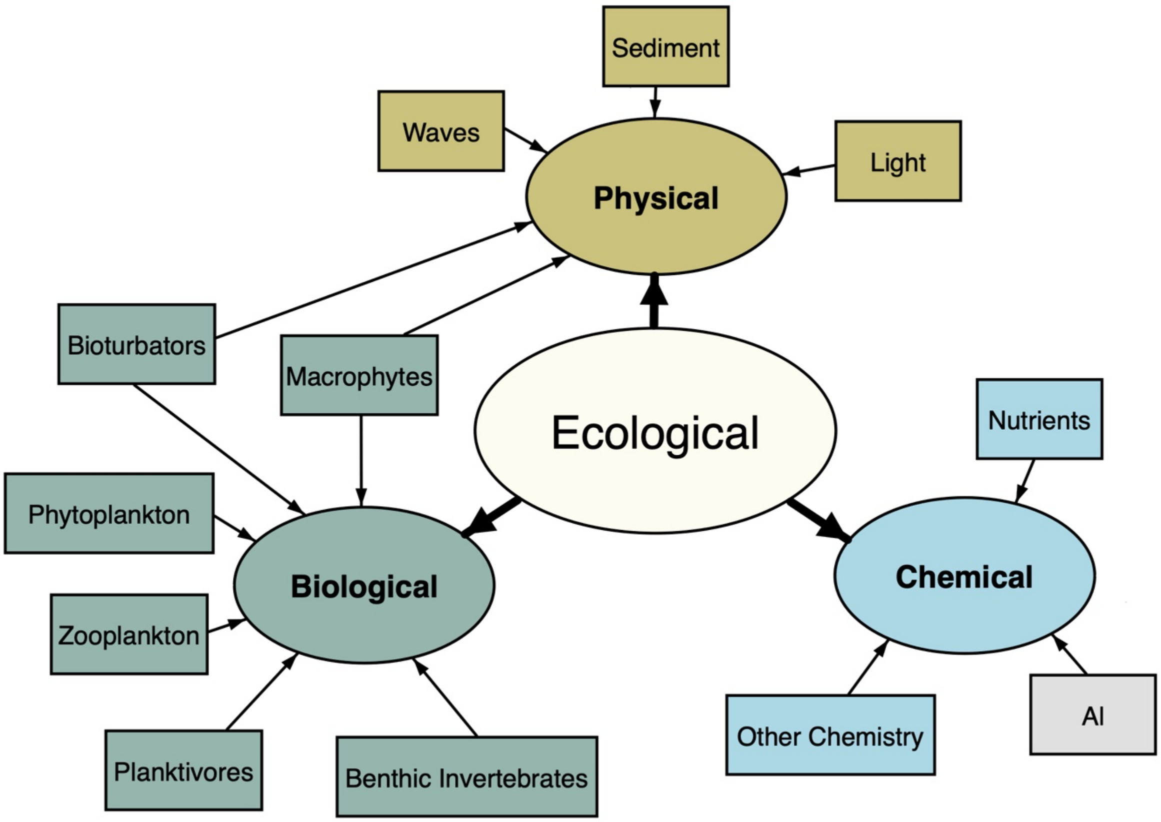
Filename: TSSD Limnocorral Ecological Study Progress Final Report 2022 Ver. 1.2
March 3, 2023

Utah Lake Limnocorral Study

Progress Report 2022

Chapter 2: Ecological Investigations



To
Rich Mickelsen, Director
Timpanogos Special Service District

Jeff Den Bleyker
Jacobs Engineering

By
David C. Richards, Ph.D.
OreoHelix Ecological, Vineyard UT 84059
Phone: 406.580.7816
Email: oreohelix@icloud.com

Brett Marshall
River Continuum Concepts, Manhattan, MT

Sam Rushforth, Ph.D., and Sarah Rushforth
Rushforth Phycology, Provo, UT

Blake Wellard

OreoHelix Ecological "Dedicated to Evaluating and Protecting the World's Ecological Health, Integrity, and Well Being, One Snail at a Time"

Cover diagram: a simplified structural equation model (SEM) of the observed (measured) variables (depicted as rectangles) and their effects on the latent physical, chemical, and biological components (depicted as ovals) of the larger latent variable ecological within Utah Lake's ecosystem. There are extensive additional links not shown between all of these components and all interact directly and indirectly to form the lakes food web and ecosystem function.

This report is the ecological section of the Timpanogos Special Service District, Utah Lake Nutrient Cycling Studies Project administered by Brigham Young University. Geochemistry results are in a separate chapter, Chapter 1.

SUMMARY

Utah Lake is a small remnant of ancient Lake Bonneville. The lake's ecosystem has been severely degraded over the past 150 years or so, since first settled by Americans of European decent, including a shift from a clearer water stable state to a highly turbid unstable state, loss of native species including loss of aquatic vegetation, mollusks and fishes, introduction of nonnative species (particularly carp), nutrient addition, water level and flow regulation, and other pollutants, to name a few. Utah Lake's water quality, foodweb, and ecosystem have been degraded to such a state that by many ecosystem measures, its resilience to future perturbation and resistance to improvement (restoration) appears to be compromised.

There is much concern as to the future of Utah Lake and what can be done to improve its condition (i.e., health, integrity), including the reduction of algal blooms. However, the focus of concern has been almost exclusively on nutrient reduction (bottom-up) and to a lesser extent invasive carp control. There has been little to no effort expended to examine or understand the importance of the lake's food web and how top-down, trophic cascades directly and indirectly effect and respond to current conditions or how biomanipulation including restoring native aquatic vegetation and mollusks and a more balanced fishery may help restore its ecosystem. Restoring Utah Lake to reduce algal blooms, improve its fisheries and ecosystem function cannot proceed without this understanding.

The overall goal of this study was to understand factors that influence nutrient cycling, algal blooms, food web dynamics, and ecosystem functioning that contribute to the impairment of the health of Utah Lake's ecosystem via in-lake mesocosm (limnocorral) experiments. Results of these ongoing studies will help direct managers to develop a holistic restoration program essential for improving the lake's health using integrated and adaptive management strategies.

We examined the direct and indirect effects of application of nutrients, carp, pelagic fishes, aquatic plants (macrophytes), and bivalves, and in particular reduction in wave action using a series of limnocorrals (mesocosms) on:

1. Phytoplankton assemblages,
2. Benthic algae (periphyton) assemblages,
3. Zooplankton assemblages and,
4. Benthic invertebrate assemblages.

We postulated that the application of these treatments would have measurable direct and indirect effects on these four assemblages and that these non-target effects needed to be addressed. In

addition, we expected that treatment effects would alter nutrient cycling and water quality in complicated interactions within the food web.

Ten large limnocorrals (mesocosms) were installed in Utah Lake near the outfall of Timpanogos Special Service District near Lindon, UT in Spring/early Summer 2022. Treatments included, macrophytes, bivalves, carp, and a combination of these, zooplanktivorous fish, nutrient additions, control corrals, and lake controls. In addition to regular weekly nutrient and chemistry data collection, we collected detailed phytoplankton, zooplankton, benthic invertebrate, and periphyton data on three occasions, start (May), middle (August), and end (October) of experiments.

Our results confirmed our hypotheses that intentional modifications of top-down, trophic cascade effects can help improve and restore Utah Lake's ecosystem function. Specifically, wind and wave, and to a lesser extent carp, induced turbidity, as well as zooplanktivorous fish predation had direct and indirect effects on:

- Phytoplankton,
- zooplankton,
- benthic invertebrates,
- benthic algae and periphyton, and
- light availability.

Reduced wave action and zooplanktivorous fish predation allowed for increased zooplankton abundance particularly larger sized individual taxa such as daphniids and copepods to prosper. Increased abundance of large-sized zooplankton likely reduced phytoplankton biovolume and likely altered the phytoplankton assemblage's relative abundances and dynamics. Wave and carp induced turbulence was mostly responsible for nutrient flux from easily suspended fine sediments. Subsequently, turbulence reduction increased light penetration to the substrate allowing benthic algae and the periphyton community to increase in biovolume and compete with phytoplankton, including potential reduction of harmful algal blooms.

All results in this study were consistent with over a century of aquatic ecological findings from other ecosystems worldwide, Utah Lake was not expected to be an exception. These findings also show that restoration of Utah Lake is straight forward and not beyond are capability. Successful science based aquatic ecosystem restoration is being conducted worldwide and a detailed discussion on the relevance of our mesocosm findings in relation to aquatic ecosystem science and restoration is included in this progress report.

Based on this study we recommend:

- Future mesocosm treatments need to be replicated focusing on wave, juvenile carp, and mollusk effects.
- More detailed analyses of response variables such as
    - mollusk growth, diets, fitness,
    - zooplankton size distributions, diets, and diversity,
    - fish fitness, diets, growth,
- Initiation of reestablishment of native aquatic macrophytes, particularly emergent vegetation throughout the lake.

- Installation of temporary wave breaks at select locations until native aquatic plants can be fully established.
- Consideration of top-layer nutrient rich sediment removal.
- Reintroduction of native mollusks.
- Management of the lake towards a more balanced fishery.

We conclude that restorative measures based on these findings especially native aquatic plant reestablishment, and implementation of what is known and currently practiced throughout the world can be prudently and expeditiously used to improve Utah Lake's foodweb, health, integrity, and resilience to future perturbation.

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Introduction

Utah Lake, a small remnant of pluvial Lake Bonneville, is a large, shallow, turbid, highly-eutrophic, slightly saline, and exceedingly regulated lake managed as a storage reservoir residing in one of the fastest growing urban areas in the U.S. Its ecosystem has been severely degraded ever since first settlement by Americans of European descent over 150 years ago (Richards 2022a) and it continues to be a highly abused ecosystem. The lake has lost its ecological integrity[1] and by most quantitative, qualitative, and bioassessment based standards is in poor health[2]. This includes a major degradation shift from a clear water state to a highly turbid state that has altered the lake's food web, water quality, and ecosystem function ((Janetski 1990, Richards 2022 a, b). Based on water quality agency (including EPA) ranking of Tolerance Value most of Utah Lake's ecosystem is considered 'very poor' and its associated degree of organic pollution can be classified as 'severe' (Richards 2022c). The lake's resilience to future perturbation and resistance to improvement (restoration) appears to be compromised (Richards 2022 a,b).

Richards (2022b) developed the first ever proof-of-concept, bioenergetic, mass balance food web model for Utah Lake that produced dozens of ecosystem metrics and indices, most of which supported the premise that Utah Lake ecosystem is impaired and dominated by only a handful of taxa including invasive Common Carp, other non-native fishes, and pollution tolerant chironomids, and that the lake energy sources are co-dominated by water column primary production and strongly respiring detritus mostly in the form of detrital 'rain'. Richards (2022b) foodweb model results also showed that the lake has low robustness (e.g., resistance to perturbation), is well below optimal trophic functioning, and despite its long geologic history is now stalled at an 'immature' early succession stage, primarily because of chronic wave action and unnatural water level fluctuations that consistently disturb unconsolidated sediments and reset the food web, thus preventing maturation and stability of the system.

There is much concern as to the future of Utah Lake and what can be done to improve its condition (i.e., health, integrity), including the reduction of algal blooms and restoration of its native biota. However, there has been little to no effort expended to examine or understand the importance of the lake's food web and how top-down, trophic cascades effect and respond to current conditions or how biomanipulation may help restore its ecosystem health despite decades of research documenting their importance worldwide. Restoring the lake cannot proceed without this understanding.

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[1] **Ecological integrity** is the sum of physical, chemical, and biological integrity. Integrity implies an unimpaired condition or the quality or state of being complete or undivided; it implies correspondence with some original condition. (Karr 1993, 1996).

[2] **Ecological health** implies a flourishing condition, well-being, vitality, or prosperity. An ecosystem is healthy when it performs all its vital functions normally and properly; a healthy ecosystem is resilient, able to recover from many stresses; a healthy ecosystem requires minimal outside care" (Karr 1996). Other more quantitative measures of 'health' are in Discussion section.

Water column vs benthic primary production

Primary production in Utah Lake has been almost completely dominated by water column phytoplankton (algae) for well over 50 years indicating an unbalanced poorly functioning ecosystem. In a healthy state, the lake should have substantially more contribution from benthic primary production, given its shallow nature (Scheffer 1998, Scheffer and Jeppesen 1998). Algal blooms, including potentially toxic cyanobacteria blooms (HABs) occur regularly during summer months. Submerged and emergent aquatic macrophytes (plants) were once abundant throughout much of the littoral zones of the lake but are now near absent. Mollusk (mussels, clams, and snails) diversity and abundance peak in the Utah Lake-Jordan River drainage and the surrounding areas in the depauperate western USA (Richards 2017a, Richards 2014). Native mussels and clams worked in conjunction with macrophytes to help stabilize sediments. Unfortunately, and almost entirely due to human activities, Utah Lake's keystone native mollusk assemblage has been near annihilated. The native mussel, *Anodonta californiensis/nutalliana* is extinct in the lake even though the lake was home to more of this ecosystem engineer than any other water body in Utah in the recent past (Richards 2014). Fingernail clams, primarily *Sphaerium* sp. historically occurred by the billions (Richards unpublished data), are near extirpated in Utah Lake and may now be below viable population levels and extinction prone (Richards personal observations). Invasive Asian clam (*Corbicula* sp.) is now the most abundant bivalve even though its numbers are unexplainably low. Of the eleven native snail taxa that historically occurred in the lake, only two tolerant taxa, *Physella* sp. and *Stagnicola* sp. remain (Holcomb et al. 2020, Richards unpublished data). The lake's once diverse benthic invertebrate assemblage is now mostly dominated by only two or three pollution tolerant chironomid (midge) and oligochaete (segmented worm) taxa (Richards 2022c). Utah Lake once supported 13 species of native fish, ten of which have been extirpated or are extinct. The lake currently only supports three of its native species including the threatened June Sucker (*Chasmistes liorus*) (Federally Threatened species), Utah Sucker (*Catastomus ardens*), and a small Utah Chub (*Gila artraria*) population that account for less than 2% relative abundance (Richards 2022 a, b). Twelve non-native and highly invasive species now account for 98% relative abundance, including the dominance by Common Carp (*Cyprinus carpio).* By most standards the lake has lost its biological integrity, a subset of ecological integrity, and is in poor health. Utah Lake's resilience to future perturbation and its resistance to improvement (restoration) appears to be compromised (Richards 2022 a, b).

Carp

Early settlers introduced several thousand European carp, *Cyprinus carpio* into Utah Lake between 1882 and 1903 where they quickly established and rapidly dominated Utah Lake's fisheries (Heckmann et al. 1981). Along with the many abuses to the ecosystem that early settlers inflicted on Utah Lake, invasive carp via bioturbation caused the near complete loss of macrophytes (aquatic plants) as well other highly detrimental direct and indirect impacts (Richards and Miller 2019 a). These impacts resulted in a rapid transition from a healthy clear water state to a degraded turbid state (Richards and Miller 2019, Scheffer et al. 1993, Vilizzi, Tarkan, and Copp 2015). It has been well documented that since the introduction of Common Carp, these voracious ecosystem engineers have caused major ecological shifts in Utah Lake and their presence is partially responsible for the lake's resistance to recovery efforts. A carp removal program was initiated in 2009 to reduce carp impacts when their biomass was estimated to be well over 50,000 tons and 95% of total fish biomass in the lake (Walsworth et al. 2020). Despite program efforts, carp continue to thwart restoration efforts including the difficult transition reversal from a highly resistant turbid state to a clearer stable state and a more balanced fishery (Richards and Miller 2019 a, Scheffer et al. 1993, Walsworth et al. 2020, Walsworth and Landom 2021). In addition, carp are highly fecund and produce billions of juveniles every year. These juveniles are zooplanktivores that have completely altered the zooplankton assemblage in the lake, reducing zooplankton's critical role in the foodweb. Our limnocorral studies continue to examine the effects of carp on phytoplankton, benthic algae, zooplankton, and benthic invertebrate assemblages.

Water clarity and turbidity

The photic zone (also known as euphotic zone) is the depth at which light penetration is sufficient for photosynthesis and the aphotic zone is the zone below the photic zone and insufficient for photosynthesis. The lower limit of the photic zone is almost universally considered as the depth at which < 1% light energy occurs (Kirk 2011). Utah Lake has a very shallow photic zone due to suspended solids (predominantly silt and calcium precipitates) and algal turbidity that varies spatially and temporally. Estimated photic zone depth using Secchi disk measurement has shown that it is often much less than 30 cm and often less than 10 cm. Except for the very shallowest locations on the lake (or sometimes under ice cover) photosynthetically available light does not penetrate to the benthos to allow for benthic primary production in which case, only heterotrophic bacterial production occurs in the benthos (Richards and Miller unpublished data).

Although Utah Lake is naturally prone to turbid conditions, likely it was much less turbid prior to settlement. This is because of past abundance of macrophytes, mollusks, and the major contribution of benthic algae to filter and stabilize the substrate compared to present day dominance by water column phytoplankton, bioturbation by invasive carp, and cessation of natural flow and water level regime.

Wind and wave action induced turbidity is a major impediment for all members of the food web. Sediment resuspension from strong waves can last for many days after a storm event on Utah Lake. Strong wave action also dislodges benthic invertebrates, including the most abundant taxon, midge larvae and is in part one of the reasons why midge larvae densities are not higher. Filter feeding invertebrate including remaining bivalve clams cease to feed when total suspended solids (TSS) reach concentrations of as little as 20 mg l^{-1} (Hornbach et al. 1984, Way et al. 1990). Even relatively pollution tolerant invasive Asian clams (*Corbicula* sp.) and less tolerant native fingernail clams (Sphaerium) initiate pseudofeces[3] production at 17 to 20 mg l^{-1} TSS (Fuji 1979, Hornbach et al. 1984, Way et al. 1990). Increasing rates of suspended solids from sediment resuspension, calcium precipitate, and increasing algal concentrations may have been partly responsible for the demise of native mussels and severe reduction in native clam populations. The invasive Asian clam, *Corbicula* sp. occurs at very high densities in most tributaries and the

[3] Pseudofeces are a specialized method of expulsion that filter-feeding bivalve mollusks (and filter-feeding gastropod mollusks) use to expel suspended particles that cannot be used as food, and which have been rejected by the animal. The rejected particles are wrapped in mucus and are then expelled without having passed through the digestive tract. Thus, although they may closely resemble the mollusk's real feces, they are not actually feces, hence the name pseudofeces, meaning false feces.

Jordan River but at low densities in the lake. High levels of suspended solids may be partially responsible. Our limnocorral studies continue to examine effects of wind and waves on phytoplankton, benthic algae, zooplankton, and benthic invertebrate assemblages.

Justification

There is much concern as to the future of Utah Lake and what can be done to improve its condition (i.e., health, integrity), including the reduction of algal blooms. However, the focus of concern has been almost exclusively on nutrient reduction (bottom-up) and to a lesser extent invasive carp or sediment resuspension control. There has been little to no effort expended to examine or understand the importance of the lake's food web and how top-down, trophic cascades directly and indirectly effect and respond to current conditions or how biomanipulation including restoring native aquatic vegetation and mollusks may help restore its ecosystem. Restoring Utah Lake to reduce algal blooms, improve its fisheries and ecosystem function cannot proceed without this understanding.

Mesocosm (limnocorral) experiments bridge the gap between highly controlled laboratory experiments that target causality of underlying mechanisms and whole level ecosystem experiments. Even though mesocosm experiments are oversimplifications of an ecosystem (i.e., limited realism), whole lake experiments, although realistic, cannot be easily justified (Stewart et al., 2013) (e.g., Utah Lake). According to Stewart et al., (2013):

> "Because mesocosms can include more biological complexity at larger scales, they are generally regarded as being more amenable for testing community-level and ecosystem-level responses to change in more realistic settings. They can also (ideally) help disentangle direct from indirect effects over intergenerational scales, especially for taxa that cannot be housed in microcosms, parameterized, due to a lack of appropriate empirical and experimental data. Field surveys typically explore correlations between climatic conditions and biological properties but cannot confirm causal relationships and have little or no predictive power. A deeper understanding of the ecological consequences …… is therefore achieved by combining multiple approaches, with mesocosms playing a central and increasingly important role."

Lake ecosystems are complex with physical, chemical, and biological components continuously interacting that are inseparably linked (i.e., foodweb). Subsequently, the contemporary mesocosm experimental paradigm is to measure as many ecological responses as feasible, thus providing scientists and managers invaluable information, which can then be incorporated into an entire ecosystem management framework.

Limnocorral Study Goals

The overall goal of these studies is to understand factors that influence nutrient cycling, algal blooms, food web dynamics, and ecosystem functioning that contribute to the impairment of the ecosystem health of Utah Lake. Results from this ongoing research will help direct managers to initiate restoration[4] needed to maintain and improve its health using an integrated and adaptive

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[4] Ecological restoration, "placing the ecosystem on a trajectory of recovery but not necessarily recovery to its former state so that it can persist, and its species can adapt and evolve (Society Ecological Restoration).

management strategy by incorporating this and other scientific findings (Richards 2021a, ongoing DWQ Utah Lake Science Panel studies, Richards 2021c, see bibliography).

The ecological component goal of the TSSD Utah Lake limnocorral study 2022 was to examine the direct and indirect effects of application of nutrients, carp, pelagic fishes, aquatic plants (macrophytes), and bivalves, and in particular reduction in wave action on:

1. Phytoplankton assemblages,
2. Benthic algae (periphyton) assemblages,
3. Zooplankton assemblages and,
4. Benthic invertebrate assemblages.

We postulated that the application of these treatments would have measurable direct and indirect effects on these four assemblages and that these non-target effects needed to be addressed. In addition, we expected that treatment effects would alter nutrient cycling and water quality in complicated interactions within the food web (see Williams et al. 2021 for more details of this project) (please review Richards et al. 2019g, Richards and Miller 2019a, and Richards and Miller 2017b for a holistic overview of Utah Lake's unique foodweb and ecology).

Hypotheses Tested

We tested the following general hypotheses[5] given the constraint that there was no treatment replication.

H_1: All corrals blocked wave action and reduced turbidity (and most eliminated large carp effects), consequently we predicted that turbidity would be lower in corrals than in the lake (one-tailed test) and light attenuation would decrease (one-tailed test)

H_2: Reduced turbidity would result in phytoplankton biovolume greater inside corrals than in the lake (one-tailed test)

> ***H_{2a}*:** Phytoplankton diversity and relative abundances would differ inside corrals than in the lake

H_3: Zooplankton abundance would be greater inside corrals than outside due to direct and indirect effects of corrals (one-tailed test)

> ***H_{3a}***: Zooplankton diversity and relative abundances would differ inside and outside of corrals

H_4: Benthic invertebrate densities would be greater inside corrals than outside due to direct and indirect effects of corrals (one-tailed test).

> ***H_{4a}*:** Benthic invertebrate diversity and relative abundances would differ inside and outside of corrals.

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[5] Post hoc hypothesis tests were also conducted during analysis as additional questions arose.

H_5: Benthic algae and periphyton would establish inside corrals because of more stable substrate and attachment surfaces on sides of corrals (presence/absence).

H_6: Nutrient addition (Corral 7) would affect biota inside treatment corral directly and indirectly. Predicted increase in phytoplankton, zooplankton, and periphyton inside corrals (one tailed test but without replication).

H_7: Zooplanktivorous fish addition treatments would directly affect zooplankton and indirectly affect phytoplankton and light attenuation.

H_8: Carp addition treatments would have direct and indirect effects on biota inside corrals.

H_9: Bivalve addition treatments would have direct and indirect effects on biota.

H_{10}: Aquatic plants (macrophytes) treatments would have direct and indirect effects on biota and could be restored to the lake.

Most mesocosm experimental treatments are considered 'pulse' type experiments. Pulse experiments are similar to pulse disturbances to an ecosystem and are short-term, relatively discrete events that are usually the result of physical forces (storms or floods) (corrals in this study), chemical inputs (nutrients in this study), or bioturbation (invasion of exotic species, carp in this study) (Brasell et al., 2021, Zhao et al. 2022), and in this study addition of zooplanktivores in a confined environment. Pulse experiments are designed to have a one-time large, exaggerated effect absent of incremental changes in treatment levels (i.e., observable rate of effect change in relation to incremental changes in treatment levels. Consequently 'pulse' experiments are expected to elicit a strong response, i.e., effect vs no effect, but absent of statistical rigor due to lack of replication. Well-designed, un-replicated pulse experimental results can provide evidence of either being consistent with and supporting known phenomena or not supporting (Carpenter and Kitchell 1996).

Methods

Limnocorrals (mesocosms)

Ten limnocorrals (mesocosms) were installed in Utah Lake near the outfall of Timpanogos Special Service District near Lindon, UT. Five corrals were established in shallow water starting on May 9, 2022, and five in deeper water starting on June 6, 2022. Experiments were fully terminated on October 11, 2022. Shallow water corrals were numbered 1 through 5 and deeper (open) water corrals 6 through 10. In addition, samples were collected outside of corrals and used as lake controls. Corral treatments are in Table 1. Fishes inadvertently entered and escaped from several corrals and likely affected outcomes. See Williams et. al. (2022a) and Den Bleyker et al. (2022) for more details on methods, treatments, and observations.

Table 1. Limnocorral (mesocosm) treatments and notes.

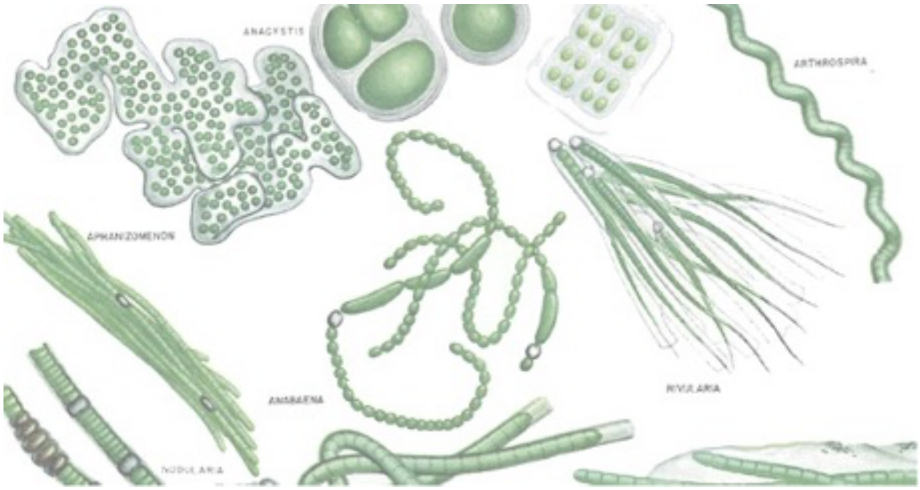
		Treatment	Notes
Shallow < 1m	*Corral 1*	Macrophytes and bivalves	Approximately 1000 *Corbicula* sp. added June. Macrophytes planted April to August
	Corral 2	Macrophytes only	Macrophytes planted April through August
	Corral 3	Macrophytes, bivalves, and carp	Macrophytes planted April through August Approximately 1000 *Corbicula* sp. added June. Carp added June
	Corral 4	Control	One large carp entered but was removed asap
	Corral 5	Control	
Deep 1 to 2 m	*Corral 6*	Zooplanktivores and lake mixing	Carp eggs were inadvertently laid on inside of corrals before deployment. Subsequently, early life stage and juvenile carp remained in corral throughout the duration of experiment. Rhodamine added June 8, 2022[a]
	Corral 7	Nutrient addition	Nutrients were added on two occasions in August. Rhodamine added June 8, 2022
	Corral 8	Carp and Zooplanktivores	Juvenile fishes entered but were removed. One large carp remained for much of the study. Rhodamine added June 8, 2022
	Corral 9	Zooplanktivores	Juvenile carp
	Corral 10	Control	

[a] Addition of rhodamine was to determine corral mixing residence time (see Williams et al. 2022b). Effects of rhodamine addition on biota are unknown.

Table 2. Latitude and longitude of ten corrals.

Corral	Latitude	Longitude
1	40.33447 °	-111.77431 °
2	40.33452 °	-111.77460 °
3	40.33452 °	-111.77475 °
4	40.33459 °	-111.77486 °
5	40.33468 °	-111.77516 °
6	40.33320 °	-111.77474 °
7	40.33311 °	-111.77476 °
8	40.33300 °	-111.77480 °
9	40.33291 °	-111.77482 °
10	40.33279 °	-111.77484 °

Phytoplankton Assemblages



We used what Utah Division of Water Quality (DWQ) refers to as an ‘integrated’ sample or what Rushforth Phycology refers to as a ‘surface’ sample to collect phytoplankton from inside and outside corrals. We inverted a 500 ml labeled plastic sample jar to elbow depth in the water and then slowly reinverted and lifted the jar to the surface to capture as much water equally at depth. Lugol’s solution was added to the samples and the samples were then placed on ice and delivered to Rushforth Phycology as soon as possible usually within one day.

All algal taxonomies were performed by Rushforth Phycology (rushforthphycology.com), the leading algal taxonomy experts for Utah Lake and surrounding aquatic ecosystems. Rushforth Phycology reported phytoplankton taxonomic results as number in stand, rank in stand, relative density, natural units mL^{-1}, cells mL^{-1}, and cell volume (μ^3 mL^{-1})[6]. The most commonly used values are cell counts (cells mL^{-1}) and cell biovolume (μm^3 mL^{-1}). Linear regression analysis showed that both were highly significantly correlated ($R^2 = 0.94$ for *A. flosaquae* combined with all other taxa, $R^2 = 1.00$ when modeled separately). Subsequently, cell biovolume (log (μm^3 mL^{-1})) was chosen for 2022 analyses.

Zooplankton Assemblages

Three charismatic microfauna that were abundant in the limnocorral study: Left photo = *Brachionus* sp., Center photo = *Daphnia pulex*, Right photo = *Ceriodaphnia* sp. Photos downloaded from internet.

[6] Cell (bio)volume values were specifically developed for Utah Lake phytoplankton by Rushforth Phycology.

Zooplankton data provided in this study afforded invaluable results necessary in our quest to understand the ecology and food web of Utah Lake and to help us determine causes of potential harmful algal blooms with the goal of ecosystem restoration. However, results presented in this report are based on limited or no replication and consequently have little statistical confirmation.

Field

We used an 80 μm mesh zooplankton net to collect zooplankton samples using a vertical tow from bottom to top of each of the corrals. Contents of net collection jars were gently sprayed using a spray bottle into sample jars. Care was taken to fill the sample jar to the brim and to keep jars upright to not allow zooplankton to dry on the sides or inside top of jar which can prevent accurate taxonomic identification. Water depth and net diameter were measured to determine zooplankton taxa counts per unit volume. The field team preserved samples to a final dilution of 70% isopropyl in properly labeled plastic sample jars and zooplankton samples were delivered to the River Continuum Concepts laboratory.

River Continuum Concepts, led by Mr. Brett Marshall, taxonomically analyzed samples, and wrote a brief summary report. The RCC lab and OreoHelix Ecological have developed the most accurate Utah Lake zooplankton taxonomic list to date derived from samples provided by OreoHelix Ecological and Wasatch Front Water Quality Council (Richards and Miller 2019) and has the nation's most qualified personnel for taxonomic identification of Utah Lake zooplankton.

Laboratory

Upon arrival at the lab, all samples were inventoried and logged into our sample tracking database which assigned unique sample identifier numbers, site codes, dates, and replicate numbers. Samples were gently rinsed through a 63-micron stainless steel sieve and rinsed into a quadrant-splitter petri dish using 75% aqueous isopropanol. The contents of the splitting dish were mixed with a pipette until the distribution of animals within quadrants appeared roughly equivalent in abundance and size. If the sample contained significant detritus, it was separated from the zooplankters under a dissecting microscope using the most effective magnification (10-100x) to ensure that no specimens were attached to the detritus removed. Once all the detritus was removed, we used a 4-sided die to randomly select one of the quadrants, which was transferred by pipette to a 6x6 gridded rectangular petri dish. Specimens were spread evenly across the gridded surface and two 6-sided dice were cast to determine which of the 36 grids was selected for identification. All specimens were removed from the selected grid and identified. After all the specimens from the first grid were removed, enumerated, and identified, another grid was randomly selected using the dice and the process was repeated until the total number of identified organisms exceeded 200 animals. If the first quarter was completely processed and the total number of animals remained below 200 animals, another quarter was randomly selected from the quadrant splitter dish using the four-sided die, and that quarter was transferred to the gridded dish and grids were randomly selected with pairs of six-sided dice. This process was repeated, when necessary, until the total number of animals exceeded 200 animals. The total number of specimens reported for a remained < 200 animals only for samples that were completely (100%) identified.

The subsample factor was used to estimate the total abundance of animals. The subsample factor is the reciprocal of the percent of the sample processed to attain 200 animals. Thus, if 10 grids were used from the first quarter of the sample, then the percentage of the sample used is 6.944% (0.25*(10/36)). In this case the total of 200 animals is corrected to density by dividing the sample abundance by 0.06944, resulting in an abundance of 2880 per sample (200/0.06944). The community density dataset applies this factor to each, and every species identified from the sample.

The fixed count method of processing zooplankton samples was selected because it provides timely and cost-effective analysis of the dominant species present and is used by state agencies as endorsed by the U.S. E.P.A. for biological assessment of lake zooplankton communities. However, there are some limitations to fixed count subsample methods, and those limitations become more relevant as the portion of the sample identified becomes very small (<~1%). Imagine two communities where there are 10 species, with 3 species being much more abundant than the others (Example 1). When we select a random subsample of 200 animals from community 2, most of the time, some taxa are omitted (Example 2). Therefore, for this report, when densities are used, we are cautious when comparing the occurrence or non-occurrence of lower abundant taxa from samples that were heavily subsampled.

<u>Example 1</u>. This example shows the abundance of two communities with the same relative abundance of 10 species. The second community (Comm2) contains 100x the number of individuals as the first community (Comm1).

TAXON	Community 1	Community 2
Copepod-1	101	10100
Copepod-2	30	3000
Copepod-3	1	100
Copepod-4	1	100
Cladoceran-1	61	6100
Cladoceran-2	1	100
Cladoceran-3	1	100
Cladoceran-4	1	100
Rotifer-1	2	200
Rotifer-2	1	100
Total	200	20000

<u>Example 2.</u> Effect of subsampling. Community 2 must be subsampled down to 200-300 animals. This example shows results of the first 8 attempts at drawing a random 201 animals from Community 2. Notice that none of the subsamples contained all ten taxa. Thus, even when these data are corrected for subsampling (multiplied by 100) there will be missing species.

Copepod-1	94	105	104	109	91	101	97	108
Copepod-2	28	37	29	26	38	31	27	34
Copepod-3	1	1	0	2	2	0	0	0
Copepod-4	2	3	0	2	0	2	1	1
Cladoceran-1	72	51	60	60	68	62	68	55
Cladoceran-2	0	1	2	0	0	2	2	0

Cladoceran-3	1	1	0	1	2	0	1	2
Cladoceran-4	1	1	0	0	0	1	0	0
Rotifer-1	2	0	6	1	0	1	5	1
Rotifer-2	0	1	0	0	0	1	0	0
Identified	201	201	201	201	201	201	201	201
TAXA	8	9	5	7	5	8	7	6

The effects of subsampling must always be considered when conducting research and the level of subsampling needs to be balanced by the goals of the research and cost effectiveness. For example, in all instances when subsampling is conducted, absence of a taxon from a sample or location cannot be concluded.

All biological sample methods used in 2022 were similar to 2021 methods and can be found in more detail in Richards et al. (2021).

Statistical Methods

Four to five letter codes were made for each phytoplankton and zooplankton taxon, typically the first two letters of the genus name and the first two letters of the species name unless there were duplicates (Table 3). Seven to eight- digit location and sampling date codes were also developed for use in analyses.

