basins during the last glacial retreat (~13,000 years ago) (reviewed in Hilfinger and Mullins, 1997). The

basins of both lakes penetrate the Syracuse and Vernon formations and lie in an east-west oriented glacial melt water channel (Sissons, 1960). The lakes were privately owned until 1927, when the surrounding land was purchased by New York State to create Green Lakes State Park (New York State Office of Parks, 2004). Green Lake itself is shaped something like a comma, the central basin being nearly circular with a drainage channel to the northeast forming the comma's tail (Figure 1). The lake is 55 m at its deepest point, has a small surface area (0.26 km^2) and is surrounded by steeply rising hills to the northwest and southeast. These features (depth, small surface area and wind shelter) all contribute to the lake's meromixis. The lake's present elevation is 127 m, approximately equal to the Erie Canal, which lies just north of the park. The majority of recharge to Green Lake is comprised of ground water that enters the monimolimnium after percolating through the Syracuse

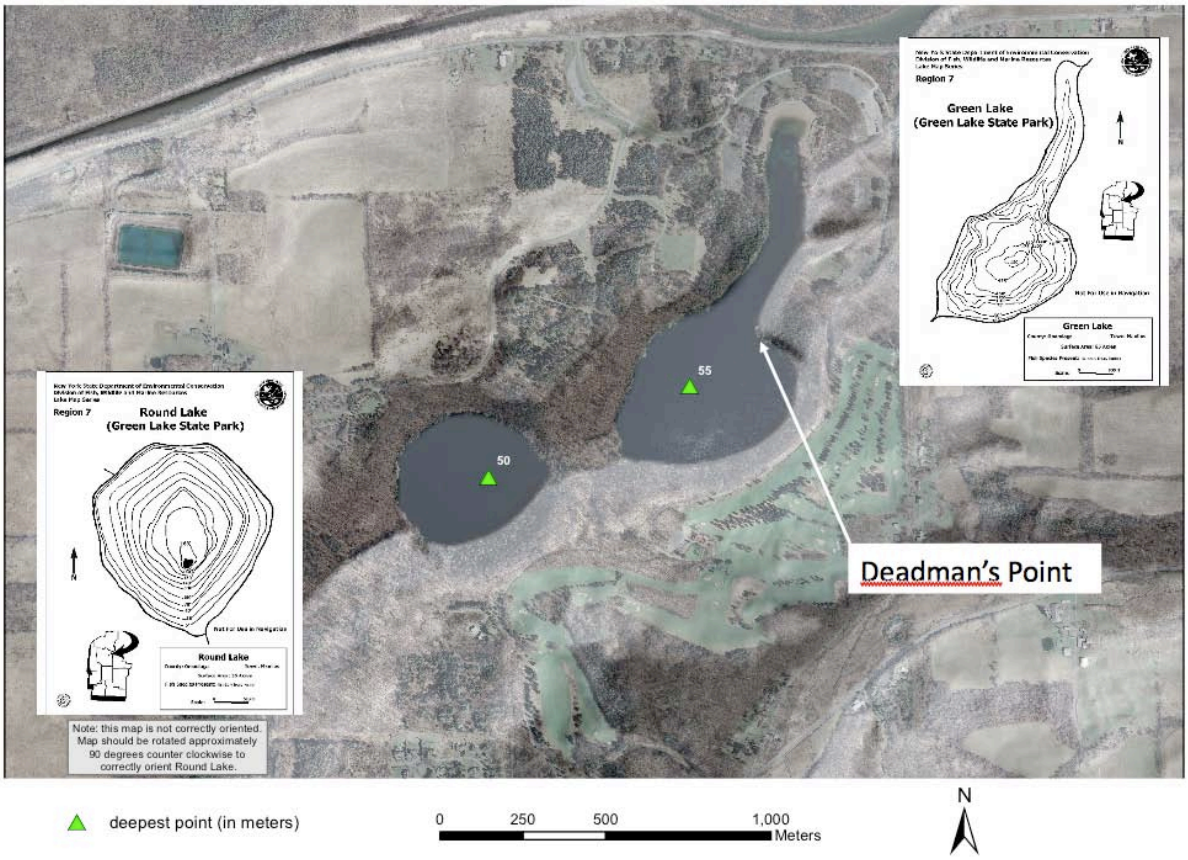

Figure 1: Satellite image of Green Lakes State Park showing Round Lake to the left and Green Lake on the right with the locations of the thrombolite at Deadman's Point and deepest water indicated. Inset bathymetric maps from the New York State Department of Environmental Conservation. Figure courtesy of Dave Tewksbury.

Formation and Vernon Shale. The ground water is saline and contains high concentrations of Ca^{2+}, Mg^{2+} and SO_4^{2-} attributed to the dissolution of dolomite ($CaMg(CO_3)_2$), gypsum ($CaSO_4$•H2O) and halite (NaCl) deposits (Thompson et al., 1990; Torgersen et al., 1981). This saline input sufficiently increases the density of the monimolimnium relative to the mixolimnium to establish stratification, thus Green Lake is a classic example of *crenogenic* meromixis (Bradley, 1929; Eggleton, 1956; Takahashi et al., 1968). To close hydrologic, isotopic and chemical balances on the lake, Takahashi et al. (1968) argued that a separate less saline ground water input must also enter the mixolimnium. A model of two ground water inputs was supported by the stratigraphic and sedimentological studies of Thompson et al. (1990) who suggested a shallow seep enters the mixolimnion along the Syracuse-Vernon contact (~10 m depth) and a deeper more saline input enters along the contact between the green and red units of the Vernon Shale (~18 m). This lower seep occurs at approximately the same depth as the *chemocline*, the transition zone lying between the mixolimnium and monimolimnium, marked by dramatic gradients in oxidized and reduced chemical species and a notable dense population of purple sulfur bacteria (Figure 2).

