Illinois-Indiana Sea Grant (IISG) Research Project Final Report

Section A. Summary

Title of Project: Drivers of microbial food web structure and function: Bottom-up and top-down controls across Lake Michigan

Completion Date: 3/1/2016; NCE thru 2/28/2017

Principal Investigator: Maureen Coleman, Assistant Professor, University of Chicago

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Abstract

In Lake Michigan, microbial communities are key mediators between changing lake chemistry and higher trophic levels. Nevertheless, microbial communities have been largely ignored by decades of Great Lakes ecosystem research (with few exceptions, e.g. toxic *Microcystis* blooms in Lake Erie). We used molecular tools to characterize microbial communities in the changing biogeochemistry of Lake Michigan (2012-2015) and across the Laurentian Great Lakes. There was significant heterogeneity in the structure of the microbial food web across depth, space, season, and year. Depth strongly structures microbial communities across the Great Lakes during summer stratification. Lake-specific differences in microbial abundance and composition were observed across the Laurentian Great Lakes. Upper lakes (Superior, Michigan, and Huron) contained fewer microbial cells and virus-like particles and differed in composition from lower lakes (Erie and Ontario). At the same time, there were strong similarities in microbial taxa observed across the biogeochemically-differentiated lakes. The two most abundant bacterial taxa – LD12 and acI-B1 – were the same across all lakes and we observed *Chloroflexi* in all samples collected at depths greater than 62 m. Four years of time series observations suggest that each of

the Great Lakes is an ecological metacommunity where microbial community structure depends on the biogeochemical conditions. Preliminary observations suggest that some taxa distributed across all five lakes (e.g., certain picocyanobacteria) contain different functional genes depending on the biogeochemical conditions of a particular lake, suggesting a capacity for local adaptation within the Great Lakes ecosystem.

Keywords

Microbes, Microbial Ecology, Food Web

Include a list of five keywords for indexing.

Lay Summary

Microorganisms consume, recycle, and transform essential nutrients and form the base of the food web in lakes. Understanding how the composition of microbial assemblages (i.e., which microorganisms are present and their relative abundance) and the functions they are able to carry out (e.g., photosynthesis) change over space and time can help us predict how ecosystems like Lake Michigan will respond to changes in the environment. We surveyed microorganisms across all five Laurentian Great Lakes over four years. The main factor that affected the composition of microbial assemblages was depth. For example, during summer stratification, the microbial community at the bottom of Lake Michigan more strongly resembled the microbial community at the bottom of Lake Ontario than the microbial community collected at the surface of Lake Michigan. Depth differences are not observed in the spring when the lakes are mixing; spring surface communities resemble deep communities. We also observed differences in the abundance and composition of microorganisms at the surface of the five Great Lakes, with the largest differences observed between the upper lakes (Superior, Michigan, and Huron) and lower lakes (Erie, Ontario). Despite these differences, many microbial

species were observed in all of the lakes. Some of these species appear to have different adaptations depending on which lake they inhabit, such as the ability to acquire and transform various forms of nitrogen. Together, our results reveal a complex microbial biogeography that is shaped by, and likely contributes to, biogeochemical variability across the Great Lakes.

Section B. Accomplishments

Introduction

Lake Michigan is in the midst of rapid ecosystem change. Some changes are readily observable – noxious algal blooms and the stunning invasion of quagga mussels, for instance – but arguably the most important changes are occurring among microscopic communities of Bacteria, Archaea, phytoplankton, and viruses. In Lake Michigan, these microbial communities are key mediators between changing lake chemistry, such as oligotrophication and altered phosphorus (P) dynamics (Hecky et al. 2004, Evans et al. 2011, Barbiero et al. 2012), and higher trophic levels, and therefore understanding their short-term responses and long-term adaptations to these conditions is of fundamental importance. Nevertheless, microbial communities have been largely ignored by decades of Great Lakes ecosystem research (with few exceptions, e.g. toxic *Microcystis* blooms in Lake Erie). To fill this urgent gap, we propose using molecular tools, in particular high-throughput DNA sequencing, to understand the role of microbial communities in the changing biogeochemistry of Lake Michigan.

While the 16S ribosomal RNA gene has emerged as a powerful marker for rapid taxonomic fingerprinting, it has limited utility for inferring biogeochemical functions. Complementing 16S rRNA, metagenomics can reveal broad patterns in community-

level metabolism as well as the functional capabilities of specific taxa (DeLong et al. 2006), and can pinpoint selective pressures differentially acting on two populations. Such analyses have recently implicated phosphorus (P) availability as the strongest driver of microbial differences between two ocean basins (Coleman and Chisholm 2010) and will likely reveal similar drivers across space and time in Lake Michigan. Going further, transcriptomics (RNA-level community gene expression) and proteomics can reveal which genes and pathways are most highly expressed in a given sample and which taxa are responsible for this expression (Frias-Lopez et al. 2008) – useful for capturing shorter term dynamics and responses to perturbations. Combined together, these approaches, along with detailed environmental characterization, afford unprecedented access to the microscale processes underlying the health of the entire Lake Michigan food web. These tools are particularly useful for inferring possible "bottom-up" controls on the microbial food web – i.e., what nutrient uptake and metabolism pathways are most prevalent. But a complete picture of the microbial food web must also include "top-down" controls and the fate of microbial cell components, whether they be transferred to higher trophic levels or recycled back to dissolved and particulate pools. In recent years, there has been growing evidence that lysis by viruses is a major source of microbial mortality. Not only does this process affect cell abundance, but it also liberates nutrients and short-circuits their transfer up the food chain – the so-called "viral shunt" (Suttle 2007). Moreover, the composition of DOM released by viral lysis is likely distinct from that released by grazing, as recently demonstrated in a marine cyanophage system (Ma et al. 2018). Much less is known about the role of viruses in freshwater systems, in particular the oligotrophic Great

Lakes.