Non-metric multidimensional scaling (NMS) ordination was used to compare phytoplankton assemblage dis(similarity) relationships statistically and visually between corrals and dates. Ordination techniques are often more informative than hypothesis-testing approaches for exploring relationships between multivariate ecological assemblages or communities (McCune and Grace 2002). In general, ordination is the ordering of objects along axes according to their (dis)similarities; the main objective of ordination is to reduce many-dimensional relationships into a small number of more easily interpretable dimensions (i.e., axes on a plot). The strongest correlation structure in the data is extracted and is then used to position objects in ordination space. Objects that are close in the ordination space are more similar than objects distant in ordination space (McCune and Mefford 2011).

NMS was used in these analyses because it has been shown to be robust and highly informative for understanding ecological relationships. NMS ordination is often more broadly applicable for ecological studies than other ordination techniques because it does not require relationships among variables to be linear (McCune and Mefford 2011, Peck 2010). NMS ordination permits the visualization of the multidimensional relationships of phytoplankton assemblages into a more easily visualized, lower dimensional space. Dimensional reduction obviously creates some distortion in relationships between samples. The level of reduction in distortion is measured as 'stress', where lower stress values equal less distortion. NMS plots with stress values of 15% (0.15) or less are typically considered to be a good representation of the data and stress values lower than 10% (0.10) are considered excellent representations (McCune and Mefford 2011, Peck 2010).

Cell biovolume (μm^3 $mL^{-}1$) was log transformed prior to all analyses to more normalize its distribution. Phytoplankton taxa with fewer than 3 occurrences in all the samples were removed prior to running NMS models in order to reduce the effects of these uncommon taxa on model performance (McCune and Mefford 2018). Several distance measures were used and evaluated including Sorensen (Bray-Curtis), Relative Sorensen, Jaccard, Euclidean, Relative Euclidean, and Morisita-Horn. NMS analysis was run for 250 iterations using the real data and 250 iterations in randomized Monte Carlo simulations. Best-fit models were selected based on stable final stress < 0.15 and 3-dimensional solutions or less. NMS ordinations were rotated using varimax rotation to maximize variation along the axes and extracted as univariate scores. Consequently, the final ordinations can be rotated either vertically or horizontally without effecting the results. Centroid labels and convex hulls of months were added to the ordinations to aid in the interpret the relationships. Post hoc proportion of variance represented by each axis was calculated based on the R^2 value between distance in the ordination space and distance in the original space.

Multiple Response Permutation Procedure (MRPP), a non-parametric multivariate method was used to formally test the hypothesis of no differences in phytoplankton assemblages between months. MRPP has the advantage of not requiring distributional assumptions such as multivariate normality and homogeneity of variance and thus is often preferred over perMANOVA for analyzing multivariate ecological data (McCune and Grace 2002). The same distance measure was used for each MRPP analyses as was for corresponding NMS models. The chance-corrected within-group test statistic, A (and associated p-value) was used to evaluate the hypothesis of no difference in groupings (McCune and Grace 2002). Post hoc multiple comparisons were also made when appropriate.

All multivariate and additional analyses including rank abundance and descriptive summary statistics were made using PC-ORD for Windows Version 7.08 (McCune and Mefford 2018) using Parallels Desktop 18 for Mac virtual platform.

Descriptive statistics were calculated for most data comparisons. Regression analyses were selected using the most appropriate model including linear, Poisson, fractional, and negative binomial. Best fit regression models were chosen based on lowest log likelihood, AIC, and BIC values. T-tests (one sample, two-sample using groups, and paired) and ANOVAs were also conducted when data were near normally distributed. Kruskal-Wallis equality of populations rank test were applied when data were not near normally distributed. Box and whisker plots were developed for non-normally distributed data. Box plots used median, 25th, 75th, lower and upper adjacent values and outside values. Graphical representations of statistical models were made using either Stata /IC 16.1 for Mac (Intel 64-bit) or Microsoft Excel for Mac (version 16.68). Details of additional statistical methods not listed here are described in Results sections. Additional statistical methods were used dependent on hypotheses (questions) for specific interactions and comparisons.

Results

Phytoplankton

Eighty-two (82) phytoplankton taxa were collected and identified from thirty-eight samples from our mesocosm study in 2022 (Table 3). Total estimated number of taxa in the study ranged from

101 to 116 based on jackknife and Chao estimators. This large number of phytoplankton taxa demonstrates that Utah Lake has very high, water column phytoplankton diversity and supports Richards (2022) foodweb model results showing that water column primary production exceeds benthic primary production. However, only a handful of phytoplankton dominated, indicating a stressed environment.

Table 3. List of phytoplankton taxa, taxon code for analysis and division collected in our mesocosm study, 2022.

Taxon	**Taxon Code**	**Algal Division**
Aulacoseira granulata (Ehrenberg) Simonsen (= *Melosira granulata*)	AUGR	Bacillariophyta
Aulacoseira granulata var. *angustissima* (Müller) Simonsen (=*Melosira granulata* var. *angustissima*)	AUGR	Bacillariophyta
centric diatoms species	CDSP	Bacillariophyta
centric diatoms species 2	CD2	Bacillariophyta
Chaetoceros muelleri Lemmermann	CHMU	Bacillariophyta
Fragilaria crotonensis Kitton	FRCR	Bacillariophyta
pennate diatoms	PD	Bacillariophyta
Actinastrum gracillimum Smith	ACGR	Chlorophyta
Actinastrum hantzschii Lagerheim	ACHA	Chlorophyta
Ankistrodesmus arcuatus Korshikov (= *Monoraphidium arcuatum* (Korshikov) Hindák)	ANAR	Chlorophyta
Ankistrodesmus falcatus (Corda) Ralfs	ANFA	Chlorophyta
Botryococcus species	BOSP	Chlorophyta
Chlamydomonas globosa Snow	CHGL	Chlorophyta
Chlamydomonas species	CHLSP	Chlorophyta
Coelastrum species	COSP	Chlorophyta
Coenococcus planktonicus Korshikov	COPL	Chlorophyta
Cosmarium species	COMSP	Chlorophyta
Crucigenia fenestrata (Schmidle) Schmidle	CRFE	Chlorophyta
Crucigenia quadrata Morren	CRQU	Chlorophyta
Desmodesmus bicaudatus (Dedusenko) .Tsarenko	DEBI	Chlorophyta
Desmodesmus bicellularis (Chodat) An, Friedl & Hegewald	DEBIC	Chlorophyta
Desmodesmus communis (Hegewald) Hegewald	DECO	Chlorophyta
Desmodesmus intermedius (Chodat) Hegewald	DEIN	Chlorophyta
Desmodesmus opoliensis (Richter) Hegewald	DEOP	Chlorophyta
Desmodesmus species	DESP	Chlorophyta
Eremosphaera gigas (Archer) Fott & Kalina (= *Oocystis gigas* Archer)	ERGI	Chlorophyta

Gregiochloris lacustris (Chodat) Marvan, Komárek & Comas (= *Quadrigula lacustris* (Chodat) Smith)	GRLA	Chlorophyta
Kirchneriella lunaris (Kirchner) Möbius (= *Kirchneriella lunata* Schmidle)	KILU	Chlorophyta
Kirchneriella species	KISP	Chlorophyta
Komma species	KOSP	Chlorophyta
Lagerheimia species	LASP	Chlorophyta
Monoraphidium contortum (Thuret) Komárková-Legnerová	MOCO	Chlorophyta
Monoraphidium convolutum (Corda) Komárková-Legnerová (= *Ankistrodesmus convolutus* Corda)	MOCOV	Chlorophyta
Mougeotia species	MOSP	Chlorophyta
Oocystis borgei Snow	OOBO	Chlorophyta
Oocystis species	OOSP	Chlorophyta
Pectinodesmus pectinatus (Meyen) Hegewald, Wolf, Keller, Friedl & Krienitz (= *Acutodesmus pectinatus* (Meyen) Tsarenko)	PEPE	Chlorophyta
Pediastrum angulosum Ehrenberg ex Meneghini	PEAN	Chlorophyta
Pediastrum duplex Meyen (= *Pediastrum duplex var. clathratum* Meyen)	PEDU	Chlorophyta
Pseudopediastrum boryanum (Turpin) Hegewald (= *Pediastrum boryanum* (Turpin) Meneghini)	PSBO	Chlorophyta
Quadrigula species	QUSP	Chlorophyta
Scenedesmus arcuatus (Lemmermann) Lemmermann	SCAR	Chlorophyta
Scenedesmus ellipticus Corda	SCEL	Chlorophyta
Schroederia setigera (Schröder) Lemmermann	SCSE	Chlorophyta
Sphaerocystis schroeteri Chodat	SPSC	Chlorophyta
Tetraëdron caudatum (Corda) Hansgirg	TECA	Chlorophyta
Treubaria setigera (Archer) Smith	TRSE	Chlorophyta
Unknown spherical chlorophyte	UNSC	Chlorophyta
Unknown spherical chlorophyte 3	UNSPCH3	Chlorophyta
Willea crucifera (Wolle) John, Wynne & Tsarenko (= *Crucigeniella crucifera* (Wolle) Komarek	WICR	Chlorophyta
Willea rectangularis (Braun) John, Wynne & Tsarenko (= Crucigenia rectangularis (Nägeli) Gay)	WIRE	Chlorophyta
Mallomonas species	MASP	Chrysophyta
Unknown spherical chrysophyte	UNSPCH	Chrysophyta
Chroomonas species	CHSP	Cryptophyta
Cryptomonas richei Fritsch Fritsch	CRRI	Cryptophyta
Cryptomonas species	CRSP	Cryptophyta

Aphanizomenon flosaquae Ralfs ex Bornet & Flahault	APFL	Cyanophyta
Aphanocapsa incerta (Lemmermann) G.Cronberg & Komárek (= *Microcystis incerta* (Lemmermann) Cronberg & Komárek)	APIN	Cyanophyta
Aphanocapsa species	APCSP	Cyanophyta
Aphanothece species	APSP	Cyanophyta
Chroococcus dispersus (Keissler) Lemmermann	CHDI	Cyanophyta
Chroococcus minor (Kützing) Nägeli	CHMI	Cyanophyta
Chroococcus turgidus (Kützing) Nägeli	CHTU	Cyanophyta
Coelosphaerium species	COSSP	Cyanophyta
Cyanodictyon planctonicum Mayer	CYPL	Cyanophyta
Dolichospermum circinalis (Brébisson) Wacklin, Hoffmann & Komárek (= *Anabaena circinalis* Rabenhorst)	DOCI	Cyanophyta
Gloeocapsa species	GLSP	Cyanophyta
Gomphosphaeria species	GOSP	Cyanophyta
Limnococcus limneticus (Lemmermann) Komárková, Jezberová, Komárek & Zapomelová (= *Chroococcus limneticus* Lemmermann)	LILI	Cyanophyta
Merismopedia glauca (Ehrenberg) Kützing	MEGL	Cyanophyta
Merismopedia species	MESP	Cyanophyta
Microcystis species	MISP	Cyanophyta
Phormidium species	PHSP	Cyanophyta
Phormidium species 4	PHSP4	Cyanophyta
Planktothrix agardhii (Gomont) Anagnostidis & Komárek (= *Oscillatoria agardhii* Gomont)	PLAG	Cyanophyta
Planktothrix species	PLSP	Cyanophyta
Snowella lacustris (Chodat) Komárek & Hindák (= *Gomphosphaeria lacustris* Chodat)	SNLA	Cyanophyta
Snowella species	SNSP	Cyanophyta
Spirulina species	SPSP	Cyanophyta
Unknown colonial cyanophyte	UNCCY	Cyanophyta
Unknown filamentous cyanophyte	UNFC	Cyanophyta
Peridinium species	PESP	Dinophyta
Unknown dinoflagellate	UNDI	Dinophyta
Euglena species	EUSP	Euglenophyta
Lepocinclis species	LESP	Euglenophyta
Phacus species	PHSP	Euglenophyta

Trachelomonas species	TRSP	Euglenophyta

Rank abundance of phytoplankton (Figure 1 and Table 4) showed that several phytoplankton taxa dominated the study area in 2022. Forty-three (52%) of the taxa occurred in < 10% of the samples. Seven taxa (9%) occurred >= 50% of the samples including four taxa that occurred >80% of the samples, CDSP (84%), OOSP (84%), CD2 (87%) and PD (95%). The abundance of Bacillariophyta (diatom) taxa throughout the study period is very unusual for Utah Lake.

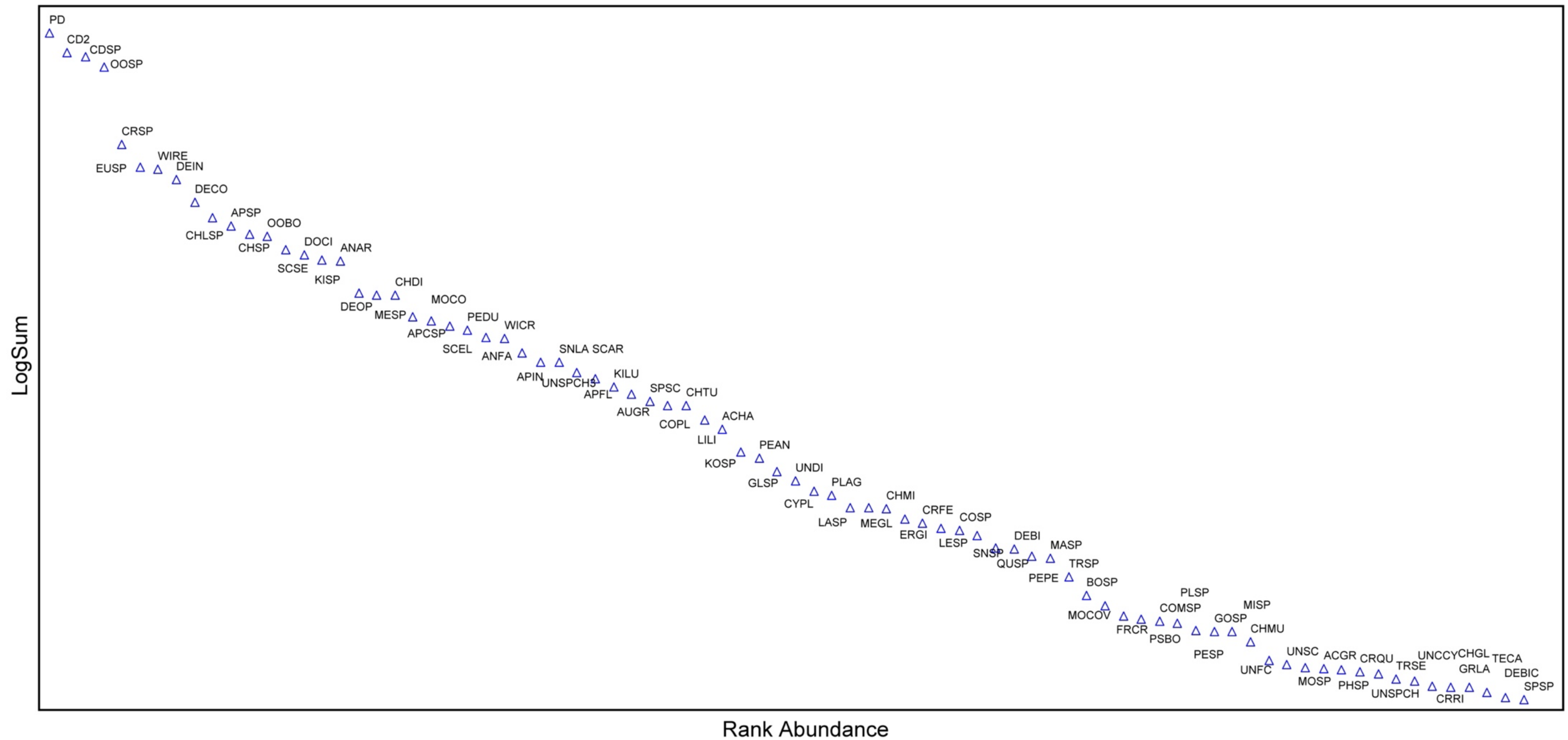


Figure 1. Rank abundances of phytoplankton encountered in our mesocosm study, 2022. logSum was used to emphasize the dominance by few taxa including pennate diatoms (PD), two centric diatom taxa (CD2, CDSP), and Oocystis sp. (OOSP). Rank abundance metrics are in Table 4.

Description of rank abundance metrics for Table 4.

Symbol	Meaning
RankAbun	Rank abundance of the species (columns) in the main matrix. Ties are assigned ranks in order of encounter, rather than averaging the ranks of the tied items. This procedure is necessary for graphing the dominance curve, so that points with ties are not piled on top of each other.
LogSum	Log base 10 of the column (species) sum.
Sum	The column (species) total.
RankFreq	Rank frequency of the species (columns) in the main matrix. Ties are assigned ranks in order of encounter, rather than averaging the ranks of the tied items. This procedure is necessary for graphing the dominance curve, so that points with ties are not piled on top of each other.
Freq	Frequency of the species (columns) in the matrix. This is simply the number of nonzero values in the column. Negative numbers are disallowed in this procedure.
Mean	The column (species) total divided by the number of rows (Sum / N).
Sdev	The standard deviation within a column, calculated as a sample standard deviation (sum of squared differences from mean, divided by N-1).
CV%	Coefficient of variation, expressed as a percentage: 100*Sdev/Mean.
V/M	Variance-to-mean ration. With count data this statistic can be used to indicate deviations from a Poisson distribution. The random expectation is V/M=1, with larger values indicating aggregation and smaller values indicate more uniform dispersion.

Table 4. Rank abundance metrics of phytoplankton taxa ell biovolumes log (μm^3 mL^{-1}) encountered in our mesocosm study 2022.

Taxon	Rank Abundance	Rank Freq	Freq	Mean	S. Dev.	CV%	V/M
PD	1	1	36	5.29	1.38	26.07	0.36
CD2	2	2	33	4.71	2.07	44.02	0.91
CDSP	3	3	32	4.58	2.28	49.85	1.14
OOSP	4	4	32	4.31	1.94	45.02	0.87
CRSP	5	8	18	2.68	2.87	107.15	3.08
EUSP	6	6	19	2.34	2.40	102.47	2.46
WIRE	7	7	19	2.30	2.35	102.07	2.40
DEIN	8	5	20	2.17	2.09	96.41	2.01
DECO	9	9	17	1.89	2.14	113.35	2.43
CHLSP	10	11	15	1.72	2.19	127.32	2.79
APSP	11	14	12	1.64	2.46	150.27	3.70
CHSP	12	21	10	1.56	2.72	174.26	4.73
OOBO	13	15	12	1.53	2.30	150.48	3.47
SCSE	14	12	14	1.42	1.89	133.34	2.52
DOCI	15	20	10	1.37	2.33	170.09	3.97
KISP	16	13	13	1.33	1.89	142.39	2.70
ANAR	17	10	16	1.32	1.59	120.39	1.92
DEOP	18	19	10	1.08	1.85	170.72	3.16

MESP	19	16	11	1.08	1.73	160.51	2.77
CHDI	20	22	10	1.07	1.82	170.41	3.11
APCSP	21	26	7	0.94	2.03	215.47	4.37
MOCO	22	17	11	0.91	1.47	160.60	2.36
SCEL	23	24	7	0.89	1.90	213.66	4.06
PEDU	24	28	6	0.87	2.04	234.72	4.79
ANFA	25	18	10	0.83	1.41	170.38	2.40
WICR	26	25	7	0.83	1.77	213.74	3.78
APIN	27	29	6	0.75	1.77	234.64	4.15
UNSPCH3	28	23	9	0.71	1.32	185.03	2.44
SNLA	29	31	5	0.71	1.86	261.15	4.85
SCAR	30	27	6	0.67	1.57	234.50	3.69
APFL	31	39	4	0.64	1.92	298.94	5.75
KILU	32	30	6	0.61	1.44	234.70	3.37
AUGR	33	32	5	0.59	1.53	261.07	4.01
SPSC	34	34	4	0.56	1.67	296.42	4.94
COPL	35	36	4	0.55	1.62	295.84	4.80
CHTU	36	35	4	0.55	1.63	297.32	4.85
LILI	37	38	4	0.50	1.49	296.23	4.41
ACHA	38	33	5	0.47	1.24	262.62	3.26
KOSP	39	37	4	0.41	1.22	295.46	3.60
PEAN	40	45	3	0.40	1.38	347.33	4.79
GLSP	41	40	3	0.37	1.27	346.85	4.41
UNDI	42	41	3	0.35	1.20	346.64	4.16
CYPL	43	44	3	0.33	1.13	346.82	3.92
PLAG	44	58	2	0.32	1.36	429.96	5.86
LASP	45	42	3	0.29	1.02	346.42	3.53
MEGL	46	43	3	0.29	1.02	346.97	3.53
CHMI	47	47	2	0.29	1.28	436.98	5.58
ERGI	48	48	2	0.28	1.18	429.96	5.09
CRFE	49	50	2	0.27	1.15	430.03	4.96
LESP	50	51	2	0.26	1.11	429.96	4.79
COSP	51	53	2	0.26	1.10	430.35	4.75
SNSP	52	54	2	0.25	1.07	430.61	4.61
QUSP	53	46	2	0.23	0.99	430.23	4.26
DEBI	54	49	2	0.23	0.99	431.04	4.25
PEPE	55	57	2	0.22	0.94	429.96	4.03
MASP	56	52	2	0.22	0.94	435.64	4.09
TRSP	57	56	2	0.19	0.83	432.02	3.60

BOSP	58	67	1	0.17	1.06	616.44	6.53
MOCOV	59	55	2	0.16	0.70	430.76	3.01
FRCR	60	80	1	0.15	0.94	616.44	5.78
PSBO	61	74	1	0.15	0.92	616.44	5.66
COMSP	62	81	1	0.15	0.91	616.44	5.59
PLSP	63	72	1	0.15	0.90	616.44	5.54
PESP	64	62	1	0.14	0.86	616.44	5.30
GOSP	65	61	1	0.14	0.85	616.44	5.25
MISP	66	63	1	*	0.85	616.44	5.25
CHMU	67	69	1	0.13	0.80	616.44	4.92
UNFC	68	75	1	0.12	0.71	616.44	4.40
UNSC	69	70	1	0.11	0.70	616.44	4.29
MOSP	70	66	1	0.11	0.69	616.44	4.23
ACGR	71	79	1	0.11	0.68	616.44	4.20
PHSP	72	68	1	0.11	0.68	616.44	4.16
CRQU	73	65	1	0.11	0.67	616.44	4.11
UNSPCH	74	60	1	0.11	0.66	616.44	4.05
TRSE	75	71	1	0.10	0.64	616.44	3.92
UNCCY	76	77	1	0.10	0.63	616.44	3.89
CHGL	77	78	1	0.10	0.61	616.44	3.76
CRRI	78	76	1	0.10	0.61	616.44	3.75
GRLA	79	59	1	0.10	0.61	616.44	3.75
TECA	80	64	1	0.10	0.59	616.44	3.62
DEBIC	81	73	1	0.09	0.57	616.44	3.52
SPSP	82	82	1	0.09	0.56	616.44	3.47

Monthly Phytoplankton Summaries

May

Phytoplankton diversity was greatest in Corral 5 (control) at the start of the study May 17, 2022, and lowest in Corral 4 (Table 5, Figure 2). There was no evidence in differences in biovolumes or taxa richness between inside and outside of corrals using t-test for biovolume ($t = -1.18$, $p = 0.29$) and visualization for taxa richness.

*Table 5. Several metrics of phytoplankton taxa on May 17, 2022, samples. Cell biovolumes log (µm³ mL⁻¹). S = Richness = number of taxa in each sample, E = Evenness = H / ln (Richness), H = Diversity = - sum (Pi*ln (Pi)) = Shannon`s diversity index, D = Simpson`s diversity index for infinite population = 1 - sum (Pi*Pi) where Pi = importance probability in element i (element i relativized by row total), effective number of taxa ENT = exp(H).*

Sample	Total Biovolume (log (μm^3 mL^{-1})	S	E	H`	D	ENT
Corral 4	7.08	9	0.99	2.17	0.88	9
Corral 5	6.82	21	0.99	3.01	0.95	20
Lake 1	6.96	14	0.99	2.62	0.93	14
Lake 2	6.96	20	0.99	2.97	0.95	19
Lake 3	6.72	10	0.99	2.29	0.90	10
Lake 4	6.49	11	0.99	2.38	0.91	11
Lake 5	6.61	12	0.99	2.47	0.91	12

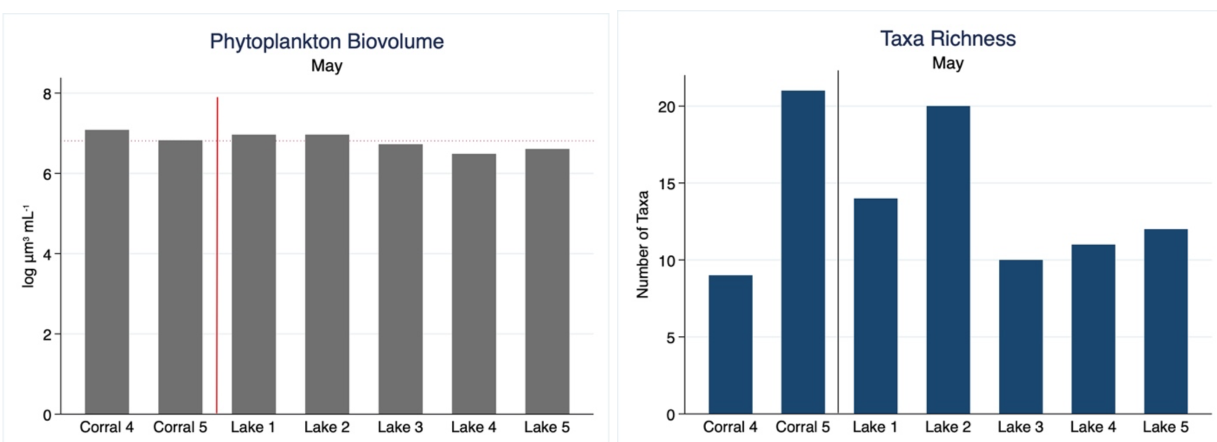


Figure 2. Comparisons of number of taxa and biovolume for corrals and lake on May 17, 2022. No evidence for difference in biovolumes or taxa richness between inside corrals and lake (ANOVA). Red dotted line is mean.

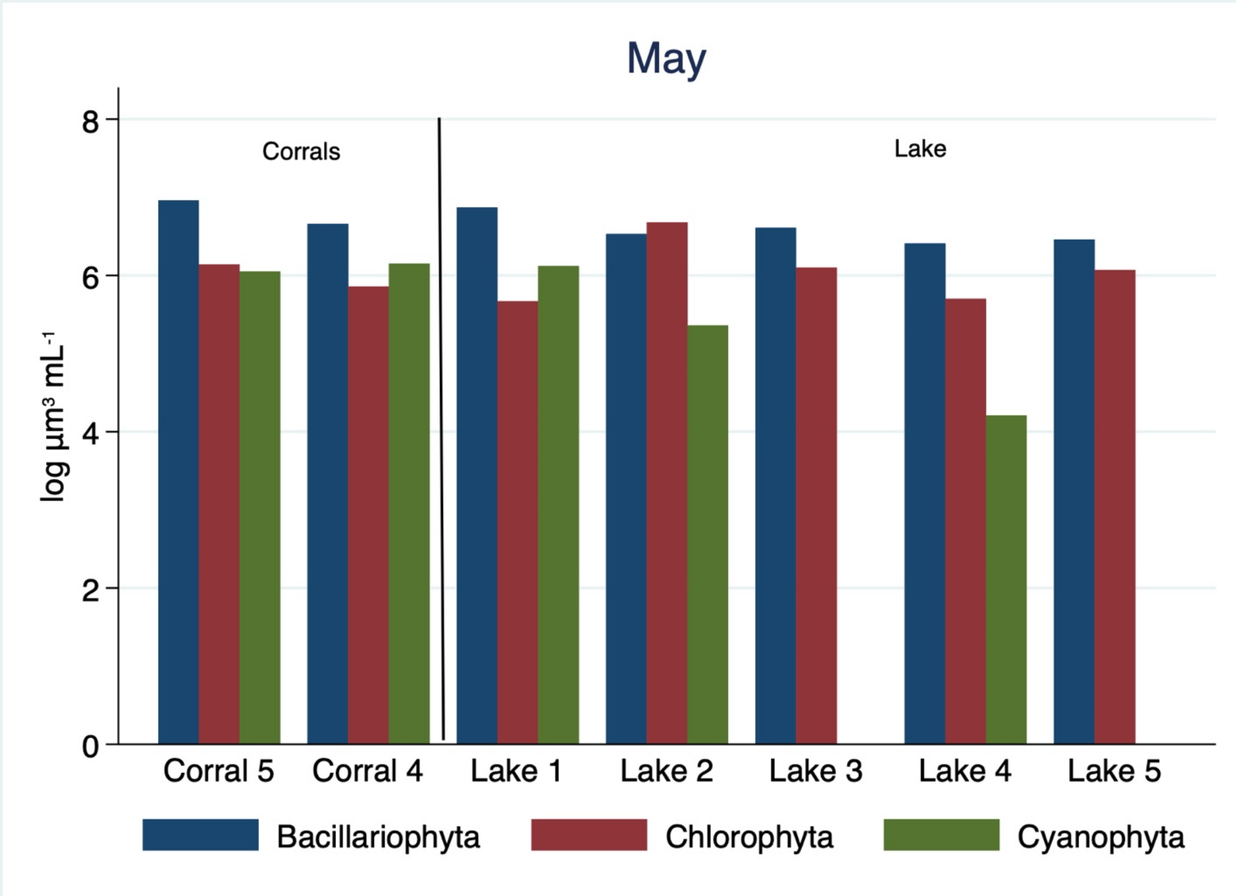


Figure 3. Comparison between Bacillariophyta, Chlorophyta, and Cyanophyta in corrals and lake replicates on May17, 2022.

There was no evidence that Bacillariophyta, Chlorophyta, and Cyanophyta biovolumes inside corrals were less than lake biovolumes, however there was evidence that Bacillariophyta biovolume was greater in Corral 4 than the lake and Cyanophyta biovolume was greater in both corrals than the lake on May 17, 2022 (Table 6). *Planktothrix agardhii* the dominant cyanophyte in Corral 5 and *Snowella lacustris* was the dominant cyanophyte in Corral 4. *Planktothrix agardhii and S. lacustris* also occurred in one of the lake samples but none of the others.

Table 6. Simple one-sample t-test comparisons between corral treatments and lake biovolumes log (μm^3 mL^{-1}) of Bacillariophyta, Chlorophyta, and Cyanophyta on May 17, 2022. Two hypotheses were tested: 1) biovolume in each treatment corral was equal to the lake mean biovolume (N = 5) and 2) biovolume in each treatment corral was less than the lake mean biovolume. A 95% confidence level was used for t-tests. Italicized t- values were considered as evidence for differences.

	Ha: Lake mean = corral biovolume	Ha: lake mean biovolume > corral biovolume
Bacillariophyta		
Corral 4	*t = -1.75, p < 0.01*[a]	t = -4.75, p = 1.00
Corral 5	t = -1.04, p = 0.36	t = -1.04, p = 0.82
Chlorophyta		
Corral 4	t = -0.53, p = 0.63	t =- 0.53, p = 0.69
Corral 5	t = -1.01, p = 0.37	t = -1.01, p = 0.19
Cyanophyta		

Corral 4	*t = -2.21, p = 0.09*[b]	t = -2.21, p = 0.95
Corral 5	*t = -2.29, p = 0.08*[c]	*t = -2.29, p < 0.96*

[a]Ha: mean lake biovolume < corral biovolume; t = -4.75, p < 0.01
[b]Ha: mean lake biovolume < corral biovolume; t = -2.21, p = 0.05
[c]Ha: mean lake biovolume < corral biovolume; t = -2.29, p = 0.04

*Table 7. Several metrics of phytoplankton taxa from May 17, 2022, samples inside and outside of corrals. Cell biovolumes log ($\mu m^3\ mL^{-1}$). S = Richness = number of sample occurrences, E = Evenness = H / ln (Richness), H = Diversity = - sum (Pi*ln (Pi)) = Shannon`s diversity index, D = Simpson`s diversity index for infinite population = 1 - sum (Pi*Pi) where Pi = importance probability in element i (element i relativized by row total). Taxa names are in Table 3.*

Taxon	Mean Biovolume	Std. Dev.	Min.	Max.	Number of sample occurrences	E	H`	D
ANAR	1.78	1.68	0.00	3.55	4	1.00	1.38	0.75
ANFA	0.87	1.49	0.00	3.20	2	1.00	0.69	0.50
APCSP	1.30	2.26	0.00	5.33	2	0.98	0.68	0.48
AUGR	0.64	1.68	0.00	4.44	1	NaN	0.00	0.00
BOSP	0.93	2.47	0.00	6.53	1	NaN	0.00	0.00
CD2	5.64	2.50	0.00	6.88	6	1.00	1.79	0.83
CDSP	5.43	0.53	4.61	6.36	7	1.00	1.94	0.86
CHDI	2.36	2.21	0.00	4.21	4	1.00	1.39	0.75
CHSP	5.20	2.75	0.00	9.45	6	0.98	1.76	0.82
COSP	0.73	1.92	0.00	5.08	1	NaN	0.00	0.00
CRSP	1.64	2.80	0.00	5.85	2	1.00	0.69	0.50
CYPL	0.59	1.56	0.00	4.13	1	NaN	0.00	0.00
DECO	3.02	2.07	0.00	4.53	5	1.00	1.61	0.80
DEIN	2.35	2.20	0.00	4.33	4	1.00	1.39	0.75
EUSP	2.09	2.62	0.00	5.19	3	1.00	1.10	0.67
FRCR	0.83	2.19	0.00	5.78	1	NaN	0.00	0.00
GRLA	0.54	1.42	0.00	3.75	1	NaN	0.00	0.00
KILU	1.18	2.01	0.00	4.25	2	1.00	0.69	0.50
LILI	0.63	1.66	0.00	4.40	1	NaN	0.00	0.00
MOCO	2.39	1.65	0.00	3.80	5	1.00	1.61	0.80
OOBO	2.36	2.95	0.00	5.90	3	1.00	1.10	0.67
OOSP	3.87	2.65	0.00	5.63	5	1.00	1.61	0.80
PD	5.68	0.23	5.34	5.89	7	1.00	1.95	0.86
PLAG	1.72	2.94	0.00	6.03	2	1.00	0.69	0.50
SCAR	1.26	2.15	0.00	4.55	2	1.00	0.69	0.50
SCSE	1.10	1.89	0.00	4.01	2	1.00	0.69	0.50
SNLA	1.65	2.82	0.00	6.15	2	1.00	0.69	0.50
SNSP	0.71	1.88	0.00	4.98	1	NaN	0.00	0.00
SPSC	1.62	2.77	0.00	5.67	2	1.00	0.69	0.50

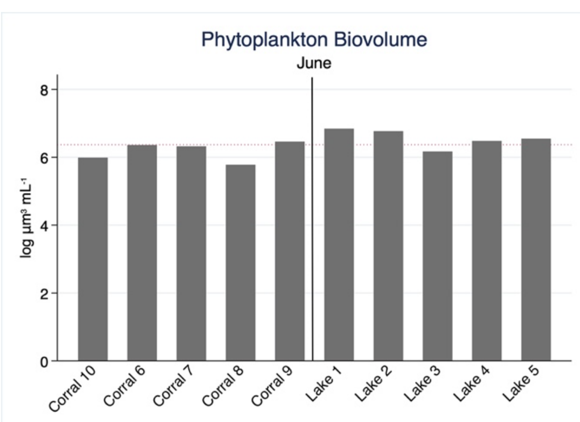
TRSE	0.56	1.48	0.00	3.92	1	NaN	0.00	0.00
WICR	2.49	2.33	0.00	4.65	4	1.00	1.39	0.75
WIRE	4.93	0.24	4.55	5.25	7	1.00	1.95	0.86

June

There was good evidence that phytoplankton biovolume was less inside corrals than outside (t = 2.18, Ha: diff = 0, p = 0.06; Ha: diff > 0, p = 0.03) (Table 8Table 7, Figure 4, Figure 5). Because of variability, there was no evidence that taxa richness differed inside and outside of corrals (Poisson regression z = -1.77, p = 0.10) on June 23, 2022, even though four of the five lake samples had greater than mean richness and four of five corrals had less than mean richness (Table 8, Figure 4,).

