Title
Seasonal 16s rRNA Inventory of Microbial Diversity and Geochemical Dynamics in the Salton Sea

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Publication Date
2023

UNIVERSITY OF CALIFORNIA
RIVERSIDE

Seasonal 16s rRNA Inventory of Microbial Diversity and Geochemical Dynamics in the Salton Sea

A Thesis submitted in partial satisfaction
of the requirements for the degree of

Master of Science

in

Earth and Planetary Sciences

by

Alyson Alanna Fresquez

September 2023

Dissertation Committee:
Professor Timothy Lyons, Chairperson
Professor Edward Schwieterman
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ACKNOWLEDGEMENTS

I sincerely thank my professor and chair of my committee, Timothy Lyons, for his generous feedback and patience. This endeavor would not have been possible without Professor Lyons' guidance and endless support. Additionally, this journey could not have been undertaken without the substantial knowledge and expertise of my defense committee, Professors Gordon Love and Edward Schwieterman.

I am also endlessly grateful for collaborating with Professor Emma Aronson and her lab group. Specifically, I acknowledge my colleague Linton Freund for their leadership and continued help in this effort. I also thank Dr. Aronson for her knowledge and insightful supervision. My deep gratitude also goes to my research colleagues, Charlie Diamond and Caroline Hung, for their abundant help, support, encouragement, insight, and dedication to this project. This project would not have been possible without all of these contributions.

ABSTRACT OF THE THESIS

Seasonal 16s rRNA Inventory of Microbial Diversity and Geochemical Dynamics in the Salton Sea

by

Alyson Alanna Fresquez

Master of Science, Graduate Program in Earth and Planetary Sciences
University of California, Riverside September 2023
Dr. Timothy Lyons, Chairperson

The Salton Sea lies at the forefront of scientific and socio-economic interests. An endorheic, polymictic lake, the Sea is characterized by elevated sulfate concentrations and sulfide eruptions within its hypersaline waters. As the lake experiences intense evaporation due to hot, arid conditions and diminishing water supply, it undergoes stratification and increasing salinity. In the summer, wind-driven mixing events cause the upwelling of anoxic hydrogen sulfide-rich bottom waters, leading to hypoxic/anoxic conditions throughout.

This study aims to elucidate the links between microbial consortia and geochemistry by teasing out spatial and temporal data for redox patterns, particularly in light of the Sea's recent shallowing and evolving thermally supported chemoclines. Water column samples were surveyed from the Sea's southern basin across three seasons and four dates, including a sulfide-rich upwelling event. Geochemical data were gathered, and microbial diversity was analyzed using 16s rRNA Amplicon sequencing.

Results reveal significant seasonal microbial assemblage variations ($p= 0.001$). Changes in microbial diversity and species richness did not significantly differ by depth ($p > 0.05$); however, there were notable changes at the chemocline, as shifts in microbial taxa reflected stratified summer waters and mixed winter/ spring waters. Microbial community composition was significantly impacted by temperature ($p= 0.001$) and oxidation-reduction potential (ORP) ($p=0.001$). Variations in diversity were evident when analyzing seasonal shifts and geochemical constituents, as modifications to metabolic pressure and electron acceptor availability determined microbial ecologies influenced by redox conditions.

Archaeal diversity was lower than bacterial diversity, with *Halobacterota* and *Nanoarchaeota* as the only two taxa found. *DS001 spp.* and *Litoricola spp.* were the most abundant genera across all samples. *Truepera spp.* was abundant in the winter and spring, while cyanobacteria *Synechococcus spp.* was abundant in August. The novel presence of *DS001* suggested the microbial capacity for detoxifying pesticides by mineralizing Methyl Parathion as a carbon source in the Sea, where this toxic contaminant is pervasive in the water, sediments, and fish species. *Actinobacteria, Gammaproteobacteria, Alphaproteobacteria,* and *Bacteroidetes* were the most prevalent microbial classes. Abundance of these taxa suggests that the Salton Sea's evolving microbial composition mirrors soda saline lake patterns, indicating a potential shift towards similar ecosystems.

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CHAPTER 1

INTRODUCTION

Salton Sea Background

The Salton Sea, situated within the Salton Trough atop the San Andreas Fault, is California's largest lake, characterized by its distinct and ever-evolving nature (Alles, n.d.; Cohen et al., 1999; Tompson, 2016). This hypersaline body is marked by complex ecological dynamics, yielding conditions that make it a unique study area.

Spanning 320 square miles and nestled 69 meters below sea level within Southern California's Imperial Valley, the Salton Sea's geological origins trace back to the Salton Sink Basin (Buckles et al., n.d., 2002). Famed for its fecund soil, the Imperial Valley benefits from centuries of silt accumulation from the Colorado River, fostering fertile farmland and an expansive river delta adjacent to the Salton Sea. The Sea's most recent wet phase initiated with a flood-induced breach of an irrigation canal in 1905, which subsequently transitioned into a terminal lake dependent solely on runoff from surrounding agricultural regions. The Sea has progressively accumulated salts so that its salinity now exceeds that of the ocean by roughly a factor of two (Cohen, 2014; Cohen et al., 1999).

Ongoing climatic shifts along with policy-related fluctuations in water influx have exposed the Salton Sea to persistent challenges. Evaporation rates remain high, and the influx of agricultural runoff exacerbates the lake's salinity, including high inputs of nutrients and sulfate via fertilizers. The resulting accumulations of chloride, sodium, and other dissolved solids (such as sulfate and bicarbonate) have led to a hyper-saline and eutrophic (nutrient-rich) environment under thermally stratified conditions (Cohen et al., 1999; Cohen et al., 2014; Douglas Barnum et al., 2017, Reese et al., 2008; Tiffany et al., 2007; Watts et al., 2001). The dynamic thermally and chemically stratified conditions have led to a complex, evolving ecosystem that impacts microbes, the wildlife (fish and birds in particular), and the human populations on the margins. This narrative will explore the intricate dynamics that define the Salton Sea and specifically will elucidate the details of spatial and temporal chemical and microbial variations that occur with depth in the lake on seasonal time scales.

Saline Lakes and Microbial Implications

Analyzing and understanding the distributions and ecologies of microorganisms worldwide is a major endeavor. Microbes have adapted to life in practically all environments (Karimi et al., 2017). Microbial populations exhibit a remarkable ability to flourish in environments characterized by extreme shifts in pH, nutrient supply, temperature, oxygen availability, and salinity (Karimi et al., 2017; Lozupone & Knight, 2007). In the face of recent human impacts, shifts in geochemical parameters are poised to induce significant modifications within the global microbial assemblage and its ecological structures (Karimi et al., 2017).

Landlocked saline lakes are among the best places to observe intricate microbial ecologies and their unique physicochemical attributes. Such lakes experience dynamic fluctuations in water levels due to agricultural practices and meteorological changes, thereby influencing water chemistry, nutrient cycling, and mixing regimens (Jones & Fleck, 2020; Watts et al., 2001). As a result, inland saline lakes undergo substantial ecological community shifts with heightened susceptibility to concomitant environmental challenges and water quality degradation (Jones & Fleck, 2020; Kjelland & Swannack, 2018; Tiffany et al., 2007; Watts et al., 2001). These lakes give us powerful opportunities to investigate the adaptations, metabolic capabilities, and interactions of microorganisms thriving in such environments (Allison & Martiny, 2008; Karimi et al., 2017; Paul & Mormile, 2017).

The Salton Sea's shallow depth, eutrophic condition, and ongoing evaporation are extreme and driving rapid change. Elevated nutrient levels (namely, nitrates and phosphates), coupled with warm temperatures, result in prolific algal growth in the surface waters (Reese et al., 2008; Tiffany et al., 2007). This combination leads to distinct layers within the water column that are partitioned into warm surface layers in the epilimnion and cooler deep waters in the hypolimnion, supported by differences in densities (Reese et al., 2008; Tiffany et al., 200; Watts et al., 2001). This stratified structure hinders the mixing of layers, further impacting the distribution of dissolved oxygen and redox conditions (Evan, n.d.; Jones & Fleck, 2020; Watts et al., 2001). The decomposition of settling algal remains under stratified conditions leads to dissolved oxygen depletion in the deep waters, ultimately giving rise to anoxic conditions within the water column (Cohen et al., 1999; Cohen et al., 2014; Natural Resources Agency, 2020; Wood et al., 2002; Reese et al., 2008; Watts et al., 2001). Thus, anaerobic microorganisms, such as sulfate-reducers, engage in anaerobic respiration, producing, for example, hydrogen sulfide as the final metabolic product [$2CH_2 + SO_4^{2-} \rightarrow H_2S + 2CHO_3$] (Reese et al., 2008; Tiffany et al., 2007). During the summer, the Sea experiences wind-driven mixing events that cause these sulfide-rich bottoms waters to mix with the surface layers, resulting in hydrogen sulfide blooms [$H_2S + 2O^2 \rightarrow SO_4^{2-} + 2H^+$] that can be temporally and spatially associated with "greentide events" (Reese et al., 2008; Tiffany et al., 2007). "Greentides" appear to be linked to surface oxidation of hydrogen sulfide that may elevate gypsum saturation through sulfate production, allowing for the spontaneous precipitation of gypsum crystals that manifest in a visible green hue (Reese et al., 2008; Tiffany et al., 2007)—although specific details remain unknown. Subsequent to these events, all available oxygen is consumed throughout the water column, resulting in significant fish and plankton die-offs (Reese et al., 2008; Tiffany et al., 2007). At other times, particularly during the summer months, oxygen deficiencies are limited to the deep and intermediate layers of the water column, with profound consequences for the ecological health and stability of the lake.

Sulfur cycling in stratified lakes involve a series of microbial transformations, with sulfate reduction and sulfide oxidation among the key steps (Gilhooly et al., 2016; Reese et al., 2008). Importantly, the Sea's seasonal stratification and hyper-productivity result in a pronounced decline in dissolved oxygen levels, giving rise to a discernible redox gradient. Specifically, when oxygen concentrations fall below 0.1mg, a redox potential of approximately -200 mV reflects these conditions, fostering the accumulation of reduced compounds, particularly hydrogen sulfide (Reese et al., 2008; Søndergaard, n.d.; Watts et al., 2001).

Building on previous microbial studies conducted in the Sea and recognizing, our study delved into the diversity of microbial community ecologies linked to the “greentide” phenomenon, seasonal variations more generally, and the complex interplay among geochemical parameters. We examined these dynamics temporally and by vertical column by characterizing the Sea’s epilimnion (0m, 2m, 3m, 4m), mixolimnion (5m, 7m), and hypolimnion (9m, 10m, 11m) in the deep central portion of the lake on four different dates spanning different seasons (June, August, December, April). We did this by extracting DNA followed by 16s RNA Amplicon sequencing (Table 1, Fig. 1). Among the seasonal collections, a “greentide” event was captured in June, marked by a substantial upsurge of sulfide-rich bottom waters. During the collection periods, the following geochemical data were recorded: oxidation-reduction potential (ORP), temperature (°C), dissolved oxygen, dissolved organic matter, turbidity, chlorophyll, and salinity (details follow below). Dissolved oxygen, ORP, and temperature readings were subsequently cross-analyzed with microbial taxa to look for possible relationships among changing water chemistry and microbial ecologies. Additionally, measurements of sulfate and sulfide concentrations were taken during three of the collection dates (August, December, and April).

As the lake continues to evolve, particularly in the face of declining water levels and attendant changes in water column redox structure and nutrient loading, this research serves as a fundamental present-day baseline for comparison to anticipated future changes. We postulate that diversity and abundances in microbial taxa have and will vary in response to shifts in water column conditions. The significance of this work is elevated by the need for geochemical and microbiological data in the face of increasing human health risks and ongoing plans for mitigation that must be finalized in light of a comprehensive biogeochemical understanding of the system (Galloway-Pena et al., 2017; Karimi et al., 2017; Nissenbaum, n.d.; Paul & Mormile, 2017).

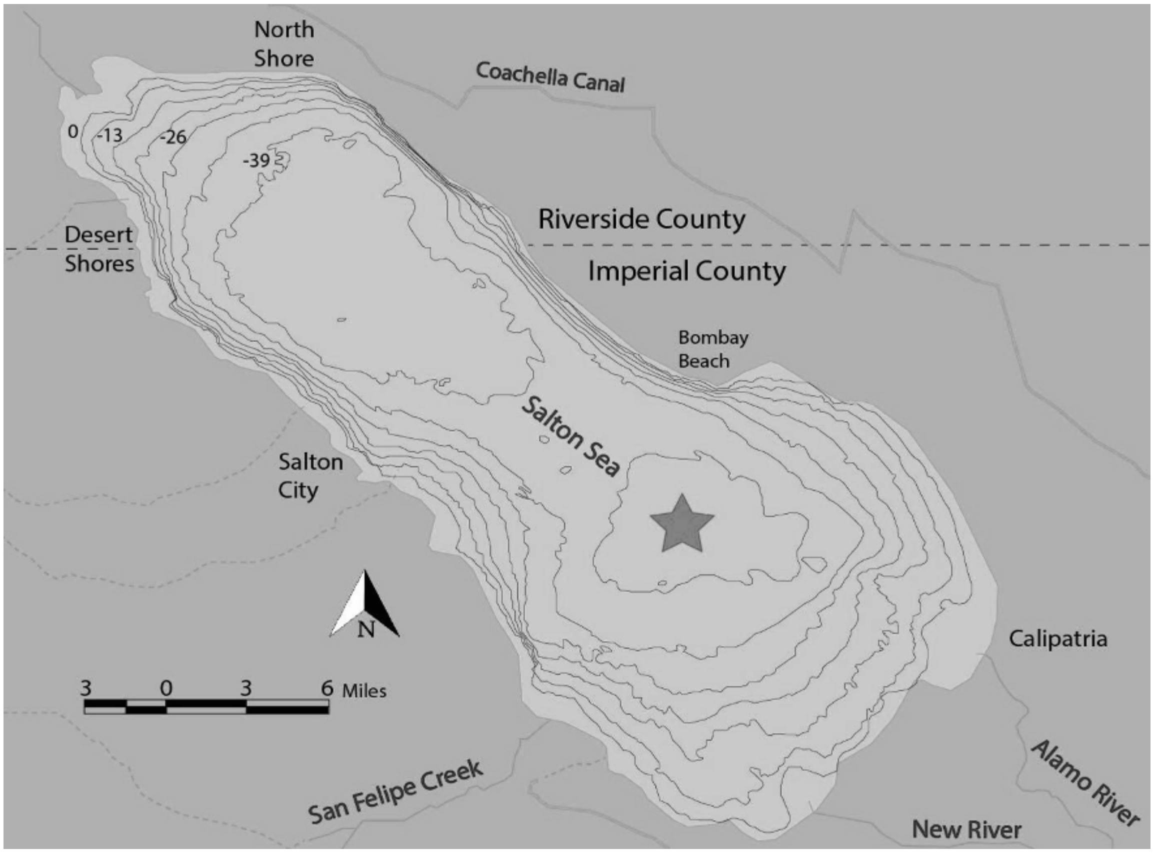


FIGURE 1. Map of the Salton Sea showing the sample location in the southern basin (star).

CHAPTER 2

METHODS

In-situ Sampling Collection

Seawater sampling and monitoring were conducted from the deepest part of the southern basin at 33.26265, -115.739 (lat., long.) on four separate occasions across three different seasons, including profiles spanning the entire water column depth (Figure 1). Specially, water was sampled at eight different depths (0m, 2m, 3m, 4m, 5m, 7m, 9m, 10m, and 11m) across the chemocline and thermocline. The first collection was during the summer season (June 15, 2021) during a hydrogen sulfide upwelling event with associated "greentide" event in the surface waters (Tiffany et al., 2007). The second collection was also during summer season (August 24, 2021) at a time with no greentide event and no significant upwelling of sulfidic bottom waters. The third collection occurred during the winter (December 21, 2021). The fourth was during the spring (April 13, 2022) The latter two also lacked hydrogen sulfide upwelling and "greentides". Water column samples collected for DNA analysis were captured using the Alexis Peristaltic Water Pump with in-situ filtering capabilities (Table 1). This device uses an accurate and precise variable speed controller for consistent flow rates to ensure the integrity of samples. Samples were collected and stored in eight one-liter acid-washed Nalgene bottles. Once collected, samples were refrigerated prior to analysis (4-6 °C).