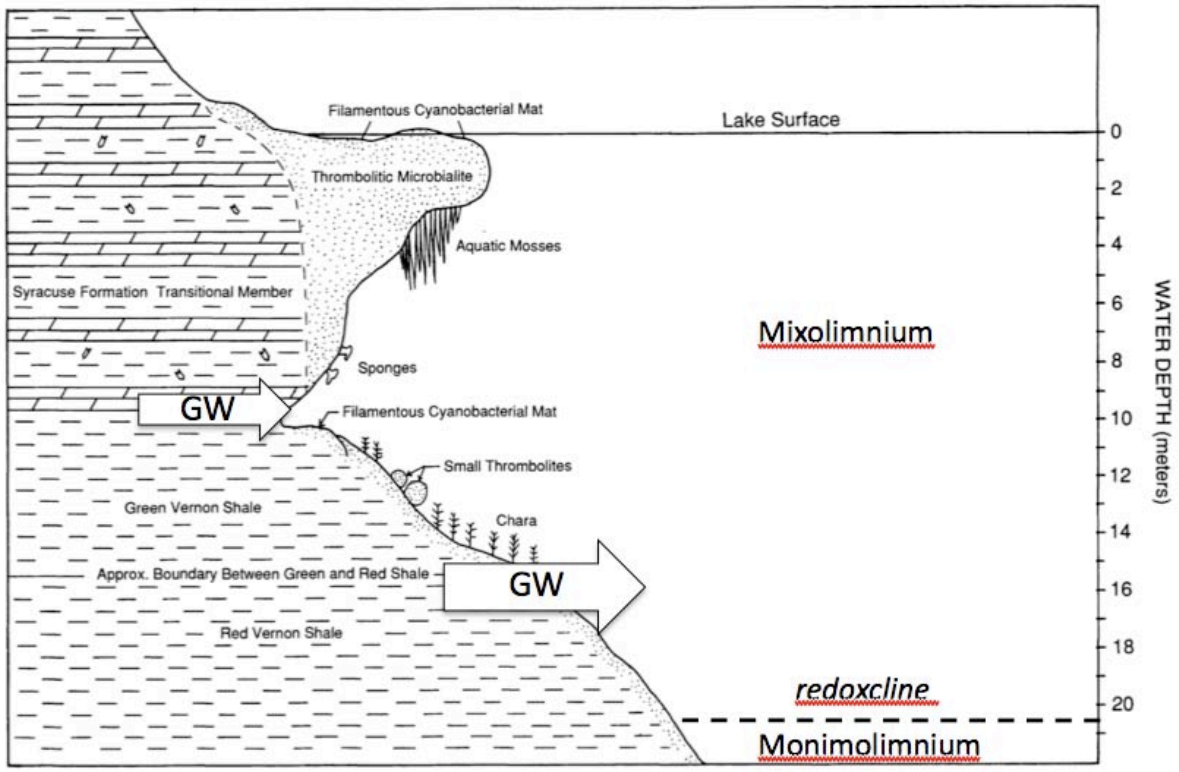

Figure 2: Profile of Green Lake at Deadman's Point illustrating local stratigraphy, points of suspected ground water entry and the present day position of the redoxcline. Figure modified from Thompson et al. 1990.

GEOMICROBIOLOGY OF GREEN LAKE

Early microbiological investigations of Green Lake relied on microscopic observations or culture based approaches (Bradley, 1929; Culver and Brunskill, 1969; Eggleton, 1956; Thompson et al., 1990). These studies established that a dense population of sulfur oxidizing phototrophs occurs at the chemocline (both purple- and green-sulfur bacteria) and that the cyanobacteria *Synechococcus* orchestrates an annual massive precipitation of calcite in the mixolimnium (termed the *whiting event*). They also showed that *Synechococcus* (and other cyanobacteria) are the dominant microbial constituents in Green Lake's calcareous bioherms (*thromobolites*).

One limitation of these prior studies was the use of culture dependent methods, which we now know miss the vast majority of microbial diversity in most natural environments (Amann et al., 1995). Recent studies have applied culture independent methods (largely DNA based) (Meyer, 2008; Meyer et al., 2011; Wilhelm and Hewson, 2012), but have been limited in spatial resolution (3-5 depths). Acquisition of aseptic samples at high spatial resolution is desirable as it permits detection of subtle changes in community composition, particularly across the chemocline where geochemical conditions change dramatically over short distances (<1 m). Given the time required to collect any single water sample, execution of a multi-level survey by repeated sampling raises the concern that the samples will not be truly contemporaneous. This could give rise to artifacts where diurnal cycles are coupled to shifts in microbial assemblage composition. To address this need we developed a low cost mulit-level sampling device to acquire synchronous aseptic samples for microbial and geochemical analysis at 0.25 m to 1.0 m resolution throughout the water column (up to 72 depths collected in one sample event). Below I describe this sampling method then discuss past and present studies of the major geomicrobial features of Green Lake adding results from our own work where relevant.

A low cost multi-level sampling device for aseptic synchronous sampling

The multi-level sampler is comprised of an anchored sampling tube held vertically in the water column to which sterile 60 ml disposable syringes are affixed (Figure 3). Windows are cut in the side of the tube at desired intervals. In Green Lake, we use 1.0 m intervals throughout the water column with additional 0.25 m intervals across the chemocline (16 to

24 m). The plunger of each syringe is predrilled to hold a pin that allows it to be locked while drawn under vacuum. The tip of each syringe is fitted with a short length of silicone tubing connected to a glass Pasture pipette that has been heat sealed at the tip and bent to create an elbow (Figure 3c). Prior to deployment, the syringes, tubes and tips are assembled and autoclaved, then carefully transported to the lake. As the sampling tube is deployed, the plunger of each syringe is pulled and locked under vacuum, a numbered float is then slipped over the pipette tip and the syringe is carefully attached to the sampling tube with the pipette tip passing through the window (Figures 3b and 3c). Once all syringes are deployed and the sampling tube is vertical (and at the correct depth), a messenger is dropped through the center of the tube. As the messenger drops it breaks each pipette tip at the elbow drawing water into the syringe. The elbow is positioned a few centimeters away from the hose to avoid contamination from the sampling hose. Once broken, the floats return the tips to the lake surface where we recover them (Figure 3d). As each float is uniquely coded we know precisely which depths have been acquired.