*Table 8. Several metrics of phytoplankton taxa from June 23, 2022, samples inside and outside of corrals. Cell biovolumes log (μm^3 mL^{-1}). S = Richness = number of taxa in each sample, E = Evenness = H / ln (Richness), H = Diversity = - sum (Pi*ln (Pi)) = Shannon`s diversity index, D = Simpson`s diversity index for infinite population = 1 - sum (Pi*Pi) where Pi = importance probability in element i (element i relativized by row total), effective number of taxa ENT = exp(H).*

Sample	Total Biovolume (log (μm^3 mL^{-1})	S	E	H`	D	ENT
Corral 6	5.99	12	1.00	2.48	0.92	12
Corral 7	6.36	18	0.99	2.87	0.94	18
Corral 8	6.32	12	0.99	2.47	0.91	12
Corral 9	5.78	22	1.00	3.08	0.95	22
Corral 10	6.46	19	0.99	2.92	0.94	19
Lake 1	6.84	28	1.00	3.32	0.96	28
Lake 2	6.77	20	0.99	2.97	0.95	19
Lake 3	6.17	13	1.00	2.55	0.92	13
Lake 4	6.48	20	0.99	2.97	0.95	19
Lake5	6.55	25	1.00	3.21	0.96	25



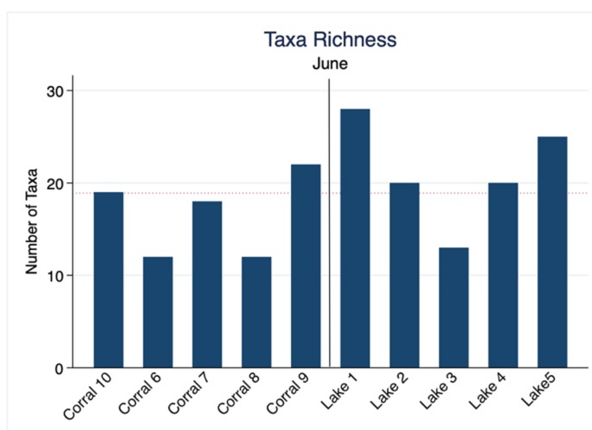


Figure 4. Comparisons of biovolume and number of taxa inside corrals vs lake in June. T-test for biovolume inside corrals vs lake t = 2.18. Ha: diff = 0, p = 0.06; Ha: diff > 0, p = 0.03. Poisson regression for taxa richness inside vs outside corrals z = -1.77, p = 0.10).

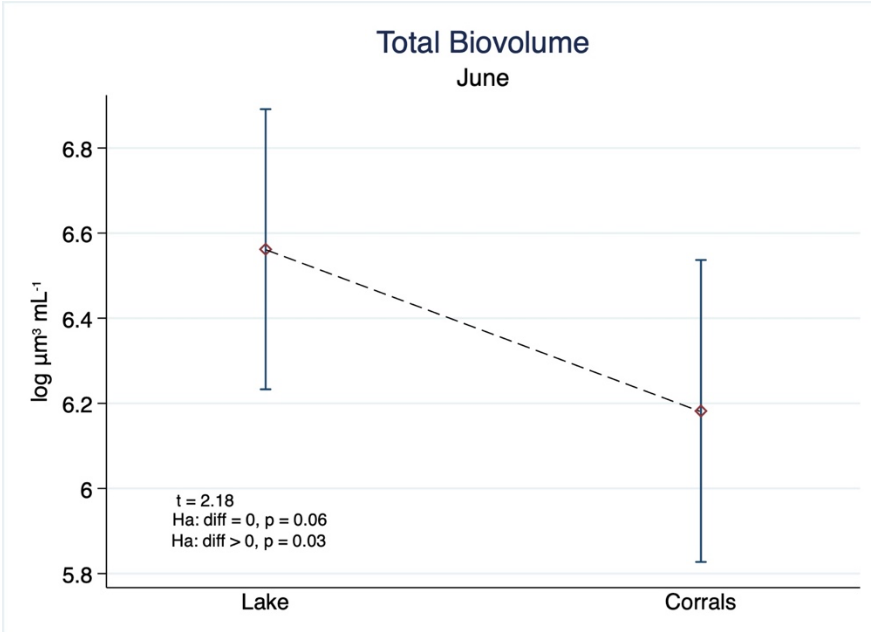


Figure 5. Comparison of total biovolume between the lake and inside corrals on June 23, 2022. Mean and 95% CIs.

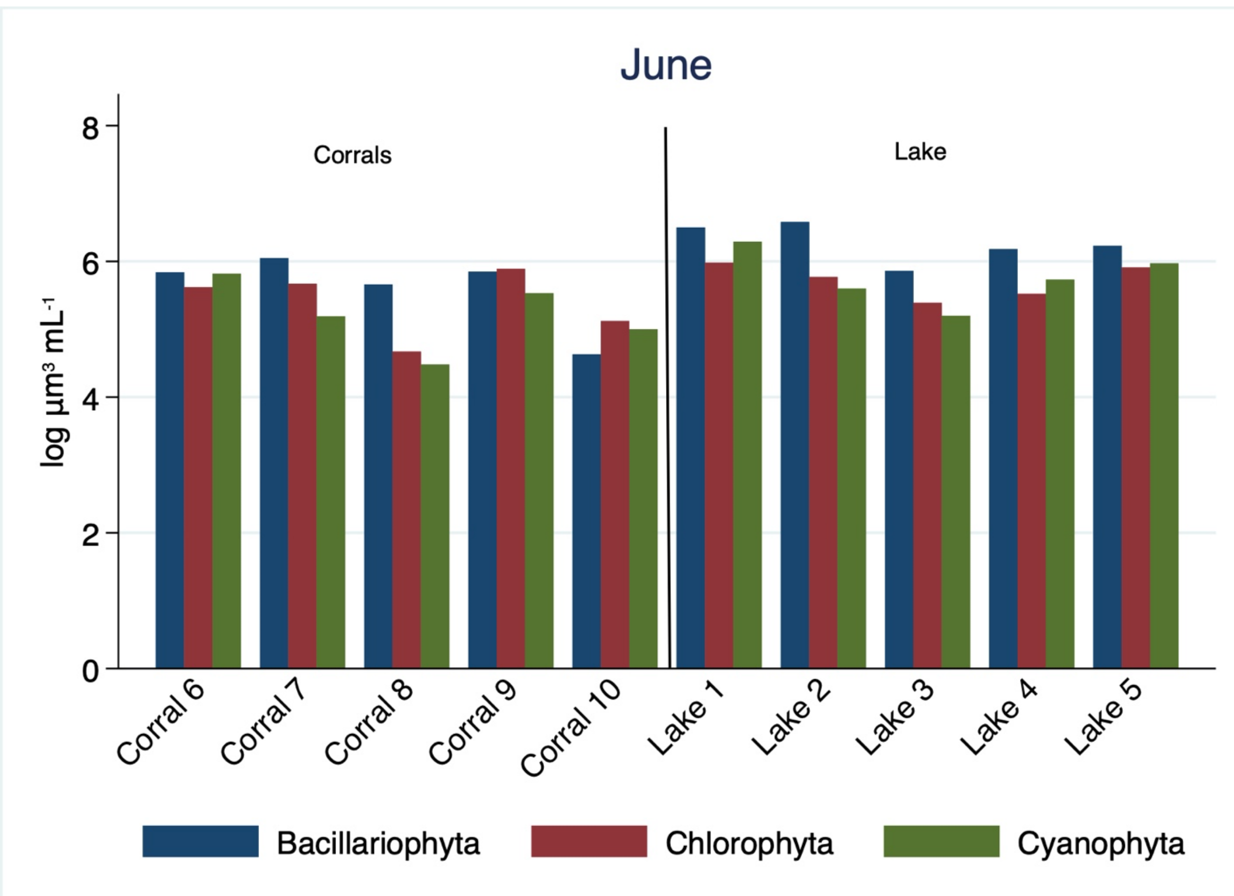


Figure 6. Comparison between Bacillariophyta, Chlorophyta, and Cyanophyta in corrals and lake replicates on June 23, 2022.

There was strong evidence that Bacillariophyta, Chlorophyta, and Cyanophyta biovolumes were less in Corrals 8, 9, and 10 than the lake on June 23, 2022 (Table 9). There was also strong evidence that Cyanophyta biovolumes were less in Corral 7 than the lake (Table 9).

Table 9. Simple one-sample t-test comparisons between corral treatments and lake biovolumes log ($\mu m^3\ mL^{-1}$) of Bacillariophyta, Chlorophyta, and Cyanophyta on June 23, 2022. Two hypotheses were tested: 1) biovolume in each treatment corral was equal to the lake mean biovolume (N = 5) and 2) biovolume in each treatment corral was less than the lake mean biovolume. A 95% confidence level was used for t-tests. Italicized t- values were considered as evidence for differences.

Division	Ha: Lake mean = corral biovolume	Ha: lake mean biovolume > corral biovolume
Bacillariophyta		
Corral 6	t = 3.36, p = 0.15	t = 3.36, p = 0.08
Corral 7	t = 1.72, p = 0.16	t = 1.72, p = 0.08
Corral 8	*t = 4.77, p = 0.01*	*t = 4.77, p < 0.01*
Corral 9	*t = 3.29, p = 0.03*	*t = 3.29, p = 0.02*
Corral 10	*t = 12.83, p < 0.01*	*t = 12.83, p < 0.01*
Chlorophyta		
Corral 6	t = 0.83, p = 0.45	t = 0.83, p = 0.23
Corral 7	t = 0.39, p = 0.72	t = 0.39, p = 0.36
Corral 8	*t = 9.25, p < 0.01*	*t = 9.25, p < 0.01*
Corral 9	t = -1.56, p = 0.19	t = -1.56, p = 0.90
Corral 10	*t = 5.26, p < 0.01*	*t = 5.26, p < 0.01*
Cyanophyta		
Corral 6	t = -0.34, p = 0.75	t = -0.34, p = 0.62
Corral 7	*t = 3.11, p = 0.04*	*t = 3.11, p < 0.02*
Corral 8	*t = 7.01, p < 0.01*	*t = 7.01, p < 0.01*
Corral 9	t = 1.25, p = 0.28	t = 1.25, p = 0.14
Corral 10	*t = 4.16, p = 0.01*	*t = 4.16, p < 0.01*

There was slight evidence that *Aphanathece* sp. (cyanophyte) had less biovolume in the corrals than in the lake on June 23, 2022 (t-test: t = 1.65, p = 0.07) but no evidence for differences for any of the other cyanophytes including *Dolichospermum circinalis* (Brébisson) Wacklin, Hoffmann & Komárek (= *Anabaena circinalis* Rabenhorst) that occurred inside and outside of corrals at this time.

The following figure compares Chrysophyta, Cryptophyta, Dinophyta, and Euglenophyta between the corrals and lake samples on June 23, 2022 (Figure 7.

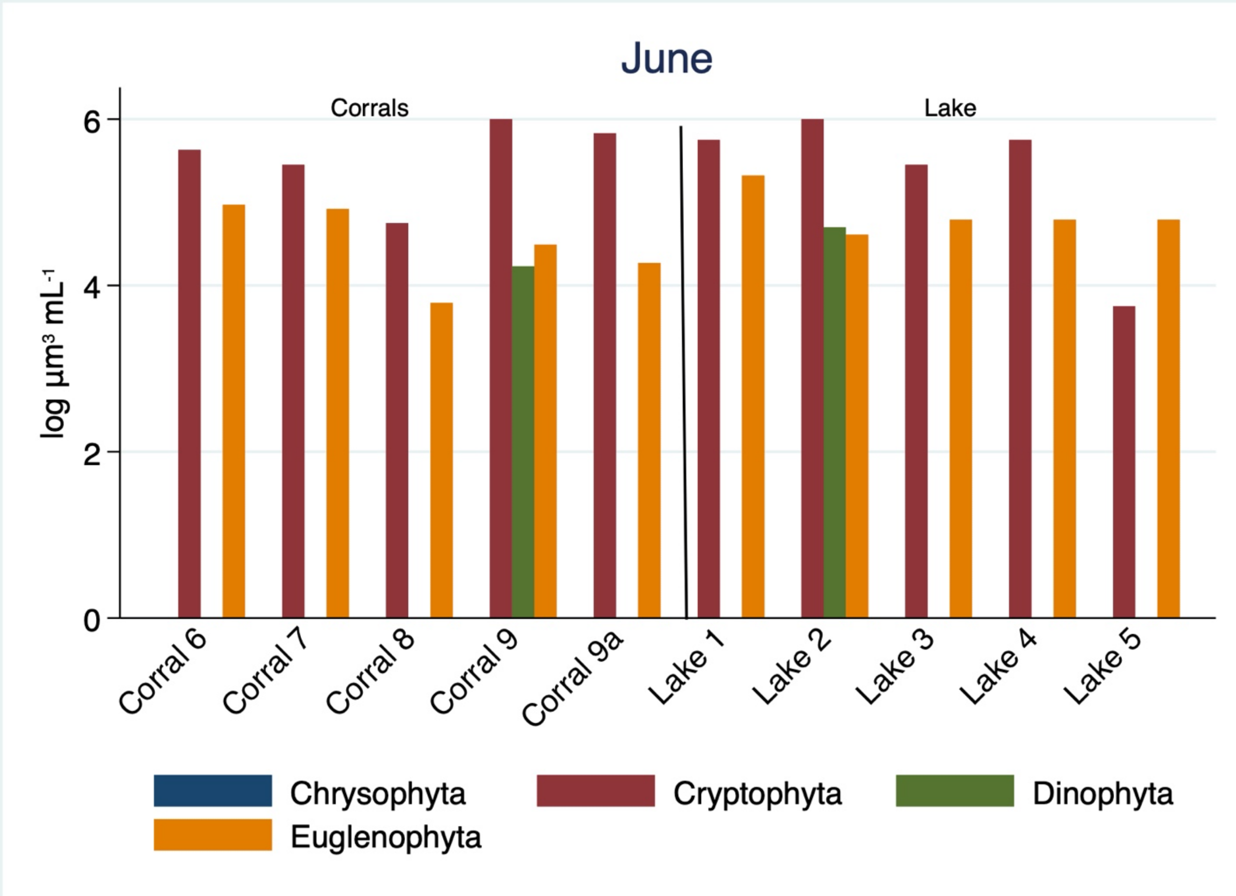


Figure 7. Comparison of Chrysophyta, Cryptophyta, Dinophyta, and Euglenophyta biovolumes inside and outside of corrals on June 23, 2022.

*Table 10. Several metrics of phytoplankton taxa from June 23, 2022, samples inside and outside of corrals. Cell biovolumes log ($\mu m^3\ mL^{-1}$). S = Richness = number of sample occurrences, E = Evenness = H / ln (Richness), H = Diversity = - sum (Pi*ln (Pi)) = Shannon`s diversity index, D = Simpson`s diversity index for infinite population = 1 - sum (Pi*Pi) where Pi = importance probability in element i (element i relativized by row total). Taxa names are in Table 3.*

Taxon	Mean biovolume	Stand. Dev.	Min	Max	Number of sample occurrences	E	H`	D
ACGR	0.38	1.27	0.00	4.20	1	NaN	0.00	0.00
ACHA	0.32	1.05	0.00	3.49	1	NaN	0.00	0.00
ANAR	1.58	1.52	0.00	3.25	6	1.00	1.79	0.83
APSP	5.19	0.57	4.16	6.11	11	1.00	2.39	0.91
CD2	5.33	0.80	4.09	6.53	11	1.00	2.39	0.91
CDSP	4.38	1.50	0.00	5.54	10	1.00	2.30	0.90
CHDI	1.78	2.07	0.00	4.38	5	1.00	1.60	0.80
CHLSP	3.57	1.83	0.00	5.16	9	1.00	2.19	0.89
CHTU	0.89	1.99	0.00	5.47	2	0.99	0.69	0.49
COPL	0.45	1.50	0.00	4.99	1	NaN	0.00	0.00
CRFE	0.93	2.06	0.00	5.18	2	1.00	0.69	0.50

CRQU	0.37	1.24	0.00	4.11	1	NaN	0.00	0.00
CRRI	0.34	1.13	0.00	3.75	1	NaN	0.00	0.00
CRSP	4.60	2.30	0.00	6.00	9	1.00	2.20	0.89
DECO	2.27	2.20	0.00	4.62	6	1.00	1.79	0.83
DEIN	2.64	2.10	0.00	4.33	7	1.00	1.95	0.86
DEOP	1.43	2.01	0.00	4.40	4	1.00	1.38	0.75
DOCI	2.89	2.77	0.00	5.64	6	1.00	1.79	0.83
EUSP	4.11	1.43	0.00	5.09	10	1.00	2.30	0.90
GLSP	0.40	1.34	0.00	4.45	1	NaN	0.00	0.00
GOSP	0.48	1.58	0.00	5.25	1	NaN	0.00	0.00
KILU	0.36	1.21	0.00	4.00	1	NaN	0.00	0.00
KISP	1.38	1.93	0.00	4.03	4	1.00	1.38	0.75
KOSP	0.36	1.18	0.00	3.92	1	NaN	0.00	0.00
LASP	1.02	1.74	0.00	3.92	3	1.00	1.10	0.67
LESP	0.90	1.99	0.00	4.92	2	1.00	0.69	0.50
MEGL	0.37	1.21	0.00	4.02	1	NaN	0.00	0.00
MESP	2.66	1.77	0.00	4.43	8	1.00	2.07	0.87
MOCO	0.73	1.26	0.00	2.89	3	0.99	1.09	0.66
MOSP	0.38	1.27	0.00	4.23	1	NaN	0.00	0.00
OOBO	2.43	2.34	0.00	5.00	6	1.00	1.79	0.83
OOSP	5.26	0.38	4.43	5.66	11	1.00	2.40	0.91
PD	5.53	0.53	4.39	6.30	11	1.00	2.39	0.91
PEPE	0.75	1.68	0.00	4.15	2	1.00	0.69	0.50
QUSP	0.80	1.77	0.00	4.53	2	1.00	0.69	0.50
SCAR	1.52	2.11	0.00	4.55	4	1.00	1.39	0.75
SCEL	2.63	2.53	0.00	5.16	6	1.00	1.79	0.83
SCSE	2.09	2.02	0.00	4.31	6	1.00	1.79	0.83
SNSP	0.41	1.35	0.00	4.48	1	NaN	0.00	0.00
SPSC	0.91	2.04	0.00	5.37	2	1.00	0.69	0.50
TRSP	0.67	1.49	0.00	4.01	2	0.99	0.69	0.50
UNCCY	0.35	1.17	0.00	3.89	1	NaN	0.00	0.00
UNDI	0.81	1.81	0.00	4.70	2	1.00	0.69	0.50
UNSPCH3	2.46	1.30	0.00	3.77	9	0.99	2.18	0.89
WICR	0.40	1.31	0.00	4.35	1	NaN	0.00	0.00
WIRE	3.61	1.82	0.00	5.16	9	1.00	2.19	0.89

July

Phytoplankton biomass was greater, and diversity was much greater in Corral 5 (control) and diversity lowest in Corral 3 that was stocked with emergent macrophytes, bivalves, and carp, (Table 11). Biovolume was lower in Corrals 2 and 3 that had macrophytes, and macrophytes, carp and bivalves, respectively.

*Table 11. Several metrics of phytoplankton taxa from July 28, 2022, samples inside and outside of corrals. Cell biovolumes log ($\mu m^3\ mL^{-1}$). S = Richness = number of taxa, E = Evenness = H / ln (Richness), H = Diversity = - sum (Pi*ln (Pi)) = Shannon`s diversity index, D = Simpson`s diversity index for infinite population = 1 - sum (Pi*Pi) where Pi = importance probability in element i (element i relativized by row total), effective number of taxa ENT = exp(H).*

Sample	Total Biovolume (log ($\mu m^3\ mL^{-1}$)	S	E	H`	D	ENT
Corral 2	6.50	13	0.99	2.55	0.92	13
Corral 3	6.40	11	0.99	2.37	0.90	11
Corral 4	6.87	18	0.99	2.85	0.94	17
Corral 5	7.45	27	1.00	3.28	0.96	27

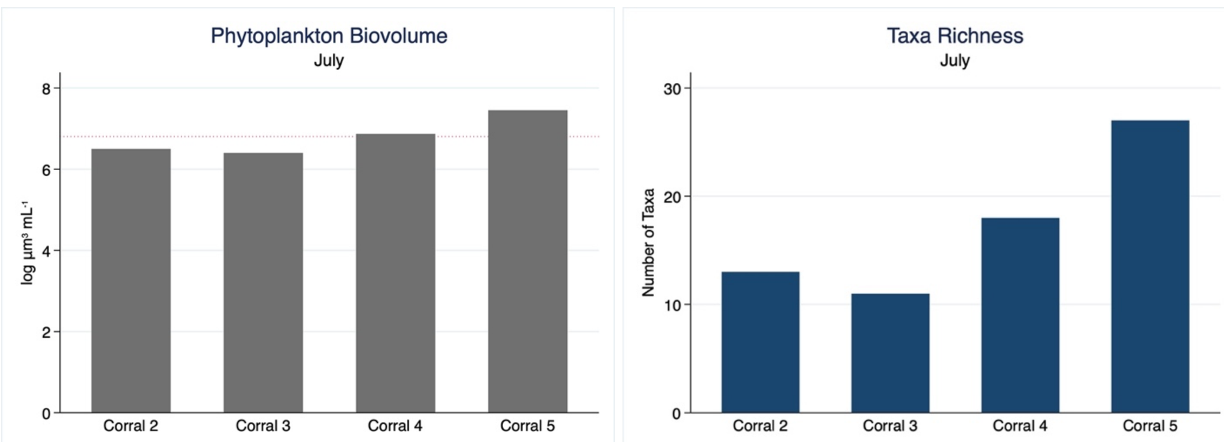


Figure 8. Comparisons of biovolume log ($\mu m^3\ mL^{-1}$) and taxa richness Corrals 2 to 5, July 28, 2022. Macrophytes were in the process of being planted in Corral 1 at this time. Red dotted line is mean.

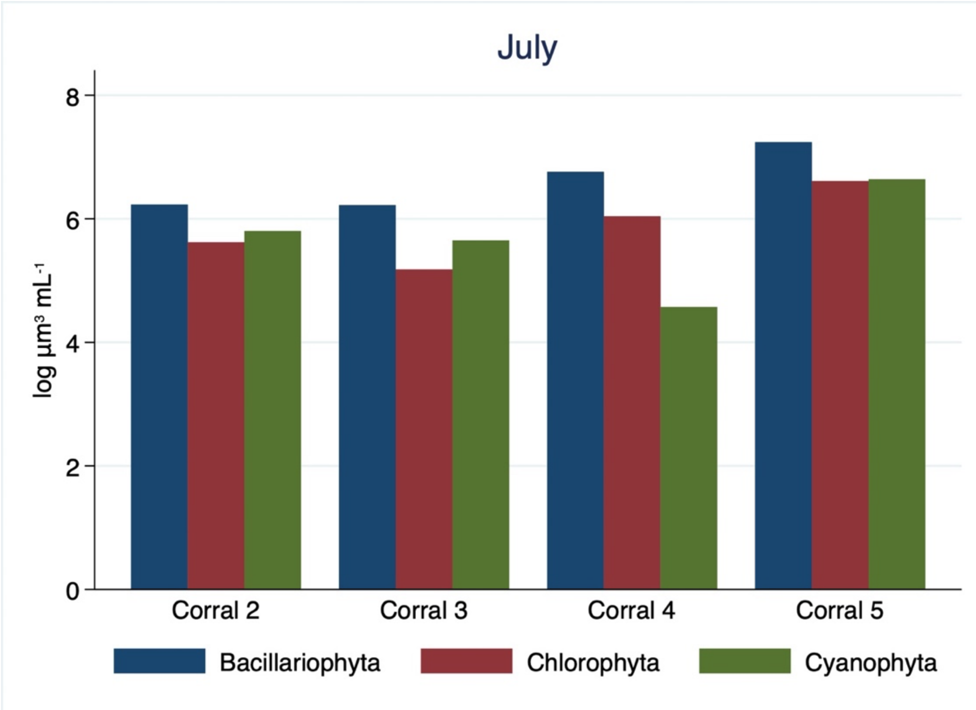


Figure 9. Comparison of Bacillariophyta, Chlorophyta, and Cyanophyta in Corrals 2 through 5 on July 28, 2022.

Several cyanophyte taxa occurred at relatively low biovolumes in the corrals on July 28, 2022, including *Aphanizomenon flosaquae*, *Gloeocapsa* sp., *Merismopedia glauca*, *Planktothrix* sp., and *Spirulina* species.

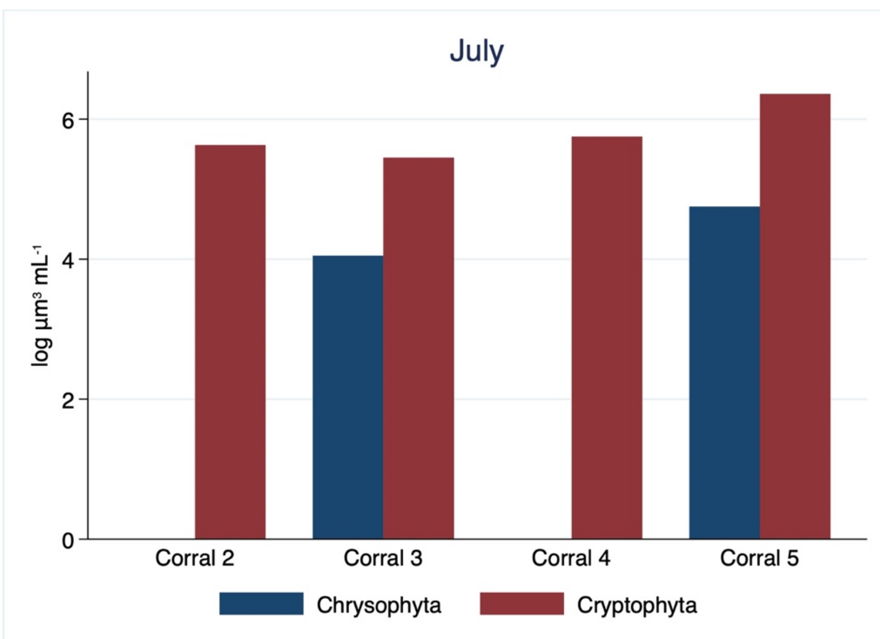


Figure 10. Comparisons of Chrysophyta and Cryptophyta biovolumes log (μm^3 mL^{-1}) in corrals on July 28, 2022.

These differences in biomass and diversity in Corral 3 vs. Corral 5 can be explained by diverse zooplankton habitat provided by macrophytes that allowed more zooplankton to graze phytoplankton, increased epiphytes growing on macrophytes that competed with phytoplankton for nutrients, and possibly macrophytes themselves up-taking sediment nutrients that otherwise would have fluxed into the water column and become available to phytoplankton in Corral 3. It was unknown if the adult carp in Corral 3 fed on zooplankton, but it is consistent with theory and our observations in other locations in Utah Lake. There was a large carp that inadvertently entered Corral 4 during this time and was subsequently removed. The carp could have lowered phytoplankton biovolume and diversity.

*Table 12. Several metrics of phytoplankton taxa from July 28, 2022, samples inside and outside of corrals. Cell biovolumes log ($\mu m^3\ mL^{-1}$). S = Richness = number of sample occurrences, E = Evenness = H / ln (Richness), H = Diversity = - sum (Pi*ln (Pi)) = Shannon`s diversity index, D = Simpson`s diversity index for infinite population = 1 - sum (Pi*Pi) where Pi = importance probability in element i (element i relativized by row total). Taxa names are in Table 3.*

Name	Mean biovolume	Stand. Dev.	Sum	Min	Max	S	E	H`	D
ACHA	1.97	2.28	7.89	0.00	4.10	2	1.00	0.69	0.50
ANAR	2.65	1.85	10.61	0.00	4.07	3	0.99	1.09	0.66
ANFA	2.55	1.73	10.21	0.00	3.81	3	1.00	1.10	0.66
APCSP	4.25	2.84	16.99	0.00	5.94	3	1.00	1.10	0.67
APFL	1.18	2.35	4.70	0.00	4.70	1	NaN	0.00	0.00
AUGR	2.33	2.71	9.31	0.00	5.05	2	1.00	0.69	0.50
CD2	2.28	2.65	9.12	0.00	4.89	2	1.00	0.69	0.50
CDSP	7.24	2.49	28.95	5.36	10.79	4	0.97	1.35	0.73
CHMI	2.77	3.30	11.09	0.00	6.53	2	0.98	0.68	0.48
COMSP	1.40	2.80	5.59	0.00	5.59	1	NaN	0.00	0.00
COPL	3.97	2.66	15.86	0.00	5.59	3	1.00	1.10	0.67
CRSP	5.80	0.39	23.19	5.45	6.36	4	1.00	1.39	0.75
DEBI	1.16	2.33	4.65	0.00	4.65	1	NaN	0.00	0.00
DECO	3.34	2.25	13.37	0.00	4.92	3	1.00	1.10	0.66
DEIN	3.25	2.18	13.00	0.00	4.63	3	1.00	1.10	0.67
DEOP	3.27	2.22	13.07	0.00	4.92	3	1.00	1.09	0.66
ERGI	2.61	3.02	10.46	0.00	5.23	2	1.00	0.69	0.50
GLSP	1.26	2.53	5.05	0.00	5.05	1	NaN	0.00	0.00
KISP	4.17	0.64	16.68	3.55	4.94	4	0.99	1.38	0.75
KOSP	0.98	1.96	3.92	0.00	3.92	1	NaN	0.00	0.00
MASP	1.19	2.37	4.75	0.00	4.75	1	NaN	0.00	0.00
MEGL	0.93	1.86	3.72	0.00	3.72	1	NaN	0.00	0.00
OOBO	1.25	2.50	5.00	0.00	5.00	1	NaN	0.00	0.00
OOSP	2.69	3.12	10.76	0.00	5.73	2	1.00	0.69	0.50
PD	6.37	0.30	25.49	6.07	6.69	4	1.00	1.39	0.75
PEAN	2.59	3.01	10.34	0.00	5.59	2	1.00	0.69	0.50

PEDU	5.58	0.49	22.31	5.13	6.28	4	1.00	1.38	0.75
PLSP	1.39	2.77	5.54	0.00	5.54	1	NaN	0.00	0.00
SCSE	2.01	2.32	8.02	0.00	4.01	2	1.00	0.69	0.50
SPSP	0.87	1.73	3.47	0.00	3.47	1	NaN	0.00	0.00
TECA	0.91	1.81	3.62	0.00	3.62	1	NaN	0.00	0.00
UNSPCH	1.01	2.03	4.05	0.00	4.05	1	NaN	0.00	0.00

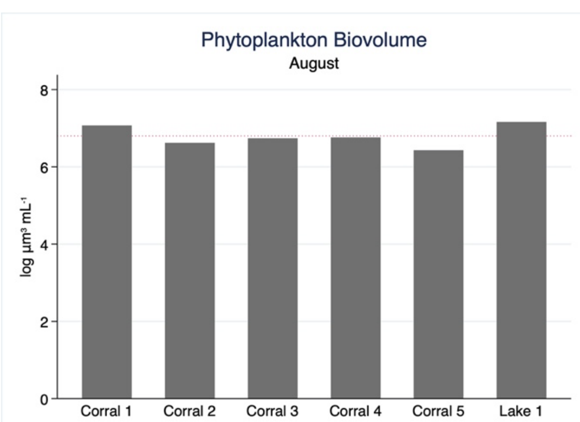
August

Shallow

Phytoplankton biovolume was slightly greater than the mean in Corral 1 and in the lake and diversity was greatest in Corral 5 (control) on August 16, 2022. Diversity was lowest in Corral 1 (macrophytes and bivalves) and Corral 2 (bivalves). Biovolume was lower than the mean in Corral 5 (control). If we assume that the one lake sample biovolume equates to lake mean = 7.16 **(**log (μm^3 mL$^-$1) then a one sample t-test suggests that there was good evidence that phytoplankton biovolume within the corrals (N = 5), despite treatment effects, was less than in the lake (t = -4.17, Ha: mean < 7.16, p < 0.01; Ha: mean = 7.16, p = 0.01).

*Table 13. Several metrics of phytoplankton taxa from August 16, 2022, samples inside and outside of corrals. Cell biovolumes log (μm^3 mL^{-1}). S = Richness = number of taxa, E = Evenness = H / ln (Richness), H = Diversity = - sum (Pi*ln (Pi)) = Shannon`s diversity index, D = Simpson`s diversity index for infinite population = 1 - sum (Pi*Pi) where Pi = importance probability in element i (element i relativized by row total), effective number of taxa ENT = exp(H).*

Name	Total Biovolume (log (μm^3 mL^{-1})	S	E	H`	D	ENT
Corral 1	7.07	11	1.00	2.39	0.91	11
Corral 2	6.62	11	0.99	2.38	0.91	11
Corral 3	6.74	17	0.99	2.81	0.94	17
Corral 4	6.76	18	0.99	2.87	0.94	18
Corral 5	6.43	27	0.99	3.28	0.96	27
Lake 1	7.16	14	0.99	2.62	0.93	14



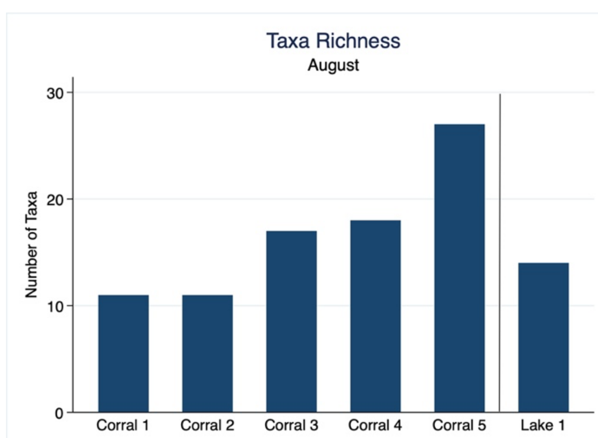


Figure 11. Comparisons of biovolume log (µm^3 mL$^-$1) and taxa richness Corrals 1 to 5, August 16, 2022. Red dotted line is mean. One sample t-test t = -4.17, Ha: mean < 7.16 p 0.007; Ha: mean = 7.16, p = 0.01. Assumes the one lake sample equates to lake mean biovolume.

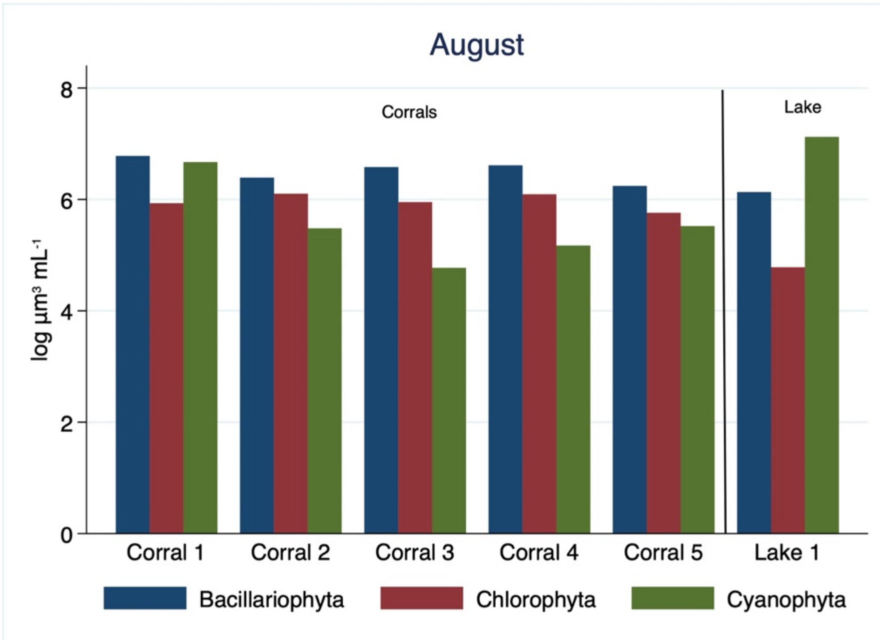


Figure 12. Comparisons of Bacillariophyta, Chlorophyta, and Cyanophyta biovolumes (log (µm^3 mL$^-$1) in corrals and lake on August 18, 2022.

