Fifty years of limnology (1969–2019) at Mahoney Lake, British Columbia, Canada

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Abstract: Mahoney Lake is a small, meromictic saline lake in south-central British Columbia noted for its unique layer of purple sulfur bacteria. First examined in 1969, this lake has undergone physical, chemical, biological, and pre-historical research to generate an understanding of how the lake and its biota function have developed through time. Advances in understanding the sulfur transformations and bacterial nutrient cycling over the last fifty years have been prolific, resulting in the description of several new taxa. Mahoney Lake is exceptional in its limnological characteristics and is an ideal site for training future limnologists.

Key words: purple sulphur bacteria, meromictic, redox

Introduction

Mahoney Lake, British Columbia, Canada is a closed-basin meromictic lake with unique stratification patterns and physical chemistry that are currently reflected as euxinic (i.e., anoxic and sulfidic) conditions. Its biota are similarly unique and diverse, having adapted to the extreme environments that developed in the Holocene. As such, it has received scientific attention for over fifty years.

Mahoney Lake is an approximately twenty hectare lake situated at ~470 metres above sea level, ten kilometres south of Okanagan Falls, British Columbia, with a catchment of about 385 ha in area. The lake has a depth of eighteen metres, however, the surface elevation fluctuates by several metres in any decade as there are no outlet streams and inlet streams are ephemeral. As such, Mahoney Lake

is acutely sensitive to water balance. The shoreline length is estimated at less than three kilometres (BC Parks 2020). It is currently bounded by the twenty nine and a half hectare Mahoney Lake Ecological Reserve on the southern side, established by the province of British Columbia in 1972, and the 3764 hectare White Lake Grasslands Protected Area, established in 2001, on the northern side. The lake is located in the Ponderosa Pine biogeoclimatic zone, with a mean annual temperature of 10.1°C and 345 mm of precipitation (1981–2010 Canadian Climate Normals from Oliver, BC).

Mahoney Lake was officially named as such in 1936, after John Mahoney who pre-empted Lot 521 in February 1908; prior to this it was identified as Alkali Lake on some 1918 land surveyor’s field notes (BC Geographical Names 2020). The Syilx peoples, the local First Nations, have for millennia interacted with this and other special lakes

in the area (e.g. Spotted Lake) and likely had given Mahoney Lake a name in the Nsyilxcən language based upon the unique character of this lake.

Here we present a three-part, comprehensive summary of the research conducted over the last fifty years. We first describe research examining the unique physical and chemical characteristics of this lake. Second, we outline the paleolimnological studies that highlight changes the lake has undergone since deglaciation in the region. Last, we highlight research in carbon and sulfur transformations and characterization of the sulfur bacterial community and suggest possible future avenues of research.

Mahoney Lake

A unique aquatic ecosystem

A Zeitgeist of the postwar period was to “improve” the sport fishery in British Columbia, specifically for brook and rainbow trout (Ashley and Nordin 1999). In the late 1960s, Halsey was tasked to investigate the overwintering capacity of a variety of inland lakes for game fish (Halsey 1968). An aeration system was eventually installed at Yellow Lake in 1969 to facilitate the salmonid fishery (Halsey and MacDonald 1971). This mandate was likely the reason for examining Mahoney Lake, as Northcote and Halsey compared four similarly sized lakes in southern British Columbia, three near the community of Penticton (White, Yellow, and Mahoney Lakes) and one (Lyons Lake) near Kamloops (Northcote and Halsey 1969). They provided physicochemical data for the lakes and their watersheds, noting that the thermal, dissolved oxygen, conductivity, and fauna profiles indicated that strong meromixis occurred in Mahoney and Lyons Lakes. Furthermore, using an echo sounder, they discovered two layers within the water column of Mahoney Lake, the lower one occurring at the chemocline which was dominated by purple sulfur bacteria at the time identified as *Thiocapsa* sp. with a jellylike consistency because of an extremely high biomass density, and an upper layer that may have been caused by phytoplankton, but that may have been ephemeral in nature. Aside from noting the presence of the distinct layer of bacteria (later photographed to be distinctly stratified (Overmann 2001), they made several im-

portant observations and speculations that directed subsequent research, for example, that the purple sulfur bacterial plate may move with seasonal light penetration, that the copepod community feeds upon the bacteria, and that warm monimolimnion temperatures may allow year-round reproduction within the zooplankton community. Lastly, they stated that Mahoney Lake is probably unsuitable for trout due to its salinity and low oxygen concentrations – for this we may be grateful that there was no artificial mixis technology installed in Mahoney Lake, setting the stage for decades of limnological research into this fascinating lake.