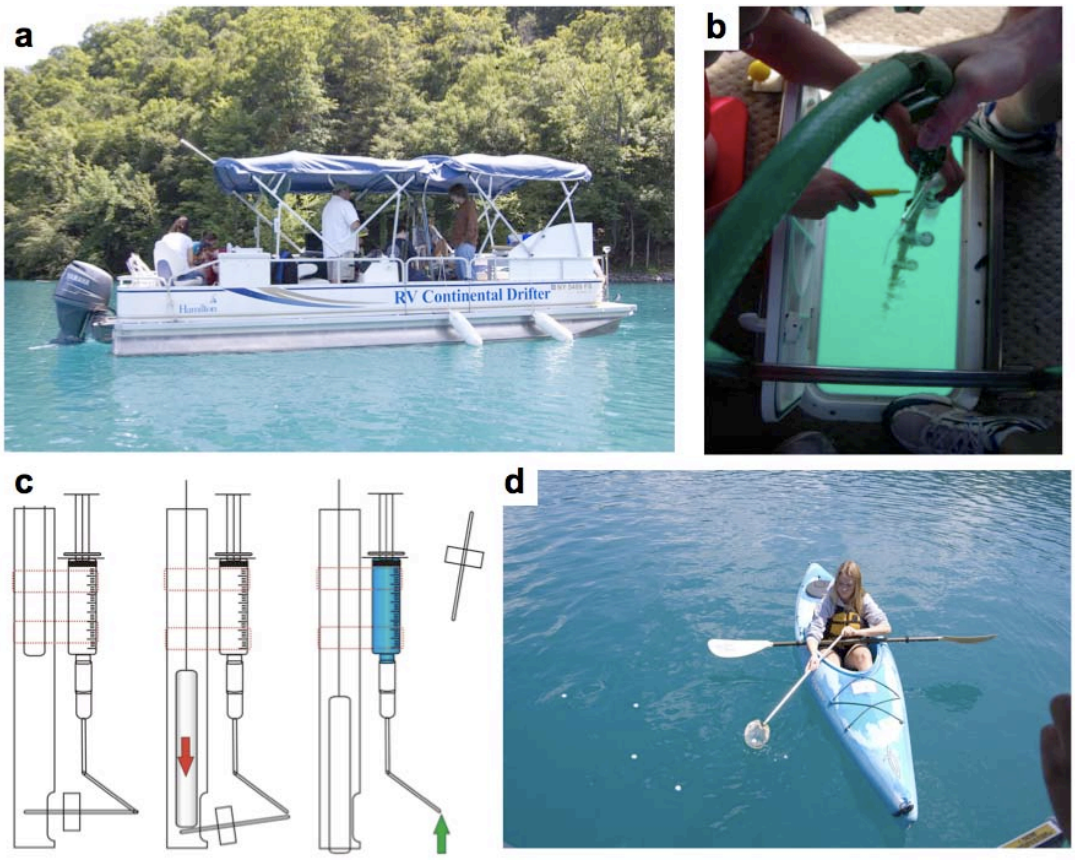

Figure 3: (a,b) Deployment and operation of the multilevel sampler. (c) Mechanism of sample collection. Sterile syringes are fitted with bent flame sealed glass Pasteur pipettes and deployed under vacuum. Each syringe is fitted with a numbered float. (d) Upon triggering, floats are collected to confirm water was collected at the target depth.

Green Lake's trophic structure

The first studies of the trophic structure of Green Lake reported an unusual absence of phytoplankton (other than the purple sulfur bacteria) (reviewed in Thompson et al., 1990). The zooplankton population exceeded phytoplankton 50,000 fold and skewed toward the chemocline, suggesting the use of purple sulfur bacteria as the primary food source (Culver and Brunskill, 1969; Jackson and Dence, 1958). However, the gut contents of lake copepods often show little evidence of purple sulfur bacteria and many instances of calcite ingestion (Brunskill, 1969; Fields, 1974). These perplexing observations were reconciled by the discovery of abundant small cyanobacteria belonging to the genus *Synechococcus* throughout the mixolimnium (Thompson et al., 1990; Thompson et al., 1997). The small size of the *Synechococcus* cells (0.5 μm) explained their omission in earlier phytoplankton surveys that expected to find algae, which are much larger. Furthermore, the nucleation and growth of calcite on the surface of *Synechococcus* cells explained the presence of high numbers of calcite crystals in the guts of copepods (see below) (Thompson et al. 1997).

Primary productivity in Green Lake was estimated at 290 g C/m^2 per year by Culver and Brunskill (1969) with 83% of this occurring in the chemocline mediated by purple sulfur bacteria (photolithoautotrophs that require sulfide for CO_2 fixation) (Thompson et al. 1990). Integrating over the entire lake, Pfennig (1978) estimated this accounts for 60 tons of carbon assimilation and 84 tons of hydrogen sulfide photoxidation per year! However, this is an underestimate of total sulfide oxidation as abiotic chemical oxidation of sulfide also occurs. Based on the distribution of major and minor sulfur isotopes at the chemocline, Zerkle et al. (2010) suggest a seasonal variation in dominance of biotic and abiotic sulfide oxidation processes. In the spring, prior to the annual whiting event when light penetration is greatest, the activity of anoxygenic phototrophs (purple and green sulfur bacteria) is at a maximum and sulfide oxidation is primarily biological. During and after the whiting event, when light is less abundant at the chemocline, abiotic oxidation of sulfide by molecular oxygen becomes dominant.

Calcite precipitation and the cyanobacteria *Synechecoccus*

The input of calcium ions from ground water into Green Lake results in supersaturation with respect to calcite throughout the water column (Takahashi et al., 1968; Brunskill, 1969).

This leads to two notable phenonmena, both of which involve calicite precipitation induced by cyanobacterial photosynthesis; an annual whiting event, in which *Synechococcus* cells induce the massive precipitation and export of calcite from the upper waters of the mixoliminum, and the formation of extraordinary thrombolytic reefs at select points along the shoreline.

