8-2023

Influence of Hydrologic History on Nitrogen Cycling in Lake Sediments

Emily Jainarain
Utah State University

INFLUENCE OF HYDROLOGIC HISTORY ON NITROGEN CYCLING IN

LAKE SEDIMENTS

by

Emily Jainarain

A thesis submitted in partial fulfillment of
the requirements for the degree

of

MASTER OF SCIENCE

in

Watershed Sciences

Approved:

Erin Rivers, Ph.D. Major Professor	Timothy Walsworth, Ph.D. Committee Member
Janice Brahney, Ph.D. Committee Member	D. Richard Cutler, Ph.D. Vice Provost of Graduate Studies

UTAH STATE UNIVERSITY
Logan, Utah

2023

ABSTRACT

Influence of Hydrologic History on Nitrogen Cycling in Lake Sediments

by

Emily Jainarain, Master of Science

Utah State University, 2023

Major Professor: Dr. Erin Rivers
Department: Watershed Sciences

Water level fluctuations in lakes cause littoral sediments to go through phases of desiccation and reinundation, which can change sediment properties and stimulate biogeochemical reactions. Limited research has been performed on the effects of drying and rewetting on nitrogen transformations in littoral sediments, therefore the contribution of internal nitrogen loading from littoral sediments with varied hydrologic history is not well understood. This study investigated the mechanisms of nitrogen release from littoral sediments of varied hydrologic history as sediments transitioned from dry to wet conditions. Nitrogen fluxes were assessed during dry summer conditions and transitional fall conditions in three field sampling campaigns across three zones (saturated, littoral, and upland) with different hydrologic histories at Utah Lake, USA. Sediment and water samples were analyzed for bioavailable nutrients (NO_3N, and NH_4-N) and sediment nitrogen cycling (denitrification, mineralization, nitrification, and microbial biomass C and N).

Our results varied considerably between zones of different hydrologic history. The lake zones displayed high levels of NH_4-N and the upland zones displayed high levels of NO_3-N and high rates of mineralization. NH_4-N was high in the winter across all zones. The littoral zones did not display significant rates of any of the tested variables, possibly due to tight coupling. The high levels of inorganic nitrogen and rates of mineralization were influenced by carbon availability, sediment moisture, and pH. If lake levels decrease and more sediments are exposed, there is potential for bioavailable nutrients to leach into the groundwater and contribute to internal nitrogen loading. Our results show that nitrogen transformations in Utah Lake vary between zones and are sensitive to changes to environmental conditions.

The results of this study will contribute to a better understanding of the influence of water level fluctuations on nitrogen cycling in Utah Lake littoral sediments. By exploring the rates of nitrogen transformations and several biogeochemical processes, insight can be gained on whether littoral sediments act as nutrient sinks or sources and how the overall nutrient budget of the lake is impacted. This study will play a critical role in developing nutrient criteria for the lake.

(41 pages)

PUBLIC ABSTRACT

Influence of Hydrologic History on Nitrogen Cycling in Lake Sediments

Emily Jainarain

Water quality is declining in freshwater lakes around the world due to environmental change and anthropogenic activities that threaten the physical, ecological, and geochemical integrity of freshwater ecosystems. Excess N and P in lakes can cause eutrophication, a major driver of water quality impairment that leads to excessive algal growth, or harmful algal blooms (HABs), and poses risks to recreation, fisheries, and public drinking water. Water level fluctuations in lakes are expected to become more frequent and intense as climate change increases periods of drought and alters precipitation patterns, and fluctuations may stimulate biogeochemical reactions in littoral sediments that add or remove bioavailable nutrients and impair water quality in lakes. This study assessed the effect of drying and rewetting on nitrogen cycling in littoral sediments at Utah Lake, a shallow, hypereutrophic lake in Utah, USA.

Nitrogen fluxes were assessed during dry summer conditions and transitional fall conditions in three field sampling campaigns across three zones (saturated, littoral, and upland) with different hydrologic histories. Sediment and water samples were analyzed for bioavailable nutrients (sediment nitrate, and sediment ammonium) and sediment nitrogen cycling (denitrification, mineralization, nitrification, and microbial biomass C and N). Our results showed considerable variability across zones. High levels of sediment ammonium were found in the lake zones and in winter across all zones, while high levels of nitrate and rates of mineralization were found in the upland zones. Carbon availability,

sediment moisture, and pH strongly influenced these results. We hypothesize that if lake levels decrease and more sediments are exposed, there is potential for bioavailable nutrients to leach into the groundwater and contribute to internal nitrogen loading.

The results of this study will contribute to the creation of an internal nutrient loading budget of Utah Lake. With this data, we will better understand the relationships between external and internal nutrient loading to Utah Lake. From there, the most significant sources of nutrients to the lake will be identified and we can begin to reduce nutrient loads in order to manage eutrophication.

ACKNOWLEDGMENTS

I would like to thank my advisor, Dr. Erin Rivers, for being an incredible mentor and friend throughout this entire process, and for the time and effort that you put into this research. This work would not have been possible without the long hours you spent in the lab and in the field. Thank you to my committee members, Dr. Janice Brahney and Dr. Tim Walsworth, for their guidance and insightful feedback on my research. Next, thank you to my lab-mate, Lily Wetterlin, for helping conduct field work and lab analyses, and for your support over the last two years. I am forever grateful for my parents, Charles and Janet Jainarain, who instilled a love of science and environmental advocacy in me at a young age, and never stopped pushing me to continue learning.

This project would not have been possible without the JEDI Graduate Research Fellowship. I am grateful to the Department of Watershed Sciences for awarding me the fellowship and taking steps toward creating a more diverse, equitable, and inclusive community of scientists. Finally, thank you to the Utah Department of Environmental Quality Division of Water Quality, who supported this work. Any recommendations expressed here are those of the author(s) and do not necessarily reflect the views of the Utah Department of Environmental Quality.

Emily Jainarain

CONTENTS

LIST OF TABLES

LIST OF FIGURES

1. INTRODUCTION

Changes in environmental conditions can influence the community structure and function of microorganisms, resulting in ecosystem-wide effects on microbially-mediated biogeochemical cycles in aquatic systems. Microbially-mediated nitrogen transformations regulate the availability of reactive nitrogen in benthic sediments and the overlying water column, which can lead to changes in water quality (Small et al., 2014, Robertson and Groffman, 2015). The rate and magnitude of microbial transformations of nitrogen are influenced by many factors, including pH, temperature, oxygen, carbon availability, and microbial community composition (Groffman et al., 1988, Schimel et al., 2007). As the climate changes and anthropogenic activities increasingly alter the environmental conditions of aquatic ecosystems, it is important to understand the resulting impact on nitrogen transformations to inform management and restoration in these systems.

Microbially-mediated nitrogen transformations, controlled by biological, chemical, and physical processes, vary in response to fluctuating environmental conditions. Redox potential controls the reducing or oxidizing capacity and varies throughout the hydrologic gradient in lake shorelines (Keddy, 2000). High redox potential promotes nitrification ($NH_4^+ \rightarrow NO_2^- \rightarrow NO_3^-$) while low redox potential promotes denitrification ($NO_3^- \rightarrow N_2$) and nitrogen fixation ($N_2 \rightarrow NO_3^-$) (Bodelier et al., 1996, Peralta et al., 2013). Changes in precipitation patterns due to climate change may result in longer periods of drought and excessive rainfall events, which can alter hydrologic regimes of water bodies (Seneviratne, 2014). Shifting precipitation patterns can cause changes in drying-rewetting cycles in water bodies, which influences oxygen availability and redox potential in sediments.