Fourteen years later, Northcote and Hall (1983) compared the adjacent Green and Mahoney Lakes (separated by less than one kilometre), both of which are considered saline. They proposed that the differences in conductivity (Green Lake = 3520 $\mu\text{S cm}^{-1}$ and Mahoney Lake = 55,000 $\mu\text{S cm}^{-1}$) and mineral composition between lakes is due to the underlying bedrock – Greenlake astride the Skaha formation that is low in alkali materials, Mahoney bounded by the Kitley Lake and Marama formations (see Church 1973 for additional discussion on these rock formations), both high in alkali minerals. Differences in bedrock contributions were later confirmed (Michel et al. 2002), with a conductivity value of 135,000 $\mu\text{S cm}^{-1}$ in October, 1981 at Mahoney Lake, though values of 5800 and 8500 $\mu\text{S cm}^{-1}$ from May and September, 1983 were observed. Differences in ion concentrations were also observed between Mahoney and Green Lakes (see Table 1).

Although the salinity of Mahoney Lake is comparable to that of marine environments, and the lake is not alkaline, it is rich in magnesium and sulfate ions which seem to be the cause of the absence of fish and the low diversity of zooplankton. Northcote and Hall (1983) additionally proposed that meromixis is maintained in Mahoney Lake not

Table 1. Ion concentrations (in mg dm^{-3}) of Mahoney and Green Lakes, British Columbia

Ion	Mahoney Lake (Oct. 1981)	Green Lake (Sept. 1983)
Na^+	4900	228
K^+	730	37
SO_4^{2-}	19440	701

due to differences in salinity, but rather local topographical differences, suggesting that the surrounding hills protect Mahoney Lake from prevailing winds whereas Green Lake is more exposed and lies parallel the main axis of the Okanagan Valley. However, one cannot help but feel they were ultimately more interested in examining the biological implications of the unique stratification of Mahoney Lake. Four distinct oxygen zones were confirmed, the surface high O₂ zone (likely originating from melting snow), a low O₂ zone at two metres depth, a moderately oxygenated zone at six metres depth, and the anoxic monimolimnion below eight metres depth. They also observe that productivity is dominated by bacterial activity, unlike Green Lake, where lake productivity was dominated by phytoplankton as in most other lakes. Finally, they associate two distinct zooplankton zones associated with the surface and six metre oxygenated layers.

The unusual, four-layer stratification of Mahoney Lake begged further investigation, both from a mixis perspective, but also with implications in productivity and nutrient cycling. Because of the unusual lake water chemistry and temperatures, Hall and Northcote (1986) developed a calibration method for dissolved solid estimation to be used at Mahoney Lake. Three publications stemmed from this period of investigation: a vernal (spring season) examination of microstratification (Northcote and Hall 1990), an autumnal (fall season) examination of mixing of the water layers (Ward et al. 1990), and an investigation into the productivity and decomposition processes occurring in spring and fall (Hall and Northcote 1990). The results suggest that indeed spring melting of snow and ice was the origin of the secondary (upper, ephemeral) chemocline in the lake and that wind is not a significant contributing factor to destratification in autumn. However the most unexpected result was that the phototrophic layer of purple sulfur bacteria was responsible for up to 66 percent of the total primary productivity in Mahoney Lake. Phytoplankton productivity in the mixolimnion was considered similar to other “normal” (i.e., oligotrophic) lakes, likely limited by phosphorus.