Whiting events

Though Green Lake is supersaturated with respect to calcite at all depths (Brunskill, 1969), there appears to be insufficient driving force to permit precipitation by homogeneous nucleation. When precipitation does occur, it happens via heterogeneous nucleation on *Synechococcus* surfaces, catalyzed by calcium adsorption and epitaxial growth of calcite around each cell (Thompson et al., 1990; Thompson et al., 1997). The cell is not passive in this process. Indeed photosynthetic activity appears necessary to drive precipitation evidenced by two observations; 1) the majority of annual calcite precipitation forms in the mixolimnium (Figure 4a)(Brunskill, 1969) where *Synechococcus* populations are abundant, and 2) precipitation peaks during the summer months when photosynthetic activity is at a maximum (driven by longer daily light exposure and elevated epilimnion temperature) (Thompson et al., 1990; Thompson et al., 1997). The mechanism of calcite biomineralization, termed *photosynthetic alkalization*, involves a shift in the chemical equilibrium in the vicinity of the cell. As cells remove bicarbonate from solution they increase the local pH, which, in turn, shifts DIC speciation to favor CO_3^{2-} (Figure 4b). The co-localization of carbonate and Ca^{2+} (by adsorption) results in sufficient supersaturation to form calcite on the cell surface. This mechanism is supported by $^{13}\delta C$ measurements made by Takahashi et al (1968) of sediment calcite (-4 per mil) and mixolimnium DIC (-7 per mil). The difference in $^{13}\delta C$ is attributed to preferential uptake of ^{12}C during photoautotrophy, leaving ^{13}C enriched carbonate on the cell exterior (Thompson et al., 1990; Thompson et al., 1997).

Brunskill (1969) quantified the vertical distribution of calcite and total sedimentation rates during the annual whiting event. The highest suspended concentrations occurred at 5 m in June and July with the total suspended calcite load reaching 35 g/m^2. Annual sedimentation of calcite following each summer whiting event forms well preserved varves, with each calcite layer separated by darker organic detrital material. Sedimentation rates have

averaged 1 mm/year for the last 200 years (Hubeny et al., 2011). The thicknesses and chemical/isotopic composition of these calcite layers have been used, among other things, to establish a record of recent anthropogenic impacts on the Green Lake watershed and to assess regional trends in precipitation and drought during the late Holocene (Hilfinger et al., 2001; Hubeny et al., 2011).

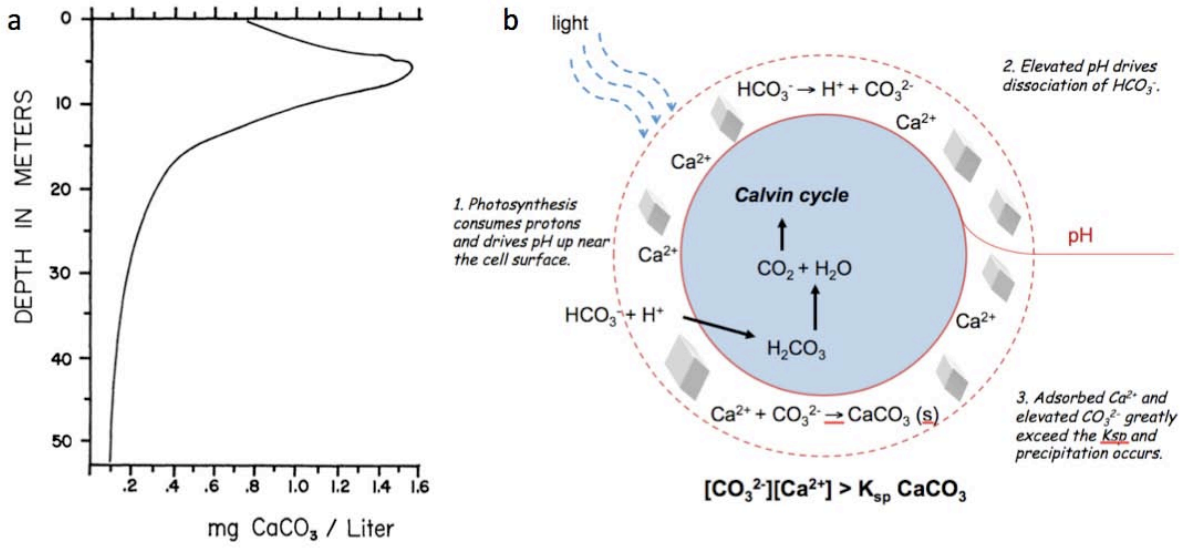

Figure 4: (a) Profile of suspended calcite concentration in late May, 1966 from Brunskill (1969). (b) Mechanism of calcite precipitation by photosynthetic alkalization. Figure modified from Thompson et al. (1997).

Green Lake thrombolites

Similar to stromatolites, thrombolites are a type of microbialite, organosedimentary deposits that grow through particle trapping or in-situ precipitation induced by cellular metabolism and nucleation on cell surfaces (Riding, 2011). Unlike stromatolites, thrombolites lack lamination and are "characterized by a macroscopic clotted fabric" (Aitken, 1967). As microbialites provide some of our earliest fossils dating to ~3.5 billion years ago (Allwood et al., 2009), examples of living microbialite systems are of great interest as they provide contemporary analogs for ancient ecosystems (Wilhelm and Hewson, 2012).

Although a few thrombolites grow along the north shore of Green Lake's central basin, the most impressive is that known as "Deadman's Point" located at intersection of the eastern shore of the central basin and the southern edge of the drainage channel (Figure 1). Extending approximately 10 m from the shore and reaching a depth of 10 m below the surface, this thromolite is significantly larger than any other in the park (Figure 2). The surface is now routinely exposed to air, the result of a 1 to 2 m drop in lake level in the early

1800's coincident with the opening of the local section of the Erie Canal (Thompson et al., 1990). Visual inspection of Deadman's Point while scuba diving shows the structure to be undercut by alcoves that lie at the contact between the lower dolostone bed of the Syracuse Formation and the green Vernon Shale (Thompson et al., 1990). Based on sedimentologic and stratigraphic evidence, Thompson et al. (1990) concluded that ground water enters the lake through these alcoves.