Project Narrative

Methods

Sampling – We conducted field sampling across Lake Michigan in April 2015 and August 2015, as part of the Cooperative Science and Monitoring Initiative (CSMI) focus year. Samples from 2015 were compared with microbial samples collected in 2012, 2013, and 2014. Our field sampling was conducted in conjunction with the EPA's Spring and Summer Survey cruises aboard the R/V *Lake Guardian*. GF/A pre-filtered samples were concentrated onto 0.2 um filters and frozen at -80°C for characterizing water column microbial communities via DNA, RNA, and protein sequencing. Additional samples were preserved in glutaraldehyde for enumerating bacterial and cyanobacterial cells via flow cytometry and virus-like-particles via microscopy.

DNA sequencing and analysis – DNA samples have been extracted and 16S rRNA amplicons have been sequenced at Argonne National Laboratory on the Illumina MiSeq platform. We analyzed 16S rRNA amplicon sequences using the mothur software (Schloss et al. 2009) and delineated taxonomic units using minimum entropy decomposition (Eren et al. 2015). We analyzed sequences from Lakes Michigan within the context of sequences from the other Laurentian Great Lakes to determine how microbial diversity is distributed within and across lakes. We additionally carried out a meta-analysis of amplicon sequencing datasets, comparing the composition and phylogenetic relationships of microorganisms from Lake Michigan and other Great Lakes to other freshwater lake and marine systems.

Viral characterization – We enumerated virus-like particles by epifluorescence microscopy using the SYBR Gold DNA stain across spring and summer samples, in both Lake Michigan and the other Great Lakes.

Results

Lake Michigan in the context of global aquatic microbial communities

To put our observations of microorganisms in Lake Michigan and the other Great Lakes into context, we compared our 16S rRNA amplicon sequencing datasets to those from other freshwater lakes and marine systems. Community composition in the Laurentian Great Lakes was similar to that observed in other freshwater systems and distinct from marine systems (Fig. 1). Our comparison of taxa across systems yielded an intriguing finding – a lineage of SAR11 (*Alphaproteobacteria*) previously only observed in marine systems was detected at very low abundance in Lake Michigan (Fig. 2). This taxon was especially abundant in samples collected in 2015. Notably, we observe this taxon in all of the Laurentian Great Lakes and it is particularly abundant in Lakes Michigan and Ontario.

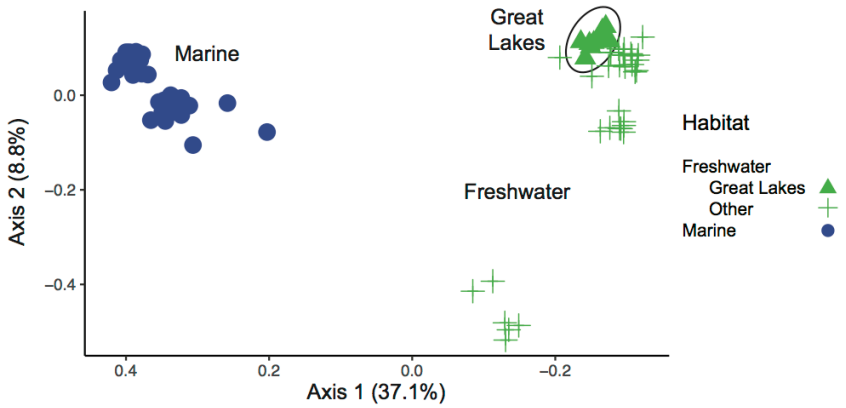


Figure 1. Principal coordinate analysis of unweighted UniFrac distances between marine and freshwater assemblages characterized by 16S rRNA V4 gene sequences.