Aphanizomenon flosaquae occurred in one corral and outside of corral and was about 10 times the biovolume outside (Table 14). *Dolichospermum circinalis* occurred in one corral but not in any other or in the lake sample (Table 14). Other cyanophyte taxa biovolumes that were found are also in (Table 14).

Table 14. Biovolumes (log (µm^3 mL$^-$1) of cyanophyte taxa found in the corrals and lake on August 16, 2022. Taxa names are in Table 3.

Site	APFL	APIN	APSP	CHDI	CHTU	CYPL	DOCI	GLSP	LILI	MESP	MISP	SNLA
Corral 1	6.56	4.89	0.00	0.00	5.77	0.00	5.34	4.45	0.00	3.73	5.25	0.00
Corral 2	0.00	0.00	5.16	4.51	0.00	3.83	0.00	0.00	0.00	0.00	0.00	5.07
Corral 3	0.00	0.00	0.00	0.00	0.00	4.43	0.00	0.00	4.51	0.00	0.00	0.00
Corral 4	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.17	0.00	0.00	0.00
Corral 5	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.00	0.00	0.00	5.37
Lake 1	7.10	0.00	0.00	0.00	5.30	0.00	5.34	0.00	0.00	0.00	0.00	0.00

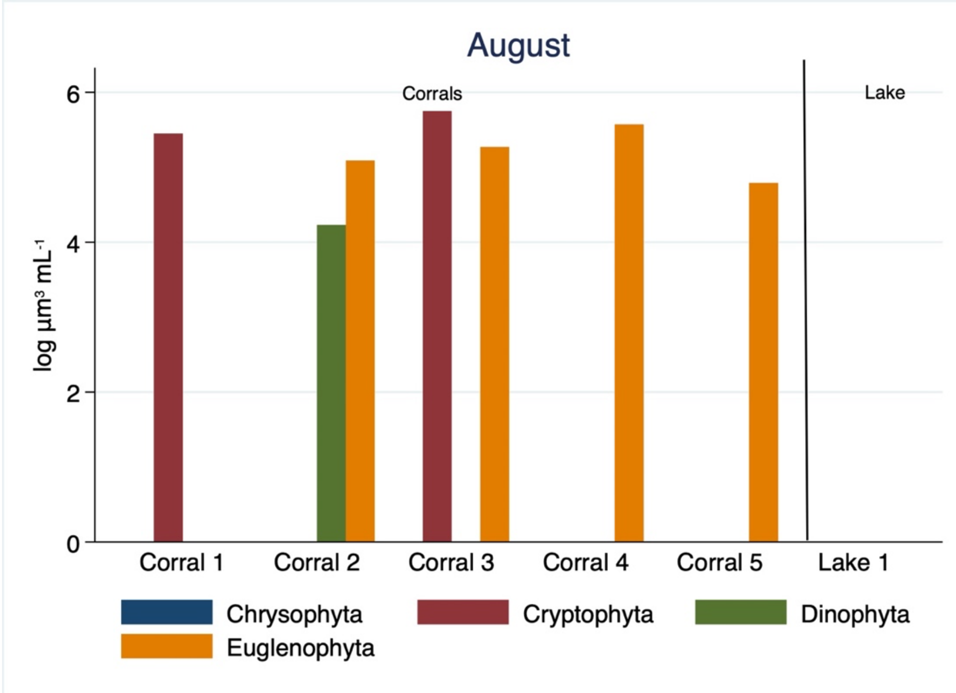


Figure 13. Comparisons of Chrysophyta, Cryptophyta, Dinophyta, and Euglenophyta biovolumes log (µm^3 mL^{-1}) in corrals and the lake on August 16, 2022.

These differences in biomass and diversity in Corral 1 vs. Corral 5 can be explained by bivalves filtering phytoplankton, diverse zooplankton habitat provided by macrophytes that allowed more zooplankton to graze phytoplankton, increased epiphytes growing on macrophytes that competed with phytoplankton for nutrients, and possibly macrophytes themselves up-taking sediment nutrients that otherwise would have fluxed into the water column and become available to phytoplankton in Corral 1.

*Table 15. metrics of phytoplankton taxa from August 16, 2022, samples inside and outside of corrals. Cell biovolumes log (µm^3 mL^{-1}). S = Richness = number of sample occurrences, E = Evenness = H / ln (Richness), H = Diversity = - sum (Pi*ln (Pi)) = Shannon`s diversity index, D = Simpson`s diversity index for infinite population = 1 - sum (Pi*Pi) where Pi = importance probability in element i (element i relativized by row total). Taxa names are in Table 3.*

Name	Mean	Std. Dev.	Sum	Min	Max	S	E	H`	D
ACHA	0.63	1.55	3.79	0.00	3.79	1	NaN	0.00	0.00
ANAR	1.63	1.79	9.79	0.00	3.47	3	1.00	1.10	0.67
ANFA	0.53	1.31	3.20	0.00	3.20	1	NaN	0.00	0.00
APCSP	0.81	1.98	4.86	0.00	4.86	1	NaN	0.00	0.00
APFL	2.28	3.53	13.66	0.00	7.10	2	1.00	0.69	0.50
APIN	0.82	2.00	4.89	0.00	4.89	1	NaN	0.00	0.00
APSP	0.86	2.11	5.16	0.00	5.16	1	NaN	0.00	0.00
AUGR	0.69	1.69	4.14	0.00	4.14	1	NaN	0.00	0.00
CD2	5.58	1.16	33.46	3.75	6.51	6	0.99	1.77	0.83
CDSP	5.38	0.79	32.29	4.61	6.73	6	1.00	1.78	0.83
CHDI	0.75	1.84	4.51	0.00	4.51	1	NaN	0.00	0.00

CHGL	0.63	1.54	3.76	0.00	3.76	1	NaN	0.00	0.00
CHLSP	1.36	2.11	8.16	0.00	4.08	2	1.00	0.69	0.50
CHMU	0.82	2.01	4.92	0.00	4.92	1	NaN	0.00	0.00
CHSP	3.81	2.96	22.86	0.00	5.92	4	1.00	1.39	0.75
CHTU	1.85	2.86	11.07	0.00	5.77	2	1.00	0.69	0.50
CRSP	1.87	2.90	11.21	0.00	5.75	2	1.00	0.69	0.50
CYPL	1.38	2.14	8.26	0.00	4.43	2	1.00	0.69	0.50
DEBI	0.68	1.65	4.05	0.00	4.05	1	NaN	0.00	0.00
DEBIC	0.59	1.44	3.52	0.00	3.52	1	NaN	0.00	0.00
DECO	1.41	2.18	8.45	0.00	4.23	2	1.00	0.69	0.50
DEIN	2.64	2.05	15.82	0.00	4.03	4	1.00	1.39	0.75
DEOP	1.36	2.11	8.15	0.00	4.23	2	1.00	0.69	0.50
DOCI	1.78	2.76	10.68	0.00	5.34	2	1.00	0.69	0.50
EUSP	3.45	2.69	20.71	0.00	5.57	4	1.00	1.39	0.75
GLSP	0.74	1.82	4.45	0.00	4.45	1	NaN	0.00	0.00
KILU	0.57	1.39	3.40	0.00	3.40	1	NaN	0.00	0.00
KISP	2.05	2.24	12.27	0.00	4.21	3	1.00	1.10	0.67
KOSP	1.31	2.02	7.84	0.00	3.92	2	1.00	0.69	0.50
LILI	2.45	2.69	14.68	0.00	5.17	3	1.00	1.10	0.67
MESP	0.62	1.52	3.73	0.00	3.73	1	NaN	0.00	0.00
MISP	0.87	2.14	5.25	0.00	5.25	1	NaN	0.00	0.00
MOCO	1.68	1.84	10.06	0.00	3.50	3	1.00	1.10	0.67
MOCOV	1.03	1.59	6.15	0.00	3.26	2	1.00	0.69	0.50
OOBO	1.67	2.58	10.00	0.00	5.00	2	1.00	0.69	0.50
OOSP	5.06	0.49	30.38	4.43	5.43	6	1.00	1.79	0.83
PD	5.80	0.13	34.80	5.71	6.05	6	1.00	1.79	0.83
PEAN	0.79	1.94	4.75	0.00	4.75	1	NaN	0.00	0.00
PEDU	0.86	2.10	5.13	0.00	5.13	1	NaN	0.00	0.00
PSBO	0.94	2.31	5.66	0.00	5.66	1	NaN	0.00	0.00
SCEL	0.81	1.98	4.86	0.00	4.86	1	NaN	0.00	0.00
SCSE	2.52	1.96	15.13	0.00	4.01	4	1.00	1.39	0.75
SNLA	1.74	2.70	10.44	0.00	5.37	2	1.00	0.69	0.50
UNDI	0.70	1.73	4.23	0.00	4.23	1	NaN	0.00	0.00
WICR	1.61	2.49	9.65	0.00	4.83	2	1.00	0.69	0.50

Deep

Results from August 16, 2022, deep water corrals (Corrals 6 to 10) were some of the most relevant in our study. We found strong evidence that Cyanophyta and total phytoplankton biovolumes (log (μm^3 mL^{-1})) were lower inside the corrals than in the lake (Figure 14). Mean cyanophyte biovolume (log (μm^3 mL^{-1})) in the lake samples = 7.08 (12,022,644), while corral mean cyanophyte biovolume = 6.04 (1,096,478) an order of magnitude less in the corrals. We attribute this almost exclusively to zooplankton grazing (see August zooplankton section).

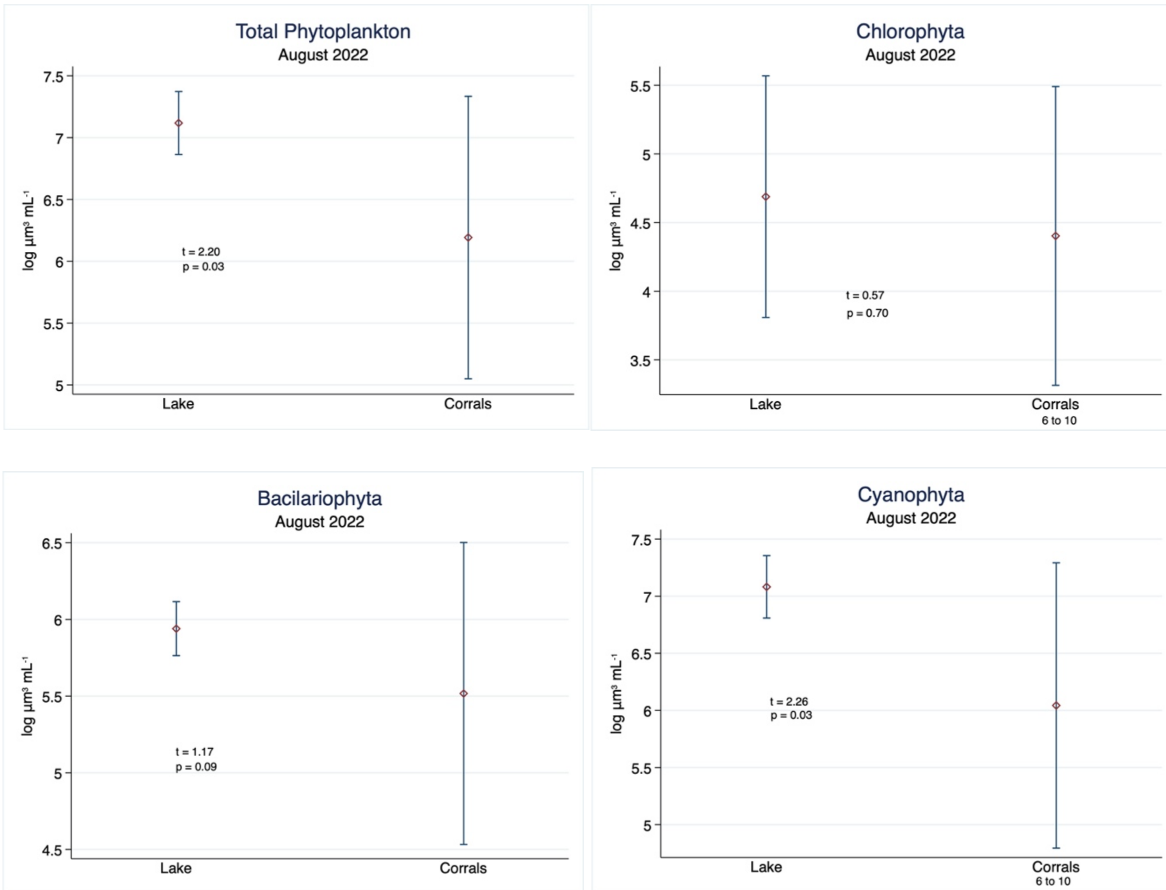


Figure 14. Comparisons of total phytoplankton, Chlorophyta, Bacillariophyta, and Cyanophyta biovolumes (log (µm^3 mL^{-1})) between corrals and the lake on August 16, 2022. Mean and 95% CIs. T-test results were based on one tailed Ha: lake biovolumes > corral biovolumes. N = 10 samples.

Table 16. Bacillariophyta, Chlorophyta, Cryptophyta, Cyanophyta, Euglenophyta, and total phytoplankton biovolumes (log (µm^3 mL^{-1})) on August 16, 2022, inside and outside of corrals.

	Bacillariophyta	**Chlorophyta**	**Cryptophyta**	**Cyanophyta**	**Euglenophyta**	**Total**
Corral 6	6.59	5.17	5.15	7.28	4.16	7.37
Corral 7	4.90	3.38	0.00	4.79	0.00	5.15
Corral 8	6.13	5.46	0.00	6.69	0.00	6.82
Corral 9	4.86	4.01	0.00	5.33	0.00	5.46
Corral 10	5.10	4.00	0.00	6.12	0.00	6.17
Lake 1	6.15	5.19	0.00	7.22	0.00	7.26
Lake 2	5.90	5.12	0.00	7.13	0.00	7.16
Lake 3	6.01	5.11	5.15	7.21	0.00	7.25
Lake 4	5.84	4.49	0.00	6.69	4.92	6.76
Lake 5	5.80	3.53	0.00	7.15	0.00	7.17

In addition to this important finding, total phytoplankton, and all phytoplankton division biovolumes were lowest in Corral 7 shortly after nutrient enrichment (13 days). Corral 7 also had the greatest abundance (378 individuals L^{-1}) of zooplankton, including the most cladocerans (311 L^{-1}) on this date (Table 34).

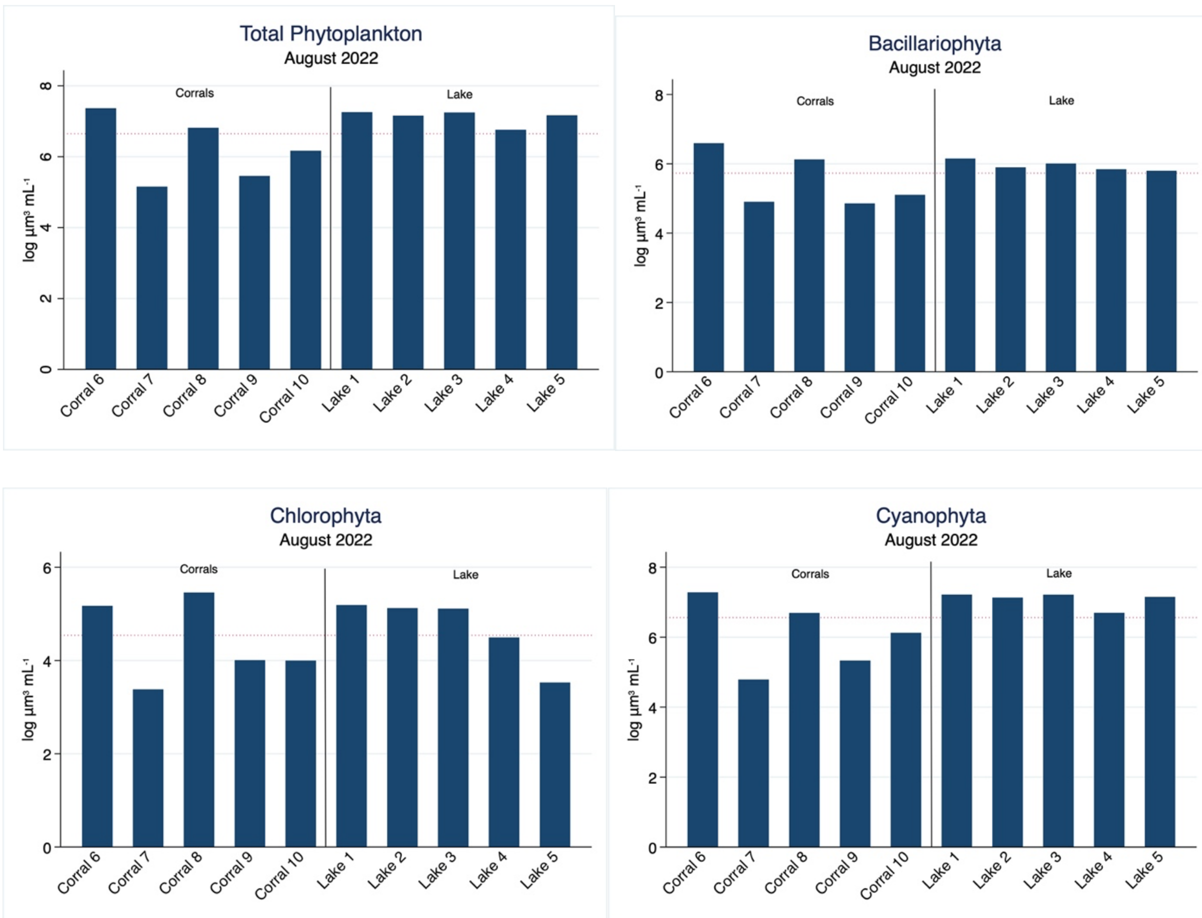


Figure 15. Comparisons of total phytoplankton, Bacillariophyta, Chlorophyta, and Cyanophyta biovolumes in each corral and lake samples collected on August 16, 2022.

October

Several metrics of phytoplankton taxa from October 11, 2022, samples inside and outside of corrals are presented in Table 17 and Table 18.

*Table 17. Several metrics of phytoplankton taxa from October 11, 2022, samples inside and outside of corrals. Cell biovolumes log (μm^3 mL^{-1}). S = Richness = number of taxa, E = Evenness = H / ln (Richness), H = Diversity = - sum (Pi*ln (Pi)) = Shannon`s diversity index, D = Simpson`s diversity index for infinite population = 1 - sum (Pi*Pi) where Pi = importance probability in element i (element i relativized by row total), effective number of taxa ENT = exp(H).*

Sample	Total Biovolume (log (μm^3 mL^{-1})	S	E	H`	D	ENT
Corral 6	5.97	11	0.995	2.386	0.9071	11
Corral 7	4.53	4	0.998	1.384	0.7489	4

Corral 8	5.41	9	0.992	2.179	0.8851	9
Corral 9	5.24	4	0.999	1.384	0.749	4
Corral 10	3.90	2	0.998	0.692	0.4987	2
Lake 1	5.73	8	0.991	2.06	0.8702	8
Lake 2	6.63	13	0.991	2.541	0.9194	13
Lake 3	6.11	7	0.997	1.939	0.8552	7
Lake 4	5.75	7	0.995	1.936	0.8545	7
Lake 5	6.27	8	0.997	2.074	0.8736	8

*Table 18. Several metrics of phytoplankton taxa from October 11, 2022, samples inside and outside of corrals. Cell biovolumes log (μm^3 mL^{-1}). S = Richness = number of sample occurrences, E = Evenness = H / ln (Richness), H = Diversity = - sum (Pi*ln (Pi)) = Shannon`s diversity index, D = Simpson`s diversity index for infinite population = 1 - sum (Pi*Pi) where Pi = importance probability in element i (element i relativized by row total). Taxa names are in Table 3.*

Name	Mean	Stand. Dev.	Sum	Minimum	Maximum	S	E	H`	D
ACHA	0.28	0.88	2.79	0.00	2.79	1	NaN	0.00	0.00
ANFA	1.19	1.54	11.91	0.00	3.20	4	1.00	1.39	0.75
APCSP	0.49	1.54	4.86	0.00	4.86	1	NaN	0.00	0.00
APFL	0.61	1.93	6.09	0.00	6.09	1	NaN	0.00	0.00
APIN	2.38	2.52	23.77	0.00	5.20	5	1.00	1.61	0.80
AUGR	0.44	1.41	4.44	0.00	4.44	1	NaN	0.00	0.00
CD2	3.81	2.13	38.13	0.00	5.87	8	0.99	2.07	0.87
CDSP	2.67	2.85	26.69	0.00	6.25	5	1.00	1.60	0.80
CHLSP	1.79	2.37	17.90	0.00	5.28	4	0.99	1.37	0.74
COSP	0.47	1.48	4.67	0.00	4.67	1	NaN	0.00	0.00
CRSP	0.55	1.72	5.45	0.00	5.45	1	NaN	0.00	0.00
DECO	0.39	1.24	3.92	0.00	3.92	1	NaN	0.00	0.00
DEIN	0.81	1.70	8.06	0.00	4.03	2	1.00	0.69	0.50
DEOP	0.42	1.34	4.23	0.00	4.23	1	NaN	0.00	0.00
DOCI	0.97	2.06	9.69	0.00	5.34	2	0.99	0.69	0.49
EUSP	0.83	1.75	8.28	0.00	4.49	2	1.00	0.69	0.50
KILU	0.76	1.60	7.58	0.00	3.88	2	1.00	0.69	0.50
KISP	0.65	1.37	6.46	0.00	3.43	2	1.00	0.69	0.50
MASP	0.35	1.09	3.45	0.00	3.45	1	NaN	0.00	0.00
MEGL	0.34	1.08	3.42	0.00	3.42	1	NaN	0.00	0.00
MESP	0.79	1.67	7.94	0.00	4.03	2	1.00	0.69	0.50
OOSP	3.78	2.04	37.77	0.00	5.33	8	1.00	2.07	0.87
PD	4.02	2.18	40.22	0.00	5.89	8	1.00	2.07	0.87
PEDU	0.56	1.77	5.59	0.00	5.59	1	NaN	0.00	0.00
PESP	0.53	1.68	5.30	0.00	5.30	1	NaN	0.00	0.00
PHSP	0.42	1.32	4.16	0.00	4.16	1	NaN	0.00	0.00

SNLA	0.51	1.60	5.07	0.00	5.07	1	NaN	0.00	0.00
UNFC	0.44	1.39	4.40	0.00	4.40	1	NaN	0.00	0.00
UNSC	0.43	1.36	4.29	0.00	4.29	1	NaN	0.00	0.00
WIRE	1.34	2.15	13.36	0.00	4.55	3	1.00	1.10	0.67

We found good evidence that bacillariophytes, chlorophytes, cyanophytes, and total biovolumes (log (μm^3 mL^{-1}) were lower in the corrals than in the lake on October 11, 2022 (Figure 16, Figure 18)

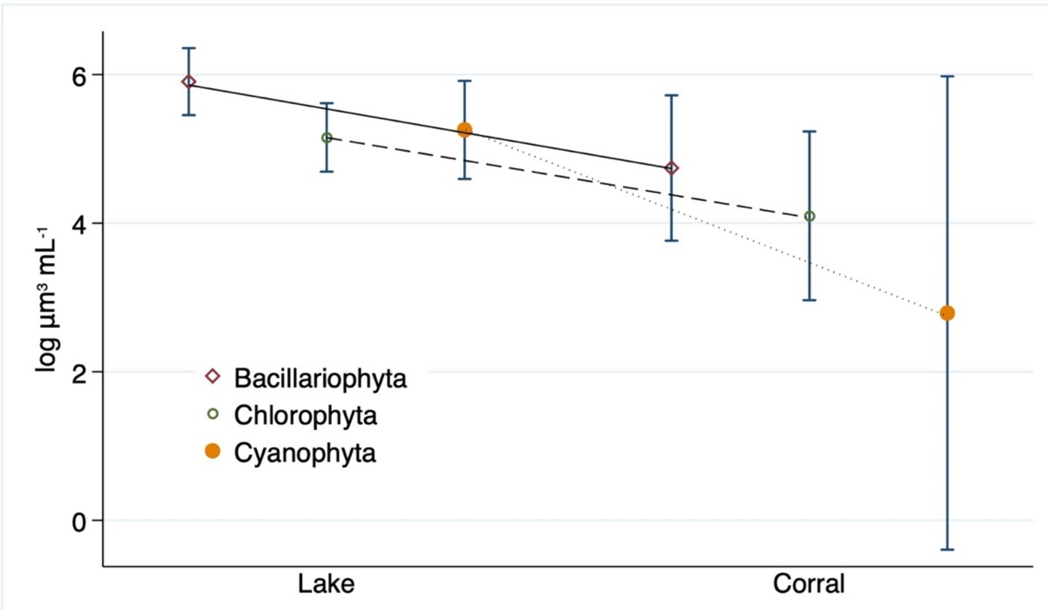


Figure 16. Comparison of bacillariophyte, chlorophyte, and cyanophyte biovolume (log (μm^3 mL^{-1}) between the lake and inside corrals on October 11, 2022. Bacillariophyta t-test: $t = 3.00$, $p = 0.01$; Chlorophyta t-test: $t = 2.07$, $p = 0.02$; Cyanophyta t-test: $t = 2.10$, $p = 0.03$.

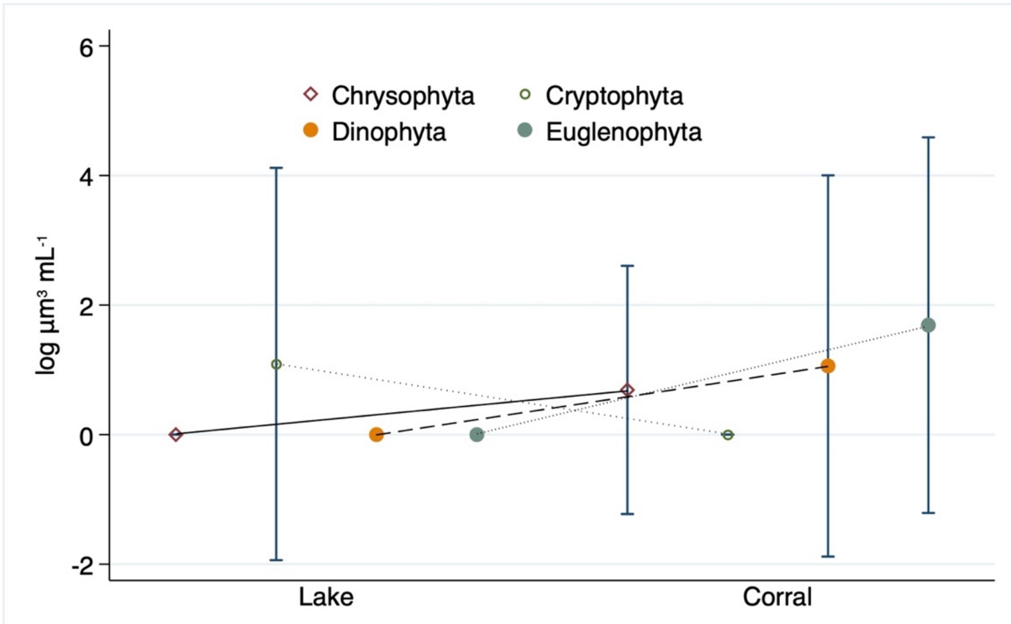


Figure 17. Comparison of Chrysophyta, Cryptophyta, Dinophyta, and Euglenophyta biovolume (log ($\mu m^3\ mL^{-1}$) between the lake and inside corrals on October 11, 2022. Mean and 95% CIs. Corrals 6 to 10 combined.

There was strong evidence that total phytoplankton biovolume was less inside the corrals than in the lake (Two sample t test: t = 2.73, p = 0.01) (Figure 18).

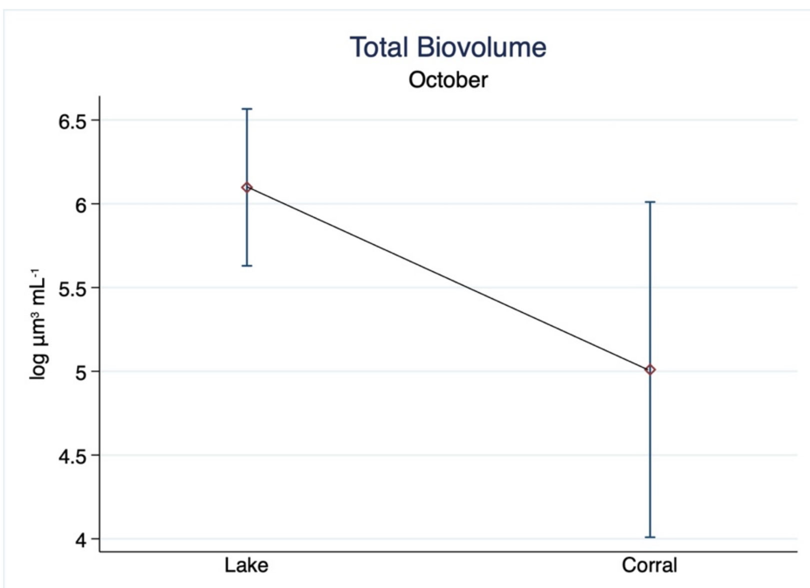


Figure 18. Comparison of total phytoplankton biovolume (log ($\mu m^3\ mL^{-1}$) between the lake and inside deep (open water) corrals on October 11, 2022. Two sample T test: t = 2.73, p = 0.01. Open water corrals 6 to 10 combined.

The following table (Table 19) shows differences in Bacillariophyta, Chlorophyta, and Cyanophyta biovolumes in Corrals 6 to 10 vs. lake biovolumes. There was strong evidence for differences in almost all instances.

Table 19. Simple one-sample t-test comparisons between corral treatments and lake biovolumes log (μm^3 mL^{-1}) *of Bacillariophyta, Chlorophyta, and Cyanophyta on October 11, 2022. Two hypotheses were tested: 1) biovolume in each treatment corral was equal to the lake mean biovolume (N = 5) and 2) biovolume in each treatment corral was less than the lake mean biovolume. A 95% confidence level was used for t-tests. Italicized t- values were considered as evidence for differences.*

Division	Ha: Lake mean = corral biovolume	Ha: lake mean biovolume > corral biovolume
Bacillariophyta		
Corral 6	*t = 1.76, p = 0.15*	*t = 1.76, p = 0.08*
Corral 7	*t = 10.99, p < 0.01*	*t = 10.99, p < 0.01*
Corral 8	*t = 3.73, p = 0.02*	*t = 3.73, p = 0.01*
Corral 9	*t = 6.07, p < 0.01*	*t = 6.07, p < 0.01*
Corral 10	*t = 13.27, p < 0.01*	*t = 13.27, p < 0.01*
Chlorophyta		
Corral 6	t = -0.28, p = 0.79	t = -0.28, p = 0.60
Corral 7	*t = 8.58, p < 0.01*	*t = 8.58, p < 0.01*
Corral 8	*t = 11.60, p < 0.01*	*t = 11.60, p < 0.01*
Corral 9	t = 1.23, p = 0.29	t = 1.23, p = 0.14
Corral 10	*t = 10.69, p < 0.01*	*t = 10.68, p < 0.01*
Cyanophyta		
Corral 6	t = 0.78, p = 0.48	t = 0.78, p = 0.24
Corral 7	*t = 4.44, p = 0.01*	*t = 4.44, p < 0.01*
Corral 8	*t = 2.42, p = 0.07*	*t = 2.42, p = 0.04*
Corral 9	*No cyanophytes*	*No cyanophytes*
Corral 10	*No cyanophytes*	*No cyanophytes*

The lower phytoplankton biovolumes inside the corrals compared within the lake at the end of the research season is consistent with universally recognized limnological theory; grazing from large abundances of zooplankton free from predation reduces phytoplankton. Even though light availability was greater within the corrals and likely increased phytoplankton production, intense grazing pressure by zooplankton compensated and kept phytoplankton biovolume lower than in the lake where predation by fishes on zooplankton occurred and phytoplankton biomass was greater.

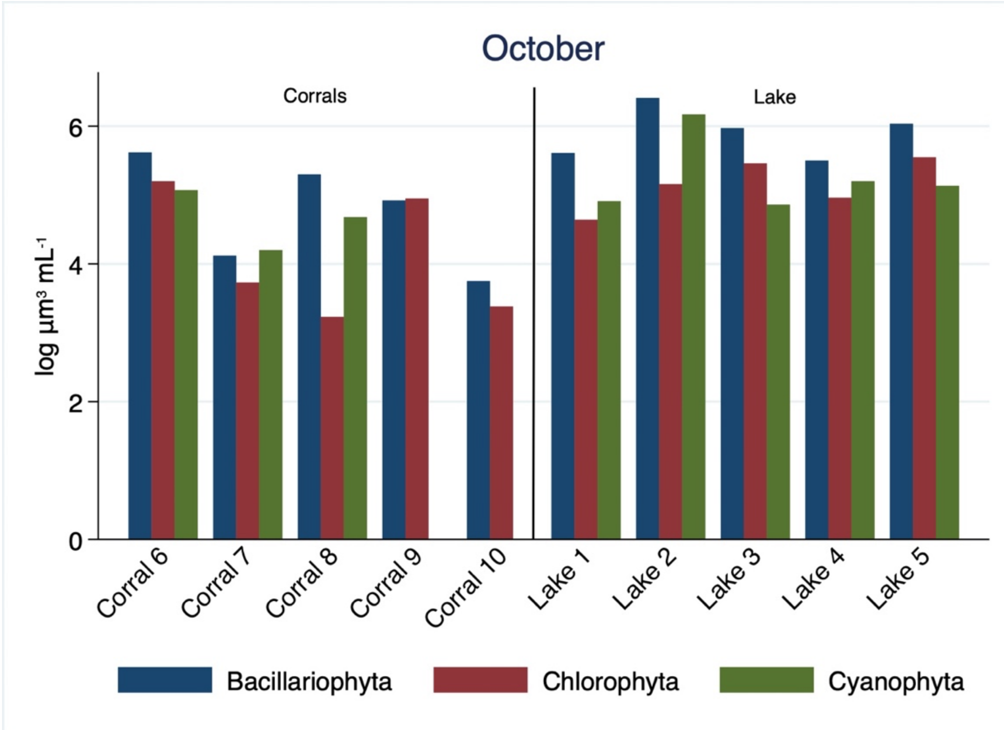


Figure 19. Comparisons of Bacillariophyta, Chlorophyta, and Cyanophyta biovolumes (log (µm³ mL⁻¹)) corrals vs. lake from October 11, 2022.