The availability and composition of carbon and nitrogen plays a key role in nitrogen transformations (Jie et al., 2009). In general, the ratio of carbon to nitrogen in lakes and the littoral zones of lakes are determined by vegetation type. Macrophytes have carbon to nitrogen ratios of 10-20. (Kaushal and Binford, 1999). High carbon to nitrogen ratios creates competition for oxygen, encouraging heterotrophic bacteria to outcompete autotrophic nitrifiers and resulting in reduced NH_4^+ oxidation (Jie et al., 2009). Additionally, a high carbon to nitrogen ratio in sediments has been shown to promote nitrogen immobilization, in which inorganic nitrogen is assimilated by microorganisms. (Nieder and Benbi, 2008). Rising temperatures due to climate change increase the duration, magnitude, and dispersal of macrophytes, potentially impacting the carbon to nitrogen ratio in lakes (Paerl et al., 2016).

Climate change and anthropogenic stressors such as diversions for consumptive water use cause complex changes in hydrology and drive internal changes in lake ecosystems (Abbott et al., 2021; Weise et al., 2016). Rising temperatures and increased evapotranspiration, combined with diversions, managed outflow, and upstream water use, result in seasonal, interannual, and long-term fluctuations of lake levels (Wurtsbaugh, 2016). Water level fluctuations cause littoral sediments to go through phases of drying and rewetting, which can change sediment properties and alter the duration of oxic and anoxic conditions (Weise et al., 2016). As sediments transition from dry to wet conditions, pulses of bioavailable nutrients may release into the water column and impact the nutrient dynamics of lakes. This biogeochemical reaction commonly occurs along the lake shoreline where water level fluctuations have the greatest effect (Zohary and Gasith, 2014; Carmignani and Roy, 2017).

The littoral zone of shallow water in lentic ecosystems is especially vulnerable to small changes in water levels resulting in large areas exposed to oxygen (Leira and Cantonati, 2008). Biogeochemical hot spots (areas that show high rates of biogeochemical reactions relative to the surrounding area) and hot moments (periods of time during which rates of biogeochemical reactions are high) develop at the interface between environmental conditions in a landscape where resources converge, typically at the intersection of hydrologic flow paths (McClain et al., 2003; Vidon et al. 2010). With fluctuations between saturated and dry conditions, the littoral zone may be a *hot spot* for microbial N transformations in lakes during *hot moments* when sediments transition from dry to flooded conditions. As littoral sediments go through periods of desiccation and rewetting, potentially significant amounts of bioavailable nitrogen (N), phosphorus (P), and carbon (C) are released from sediments into the water column (Baldwin and Mitchell, 2000; Birch, 1960; McComb and Qiu, 1998; Scholz et al., 2002). Microorganisms adapt to the slow change in osmotic potential during periods of drought; however, when sediments are reinundated with rising water levels, the rapid change in osmotic pressure induces cell lysis. This cell lesion releases bioavailable nutrients that were previously bound in the microbial biomass, causing a flux of N, P, and C into the water column (Kieft, 1987). Nutrient availability is affected by biologically mediated processes that are highly dependent on oxidation state (Peralta et al., 2013) and hydrologic stress of sediments may be a major control in nutrient release.

Investigating rates of nitrogen transformations in sediments that undergo periods of desiccation and inundation provides insights into mechanistic controls of nutrient dynamics in lake littoral zones. The majority of drying-rewetting nitrogen cycling investigations have been conducted in the summer, and little is known about how nitrogen cycling processes are impacted by the transition of growing season to dormant season. The goal of this study was to better understand how the hydrologic history of lakebed sediments has shaped microbial nitrogen transformations and how nitrogen transformations are impacted by seasonal change. Specifically, the objectives of this study were to 1) identify the differences in the availability of nitrogen and rates of nitrogen transformations among sediments with different hydrologic histories and 2) identify how nitrogen transformations are impacted by changes in environmental conditions. We analyzed sediment samples from four locations around a lake with three contrasting hydrologic histories (perennially saturated, intermittent dry-wet, and perennially dry) for sediment chemistry, benthic nitrogen cycling, and benthic carbon cycling during late summer, fall, and winter conditions.

2. METHODS

2.1 Study Site

Utah Lake (40.214741, -111.796658), located in northern Utah, USA, is an unstratified, shallow freshwater lake. The depth of the lake is mostly uniform, averaging 2.8 m with a maximum depth of 6 m (Randall, et. al. 2019). Utah Lake is a remnant of Pleistocene Lake Bonneville and was formed about 8000 years ago. Utah Lake is eutrophic with frequent harmful algal blooms, caused by high concentrations of phosphorus and nitrogen. The contributing watersheds are mixed use, with high agricultural and urban land use that contribute high loads of nutrients into the lake and (Randall, et. al. 2019).

Because of the low-gradient bathymetry of Utah Lake, annual water level fluctuations of 3-4 feet throughout the year cause frequent drying and rewetting of littoral sediments. The main causes of the fluctuations are evaporation, precipitation patterns, managed outflow, and upstream diversions used for irrigation, agriculture, and drinking water. Approximately 10-15% of Utah Lake is littoral and impacts of drying and wetting affect a large proportion of lakebed sediments.

2.2 Field Sampling

Carbon and nitrogen pools and fluxes were assessed in three field sampling events in September, October, and December 2021. Average temperatures during the sampling events were 24.2, 11.7, and 7.8 ◦C (September - December). Rainfall amounts for the month prior to sampling events were 62, 112.5, and 38.4 mm (September - December).

Four sampling locations were selected around Utah Lake representing low-gradient bathymetry with littoral zones that are substantially impacted by wetting and drying (Figure 1). At each location, three zones were sampled to represent distinct hydrologic conditions: perennially dry (upland), intermittent dry-wet (littoral), and saturated (lake). The littoral zones were moist but were never inundated during the period of sampling. At each of the three zones at each location, composite sediment samples were collected, composed of four sediment cores (7.52 cm diameter x 15 cm depth). All sediment samples were put on ice for transport. Upon returning to the laboratory sediment samples were refrigerated at 4°C until analysis (<2 weeks).

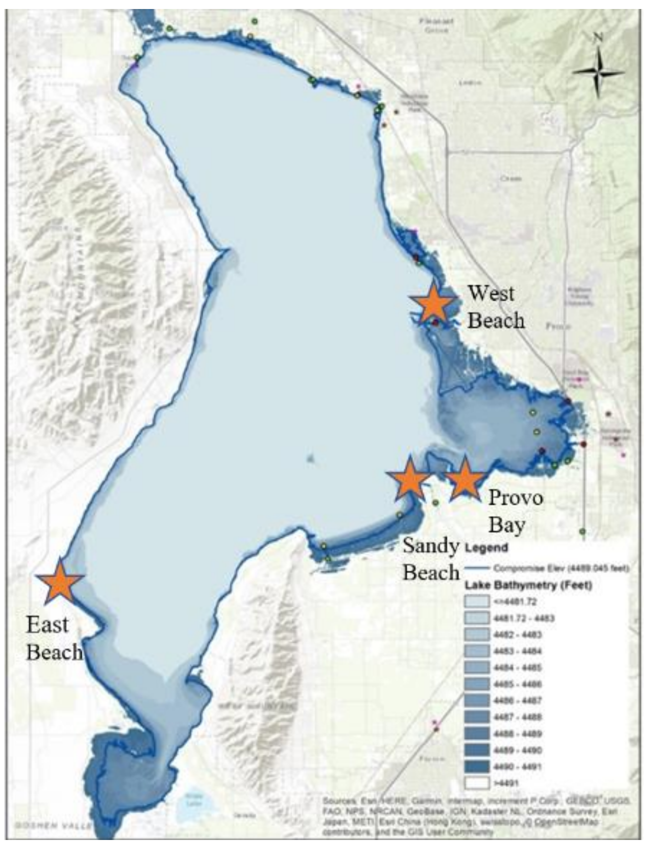

Figure 1. Areas of Utah Lake that were continuously wet for the period of 2010 – 2020 (light blue) versus those that were periodically dry (dark blue bands). Stars represent sampling locations at Utah Lake.