Overmann et al. (1991) examined the purple sulfur bacteria layer in Mahoney Lake, reclassifying the dominant species as *Amoebobacter purpureus* (later reclassified as *Lamprocystis purpurea* comb. nov by Imhoff (2001) and further confirmed

by Hamilton et al. (2014) as *Thiohalocapsa*, thus it is referred to here by the name *Thiohalocapsa* sp. strain ML1) and lesser populations of *Thiocapsa roseopersicina*, *Rhodobacter capsulatus*, *Chloroherpeton thalassium*, and *Prosthecochloris aestuarii*. They determined that the concentration of bacteriochlorophyll *a* was up to 20,900 µg dm⁻³, the highest value observed in any natural body of water to date (nine times higher than the next reported value), with primary productivity amounting to fifteen milligrams of carbon per square metre per hour within the bacterial plate. In subsequent years, record concentrations of 27,500 µg bacteriochlorophyll-*a* per litre were detected (Overmann et al. 1994). Overmann et al. (1991) also investigated the flux of sulfide within the water column, recognizing the redox roles of a variety of bacteria within the layer itself, including purple non-sulfur bacteria which recycled organic carbon. They further suggested that the meromictic structure of the lake reduces bacterial losses to sedimentation and decay, allowing the higher concentrations of bacteria to persist. Overmann also notes that the growth of *Thiohalocapsa* sp. strain ML1 (formerly *A. purpureus*) is slow, since only 10 percent of the cells receive sufficient light energy for photosynthetic growth due to the extreme self-shading within the bacterial layer (Overman 1997).

Subsequently, the research focus at Mahoney Lake diverged along two different avenues of investigation, the first following the purple sulfur bacteria, and the second investigating the pre-history or development (paleolimnology) of the lake itself.

Mahoney Lake: Paleolimnology

Overmann et al. (1993) examined fossil pigments from a sediment core taken from Mahoney Lake in 1985, which was subsequently stored at the University of British Columbia under the care of Ken Hall. Pigments from aquatic algae, plants, and bacteria are long recognized to be resistant to decomposition or alteration in sediment and thus are an ideal archival proxy for productivity (Leavitt and Hodgson 2001). Using high-performance liquid chromatography, Overmann et al. were able to match the then currently 97 percent dominating *Thiohalocapsa* sp. strain ML1's okenone pigment to the presence of okenone pigments dating back to 11,000 years before present, though peaking in the

early Holocene once sediments changed from inorganic to organic material. Deposition of Mazama ash was noted as significant in this lake, with nearly one metre of tephra preserved in the sediments. This contrasts with only eight centimetres of Mazama tephra at nearby Lake of the Woods, British Columbia (Heinrichs et al. 2004), which is more typical of most Mazama tephra layers in lakes within the region (Buckland et al. 2020). Okenone pigments decreased significantly during tephra deposition in Mahoney Lake, but reached their highest concentrations during the last few thousand years. Surprisingly, no carotenoid pigments from purple non-sulfur bacteria nor any from green sulfur bacteria were found in the fossil record, suggesting the dominant purple sulfur bacteria community was an early and long-standing community at Mahoney Lake.

Lowe et al. (1997) used the same sediment core to examine whether or not the lake has always been meromictic, applying the rationale that low lake levels would allow mixing by wind, whereas high lake levels would maintain a separate, non-mixing layer. By examining the core for the presence of varves, they determined that meromictic conditions were established by about 9000 yr BP, shortly after the sediment changed from inorganic mud to organic gyttja at 10,000 yr BP. Meromixis was intermittent throughout the Holocene, interrupted by periods of water evaporation and ensuing deposition of marl, such that they were able to infer a record of “effective precipitation” for Mahoney Lake and compare that record with other regional paleoclimate records. Curiously, the “effective precipitation” (precipitation over and above what is lost by evaporation) record does not accurately follow either the glacial retreat/advance patterns or forest development patterns from other paleoenvironmental studies. Lowe et al. (1997) note a nearly four metre decrease in lake level between 1982 and 1995, together suggesting that this lake is much more sensitive to climatic changes than perhaps other lakes, and that the dominating Pacific weather system (wet vs dry winter) has a greater influence on lake level than general climatic trends.