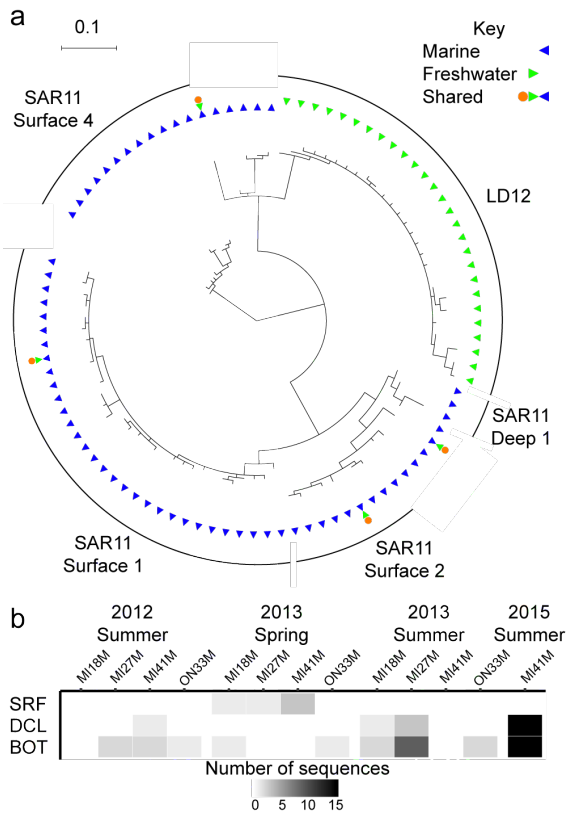
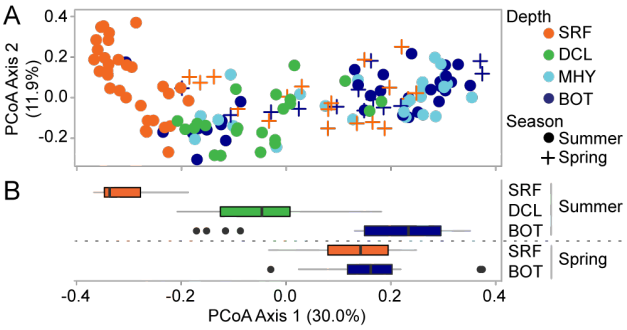


Figure 2. Observations of non-LD12 SAR11 (*Alphaproteobacteria*) in the Great Lakes. (a) 16S rRNA V4 region gene tree constructed using representative sequences from each SAR11 node. The first ring indicates whether nodes were found only in marine (blue) or freshwater samples (green) while the second ring indicates the nodes that are shared across habitat type (orange). (b) Number of non-LD12 SAR11 clade sequences detected in select stations on Lakes Michigan and Ontario.

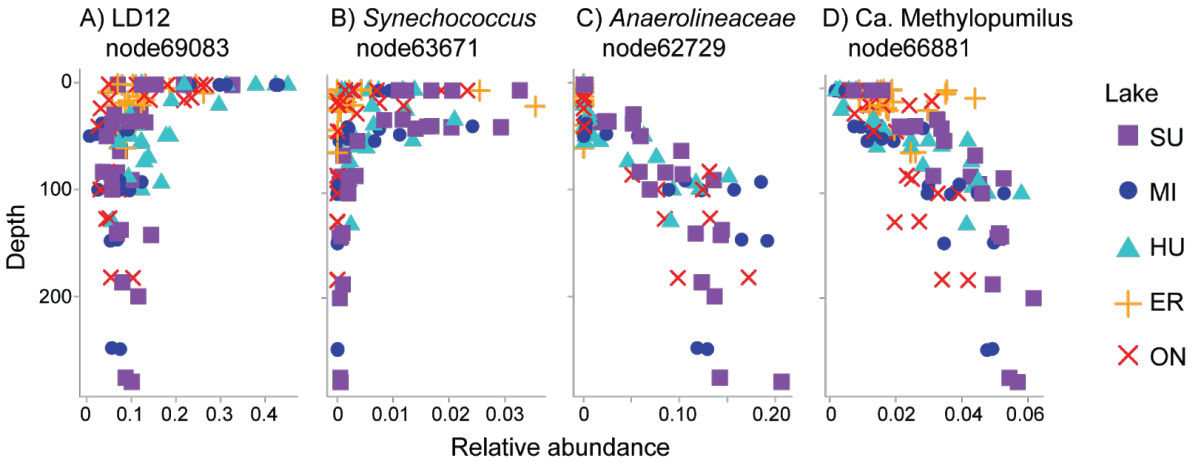
Microbial diversity across the Laurentian Great Lakes is primarily shaped by depth

Microbial communities across the Great Lakes were strongly structured by depth in deep lakes (i.e., excluding shallow lake Erie) during summer stratification (Fig. 3, PERMANOVA: Depth R^2=0.36, p<0.001, Lake R^2=0.17, p<0.001). Summer surface communities were distinct from those characterized from spring samples, with surface communities resembling the communities surveyed in deep waters during spring and summer. Changes in the composition of microorganisms with depth during summer stratification were observable at the phylum level. Phyla enriched in deep waters include *Chloroflexi*, *Nitrospirae* and *Planctomycetes*; *Cyanobacteria* were enriched in surface waters. Taxonomic units (i.e., Minimum Entropy Decomposition nodes) exhibiting differences in surface and deep water sampled included a number of the most abundant taxa. Surface-enriched taxa included an LD12 node, the most abundant taxon in the

dataset, and a *Synechococcus* node, which was also abundant in deep chlorophyll layer samples (Fig. 4A, B). A deepwater specialist node identified as *Chloroflexi* was nearly absent in surface samples while comprising 5-20% of samples collected below 100m (Fig. 4C). In contrast, a Ca. Methylopumilus node generally increased in relative abundance with depth but was observed in many surface samples (Fig. 4D).