2.3 Analysis of Sediment and Water Samples

Sediment samples were analyzed for bioavailable nutrients (PO_4-P, NO_3-N, and NH_4-N), microbial biomass C and N, and sediment nitrogen cycling rates (denitrification, mineralization, nitrification).

Sediment Physiochemical Properties

For each zone, composite sediment samples were subsampled and analyzed for sediment dry mass, moisture content, organic matter content, bulk density, pH, and extractable nutrients using standard methods (Robertson et al., 1999). To determine sediment gravimetric water content, field-moist subsamples were weighed, oven dried at 105 °C until there was no further mass loss, and then reweighed. To determine sediment pH, equal portions of sediment samples and DI water were mixed, equilibrated for 30 minutes, and pH was measured using a multiparameter probe (YSI Inc., Yellow Springs OH). Organic matter content was analyzed by loss on ignition, in which subsamples that were previously analyzed for dry mass and moisture content were burned (ashed) in a muffle furnace at 550 °C for four hours and then reweighed. To measure exchangeable ions in the sediment matrix, 40 mL of KCl was added to 10 g of sediment from each zone (2 replicates per sample) (Robertson et al., 1999). The samples were mixed, settled, and filtered through Whatman Grade 42 filter paper (2.5 µm pore size) using gravimetric filtration. Once the samples were filtered, they were frozen until analysis.

Benthic Nitrogen Cycling

The chloroform fumigation-incubation method (CFIM) was used to estimate microbial biomass C and N (Jenkinson and Powlson, 1976). Duplicate subsamples of 10 g from the composite soil sample of each zone were placed inside 50 ml glass beakers. Two treatments, control and fumigated, were used. Samples designated for fumigation were placed in a vacuum desiccator lined with moist paper towels. Acid washed chloroform and boiling chips were placed in a 50 ml beaker in the center of the desiccator. The desiccator was sealed, placed in a laboratory hood, and evacuated, allowing the chloroform to boil for approximately one minute. Samples were incubated for 24 hours in the chloroform vapor-saturated atmosphere. At the end of the incubation period, the desiccator was vacuum air-flushed 6 times to remove the chloroform. Samples were removed from the desiccator, placed in quart wide mouth mason jars, and sealed with lids fitted with rubber septa for gas sampling. Fumigated samples were inoculated with 0.2 g of fresh sediments. Concurrently, unfumigated sediment samples are placed in canning jars and treated in the same fashion, serving as controls. The fumigated and control samples were placed in an incubator at 25 °C for 10 days. At the end of the incubation period, 5 mL headspace samples were extracted and analyzed immediately for carbon dioxide on a Shimadzu GC-2014 gas chromatograph (Shimadzu Scientific Instruments). Following the analysis, a final nutrient extraction was performed on all samples (control and fumigated) using a 2M KCl solution, filtered with Whatman Grade 42 filter paper (2.5 µm pore size), and stored in a freezer.

Using the gas chromatograph results, microbial biomass carbon was calculated as:

$$\left(1.73 * Fumigant\,\frac{\mu g\ C}{g\ soil}\right) - \left(0.56 * Control\,\frac{\mu g\ C}{g\ soil}\right)$$

and microbial biomass nitrogen was calculated as:

$$Microbial\ Biomass\ C\left(0.56\left(\frac{Control\ DIN}{Fumigant\ DIN}\right)\right) + 0.095$$

Fumigant and control μg C per g soil were calculated using the results from the gas chromatograph. Coefficients 1.73, 0.56, and 0.095 are derived from the regression of chloroform-fumigation incubation biomass C and N data against microscopic biomass of soils (Horwath et al., 1996). Fumigant and control DIN (dissolved inorganic nitrogen) were calculated using the final KCl extraction results for NO_3^- and NH_4^+ (described below).

Nutrient Analysis

Initial sediment KCl extract solutions and control and fumigated KCl extract solutions were analyzed for NH_4-N, NO_3-N, and PO_4-P on a SEAL AQ300 water chemistry analyzer using standard methods (Robertson et al., 1999).

Using the nutrient chemistry results, potential net nitrification was calculated as:

$$\frac{(Final\ Control\ NO_3 - Initial\ NO_3)}{Incubation\ Time}$$

Potential net mineralization was calculated as:

$$\frac{(Final\ Control\ NO_3 + Final\ Control\ NH_4) - (Initial\ NO_3 + Initial\ NH_4)}{Incubation\ Time}$$

Final Control NO_3 and NH_4 were calculated using the nutrient chemistry results from the incubated samples. Initial NO_3 and NH_4 were calculated using the nutrient chemistry results from the initial KCl extraction.

Denitrification

The chloramphenicol-amended, acetylene block method was used to measure microbial denitrification rates. Acetylene gas is used to block the conversion of N_2O (intermediate product) to N_2 (final product of denitrification) to permit the quantification of N_2O (Bernhardt and Schlesinger, 2012). Chloramphenicol inhibits microbial growth during the experimental period (Smith and Tiedje 1979). Sediment microcosms were prepared by adding 10 g sediment and 10 mL unfiltered lake water to 125 mL Erlenmeyer flasks capped with airtight neoprene septa. Microcosms were flushed and evacuated with vacuum-helium cycles to force anaerobiosis. The microcosm headspace was equilibrated to atmospheric pressure and amended with 10 mL acetylene gas. Headspace samples were extracted using a 5 mL airtight syringe and immediately injected and analyzed on a Shimadzu GC-2014 gas chromatograph. Samples were taken hourly for three hours, and denitrification rates were determined by the rate of N_2O production during the experimental period.

2.4 Statistical Analysis

A two-way analysis of variance was used to determine effects of zones, seasons, and their interactions on sediment physiochemistry and microbial N cycling variables using the *lmerTest* package in R statistical programming (v4.2.1; R Core Team, 2023). Post-hoc pairwise comparison tests were performed on significant effects ($\alpha = 0.05$) using least-squares means (*lsmeans* R package). Multiple linear regressions were developed to assess the relationships between sediment physiochemistry and microbial N cycling variables. A both-direction stepwise multiple linear regression was performed by using the "step" function in R. Akaike's information criterion (AIC) was used to compare variables and identify those that best explain the variance in N cycling variables. To meet parametric statistical assumptions, the data were normalized by log-transforming all variables except net N mineralization and nitrification. Due to the presence of negative and positive values in these variables, a cubed-root transformation was used.

3. RESULTS

3.1 Sediment Chemistry

Sediment NH_4-N ranged from 0.014-7.52 µg -N/g-dry sediment (Table 1.1). An effect of season (p-value < 0.0001) and zone (p-value < 0.05) on NH_4-N was observed, and the interaction between zone and season was significant (p-value < 0.1, Figure 2). The highest concentrations of sediment NH_4-N were observed in the lake zones, and sediment NH_4-N was highest during December and lowest in October. Sediment NO_3-N ranged from 0-31.4 µg -N/g-dry sediment (Table 1.1). There was not an effect of season on NO_3-N, but there was a significant effect of zone on NO_3-N (p-value < 0.05), with the highest amount of sediment NO_3-N in the upland zones (Figure 3). Sediment organic matter (sed-OM) ranged from 4-20 g-OM/kg. No effect of zone or season was found in sed-OM (p-value > 0.1).

Table 1

Average values of sediment physiochemistry and microbial N cycles variables for each month at each zone. Standard deviations are in parentheses.