Heinrichs et al. (1997) also used the same sediment core to reconstruct paleosalinity examining sub-fossil chironomid and diatom remains. Using the rationale that during periods of low effective moisture, the water balance of this closed-basin lake would favour high salinity, whereas during cool-

er or wetter periods, the lake would favour more freshwater conditions. The proxies both indicate fresh water conditions occurred prior to 9800 yr BP, with a subsequent shift to saline conditions (about thirty grams per litre) thereafter. This dramatic difference was considered to reflect the loss of glacial water input into the system (Heinrichs 1995). Refinements to the models used for calculating paleosalinities support the large shift from freshwater to saline conditions early in the Holocene (Heinrichs et al. 2001), and weakly support the idea of cooling during the last few millennia (Heinrichs and Walker 2006). The impacts of regional climate fluctuations have generally been observed in other local lakes using a variety of proxies (Walker and Pellatt 2008).

In a ground-breaking, environmental DNA study (Coolen and Overmann 1998), genetic material from purple sulfur bacteria was sequenced for the first time from lake sediment (Parducci et al. 2017), specifically, from the same sediment core used in the preceding studies. Coolen and Overmann (1998) used the 16S rRNA gene fragments from *Thiohalocapsa* sp. strain ML1 (formerly *A. purpureus*) from the chemocline and compared them against samples from the sediment as far back as 9100 years old, confirming that they were 99.2 percent identical. Thus they confirm that it was this bacteria species that was present from early on in the lake's history, persisting through both meromictic and holomictic stages.

The last study to use this sediment core was that by Hall and Northcote (2000), tracking geochemical changes. The total phosphorus curve showed a decrease following deglaciation, suggesting that availability of this nutrient was greater from pulverized glacial flour, as no new sources were available thereafter. The calcium and magnesium curves were suggested to be correlated with evaporative conditions, such that peaks in the early- (approximately 10,000-7000 yr BP) and mid- (6000-4000 yr BP) Holocene were relatively dry periods. This generally supports the pattern identified by Lowe et al. (1997) with lake levels. Maximum productivity in the lake occurred after 5000 yr BP, with peaks in total nitrogen and organic matter in the sediment. A relatively recent decline in productivity (i.e. during the last 1000 years) may be due to unfavourable conditions for the sulfur bacteria.

It has to be kept in mind, however, that photosynthetic production of anoxygenic phototrophic

purple sulfur bacteria depends on the presence of sulfide, which in Mahoney Lake is formed by sulfur- and sulfate-reducing bacteria as in other non-geothermal lakes. Ultimately, anoxygenic photosynthesis is therefore fueled indirectly by organic carbon that has been produced by oxygenic photosynthesis within or outside the ecosystem (Overmann et al. 1993). In the case of Mahoney Lake, the high ratio of primary production of purple sulfur bacteria to that of phytoplankton most likely is due to a substantial input of allochthonous organic matter. The input of purple sulfur bacterial biomarkers into bottom sediments is therefore determined by a complex interplay of light availability, allochthonous organic carbon concentrations, and sulfide availability/production in the chemocline, as well as the death and sedimentation rates of the purple sulfur bacterial cells.

Paleolimnological research was renewed by researchers from the University of Pittsburgh (UP) and Indiana University – Purdue University of Indianapolis (IUPUI), who returned to Mahoney Lake in 2015 in order to study its sulfur cycle, paying particular attention to organic sulfur (i.e., sulfur incorporated into organic matter during diagenesis – aka sulfurization). The relative abundances of inorganic, organic, and elemental sulfur can be used to reconstruct (paleo)environmental redox conditions. Relative to the long-standing proxies and interpretive framework developed for pyrite formation and deposition, studies focused on the organic sulfur record are limited. The major obstacles associated with the interpretation of the organic sulfur record are related to unknowns surrounding the timing and pathway(s) of formation of individual organic sulfur compounds and the extent to which organic sulfur isotope compositions, both bulk and molecular, record primary depositional conditions or are diagenetically overprinted. The coupled cycling of sulfide oxidation and sulfate reduction were explored from the water column and a sediment core obtained in 2006, demonstrating that pyrite (FeS_2) deposited in the lake was generated in the water column (Gilhooly et al. 2016). Gilhooly III et al. (2016) confirmed that this sulfur derives from minerals of the Kitley formation.