< Figure 3. Microbial communities were strongly structured by depth during summer stratification. Principal coordinate analysis of pairwise Bray-Curtis similarities calculated between samples collected at several depths from each of the five Great Lakes during spring and summer surveys (A). Boxplots of principal coordinate axis 1 values (median +/- quartiles) for surface (SRF), deep chlorophyll layer (DCL), and 10 m from the bottom (BOT) samples collected from the four deep lakes highlight differences observed across depths (B).



^ Figure 4. Depth distribution of four MED nodes (i.e., taxonomic units) during summer stratification. Surface enriched nodes include *Alphproteobacteria* LD12 node69083 (A) and *Cyanobacteria Synechococcus* node63671 (B). Bottom enriched nodes include *Chloroflexi Anaerolineaceae* node62729 (C) and *Betaproteobacteria* LD28 node66881 (D).

Diversity patterns across lakes are driven by lake-specific as well as ubiquitous taxa

Given the overarching influence of depth on microbial communities across the Laurentian Great Lakes, we focused on summer surface samples to compare communities observed across lakes. Community composition differed between the

upper lakes (Superior, Michigan, Huron) and the lower lakes (Erie, Ontario), potentially reflecting differences in nutrient availability and productivity (Fig. 5).

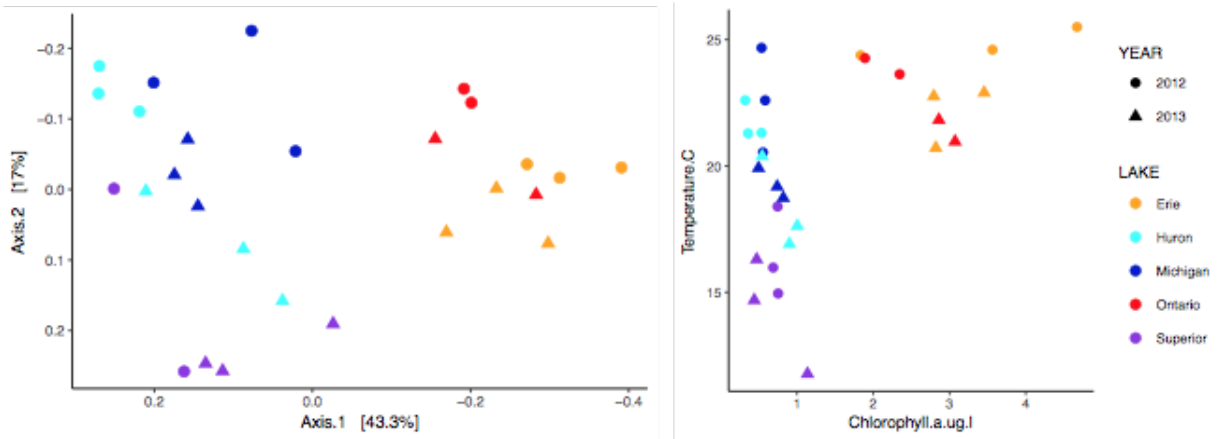


Figure 5. Microbial community composition across the Great Lakes correlates with productivity and temperature. Principal coordinate analysis of pairwise Bray-Curtis similarities calculated between summer surface samples collected from each of the five Great Lakes (A). The same samples compared based on temperature and chlorophyll a measurements (B).

Great Lakes microbial communities are composed of abundant taxa ubiquitously distributed throughout the lakes as well as taxa with a lake-specific distribution (Fig. 6). While the second most abundant taxon, classified as acI-B1, was significantly more abundant in lower lakes compared to upper lakes, it comprised an average of at least 4% of sequences in each lake. Additional taxa contributing to community level differences observed between upper and lower lakes included a taxon classified as acI-C2 which comprised nearly 10% of microbial sequences from Lakes Erie and Ontario and was rarely detected in the upper lakes.