Zone	Date	MBC (ug C/g Sediment)	MBN (ug N/g Sediment)	Mineralization (ug-N/g dry Sediment/day)	Nitrification (ug-N/g dry Sediment/day)	Respiration (ug C/g Sediment/day)	Sediment NO3 (ug-N/g dry Sediment)	Sediment NH4 (ug-N/g dry Sediment)	Organic Matter Content
Lake	September	1319.2 (1085.1)	12402.24 (8235.01)	-0.95 (0.79)	-0.01 (0.1)	77.33 (42)	0.55 (0.83)	2.06 (1.95)	0.03 (0.02)
	October	629 (313.9)	4985.43 (3730.9)	-0.35 (0.51)	0.29 (0.5)	52.35 (20.87)	1.2 (1.32)	1.08 (0.44)	0.05 (0.02)
	December	686.35 (394.31)	920.51 (1367.1)	-1.09 (0.93)	0.26 (0.18)	26.18 (21.75)	0.33 (0.22)	4.69 (1.33)	0.04 (0.02)
Littoral	September	854.7 (662.8)	1732.23 (1371.3)	-0.24 (0.48)	0.25 (0.4)	56.19 (33.3)	0.68 (0.89)	0.98 (0.93)	0.04 (0.04)
	October	514.24 (267.46)	404.46 (334.9)	0.02 (0.97)	0.09 (0.82)	27.48 (21.03)	4.72 (6.06)	0.26 (0.27)	0.04 (0.03)
	December	756.92 (416.04)	709.27 (464.25)	-0.36 (1.73)	0.18 (0.167)	21.53 (10.84)	1.11 (1.5)	3.83 (2.6)	0.04 (0.02)
Upland	September	277.68 (423.4)	660.16 (1060.4)	0.31 (0.88)	0.31 (0.82)	32.61 (37.7)	5.25 (7.14)	0.34 (0.23)	0.04 (0.03)
	October	599.73 (528.5)	724.35 (1151.05)	3.58 (6.54)	3.63 (6.57)	32.81 (35.75)	11.21 (13.6)	0.15 (0.11)	0.05 (0.05)
	December	973.74 (837.6)	1620.51 (1951.05)	-0.33 (1.88)	1.43 (1.62)	41.56 (44.47)	10.1 (11.55)	5.17 (1.66)	0.1 (0.08)

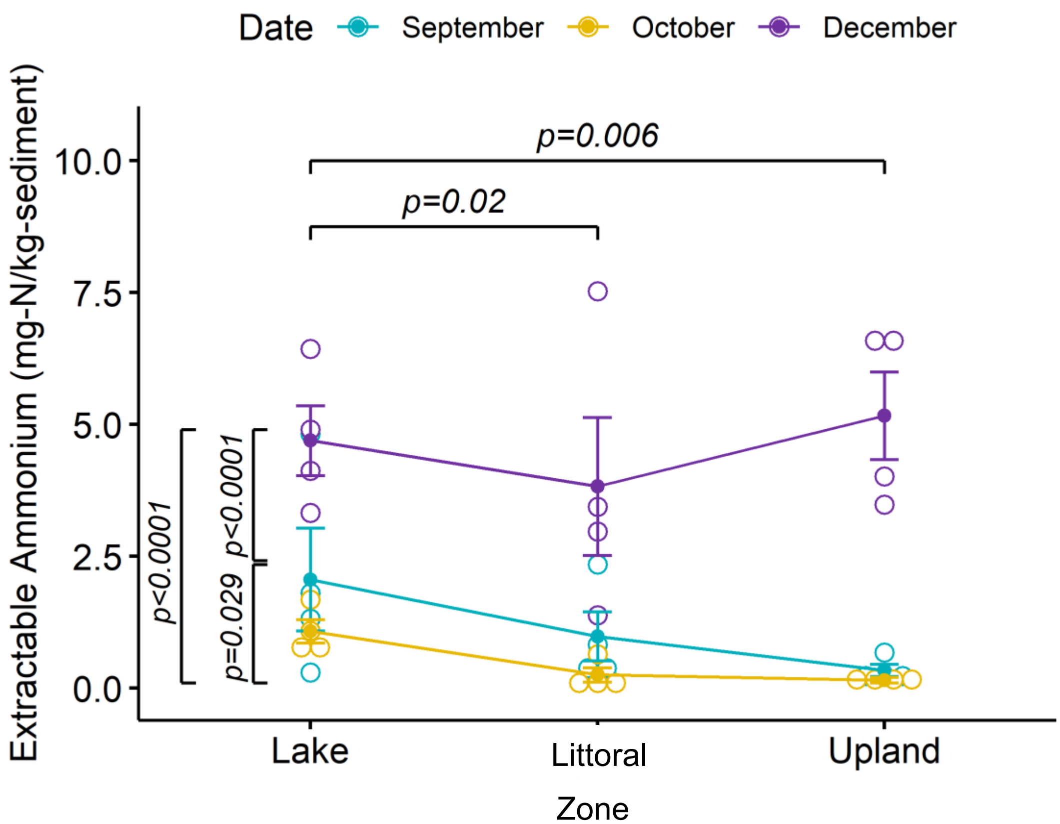

Figure 2. Sediment ammonium concentrations in lake, littoral, and upland sediments at Utah Lake in September, October, and December 2021. P-values indicate pairwise differences ($p < 0.1$).

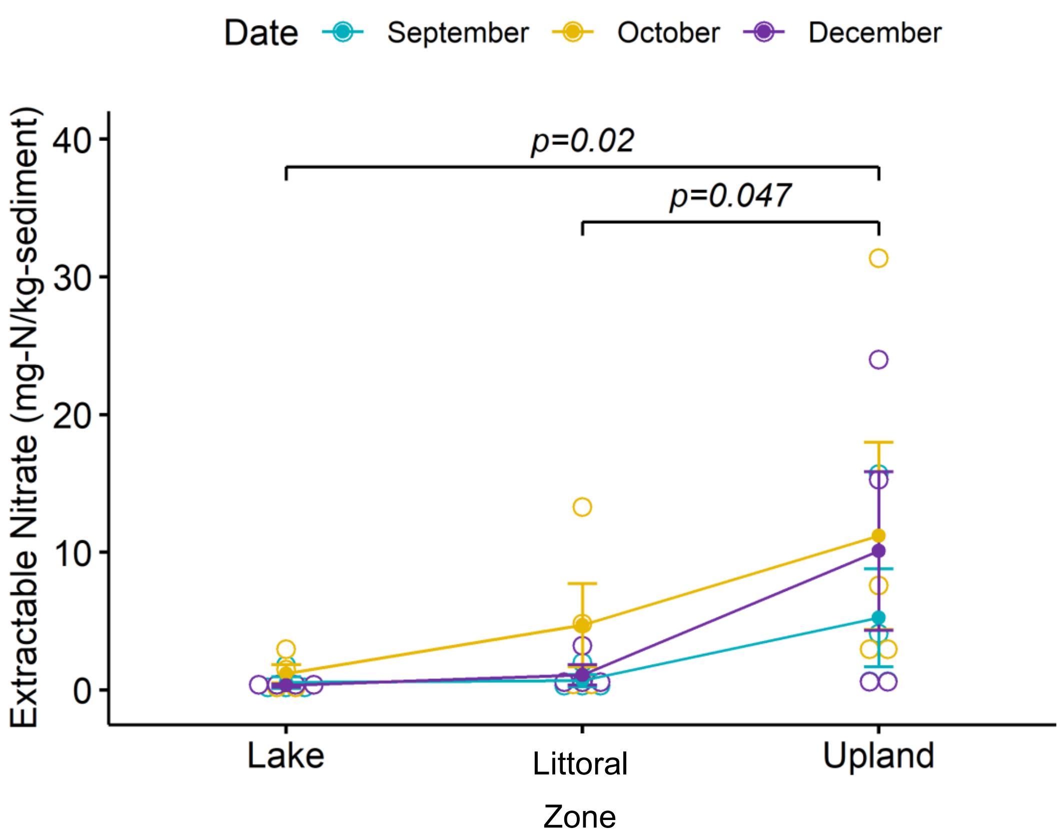

Figure 3. Sediment nitrate concentrations in lake, littoral, and upland sediments at Utah Lake in September, October, and December 2021. P-values indicate pairwise differences (p < 0.1).