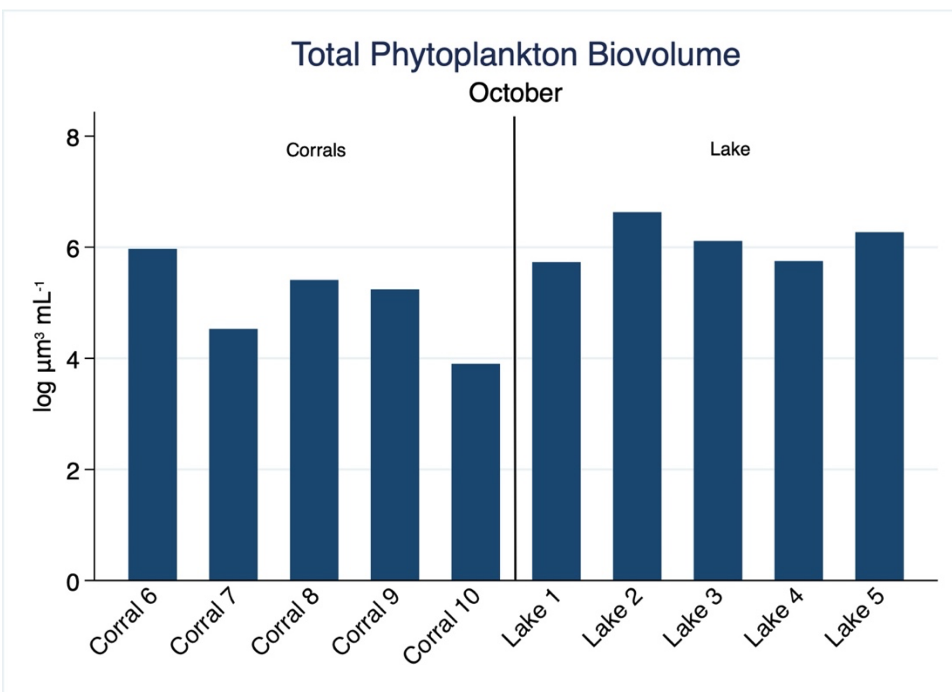


Figure 20. Comparisons of phytoplankton biovolumes (log (µm³ mL⁻¹)) corrals vs. lake from October 11, 2022.

Aphanizomenon flosaquae only occurred in one lake sample and *Dolichospermum circinalis* only occurred in one corral (Corral 8) and one lake sample on October 11, 2022 (Table 20*)*. Other cyanophyte taxa biovolumes are in Table 20.

Table 20. Biovolumes (log (µm^3 mL$^-$1) of cyanophyte taxa found in the corrals and lake on October 11, 2022. Taxa names are in Table 3.

SiteCode	APFL	APIN	DOCI	MEGL	MESP	PHSP	SNLA	UNFC
Corral 10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Corral 6	0.00	0.00	0.00	0.00	0.00	4.16	5.07	0.00
Corral 7	0.00	4.20	0.00	0.00	0.00	0.00	0.00	0.00
Corral 8	0.00	0.00	4.35	0.00	0.00	0.00	0.00	4.40
Corral 9	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Lake 1	0.00	4.89	0.00	3.42	0.00	0.00	0.00	0.00
Lake 2	6.09	4.59	5.34	0.00	3.91	0.00	0.00	0.00
Lake 3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Lake 4	0.00	5.20	0.00	0.00	0.00	0.00	0.00	0.00
Lake 5	0.00	4.89	0.00	0.00	4.03	0.00	0.00	0.00

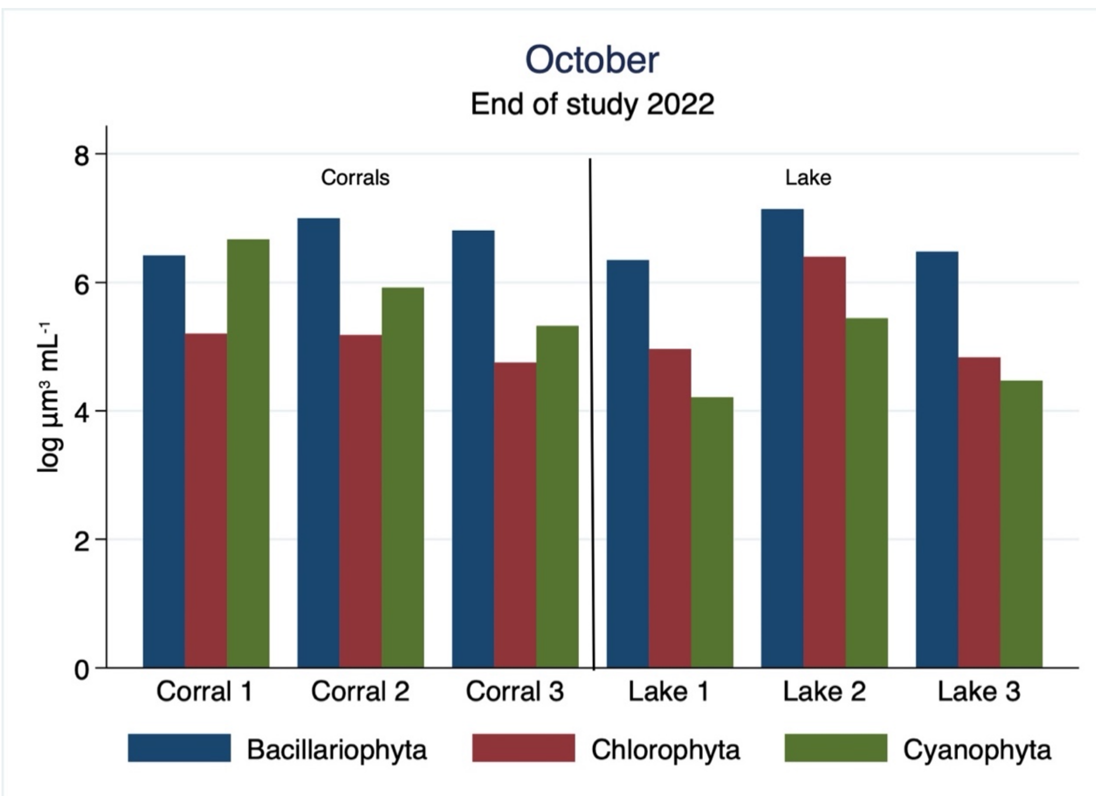


Figure 21. Comparisons of Bacillariophyta, Chlorophyta, and Cyanophyta biovolumes (log (µm^3 mL$^-$1) between inside corrals and lake on October 4, 2022. no significant difference for any division between corrals and lake.

Phytoplankton Taxa Assemblages

Seasonal

Nonmetric multidimensional scaling (NMS) showed that there was a seasonal progression in phytoplankton assemblages and assemblages differed by month (Figure 22). The best fit NMS model was a 3-dimensional solution using a Relative Sorenson distance measure that generated a final stress = 13.34, final instability = 0.006, at 100 iterations. Axis 1 $R^2 = 0.41$, Axis 2 $R^2 = 0.25$, Axis 3 $R^2 = 0.18$ for total $R^2 = 0.84$. Caution is needed to interpret this NMS model as locations of sample sites and taxa are not exact (McCune and Mefford 2011). However, Multiple Response Permutation Procedure (MRPP) provided strong evidence that assemblages differed each month (MRPP $A = 0.20$, $p < 0.001$) and pairwise comparisons between all months were <= 0.05. Complete NMS and MRPP results are available upon request.

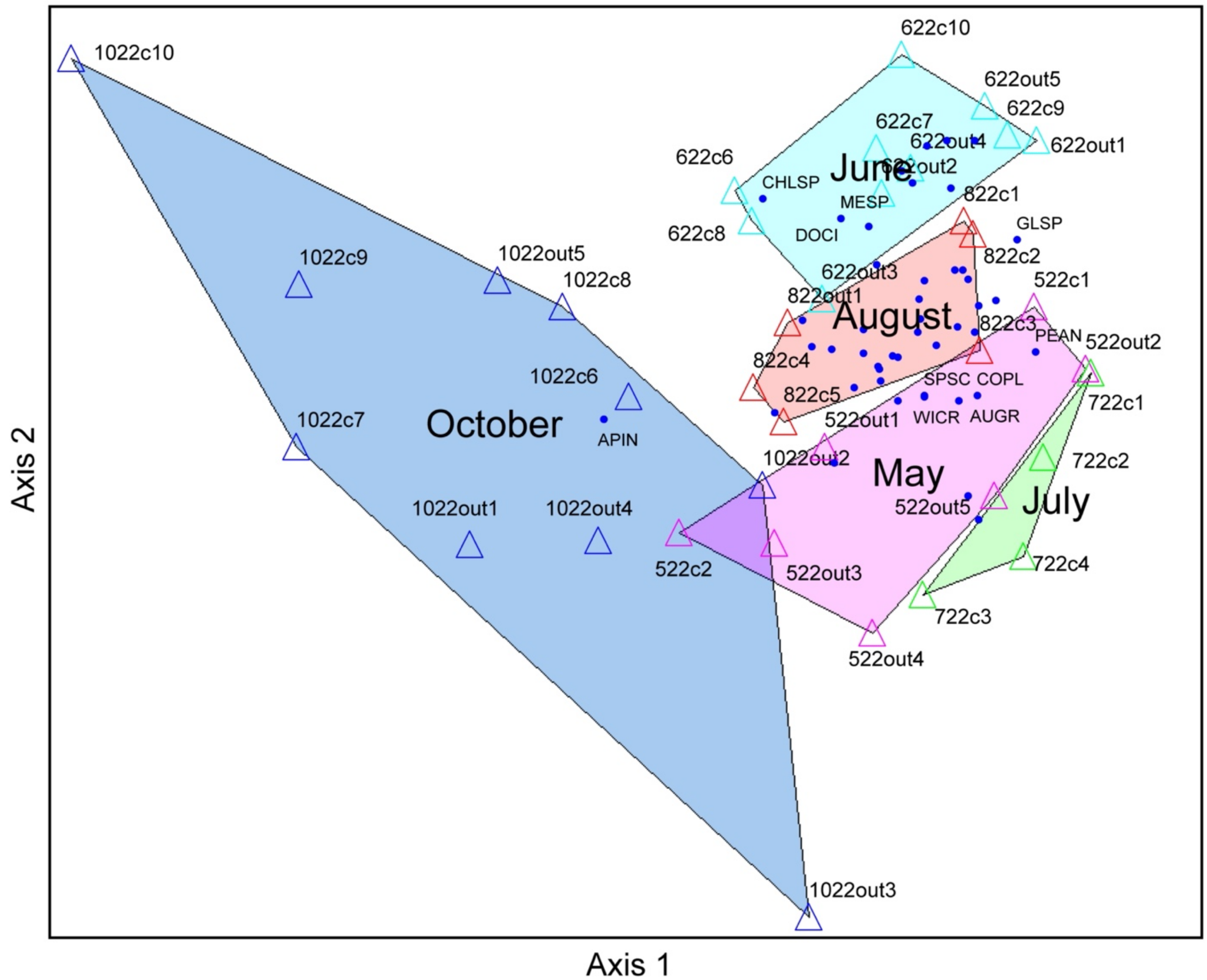


Figure 22. NMS Axis 1 and Axis 2 showing differences in phytoplankton taxa assemblages among months. Only Axis 1 and Axis two figure are presented.

May and June

Corrals vs. Lake

No useful NMS model was found for May and June phytoplankton taxa assemblages. MRPP for May taxa assemblages provided no evidence for differences inside and outside shallow corrals (MRPP *A* = -0.07, p = 0.83), although MRPP for June taxa provided some evidence for differences in assemblages inside and outside deep (open water) corrals (MRPP *A* = 0.06, p = 0.08). MRPP results available upon request.

October

Corrals vs. Lake

Nonmetric multidimensional scaling (NMS) clearly showed that phytoplankton assemblages differed between the lake and within the corrals (Figure 23 and Figure 25). The best fit NMS model was a 2-dimensional solution with a final stress = 7.12, final instability < 0.001, at 57 iterations. Axis 1 R^2 = 0.72, Axis 2 R^2 = 0.016 for total R^2 = 0.88. Interpretation of this NMS model is straightforward with very little interpretation error (McCune and Mefford 2011). Multiple Response Permutation Procedure (MRPP) provided evidence that assemblages differed between the lake and inside the corrals in October (MRPP *A* = 0.04, p = 0.07). Complete NMS and MRPP results available upon request.

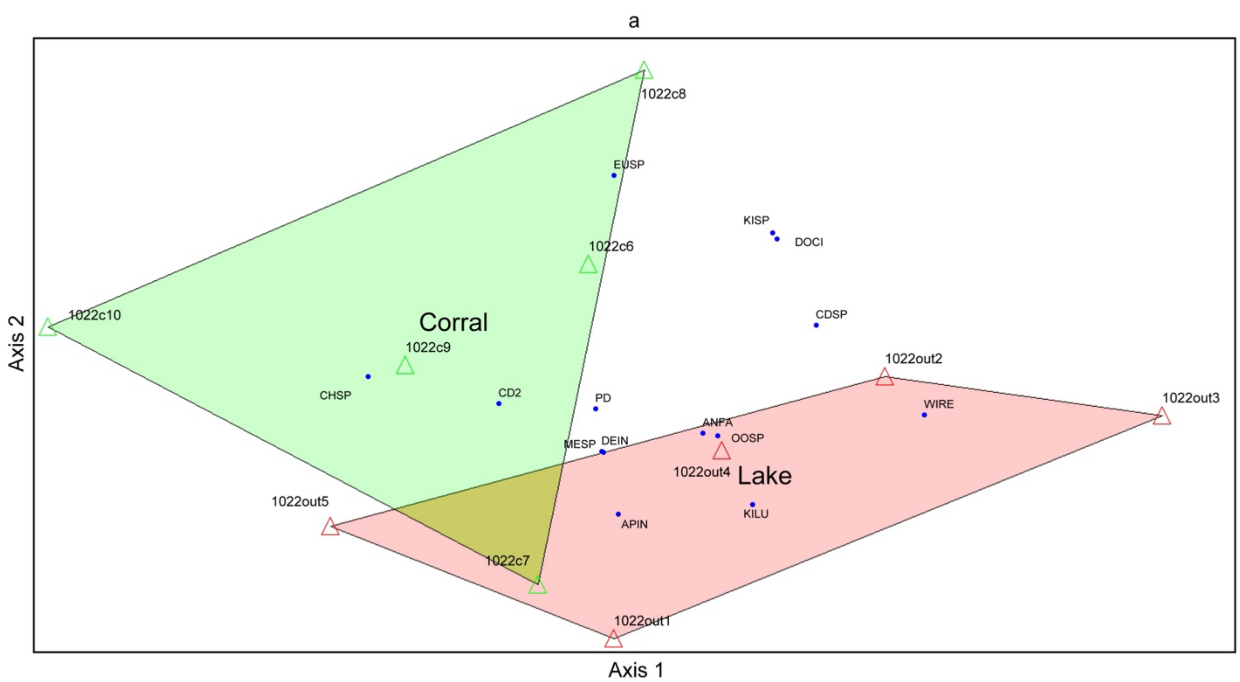


Figure 23.

Phytoplankton Divisions

Seasonal

The best fit NMS model using a Relative Sorensen distance measure was a 2-dimensional solution with a final stress = 7.04, final instability < 0.001, at 30 iterations. Axis 1 R^2 = 0.83, Axis 2 R^2 = 0.13 for total R^2 = 0.95. NMS based on phytoplankton divisions (e.g., Cyanophyta etc.) showed that phytoplankton assemblages mostly differed between months except October had much overlap will all months. (Figure 24). Interpretation of this NMS model is straightforward with little interpretable error (McCune and Mefford 2011). Multiple Response

Permutation Procedure (MRPP) provided strong evidence that assemblages differed (MRPP *A* = 0.19, $p < 0.001$). MRPP pairwise comparisons showed that assemblages differed between most months except May vs August, May vs. October, and August vs. October. Complete NMS and MRPP results available upon request.

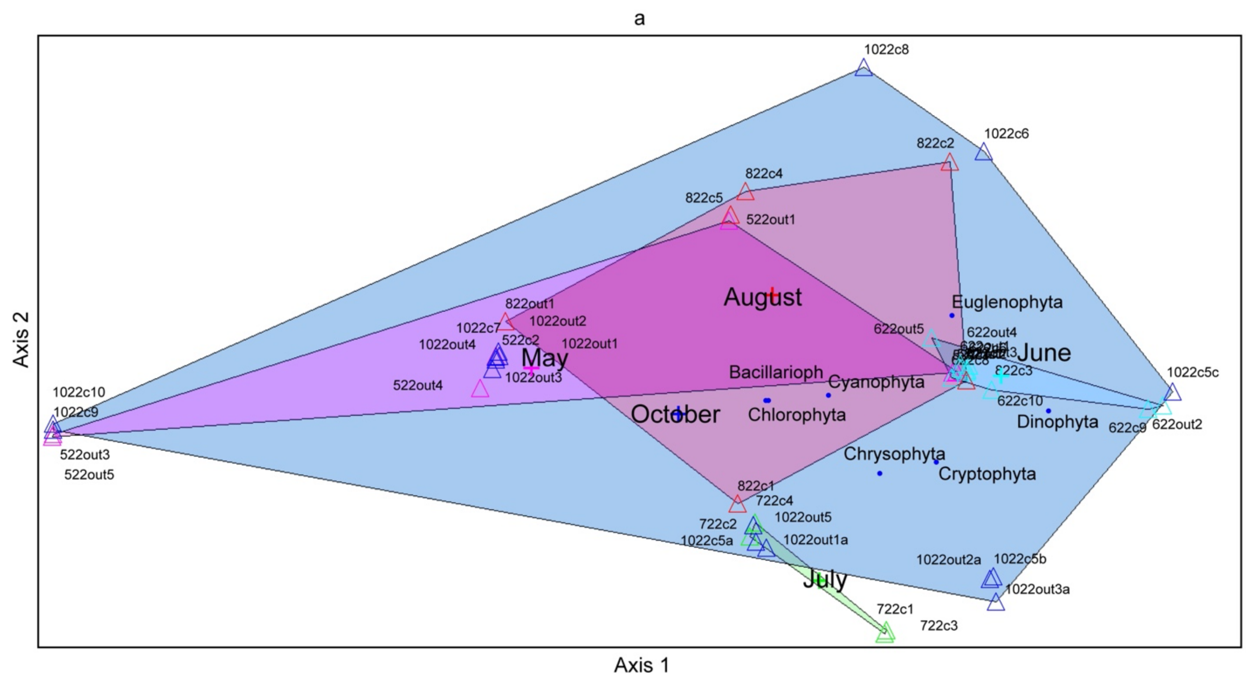


Figure 24.

October Divisions

Corrals vs. Lake

NMS based on phytoplankton divisions (e.g., Cyanophyta etc.) showed that phytoplankton assemblages differed inside and outside of corrals in October (Figure 25). The best fit NMS model using a Morisita-Horn distance measure was a 2-dimensional solution with a final stress = 0.01, final instability < 0.001, at 35 iterations. Axis 1 $R^2 = 0.78$, Axis 2 $R^2 = 0.18$ for total $R^2 =$ 0.96. Interpretation of this NMS model is straightforward with little interpretable error (McCune and Mefford 2011). Multiple Response Permutation Procedure (MRPP) provided strong evidence that assemblages differed inside and outside of corrals (MRPP *A* = 0.12, p =0.01). Complete NMS and MRPP results available on request.

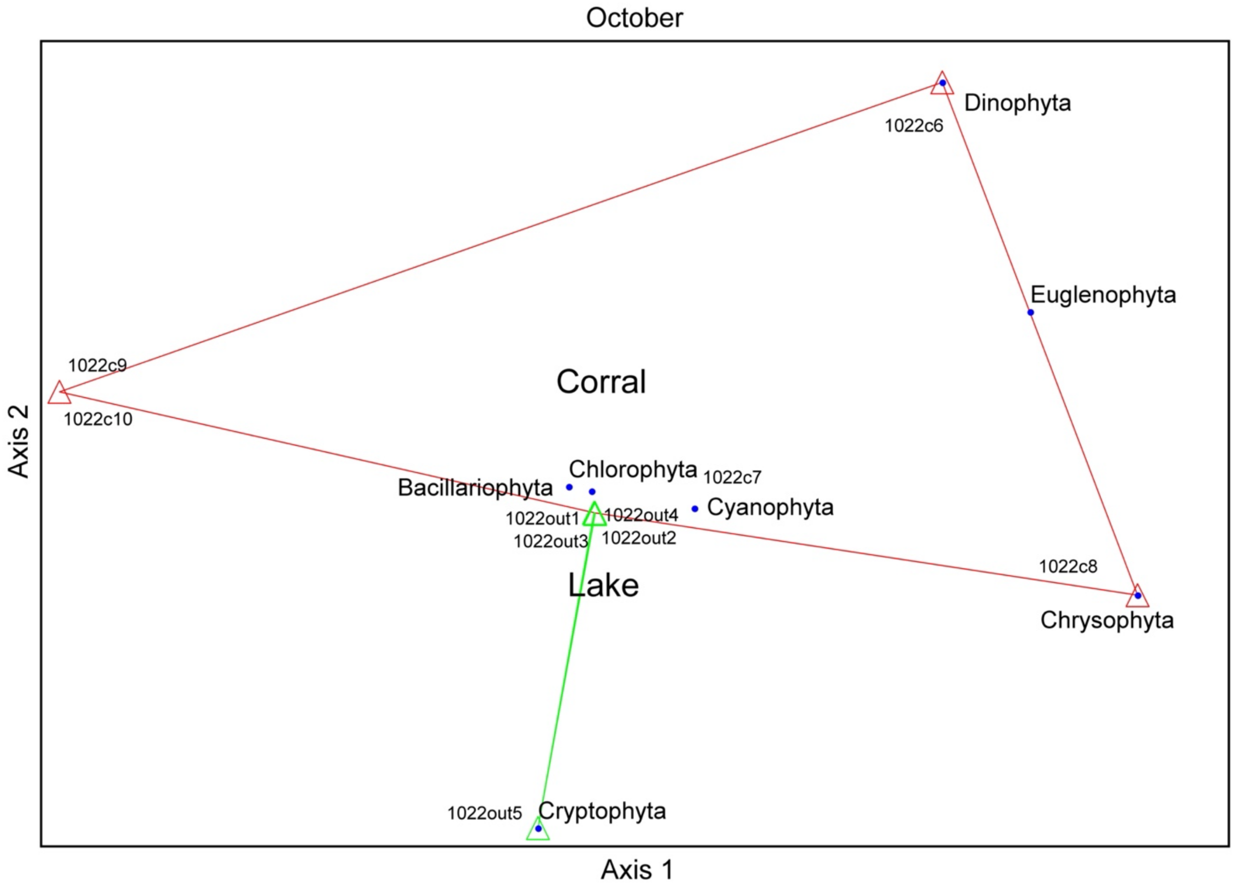


Figure 25. NMS ordination axis 1 and 2 of phytoplankton divisions from October 11, 2022, sampling event.

Zooplankton

May

As predicted, we found strong evidence that zooplankton abundances (individuals L^{-1}) were greater inside corrals than in the lake on May 17, 2022 (see following Tables and Figures). Zooplankton abundances did not seem to follow the same patterns as did phytoplankton biovolumes **(**log (μm^3 $mL^{-}1$) on May 17, 2022 (see section: Phytoplankton, May).

Aquatic ecologists often discuss zooplankton as groups, Orders, Families, or Taxa (species). All four groupings were analyzed in this report. There were only four zooplankton groups, orders, and families and seven abundant species on May 17, 2022, therefore results presented are very similar (see following Tables and Figures). The limited number of zooplankton taxa signifies a stressed ecosystem. Corral 1 (macrophytes and bivalves) was the only treatment corral that had zooplankton abundances less than or equal to lake abundances. This could be because of the ongoing stocking of macrophytes into the corral at this time but needs further investigation.

Table 21. Zooplankton taxa collected in mesocosm study May 17, 2022.

Group	Order	Family	Taxon
Copepods	Cyclopoida	Cyclopidae	*Acanthocyclops americanus* (imm)

Copepods	Cyclopoida	Cyclopidae	*Acanthocyclops americanus*
Copepods	Calanoida	Diaptomidae	Diaptomidae
Copepods	Calanoida	Diaptomidae	*Leptodiaptomus sicilis*
Copepods	Calanoida	Diaptomidae	*Leptodiaptomus siciloides*
Cladocerans	Cladocera	Daphniidae	*Ceriodaphnia dubia*
Cladocerans	Cladocera	Daphniidae	*Daphnia ambigua* sp. 2
Cladocerans	Cladocera	Daphniidae	*Daphnia mendotae*
Cladocerans	Cladocera	Daphniidae	*Daphnia pulex* gr.
Cladocerans	Cladocera	Chydoridae	Chydorus brevilabrus
Cladocerans	Cladocera	Sididae	*Diaphanosoma* cf. Heberti
Cladocerans	Cladocera	Bosminiidae	*Bosmina longirostris* complex
Rotifers	Plioma	Brachionidae	*Brachionus variabilis*

Group Level

Zooplankton group level analyses are presented in the following tables and graphs.

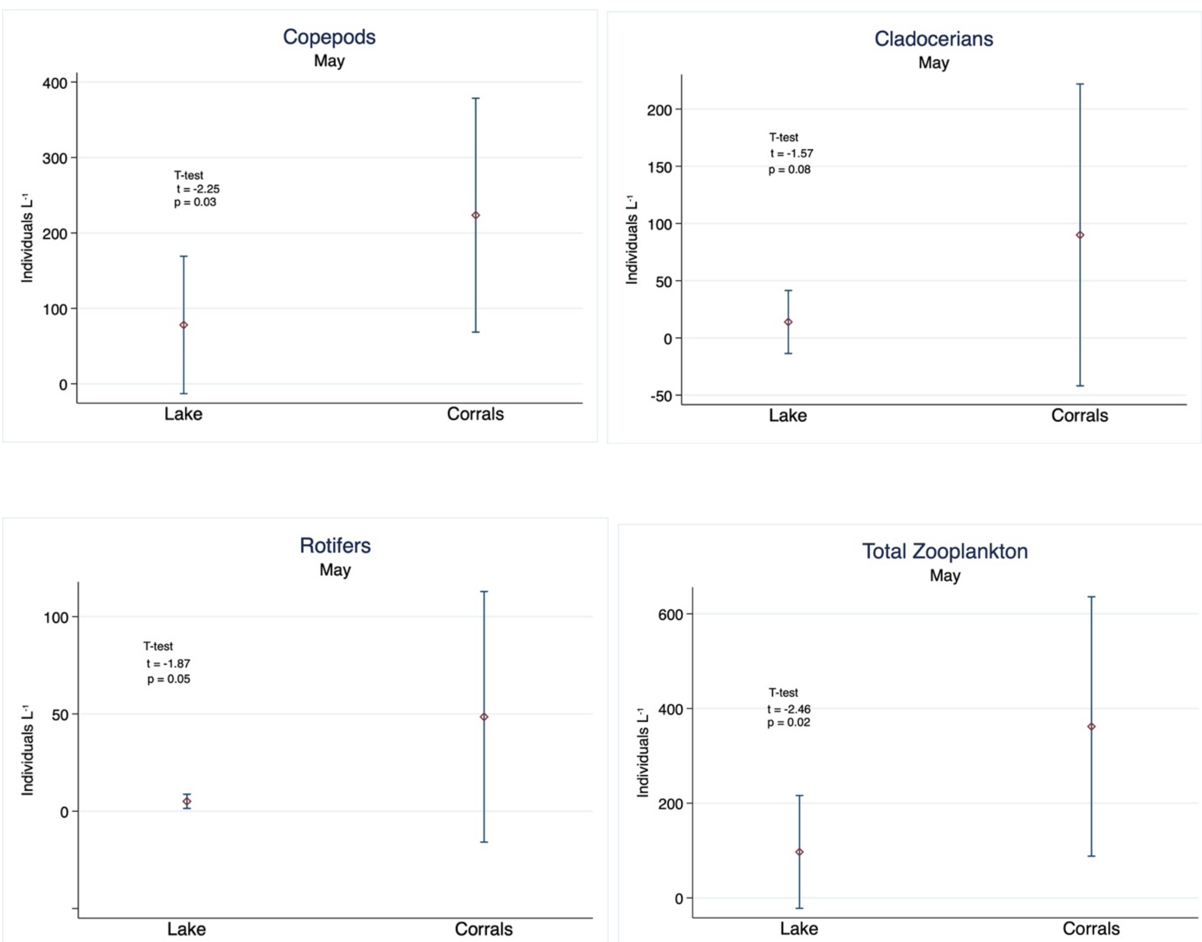


Figure 26. Mean and 95% CIs individuals L^{-1} for zooplankton groups (and total) copepods, cladocerans, rotifers, and total. T-tests results were based on Ha: difference in lake < corrals.

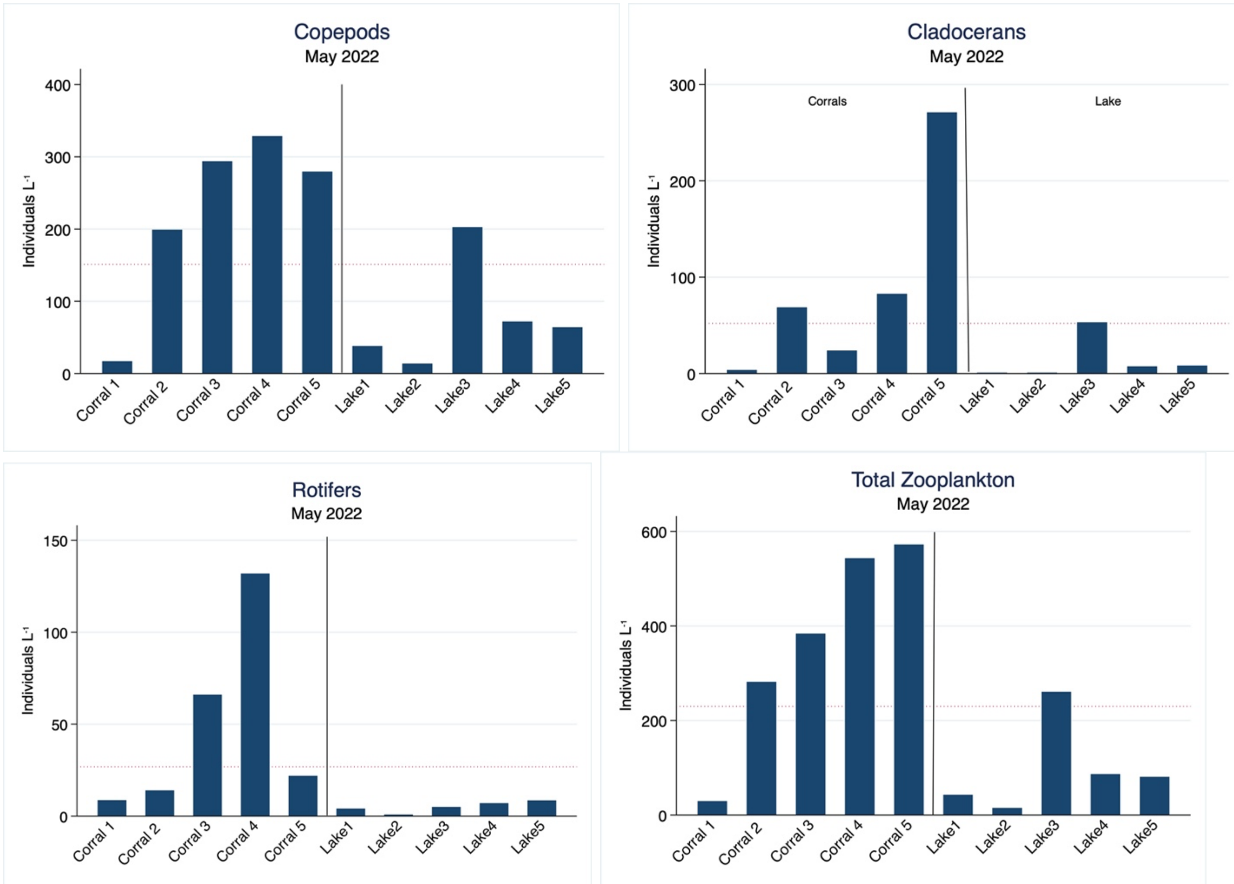


Figure 27. Comparisons of zooplankton Group abundances inside and outside corrals on May 17, 2022.

Table 22. Simple one-sample t-test comparisons between corral treatments and lake zooplankton group abundances (individuals L^{-1}). On May 17, 2022. Two hypotheses were tested: 1) abundances in each treatment corral was equal to the lake mean abundances (N = 5) and 2) zooplankton abundance in each treatment corral was less than the lake mean abundance. A 95% confidence level was used for t-tests. Italicized t- values were considered as evidence for differences.

Copepods	Ha: lake = corrals	Ha: lake < corrals
Corral 1	t = 1.86, p = 0.13	t = 1.86, p 0.93[a]
Corral 2	*t = -3.69, p 0.02*	*t = -3.69, p = 0.01*
Corral 3	*t = -6.58, p < 0.01*	*t = -6.58, p < 0.01*
Corral 4	*t = -7.64, p < 0.01*	*t = -7.64, p < 0.01*
Corral 5	*t = -6.14, p < 0.01*	*t = -6.14, p < 0.01*
Cladocerans		
Corral 1	t = 1.04, p = 0.36	t = 1.04, p = 0.82
Corral 2	*t = -5.51, p < 0.01*	*t = -5.51, p < 0.01*
Corral 3	t = -1.00, p = 0.37	t = -1.00, p = 0.19
Corral 4	*t = -6.94, p < 0.01*	*t = -6.94, p < 0.01*

Corral 5	*t = -25.92, p = 0.00*	*t = -25.92, p = 0.00*
Rotifers		
Corral 1	*t = -2.71, p = 0.05*	*t = -2.71, p = 0.03*
Corral 2	*t = -6.79, p < 0.01*	*t = -6.79, p < 0.01*
Corral 3	*t = -46.57, p < 0.01*	*t = -46.57, p < 0.01*
Corral 4	*t = -96.81, p = 0.00*	*t = -96.81, p = 0.00*
Corral 5	*t = -12.85, p < 0.01*	*t = -12.85, p < 0.01*

[a]*Ha:lake > corrals t = 1.86, p = 0.07*

Order Level

Zooplankton order level analyses are presented in the following tables and graphs.

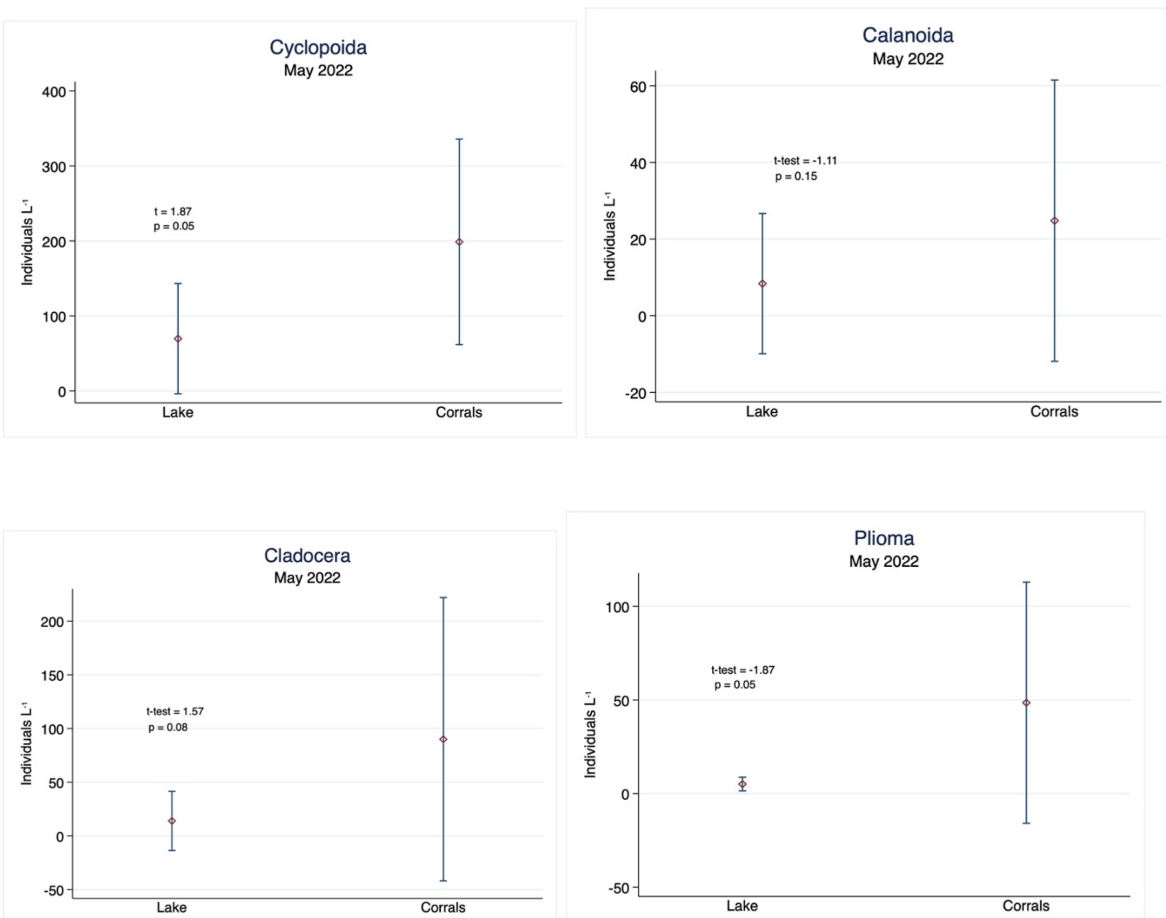


Figure 28. Mean and 95% CIs individuals L^{-1} for zooplankton Orders Cyclopoida, Calanoida, Cladocera, and Plioma. T-tests results were based on Ha: difference in lake < corrals. Totals are the same for groups in Figure 26.