In-situ Geochemical Water Colum Profiles

To investigate the seasonal variation of the lake stratification, a calibrated YSI EXO 2 Multiparameter Water Quality Sonde (YSI Incorporated, Yellow Springs, OH, USA) was used for determining temperature, salinity, chlorophyll, turbidity, dissolved organic matter, dissolved oxygen, and oxidation-reduction potential (ORP) throughout the water column. Samples collected for sulfide analyses were subjected to filtration using a 0.4-micron filter, followed zinc acetate preservation to determine their concentrations. Additional samples were treated with $BaCl_2$ for analysis of sulfate concentrations.

Laboratory DNA Extraction and Sequencing

Water samples were processed immediately after collection by vacuum filtration. A flow-through pre-filtration step with a 5-micron filter was followed by a 0.2-micron filter. DNA was extracted from filtered seawater with DNeasy PowerWater Kit QIAGEN. DNA purity and yields were checked by a Nanodrop analysis. Nanodrops quantify a sample's total DNA, RNA, and protein before downstream amplification. Extracts were purified using a bead-clean-up protocol. Magnetic beads bind to the DNA library. The magnet pulls the beads to one side so that all contaminants and artifacts are washed away. This step removes buffers, contaminants, and nucleotides from the sample to ensure pure DNA for downstream analysis. 16s RNA genes were amplified, and sequencing was performed with an Illumina MiSeq (2x300). V3-V4 was the target region, which contains the maximum nucleotide heterogeneity and displays the maximum discriminatory power.

16s rRNA Amplicon Data Analysis

Processing and quality screening of 16s rRNA sequences were accomplished with FASTQC and the DADA2 (Divisive Amplicon Denoising Algorithm) package by graduate student Linton Freund. FASTQC provided a thorough report on the quality of sequences as well as identification of primers still attached to sequences. The Eestats2 program was used to determine how many reads at each length have the quality required to exceed the three error thresholds: 0.5%, 1%, 2%. To decontaminate, trim sequences, cut primers and adapters, and the bbduk program was used. Within DADA2, chimeras and primer impurities were removed, as reads were trimmed and refined. Sequence variants that were potentially extrapolated by error were identified and filtered. DADA2 was used to infer that the concluding amplicon sequence variants (ASVs) calculated to be authentic variants. ASVs are analyzed identically as traditional operational taxonomic units (OTUs); however, ASVs are assigned based on 99% sequence identity, which serves as a true representation of biological sequences. All ASVs were taxonomically classified using the SILVA reference database (NRv132), Ribosomal Database Project, and the DADA2 package. ASV sequence counts were transmuted with a biomass modification by multiplying the proportion of each ASV's presence by each sample's total sequence count by the estimated number of total cells in the sample. Downstream analyses were performed using these biomass-weighted relative abundances. Distinctive abundances of ASVs within each depth and seasonal collections were executed using phyloseq.

Multivariate analysis was undertaken using the vegan package in R (R Core Team, 2022). Data formatting, transformation (data frames), and filtering were done by running the ASV count table, ASV taxonomy table, and the metadata through the vegan package in R. The vegan package was also used to calculate species richness and alpha diversity (Shannon-Wiener index). The ASV rarefaction curve was distinguished in R (Appendix Q). Figures were made using ggplot2 and ggpubr in R. To investigate if our data are normally distributed, the Shapiro-Wilk test was used. In pair-wise fashion, the Wilcoxon Test approach was used to compare means among the samples. A Pearson parametric correlation plot and Pearson's Product-moment correlation test were used to assess the magnitude and direction of the linear association between the continuous variables within the dataset. Analysis of Variance (ANOVA) and Kruskal-Wallis Test (Non-parametric) analyses were performed to compare the means across all sample dates. Fligner-Killeen and ANOVA statistical analyses were performed to determine whether microbial diversity and species richness differed significantly by depth. As Shannon Diversity is a continuous number, linear regression analysis (parametric testing) was performed in R to test if environmental factors helped predict Shannon Diversity and Species Richness.

Sulfate - Sulfide Concentrations Sample Characterization and Methods

Water column samples collected for sulfide and sulfate concentration determinations were filtered in-situ at 0.4 micron, preserved immediately with powdered zinc acetate, and subsequently chilled upon storage to slow down the growth of microbes.

The total dissolved sulfide $[\Sigma S^{2-} = H_2S + HS^- + S^{2-}]$ concentration in the water column was determined from 1 mL sample aliquots dispensed into 2 mL microcentrifuge tubes pre-filled with 0.5 mL of 20% zinc acetate, and samples were then vortexed for 5 s and stored at 4°C in the dark. Sulfide concentrations were determined colorimetrically using the Cline method (Broenkow & Cline, 1969). Sulfate concentrations were determined gravimetrically from the same filtered samples preserved with powdered zinc acetate. Sulfate concentrations determined through this method were comparable with those publicly available from the Bureau of Reclamation.

TABLE 1. Sampling locations and water depths.

Collection Date	Depth (meters)	Collection Location: Latitude (N)	Collection Location: Longitude (W)
15-Jun-21	2	33.26265	-115.739
15-Jun-21	5	33.26265	-115.739
15-Jun-21	10	33.26265	-115.739
24-Aug-21	0	33.26265	-115.739
24-Aug-21	3	33.26265	-115.739
24-Aug-21	4	33.26265	-115.739
24-Aug-21	5	33.26265	-115.739
24-Aug-21	7	33.26265	-115.739
24-Aug-21	9	33.26265	-115.739
24-Aug-21	10	33.26265	-115.739
24-Aug-21	11	33.26265	-115.739
22-Dec-21	0	33.26265	-115.739
22-Dec-21	3	33.26265	-115.739
22-Dec-21	4	33.26265	-115.739
22-Dec-21	5	33.26265	-115.739
22-Dec-21	7	33.26265	-115.739
22-Dec-21	9	33.26265	-115.739
22-Dec-21	10	33.26265	-115.739
22-Dec-21	11	33.26265	-115.739
13-Apr-21	0	33.26265	-115.739
13-Apr-21	3	33.26265	-115.739
13-Apr-21	4	33.26265	-115.739
13-Apr-21	5	33.26265	-115.739
13-Apr-21	7	33.26265	-115.739
13-Apr-21	9	33.26265	-115.739
13-Apr-21	10	33.26265	-115.739
13-Apr-21	11	33.26265	-115.739

CHAPTER 3

RESULTS and DISCUSSION

Chemical Properties of Water Column

Temperatures throughout the water column vary through the year between 25°C - 31°C in the summer season and 15°C- 25°C in the winter and spring, with the highest temperatures seen in the surface layers (Figure 2). Salinity conditions showed minimal fluctuation, varying between 57 and 61, showing substantial recent increases (e.g., compared to 40-45 g l-1; Watts et al., 2001). Other chemical constituents, Chlorophyll (RFU), Turbidity (FNU), and Dissolved Organic Matter (RFU) exhibited strong agreement and consistent values with depth in the winter and spring seasons but varied notably during the June collection, with elevated levels in the surface layers to about 5 meters depth (Figure 2). Conversely, Dissolved Oxygen (%) and Oxidation-Reduction Potential (mV) levels exhibited substantial differences between seasons, with Dissolved Oxygen values reaching zero and ORP registering negative values during the greentide event. Notably, June was marked by anoxic conditions where oxygen concentrations reached zero, and negative ORP values were observed at depths of 3 meters and below (Figure 3). Seasonality variations were also evident when sulfate and sulfide concentrations were observed for August, December, and April (Figure 4). While sulfate and sulfide concentrations were not measured during the June collection, patterns were apparent when comparing the summer to winter and spring. Sulfate levels in the water column ranged from 160-200 *mM*, with comparatively higher concentrations observed during the winter and spring, which may be attributed to many different factors but is likely associated with the high sulfate loading from the agricultural runoff, coupled with, presence of oxygen throughout the water column resulting in limited conversion to sulfide (0-10 μm). In contrast, the summer months revealed elevated sulfide concentrations in the deeper layers (10-70 μm), which is possibly linked to the 5 mm decrease in sulfate levels at the chemocline, where the absence of oxygen, promotes sulfate reduction, consequently leading to increased sulfide production (Figure 4). However, at this stage these suggestions are only observed correlations between sulfate and sulfide. Further analysis is needed to point out the causations for these results.

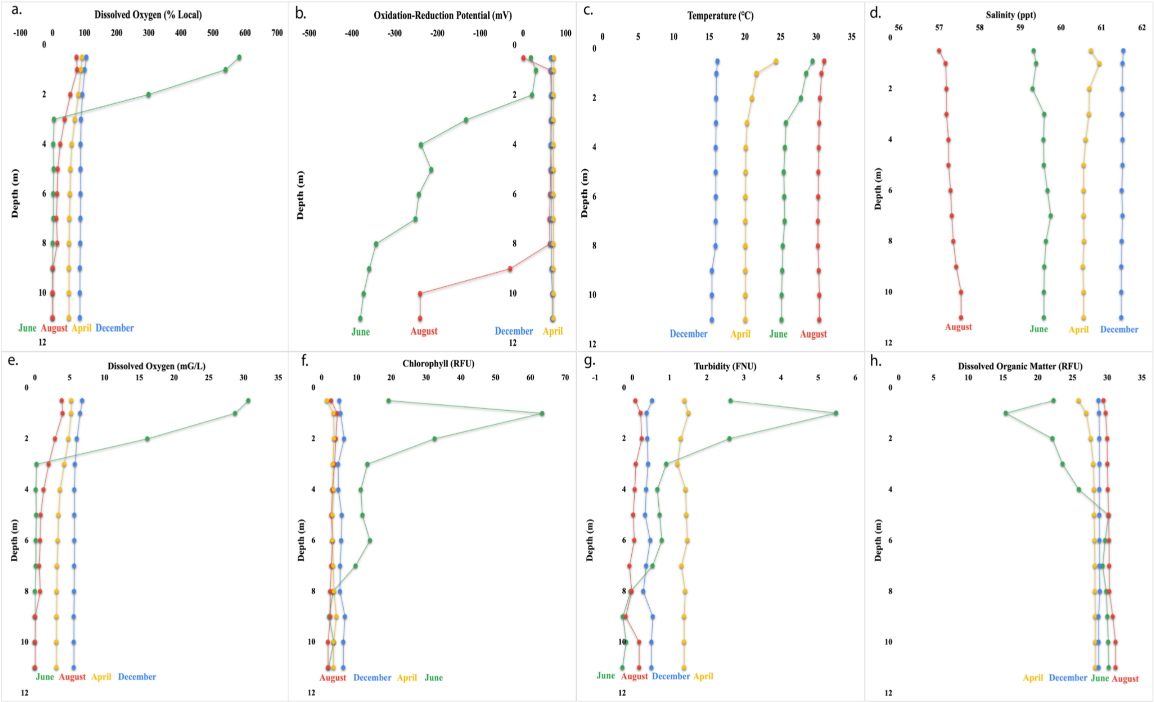


FIGURE 2. Depth profiles of the geochemical parameters of the Salton Sea water column across all four sample months: dissolved oxygen (% Local) (a), oxidation-reduction potential (mV) (b), temperature (℃)(c), salinity (ppt) (d), dissolved oxygen (mG/L) (e), chlorophyll (RFU) (f), turbidity (FNU) (g), dissolved organic matter (RDU) (h).

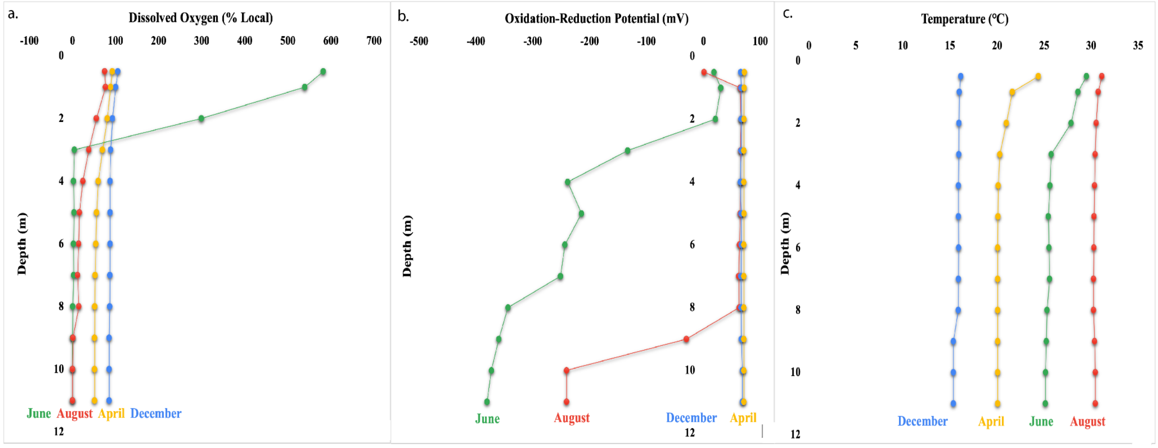


FIGURE 3. Depth profiles of dissolved oxygen (a), oxidation-reduction potential (b), and temperature (c) of the water column across all four sample months.

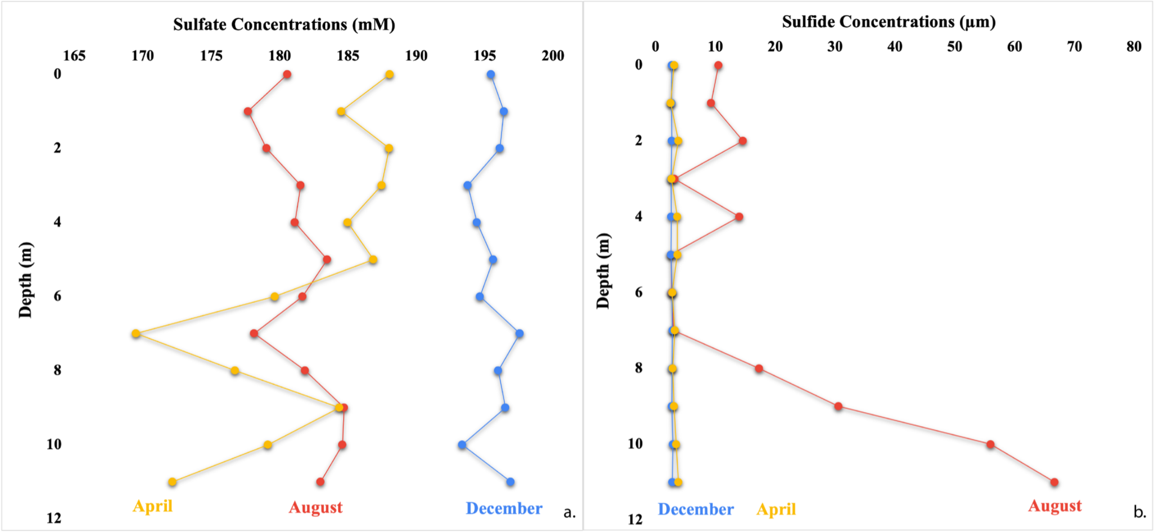


FIGURE 4. Depth profiles of sulfate (mM) (a) and sulfide (µm) (b) concentrations of the water column across all three sample months.

Taxonomic Diversity in the Salton Sea

A total sample size of 45,097 ASVs was identified, with a total count of 590,589. A total number of 44,921 unique bacterial ASVs, with a count of 590,262, and 176 archaeal ASVs, with a count of 327, were cataloged from filtered water samples. *Actinobacteriota* was the most abundant phylum, representing 42% of the data. *Proteobacteria* were the second most abundant, covering 25 % of the data, and *Bacteroidota* was the third most abundant, representing 16% of the data. The four most abundant classes were *Actinobacteria*, *Gammaproteobacteria*, *Bacteroidia*, and *Alphaproteobacteria*. *DS001* was the most abundant genus. *Litoricola* was the second most abundant genus, and *Truepera* was the third most abundant (Appendix P). Only two archaeal classes were found. *Nanoarchaeia* represented $5.4\ x\ 10^{-4}$ % (total count of 324) of the data, while *Methanosarcinia* only covered $5.8\ x\ 10^{-6}$% (total count of 3) of the data.

Microbial Shannon Diversity and Species Richness by Vertical Column

ANOVA and Fligner-Killeen analyses results indicated that microbial Shannon diversity did not significantly differ with depth (Appendices A, B, and C). Alongside this, ANOVA and Fligner-Killeen analyses also revealed that species richness did not differ significantly with depth (Appendices A, B, and C).

Although there were no statistically significant differences with depth, there are still notable disparities in stratification trends in Shannon diversity and species richness in the vertical column. The highest microbial Shannon diversity was at 10 meters depth, and the lowest was at 9 meters depth (Figure 5). These findings suggest a discernible shift in microbial communities between 9 and 10 meters, coinciding with dissolved oxygen, ORP, and temperature variations in this region of the water column. The depletion of oxygen and negative ORP values in the deeper regions that mark the chemocline support the notion of divergent microbial communities in deeper waters, ultimately indicating an ecosystem characterized by high biodiversity for species capable of thriving in low oxygen conditions. Additionally, our analysis revealed that the highest patterns of species richness resided at 10- and 11-meters depth, with the lowest at 9 meters depth. The overall suggestion is a vertical stratification of species richness influenced by the redox gradient.