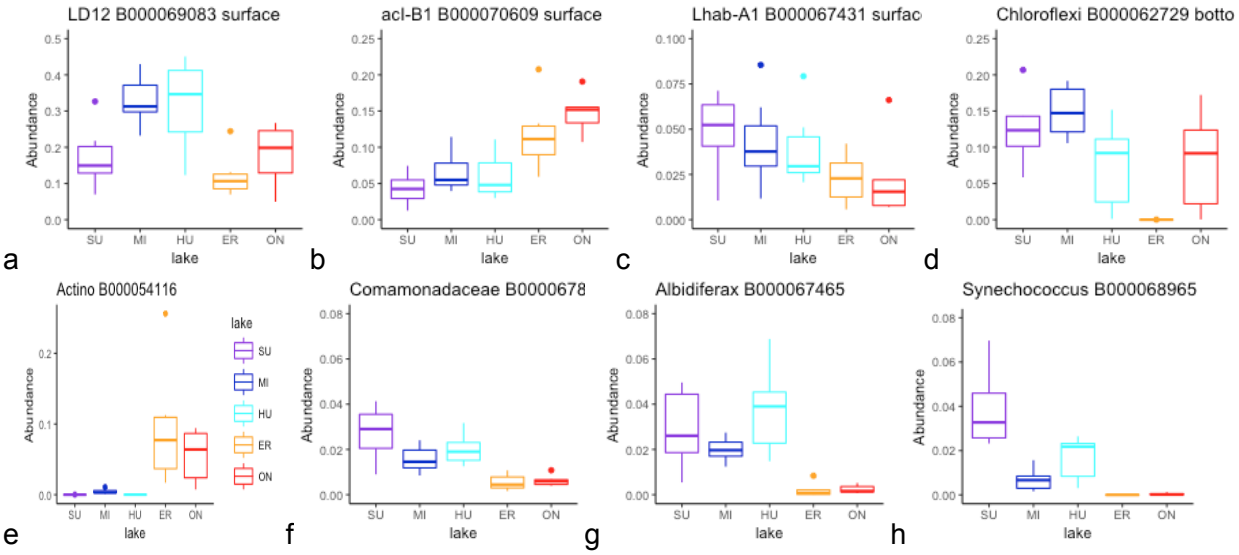


Figure 6. Microbial diversity across the Laurentian Great Lakes is shaped by abundant, cosmopolitan MED nodes and nodes with a region-specific distribution. The four most abundant nodes were generally observed at high abundance in each lake: (A) LD12 node 69083, (B) acI-B1 node 70609, (C) Lhab-A1 node 67431, and (D) Chloroflexi node 62729. Chloroflexi distribution is shown in bottom samples as it is a deepwater specialist. Nodes exhibiting significant differences in abundance between lower lakes (ER and ON) and upper lakes (SU, MI, HU) include (E) acI-C2 node 54116, (f) betI-A node 67838, (g) betI unclassified node 67465, (h) *Synechococcus* node 68965.

Patterns in microbial diversity across the Great Lakes change from year to year

Each year, microbial communities in samples collected from the upper lakes are generally more similar to each other than microbial communities from the lower lakes. When we compare microbial community composition across multiple years, we see one example where communities sampled from an upper lake that tends to have cooler temperatures (Lake Michigan) in a warmer year (2012) resemble communities from samples collected from a lower lake that tends to have warmer temperatures (Lake Ontario) in a cooler year (2015; Fig. 7). This result emphasizes the shared pool of microorganisms across lakes and suggests that changing environmental conditions

might cause the composition of microorganisms in one lake to begin to resemble the composition of microorganisms in a different lake.

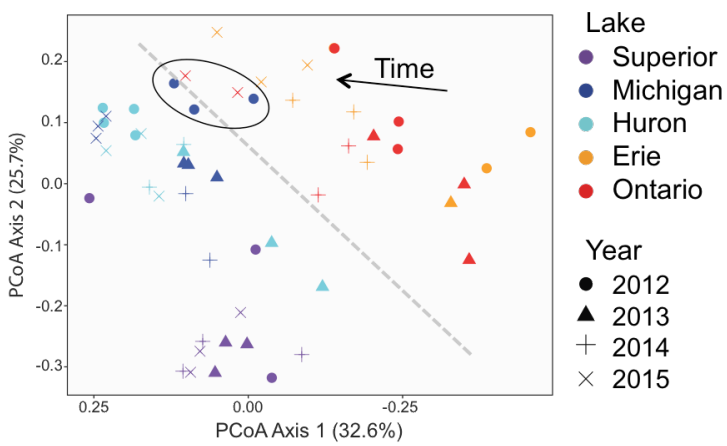


Figure 7. Changes in summer surface microbial community composition through time. Principal coordinate analysis of pairwise Bray-Curtis similarities calculated between summer surface samples collected from each of the five Great Lakes between August 2012 and August 2015.

Cross-lake and year-to-year variation in cyanobacterial distribution and function

To better understand the distribution of microorganisms across the Great Lakes, we focused on taxa within the Cyanobacteria. The distribution of cyanobacterial nodes across the Great Lakes is similar to patterns observed at the microbial community level. Certain nodes have a cosmopolitan distribution across lakes while others appear to be specialists that are enriched in the upper or lower lakes (Fig. 8A). Dominant nodes also change through time (Fig. 8B). We are starting to analyze the genomes of cyanobacteria that we observe across all the Great Lakes to characterize specific adaptations to biogeochemical conditions in the different lakes. For example, one type of cyanobacteria has a gene for a nitrate/nitrite transporter in Lakes Erie and Ontario where nitrate concentrations are lower while we do not detect this gene in the upper lakes where nitrate concentrations are higher (Fig. 9).