3.2 Benthic Nitrogen Cycling

Net nitrification ranged from -1.1-13.5 µg -N/g-dry sediment/day (Table 1.1). The negative values indicate that NO_3-N is being consumed, likely due to denitrification. There was no effect of zone or season on net nitrification (p-value > 0.1). Net mineralization rates ranged from -2.9-13.3 µg -N/g-dry sediment/day (Table 1.1). Negative mineralization rates indicate net N immobilization through microbial uptake, or denitrification. There was an effect of zone on net mineralization where higher mineralization was observed in the upland zones than the lake zones (Figure 4, p-value < 0.05). The littoral zones were not significantly different than the upland or lake zones (p-value > 0.1). Values ranged from -2.02-0.31 in the lake zone, -2.8-1.2 in the littoral zone, and -2.6-13.4 µg -N/g dry sediment/day in the upland zone. There was no effect of season on net mineralization (p-value > 0.1).

Microbial Biomass N

Microbial biomass N ranged from 5.31 - 23059.98 µg -N/g-dry sediment (Table 1). There was an effect of zone and an interaction of zone and season (p-value < 0.05). The highest microbial biomass N was observed in the lake zone (p-value < 0.5). The lake zones showed a seasonal decline in microbial biomass N, whereas the littoral and upland zones did not show distinct seasonal changes (Figure 5, p-value < 0.05). There was no effect of season on microbial biomass N (p-value > 0.1).

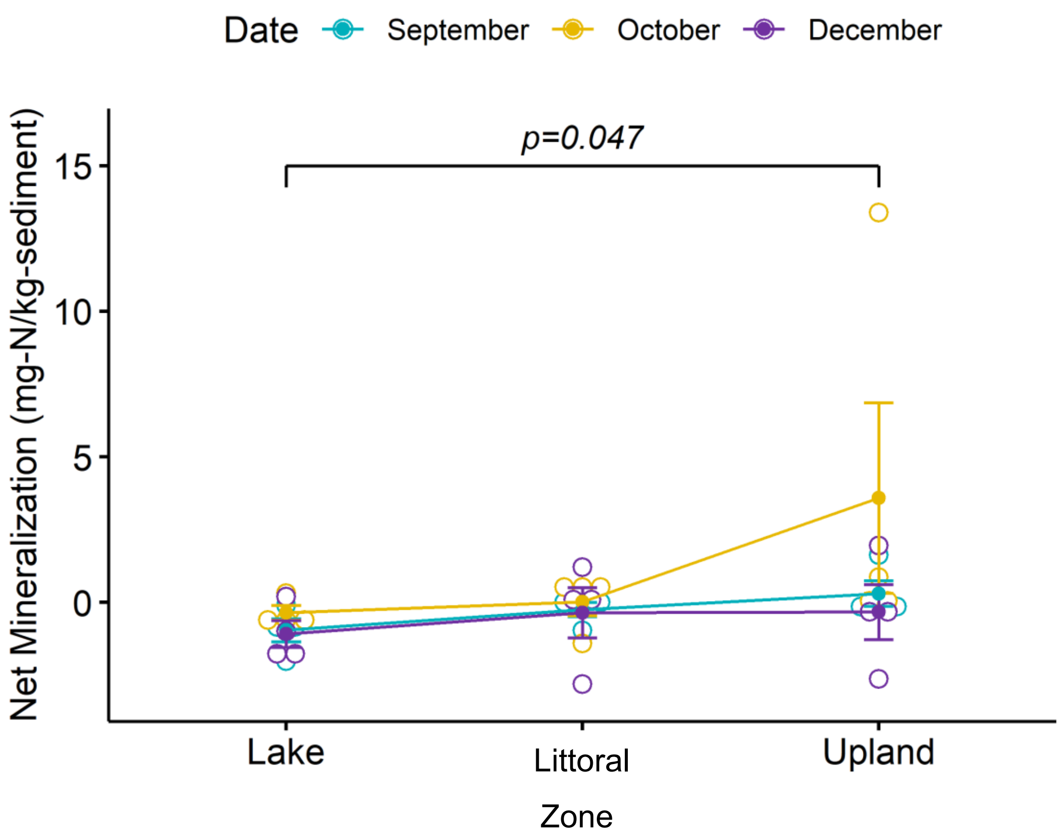

Figure 4. Net nitrogen mineralization rates in lake, littoral, and upland sediments at Utah Lake in September, October, and December 2021. P-values indicate pairwise differences ($p < 0.1$).

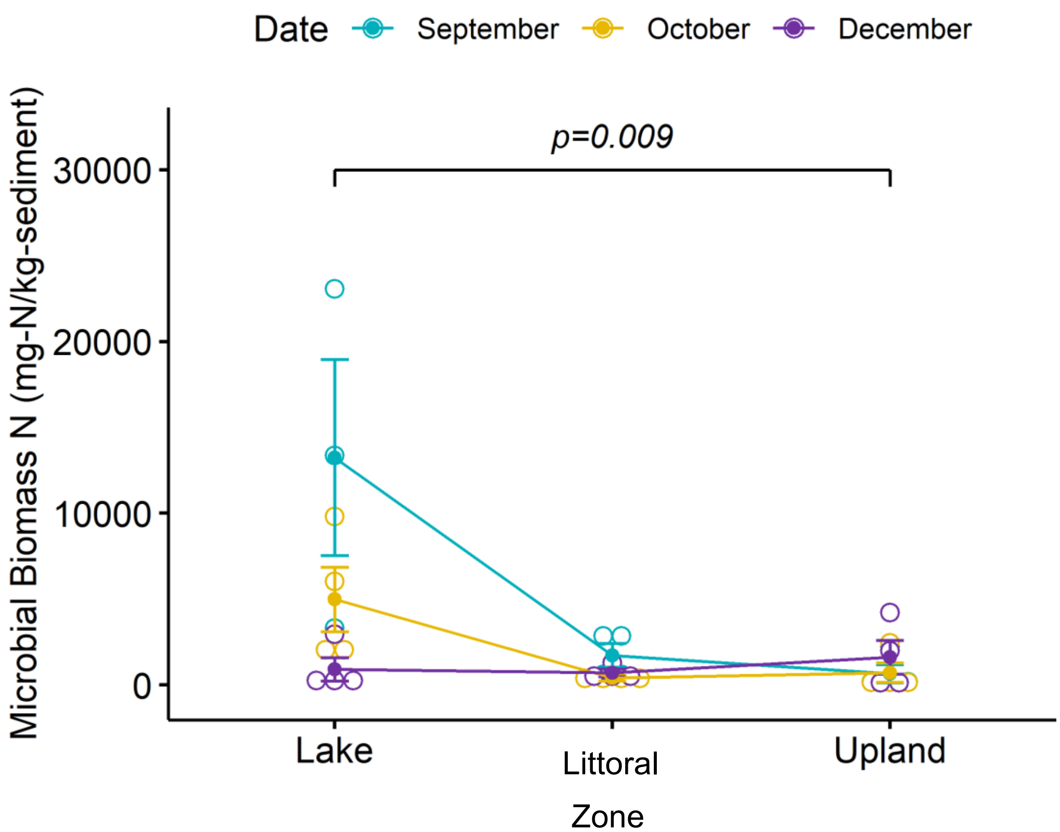

Figure 5. Microbial biomass nitrogen in lake, littoral, and upland sediments at Utah Lake in September, October, and December 2021. P-values indicate pairwise differences (p < 0.1).