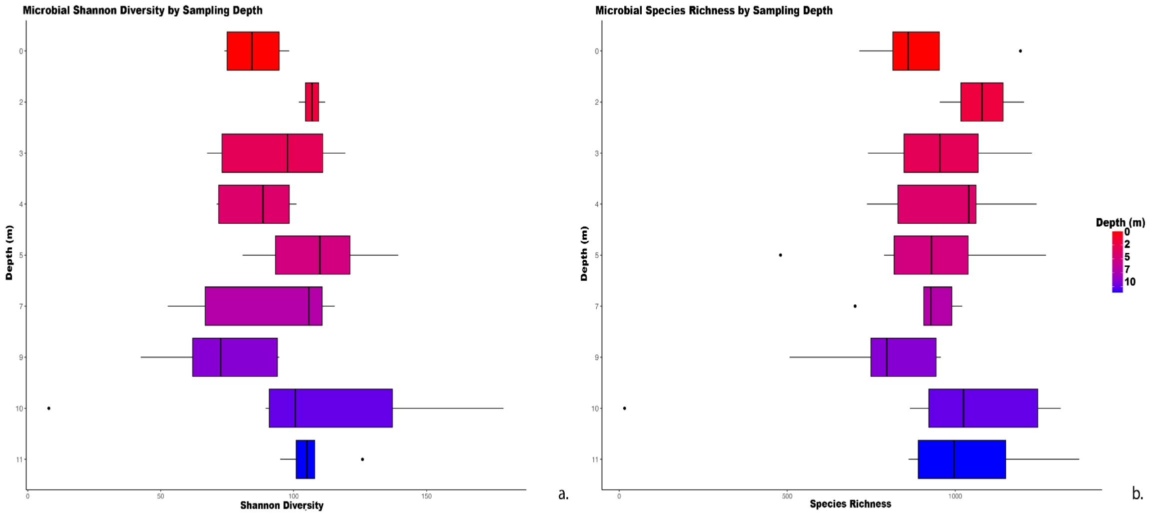


FIGURE 5. Boxplot of alpha (α) Shannon diversity and species richness by depth (vertical column), including all sample month data.

Microbial Shannon Diversity and Species Richness by Season

June showed a significantly higher average Shannon Diversity compared to all other sample months ($p <= 0.01$) (Figure 6). Additionally, analyses showed that December had a significantly higher Shannon Diversity relative to August ($p <= 0.01$). However, no significance in Shannon Diversity between December and April and August and April was observed. A likely cause for this, ties to the "greentide" event in June, characterized by comprehensive wind-induced mixing of the water column and effective transport of the deep hydrogen sulfide-rich waters vertically at locations across the lake, which facilitated the dispersion of diverse microbial species and communities throughout the water column (more below in the Synthesis).

The highest species richness was observed in August. August, June, and December had significantly higher average species richness values compared to April ($p <= 0.01$). Overall, species richness was highest in the summer months. As summer temperatures were warmer and oxygen was less abundant, an increase in productivity and proliferation of species well adapted to low redox conditions was observed.

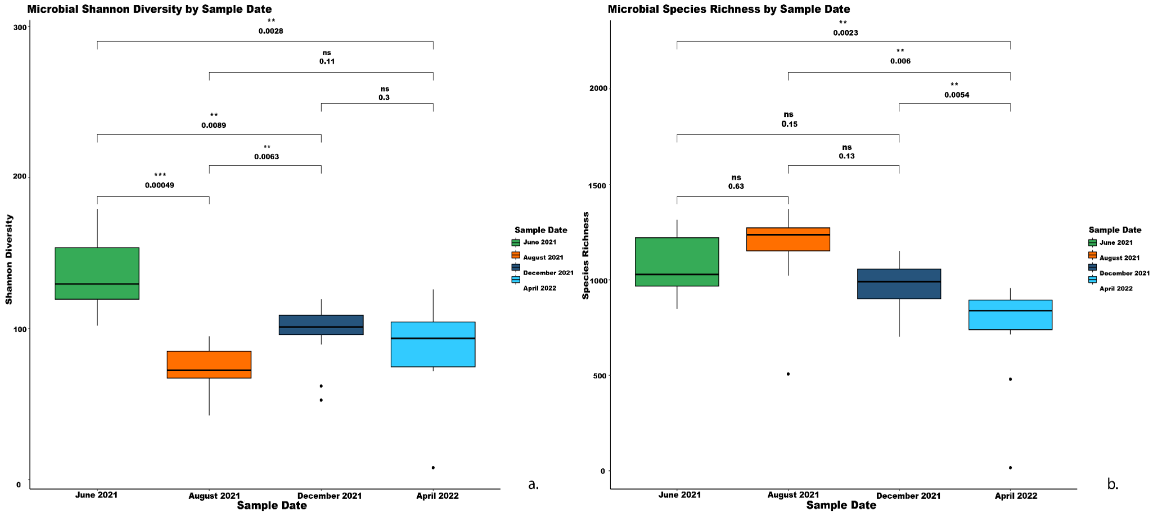


FIGURE 6. Boxplot of alpha (α) Shannon diversity and species richness by sample month. The * indicates significance magnitudes, * being p < = 0.05, ** being p< = 0.01, * being p <= 0.001, and **** being p < = 0.0001. The ns symbol stands for *not significant*.**

Microbial Diversity and Richness Cross-Correlated with Temperature, Oxidation-Reduction Potential, and Dissolved Oxygen

Distinct seasonal and stratification trends were identified when examining the cross-correlation between Shannon Diversity and the three geochemical parameters: temperature, dissolved oxygen, and ORP (Figure 7). Microbial Shannon diversity peaked in June (greentide day), coinciding with negative ORP values and diminished dissolved oxygen levels throughout most of the water column. Additionally, high variation with microbial Shannon diversity at deeper depths relative to the surface was observed, which aligned with the Sea's higher temperatures and thermal stratification, as bottom waters were characterized by low ORP and dissolved oxygen values. In contrast, less variation in Shannon diversity was recorded in Winter (December) and Spring (April), as the lake was not thermally stratified. Likewise, species richness was highest in the summer, specifically at deeper depths, and lower in the winter and spring seasons (Figure 8).

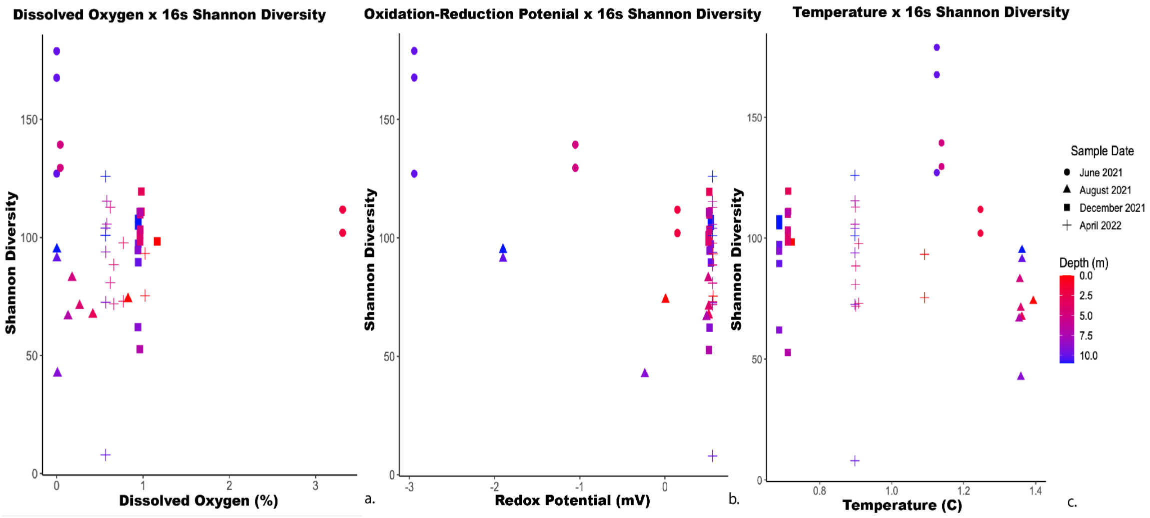


FIGURE 7. Alpha (α) Shannon diversity cross-correlated with dissolved oxygen (a), Oxidation-Reduction Potential (b), and temperature (c) by depth and sample month. Color shade indicates depth. Shape indicates sample month.

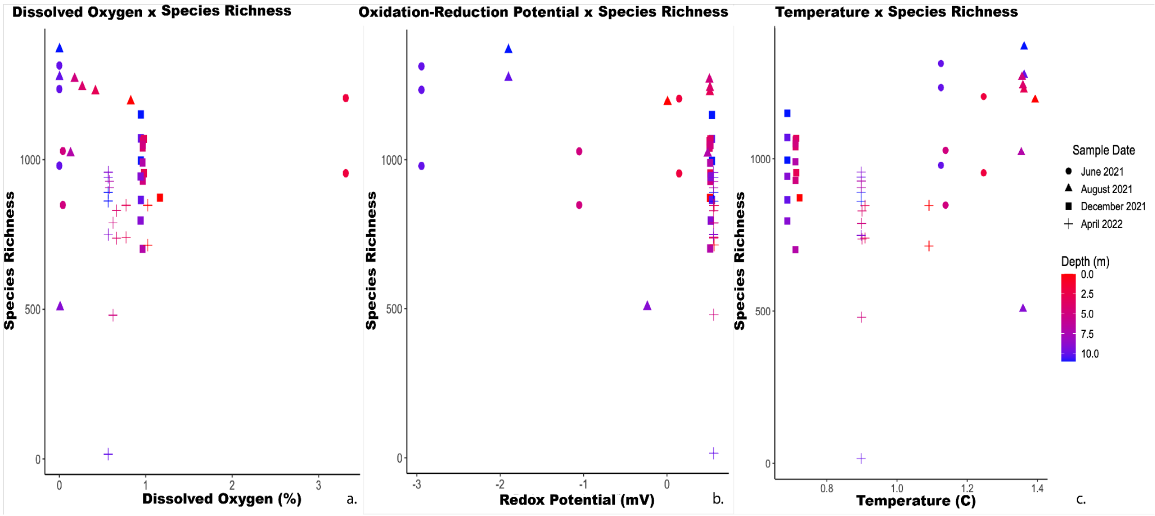


FIGURE 8. Species richness cross-correlated with dissolved oxygen (a), Oxidation-Reduction Potential (b), and temperature (c) by depth and sample month. Color shade indicates depth. Shape indicates sample month.

Statistical Significance of Environmental Variance

The Shapiro-Wilk test was employed to assess Shannon diversity, species richness, and the various environmental variables, including dissolved oxygen, oxidation-reduction potential, temperature, chlorophyll, turbidity, and dissolved organic matter (Appendix D). As salinity was consistent throughout the all-sample months, it was not included in statistical testing. Shannon diversity did not significantly deviate from a normal distribution, while species richness differed appreciably from a normal distribution. Other than salinity, all tested geochemical and physical parameters differed significantly from a normal distribution: temperature, dissolved oxygen, oxidation-reduction potential (ORP), turbidity, chlorophyll, and dissolved organic matter.

Nonparametric tests were conducted to compare the environmental variables by sample date. Due to the absence of a normal distribution in the data, nonparametric tests were performed to eliminate any assumptions regarding the underlying distribution of the data. A Kruskal-Wallis Test was employed to determine if there were statistically significant differences in the environmental variables based on their medians, while the Pairwise Wilcoxon test was used to compare each environmental variable between sample months (seasons) (Appendix E and F). The variance in dissolved oxygen between sample months showed a statistical significance for the summer compared to winter and spring and a statistical significance between winter and spring. Specifically, there was a significant difference in dissolved oxygen between August and December and December and April ($p <0.001$). ORP variance was statistically significant across all sample months (across all seasons ($p < 0.001$). Temperature variance showed a significant statistical difference across all sample months ($p < 0.001$). Turbidity, chlorophyll, and dissolved organic matter exhibited a significant statistical difference between seasons ($p < 0.001$).

Environmental Variable Correlation

The interrelationship of these environmental variables was investigated to ascertain potential trends among these geochemical parameters that could exert influence or drive one another (Figure 9, Appendix G). A positive correlation was identified between dissolved oxygen and ORP, while a negative correlation was observed between dissolved oxygen and temperature. Similarly, a negative correlation was observed for ORP and temperature, lending support to the notion that elevated lake temperatures lead to reduced availability of dissolved oxygen, consequently resulting in diminished ORP, indicative of an increasingly reducing aquatic environment. Additionally, ORP and dissolved oxygen correlated positively with turbidity, while a negative correlation was observed with temperature. Chlorophyll appeared to correlate positively with dissolved oxygen, temperature, and turbidity.

Pearson's Product-moment correlation analysis revealed that the positive correlation between dissolved oxygen and ORP was statistically significant ($p < 0.001$) (Appendix G). Further, the negative correlation between temperature and ORP was statistically significant ($p < 0.001$). Dissolved oxygen was observed to have a statistically significant positive correlation with chlorophyll ($p <0.001$), while ORP's positive correlation with chlorophyll was not statistically significant. Additionally, dissolved oxygen, ORP, and chlorophyll were observed to have a statistically significant negative correlation with dissolved organic matter.

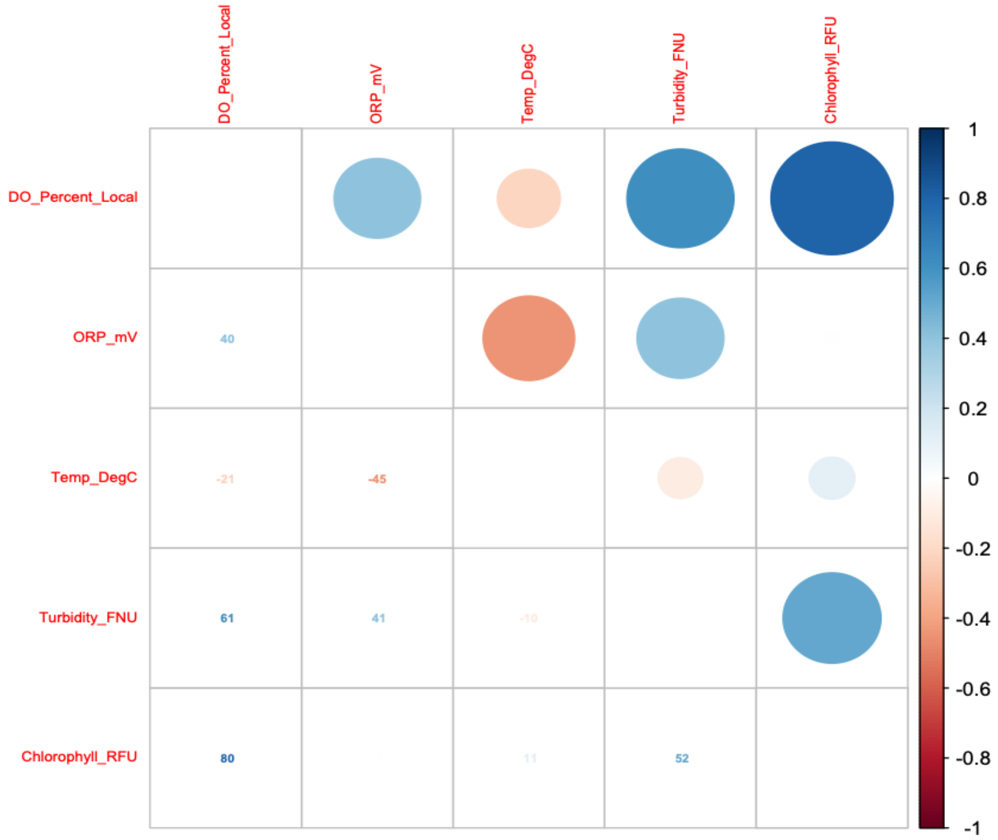


FIGURE 9. Pearson-Correlation Plot of geochemical parameters. Negative correlations are indicated in red, and positive correlations are in blue. Color size and intensity are proportional to the correlation coefficients. On the right side of the plot, the legend shows the correlation coefficients and the reciprocating colors.