Recently, Wilhelm and Hewson (2012) examined the diversity of cyanobacteria in thrombolite surface samples collected at multiple water depths along north, west and south facing aspects of Deadman's Point. They observed high taxonomic richness, identifying 123 operationally defined taxanomic units (OTUs) based on automated ribosomal intergenic spacer analysis (ARISA). This is approximately four times the richness observed for cyanobacteria in Bahamian stromatolites (Foster et al., 2009). A general trend of increasing taxonomic richness and diversity was observed with depth, yet the highest similarity between communities on all faces of the thrombolite occurred at the greatest depth sampled (2 m). Likely drivers of diversity include variation in solar irradiation, temperature and habitat stability. Dissimilarities between assemblages at shallow depths were attributed to more frequent habitat disturbance and allochtonous inputs (e.g., rainfall, runoff and ice).

Interestingly, none of the dominant internally transcribed spacer lengths (the ARISA molecular fingerprints used to define each OTU) matched those expected for *Synechococcus* species, which clearly comprise the dominant cyanobacterial population in the mixolimnium (Wilhelm and Hewson 2012). This suggests that other, as yet unidentified, cyanobacterial populations contribute to thrombolite formation at Green Lake.

Green Lake chemocline and monimolimnium

A review of the Green Lake literature reveals some variation in the chemocline depth. This is attributable, in part, to inconsistent definitions. Eggleton (1956) did not use the term *chemocline* but he did describe the lake's characteristic chemical gradients. He reported that oxygen "dropped rapidly in concentration between the 15- and 20-meter depths and was never present in any demonstrable amount below 22 m" (Eggleton 1956, pp. 366). This description remains accurate today (Figure 5a). Takahashi et al. (1968) appears to be the first to use the term chemocline with regard to Green Lake, defining it (at 18 m) simply as the

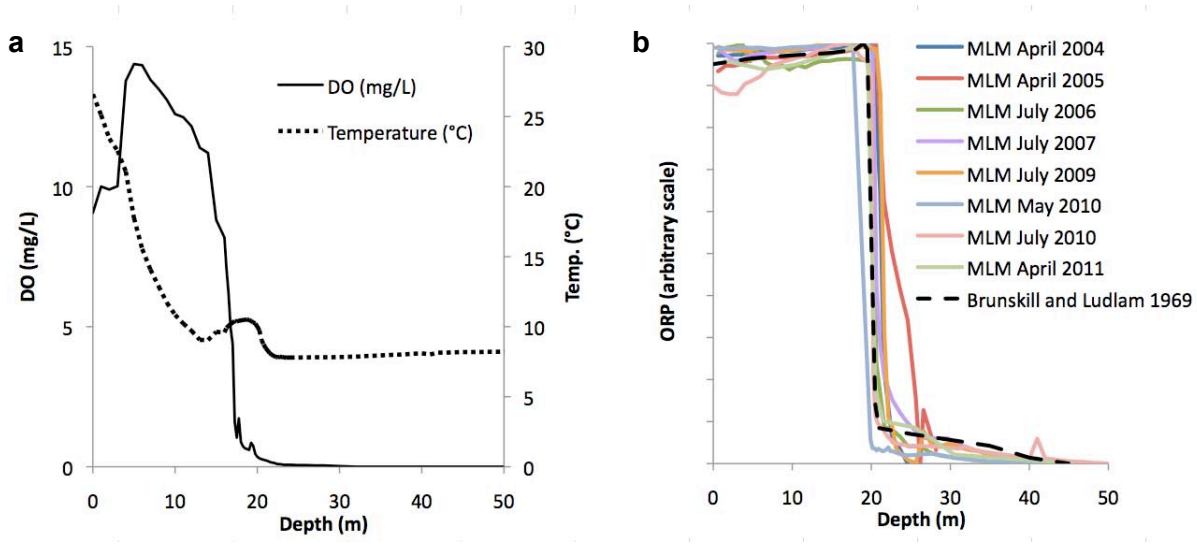

Figure 5: (a) Dissolved oxygen and temperature profiles in Green Lake for July 2008. The redoxcline was located at 20.5 meters. (b) Compilation of oxidation reduction potential measurements made between 2004 and 2011 compared to the measurement of Brunskill and Ludlam (1969).

depth that separates the mixolimnium from the monimolimnium. Using the same definition, Culver and Brunskill (1969) reported that the chemocline extended from 17.5 m to 20 m. However, geochemical profiles from 1974 and 1975 clearly show the chemocline at shallower depths with measurable methane at 15 m and elevated concentrations of methane and sulfide at 17 m (Torgersen et al., 1981). A slightly lower chemocline is indicated between 1985 and 1988 by reports of the purple sulfur bacterial plate (a layer of dense growth) between 16-18 m (Thompson et al., 1990). Recent studies from 2007 and 2008 used oxidation-reduction potential (ORP) to locate the chemocline at 20.5 m (Meyer et al., 2011; Zerkle et al., 2010), although this may more precisely be called the *redoxcline*. Comparing these reports with our surveys of ORP from 2004-2010 and that of Brunskill and Ludlum (1969) we see the redoxcline of Green Lake appears remarkably consistent (Figure 5b). Although Torgerssen et al. (1981) did not report ORP, the sulfide levels they measured assure the redoxcline must also have risen in the 1974-75 period. The cause of this apparent decades long rise and fall of the chemocline/redoxcline is not known. Although seasonal variations in the elevation of the lake occur (differences of ~20 cm have been observed by the author), these are insufficient to account for the relatively large shifts in the chemocline depth observed over the last 40 years.

The most impressive feature of the chemocline is the purple color caused by the high density of purple sulfur bacteria (less obvious are the green sulfur bacteria that live slightly

lower in the water column). The concentration of cells in the plate is so great (10^6 to 10^7 cells/ml) that virtually no light penetrates below the chemocline and solar absorption creates a thermal "bump" in the temperature profile (Culver and Brunskill, 1969) (Figure 5a).