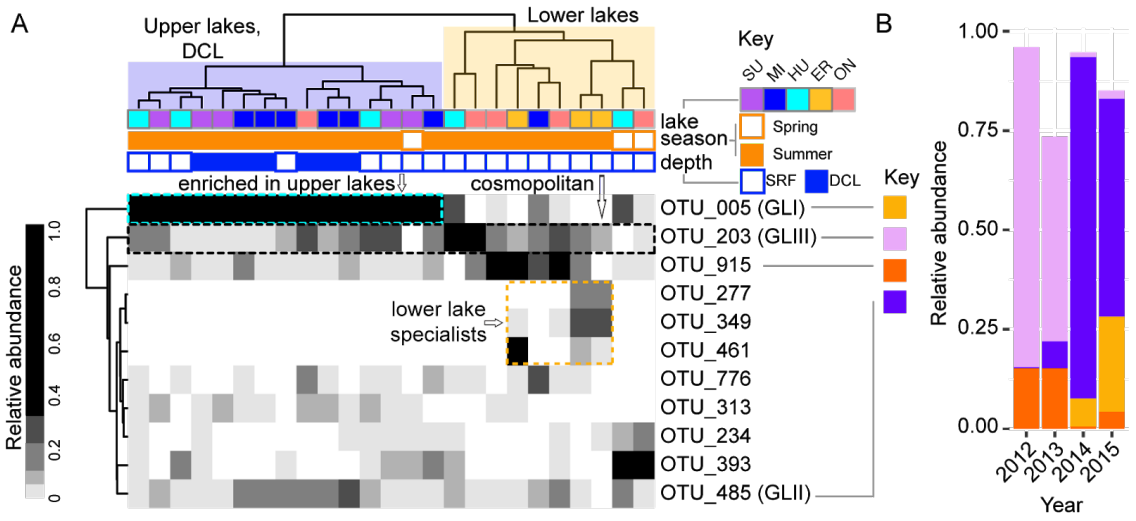


Figure 8. Cyanobacterial oligotypes (16S rRNA V4-V5 region) through time and space. (A) Heatmap showing relative abundance of oligotypes in 2012. (B) Oligotype composition over 4 years at a Lake Ontario station.

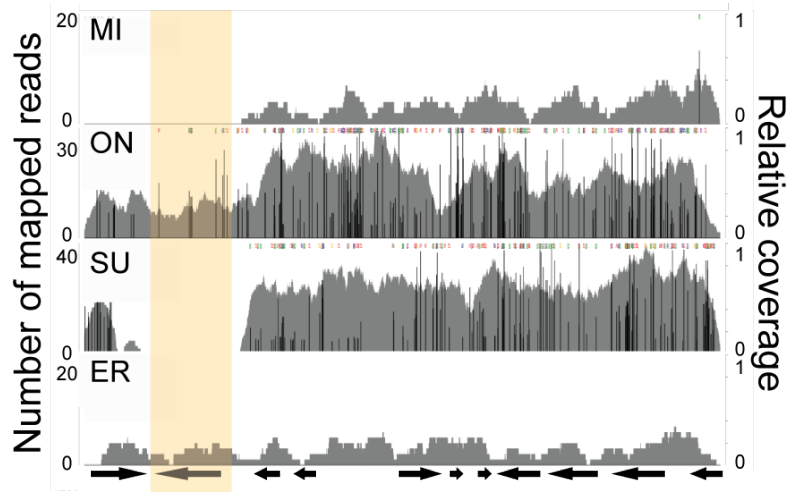


Figure 9. Mapping of six metagenomes to a genome fragment representing GLIII (from Lake Erie culture ER1303). Vertical black lines correspond to single nucleotide polymorphisms. A gene annotated as a nitrate/nitrite transporter (highlighted in orange) appears to be absent from Michigan and Superior and present in lower-NO_3^- Ontario and Erie, while the neighboring genes are present at varying levels in all samples.

Viral abundance differs across lakes and is correlated with bacterial abundance

To enhance our understanding of how viruses contribute to microbial food webs across the Great Lakes, we estimated the concentration of viruses and used metagenomics to identify the types of viruses we observe. The upper lakes tended to have a lower concentration of virus-like particles than the lower lakes (Fig. 10a). Concentration of virus-like particles increased with the concentration of bacterial cells

(Fig. 10b). The main types ('species') of virus that we observe in Lakes Erie, Michigan, and Superior are similar in each lake. These abundant Great Lakes viruses are most similar to bacteriophage sequenced from the Mediterranean Sea; they have not been cultured, and host information is not known (Fig. 11). Among the abundant types of virus (>1% contribution to viral genomic sequences) observed in Lake Michigan was a phage predicted to infect LD12 cells (in the 'Pelagibacteriales' group), which are the most abundant type of bacteria in Lake Michigan. We also detected a number of abundant cyanophage – phage that infect cyanobacteria – in Lake Erie.

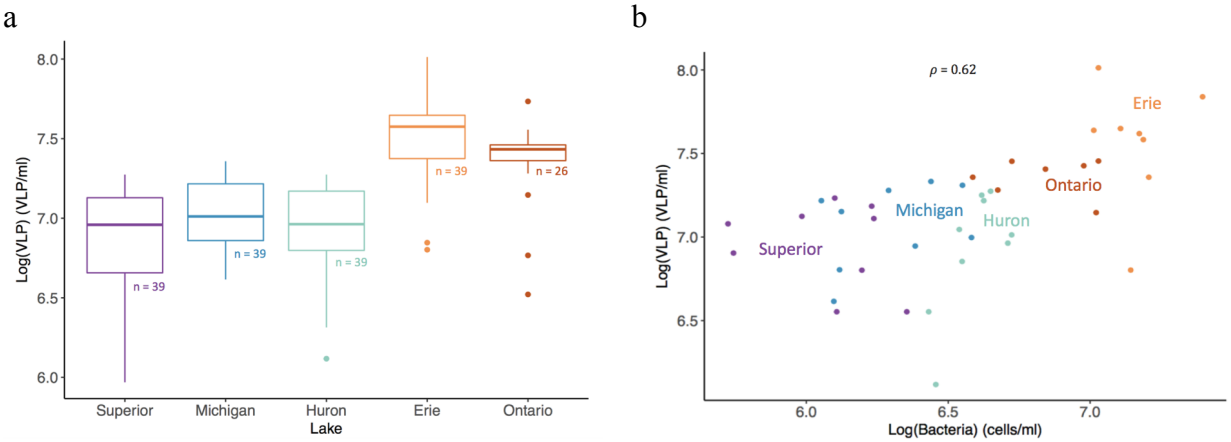


Figure 10. Lake-specific differences are observed in viral abundance across the Laurentian Great Lakes. Concentration of virus-like particles (VLP) differs across lakes (a) is correlated with the concentration of bacterial cells (b). Spearman correlation coefficient ρ=0.62.