Linear Regression Shannon Diversity and Species Richness

Linear regression analyses were performed to examine the relationship between environmental variables and Shannon Diversity and species richness (Appendices H and I). Results indicated that dissolved oxygen, temperature, and dissolved organic matter were not statistically significant predictors of Shannon diversity, while ORP was a significant predictor ($p < 0.001$). A subgroup analysis was conducted to further investigate the significance of ORP in predicting Shannon diversity and distinguishing between summer and non-summer months. This effort revealed that ORP was only a significant predictor of Shannon diversity during summer, whereas no significant relationship was observed during the winter or spring. Dissolved oxygen and dissolved organic matter were found to have no statistically significant influence on species richness. However, in contrast to Shannon diversity, temperature was a significant predictor of species richness ($p < 0.001$). In addition, ORP was identified as a significant predictor of species richness. However, ORP differed from Shannon diversity, as ORP was a statistically significant predictor for species richness in winter and spring instead of summer ($p < 0.001$).

These trends suggest that temperature serves as a reliable predictor for the number of species in a given location. However, it remains unclear which specific taxa dominate the community. Thus, temperature may facilitate a greater number of organisms inhabiting a community, but it does not provide insights into their potential significance or contributions to the overall composition of the community.

Upon evaluation of the results of ORP as a significant predictor of species richness and Shannon diversity, an observed increase in the number of species can be attributed to the decrease in ORP, indicating the potential for proliferation, survival, and success of species within the community under reduced ORP conditions. Based on subgroup linear analysis, ORP significantly predicted Shannon diversity in the summer months and species richness in the winter and spring ($p < 0.001$). Thus, when considering the observed seasonal variations for ORP, it becomes evident that ORP effectively predicts species' proliferation, success, and abundance in the summer months. However, during the winter and spring, ORP is only able to predict the number of species in a given niche without providing precise information regarding the dominant taxa.

It is important to mention that linear models may not be effective in predicting Shannon diversity in the community (as Shannon diversity is continuous data), but they can be valuable in predicting species richness. This relationship further highlights the interconnectedness and complexity of ecological systems, emphasizing the need to consider all factors and ecological interactions.

Microbial Relative Abundance

Archaeal Composition

Archaeal diversity throughout the water column was significantly lower than bacterial diversity. *Halobacterota* and *Nanoarchaeota* were the only two archaeal taxa found. From these phyla, the classes observed were *Methanosarcinia* and *Nanoarchaeia* (Figure 10). *Nanoarchaeia* was observed throughout all seasons and at all depths.

Woesearchaeales, an order from the class *Nanoarchaeia,* was most abundant, while *Methanosarciniales,* an order from class *Methanosarcinia*, was found only in April and August.

Bacterial Composition by Microbial Class and Family

The class *Actinobacteria* exhibited the highest relative abundance, accounting for (> 20-50 %) of the samples (Figure 10). *Gammaproteobacteria* followed suit with abundance ranging from (> 10-30 %) and most prevalent at deep depths during December and April and shallower depths during June and August. *Bacteroidia* and *Alphaproteobacteria* (>10- 20%) were also abundant throughout the seasons, particularly at intermediate and deeper depths. *Bacilli* and *Clostridia* were abundant in June (>10 %). *Rhodothermia* and *Acidiomicrobia* were only abundant in the December collection, *Deinococci* was only relatively abundant in the April collection (>10 %), and *Cyanobacteria* appeared to be abundant in the August collection (>10 %). Our analysis indicated that *Actinobacteria, Gammaproteobacteria, Alphaproteobacteria,* and *Bacteroidetes* were the predominant bacterial taxa across all samples. These findings were consistent with previous analyses in 2005 that found *Gammaproteobacteria, Alphaproteobacteria,* and *Bacteroidetes* to dominant the Sea water; however, we recorded a shift in abundance of these communities, with *Actinobacteria* emerging as the dominant taxon, surpassing *Gammaproteobacteria,* the dominant taxa in the 2005 water column findings (Dillon et al., 2009). Additionally, these findings corroborated the observation that cyanobacteria play a minor role in population composition (Dillon et al., 2009), in contrast to previous results from the water column in September 2005 (Swan et al., 2010).

Microbacterieacae was the most abundant family (>15-30%) across all sample months. *Nitriliruptoraceae* showed a high relative abundance in August, December, and April, but not June (Figure 11). *Fusibacteraceae* and *Flavobacteriaceae* were only abundant in June (> 5-15%), while *Cyanobiaceae* was highly expressed only in August (> 5-10%). *Litoricolaceae* was relatively abundant in the summer months and spring. *Rhodobacteraceae* showed its highest abundance in June (> 5-15 %), followed by April (> 5-10%). *Trueperaceae* and *Balenolaceae* were only relatively abundant in December and April (> 5-10%). An *unknown* family was also relatively abundant across all seasons (> 20%)

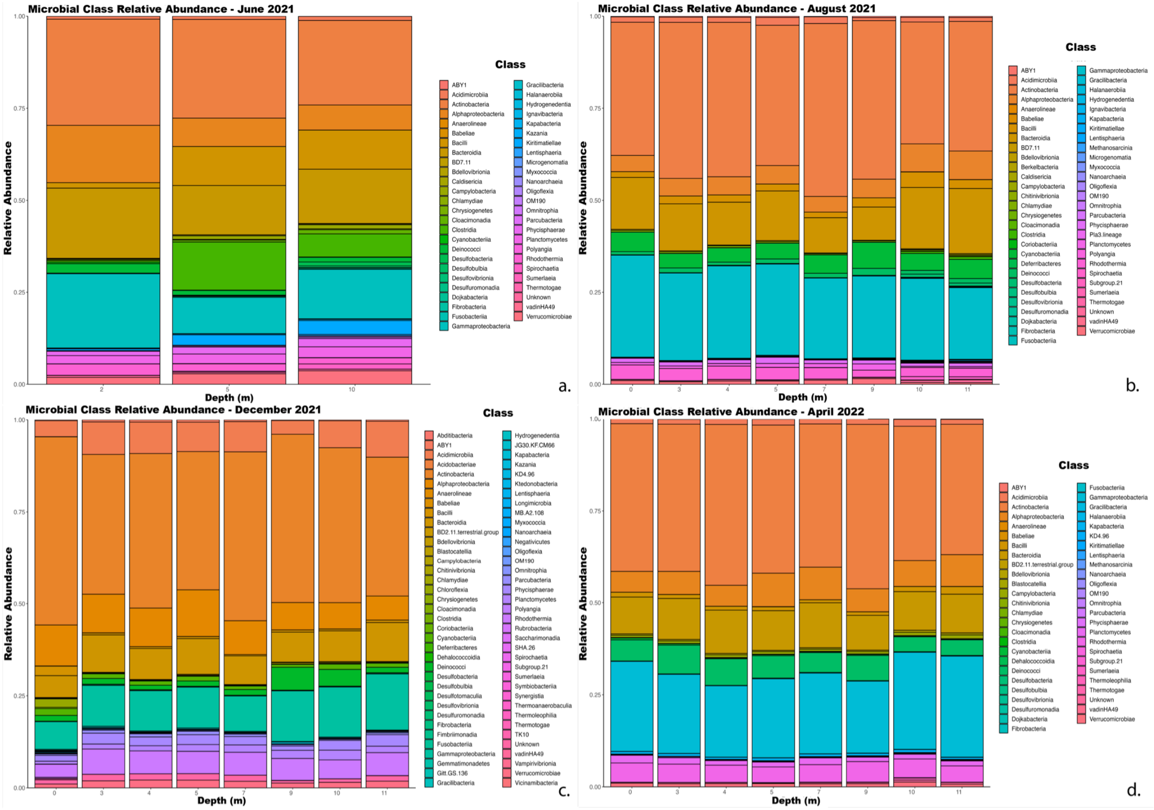


FIGURE 10. Relative abundance of microbial class by sample month with depth: June (a), August (b), December (c), April (d).

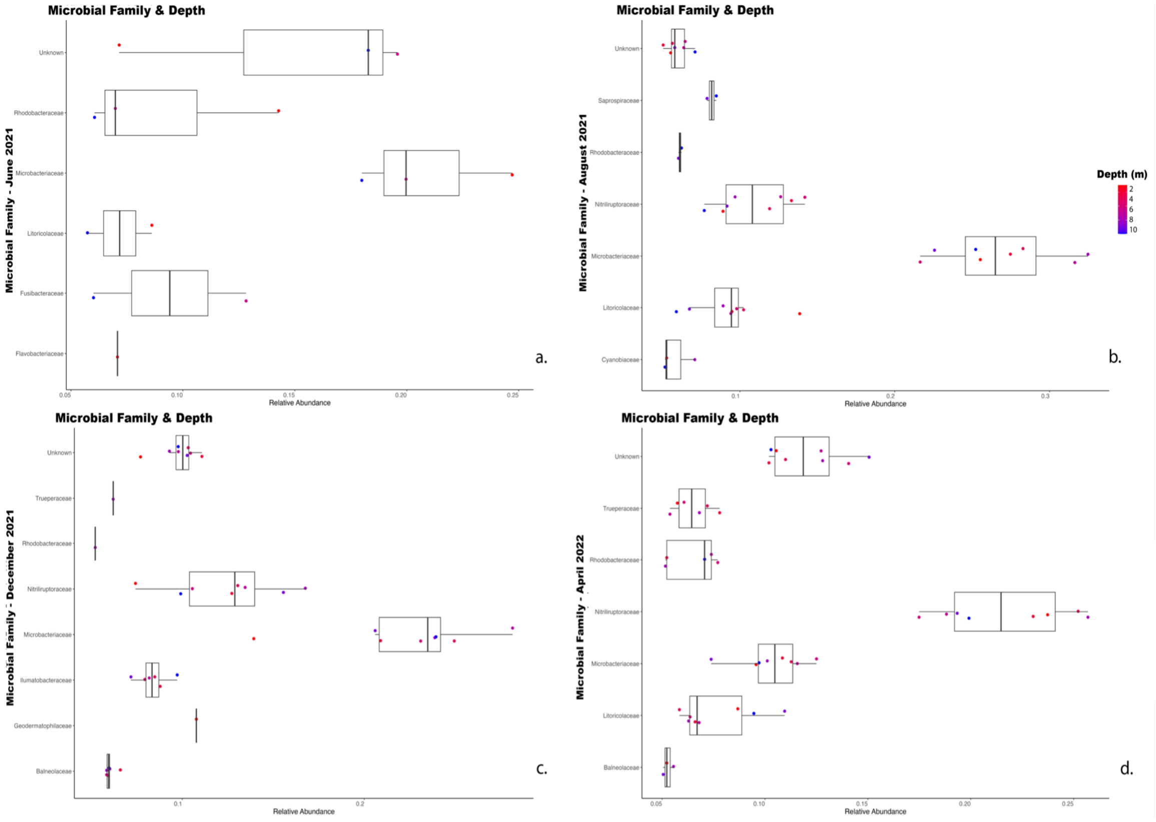


FIGURE 11. Relative abundance of microbial family with depth for each sample month: June (a), August (b), December (c), and April (d). Color shade indicates depth.

Microbial Genera at Depth by Sample Month

DS001 was the most abundant genus across all samples, seasons, and depths (>50 %) (Figure 12). *DS001* was expressed predominantly in August, followed by December, June, with the lowest expression in April. *Litoricola* appeared to be the most abundant in April, followed by August, with some samples having a relative abundance for this genus of greater than 20%. *Truepera* appeared to be the most abundant in April, followed by December (>15%). *Fusibacter* was abundant only in June (>10-20%), expressed predominantly at middle depths. *Synechoccus.CC902* was only abundant in August.

These microbial community results not only reveal the variations with season, but the observed microbial ecologies in June revealed the discernible impacts of the "greentide" events. We observed a robust correlation with existing freshwater trends and taxa commonly found in marine settings. likely influenced by the high temperatures, high salinity, sulfidic conditions, high nutrient levels, and reduced redox state, making it difficult to distinguish the impacts of specific parameters. The following synthesis addresses these organisms, the geochemical conditions (specifically in light of the "greentide" phenomenon), and their possible roles throughout the lake in both temporal and spatial (vertical column) contexts. As 16s rRNA analysis can only identify and characterize the taxa present, we can only speculate on the specific functions of these microbes.

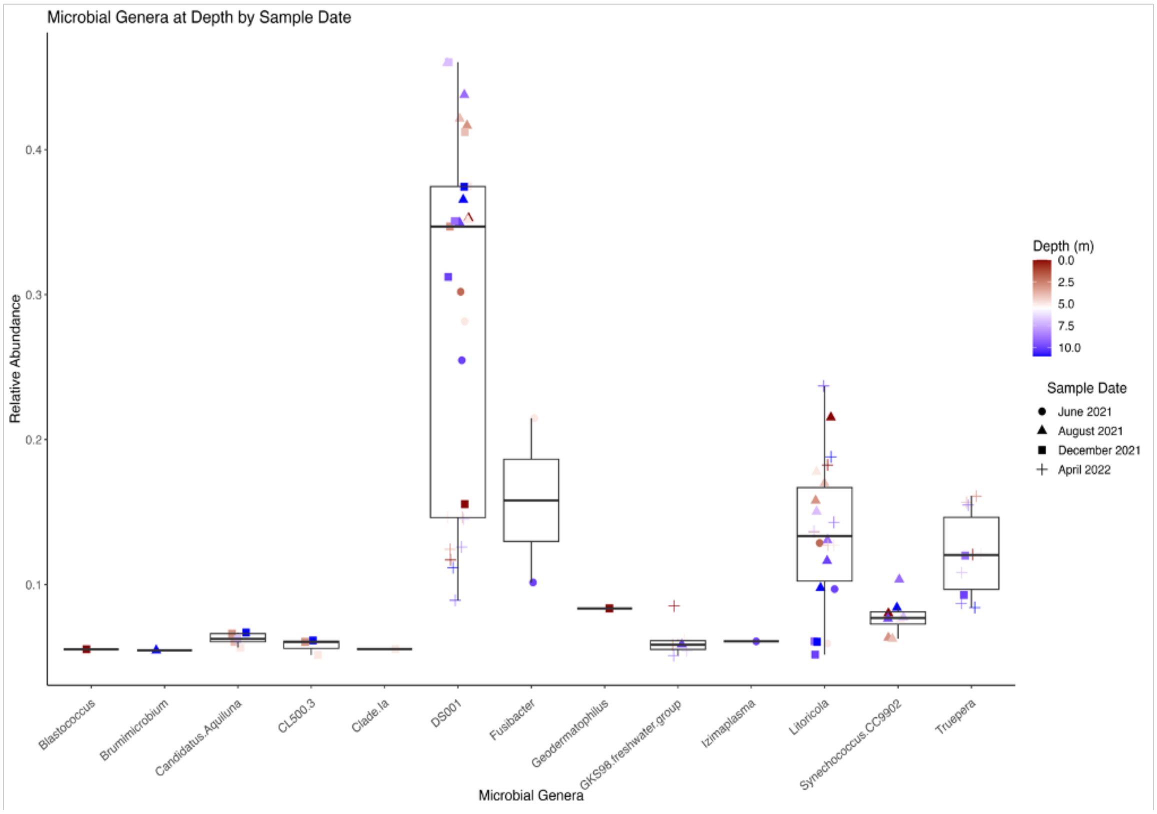


FIGURE 12. Relative abundance of microbial genera with depth and be sample month. Color shading indicates depth. Shape indicates the sample month.

CHAPTER 4

SYNTHESIS

Seasonal Microbial Community Diversity Trends

The observed changes in microbial community composition within the water column samples collected in June, August, December, and April indicated a response to seasonal fluctuations in physio-chemical conditions (temperature, dissolved oxygen, oxidation-reduction, nutrients, turbidity, sulfate, sulfide). Notably, prominent seasonal variations were observed in association with fluctuations in dissolved oxygen and redox state, which impacted the dynamics of microbial ecologies (Holdren & Montaño, 2002; Reese et al., 2008; Watts et al., 2001). Higher microbial diversity and species richness assemblage were identified in the summer months. Specifically, June showed the highest diversity ($p < 0.01$), while the highest species richness ($p < 0.001$) occurred during August. Conversely, the spring (April) exhibited the lowest species richness and diversity. Although dissolved oxygen, dissolved organic matter, and temperature were not significant predictors of Shannon diversity when performing linear regression analysis, ORP was a significant predictor ($p < 0.001$). Temperature and ORP were significant predictors of species richness ($p < 0.001$), while dissolved oxygen and dissolved organic matter were not. These findings contrasted considerably with previous seasonal trends recorded in 2005, which found spring to exhibit higher diversity and species richness (Dillon et al., 2009). However, in line with other prior investigations, our findings suggest that seasonal variations in microbial communities within eutrophic shallow freshwater systems are linked to changes in geochemical determinants, particularly nutrient-mediated relationships (Eiler & Bertilsson, 2007; Muylaert et al., 2002).