The characteristics of the chemocline that make it an ideal habitat for purple sulfur and green sulfur bacteria are the abundance of light from above and the continuous provision of hydrogen sulfide from below. These nutritional requirements reflect the metabolic peculiarities of these bacteria, which are examples of anoxygenic photoautotrophs (organisms that use light to generate energy but do not produce oxygen). This process relies on photo-excitation and transport of electrons in closed circuits within photosynthetic reactive centers that ultimately drive production of adenosine triphosphate (ATP), the principal energy currency of life (Madigan et al., 2011). In addition to light, all autotrophs also require a source of electrons to assimilate inorganic carbon. This need arises from the fact that carbon, as it is found in CO_2, is fully oxidized (+IV oxidation state) and in order to form the carbon-carbon bonds comprising biological macromolecules a lower average oxidation state must be achieved. In oxygenic photosynthesis (the type of photosynthesis used by cyanobacteria and algae), the organism derives electrons for carbon fixation from the photo-driven oxidation of water (producing diatomic oxygen as a byproduct). As the electrons used for energy generation during anoxygenic photosynthesis remain in a closed circuit, they are not available for carbon fixation and an external source of reducing power is needed. This need is fulfilled by the oxidation of sulfide, producing zero-valent sulfur (S^0), which accumulates intracellularly or extracellularly depending on the species (Madigan et al., 2011).

The most notable features of the monimolimnium are the stable temperature and pH profiles, lack of light and the presence of reduced chemical species, particularly sulfide, which makes itself immediately apparent during sampling. In a recent study of sulfur isotope geochemistry in the monimolimnium, Zerkel et al. (2010) found evidence of sulfur disproportionation (SD) at and just below the chemocline. Thiosulfate, sulfite and zero valent sulfur (including polysulfides) are common substrates for bacterial sulfur disproportionation and are present in the chemocline and monimolimnium of Green Lake (Zerkle et al., 2010). Interestingly, gene sequences for *Desulfocapsa*, a bacteria capable of SD have been recovered from Green Lake (Meyer, 2008). In the case of zero valent sulfur

disproportionation, low ambient sulfide concentrations are required. Thus this mechanism may only be significant near the upper portion of the chemocline although the authors suggest syntrophic associations with sulfide consuming partners may make disproportionation favorable at greater depths (Zerkle et al. 2010). Such syntrophic associations have been speculated between *Desulfocapsa* sp. and the sulfide oxidizing phototroph *Lamprocystis* in lake Cadagno, Switzerland (Peduzzi et al., 2003; Tonolla et al., 2003).

Molecular approaches to characterizing Green Lake's microbial diversity

The earliest taxonomic identifications of bacteria in Green Lake relied on microscopy. Eggleton (1956) reported discovering the purple sulfur bacteria in 1935, identifying them as *Lamprocystis roseopersicina*. Subsequent studies identified *Chromatium*- and *Thiocystis*-like purple sulfur bacteria and the green sulfur bacteria *Chlorobium phaeobacteroides* (Culver and Brunskill, 1969). In a recent study of carotenoid biomarkers in Green Lake, Meyer et al. (2011) used clone library construction and 16s rRNA gene sequencing to characterize the bacterial community in two water samples (one in the chemocline and one in the monimolimnium). They found the purple sulfur bacteria and green sulfur bacteria respectively comprised 25% and 15% of the sequences recovered from the chemocline (20.5 m). Four phylotypes of purple sulfur bacteria were identified including some closely related to *Chromatium okenii* and *Thiocystis*. The green sulfur clones were related to *Chlorobium phaeobacteroides*, affirming the findings of the early microscopy studies. In contrast, the mixolimnium sequences from 25.0 m were dominated by bacteroidetes (27%), followed by sulfate reducing δ-proteobacteria (22%), and ε-proteobacteria (14%) (Meyer et al., 2011). These groups are common members of anoxic communities, representing a wide diversity of metabolic capabilities including substrate hydrolysis, fermentation and anaerobic respiration (Madigan et al., 2011). The ε-proteobacteria are particularly known for their versatility in mediating redox reactions with sulfur compounds (Campbell et al., 2006).

Small ribosomal subunit gene sequencing is a powerful tool for microbial diversity analysis, however, the time and cost of clone library construction made this an impractical choice for analyzing large numbers of samples in the recent past. Next generation high-

throughput sequencing methods such as the Illumina platforms have overcome this limitation (Logares et al., 2012). For our high-resolution surveys we used an alternative gene-based technique known as terminal restriction fragment length polymorphism (TRFLP). This approach involves the amplification of 16s rRNA genes from environmental samples via the polymerase chain reaction (PCR) using fluorescently tagged primers. The PCR products are then digested with restriction enzymes that cleave the sequences at specific sites. Finally the size and abundance of the terminal fragments (easily identified by their fluorescent tag) are quantified. In closely related organisms the 16S rRNA sequences are similar, therefore the restriction sites will occur at many of the same locations and similar terminal fragments will result. In distant relatives the terminal fragment sizes will differ. Thus the diversity of TRFLP peaks in a given sample reflects genetic diversity in the microbial community. The usefulness of combining of high-resolution sampling with low cost molecular finger printing is illustrated in Figure 6, which presents TRFLP results for 29 samples collected using the multi-level sampler in July of 2008. Note the stark contrast in community composition above and below the redoxcline (20.5 m). When TRFLP results are combined with clone library analysis, it is possible to assign putative identities to specific fragments at least at the class or order level (as shown in Figure 6). The magnitude of each peak provides a semi-quantitative measure of abundance, allowing us to visualize the distribution of specific groups such as the *Synechecoccus* population, which skews toward the chemocline before abruptly disappearing at the redoxcline. This pattern is similar to the skewed distribution of copepods reported by Culver and Brunskill (1969), suggesting that cyanobacterial harvesting may offer an additional explanation for the copepod distribution other than the grazing of purple-sulfur bacteria.

Final remarks

After 170 years of study, Green Lake continues to fascinate us. Most of this past work addressed the geologic and limnologic characteristics of the lake. With the advent of low-cost high-throughput sequencing, we are now able to interrogate the composition of microbial communities in ways that were impractical just a decade ago. Because it is an ideal natural laboratory, we are likely to see several new and exciting studies from Green Lake in the

decades ahead addressing complex links between biogeochemical dynamics, community composition and metabolic function that will have impact far beyond the bounds of the park.