Because Mahoney Lake represents an end-member of extreme, environmental euxinia, it provides an excellent location for detailed studies of organic matter sulfurization. Therefore, water col-

umn samples and a composite ca. four metre long sediment core were recently acquired. Bulk measurements of inorganic sulfur, organic sulfur, carbon and nitrogen abundance and isotope compositions, as well as redox trace metal measurements on samples from the sediment core have been completed. Sulfur isotopes of individual organic sulfur compounds were also measured. Similar bulk analyses were also performed on water column samples of dissolved and particulate organic matter. Data from these analyses have yet to be published, but have revealed insights into the complex interplay of the coupled biogeochemical cycles of carbon, sulfur, and iron, with important implications for interpretation of the geologic record and reconstruction of (paleo)environmental conditions.

In addition to their sulfur work, the UP and IUPUI researchers also analyzed molecular biomarker proxies in water column particulate organic matter as well as in the surface sediments. Specifically, they catalogued the structural diversity and abundance of bacteriohopanepolyols (BHPs) – a promising class of hopanoid biomarkers used for tracing microbial activity and reconstructing (paleo) environmental conditions. They found distinct differences among the BHP compositions and oxic, suboxic, and euxinic water column conditions. The BHP compositions within the water column were also found to be distinctly different from those within the surface sediments. The results mentioned are currently in preparation for publication and have great potential to provide new and complementary information related to environmental and microbial dynamics throughout Earth's evolution and especially during times of extreme environmental transitions (e.g., oceanic anoxic events).

Purple sulfur bacteria and more

With the recognition that the sulfur bacteria of Mahoney Lake were not only highly abundant but also the key drivers of most geochemical processes, additional characterization of the sulfur transformations and bacterial communities commenced. What may have begun as just an anomalous oddity worth a quick second look, the sulfur bacteria story has gone on to capture the imagination of astrobiologists. Upon returning to Mahoney Lake, Overmann et al. found two new strains (06511 and SSP1) of a sulfur bacteria from the littoral sediments,

newly described as *Thiorhodovibria winogradskyi* gen. nov. and sp. nov (Overman et al. 1992)). Of particular interest is the fact that these bacteria are exposed to and thus naturally tolerant of sunlight and oxygen, as well as highly saline conditions during periods of evaporation.

The dominant sulfur bacteria in the water column, *Thiohalocapsa* sp. strain ML1 (formerly *A. purpureus*), was documented to form aggregates that remain buoyant due to cell surface hydrophobicity when sulfide was depleted. With normal concentrations of sulfide, gas vesicles allow the bacteria to remain buoyant. These paired mechanisms were proposed to maintain the specific depth of the bacterial community layer (Overmann and Pfennig 1992). With fluctuating amounts of sulfide in the water column during the year, the populations of *Thiohalocapsa* sp. strain ML1 were observed to adapt accordingly (Overmann et al. 1994). Minimum late summer sulfide concentrations trigger the die-off in *Thiohalocapsa* sp. strain ML1 (Overmann, Beatty, Krouse et al. 1996). Excess bacterial cells then enter the mixolimnion during autumn. Wind-driven erosion of the surface of the chemocline population eventually deposits visible, bright purple masses on the littoral sediment (Overmann, Beatty and Hall 1996). In yet another bizarre twist, the excess *Thiohalocapsa* sp. strain ML1 cells that were not able to survive and ended up in the oxygen-containing mixolimnion acted as a significant phosphorus source for aerobic, heterotrophic bacteria which are otherwise limited by this nutrient throughout the rest of the year.

Bacteria are not the only (interesting) biological resident in the water column. With this abundant primary producing bacterioplankton community, it makes ecological sense that there would be a secondary trophic network. Heterotrophic flagellates, ciliates, rotifers, and calanoid copepods (e.g. *Diaptomus connexus*) have been observed (Overmann, Hall, Northcote, Ebenhöf et al. 1999). Because of the salinity of the water itself, fish are not able to survive, which would otherwise feed upon the copepod community. Whereas most lakes would have copepods feeding upon a 'lower' trophic herbivore, here they also feed directly upon the purple sulfur bacteria (Overman, Hall, Northcote and Beatty 1999).