Actinobacteria, Gammaproteobacteria, Alphaproteobacteria, and *Bacteroidota* were detected as the most abundant lineages across all seasonal collections. These are microbes found to be most related to marine systems and hypersaline lakes (Humayoun et al., 2003; Jensen et al., 2017; Mutlu et al., 2008; Rojas et al., 2018; Vavourakis et al., 2019). *Microbacteriaceae* emerged as the most relatively abundant family, consistent with Actinobacteria's aerobic, heterotrophic nature. The family *Microbacteriaceae* has shown prevalence in the epilimnion of the saline euxinic ecosystem of Mahoney Lake in British Columbia, as well as in the Salton Sea during periods of elevated sulfide concentrations (Grossart et al.,2009; Klepac-Ceraj et al., 2012; Swan et al., 2010). *Actinobacteria* lineages are abundant in the surface waters of alkaline Mono Lake, consistent with preference for soda lakes and the Salton Sea, which are low in dissolved oxygen concentrations, have elevated mineral content (particularly in salts and carbonates), and high in salinity (Humayoun et al., 2003; Vavourakis et al., 2019). The abundance of DS001 was evident in all samples, showcasing its prevalence in environments characterized by high salinity, such as oceanic phytoplankton blooms and desert hypersaline lakes (Salazar et al., 2020; Yang et al., 2015).

Interestingly, the observation of *DS001* as the most abundant genus potentially captured a unique metabolic process in the Salton Sea. *DS001* has been found to participate in a bioremediation metabolic process identified as the degradation of Methyl Parathion

(MP), as *DS001* can use MP as a carbon source (Jamaluddin & AK, 2015; Kumar et al., 2018; Pakala et al., n.d.; Zhao et al., n.d.). Methyl Parathion is an acutely toxic organophosphate, specifically a highly active thiophosphorus ester insecticide developed in the 1940s and first registered in the US in 1954, but it was restricted in 1978 (Hertel et al., 1993; Jamaluddin & AK, 2015).

The toxic contaminant Methyl Parathion has been found in water column and sediments of the Salton Sea, as well as in the organs of fish species from the lake (Moreau et al., 2007). The ability of *DS001* to mineralize MP as a carbon source highlights the capabilities of microbes to detoxify harmful pesticides in the Salton Sea. The possibility of this metabolic process in the Sea highlights ubiquitous distributions of microorganisms and their high specificity and nutritional versatility in hazardous environments (Kumar et al., 2018; Pakala et al., n.d.; Prakash Verma et al., n.d.; Salazar et al., 2020; Yang et al., 2015; Zhao et al., n.d.). *DS001* has not been identified in previous Salton Sea microbial studies, suggesting that our findings may be an indicator of evolving conditions as the Sea continues to desiccate.

The ample abundance of *Gammaproteobacteria* lineages (e.g., *Pseudomonadales,* specifically the genus, *Litoricola* [known for its sulfate reduction capabilities and marine systems]) throughout the year can be attributed to the occurrence and utilization of sulfur compounds throughout the sea, consistent with microorganisms observed under high sulfide concentrations and specifically sulfidic (euxinic) conditions in the water column (Salazar et al., 2020; Swan et al., 2010). The measured abundance of

Alphaproteobacteria and *Bacteroidota* throughout the year further reflects the geochemical conditions, as Bacteroidetes are more abundant at higher salinities, and *Alphaproteobacterial spp*. are found to be both sulfate and saline-tolerant, including both obligate aerobic phototrophs and chemosynthetic sulfide oxidizers (Dillon et al., 2009: Demergasso et al., 2004; Klepac-Ceraj et al., 2012).

Microbial Communities and Impacts on the "Greentide" Day in June

In June, an observed increase in sulfate-reducing and sulfide-oxidizing bacteria coincided with the vertical dispersion of hydrogen sulfide throughout the water column. *Fusibacteraceae* appeared abundant at deeper depths in June, a family of *Firmicutes* known for their sulfate reducing metabolic capability (Aüllo et al., 2013; Bozo-Hurtado et al., 2013; Q. Huang, 2014; Swan, Ehrhardt, et al., 2010). The family's appearance strongly correlated with the geochemical conditions linked to the "greentide" event, as the upwelling of sulfide to the surface waters facilitated anaerobic, euxinic conditions throughout the aquatic layers (Figs 8 and 9). This is observation was further supported by prior microbial studies in which the anaerobic *Firmicutes spp*. prevailed in low sulfide regions, hypersaline lakes and saline lake sediments, consistent with their ability to assimilate reduced sulfur compounds (Dillon et al., 2009; Klepac-Ceraj et al., 2012; Swan et al., 2010, Mesbah et al., 2007).

The heightened relative abundance of *Alphaproteobacterial* family (purple non-sulfur bacteria), *Rhodobacteraceae*, in June also correlated with the lake-wide disrupted thermal stratification, resulting in the prevalence of sulfur-oxidizing species (Figure 9).

Rhodobacterales spp. are recognized in marine systems as facultative microorganisms capable of heterotrophic growth when oxygen is present or photoautotrophic growth via the Calvin cycle under anaerobic conditions (Kopejtka et al., 2017; Pohlner et al., 2019).

Previous Salton Sea studies found *Rhodobacterales* to dominate in the summer waters subsequent to a wind-induced upwelling event (Swan et al., 2010). Additionally, their notable appearance in the Black Sea's aerobic zone further suggests that these species are frequently associated with sulfur oxidation (Dillon et al., 2009; Kopejtka et al., 2017). Coupled with this, a strong signal of *Flavobacteriaceae* in the surface waters in June is consistent with isolation of these microbes in the surface waters and mixolimnion of saline, eutrophic soda lakes (Humayoun et al., 2003; Klepac-Ceraj et al., 2012). The presence of this family suggests the potential for enhanced growth under the high salinity levels (59-60 ppt) and overall high productivity of those surface waters during June (e.g., as expressed in elevated chlorophyll) (Figure 2).

An *unknown* lineage dominated all the sampled months but remains elusive. However, we can speculate that this species is linked to the heightened presence of sulfate reduction and sulfide oxidation within the waters. Among the main factors observed in June is the potential coexistence and interactions among sulfate-reducing and sulfide-oxidizing microbes within a shared ecological niche—a process described as a “cryptic sulfur cycle” when identified in deep marine sediments and oxygen minimum zones (e.g., Crowe et al., 2018). The microbial lineages observed in June reflect the lake’s redox conditions, characterized by the depletion of dissolved oxygen below 3 meters depth and a negative oxidation-reduction potential (ORP), signifying the lake's overall reducing conditions.

Microbial Communities on Non-Greentide Days Coupled with Recorded Sulfate-Sulfide Concentrations

Populations observed during a non-greentide summer day in August differed from the event day, as microbial communities reflected the lakes' thermal stratification and differences in redox state in the hypolimnion rather than the observed upwelled oxygen depleted waters to the epilimnion. Although August samples were still dominated by *Actinobacteria- Microbacteriaceae*, an elevated abundance of *Cyanobiaceae* was recorded, dominated by *Synechococcus sp. CC902*, a genus similar to halotolerant marine cyanobacterium (Figs 10 and 11) (Palenik, 2001; Stoddard et al., 2007). *Synechococcus spp.* are closely related to marine isolates, contributing to picophytoplankton organic matter (Carmichael & Li, 2006; Reifel et al., 2002). However, the observed abundance of this cyanobacteria lineage may be explained by sulfide potentially serving as a resource during anoxygenic growth, thereby facilitating the further oxidation of sulfide (Luo & Mitsui, 1996). Additionally, the *Synechococcus spp. (strain SS-1)* was previously recorded in the Salton Sea and is identified for its ability to produce microcystins (Reifel, et al., 2010; Zhou et al., 2017). Thus, it is possible that as cyanobacteria blooms increase in the Sea (due to elevated nutrient-loading and evaporation), heightened exposure of bird populations to cyanotoxins will increase. Toxicity of microcystins specifically target and damage organs systems, potentially posing a deeper threat to wildlife and amplifying the need for proactive measures to protect the health of this ecosystem (Zhou et al., 2017). It is important to add larger-celled organisms were not identified in this study, as prefiltering steps may have been removed them from samples used for 16s rRNA analysis.

Aside from the observed abundance of *Cyanobacteria*, an elevated presence of *Saprospiraceae* was measured in the hypolimnion of August (Figure 9). *Saprospiraceae* spp. are gram-negative, aerobic, or facultative anaerobes typically known for their roles in the decomposition of organic material in aquatic ecosystems. Some have been found to be associated with the degradation of pollutants, highlighting their potential applications in bioremediation (Kwon et al., 2019; Oliveira et al., 2023). It is possible to speculate that *Saprospiraceae* bacteria were participating as decomposers due to the high biomass and dissolved organic matter observed in the Sea. However, several studies have reported sulfate-reducing spp. within this family in various settings, including anaerobic digesters and marine sediments (Raulf et al., 2014; Tonanzi et al., 2021; Y. Xia et al., 2008). As the presence of this family was abundant at deeper depths, members observed could have been involved in sulfate reduction in the hypolimnion of the lake when dissolved oxygen was unavailable (Figure 2). The recorded increase in sulfide levels in the bottom waters further signals their possible role as sulfate reducers, converting organic matter and sulfate to sulfide (Figure 4).

Microbacteriaceae and *Rhodobacteraceae* spp. continued to dominate in the winter and spring, however, contrasting with the summer months. Abundances of *Nitriliruptoraceae spp., Balneolaceae spp.,* and *Trueperaceae spp.* were recorded (Figure 9).

Nitriliruptoraceae spp. are thermophilic and commonly isolated from hot springs, soda lakes, and hydrothermal vent systems (Li et al., 2015; Sorokin et al., 2009). They are widely known for metabolizing nitriles, possessing enzymes capable of converting nitriles into amides and degrading them into ammonia and carboxylic acids (Sorokin et al., 2009). Although their presence in the Salton Sea can be attributed to several factors, high temperatures and high nutrient loading (nitrates and phosphates) are central (Buckles et al., n.d.; Cohen et al., 1999). Moreover, their presence may contribute to the biogeochemical cycling of nitrogen, generating bioavailable ammonia for organisms to use as a nitrogen source throughout the Sea.

Balneolaceae is a family classified as facultative anaerobes, typically found in hot springs environments and some marine solar salterns (Urios et al., 2006; Xia et al., 2016). The recorded abundance of *Balneolaceae* correlated with the Sea's available oxygen and overall high sulfate concentrations. At this stage, the functionality of *Balneolaceae* in the Sea remains unknown, but it is reasonable to suggest that members were participating as aerobic organisms, using oxygen as their terminal electron acceptors when oxygen was available throughout the water column and transforming to anaerobic metabolism in the absence of oxygen, instead using sulfate, nitrate, or other organic compounds as electron acceptors. Additionally, the abundance of *Trueperaceae* was identified—a family belonging to Deinococci identified as gram-positive haloalkaliphilic extremophile and often found in hot springs and hydrothermal vents (Albuquerque et al., 2005; Ivanova et al., 2011). From this family, the genus, *Truepera* was specifically abundant in oxygenated waters in the Sea. This genus is chemo-organotrophic and aerobic, known for its ability to degrade complex organic compounds and oxidize sulfur compounds (Ivanova et al., 2011; Banfield, 2017; Vavourakis et al., 2018). The recorded observation of this genus further reflects the oxidizing conditions of December and April waters, along with characterizing the Salton Sea's ongoing desiccation and eutrophic conditions.

A notable characteristic of the recorded genera in the winter and spring is that extremophile aerobic species dominate. When considering sulfide concentrations during these seasons, it's apparent there was less conversion of sulfate to sulfide due oxygen saturation. (Figs 3 and 4). Sulfate reducers were not abundant in the water column during these seasons, as the lake was oxidizing. Regardless of the season, sulfate concentrations are always high in the Sea due to the influx of fertilizers from agricultural runoff, thereby yielding sulfate as a non-limiting factor (Buckles et al., 2002; Cohen et al., 2014; Holdren & Montaño, 2002; Jones & Fleck, 2020; Vogl & Henry, 2002). Given the high salinities in the water column during the winter and spring (peaking between 60-62 ppt), these high salt contents may have contributed to shaping the microbial communities, such as the extremophiles observed.

Vertical Column Patterns

Community stratification was reflected in the taxonomic composition across the horizons. Although changes in Shannon diversity and species richness were not statistically significant with depth (Appendix A, B, C, J, and K), clear patterns were observed throughout the vertical column. The greatest Shannon diversity and species richness levels were observed in the bottom waters at 10 and 11 meters (Figure 5), indicating an ecosystem characterized by a biodiversity heightened by species adapted to thrive in anoxic, euxinic conditions. As density-driven stratification shapes oxygen and nutrient availability and potential shifts in electron acceptor availability. Moreover, observed microbial populations reflected the contrast in vertically stratified waters in the summer, influenced by strong negative redox gradients, and the thoroughly mixed waters in the winter and spring.

Genera's *DS001, Litoricola,* and *Truepera* were the most abundant genera (Figure 12). *DS001* and *Litoricola* were the most abundant at all depths, while *Truepera* was only abundant in the mixolimnion (3,4,5,7,9 meters depth) (Appendix P). *Truepera* is best known for its extreme resistance to ionizing radiation and optimum growth at high temperatures in hot spring environments but has also been identified in harsh lake environments undergoing evaporation (Albuquerque et al., n.d.; Ivanova et al., 2011; Sirisena et al., 2018). The presence of this genus in the oxygenated layers Salton Sea is consistent with the idea that *Truepera* and *Deinococccus* may have similar ecological niches in saline systems because of their resistance to desiccation and halotolerance (Albuquerque et al., 2005; Molina-Menor et al., 2019). Additionally, the abundance of *Litoricola* lineages at all depths correlated with their known sulfate reduction capabilities and high sulfide concentrations throughout the water column during the summer (Figure 3). The measured abundance of *DS001* at all depths further reveals the extent to which high agricultural runoff impacts the Salton Sea. As mentioned previously, in contrast to prior microbial analyses of the Salton Sea, the identification of this genus is novel and may reflect the changing conditions in the Salton Sea, such as the ability for microorganisms to find a suitable niche with the lake's environment, promptly evolving to mitigate eutrophication (Cohen et al., 1999; Jones & Fleck, 2020).

As the June sample collection was a greentide day, the chemocline was observed at between 2-3 meters depth, as dissolved oxygen, ORP, dissolved organic matter, chlorophyll, and turbidity all decreased relative to the winter-spring data (Figure 1). The notable abundance of *Flavobacteriaceae* and *Rhodobacteraceae* in shallow waters and the abundance of *Fusibacteraceae* throughout the water column further illustrated the observable shift in microbial consortia following the disruption of the former thermally and redox stratified waters.

As August sampling was on a typical summer day with temperature-dependent vertical stratification and no upward mixing and "greentide" event, the chemocline occurred between 8-9 meters depth, where sulfide concentrations increased in concert with a shift in ORP (Figs 2, 3, and 4). In phase with these geochemical transitions, we observed increased shifts in microbial lineages of *Rhodobacteraceae, Saprospiraceae,* and *Litoricolaceae* at bottom water depths, coincident with shifts in oxygen availability, redox state at the chemocline. *Cyanobacteraceae* appeared to be abundant in the surface waters as well as at 6-8 meters depth, with the latter likely attributable to the sedimentation of organic material into deeper waters. In contrast, waters collected during December and April were well mixed throughout. Since the lake was characterized by polymictic conditions at these times, a chemocline was not distinguishable from our records (Figure 2). This observation was further supported when considering cross-correlation trends of temperature, dissolved oxygen, and ORP coupled with microbial Shannon diversity and species richness (Figs 7 and 8). Clearly, mixing of the water column and the replenishment of oxygen throughout the lake resulted in similar species throughout, leading to less variation in richness and diversity (Figs 7 and 8). Alongside this, sulfide concentrations in December and April remained consistently low, hovering around 2-3 µm, suggesting a reduction in sulfide production due to the prevalence of oxygen-rich waters (Figure 4). Although sulfide concentrations were consistently low, there were more differences in sulfate concentrations in April relative to December (Figure 4). In April's surface waters, sulfate concentrations remained between 185-190 mM, dipped to 170 mM at 6-7 meters depth, elevated again to 185 mM, and then dipped again to around 170 mM in the bottoms waters (Figure 4). These sulfate fluctuations are not expressed in microbial signature, nor can any particular geochemical process explain these fluctuations. Moreover, observed microbial lineages in April and December were mixed throughout all depths (Figure 10).