Denitrification results were inconclusive, with negative rates of N_2O production, and were not included in analyses or results.

3.3 Benthic Carbon Cycling

Potential sediment respiration rates ranged from 4.9-134.4 µg -C/g-sediment/day (Table 1). There was no effect of zone or season on respiration (p-value > 0.1). Microbial biomass C ranged from 24.9 – 2685.6 µg -C/g-sediment/day (Table 1). There was no effect of zone or season on microbial biomass C (p-value > 0.1).

3.4 Multiple Linear Regression

The multiple linear regression analysis showed potential controls on mineralization, nitrification, microbial biomass C and N, and respiration (Table 2). All variables were influenced by pH except microbial biomass C, and sediment moisture influenced all variables except mineralization. The most important predictor variable was sed-OMC for three out of the five models. Sediment OMC, pH (negative relationship), and sediment NH_4-N (negative relationship) accounted for 47% of the variance in mineralization results, and sed-OMC was the strongest predictor variable in the mineralization model. Sediment OMC, pH, sediment moisture, and MBN (negative relationship) accounted for 39% of the variance in nitrification results, and sed-OMC was the strongest predictor variable in the nitrification model. Sediment moisture accounted for 77% of the variance in microbial biomass C results and was the strongest predictor variable. Sediment moisture and pH accounted for 65% of the variance in microbial biomass N results, and pH was the most important predictor variable for the microbial biomass N model. Sediment OMC, pH, sediment moisture, NH4-N (negative relationship), and microbial biomass N accounted for 88% of the variance in respiration results, and sed-OMC was the strongest predictor variable for the respiration model.

Table 2

Multiple linear regression model comparisons.

Mineralization	OMC - pH - Sediment NH4	0.47	2.80E-05	3	Sediment NO3, MBC, Sediment Moisture, MBN
Nitrification	OMC + pH + Sediment Moisture - MBN	0.39	0.00064	4	Sediment NH4, Sediment NO3, MBC
MBC	Sediment Moisture	0.77	1.20E-12	1	OMC, pH, Sediment NO3, Sediment NH4
MBN	pH + Sediment Moisture	0.65	1.04E-08	2	OMC, Sediment NO3, Sediment NH4
Respiration	OMC + pH + Sediment Moisture - Sediment NH4 + MBN	0.88	5.65E-14	5	Sediment NO3, MBC

4. DISCUSSION

The availability of nitrogen shapes the structure and community of microorganisms, which drives nitrogen transformations and availability (Yao et al., 2022). In this study, lakebed sediments were analyzed for sediment chemistry, benthic nitrogen cycling, and benthic carbon cycling across a hydrologic gradient. The results showed heterogeneity across hydrologic zones and seasons, and the investigated processes were highly variable. The upland zones displayed high rates of mineralization and levels of NO_3-N, the lake zone sediments displayed high levels of NH_4-N, and the littoral zones did not display high rates of nitrogen transformation or high levels of inorganic nitrogen. The littoral zones did not appear to be the hypothesized hot spots of nitrogen transformations, potentially due to tight coupling of processes or because they are characterized by short-term hot moments that go undetected, rather than long-term hot spots of activity. Carbon availability was found to play a strong role in the mineralization, respiration, and nitrification results, suggesting that the lake system is sensitive to carbon inputs. Our results show that nitrogen transformations were sensitive to environmental change, specifically carbon availability, sediment moisture, and pH. The data from this study will be used to create an internal nutrient loading budget for Utah Lake, in order to develop nutrient criteria.

4.1 Sediment Chemistry

We found that NH_4-N was significantly lower in September and October than in December across all zones. Utah Lake was warm and dry in September, cooler in October, and cold and below freezing in December. Algal presence in the lake in

September suggests high rates of NH_4-N assimilation during algal production during the summer. High NH_4-N coupled with low microbial biomass N across all zones in December suggests that microbial biomass turnover during seasonal senescence and freezing temperatures released high amounts of NH_4-N. Freezing temperatures cause microbial cell lysis, stimulating the release of bioavailable nutrients with limited re-establishment of the microbial biomass due to low temperatures. Austin and Strauss (2011) found that NH_4-N increased due to microbial turnover from sediment desiccation. The mineralization of microbial biomass can create high levels of NH_4-N in sediments, allowing for the possibility of NH_4-N to leach or transport downstream. Sediment NH_4-N was significantly higher in the lake zones than the upland zones and littoral zones across all seasons, and we hypothesize this is due to high concentrations of algal biomass and algal senescence.

The upland zones had significantly higher NO_3-N than the littoral zones or lake zones. Algal uptake of NO_3-N and denitrification may have been responsible for the low values in the lake and littoral zones. The higher NO_3-N levels in the upland zones were likely due to the suppression of denitrification, which favors anoxic conditions (Peralta et al., 2013). Denitrification rates are sensitive to changes in sediment moisture and are reduced in upland soils due to oxic conditions (Peralta et al., 2013). In the absence of denitrification, there is potential for NO_3-N leaching or loading through runoff or percolation to groundwater.

4.2 Benthic Nitrogen and Carbon Cycling

The lake zones had significantly lower rates of mineralization than the upland zone, and N immobilization was observed in all zones (as indicated by negative values of net N mineralization). The lake zones were characterized by high moisture content compared to the upland zones. The upland zones had significantly higher rates of mineralization. Mineralization favors oxic conditions, low C:N ratios, moist soils, and warm temperatures, all of which may contribute to high rates of mineralization in the upland zones (Johnson et al., 2005). Organic matter is required in order for mineralization to occur, and our results indicate that mineralization was primarily driven by sed-OMC. Net NH_4-N immobilization is the process that converts inorganic N into organic N (Yao et al., 2022). A high C:N ratio is required for N immobilization to take place. For example, the presence of aquatic vascular plants with high C:N ratios like shallow water macrophytes may cause nitrogen transforming microorganisms to immobilize NH_4-N to add to their biomass. This is due to the lack nitrogen supply from the vascular plants for the microorganisms to utilize. When microorganisms die, organic matter from microbial biomass is mineralized into NH_4-N (Nevins et al., 2020), and the NH_4-N may become immobilized again, be assimilated by algae, or converted to NO_3-N by nitrification.

OMC had a strong positive influence on nitrification results. Brierley et al. (2001) showed that organic nitrogen promoted nitrification in an acidic forest soil, but the addition of nitrate had an inhibitory effect unless the soil was supplied with a readily available carbon source, such as acetate. When C:N ratios are high, heterotrophic bacteria outcompete autotrophic bacteria for oxygen. The relationship between nitrate production and heterotrophic bacteria is not well understood in soils and sediments, but there are many potential mechanisms for nitrate production to occur (Martikainen, 2022).

Microbial biomass N was higher in the lake zones than the upland zones, and there was a seasonal decline of microbial biomass N in the lake zones. Our results showed that pH and sediment moisture had a positive influence on microbial biomass N. This may explain the high quantity of microbial biomass in the lake zones, as the lake sediments had the highest moisture content. Michaud et al., (2006) showed that heterotrophic bacteria produce high quantities of microbial biomass, and a high C:N ratio in the lake zones may explain the high lake biomass. Microbial biomass N and pH were highest in the lake zone, and the multiple linear regression showed a strong positive influence of pH on microbial biomass N. Microbial biomass showed seasonal patterns in lake sediments, with the highest biomass occurring in late summer and early fall (Steger et al., 2011). The seasonal decline may be explained by warm temperatures in the summer creating ideal conditions for increased microbial biomass, and microbial turnover occurring during the freezing temperatures in the winter. Respiration was similar across all zones and seasons. The strongest predictor variable was sed-OMC. While sed-OMC was a strong predictor variable, its effect on respiration was subject to its interaction with other variables. It is likely that because respiration is sensitive to OMC, it followed similar patterns.