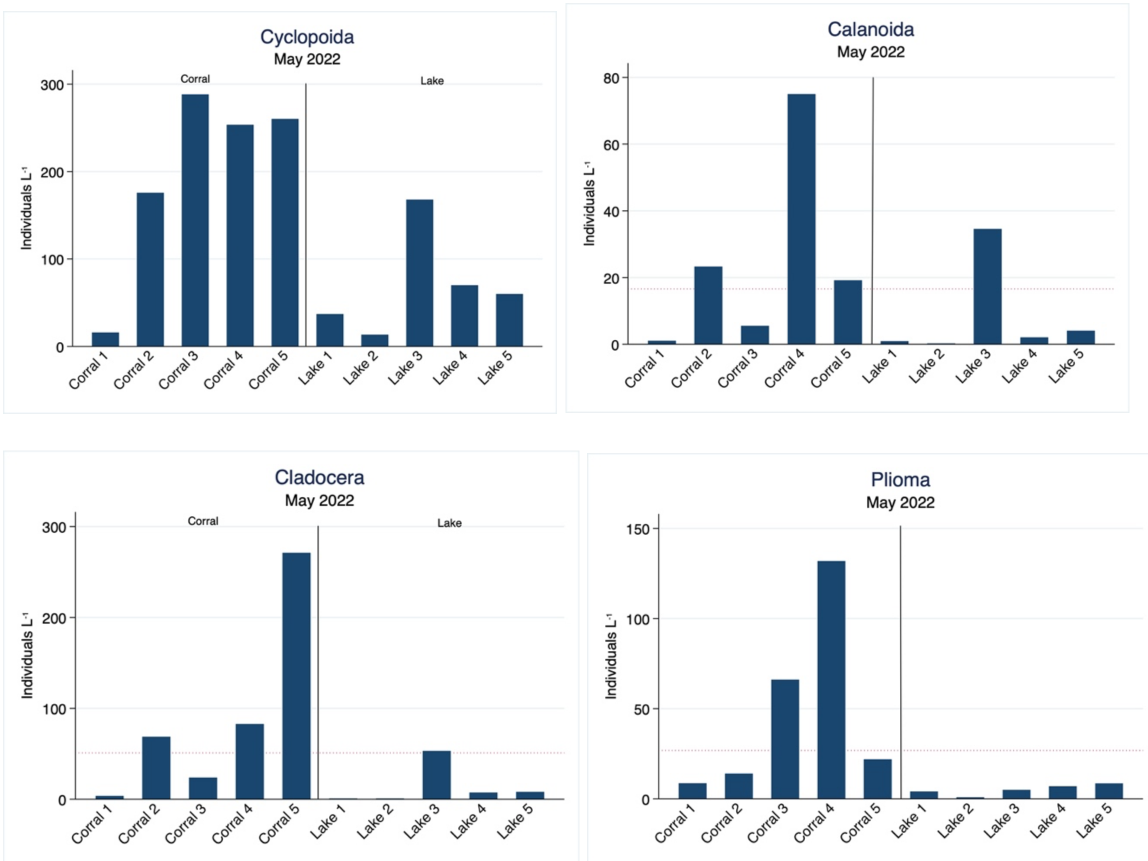


Figure 29. Comparisons of zooplankton Order abundances inside and outside corrals on May 17, 2022.

Table 23. Simple one-sample t-test comparisons between corral treatments and lake zooplankton Order abundances (individuals L^{-1}). On May 17, 2022. Two hypotheses were tested: 1) abundances in each treatment corral was equal to the lake mean abundances (N = 5) and 2) zooplankton abundance in each treatment corral was less than the lake mean abundance. A 95% confidence level was used for t-tests. Italicized t- values were considered as evidence for differences.

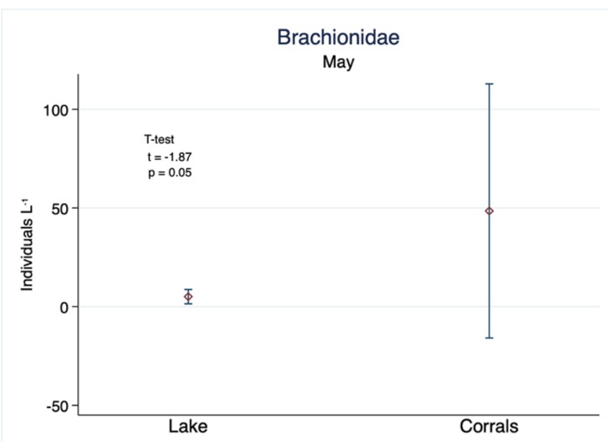
Cyclopoida	Ha: lake = corrals	Ha: lake < corrals
Corral 1	t = 2.03, p = 0.11	t = 1.86, p 0.94[a]
Corral 2	*t = -4.01, p 0.02*	*t = -4.01, p = 0.01*
Corral 3	*t = -8.26, p < 0.01*	*t = -8.26, p < 0.01*
Corral 4	*t = -6.95, p < 0.01*	*t = -6.95, p < 0.01*
Corral 5	*t = -7.20, p < 0.01*	*t = -7.20, p < 0.01*
Calanoida		
Corral 1	t = 1.11, p = 0.33	t = 1.11, p = 0.84
Corral 2	*t = -2.26, p = 0.09*	*t = -2.26, p = 0.04*
Corral 3	t = 0.44, p = 0.69	t = 0.44, p = 0.66
Corral 4	t = -10.12, p < 0.01	t = -10.12, p < 0.01
Corral 5	t = -1.64, p = 0.18	t = -1.64, p = 0.09

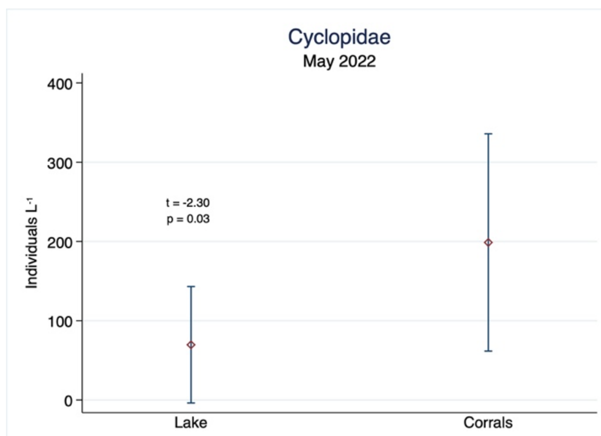
Cladocera		
Corral 1	t = 1.04, p = 0.36	t = 1.04, p = 0.82
Corral 2	*t = -5.51, p = 0.01*	*t = -5.51, p < 0.01*
Corral 3	t = -1.00, p = 0.37	t = -46.57, p = 0.19
Corral 4	*t = -6.94, p < 0.00*	*t = -6.94, p < 0.00*
Corral 5	*t = -25.92, p = 0.00*	*t = -25.92, p = 0.00*
Plioma		
Corral 1	*t = -2.70, p = 0.05*	*t = -2.70, p = 0.02*
Corral 2	*t = -6.79, p < 0.01*	*t = -6.79, p < 0.01*
Corral 3	*t = -46.58, p = 0.00*	*t = -46.58, p = 0.00*
Corral 4	*t = -96.12, p = 0.00*	*t = -96.12, p = 0.00*
Corral 5	*t = -12.85, p < 0.01*	*t = -12.85, p < 0.01*

[a]*Ha:lake > corrals t = 2.03, p = 0.06*

Family Level

Zooplankton family level analyses are presented in the following tables and graphs.





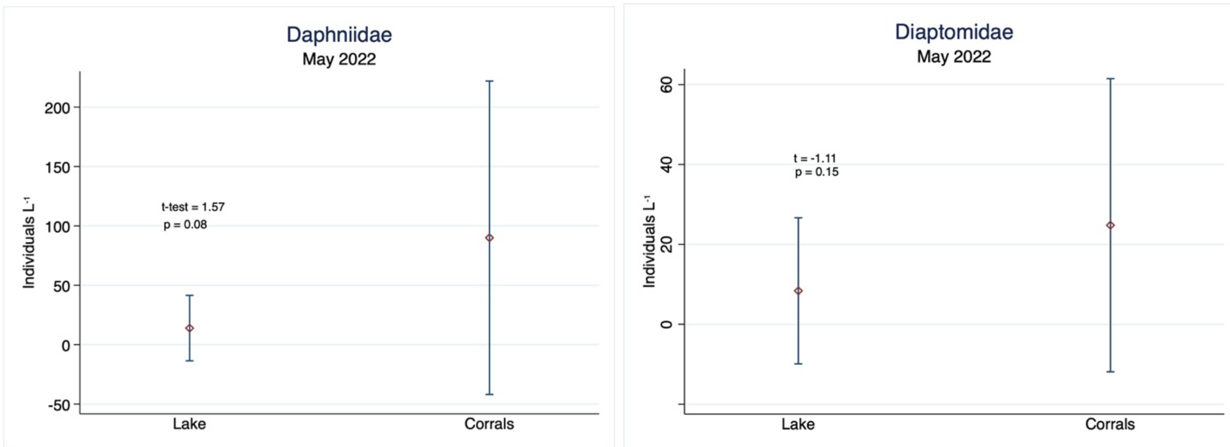


Figure 30. Mean and 95% CIs individuals L^{-1} for zooplankton Families Brachionidae, Cyclopidae, Daphniidae, and Diaptomidae. T-tests results were based on Ha: difference in lake < corrals. Totals are the same for groups in Figure 26.

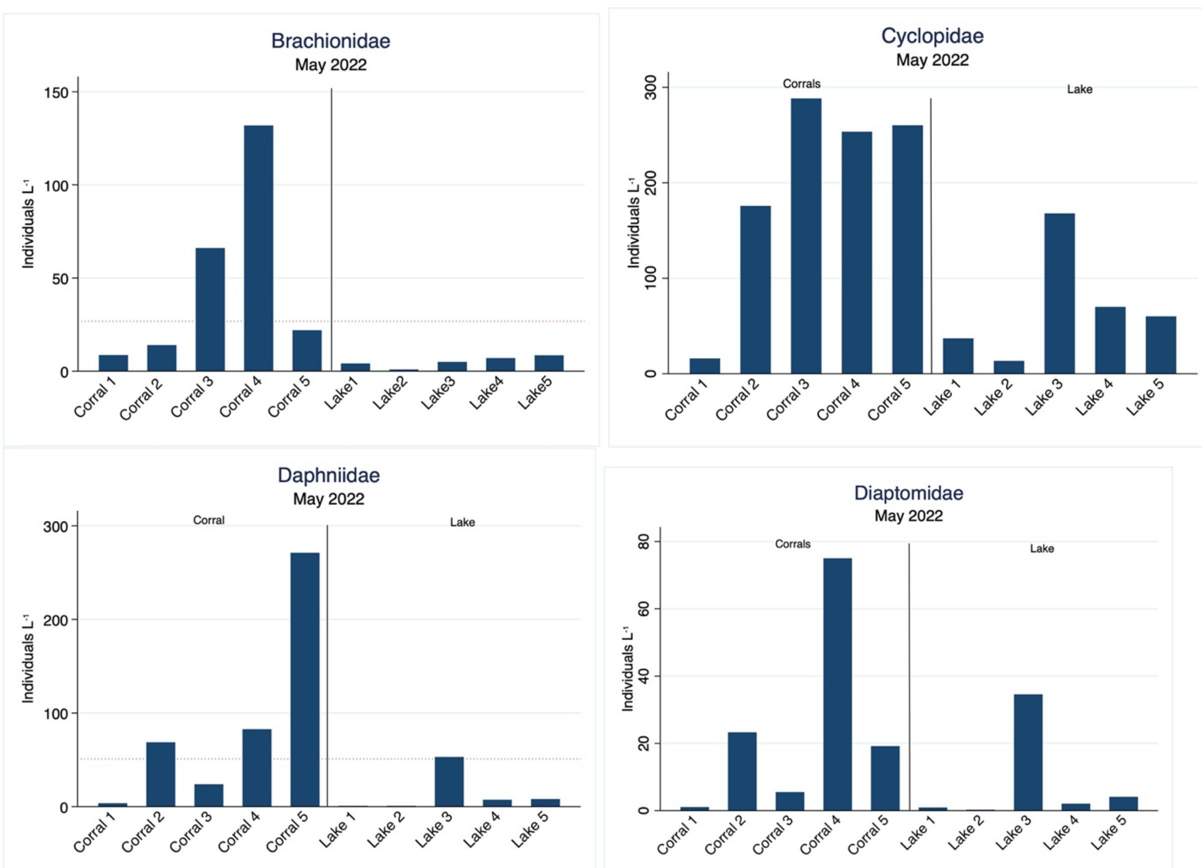


Figure 31. Comparisons of zooplankton Family abundances inside and outside corrals on May 17, 2022.

Table 24. Simple one-sample t-test comparisons between corral treatments and lake zooplankton Family abundances (individuals L^{-1}) on May 17, 2022. Two hypotheses were tested: 1) abundances in each treatment corral was equal to the lake mean abundances (N = 5) and 2) zooplankton abundance in each treatment corral was less than the lake mean abundance. A 95% confidence level was used for t-tests. Italicized t- values were considered as evidence for differences.

	Ha: lake = corrals	Ha: lake < corrals
Brachionidae		

Corral 1	$t = -2.71, p = 0.05$	$t = -2.71, p = 0.03$
Corral 2	$t = -6.79, p < 0.01$	$t = -6.79, p < 0.01$
Corral 3	$t = -46.57, p < 0.01$	$t = -46.57, p < 0.01$
Corral 4	$t = -96.81, p = 0.00$	$t = -96.81, p = 0.00$
Corral 5	$t = -12.85, p < 0.01$	$t = -12.85, p < 0.01$
Cyclopidae		
Corral 1	$t = 2.03, p = 0.11$	$t = 2.03, p = 0.94$[a]
Corral 2	$t = -4.01, p = 0.02$	$t = -4.01, p = 0.01$
Corral 3	$t = -8.26, p < 0.01$	$t = -8.26, p < 0.01$
Corral 4	$t = -6.95, p < 0.01$	$t = -6.95, p < 0.01$
Corral 5	$t = -7.20, p < 0.01$	$t = -7.20, p < 0.01$
Daphniidae		
Corral 1	$t = 1.04, p = 0.36$	$t = 1.04, p = 0.82$
Corral 2	$t = -5.51, p = 0.01$	$t = -5.51, p < 0.01$
Corral 3	$t = -1.00, p = 0.37$	$t = -46.57, p = 0.19$
Corral 4	$t = -6.94, p < 0.00$	$t = -6.94, p < 0.00$
Corral 5	$t = -25.92, p = 0.00$	$t = -25.92, p = 0.00$
Diaptomidae		
Corral 1	$t = 1.11, p = 0.32$	$t = 1.11, p = 0.84$
Corral 2	$t = -2.26, p = 0.09$	$t = -2.26, p = 0.04$
Corral 3	$t = 0.44, p = 0.69$	$t = 0.44, p = 0.66$
Corral 4	$t = -10.12, p < 0.01$	$t = -10.12, p <0.01$
Corral 5	$t = -1.64, p = 0.18$	$t = -1.64, p = 0.09$

[a]Ha: Lake > corral $t = 2.03, p = 0.06$

Taxa Level

All of the common zooplankton species were more abundant within the corrals than in the lake on May 17, 2022 (see following figures).

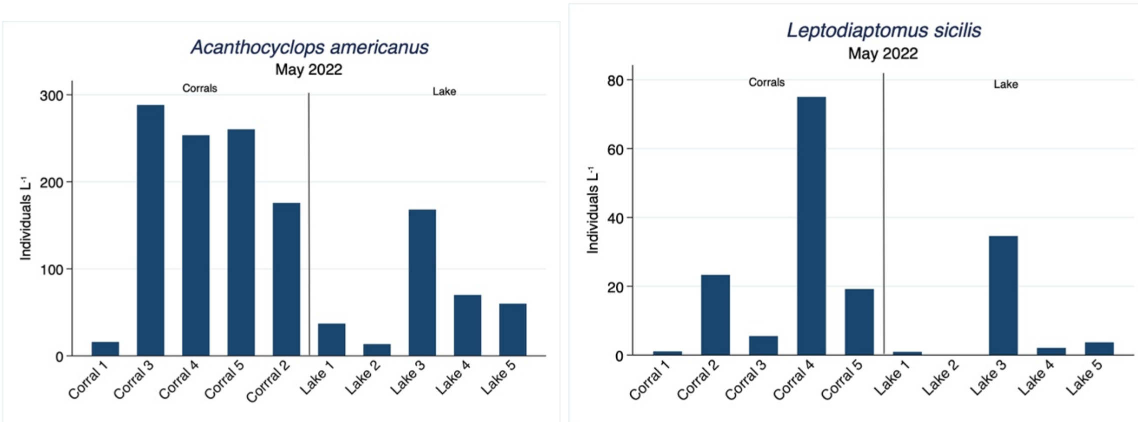


Figure 32. One species of Cyclopidae copepod, Acanthocyclops americanus and one species of Diaptomidae, calanoid copepod, Leptodiaptomus sicilis occurred in abundance on May 17/18, 2022.

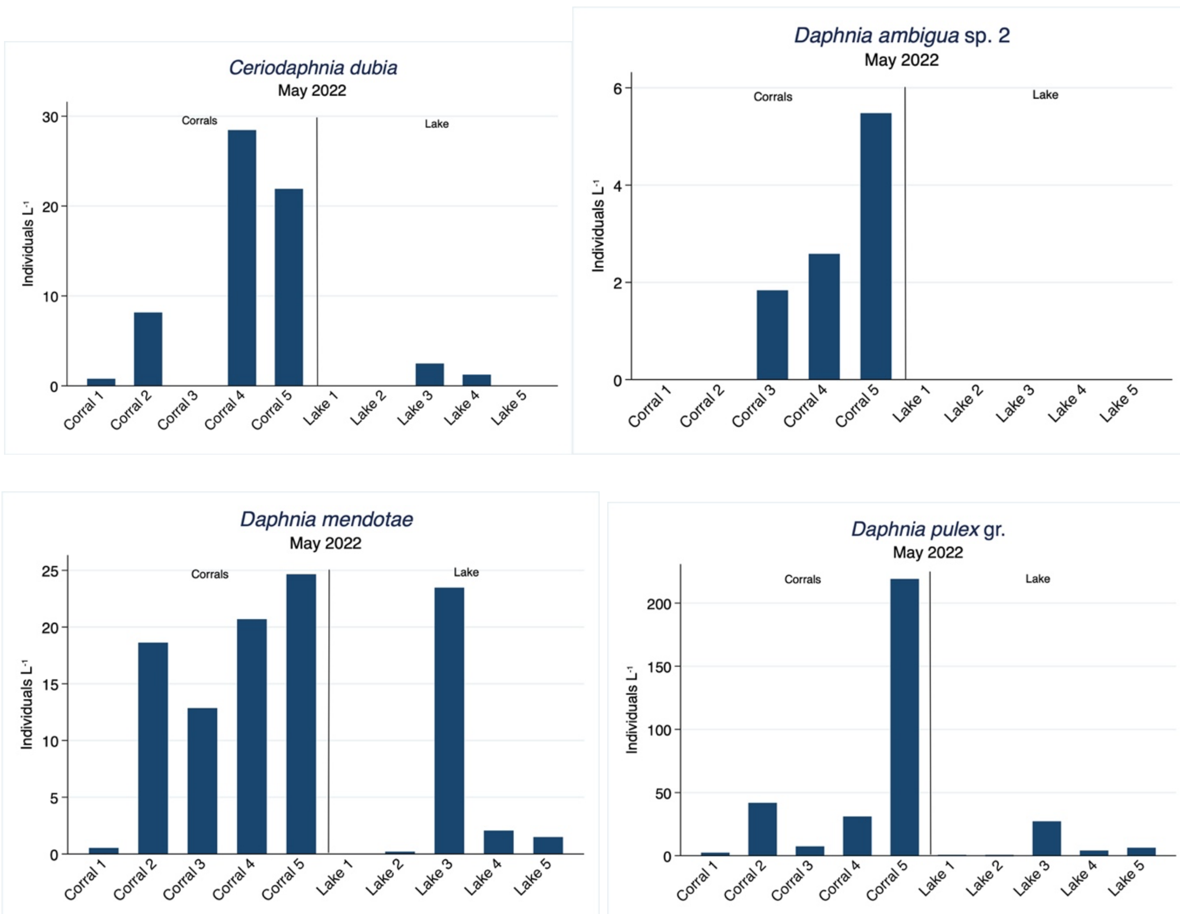


Figure 33. Four species of cladocerans in Family Daphniidae occurred in abundance on May 17-18, 2022, Ceriodaphnia dubia, Daphnia ambigua, D. mendotae, and D. pulex gr.

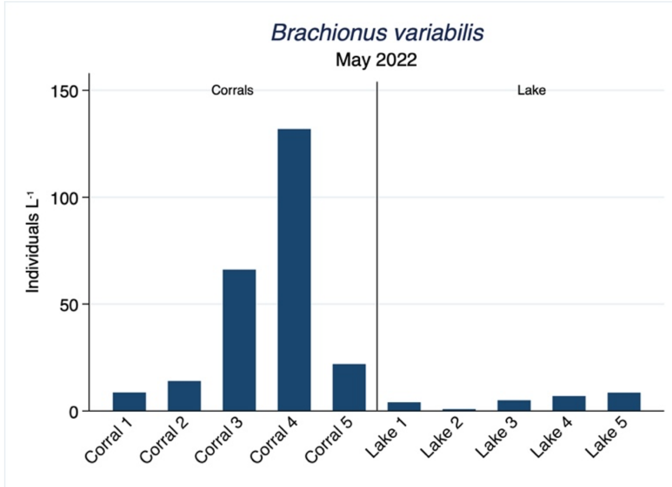


Figure 34. One species of rotifer, Brachionus variabilis (Family Brachionidae, Order Plioma) occurred in abundance more so in corrals than the lake.

Four additional taxa were collected but only occurred at low abundance and only in one sample, *Leptodiaptomus siciloides*, *Chydorus brevilabrus*, *Diaphanosoma* cf. Heberti, and *Bosmina longirostris* complex.

June

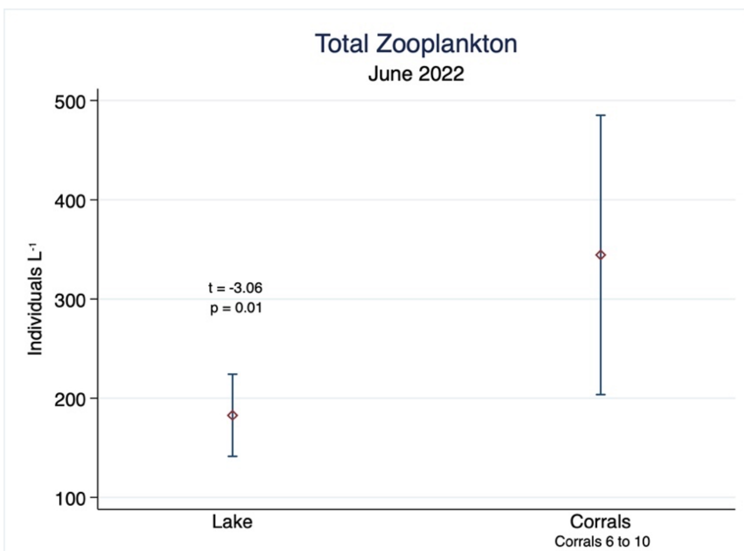


Figure 35. Comparison of total zooplankton abundance (L-1) inside and outside of open water corrals (6 to 10) on June 23, 2022. Mean and 95% CIs. T-test results based on one tailed Ha: lake abundance > corral abundance.

Table 25. Zooplankton Groups Copepod, Cladoceran, Rotifer, and total abundances L^{-1} in the lake and in Corrals 6 to 10 on June 23, 2022. Ha: Copepod Corrals > Lake abundance, t = -0.05, p = 0.48; Ha: Cladoceran Corrals < Lake abundance, t = -3.42, p =0.01; Ha: Rotifer corrals > lake abundance, t = -0.72, p = 0.25.

Site Code	Copepod	Cladoceran	Rotifer	Total
Lake 1	40.85	79.99	11.35	132.18
Lake 2	74.59	113.90	18.14	206.63

Lake 3	78.01	108.86	18.14	205.01
Lake 4	90.77	68.08	6.05	164.89
Lake 5	55.34	138.79	10.89	205.01
Corral 6	46.37	334.64	26.21	407.21
Corral 7	57.83	174.63	15.88	248.33
Corral 8	48.99	322.94	1.81	373.74
Corral 9	70.56	130.02	9.07	209.65
Corral 10	120.20	328.84	34.02	483.05

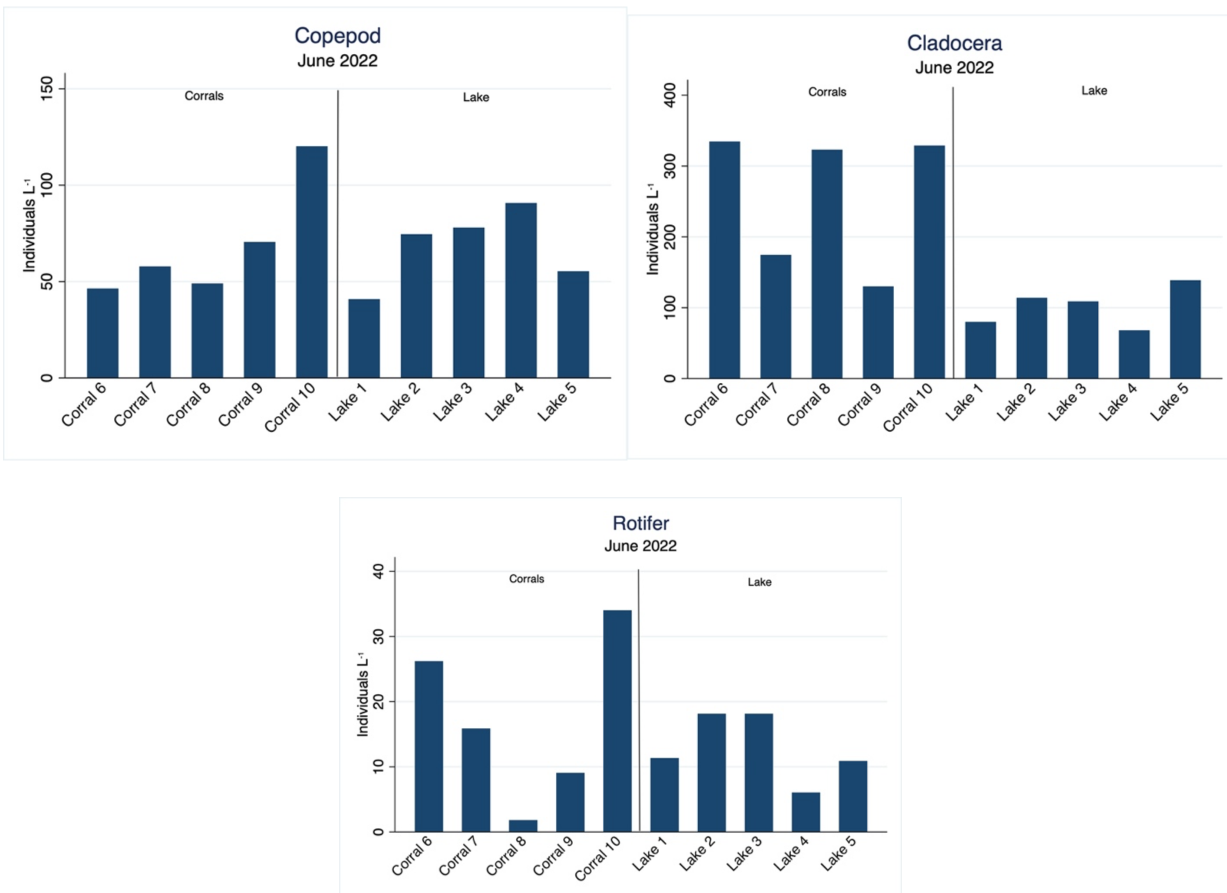


Figure 36. Comparisons of zooplankton Group abundances inside and outside corrals on June 23, 2022.

Table 26. Simple one-sample t-test comparisons between corral treatments and lake zooplankton Group abundances (individuals L^{-1}) on June 23, 2022. Two hypotheses were tested: 1) abundances in each treatment corral was equal to the lake mean abundances (N = 5) and 2) zooplankton abundance in each treatment corral was less than the lake mean abundance. A 95% confidence level was used for t-tests. Bold t- values were considered as evidence for differences.

	Ha: lake = corrals	*Ha*: lake < corrals
Copepod		
Corral 6	**t = 2.44, p = 0.07**	t = -2.71, p = 0.96[a]

Corral 7	t = 1.14, p = 0.32	t = 1.14, p = 0.84
Corral 8	t = 2.14, p = 0.10	t = 2.14, p = 0.95[b]
Corral 9	t = -0.30, p = 0.78	t = -0.30, p = 0.39
Corral 10	**t = -5.92, p < 0.01**	**t = -5.62, p < 0.01**
Cladocera		
Corral 6	**t = -18.46, p < 0.01**	**t = -18.46, p < 0.01**
Corral 7	**t = -5.77, p < 0.01**	**t = -5.77, p < 0.01**
Corral 8	**t = -17.53, p < 0.01**	**t = -17.53, p < 0.01**
Corral 9	**t = -2.23, p < 0.09**	**t = -2.23, p < 0.04**
Corral 10	**t = -5.71, p < 0.01**	**t = -5.71, p < 0.01**
Rotifer		
Corral 6	**t = -5.71, p < 0.01**	**t = -5.71, p < 0.01**
Corral 7	t = -1.27, p = 0.27	t = -1.27, p = 0.14
Corral 8	**t = 4.77, p = 0.01**	t = 4.77, p = 0.99[c]
Corral 9	t = 1.65, p = 0.17	t = 1.65, p = 0.91[d]
Corral 10	**t = -9.01, p < 0.01**	**t = 9.01, p < 0.01**

[a]Ha: lake abundance > corral abundance, t = 2.44, p = 0.04. Note: Corral 6 had many juvenile carp that inadvertently entered corral.
[b]Ha: lake abundance > corral abundance, t = 2.14, p = 0.05. Note: Corral 8 had zooplanktivores.
[c]Ha: lake abundance > corral abundance, t = 4.77, p < 0.01. Note: Corral 8 had zooplanktivores.
[d]Ha: lake abundance > corral abundance, t = 1.65, p = 0.09. Note: Corral 9 possible treatment effect or subsampling effect. Needs further interpretation.

July

Results from zooplankton samples collected on July 28, 2022, in the shallow water corrals and lake. Because only one lake sample was collected on this date, we could not find evidence of treatment effects on zooplankton.

Group

The following tables (Table 27, Table 28) show zooplankton groups and orders biovolume in shallow water corrals and lake on July 28, 2022.

Table 27. Copepod, cladoceran, rotifer, and total zooplankton abundances (L^{-1}) on July 28, 2022, inside and outside of corrals.

	Copepods	Cladocerans	Rotifers	Total
Lake 1	23.04	169.95	1.92	194.91
Corral 1	35.61	56.56	15.71	107.88
Corral 2	110.87	108.67	2.20	221.73
Corral 3	22.72	41.28	0.64	64.64
Corral 4	27.65	49.16	0.38	77.19
Corral 5	26.50	35.71	4.03	66.24

Order

Table 28. Calanoida, Cladocera, and Plioma abundances (L^{-1}) on July 28, 2022, inside and outside of corrals

	Calanoida	Cladocera	Plioma
Lake 1	23.04	169.95	1.92
Corral 1	35.61	56.56	15.71
Corral 2	110.87	108.67	2.20
Corral 3	22.72	41.28	0.64
Corral 4	27.65	49.16	0.38
Corral 5	26.50	35.71	4.03

Family

Family level zooplankton abundances (L^{-1}) on July 28, 2022, inside and outside of corrals are in Table 29.

Table 29. Family level zooplankton abundances (L^{-1}) on July 28, 2022, inside and outside of corrals

	Cyclopidae	Diaptomidae	Daphniidae	Moinidae	Bosminidae	Ilyocryptidae	Brachionidae	Asplanchnidae
Lake 1	23.04	0.00	26.88	141.14	0.96	0.96	1.92	0.00
Corral 1	35.61	0.00	28.28	22.52	5.24	0.52	15.71	0.00
Corral 2	110.87	0.00	61.47	46.10	1.10	0.00	1.10	1.10
Corral 3	22.72	0.00	26.24	14.40	0.64	0.00	0.64	0.00
Corral 4	27.27	0.38	27.27	21.89	0.00	0.00	0.38	0.00
Corral 5	26.50	0.00	19.01	16.71	0.00	0.00	3.46	0.58

August

By August we were able to document the cumulative effects of the corrals and treatments on zooplankton in both the shallow water corrals and deeper water corrals.

Shallow Water: Corrals 1 to 5

Groups

There was strong evidence that copepods, cladocerans, and rotifers were more abundant within the shallow water corrals (Corrals 1 to 5) than in the lake on August 16, 2022 (Table 30, Figure 37).

Table 30. Copepod, Cladoceran, Rotifer, and total zooplankton abundance (L^{-1}) on August 16, 2022.