Archaeal Observations and Implications

The recorded presence of archaea was considerably lower than bacteria (~ < 1%). Although *Halobacterota* and *Nanoarchaeota* were the only taxa found, both are identified in high temperature environments and under high salinity conditions (Figure 8) (Andrei et al., 2012; Munson-McGee et al., 2015; Weng et al., 2014). *Halobacterota* thrive under high salt concentrations, such as alkaline salt lakes, solar salterns, and the Dead Sea specifically, while *Nanoarchaeota* have been found to thrive in hydrothermal vents (Klindworth et al., 2014; Munson-McGee et al., 2015; Weng et al., 2014). *Woesearchaeales* was the most observed archaeal order throughout all seasons at the Sea, which is a lineage with an anaerobic heterotrophic metabolism (W.-C. Huang et al., 2021; Liu et al., 2018). Importantly, *Woesearchaeales* are important in aiding fermentation in other organisms, highlighting their potential symbiotic (syntrophic) relationship with methanogenic archaea (W.-C. Huang et al., 2021; Liu et al., 2018). Additionally, the other observed archaeal order was *Methanosarcina,* an anaerobic methanogen previously recorded in the Salton Sea water column and known to metabolize compounds such as methylsulfides (including dimethylsulfide) and methylamines (Begmatov et al., 2021). Notably*, Methanosarcinia* was only found in April and August at intermediate depths of 4 and 9 meters in April, and 5 meters in August (Figure 10). This is important as all methanogens are strict obligate anaerobes, and oxygen was abundant during those months and at those depths (Figure 2). However, species from *Methanosarcinia* have been observed to have a heightened oxygen tolerance (Jasso-Chávez et al., 2015). Interestingly, some lineages of *Methanosarcina* have been found to develop primitive forms of hemoglobin (referred to as "protoglobins") that bind to oxygen, possibly serving as a strategy to safeguard the microbes through O_2 detoxification (Allen Freitas et al., 2004).

Although we have not confirmed that *Methanosarcina* lineages in the Salton Sea are capable of resistance to oxygen stress, it encourages additional analyses. Moreover, the presence of these taxa in the Salton Sea could suggest interactions among the observed organisms, as the metabolism of *Methanosarcina* in the Salton Sea waters could have been bolstered by the presence of *Woesearchaeales,* acknowledging the potential for *Woeseachaeales* to contribute to *Methanosarcina's* fermentation process.

Environmental Parameters Influence on Microbial Community Ecologies

Ultimately, it is clear that the chemical composition of the lake is shaped by microbial community ecology and vice versa—as related to other environmental parameters such as temperature, water column mixing, and ORP. As Kruskal-Wallis and Pairwise statistical analyses showed, temperature and ORP were statistically significant as different across all sample months, while differences in dissolved oxygen, dissolved organic matter, chlorophyll, and turbidity were only statistically significant between certain months ($p < 0.001$) (Appendix E and F). These results highlight the varying lake water chemistry observed between seasons.

When analyzing the relationships among these environmental variables, the interconnectivity between factors becomes evident (Figure 9). As the significant coherence between dissolved oxygen, ORP, and temperature is apparent through all analyses ($p = 0.001$), the connection between these factors coupled with turbidity, dissolved organic matter, and chlorophyll is important to discuss.

ORP and dissolved oxygen correlated positively with turbidity, while a negative correlation was observed between turbidity and temperature (Figure 9, Appendix G). The association between increased ORP values and elevated turbidity levels can be attributed to the introduction of oxidizing agents into the water due to higher concentrations of soils and other particles from agricultural runoff (Alles, 2011; Holdren & Montaño, 2002; Re et al., n.d.). Consequently, this influx of oxidizing agents—such as iron, manganese, and nitrate—contributes to elevated ORP levels hence ultimately to more oxygen availability (Alles, 2011; Holdren & Montaño, 2002; Re et al., n.d.; Vogl & Henry, 2002). However, the increase in temperature correlated with the decrease in turbidity is likely caused by summer mixing conditions, as well as the overall shallowness and polymictic nature of the Salton Sea, leading to improved water clarity from constant mixing.

When considering the significant negative correlation between dissolved organic matter and the following parameters—dissolved oxygen, ORP, and chlorophyll ($p < 0.001$) (Appendix G)—it becomes apparent that variations in organic matter and productivity significantly influence and alter redox state, further yielding changes in microbial composition. Decreases in DOM can lead to decreases in bacterial respiration that drive an increase in dissolved oxygen concentrations and a decrease in the consumption of nutrients that would be available for phytoplankton growth, yielding conditions favorable for algal growth and causing an increase in chlorophyll conditions (Reinthaler et al., 2008).

Enhanced chlorophyll concentrations can also hinder the mixing of the water column, as warm surface layers, characterized by algae and other suspended particulates, contribute to impeding the mixing process by an increased density gradient between the upper strata and the cooler waters below (Filazzola et al., 2020; Watts et al., 2001). Lower chlorophyll concentrations can also alter microbial communities and their metabolic activities by leading to a shift in the balance between organic matter consumption and production, potentially yielding an increase in dissolved organic matter (Nissenbaum,1975.; Reese et al., 2008; Reinthaler et al., 2008; Watts et al., 1999). Notably, the occurrence of *Gammaproteobacteria* and *Bacteroidetes* populations have been shown to be altered by algal-derived organic matter (Klindworth et al., 2014; Yang et al., 2015).

Chlorophyll observed to have a positive correlation with dissolved oxygen, temperature, and turbidity (Figure 9, Appendix G). The positive correlation between temperature and chlorophyll is likely due to warm lake temperatures fostering ideal growth conditions for chlorophyll-containing organisms (like algae, phytoplankton), as higher temperatures often coincide with increased sunlight, facilitating higher photosynthetic rates (Filazzola et al., 2020). Additionally, elevated temperatures often interact with other factors, like nutrient levels, that create conditions conducive to algal growth, and subsequently, increased chlorophyll content (Filazzola et al., 2020). Chlorophyll concentrations may exhibit a positive correlation with turbidity due to algal proliferation, as the growth of algae releases organic matter particulates into the water (Filazzola et al., 2020). Although the positive correlation between ORP and chlorophyll was not significant, it was clear that suggestions of this positive trend could have been shaped by dissolved oxygen availability and seasonal temperatures, as Pearson's Product-moment results revealed a significant positive correlation between chlorophyll and dissolved oxygen ($p < 0.001$) (Appendix G). Even though these results are striking because chlorophyll reflects photosynthesis that releases oxygen, altering ORP levels accordingly, a possible cause for this result may be due to seasonal variability. Since the data is collected over different seasons, seasonal variability can introduce noise and affect the ability to detect significant correlations. Additionally, other possible reasons for this observation may be because there are nuanced interactions between multiple environmental parameters that both alter ORP and chlorophyll levels. These relationships can complicate the correlation analysis and making it harder to realize statistical significance.

These correlations illustrate the connections between the eutrophic environment, elevated temperatures, and their consequential effects in shaping the physiochemical constituents, contributing to microbial lineages observed and their seasonal differences.

Evolution of the Salton Sea and Primary Inferences

The sulfur cycle in a stratified lake involves a series of microbial transformations, with sulfate reduction and sulfide oxidation as key steps. Importantly, the unique properties and seasonal effects of the Salton Sea contribute to the lake's stratification, resulting in distinct redox conditions throughout the layers. As a result, these conditions play a curial role in shaping microbial metabolisms. The observed lineages, such as *Flavobacteriaceae, Fusibacteraceae, Rhodobacteraceae,* and *Saprospiraceae*, responded and thrived in the thermally stratified anoxic and euxinic layers. Although we did observe taxa suggested to be participating in the sulfur cycle, considering the "greentide" event in June and the overall high sulfate/sulfide concentrations throughout the seasons and varying O_2 contents, it is surprising that specific sulfate-reducing species such as *Desulfobacteria (spp, Desulfovio*) and sulfide-oxidizing species such as *Actinobacteria Streptomyces spp.* were only found in small quantities (*Desulfobrivio* – count of 121

$[2.0\ x\ 10^{-4}\ \%]$ and *Streptomyces* – count of 70 $[1.18\ x\ 10^{-4}\%]$). This observation could be due to sulfate reduction happening primarily in the bottom sediments (Dillon et al., 2009; Swan, et al., 2010). Further analysis of sulfate and sulfide concentrations and, more importantly, rates of sulfate reduction, coupled with metagenomic functional analysis, would further illustrate the effects of the sulfur cycle and how changes in the sulfur cycle affect the microbial community ecologies.

The abundance of *DS001, Litoricola*, and *Truepera* throughout the Sea emphasize the ability of microorganisms to acclimate to varying environmental conditions, given their responsiveness to alterations. With the increasing evaporation, nutrient, and salinity saturation, their appearance can suggest that the Salton Sea microbes will continue to evolve not only to withstand such conditions (Allison & Martiny, 2008; Q. Huang, 2014; Karimi et al., 2017; Lozupone & Knight, 2007). Specifically, the leading prevalence of *DS001* and its capacity to utilize the toxic contaminant, MP as a carbon source for mineralization, spotlights the potential of microbial detoxification in throughout the Sea. Such dominance of microbial degradation could be an indicator of secondary ecological succession, as microbes might be taking advantage of available resources and environmental conditions, potentially leading to changes in nutrient cycling and ecosystem dynamics. However, it's important to acknowledge, secondary ecological succession does not mean the ecosystem will result in stability. Although the sensitivity of microbial populations may be adapting to mitigate eutrophication, several factors, such as ecological, climatic, and anthropogenic factors also alter the trajectory of the lake.

While salinity exhibited a stable trend over the seasons, and uniform with depth, the consistently high levels mold the Sea's structure and ecological dynamics. Aside from temperature playing a role, high salinity can also influence the physical structure of the lake, affecting the density, leading to stratification and altered mixing patterns. These changes contribute to overall nutrient and oxygen availability throughout the lake, further influencing the distribution of species (Karimi et al., 2017). Additionally, if the lake's salinity remains uniformly high over time, it might affect the ability of organisms to migrate or colonize the lake, thus evolutionary pressures will prevail, and diversity trends may change. Microorganisms more tolerant of high salinity may thrive and pass on their genetic traits to the next generations.

Based on these findings, it is possible to infer that the nature of the Salton Sea might be evolving to mimic a soda saline lake, as the characteristics observed correlate with certain patterns commonly found in freshwater alkaline systems, such as Mono Lake (Humayoun et al., 2003). In addition to elevated salinity, high biomass production, restricted inflow and outflow, and seasonal variations, the observed abundance of *Actinobacteria* in the Salton Sea aligns with trends in alkaline microbial composition, as *Actinobacteria* sequences have also been found to dominate waters in Mono Lake (Humayoun et al., 2003). Additionally, the abundances of *Proteobacteria, Firmicutes,* and *Bacteroidetes* in the Sea further supports this observation, as these taxa are generally found to dominant soda lake systems (Cotta et al., 2022; B. E. Jones et al., 1998; Teske et al., 2016). Although the Salton Sea's pH tends to be around 7.5- 8.5 (Watts et al., 2001), and alkaline systems are typically characterized by pH values ranging 9-12, there are saline soda lakes with pH’s that fall in the range of 8-9 (Cotta et al., 2022; Jones et al., 1998; Sorokin et al., n.d.). While the Salton Sea exhibits differences in this regard, the abundance of microbial populations observed in this study resembles compositional patterns found in soda lakes (Jones et al., 1998; Sorokin et al., n.d.). Additionally, the presence and distribution of microbial populations can influence the pH and chemical composition of the lake; so, it is possible the pH of the Salton Sea could alter in response to microbial ecologies (Humayoun et al., 2003; Jones et al., 1998; Sorokin et al., n.d.; Vavourakis et al., 2019). Despite pH being an important factor in characterizing alkaline lakes, it appears to have a less significant impact in shaping microbial composition.

Furthermore, the observed differences between previous studies and our findings may be reasonably explained by ongoing desiccation and high nutrient loading in the Salton Sea, increasing salinity and the likelihood of hydrogen sulfide mixing.

CHAPTER 5

CONCLUSION AND SIGNIFICANCE

Analysis of microbial communities in the seasonally euxinic, polymictic Salton Sea suggests that microbial ecologies ultimately reflect the water column's seasonal geochemical dynamics and associated redox state. This research serves as a reference point to further understand the importance of changing lake conditions and their influence on microbial communities. Overall, diversity and species richness significantly differed throughout the seasons, consistent with changes in seasonal lake stratification. Although diversity and species richness did not vary significantly with depth, notable relationships were observed at the chemocline, which was reflected in microbial taxa.

Microbial populations' responsiveness to environmental conditions and the reciprocal influence of environments on these populations position them as primary indicators of shifts within ecosystems. As the Salton Sea is a unique system and the trajectory is unknown, our findings infer the microbial taxa composition resembles that of soda saline lakes, reflecting their adaptations to the lake's eutrophication, salinity, and other physiochemical factors. While the Salton Sea's pH varies from sodic/ alkalinic systems, it doesn't appear to be the main driver of microbial populations. These novel inferences are thought-stimulating and warrant further investigation.

Although the presence of many taxa was important, the appearance of the genera *DS001* and *Synechococcus* presented intriguing insights into the potential dynamics of the Salton Sea, impacting both its inhabitants and human populations. While the occurrence of

Synechococcus strains capable of producing microcystins raises concerns about potential cyanobacteria blooms, which could elevate cyanotoxin exposure for birds (due to nutrient-loading and evaporation), the dominant abundance of *DS001* offers a contrasting perspective (Luo & Mitsui, 1996; Palenik, 2001; Stoddard et al., 2007). This dominance may indicate extensive microbial degradation, suggesting the proliferation of pollutant-detoxifying microorganisms throughout the sea, possibly contributing to mitigating eutrophication(Kumar et al., 2018; Pakala et al., 2007). These findings hint at the potential trajectory of the ecosystem moving toward maturity by addressing stressors through bioremediation (Kumar et al., 2018). However, comprehending ecosystem stability entails recognizing its interconnected nature, as no element operates in isolation.

The fate of the Salton Sea hinges on its declining water supply and the necessity for proactive measures to reverse this trend. Addressing the impending challenges requires a comprehensive understanding of the intricate links between geochemistry, microbial ecology, mixing dynamics, and the broader context of climatic shifts. In the future, integrating compositional diversity analysis with metagenomic research could unveil the functionality of these taxa and their contribution to upholding ecosystem stability despite extreme conditions. This synergistic approach would not only enhance our understanding of the lakes' health by detecting changes in composition and function that signal shifts in ecosystem conditions, but it could aid in detecting emerging contaminants in the water, particularly important for understanding the potential impacts of human activities on the ecosystem and its inhabitants. Moreover, exploring these realms allows insights into the fate of the Salton Sea.