4.3 Hydrologic History

The lake zones were characterized by low rates of mineralization and NO_3-N compared to the upland zones, and high levels of NH_4-N compared to the littoral and upland zones. Due to the presence of summer algal blooms, it is possible that nitrogen fixation supplied NH_4-N to the lake zones. In the littoral zone, NO_3-N was lower than the upland zone, and NH_4-N was lower than the lake zone. We hypothesize that tightly coupled cycles are the cause of the low and insignificant rates of nitrogen transformation. The upland zones had the highest amount of bioavailable nitrogen and the highest rates of mineralization. Due to the potential lack of denitrification, the NO_3-N either leaches into the ground or it is immobilized by vegetation.

It was expected that the highest rates of nitrogen transformations and levels of bioavailable nitrogen would occur in the littoral zones. We expected the littoral zones to be a hot spot due to frequent shifts in environmental conditions, particularly variability in redox potential due to fluctuating water levels. Fromin et al. (2010) observed that sediments with frequent water level fluctuations displayed a stronger stimulation of microbial potentials upon rewetting. The littoral zones showed similarities to lake and upland sediments, however, it is not evident whether fluctuating hydrology creates a long-term hot spot of nitrogen transformations in littoral sediments. It is more likely that hot moments of nitrogen transformations occur in littoral sediments in the period following reinundation, however, we were unable to capture hot moments with our study design. We hypothesize that nitrogen transformations are tightly coupled in the littoral zones, resulting in the removal of nitrogen from the system through denitrification. We cannot test this hypothesis due to the issues with our denitrifcation analyses, but our ANOVA results suggest that denitrification is occurring. Although the lake levels did not reach the upland zones, studies have shown that rainfall can stimulate biogeochemical reactions after extended periods of desiccation (Pinto et al., 2021, Fromin et al., 2010). If reinundation caused microbial biomass turnover in the upland zones, it was most likely due to rain rather than the fluctuating lake levels of Utah Lake.

4.4 Ecological Implications

Water level fluctuations in lakes are expected to become more frequent and intense as climate change increases periods of drought and alters precipitation patterns (Leira and

Cantonati, 2008), and fluctuations may stimulate biogeochemical reactions in littoral sediments that impair water quality in lakes. Studies suggest that duration of desiccation strongly influences the mechanisms of nitrogen release from littoral sediments upon rewetting (Fromin et al., 2010, Austin and Strauss 2011, Steinman et al., 2014). It has been documented that N-limitation or co-limitation has a strong influence on water quality, and seasons play a major role in determining the role of nitrogen (Wu et al., 2017). The recovery of eutrophic lakes is often delayed when internal nutrient loading from littoral sediments is high, and fluctuations in sediment moisture may contribute to loading. With better understanding about the role of drying and rewetting on nitrogen dynamics in lake sediments, internal nutrient loading models can take the effects of water level fluctuations into account for restoration and management decisions.

Utah Lake is a hypereutrophic lake, with high nutrient inputs from the surrounding watershed. Our results demonstrate that the system is highly sensitive to carbon inputs, and nitrogen transformations are influenced by the high C:N ratio. The average rates of N mineralization in the lake zones were negative, indicating net N immobilization, which typically corresponds to a high C:N ratio. Research is limited regarding the impact of carbon composition and availability on nitrogen transformations in sediments, specifically heterotrophic nitrification, but our results show that carbon availability had a significant positive relationship with rates of nitrogen transformations (Martikainen, 2022). This study is among several that are investigating nutrient loading in Utah Lake, in order to develop a nutrient budget. The combined studies will help form a bigger picture and aid in determining the greatest contributors of nutrient loading to Utah Lake.

5. CONCLUSION

Our results showed considerable variation in nitrogen transformations across zones of different hydrologic history around Utah Lake. The lake sediments displayed low levels of sediment NO_3-N and rates of mineralization, and high levels of sediment NH_4-N and microbial biomass N. On average, net N immobilization occurred more than net N mineralization. Our multiple linear regression analyses indicated that pH, sediment moisture, and carbon availability are the primary factors controlling these processes in Utah Lake sediments. We hypothesized that the littoral zone would be a hotspot for nitrogen transformations, but the littoral zone displayed low or insignificant rates of nitrogen transformations, likely due to tightly coupled mineralization-nitrification and nitrification-denitrification. The upland zones had the highest amounts of bioavailable nutrients. This may be due to low sediment moisture, increased oxygen availability, and low carbon availability. Sediment-OMC had the strongest influence on nitrification, mineralization, and respiration. Utah Lake receives nutrient inputs from wastewater treatment plants and nearby agriculture and urban development. The results of this study highlight the sensitivity of nitrogen transformations to organic matter inputs.

More research on the effect of dry-wet cycles on nitrogen transformations in lake sediments is needed to understand the underlying mechanisms of nitrogen release from littoral sediments. Future research should also consider community composition, as microbial adaptation to hydrology may impact microbial function (Peralta et al., 2013). Additional efforts are needed to understand if drying-rewetting cycles impact the nitrogen dynamics in the littoral zones of Utah Lake. The significantly higher amounts of winter NH_4-N, mineralization, and NO_3-N in the upland zones suggest that if lake levels decrease and more sediments are exposed, there is the potential for greater production of bioavailable nutrients that can then leach into the groundwater and contribute to nutrient loading. It has been shown that nitrate seeped into groundwater can contribute up to 36% of added nitrogen to lakes (Keeney et al., 1971). We expect that groundwater seepage into Utah Lake contains bioavailable nitrogen from external inputs, and levels could increase in the winter due to both the potential leaching of NO_3-N in the upland zone and the lack of microorganisms and vegetation to uptake bioavailable nitrogen.

REFERENCES

Bailey, V. L., Peacock, A. D., Smith, J. L., & Bolton Jr, H. (2002). Relationships between soil microbial biomass determined by chloroform fumigation–extraction, substrate-induced respiration, and phospholipid fatty acid analysis. *Soil Biology and Biochemistry*, *34*(9), 1385-1389.

Baldwin, D. S. (1996). Effects of exposure to air and subsequent drying on the phosphate sorption characteristics of sediments from a eutrophic reservoir. Limnology and Oceanography, 41(8), 1725-1732.

Baldwin DS, Mitchell AM (2000) The effects of drying and re-flooding on the sediment and soil nutrient dynamics of lowland river-floodplain systems: a synthesis. Regul Rivers Res Manag 16:457–467

Beklioglu, M., Romo, S., Kagalou, I., Quintana, X., & Bécares, E. (2007). State of the art in the functioning of shallow Mediterranean lakes: workshop conclusions. *Hydrobiologia*, *584*, 317-326.

Bodelier, P., Libochant, J. A., Blom, C. W. P. M., & Laanbroek, H. J. (1996). Dynamics of nitrification and denitrification in root-oxygenated sediments and adaptation of ammonia-oxidizing bacteria to low-oxygen or anoxic habitats. *Applied and Environmental Microbiology*, *62*(11), 4100-4107.

Brierley EDR, Wood M 2001: Heterotrophic nitrification in an acid forest soil: isolation and characterisation of a nitrifying bacterium. Soil Biol. Biochem., 33, 1403–1409.