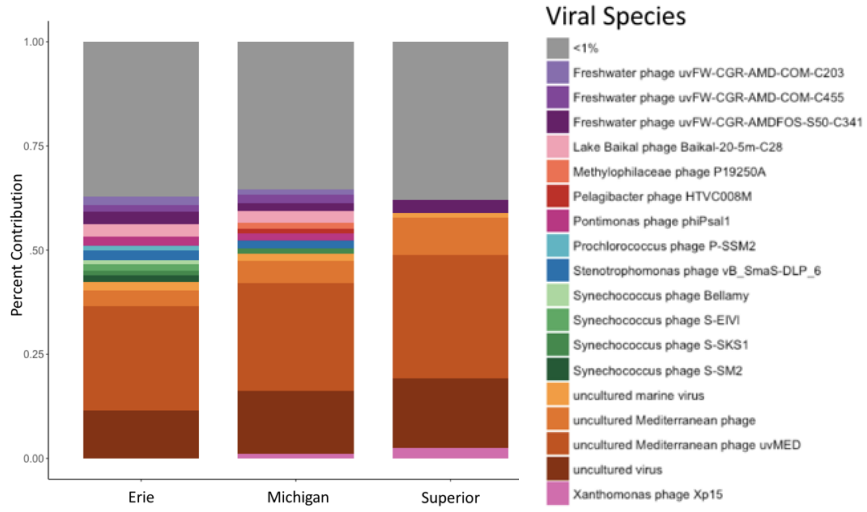


Figure 11. Percent contribution of different types of viruses 'Viral Species' to viral DNA collected from Lakes Eric, Michigan, and Superior.

Conclusions

There is significant heterogeneity in the structure of the microbial food web across depth, space, season, and year both in Lake Michigan as well as across the Laurentian Great Lakes system. Depth strongly structures microbial communities across the Great Lakes during stratified periods. Lake-specific differences in microbial abundance and composition were observed across the Laurentian Great Lakes. Upper lakes (Superior, Michigan, and Huron) contained fewer microbial cells and virus-like particles and differed in composition from lower lakes (Erie and Ontario). There were also striking similarities in microbial taxa observed across the biogeochemically-differentiated lakes. The two most abundant taxa – LD12 and acI-B1 – were the same across all lakes and we observed *Chloroflexi* in all samples collected at depths greater than 62 m. Four years of time series observations suggest that each of the Great Lakes is an ecological metacommunity where microbial community structure depends on the biogeochemical conditions. Preliminary observations suggest that some taxa distributed across all five lakes (e.g., certain picocyanobacteria) contain different functional genes depending on the biogeochemical conditions of a particular lake, suggesting a capacity for local environmental adaptation. The abundance of viruses correlates with bacterial abundance and is highest in Lakes Erie and Ontario, suggesting an important role for viruses in biogeochemical cycling and ecological processes.

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Recommendations

- Use data collected from other Great Lakes to augment what is known about the microbial food web in Lake Michigan. Changes in microbial communities across the Great Lakes may provide key insights into how communities within Lake Michigan will respond to ecosystem changes that occur over time.
- Careful consideration should be given to the depth(s) of sample collection when designing studies investigating microorganisms in the Great Lakes.

- Viral communities appear to be abundant and active in Lake Michigan and throughout the Great Lakes, and time-series monitoring of viral communities should be considered.

Outreach accomplishments

- We designed and presented ‘Microbes! Exploring Invisible Worlds’ to middle school girls at Expanding Your Horizons Chicago held on March 25, 2017. During our lesson, students designed their own microbe, choosing which adaptations to bestow upon their microbes in relation to their environment.

Potential Applications, Benefits and Impacts

- Our survey of microbial community composition across depth, lake, season, and year can help inform sampling strategies and selection of focal microbial taxa for future investigations.
- Distribution of taxonomic groups with well-defined functional contributions (e.g., cyanobacteria carry out photosynthesis) and functional genes can be used to develop predictive models of biogeochemical cycling in Lake Michigan and the other Great Lakes and predict how ecosystems will respond to perturbations.