APPENDIX

SUPPLEMENTAL FIGURES AND TABLES

A. ANOVA Test Results

Species Richness	Df	Sum Squared	Mean Squared	F-value	Pr(>F)
Depth (m)	1	31	31	0.001	0.982
Residuals	44	2658080	60411		

Shannon Diversity	Df	Sum Squared	Mean Squared	F-value	Pr (>F)
Depth (m)	1	453	452.7	0.523	0.474
Residuals	44	38108	866.1		

B. Compare Means ANOVA Results

Variable	p	p.adj	p.format	p.signif	method
Species Richness x Depth	0.869	0.87	0.87	ns	ANOVA
Shannon Diversity x Depth	0.458	0.46	0.46	ns	ANOVA

C. Fligner-Killeen Test of Homogeneity of Variances Results

Fligner-Killeen Test of Homogeneity of Variances	Chi-squared	df	p-value
Species Richness x Depth	3.1082	8	0.9274
Shannon Diversity x Depth	7.6758	8	0.4658

D. Shapiro-Wilk Normality Test Results

Parameter	**W-value**	**p-value**
Shannon Diversity	0.95502	0.07334
Species Richness	0.92164	0.00428
Dissolved Oxygen (% Local)	0.7171	3.406e-08
Temperature (°C)	0.85787	4.186e-05
Oxidation-Reduction Potential (mV)	0.5175	3.277e-11
Dissolved Organic Matter (RFU)	0.75744	1.997e-07
Turbidity (FNU)	0.89662	0.0005629
Chlorophyll (RFU)	0.47751	1.044e-11

E. Kruskal-Wallis Rank Sum Test Results

Kruskal-Wallis Rank Sum Test	**Chi-squared**	**df**	**p-value**
Dissolved Oxygen (% Local) x Sample Month	21.995	3	6.537e-05
Oxidation-Reduction Potential (mV) x Sample Month	40.702	3	7.565e-09
Temperature (°C) x Sample Month	42.106	3	3.81e-09
Dissolved Organic Matter (RFU) x Sample Month	30.274	3	1.208e-06
Turbidity (FNU) x Sample Month	29.535	3	1.729e-06
Chlorophyll (RFU) x Sample Month	33.658	3	2.339e-07

F. Pairwise-Wilcox Rank Sum Test Results

Pairwise Wilcox Rank Sum Test				
Dissolved Oxygen (% Local) x Sample Month		June	August	December
	August	1.0000	-	-
	December	0.68634	0.00057	-
	April	0.68634	0.01408	0.00102
Oxidation-Reduction Potential (mV) x Sample Month		June	August	December
	August	0.42636		-
	December	0.00116	0.00192	-
	April	0.00109	0.00054	8.3e-06
Temperature (°C) x Sample Month		June	August	December
	August	0.00817	-	-
	December	0.00116	0.00057	-
	April	0.00116	0.00057	8.6e-06
Dissolved Organic Matter (RFU) x Sample Month		June	August	December
	August	0.87282	-	-
	December	0.68200	0.00055	-
	April	0.68634	0.00057	8.5e-06
Turbidity (FNU) x Sample Month		June	August	December
	August	1.0000	-	-
	December	1.0000	0.00055	-
	April	0.67329	0.00052	8e-06
Chlorophyll (RFU) x Sample Month		June	August	December
	August	0.02597	-	-
	December	1.0000	0.00057	-
	April	0.00530	0.17466	8.6e-06

G. Pearson's Product Moment Test Results

Correlated Parameters	t-value	df	p-value	Confidence Interval	Sample Estimate (Correlation)
Dissolved Oxygen (% Local) x Oxidation-Reduction Potential (mV)	2.9448	45	0.005099	0.129773 - 0.617813	0.4019602
Dissolved Oxygen (% Local) x Temperature (℃)	-1.4579	45	0.1518	-0.47082176 - 0.07965663	-0.212368
Dissolved Oxygen (% Local) x Chlorophyll (RFU)	8.9701	45	1.397e-11	0.6670690 - 0.8845699	0.8008289
Dissolved Oxygen (% Local) x Dissolved Organic Matter (RFU)	-13.149	45	< 2.2e-16	-0.9379962 - -0.8110726	-0.8907679
Oxidation-Reduction Potential (mV) x Temperature (℃)	-3.3799	45	0.001507	-0.6527801 - -0.1869516	-0.4499616
Oxidation-Reduction Potential (mV) x Chlorophyll (RFU)	0.061745	45	0.951	-0.2786994 - 0.2955896	0.009204027
Oxidation-Reduction Potential (mV) x Dissolved Organic Matter (RFU)	-2.7601	45	0.00833	-0.6018984 - -0.1047813	-0.380499
Chlorophyll (RFU) x Dissolved Organic Matter (RFU)	-6.684	45	3.002e-08	-0.8256437 - -0.5250903	-0.7058266

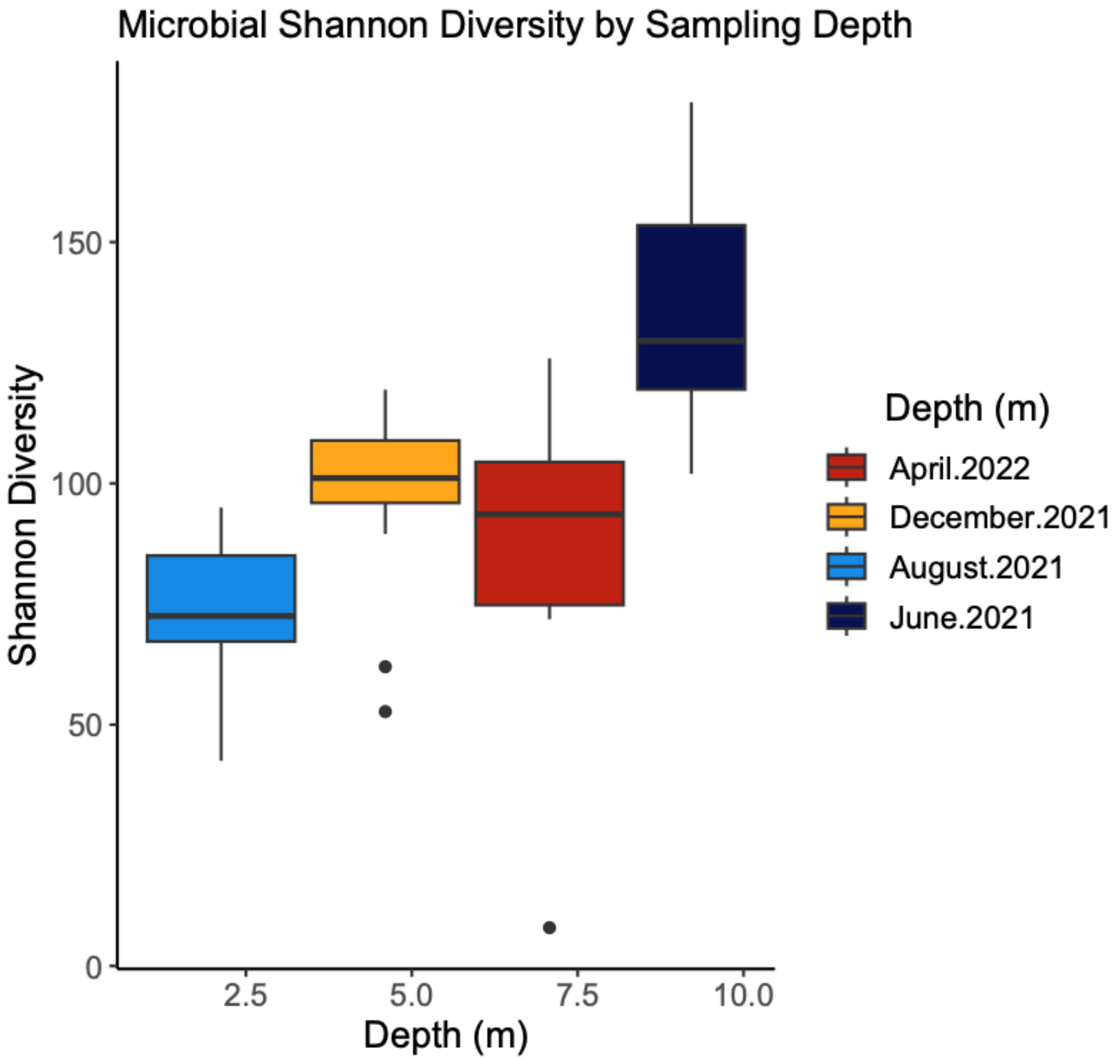
H. Shannon Diversity Linear Regression Analysis Results

Shannon Diversity Linear Regression **Variable**	**Estimate**	**Std. Error**	**t-value**	**Pr(>|t|)**
(Intercept)	96.248	4.361	22.070	<2e-16 ***
Dissolved Oxygen (% Local)	-1.267	4.380	-0.289	0.774
(Intercept)	96.125	3.694	26.023	< 2e-16 ***
Oxidation-Reduction Potential (mv)	-15.456	3.701	-4.176	0.000138 ***
(Intercept)	96.310	4.355	22.116	<2e-16 ***
Temperature (°C)	-2.090	4.400	-0.475	0.637
-Not Summer Months -				
(Intercept)	184.18	96.38	1.911	0.0659
Oxidation-Reduction Potential (mV)	-204.89	216.23	-0.948	0.3512
-Summer Months -				
(Intercept)	82.795	8.492	9.749	2.41e-07 ***
Oxidation-Reduction Potential (mV)	-21.466	5.222	-4.110	0.00123 **
(Intercept)	96.2672	4.3626	22.067	<2e-16 ***
Dissolved Organic Matter (RFU)	0.9396	4.3627	0.215	0.83

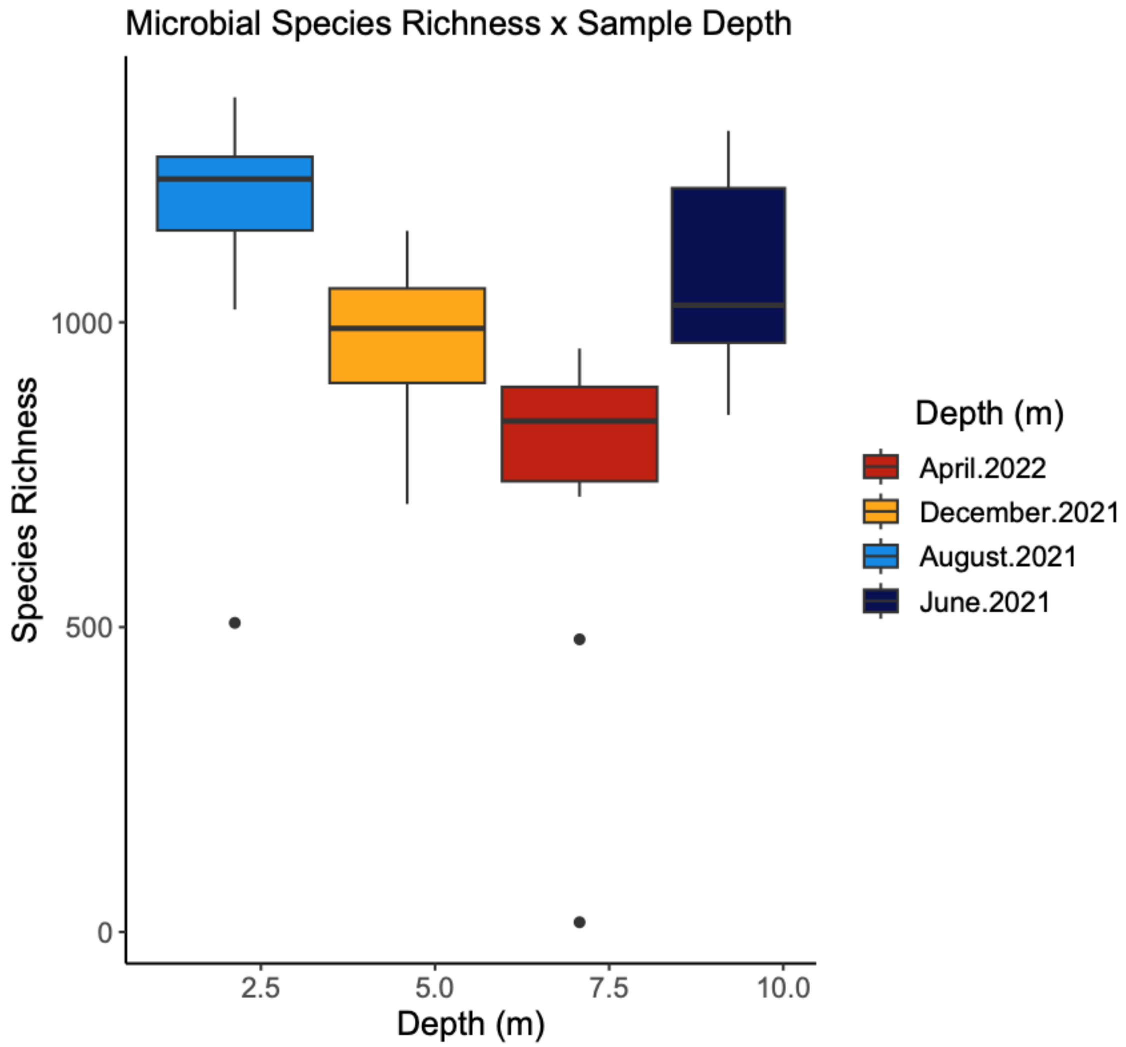
I. Species Richness Linear Regression Analysis Results

Species Richness Linear Regression **Variable**	**Estimate**	**Std. Error**	**t-value**	**Pr(>|t|)**
(Intercept)	943.035	36.228	26.030	<2e-16 ***
Dissolved Oxygen (% Local)	-6.879	36.389	-0.189	0.851
(Intercept)	942.28	33.40	28.213	2e-16 ***
Oxidation-Reduction Potential (mv)	-93.50	33.46	-2.794	0.00768 **
-Not Summer Months - (Intercept)	2941.6	793.7	3.706	0.000883 ***
Oxidation-Reduction Potential (mV)	-4670.4	1780.6	-2.623	0.013749 *
-Summer Months - (Intercept)	1085.45	73.42	14.784	1.65e-09 ***
Oxidation-Reduction Potential (mV)	-27.29	45.15	-0.605	0.556
(Intercept)	941.51	34.38	27.383	<2e-16 ***
Temperature (°C)	76.92	34.74	2.214	0.032 *
(Intercept)	943.20	35.46	26.597	<2e-16 ***
Dissolved Organic Matter (RFU)	49.50	35.46	1.396	0.17

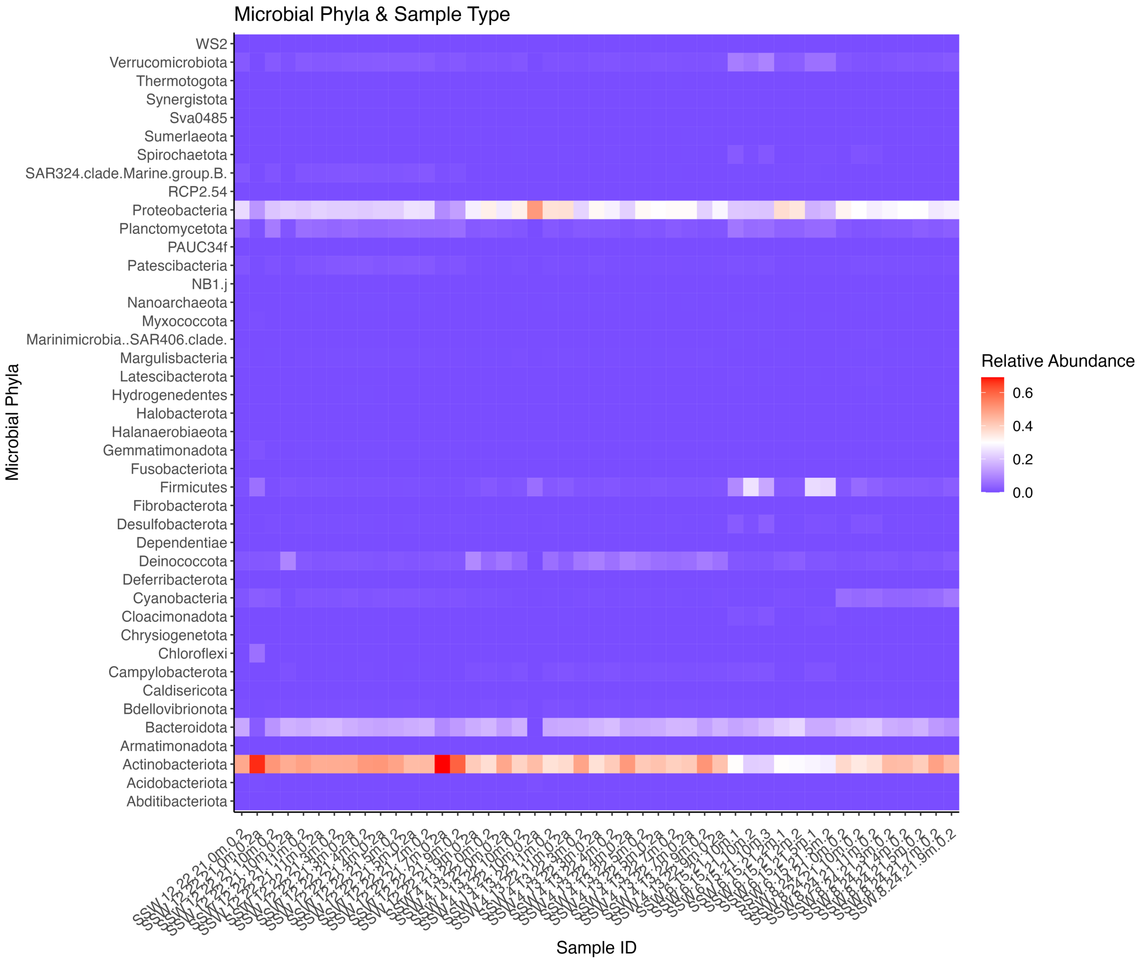
J. Microbial Shannon Diversity by Sampling Depth considering Sample Months. Colors indicate the Sample month.