Sample	Copepods	Cladocerans	Rotifers	Total
Lake 1	2.86	21.60	0.00	24.46
Lake 2	2.86	21.37	0.00	24.23
Lake 3	7.77	88.23	0.00	96.00
Lake 4	8.23	61.37	1.03	70.63
Lake 5	0.51	2.49	0.00	3.00
Corral 1	54.09	208.11	1.18	263.37

Corral 2	27.57	59.25	0.00	86.82
Corral 3	22.63	87.95	0.00	110.58
Corral 4	24.69	277.07	0.00	301.76
Corral 5	4.57	191.09	0.00	195.66

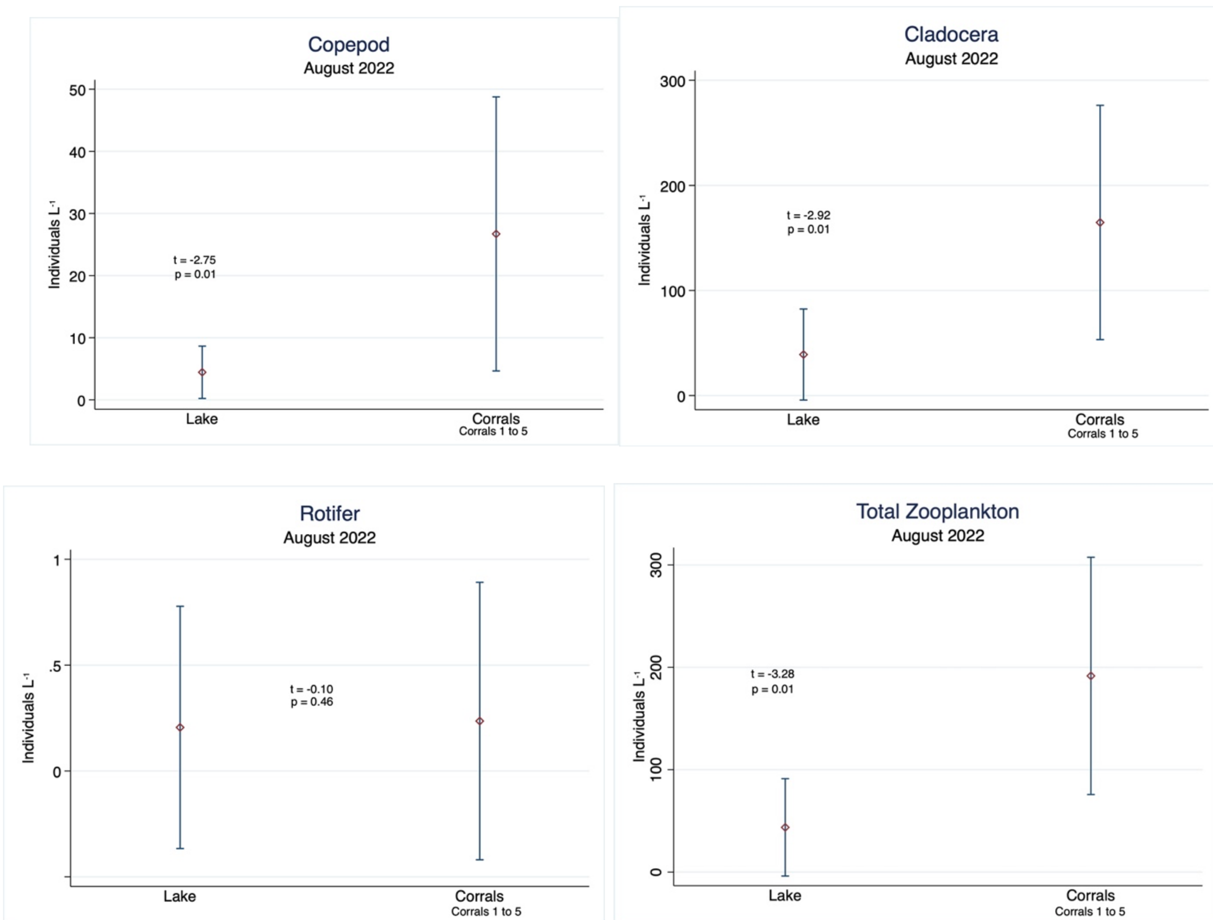


Figure 37. Comparison of Copepod, Cladocera, Rotifer, and total zooplankton abundance (L^{-1}) on August 16, 2022. Mean and 95% CIs. T-test one tailed Ha: lake abundance < corral abundance.

We found strong evidence that Corrals 1 to 4 had more copepods than the lake but no evidence that Corral 5 (one of the controls) had more copepods than the lake (Table 31) on August 16, 2022. We also found strong evidence that Corrals 1, 3, 4, and 5 had more cladocerans than did the lake but no evidence that Corral 2 did (Table 31). Corral 2 treatment was bivalves only and it is possible that bivalves filtered the cladocerans and not the copepods or that bivalves selectively fed on different phytoplankton taxa, which in turn altered zooplankton diet and disfavored cladocerans. Phytoplankton diversity was lower in Corrals 1 and 2 than the other corrals or lake in August. More research is needed.

Table 31. T-test comparisons of Copepod and Cladocera abundances (L^{-1}) between each corral and lake samples on August 16, 2022.

	Ha: lake = corrals	*Ha*: lake < corrals
Copepod		

Corral 1	**t = -32.77, p < 0.01**	**t = -32.77, p < 0.01**
Corral 2	**t = -15.27, p < 0.01**	**t = -15.27, p < 0.01**
Corral 3	**t = -12.00, p < 0.01**	**t = -12.00, p < 0.01**
Corral 4	**t = -13.36, p < 0.01**	**t = -13.36, p < 0.01**
Corral 5	t = -0.08, p = 0.94	t = -0.08, p = 0.47
Cladocera		
Corral 1	**t = -10.84, p < 0.01**	**t = -10.84, p < 0.01**
Corral 2	t = -1.30, p = 0.26	t = -1.30, p = 0.13
Corral 3	**t = -3.14, p = 0.04**	**t = -3.14, p = 0.02**
Corral 4	**t = -15.25, p < 0.01**	**t = 15.25, p < 0.01**
Corral 5	**t = -9.75, p < 0.01**	**t = -9.75, p < 0.01**

Rotifers only occurred in on lake sample at 1.03 individuals L^{-1} and one corral, Corral 1 at 1.18 individuals L^{-1}.

Order

Calanoida, Cladocera, and Plioma abundances (L^{-1}) abundances on August 16, 2022, are in Table 32.

Table 32. Calanoida, Cladocera, and Plioma abundances (L^{-1}) abundances on August 16, 2022.

	Calanoida	Cladocera	Plioma
Lake 1	2.86	21.60	0.00
Lake 2	2.86	21.37	0.00
Lake 3	7.77	88.23	0.00
Lake 4	8.23	61.37	1.03
Lake 5	0.51	2.49	0.00
Corral 1	54.09	208.11	1.18
Corral 2	27.57	59.25	0.00
Corral 3	22.63	87.95	0.00
Corral 4	24.69	277.07	0.00
Corral 5	4.57	191.09	0.00

Family

Zooplankton family abundances (L^{-1}) on August 16, 2022, are in Table 33.

Table 33. Zooplankton family abundances (L-1) on August 16, 2022.

	Cyclopidae	Diaptomidae	Daphniidae	Chydoridae	Moinidae	Sididae	Bosminidae	Brachionidae	Asplanchnidae
Lake 1	2.86	0.00	9.71	0.00	11.77	0.00	0.11	0.00	0.00

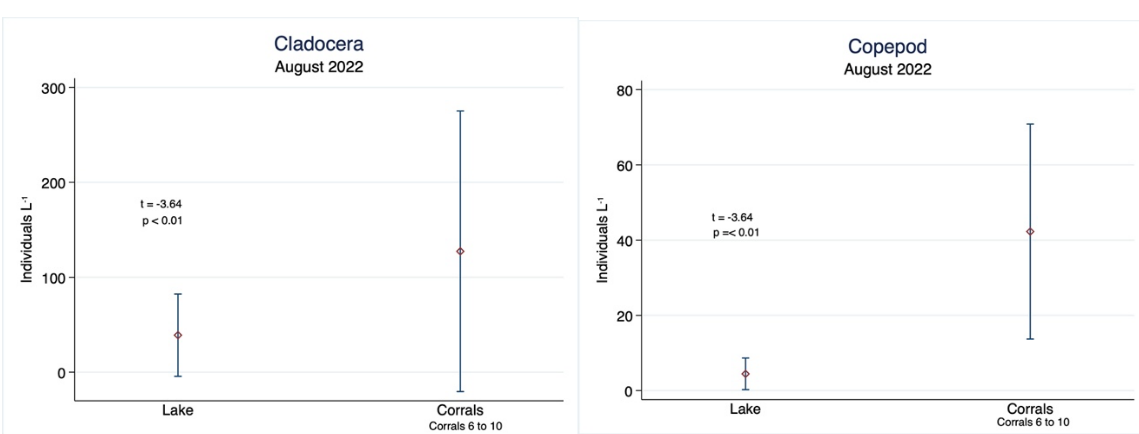
Lake 2	2.86	0.00	12.91	0.00	8.23	0.00	0.23	0.00	0.00
Lake 3	7.77	0.00	55.77	0.00	31.09	0.00	1.37	0.00	0.00
Lake 4	7.89	0.34	40.46	0.00	20.92	0.00	0.00	1.03	0.00
Lake 5	0.51	0.00	1.74	0.00	0.71	0.00	0.03	0.00	0.00
Corral 1	54.09	0.00	129.34	0.00	78.78	0.00	0.00	0.00	1.18
Corral 2	27.57	0.00	30.45	0.00	28.80	0.00	0.00	0.00	0.00
Corral 3	22.12	0.51	37.03	0.00	50.92	0.00	0.00	0.00	0.00
Corral 4	19.20	5.49	215.35	0.00	61.72	0.00	0.00	0.00	0.00
Corral 5	4.57	0.00	188.34	0.00	2.74	0.00	0.00	0.00	0.00

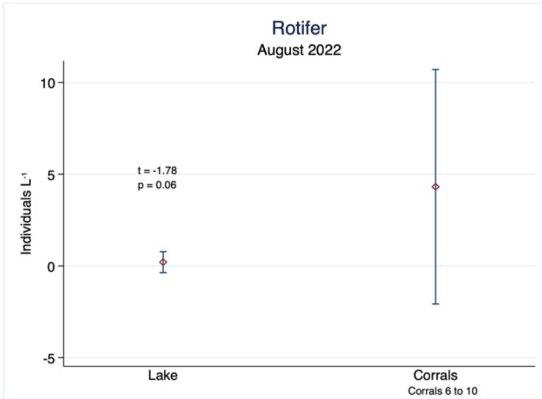
Deeper Water Corrals: Corrals 6 to 10
Group

There was strong evidence that zooplankton total abundance was greater in the corrals than in the lake on August 16, 2022 (Table 34, Figure 38). Of particular interest is that total zooplankton abundance was greatest in Corral 7, the nutrient addition corral (Table 34). Corral 7 zooplankton abundance (378.41 L^{-1}) was eight times greater than mean lake abundance (46.23 L^{-1}).

Table 34. Copepod, Cladoceran, Rotifer, and total zooplankton abundance (L^{-1}) in open water area on August 16, 2022.

	Copepods	Cladocerans	Rotifers	Total
Lake 1	2.86	21.60	0.00	24.46
Lake 2	2.86	21.37	0.00	24.23
Lake 3	7.77	88.23	0.00	96.00
Lake 4	8.23	61.37	1.03	70.63
Lake 5	0.51	2.49	0.00	3.00
Corral 6	40.74	14.26	4.07	59.07
Corral 7	66.99	311.42	0.00	378.41
Corral 8	17.75	35.21	13.09	66.05
Corral 9	64.20	163.05	3.06	230.30
Corral 10	21.73	112.72	1.36	135.81





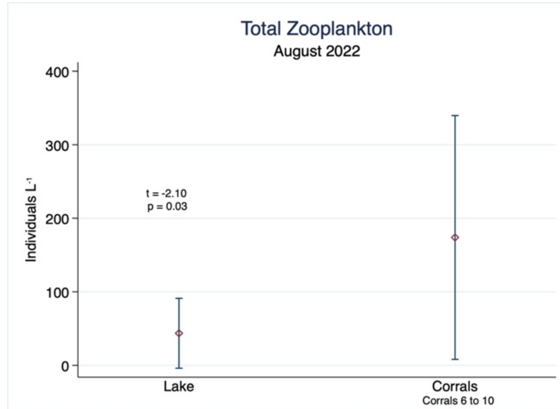


Figure 38. Comparisons of Cladocera, Copepod, Rotifer, and total zooplankton abundance (L^{-1}) inside and outside of corrals on August 16, 2022, in open water area. Mean and 95% CIs. T-test one tailed Ha: lake abundance > corral abundance.

Order

Calanoida, Cladocera, and Plioma abundances(L^{-1}) in open water area corrals and lake on August 16, 2022, are in Table 35.

Table 35. Calanoida, Cladocera, and Plioma abundances(L^{-1}) in open water area corrals and lake on August 16, 2022.

	Calanoida	Cladocera	Plioma
Lake 1	2.86	21.60	0.00
Lake 2	2.86	21.37	0.00
Lake 3	7.77	88.23	0.00
Lake 4	8.23	61.37	1.03
Lake 5	0.51	2.49	0.00
Corral 6	40.74	14.26	4.07
Corral 7	66.99	311.42	0.00
Corral 8	17.75	35.21	13.09
Corral 9	64.20	163.05	3.06

Family

Zooplankton family abundances (L^{-1}) in lake and open water area corrals on August 16, 2022, are in Table 36.

Table 36. Zooplankton family abundances (L^{-1}) in lake and open water area corrals on August 16, 2022.

	Cyclopidae	Diaptomidae	Daphniidae	Chydoridae	Moinidae	Sididae	Bosminidae	Brachionidae	Asplanchnidae
Lake 1	2.86	0.00	9.71	0.00	11.77	0.00	0.11	0.00	0.00
Lake 2	2.86	0.00	12.91	0.00	8.23	0.00	0.23	0.00	0.00
Lake 3	7.77	0.00	55.77	0.00	31.09	0.00	1.37	0.00	0.00
Lake 4	7.89	0.34	40.46	0.00	20.92	0.00	0.00	1.03	0.00
Lake 5	0.51	0.00	1.74	0.00	0.71	0.00	0.03	0.00	0.00

Corral 6	40.74	0.00	9.93	0.00	3.82	0.00	0.51	4.07	0.00
Corral 7	63.37	3.62	287.88	0.00	21.73	1.81	0.00	0.00	0.00
Corral 8	9.89	7.86	23.28	0.29	8.44	0.29	2.91	11.64	1.45
Corral 9	63.18	1.02	144.70	0.00	17.32	1.02	0.00	3.06	0.00
Corral 10	19.69	2.04	107.29	0.00	5.43	0.00	0.00	1.36	0.00

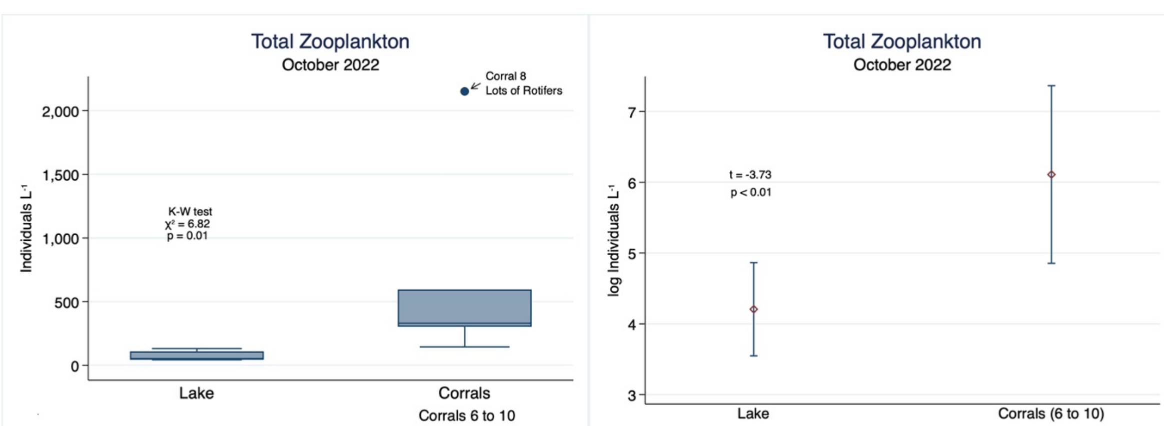
October

Groups

There was good to strong evidence that the zooplankton groups copepods, cladocerans, rotifers, and total zooplankton abundance (L^{-1}) within the corrals was greater than in the lake on October 11, 2022 (Table 37, Figure 39). There was strong evidence that total zooplankton in each of the corrals was greater than any of the lake samples (Table 37). Corral 7, the nutrient enriched corral had the lowest total abundance, while Corral 8 had the highest total abundance due to very large numbers of rotifers (Table 37).

Table 37. Copepod, Cladoceran, Rotifer, and total zooplankton abundances (L-1) on October 11, 2022, inside and outside of corrals.

	Copepods	**Cladocerans**	**Rotifers**	**Total**
Lake 1	18.97	28.34	0.00	47.31
Lake 2	48.28	81.74	0.55	130.57
Lake 3	27.43	19.43	1.14	48.00
Lake 4	18.84	23.05	0.37	42.25
Lake 5	75.43	33.37	0.00	108.80
Corral 6	302.56	16.00	11.64	330.20
Corral 7	25.13	119.02	0.00	144.15
Corral 8	258.63	124.14	1769.02	2151.79
Corral 9	82.01	510.61	2.65	595.27
Corral 10	18.91	280.75	2.91	302.56



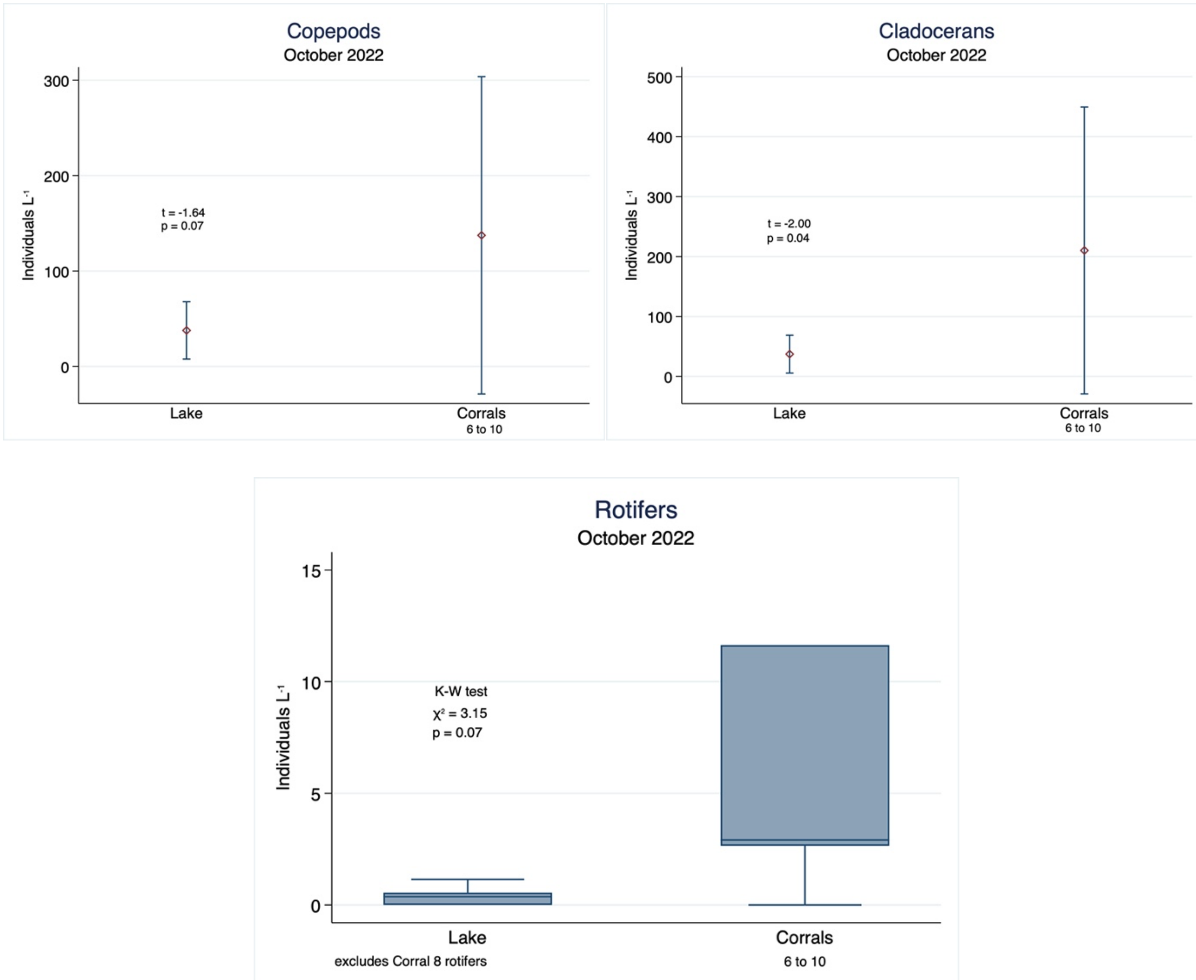


Figure 39.

One lake sample was collected near shallow water Corral 5 and inside Corral 5 just prior the end of study on October 11, 2022. Copepods, cladocerans, and rotifers were much more abundant within Corral 5 than the lake sample. No statistical support for this difference was available due to only one sample.

	Copepods	**Cladocerans**	**Rotifers**	**Total**
Lake	17.44	17.97	0.18	35.59
Corral 5	217.09	21.15	1.41	239.65

Order

Zooplankton order level was similar to group levels except for Calanoida and Harpacticoida on October 11, 2022. Group cladocerans were inclusive of order Cladocera, and group rotifers was inclusive of order Plioma (Figure 39,Table 38). There was evidence that Calanoida were more abundant in the corrals on October 11,2022 and there was strong evidence that Harpacticoida were more abundant in the lake than corrals (Figure 40). In fact, no harpacticoids were found in the corrals (6 to 10) in October.

Table 38. Calanoida, Harpacticoida, Cladocera, and Plioma abundances (L^{-1}) on October 11, 2022 inside and outside of corrals.

	Calanoida	Harpacticoida	Cladocera	Plioma
Lake 1	4.34	1.14	28.34	0.00
Lake 2	12.07	3.29	81.74	0.55
Lake 3	3.66	1.60	19.43	1.14
Lake 4	3.29	2.01	23.05	0.37
Lake 5	6.86	2.74	33.37	0.00
Corral 6	112.01	0.00	16.00	11.64
Corral 7	12.56	0.00	119.02	0.00
Corral 8	103.45	0.00	124.14	1769.02
Corral 9	2.65	0.00	510.61	2.65
Corral 10	4.36	0.00	280.75	2.91

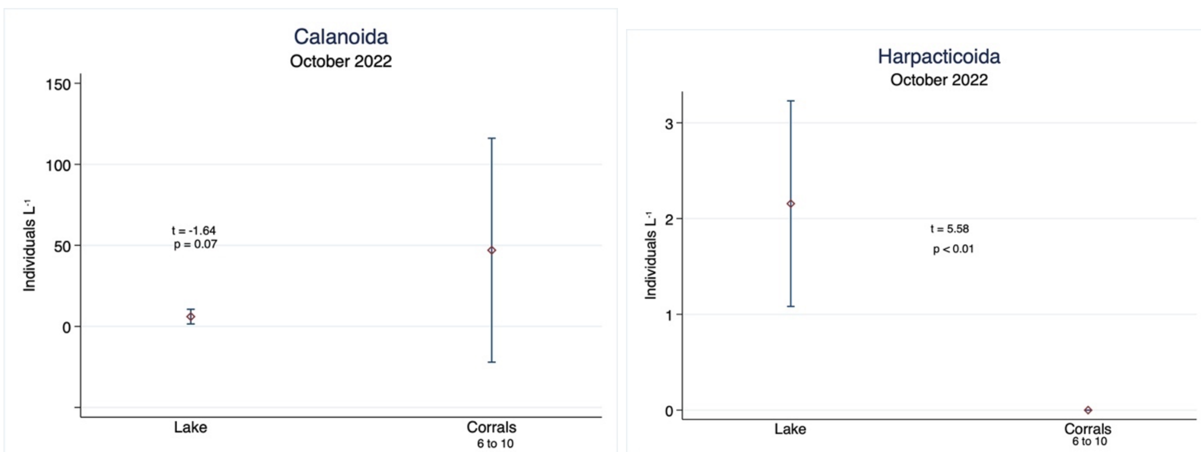


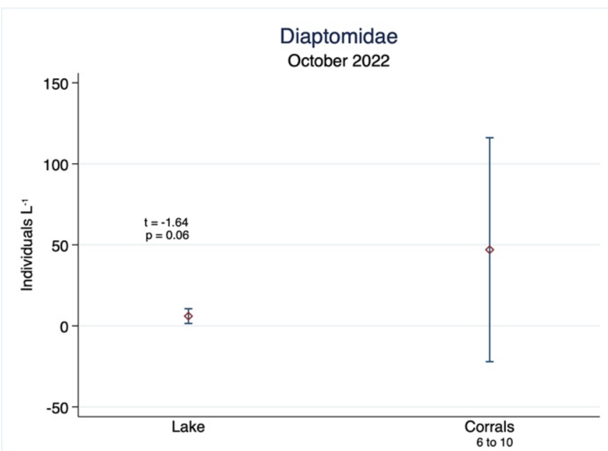
Figure 40. Comparison of Calanoida and Harpacticoida abundances inside and outside of corrals on October 11, 2022.

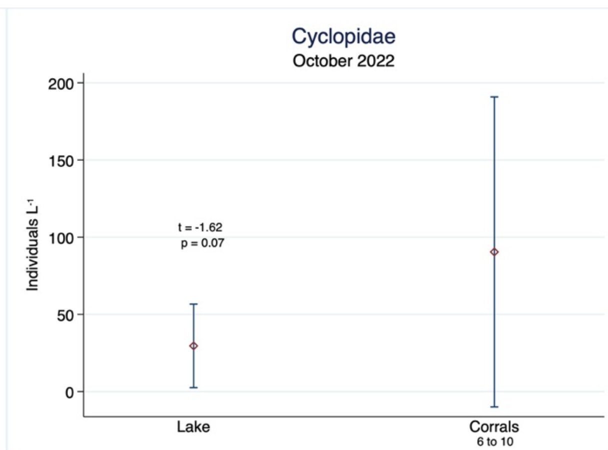
Family

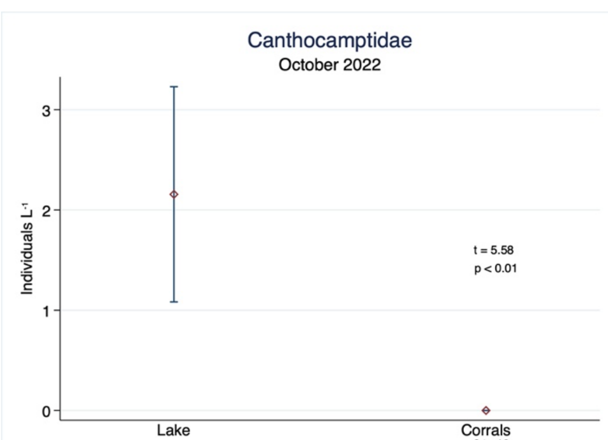
Zooplankton family level abundances (L^{-1}) inside and outside of corrals on October 11, 2022, are in Table 39. Note: Daphnids were much greater in corrals 9 and 10.

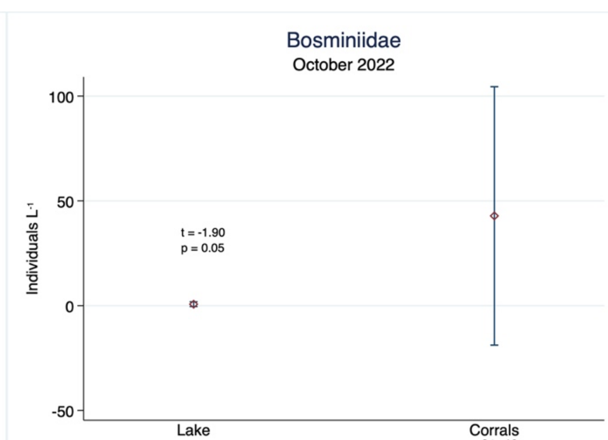
Table 39. Zooplankton family level abundances (L^{-1}) inside and outside of corrals on October 11, 2022.

	Cyclop	Diaptom	Canthocampt	Daphni	Chydor	Bosmin	Ilyocrypt	Brachion	Asplanchn	Lecan
Lake1	13.49	4.34	1.14	27.89	0.23	0.00	0.23	0.00	0.00	0.00
Lake2	32.92	12.07	3.29	72.96	5.49	2.19	1.10	0.55	0.00	0.00
Lake3	22.17	3.66	1.60	19.20	0.00	0.00	0.23	0.69	0.46	0.00
Lake4	13.54	3.29	2.01	22.32	0.00	0.37	0.37	0.37	0.00	0.00
Lake5	65.83	6.86	2.74	32.00	0.00	0.91	0.46	0.00	0.00	0.00
Corral6	190.56	112.01	0.00	13.09	0.00	2.91	0.00	5.82	5.82	0.00
Corral7	12.56	12.56	0.00	76.04	39.67	3.31	0.00	0.00	0.00	0.00
Corral8	155.18	103.45	0.00	10.35	0.00	113.80	0.00	1706.95	31.04	31.04
Corral9	79.37	2.65	0.00	481.50	10.58	18.52	0.00	0.00	2.65	0.00
Corral10	14.55	4.36	0.00	203.65	1.45	75.64	0.00	2.91	0.00	0.00









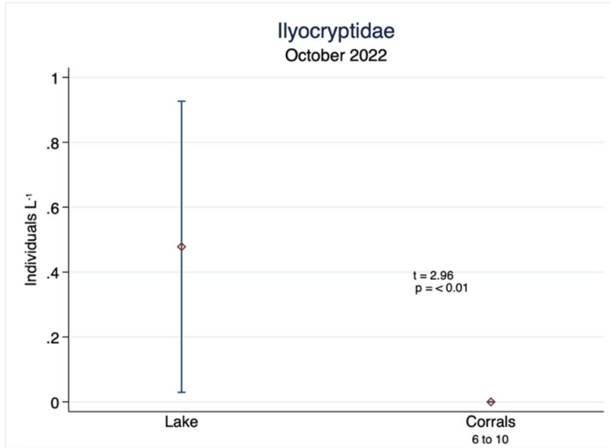


Figure 41.Comparisons of zooplankton family level abundances inside and outside of corrals on October 11, 2022. All families that were significantly different

All the families that occurred in shallow water samples were more abundant inside Corral 5 than in the lake, particularly Cyclopidae (Table 40). No statistical support for this difference was available due to only one sample from the lake and from Corral 5.

Table 40. Zooplankton family level abundances inside and outside of Corrals 5 on October 11, 2022.

	Cyclopidae	**Canthocamptidae**	**Daphniidae**	**Bosminidae**	**Ilyocryptidae**	**Brachionidae**	**Asplanchnidae**
Lake	10.04	7.40	17.62	0.35	0.00	0.00	0.18
Corral 5	187.49	29.60	16.92	2.82	1.41	1.41	0.00

Taxa

Zooplankton taxa abundances (L^{-1}) inside and outside of corrals on October 11, 2022, are in Table 41.

Table 41. Zooplankton taxa abundances (L^{-1}) inside and outside of corrals on October 11, 2022.

Taxon	Lake					Deep					Shallow	
	Lake 1	**Lake 2**	**Lake 3**	**Lake 4**	**Lake 5**	**Corral 6**	**Corral 7**	**Corral 8**	**Corral 9**	**Corral 10**	**Lake**	**Corral 5**
Acanthocyclops americanus (imm)	10.51	31.27	21.71	12.99	64.46	178.92	11.90	144.83	74.08	13.09	7.58	80.35
Acanthocyclops americanus	2.97	1.65	0.46	0.55	1.37	11.64	0.66	10.35	5.29	1.45	2.47	107.14
Diaptomidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.65	0.00	0.00	0.00
Leptodiaptomus sicilis female	0.00	10.97	0.00	1.65	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Leptodiaptomus sicilis male	0.00	1.10	0.00	0.55	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Leptodiaptomus siciloides female	4.11	0.00	3.20	0.73	5.94	104.73	11.24	93.11	0.00	2.91	0.00	0.00
Leptodiaptomus siciloides male	0.23	0.00	0.46	0.37	0.91	7.27	1.32	10.35	0.00	1.45	0.00	0.00
Attheyella sp.	1.14	3.29	1.60	2.01	2.74	0.00	0.00	0.00	0.00	0.00	7.40	29.60
Ceriodaphnia dubia	25.83	70.77	18.06	17.74	30.63	10.18	13.22	10.35	126.99	26.18	17.44	15.51
Daphnia mendotae	2.06	2.19	0.69	3.29	0.46	1.45	2.64	0.00	63.50	24.73	0.00	0.00
Daphnia pulex gr.	0.00	0.00	0.46	1.28	0.91	1.45	60.17	0.00	291.02	151.28	0.18	1.41
Daphnia retrocurva	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.45	0.00	0.00
Coronatella cf. *circumfimbriata*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	10.58	1.45	0.00	0.00
Leydigia louisi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Pleuroxus aduncus	0.23	5.49	0.00	0.00	0.00	0.00	39.67	0.00	0.00	0.00	0.00	0.00
Bosmina longirostris complex	0.00	2.19	0.00	0.37	0.91	2.91	3.31	113.80	18.52	75.64	0.35	2.82
Ilyocryptus sp.	0.23	1.10	0.23	0.37	0.46	0.00	0.00	0.00	0.00	0.00	0.00	1.41
Brachionus variabilis	0.00	0.55	0.46	0.37	0.00	4.36	0.00	0.00	0.00	0.00	0.00	0.00
Brachyonus angularus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	103.45	0.00	0.00	0.00	0.00
Brachionus sp. *Almenara*	0.00	0.00	0.23	0.00	0.00	1.45	0.00	41.38	0.00	2.91	0.00	1.41
Keratella valga	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1562.12	0.00	0.00	0.00	0.00
Asplanchna sp.	0.00	0.00	0.46	0.00	0.00	5.82	0.00	31.04	2.65	0.00	0.18	0.00

Lecane sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	31.04	0.00	0.00	0.00	0.00

Zooplankton Grazing on Phytoplankton

We found strong evidence of zooplankton grazing control of phytoplankton using June through October data ($R^2 = 0.56$, $p < 0.01$). There was a seasonal effect that had to be modeled as part of the linear regression results shown in Figure 42.

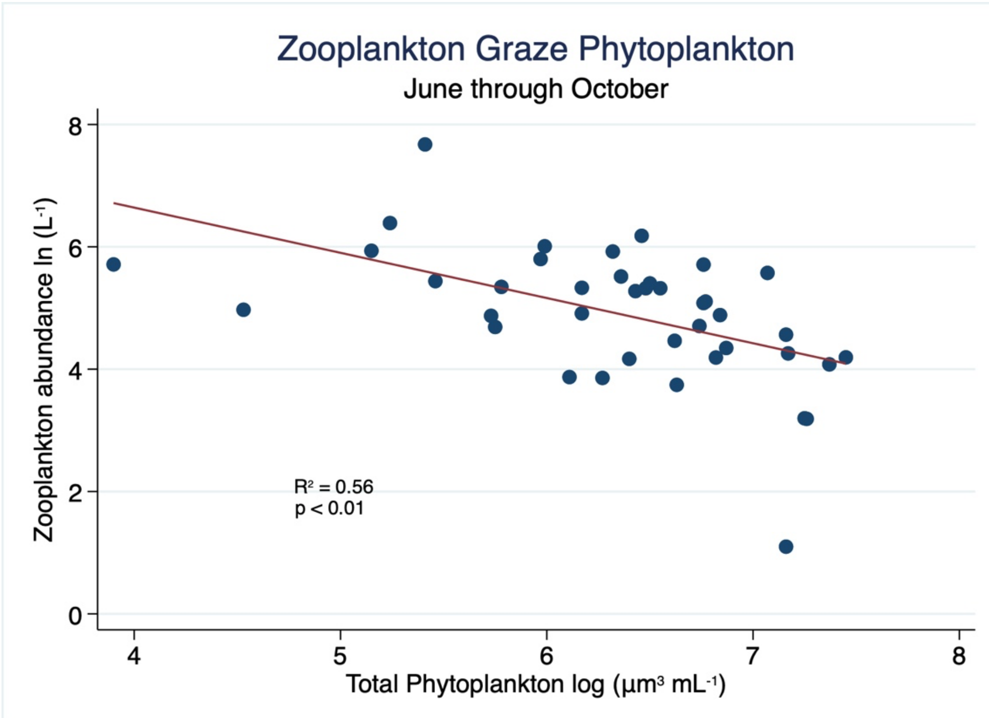


Figure 42. Relationship between total phytoplankton biovolume (log (μm^3 mL^{-1}) and zooplankton abundance ln (L^{-1}) for June through October data. Based on best fit linear regression model that included months as categorical variable.