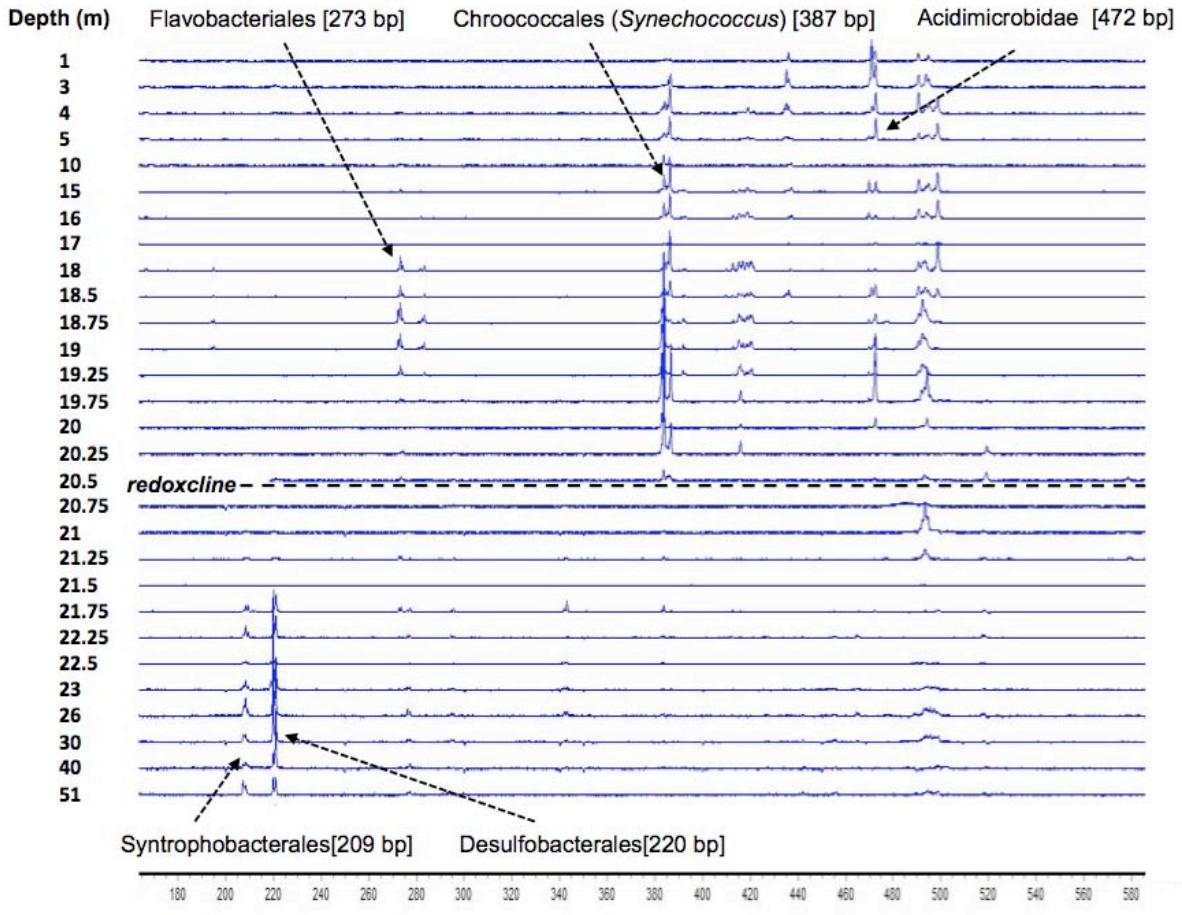

Figure 6: Example distribution of TRFLP identified taxonomic groups through the Green Lake water column. (6FAM labeled forward fragments from the Rsa1 digest of bacteria amplicons). Taxanomic assignments based on matching virtual digests of clone library sequences prepared at 13 depths (data not shown).

Acknowledgements

My thanks to the many students and collaborators who have worked with me on Green Lake: Nikola Baniski, Dr. Eric Boyd (Montanta State University), Falon Chipidza, Professor Eugene Domack (Hamilton College), Professor Jinnie Garrett (Hamilton College), Meghan Greisbach, Sean Linehan, Professor Lorraine Olendzenski (St. Lawrence University), Libby Penderey, Sarah Powell, Greg Ray, Amy Rumack, Valerie Valant, and Bruce Wegter. I am particularly thankful to the Green Lake State Park Manager Jim Semar and staff for providing access to the lake and for kindly permitting us to use park boats in support of our

work. Thanks also to David Tewksbury for preparing Figure 1 in this manuscript. Funding for this work was provided, in part, by NSF SGER grant ANT-0624020.

REFERENCES

Aitken, J.D., 1967, Classification and environmental significance of cryptalgal limestones and dolomites with illustrations from the Cambrian and Ordovician of southwestern Alberta: Journal of Sedimentary Petrology, v. 37, p. 1163-1178.

Allwood, A.C., Grotzinger, J.P., Knoll, A.H., Burch, I.W., Anderson, M.S., Coleman, M.L., and Kanik, I., 2009, Controls on development and diversity of Early Archean stromatolites: Proceedings of the National Academy of Sciences of the United States of America, v. 106, p. 9548-9555.

Amann, R.I., Ludwig, W., and Schleifer, K.H., 1995, Phylogenetic identification and in situ detection of individual microbial cells without cultivation: Microbiological Reviews, v. 59, p. 143-169.

Bradley, W.H., 1929, Algae reefs and oolites of the Green River Formation, *in* Survey, U.S.G., ed.: U. S. Geological Survey Professional Paper, p. 203-223.

Brunskill, G.J., 1969, Fayetteville Green Lake, New York ; [Part] 2, Precipitation and sedimentation of calcite in a meromictic lake with laminated sediments: Limnology and Oceanography, v. 14, p. 830-847.

Brunskill, G.J., and Ludlam, S.D., 1969, Fayetteville Green Lake, New York ; [Part] 1, Physical and chemical limnology: Limnology and Oceanography, v. 14, p. 817-829.

Campbell, B.J., Engel, A.S., Porter, M.L., and Takai, K., 2006, The versatile epsilon-proteobacteria: key players in sulphidic habitats: Nature Reviews Microbiology, v. 4, p. 458-468.