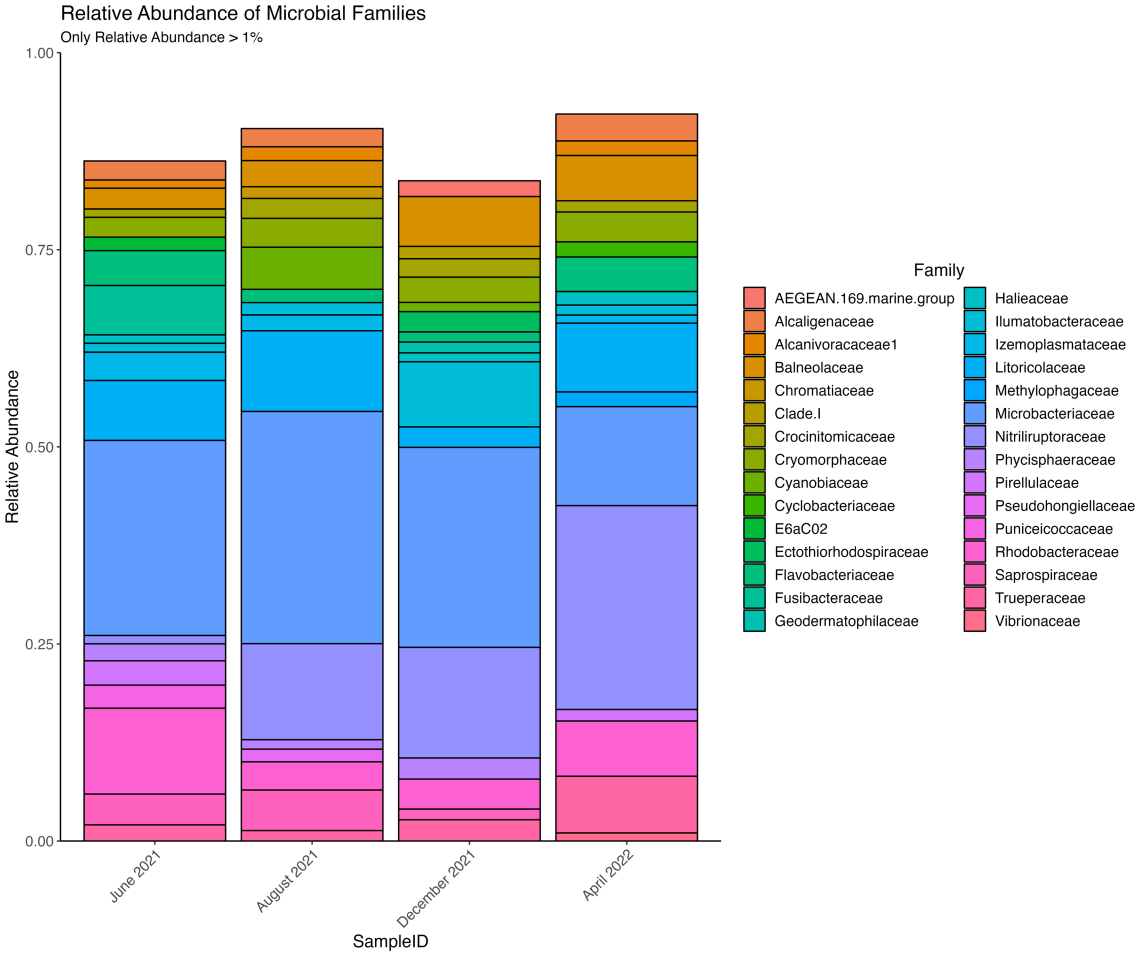
K. Microbial Species Richness by Sampling Depth considering Sample Months. Colors indicate the Sample month.



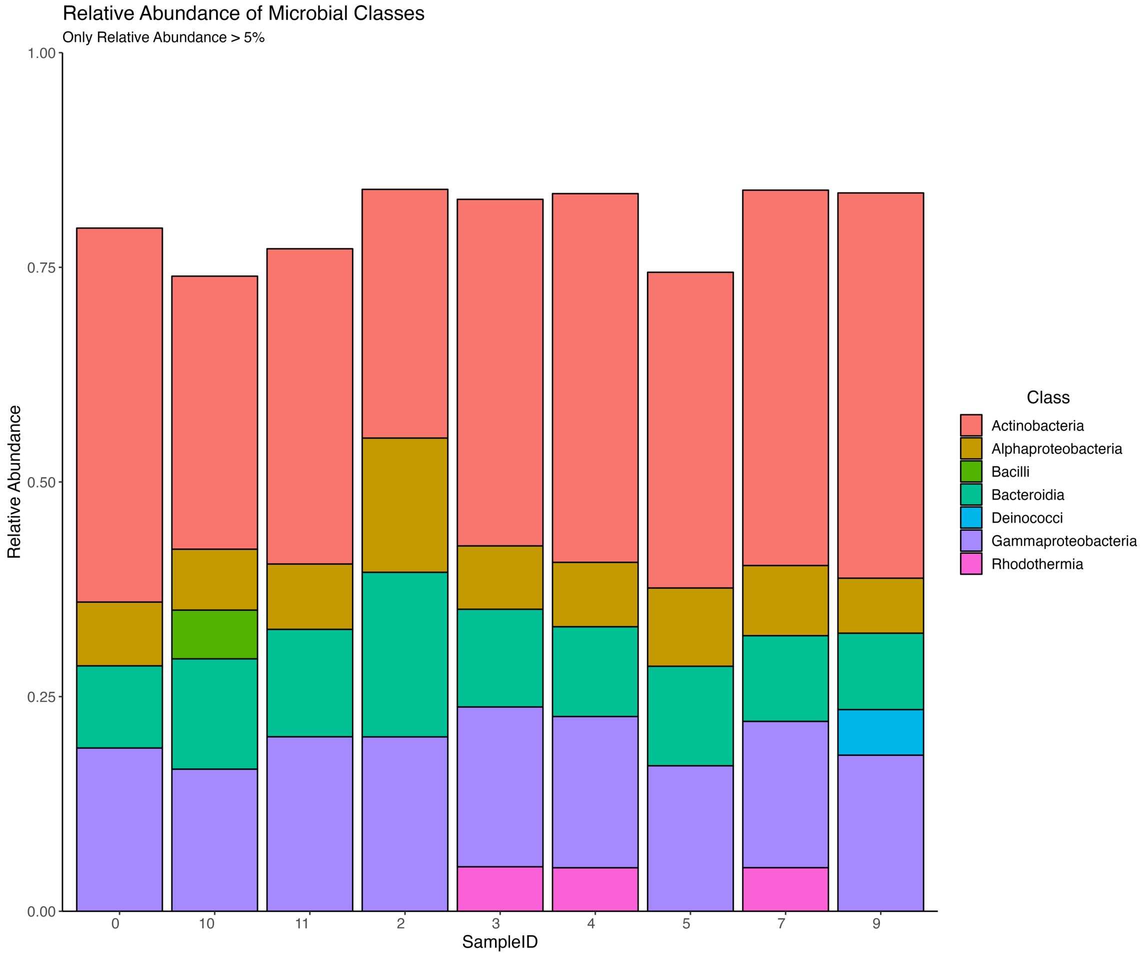
L. Heat Map of Microbial Phyla Relative Abundance by Sample ID.



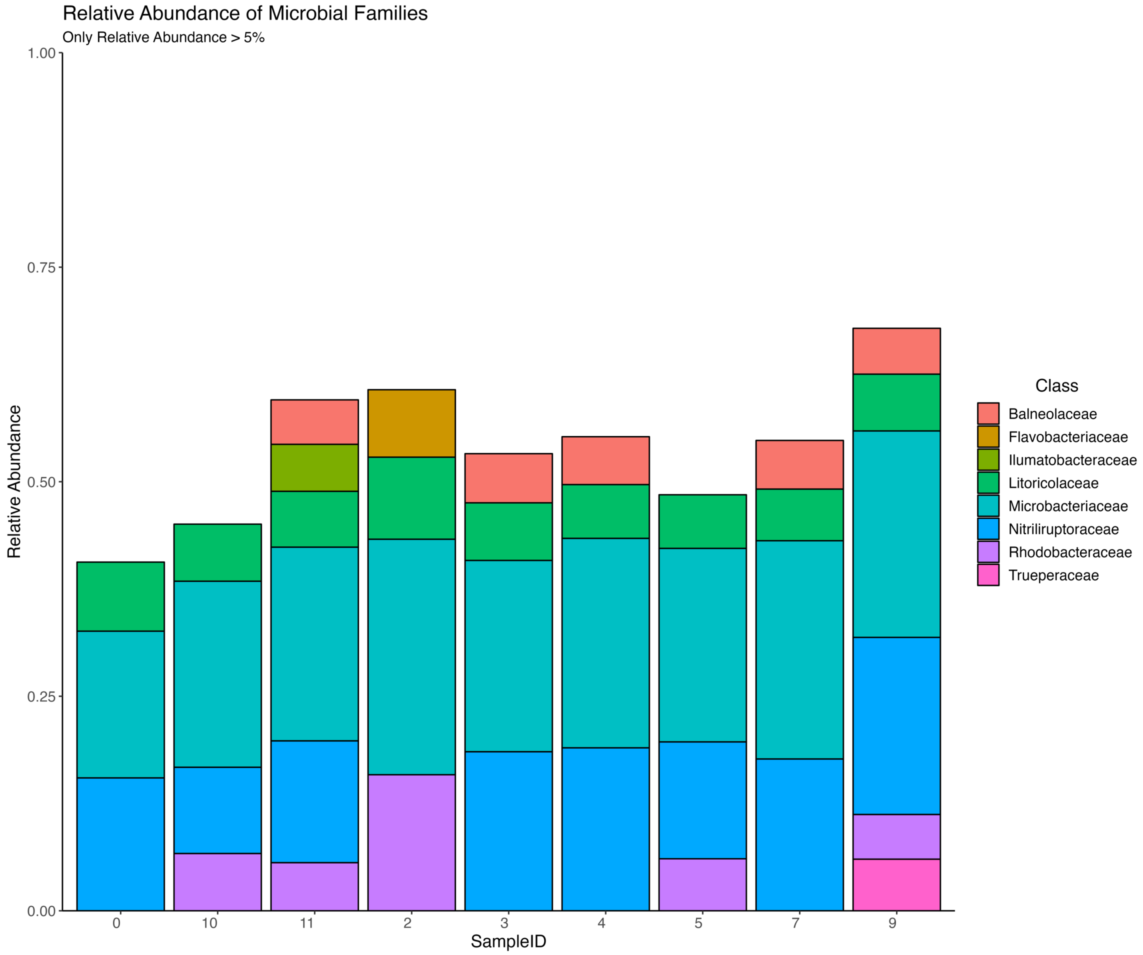
M. Microbial Family Relative Abundance of > 1% by Sample ID (Sample Month).



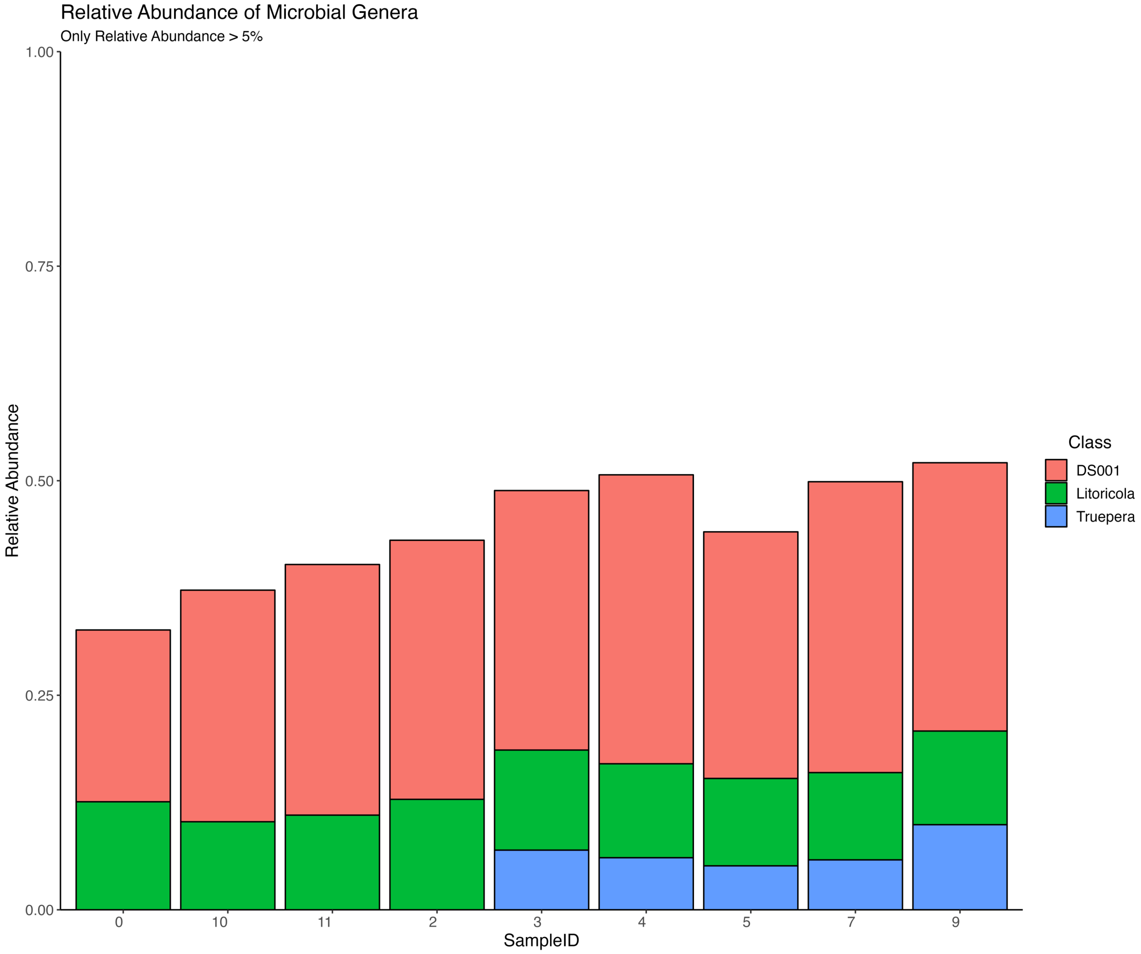
N. Microbial Class Relative Abundance of > 5 % by Sampling Depth considering all sample collections.



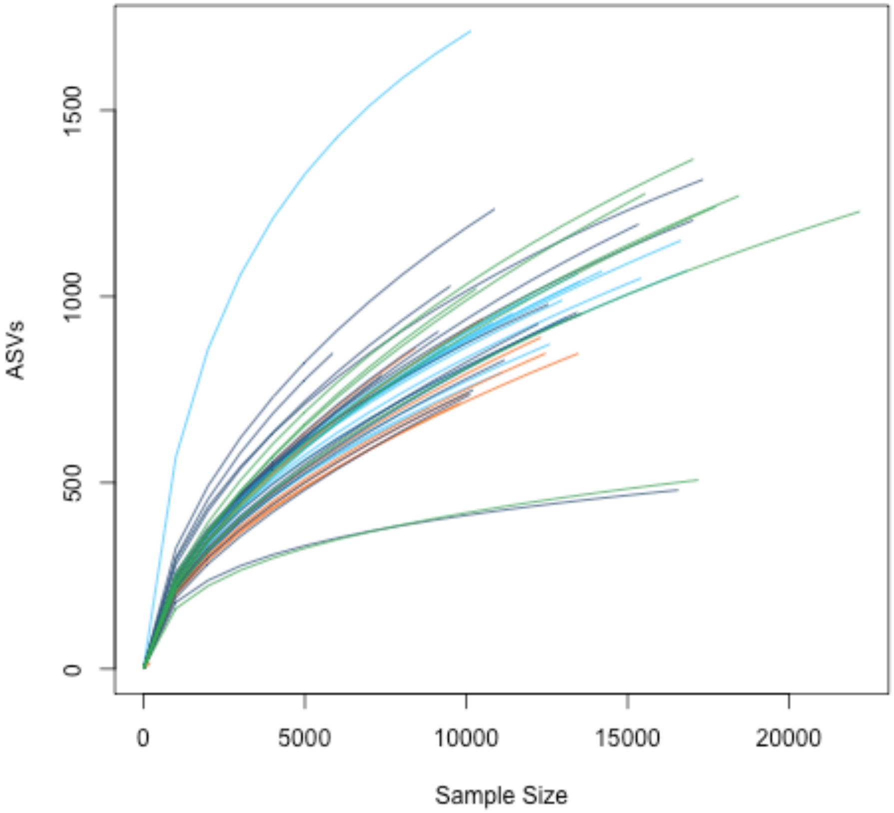
O. Microbial Family Relative Abundance of > 5 % by Sampling Depth considering all sample collections.



P. Microbial Genera Relative Abundance of > 5% by Sampling Depth considering all sample collections.



Q. Rarefaction Curve of ASV table. Each curve is colored based on its sample category (sample ID).



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