The bacterial community of Mahoney Lake is not limited to only a few species of purple sulfur bac-

teria in the layer or plate at the chemocline. Yurkova et al. (2002) documented thirty-one strains of obligate aerobic phototrophic bacteria, along with two new purple non-sulfur bacteria, from the mixolimnion using classical microbial methodology. From these same samples, Rathgeber et al. (2005) were able to isolate eight strains of Gram-negative pink-purple bacteria within the Alphaproteobacteria. They proposed a new genus of bacteria with a species classified as *Roseicyclus mahoneyensis* gen. nov., sp. nov. Beneath the chemocline, in the deep, dark, saline hypolimnion, a diverse community of bacteria also occurs (Klepac-Ceraj et al. 2012). In sulfate-rich ecosystems such as Mahoney Lake, sulfur compounds are the main inorganic compounds used by the anaerobic heterotrophic bacteria degrading organic carbon in anoxic layers. Sulfate-reducing and sulfur-reducing bacteria were indeed detected and highly active within the chemocline population of *Thiohalocapsa* sp. strain ML1 (formerly *A. purpureus*) and below (Overmann, Beatty, Krouse et al. 1996). Variation in abundance between the Epsilon proteobacteria and Deltaproteobacteria at seven and eight metres depth, respectively, is likely due to different metabolic processing of sulfur between the bacterial types, with sulfate and sulfur reduction occurring at lower depths by the Deltaproteobacteria. These bacteria are similar to those residing near methane seeps in deep ocean environments or hypersaline sediments.

New directions

There has been progress in technologies/methodologies that has meant Mahoney Lake is once again a site for novel research. Bovee (2014) and Bovee and Pearson (2014) examined individual lipid biomarkers and carbon isotopes of the basinal sediment, comparing it to both water column and littoral sediments. They found that the littoral and basinal sediments were similar, but that the materials were not generated from the bacterial community within the water column. Instead, it was the shoreline microbial community and allochthonous materials that generated the deep basin sediments, moving laterally, downslope through the density gradient prior to deposition. The bacterial community within the water column appears to be recycled within the water column itself as predicted by earlier modelling of the carbon cycle (Overmann 1997).

Hamilton et al. (2014) used metagenomic sequencing of the bacterial plate to elucidate the various bacterial participants in the sulfur cycle (oxidation and reduction). The main purple sulfur bacteria *Thiohalocapsa* sp. strain ML1 (formerly *A. purpureus*, later *L. purpurea*) was the dominant primary producer, however, a host of oxidizing and reducing organisms were identified from genomic markers. Again, using genetic analyses, Hamilton et al. (2016) found little evidence for organisms capable of oxidation below the chemocline, rather they found numerous populations that were reducers of sulfur. They identified a new taxonomic lineage in the Fibrobacteres+Chlorobi+Bacteroidetes superphylum from samples below the bacterial plate / chemocline, proposing the name *Candidatus Aegiribacteria* MLS_C, after Aegir, the Norse God of the Sea.

Mahoney Lake represents a unique ecosystem that is sufficiently simple to serve as a model system for elucidating the processes that occurred in a stratified oxic-anoxic system of the geological past. Being distinct, it has gained the interest of a number of special interest groups. NASA has identified the lake important from an astrobiological perspective (Gronstahl 2016). The unusually harsh conditions here may be an analogue for environments on exoplanets.

Future studies of Mahoney Lake will improve our understanding and the interpretation of sedimentary deposits of the geological record even further. It has also been proposed that Mahoney Lake be considered an ideal teaching site for future limnologists due to its unique characteristics and long history of research (Northcote and Hall 2008). Many interesting research questions from Mahoney Lake can yet be asked, e.g.: is the sulfur trophic web consistent through the lake's history? Have geological strata similar to the Kiteley Lake formation led to similar sulfur bacterial communities elsewhere? How will future climate and environmental changes affect Mahoney Lake? As an Ecological Reserve, it should be noted that a permit to conduct future research answering these and other questions is required from BC Parks.

Conclusion

Mahoney Lake continues to inspire new lines of inquiry into, for example biology, limnology,

and taphonomy, as well as the next generation of research scientists. From a rather humble start in measuring oxygen, conductivity and temperature values, the emerging story of this lake reflects not only our limited understanding of aquatic processes, it allows us to trip over our lack of imagination in recognizing how unique one lake can be. Further, it emphasizes the value in intense, in-depth studies of single sites vs. a one-and-done analysis of multiple sites.

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