Corstanje R, Reddy KR (2004) Response of biogeochemical indicators to a drawdown and subsequent reflood. J Environ Qual 33:2357–2366

De Groot, C. J., & Van Wijck, C. (1993). The impact of desiccation of a freshwater marsh (Garcines Nord, Camargue, France) on sediment-water-vegetation interactions. Hydrobiologia, 252(1), 83-94.

Horwath, W. R., Paul, E. A., Harris, D., Norton, J., Jagger, L., & Horton, K. A. (1996). Defining a realistic control for the chloroform fumigation-incubation method using microscopic counting and 14C-substrates. *Canadian Journal of Soil Science*, *76*(4), 459-467.

Jenkinson, D.S., Powlson, D.S., 1976. The effects of biocidal treatments on metabolism in soil—
V: A method for measuring soil biomass. Soil Biol. Biochem. 8, 209–213.

Jie, H. U., Daping, L. I., Qiang, L. I. U., Yong, T. A. O., Xiaohong, H. E., Xiaomei, W. A. N. G., ... & Ping, G. A. O. (2009). Effect of organic carbon on nitriffication efficiency and community composition of nitrifying bioffilms. *Journal of Environmental Sciences*, *21*(3), 387-394.

Kaushal, S., & Binford, M. W. (1999). Relationship between C: N ratios of lake sediments, organic matter sources, and historical deforestation in Lake Pleasant, Massachusetts, USA. *Journal of Paleolimnology*, *22*, 439-442.

Keeney, D. R., Chen, R. L., & Graetz, D. A. (1971). Importance of denitrification and nitrate reduction in sediments to the nitrogen budgets of lakes. *Nature*, *233*(5314), 66-67.

Keddy, P. A. (2010). *Wetland ecology: principles and conservation*. Cambridge university press.

Leira, M., & Cantonati, M. (2008). Effects of water-level fluctuations on lakes: an annotated bibliography. In *Ecological effects of water-level fluctuations in lakes* (pp. 171-184). Springer, Dordrecht.

Liu, C., Du, Y., Chen, K., Ma, S., Chen, B., & Lan, Y. (2019). Contrasting exchanges of nitrogen and phosphorus across the sediment–water interface during the drying and re-inundation of littoral eutrophic sediment. *Environmental Pollution*, *255*, 113356.

Mao, C., Song, Y., Peng, Y., Kang, L., Li, Z., Zhou, W., ... & Yang, Y. (2023). Patterns and drivers of anaerobic sediment nitrogen transformations across thermokarst lakes. *Global Change Biology*.

Martikainen, P. J. (2022). Heterotrophic nitrification–An eternal mystery in the nitrogen cycle. *Soil Biology and Biochemistry*, *168*, 108611.

McClain, M. E., Boyer, E. W., Dent, C. L., Gergel, S. E., Grimm, N. B., Groffman, P. M., ... & Pinay, G. (2003). Biogeochemical hot spots and hot moments at the interface of terrestrial and aquatic ecosystems. *Ecosystems*, 301-312.

Mcgowan S, Leavitt PR, Hall RI (2005) A whole-lake experiment to determine the effects of winter droughts on shallow lakes. Ecosystems 8:694–708

Michaud, L., Blancheton, J. P., Bruni, V., & Piedrahita, R. (2006). Effect of particulate organic carbon on heterotrophic bacterial populations and nitrification efficiency in biological filters. *Aquacultural engineering*, *34*(3), 224-233.

Mitchell, A., & Baldwin, D. S. (1998). Effects of desiccation/oxidation on the potential for bacterially mediated P release from sediments. *Limnology and oceanography*, *43*(3), 481-487.

Nieder, R., & Benbi, D. K. (2008). Carbon and nitrogen transformations in soils. *Carbon and nitrogen in the terrestrial environment*, 137-159.

Padisák, J., & Reynolds, C. S. (2003). Shallow lakes: the absolute, the relative, the functional and the pragmatic. *Hydrobiologia*, *506*, 1-11.

Paerl, H. W., Gardner, W. S., Havens, K. E., Joyner, A. R., McCarthy, M. J., Newell, S. E., ... & Scott, J. T. (2016). Mitigating cyanobacterial harmful algal blooms in aquatic ecosystems impacted by climate change and anthropogenic nutrients. *Harmful Algae*, *54*, 213-222.

Peralta, A. L., Ludmer, S., & Kent, A. D. (2013). Hydrologic history influences microbial community composition and nitrogen cycling under experimental drying/wetting treatments. *Soil Biology and Biochemistry*, *66*, 29-37.

Peverly JH, Kopka RJ (1991) Changes in AL, Mn and Fe from sediments and aquatic plants after lake drawdown. Water Air Soil Pollut 57–58:399–410

Pinto, R., Weigelhofer, G., Brito, A. G., & Hein, T. (2021). Effects of dry-wet cycles on nitrous oxide emissions in freshwater sediments: a synthesis. *PeerJ*, *9*, e10767.

Qiu, S., & McComb, A. J. (1994). Effects of oxygen concentration on phosphorus release from reflooded air-dried wetland sediments. *Marine and Freshwater Research*, *45*(7), 1319-1328.

Qiu, S., McComb, A., (1995). Planktonic and microbial contributions to phosphorus release from fresh and air-dried sediments. Mar. Freshw. Res. 46, 1039–1045.

Qiu S, McComb AJ (1996) Drying-induced stimulation of ammonium release and nitrification in reflooded lake sediment. Mar Freshw Res 47:531–536

Robertson, G.P., Coleman, D.C., Sollins, P., Bledsoe, C.S., 1999. Standard soil methods for long-term ecological research. Oxford University Press on Demand.

Robertson, G.P., Groffman, P.M., 2015. Nitrogen transformations, in: Soil Microbiology, Ecology and Biochemistry. Elsevier, pp. 421–446.

R Core Team, 2023. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Schimel, J., Balser, T. C., & Wallenstein, M. (2007). Microbial stress-response physiology and its implications for ecosystem function. *Ecology*, *88*(6), 1386-1394.

Seneviratne, S., Nicholls, N., Easterling, D., Goodess, C., Kanae, S., Kossin, J., ... & Zwiers, F. W. (2012). Changes in climate extremes and their impacts on the natural physical environment.

Small, G. E., Cotner, J. B., Finlay, J. C., Stark, R. A., & Sterner, R. W. (2014). Nitrogen transformations at the sediment–water interface across redox gradients in the Laurentian Great Lakes. *Hydrobiologia*, *731*, 95-108.

Vidon, P., Allan, C., Burns, D., Duval, T. P., Gurwick, N., Inamdar, S., ... & Sebestyen, S. (2010). Hot spots and hot moments in riparian zones: potential for improved water quality management 1. *JAWRA Journal of the American Water Resources Association*, *46*(2), 278-298.

Weise, Lukas & Ulrich, Andreas & Moreano, Matilde & Gessler, Arthur & Kayler, Zachary & Kristin, Steger & Zeller, Bernd or Bernhard & Rudolph, Kristin & Knezevic-Jaric, Jelena & Premke, Katrin. (2016). Water level changes affect carbon turnover and microbial community composition in lake sediments. FEMS Microbiology Ecology. 92. fiw035. 10.1093/femsec/fiw035

Wurtsbaugh, W. A. (2016). It takes two to tango: when and where dual nutrient (N & P) reductions are needed to protect lakes and downstream ecosystems. *Environmental science & technology*, *50*(20), 10805-10813.

Wurtsbaugh, W. A., Paerl, H. W., & Dodds, W. K. (2019). Nutrients, eutrophication and harmful algal blooms along the freshwater to marine continuum. *Wiley Interdisciplinary Reviews: Water*, *6*(5), e1373.

Zhou, J., Leavitt, P. R., Zhang, Y., & Qin, B. (2022). Anthropogenic eutrophication of shallow lakes: Is it occasional?. *Water Research*, *221*, 118728.