Clark, J.V.H., 1849, Onandaga; or reminisences of earlier and later times: Syracuse, New York, Stoddard and Babcock.

Culver, D.A., and Brunskill, G.J., 1969, Fayetteville Green Lake, New York. V. Studies of primary production and zooplankton in a meromictic marl lake: Limnology and Oceanography, v. 14, p. 862-873.

Eggleton, F.E., 1931, A limnological study of the frofundal bottom fauna of certain fresh-water lakes: Ecological Monographs, v. 1, p. 231-331.

—, 1956, Limnology of a meromictic, interglacial, plunge-basin lake: Transactions American Microscopical Society, v. 75, p. 334-378.

Fields, T.C., 1974, Vertical migration of Diaptomus sicilis Forbes in Fayetteville Green Lake: Syracuse, State University of New York.

Foster, J.S., Green, S.J., Ahrendt, S.R., Golubic, S., Reid, R.P., Hetherington, K.L., and Bebout, L., 2009, Molecular and morphological characterization of cyanobacterial diversity in the stromatolites of Highborne Cay, Bahamas: Isme Journal, v. 3, p. 573-587.

Hilfinger, M.F., and Mullins, H.T., 1997, Geology, Limnology and Paleoclimatology of Green Lakes State park, New York, *in* Rayne, T.W., Bailey, D.G., and Tewksbury, B.J., eds., Field Trip Guid for the 69th Annual Meeting of the New York State Geological Association, New York State Geological Association.

Hilfinger, M.F., Mullins, H.T., Burnett, A., and Kirby, M.E., 2001, A 2500 year sediment record from Fayetteville Green Lake, New York: evidence for anthropogenic impacts and historic isotope shift: Journal of Paleolimnology, v. 26, p. 293-305.

Hubeny, J.B., King, J.W., and Reddin, M., 2011, Northeast US precipitation variability and North American climate teleconnections interpreted from late Holocene varved sediments: Proceedings of the National Academy of Sciences of the United States of America, v. 108, p. 17895-17900.

Jackson, D.F., and Dence, W.A., 1958, Primary productivity in a dichothermic lake: The American Midland Naturalist, v. 59, p. 511-517.

Logares, R., Haverkamp, T.H.A., Kumar, S., Lanzen, A., Nederbragt, J., Quince, C., and Kauserud, H., 2012, Environmental microbiology thorugh the lens of high-throughput DNA sequencing: Synopsis of current platforms and bioinformatic approaches: Journal of Microbiological Methods, v. 91, p. 106-113.

Madigan, M.T., Martinko, J.M., Stahl, D.A., and Clark, D.P., 2011, Brock Biology of Microorganisms, Benjamin Cummings.

Meyer, K.M., 2008, Biogeochemistry of Oceanic Euxinia in Earth History: Numerical modeling and evaluation of biomarkers using modern analogs, The Pennsylvania State University.

Meyer, K.M., Macalady, J.L., Fulton, J.M., Kump, L.R., Schaperdoth, I., and Freeman, K.H., 2011, Carotenoid biomarkers as an imperfect reflection of the anoxygenic phototrophic community in meromictic Fayetteville Green Lake: Geobiology, v. 9, p. 321-329.
New York State Office of Parks, R., and Historic Preservation, 2004, New York's Heartland: The development of the state parks program in central New York 1925-1950, The Preservationist, Volume 8, p. 14-19.
Peduzzi, S., Tonolla, M., and Hahn, D., 2003, Isolation and characterization of aggregate-forming sulfate-reducing and purple sulfur bacteria from the chemocline of meromictic Lake Cadagno, Switzerland: Fems Microbiology Ecology, v. 45, p. 29-37.
Pfennig, N., 1978, General physiology and ecology of photosynthetic bacteria: New York, Plenum Press.
Riding, R., 2011, Microbialites, stromatolites, and thrombolites, *in* Reitner, J., and Theil, V., eds., Encyclopedia of Geobiology: Encyclopedia of Earth Sciences Series, Springer, p. 635-654.
Sissons, J.B., 1960, Submarginal, marginal and other glacial drainage in the Syracuse-Oneida area, New York: Geological Society of America Bulletin, v. 71, p. 1575-1588.
Takahashi, T., Broecker, W., Li, Y.H., and Thurber, D., 1968, Chemical and isotopic balances for a meromictic lake: Limnology and Oceanography, v. 13, p. 272-292.
Thompson, J.B., Ferris, F.G., and Smith, D.A., 1990, Geomicrobiology and sedimentology of the mixolimnion and chemocline in Fayetteville Green Lake, New York: Palaios, v. 5, p. 52-75.
Thompson, J.B., SchultzeLam, S., Beveridge, T.J., and DesMarais, D.J., 1997, Whiting events: Biogenic origin due to the photosynthetic activity of cyanobacterial picoplankton: Limnology and Oceanography, v. 42, p. 133-141.
Tonolla, M., Peduzzi, S., Hahn, D., and Peduzzi, R., 2003, Spatio-temporal distribution of phototrophic sulfur bacteria in the chemocline of meromictic Lake Cadagno (Switzerland): Fems Microbiology Ecology, v. 43, p. 89-98.
Torgersen, T., Hammond, D.E., Clarke, W.B., and Peng, T.H., 1981, Fayetteville, Green Lake, New York; (super 3) H- (super 3) He water mass ages and secondary chemical structure: Limnology and Oceanography, v. 26, p. 110-122.
Vanuxem, L., 1839, Third annual report of the geological survey of the Thrid District: Documents of the Assembly of the State of New York, Sixty-second Session, v. 5, p. 241-285.
Wilhelm, M.B., and Hewson, I., 2012, Characterization of Thrombolitic Bioherm Cyanobacterial Assemblages in a Meromictic Marl Lake (Fayetteville Green Lake, New York): Geomicrobiology Journal, v. 29, p. 727-732.
Zerkle, A.L., Kamyshny, A., Kump, L.R., Farquhar, J., Oduro, H., and Arthur, M.A., 2010, Sulfur cycling in a stratified euxinic lake with moderately high sulfate: Constraints from quadruple S isotopes: Geochimica Et Cosmochimica Acta, v. 74, p. 4953-4970.