International Implications

None identified

Section C. Outputs

Media Coverage

NA

Publications

Journal publications

- Paver, S. F., D. J. Muratore, R. J. Newton, M. L. Coleman. “Re-evaluating the salty divide: phylogenetic specificity of transitions between marine and freshwater systems” Accepted for publication in *mSystems*. Available as a pre-print on bioRxiv, June 2018: https://doi.org/10.1101/347021
- Paver, S. F., R. J. Newton, M. L. Coleman. “Microbial communities across Earth’s largest freshwater ecosystem. *In preparation for submission, Fall 2018.*

Oral presentations

- Coleman, M. L. “Microbial Ecosystems Biology in the Laurentian Great Lakes”. Omics Approaches to Freshwater Microbial Communities and CHABs, Symposium held at Bowling Green State University, April 2015.
- Coleman, M. L. “Top-down, bottom-up, and sideways: Nutrients and viral infection in picocyanobacteria”. American Society for Microbiology Annual Meeting, New Orleans, May 2015.
- Paver, S. F., R. J. Newton, M. L. Coleman. “Microbial diversity across the Laurentian Great Lakes through space and time”. The International Association for Great Lakes Research Annual Conferences, Detroit, May 2017.
- Coleman, M. L. “The Deep Blue (Inland) Seas: Illuminating Microbial Activity in Earth’s Largest Freshwater Ecosystem”. 13th Annual DOE Joint Genome Institute Genomics of Energy & Environment Meeting, San Francisco, CA, March 2018.
- Coleman, M. L. “The Deep Blue (Inland) Seas: Illuminating Microbial Activity in Earth’s Largest Freshwater Ecosystem”. University of Illinois Urbana-Champaign, Urbana, March 2018.
- Coleman, M. L. “The Deep Blue (Inland) Seas: Illuminating Microbial Activity in Earth’s Largest Freshwater Ecosystem”. University of Wisconsin Milwaukee, Milwaukee, April 2018.
- Podowski, J. C. Microbial Genomic Diversity across the Laurentian Great Lakes. The International Association for Great Lakes Research Annual Conferences, Toronto, June 2018.

Poster presentations

- Coleman, M. L., S. F. Paver, J. G. Vargas, R. J. Newton. “Drivers of Diversity across the Laurentian Great Lakes” 11th Annual DOE Joint Genome Institute Genomics of Energy & Environment Meeting, Walnut Creek, CA, March 2016.

- Paver, S. F., J. G. Vargas, M. L. Coleman. “Drivers of microbial community structure and genome diversification in oligotrophic inland seas”, International Society for Microbial Ecology, Montreal, August 2016.
- Paver, S. F., D. J. Muratore, R. J. Newton, M. L. Coleman. “Re-Evaluating the Salty Divide: A Meta-Analysis of 16S rRNA Gene Sequences from Marine and Freshwater Systems.” 12th Annual DOE Joint Genome Institute Genomics of Energy & Environment Meeting, Walnut Creek, CA, March 2017.
- Podowski, J.C., Paver, S.F., and Coleman, M.L. 2017. Elusive Freshwater Chemolithotrophs: Metagenome Assembled Genomes (MAGs) provide insight into Archaeal and Bacterial Nitrifiers from the Laurentian Great Lakes. AbSciCon, Mesa, AZ, March 2017.
- Anderson, M. R., S. F. Paver, J. G. Vargas, J. C. Podowski, A. R. Watson, P. K. Byl, M. W. Wasney, M. L. Coleman. Genomic insights into the phylogeny and metabolism of novel bacterial taxa from the Great Lakes. The International Association for Great Lakes Research Annual Conferences, Detroit, May 2017.
- Podowski, J.C., Paver, S.F., Newton, R.J., and Coleman, M.L. 2018. Genome-centric metagenomics reveals community and functional differences across the Laurentian Great Lakes. JGI User Meeting, San Francisco, CA, March 2018

Undergraduate/ Graduate Names and Degrees *(all Univ. of Chicago)*

Justin Podowski (Ph.D. student, Geophysical Sciences)

Gabriel Vargas (Ph.D. student, Geophysical Sciences)

Mark Anderson (Ph.D. student, Geophysical Sciences)

Daniel Muratore (post-postbaccalaureate, Biological Sciences)

Kyra Grantz (undergraduate, Geophysical Sciences)

Diana Bojanova (undergraduate, Geophysical Sciences)

Michael Wasney (undergraduate, Geophysical Sciences)

Shane Coffield (undergraduate, Geophysical Sciences)

Petra Byl (undergraduate, Geophysical Sciences)

Anastasia Bernat (undergraduate, Geophysical Sciences)

Project Partnerships

We have continued our collaboration with the EPA (Glenn Warren, Todd Nettesheim), which has allowed us to conduct our field sampling aboard the *Lake Guardian* and to integrate our biological data with their ongoing water quality monitoring. We also continue to collaborate with co-PI’s Ryan Newton (UW-Milwaukee) and Stuart Jones (Notre Dame).

Related Projects

Teasing apart coexisting picocyanobacteria and their contributions to biogeochemistry, DOE Joint Genome Institute, award for DNA sequencing services, awarded FY 2017

Integrated Ecosystem Genomics across a Vast and Vital Freshwater System, DOE Joint Genome Institute, award for DNA sequencing services, awarded FY 2018

Teasing apart coexisting cyanobacteria in the Laurentian Great Lakes. National Science Foundation Biological Oceanography, PI M. Coleman with co-PIs J. Waldbauer, A. Thompson, $698,196, 2018-2021

Awards and Honors

none

Patents/ Licenses

none

Section D. Metadata for Data Management Plan

Amplicon, metagenomic, and metatranscriptomic sequencing data will become freely available upon publication