Table 42. Best-fit linear regression of phytoplankton biovolume (log (μm^3 mL^{-1}) as a function of zooplankton abundance ln(L^{-1}) using June through October data.

Source	SS	df	MS			
				Number of obs	=	40
				F(4, 35)	=	11.34
Model	13.079751	4	3.26993775	Prob > F	=	0.0000
Residual	10.0946258	35	.28841788	R-squared	=	0.5644
				Adj R-squared	=	0.5146
Total	23.1743768	39	.59421479	Root MSE	=	.53705

logPhytopl~n	Coef.	Std. Err.	t	P>|t|	[95% Conf.	Interval]
logZoo	-0.31	0.09	-3.53	0.00	-0.48	-0.13
Month						
July	0.20	0.31	0.64	0.53	-0.43	0.83
August	0.06	0.24	0.24	0.81	-0.43	0.55
October	-0.89	0.25	-3.57	0.00	-1.40	-0.38
_cons	8.02	0.51	15.63	0.00	6.98	9.06

In addition, we found a strong effect of zooplankton grazing on phytoplankton biovolume ($R^2 = 0.86$, $p < 0.01$) including treatment effects, based on August 16, 2022, sampling event (Figure 43).

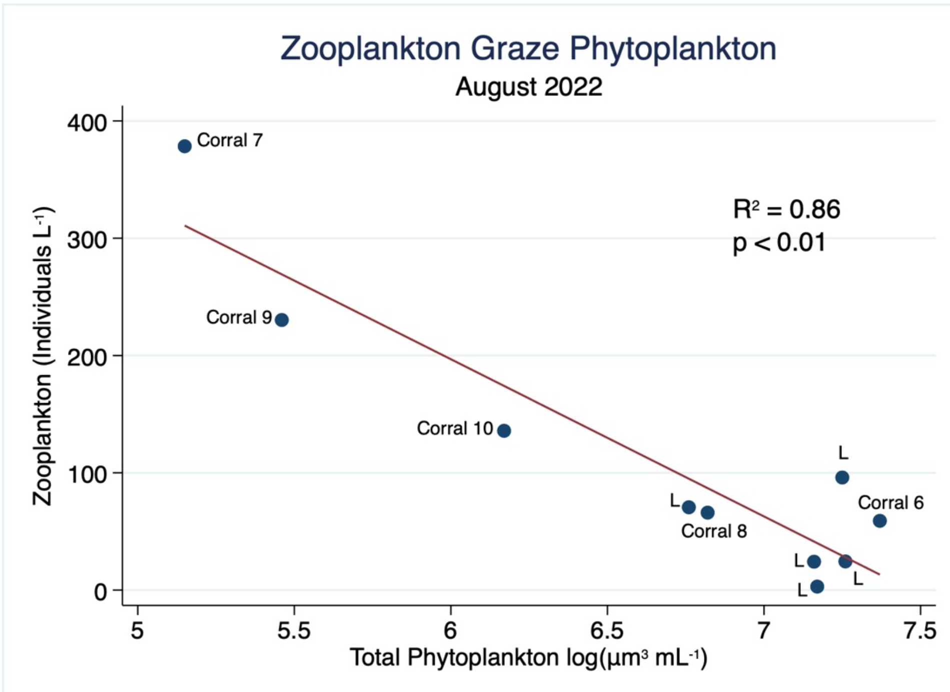


Figure 43. Relationship between total phytoplankton biovolume (log ($\mu m^3\ mL^{-1}$) and zooplankton abundance (L^{-1}) on August 16, 2022. L = lake samples.

Corrals 6 and 8 intentionally (and unintentionally) contained juvenile fishes during this time. Juvenile fishes consumed zooplankton reducing their abundance that consequently allowed phytoplankton biovolume to increase within the corrals similar to lake levels and for zooplankton abundances to remain similar to lake abundances (Figure 43). Corral 10 was the control and had greater zooplankton abundance than Corrals 6 and 8 and the lake but less than Corrals 7 and 9 (Figure 43).

Corral 7 treatment effects were the most dramatic and interesting (Figure 43). Corral 7 was dosed with phosphorus on August 3rd (and again on the 17th). Phytoplankton and zooplankton samples were collected on August 16, 2022, thirteen days after the first nutrient treatment. Our interpretation for Corral 7 treatment effects is that nutrient addition allowed phytoplankton to spike almost immediately (see Chl a results) followed closely by zooplankton grazer abundance that subsequently devoured phytoplankton. When we sampled on August 16, 2022, zooplankton had already reduced phytoplankton biovolume to the lowest levels observed in August. In addition, we observed dense periphyton (filamentous green algae) on the bottoms and sides of Corral 7. This periphyton likely competed with phytoplankton for nutrients and as we show later, provided habitat for thousands of zooplankton.

There was some evidence for zooplankton taxa feeding preferences based on August 16, 2022, samples (Table 43) although determining zooplankton feeding preference was not a goal of our study and the sample size was small (N = 10). It appeared that the five most common zooplankton taxa actively fed on *Aphanizomenon flosaquae* and pennate diatoms (Table 43), however more research to verify is required. We didn't find evidence for zooplankton grazing effects on other cyanophytes including *Aphanocapsa* sp., *Microcystis aeruginosa*, and *Snowella lacustris* (Table 43). Other correlations between zooplankton taxa and phytoplankton taxa on August 16, 2022, are in (Table 43). These relationships demonstrate the need for more intensive research on zooplankton diets in Utah Lake and how their populations can be manipulated to help control algal blooms.

Table 43. Correlations, r between phytoplankton taxa and zooplankton taxa that occurred in the corrals and lake on August 16, 2022. Correlations that were considered evidence for relation ($p < 0.05$) are in bold.

	Acanthocyclops americanus (imm)[1]	*Acanthocyclops americanus*[1]	*Leptodiaptomus siciloides Female*[1]	*Leptodiaptomus siciloides Male*[1]	*Ceriodaphnia dubia*[2]	*Daphnia mendotae*[2]	*Daphnia pulex gr.*[2]
Aphanizomenon Flosaquae[3]	**-0.80**	**-0.74**	-0.16	**-0.96**	**-0.78**	**-0.72**	**-0.88**
Aphanocapsa sp.[3]	-0.31	-0.35	-0.37	-0.50	-0.44	-0.35	-0.27
Centric diatoms [4]	-0.44	-0.52	0.02	**-0.71**	-0.43	**-0.76**	**-0.92**
Centric diatoms sp. 2[4]	-0.29	-0.34	-0.39	-0.57	-0.31	-0.41	-0.54
Chlamydomonas sp.[5]	0.22	0.18	0.29	0.13	0.01	-0.04	0.07
Kirchneriella lunaris[5]	**-0.62**	**-0.59**[a]	-0.39	-0.57	-0.32	-0.38	-0.54
Microcystis aeruginosa[3]	-0.46	-0.39	-0.31	-0.46	-0.12	-0.02	-0.43
Oocystis sp.[5]	-0.30	0.00	0.19	-0.20	-0.12	0.16	-0.29
Pennate diatoms[4]	**-0.81**	**-0.77**	0.19	**-0.82**	-0.64	**-0.77**	**-0.94**
Snowella lacustris[3]	0.00	0.14	0.21	-0.18	-0.36	-0.28	-0.28

[1]= copepod, [2] = cladoceran, [3] = cyanophyte, [4] = bacillariophyte, [5] = chlorophyte
[a] $p = 0.07$, when *A. americanus* immatures were combined with *A. americanus* adults $p = 0.05$

Results presented in this section demonstrate the trophic cascade and top-down control effects that will be discussed at length in the Discussion. This includes effects of wave action, carp bioturbation, zooplankton grazing, planktivores, benthic and periphytic algae, and macrophytes.

Benthic Invertebrates

Observed total benthic invertebrate densities (m^{-2}) were greater inside corrals than in the lake with strong evidence for greater densities in the corrals in May and August (Figure 45). Benthic invertebrate densities in Corral 7 (nutrient addition) in October were much greater than the other corrals and lake because there was a large abundance of zooplankton inside thick mats of benthic filamentous algae which was unexpected (see next section).

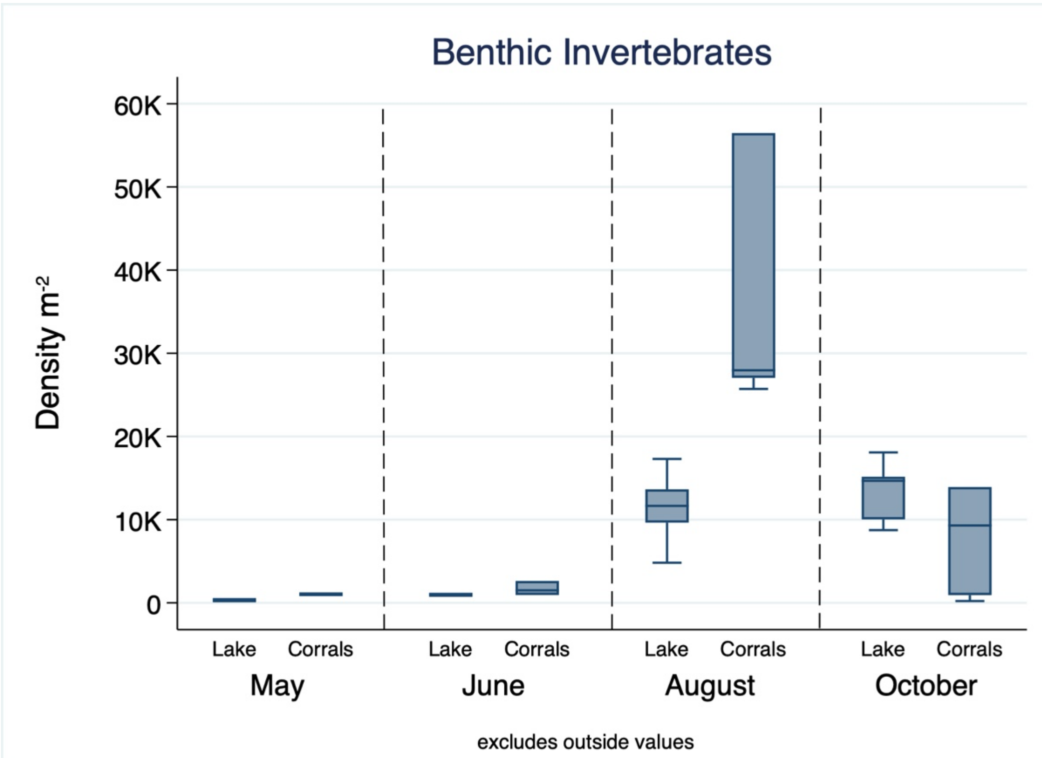
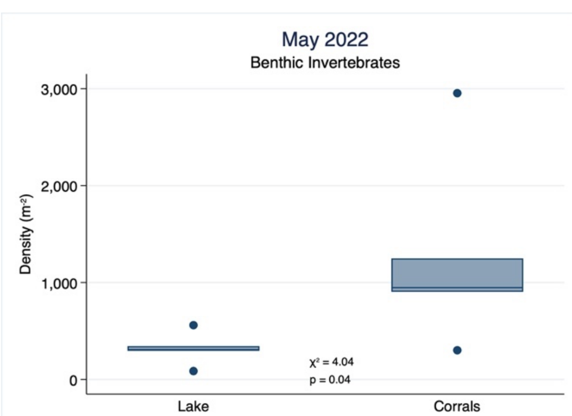
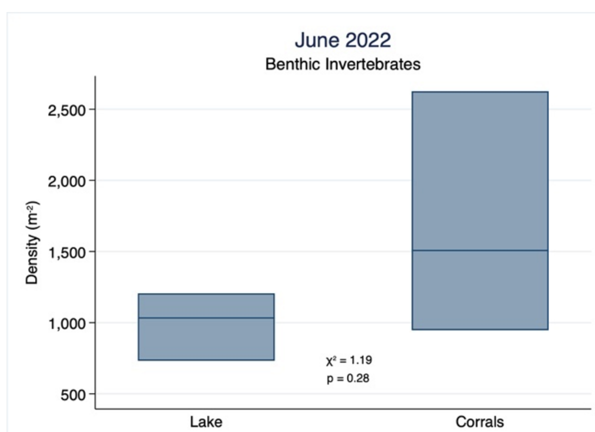


Figure 44. Comparisons between benthic invertebrate densities (m^{-2}) inside corrals and in lake by month.

The following figure (Figure 44) shows a little more detail on the comparisons between densities inside corrals and in the lake by month. This figure also includes outside values.





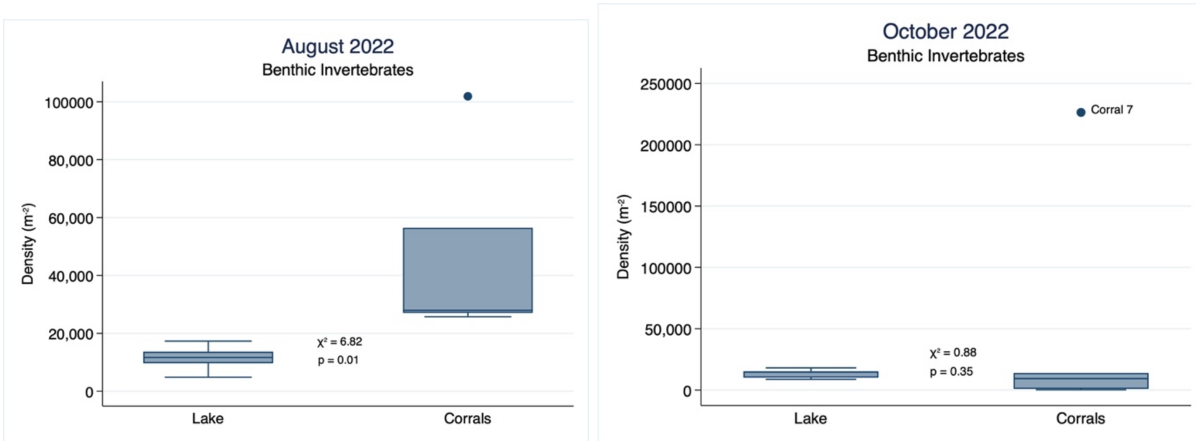


Figure 45. Comparisons between benthic invertebrate densities (m^{-2}) inside corrals and in lake by month with outside values.

The best-fit regression model of benthic invertebrate densities comparing inside corrals with lake based on month (temporal) variability was the negative binomial regression model shown in Table 44. This model was evaluated because densities were mostly count data and the distribution of values was close to negative binomial distribution.

Table 44. Best fit negative binomial regression model of benthic invertebrate densities as a function of inside or outside of corrals and month (temporal) factors. August densities were used as baseline for monthly comparisons and incidence rates were used for easier interpretations.

```
Negative binomial regression                    Number of obs     =         36
                                                LR chi2(4)        =      57.30
Dispersion     = mean                           Prob > chi2       =     0.0000
Log likelihood = -345.34688                     Pseudo R2         =     0.0766
```

total	IRR	Std. Err.	z	P>|z|	[95% Conf.	Interval]
inoutcode						
Corrals	3.47	1.01	4.26	0.00	1.96	6.15
monthcode						
May	0.03	0.01	-9.31	0.00	0.01	0.06
June	0.06	0.03	-6.28	0.00	0.02	0.14
October	1.10	0.43	0.25	0.80	0.52	2.36
_cons	12595.83	3991.24	29.79	0.00	6768.72	23439.42
/lnalpha	-0.29	0.21			-0.71	0.13
alpha	0.75	0.16			0.49	1.14

```
Note: Estimates are transformed only in the first equation.
Note: _cons estimates baseline incidence rate.
LR test of alpha=0: chibar2(01) = 7.0e+05              Prob >= chibar2 = 0.000
```

Table 45. Predicted means, standard deviation, and 95% CIs for benthic invertebrate densities inside corrals and in lake for each month sampled based on regression model in Table 44.

	Marginal Mean	Std. Dev.	95% LCI	95%UCI
May Lake	342	108	131	554
May Corrals	1,188	363	476	1,900
June Lake	739	271	208	1,270
June Corrals	2,564	1,036	534	4,595
August Lake	12,596	3,991	4,773	20,419
August Corrals	43,710	13,286	17,670	69,750
October Lake	13,893	4,348	5,371	22,415
October Corrals	48,212	14,823	19,158	77,265

The following figure, Figure 46 shows predicted benthic invertebrate densities inside and outside of corrals for each month sampled based on best fit regression model results in Table 44 and Table 45.

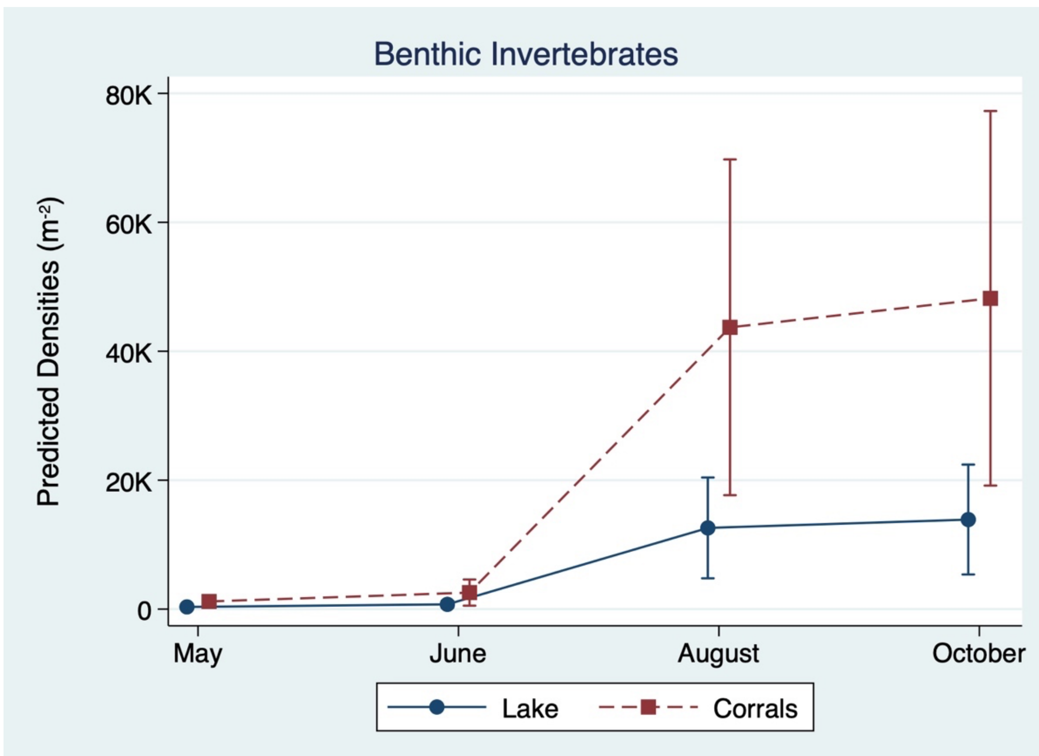


Figure 46. Estimated mean and 95% CIs of benthic invertebrate densities (m^{-2}) inside and outside of corrals by month based on regression model results in Table 44 and Table 45.

Multiple comparisons of densities inside and outside of corrals for each month based on regression model results (Table 44 and Table 45) suggested that there was strong evidence that corral benthic invertebrate densities were greater than lake densities for each month (Table 46).

Table 46. Contrast and pairwise comparisons of corrals vs lake and monthly benthic invertebrate densities based on best fit regression model results in Table 44, Table 45, and Figure 46.

Corrals vs. Lake	Contrast	Std. Err.	z	p	95% LCI	95% UCI
May	846	316	2.68	0.007	227	1,465

June	1,825	863	2.12	0.034	134	3,517
August	31,114	11,543	2.7	0.007	8,490	53,739
October	34,319	12,916	2.66	0.008	9,003	59,635

Based on the regression model results compared with the non-parametric analysis, we suggest that indeed benthic invertebrate densities were greater within the corrals than in the lake during all four monthly sample events. And as we will show next, there were important differences in densities due to treatment effects, including differences in individual taxa densities.

The following tables (Table 47 to Table 62) and figures (Figure 47 to Figure 50) show and compare benthic invertebrate densities (m^{-2}) inside and outside of corrals for May, June, August, and October sampling events.

May

Table 47. Densities (m^{-2}) of benthic invertebrate groups inside and outside of corrals on May 18, 2022.

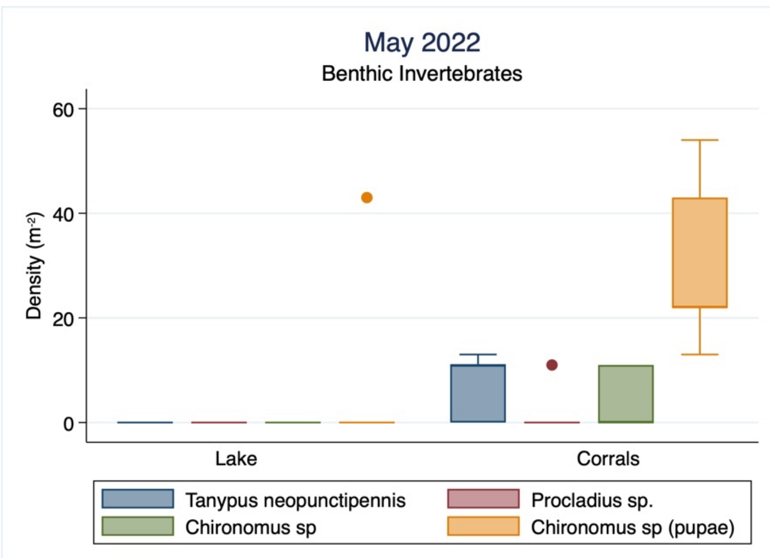
Site	**Corixidae**	**Chironomidae**	**Tipulidae**	**Nematoda**	**Annelida**	**Bivalve**	**Ostracoda**	**Copepoda**	**Cladocera**	**Amphipoda**	**Total**
Lake 1	0	43	0	43	0	0	0	0	0	0	86
Lake 2	0	258	0	43	43	0	0	0	0	0	344
Lake 3	0	301	0	0	258	0	0	0	0	0	560
Lake 4	0	258	0	0	43	0	0	0	0	0	301
Lake 5	0	258	0	0	43	0	0	0	0	0	301
Corral 1	0	215	0	0	86	0	0	0	0	0	301
Corral 2	0	914	0	13	2,014	0	0	13	0	0	2,954
Corral 3	0	388	0	22	538	0	0	0	0	0	947
Corral 4	0	624	0	11	603	0	0	0	11	0	1,249
Corral 5	0	301	0	22	570	0	0	0	11	0	904

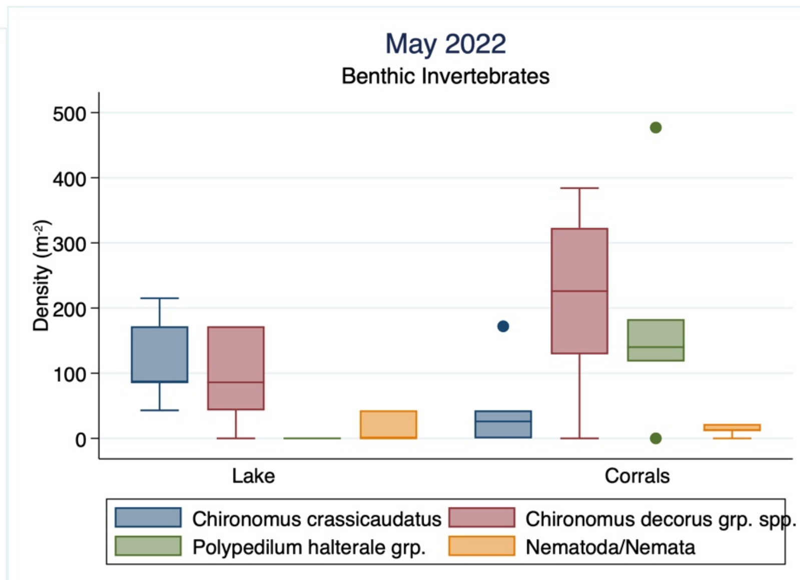
Table 48. Densities (m^{-2}) of benthic insects inside and outside of corrals on May 18, 2022. Note: All insects were Family Chironomidae (midges).

Site	*Tanypus neopunctipennis*	*Procladius* sp.	*Chironomus* sp.	*Chironomus* sp. (pupae)	*Chironomus crassicaudatus*	*Chironomus decorus* grp. spp.	*Polypedilum halterale* grp.
Lake 1	0	0	0	0	43	0	0
Lake 2	0	0	0	0	215	43	0
Lake 3	0	0	0	43	86	172	0
Lake 4	0	0	0	0	86	172	0
Lake 5	0	0	0	0	172	86	0
Corral 1	0	0	0	43	172	0	0
Corral 2	13	0	0	13	26	384	477
Corral 3	0	11	11	22	0	226	118
Corral 4	11	0	11	54	43	323	183
Corral 5	11	0	0	22	0	129	140

Table 49. Densities (m^{-2}) of benthic invertebrate non-insects inside and outside of corrals on May 18, 2022.

		Oligochaeta	Oligochaeta	Copepoda	Cladocera
Site	Nematoda/Nemata	Oligochaeta	Naididae	Diaptomidae	*Daphnia pulex* gr.
Lake 1	43	0	0	0	0
Lake 2	43	0	43	0	0
Lake 3	0	172	86	0	0
Lake 4	0	43	0	0	0
Lake 5	0	43	0	0	0
Corral 1	0	86	0	0	0
Corral 2	13	1,709	305	13	0
Corral 3	22	527	11	0	0
Corral 4	11	570	32	0	11
Corral 5	22	495	75	0	11





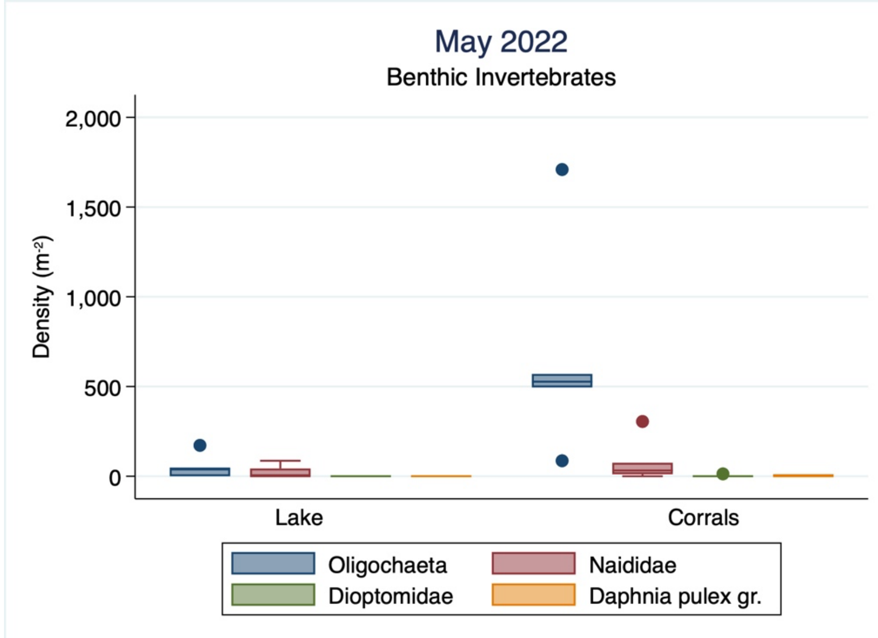


Figure 47. Comparisons of benthic invertebrate taxa densities (m-2) inside corrals and in the lake May 18, 2022.

June

Table 50. Densities (m^{-2}) of benthic invertebrate groups inside and outside of corrals on June 24, 2022.

Site	**Corixidae**	**Chironomidae**	**Tipulidae**	**Nematoda**	**Annelida**	**Bivalve**	**Ostracoda**	**Copepoda**	**Cladocera**	**Amphipoda**	**Total**
Lake 1	0	344	0	0	689	0	0	0	0	0	1,033
Lake 2	0	474	0	86	172	0	0	0	0	0	732
Lake 3	0	474	0	0	732	0	0	0	0	0	1,206
Corral 6	0	1,808	0	0	818	0	0	0	0	0	2,626
Corral 8	0	732	0	0	215	0	0	0	0	0	947
Corral 10	0	388	0	0	1,119	0	0	0	0	0	1,507

Table 51. Densities (m^{-2}) of benthic invertebrate insect taxa inside and outside of corrals on June 24, 2022. Note: all insects were Chironomidae.

Site	*Tanypus neopunctipennis*	*Procladius* sp.	*Chironomus* sp.	*Chironomus* sp. (pupae)	*Chironomus crassicaudatus*	*Chironomus decorus* grp. spp.
Lake 1	0	86	0	43	172	43
Lake 2	0	43	0	0	43	388

Lake 3	0	0	0	43	215	215
Corral 6	0	43	43	0	1,550	172
Corral 8	0	86	0	0	43	603
Corral 10	43	43	0	43	129	129

Table 52. June non-insects Densities (m^{-2}) of benthic invertebrate non-insects inside and outside of corrals on June 24, 2022.

		Oligochaeta	Oligochaeta	Lumbricidae
Site	Nematoda/Nemata	Oligochaeta	Naididae	*Eiseniella* sp.
Lake 1	0	388	172	129
Lake 2	86	43	0	129
Lake 3	0	474	215	43
Corral 6	0	603	215	0
Corral 8	0	215	0	0
Corral 10	0	861	86	172

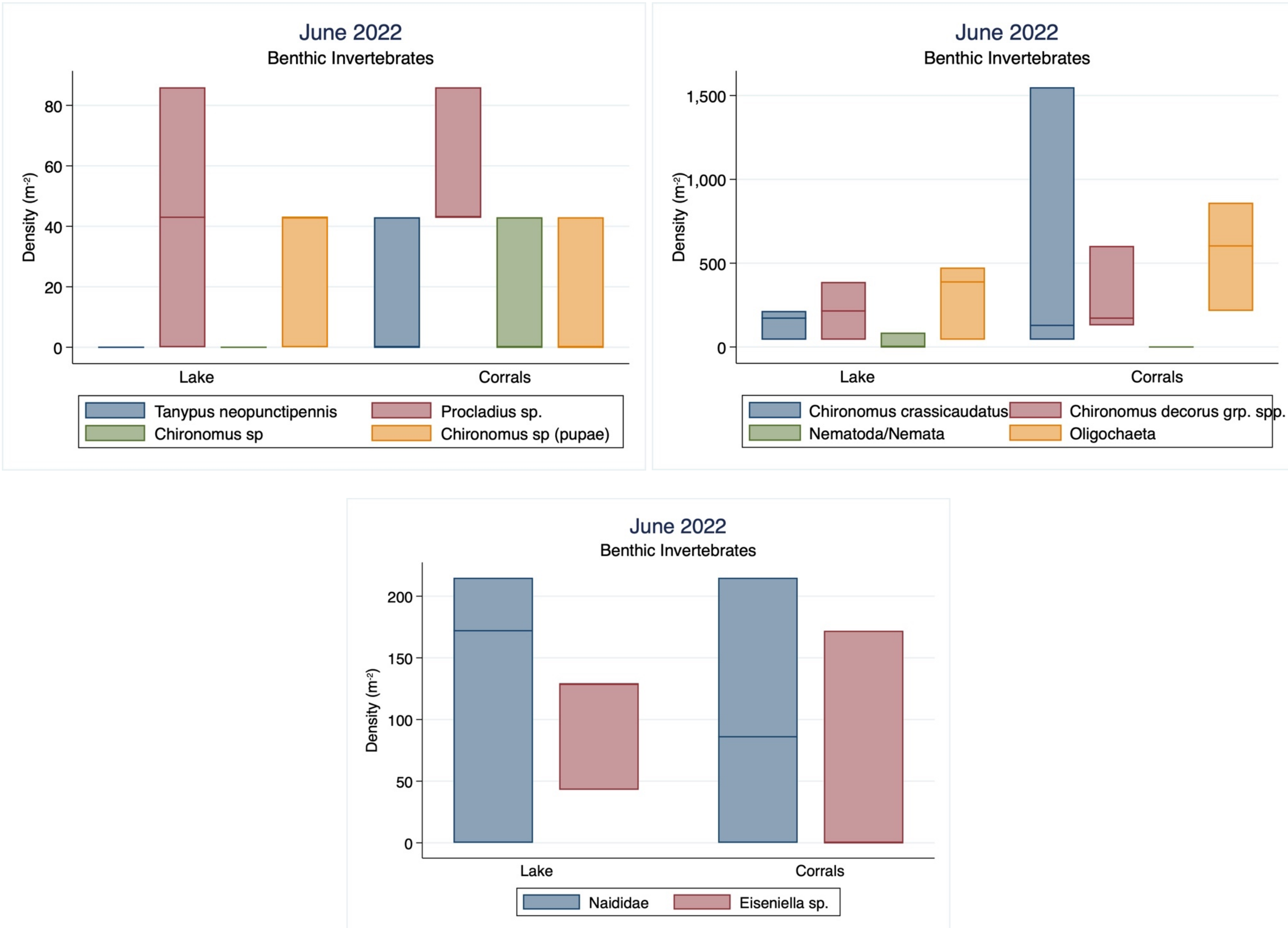


Figure 48. Comparisons of benthic invertebrate taxa densities (m^{-2}) inside corrals and in the lake June 24, 2022.

August

Table 53. Densities (m^{-2}) of benthic invertebrate groups inside and outside of corrals on August 16, 2022. August note: no zooplankton in August

Site	**Corixidae**	**Chironomidae**	**Tipulidae**	**Nematoda**	**Annelida**	**Bivalve**	**Ostracoda**	**Copepoda**	**Cladocera**	**Amphipoda**	**Total**
Lake 1	0	9,338	0	230	7,731	0	0	0	0	0	17,299
Lake 2	0	4,521	0	258	4,865	0	0	0	0	0	9,644
Lake 3	0	5,109	0	287	6,257	0	0	0	0	0	11,654
Lake 4	0	6,613	0	276	6,751	0	0	0	0	0	13,640
Lake 5	0	3,444	0	172	1,206	0	0	0	0	0	4,822
Corral 1	0	14,324	0	2,204	39,667	275	0	0	0	0	56,471
Corral 2	0	12,335	0	525	15,091	0	0	0	0	0	27,951
Corral 3	0	6,659	0	574	18,485	0	0	0	0	0	25,719
Corral 4	0	13,400	0	0	13,651	0	0	0	0	0	27,051
Corral 5	0	21,574	0	0	80,328	0	0	0	0	0	101,901

Table 54. Densities (m^{-2}) of benthic invertebrate insect taxa inside and outside of corrals on August 16, 2022.

Site	*Tanypus neopunctipennis*	*Procladius* sp.	Chironominae: Chironomini	*Chironomus* sp	*Chironomus* sp (pupae)	*Chironomus crassicaudatus*
Lake 1	842	77	0	0	0	2,832
Lake 2	258	0	0	43	0	1,808
Lake 3	574	115	0	57	0	1,607
Lake 4	1,033	0	0	0	69	3,169
Lake 5	560	0	0	0	0	1,206
Corral 1	1,102	1,653	0	0	0	1,377
Corral 2	853	640	131	131	131	1,263
Corral 3	919	230	0	0	115	2,870
Corral 4	1,002	125	0	0	125	3,507
Corral 5	2,504	1,669	0	0	0	876

Table 55. Densities (m^{-2}) of benthic invertebrate insect taxa inside and outside of corrals on August 16, 2022. Continued.

Site	*Chironomus decorus* grp. spp.	*Cryptochironomus* sp.	*Polypedilum halterale* grp.	*Glyptotendipes* sp.	*Glyptotendipes* (pupae)	*Cladotanytarsus* sp.
Lake 1	2,526	0	77	0	0	2,985
Lake 2	1,851	0	0	0	0	560
Lake 3	2,239	0	57	0	0	459
Lake 4	1,998	0	0	0	0	344
Lake 5	1,636	0	0	0	0	43
Corral 1	5,785	0	0	3,306	275	826
Corral 2	4,199	0	0	4,855	0	131
Corral 3	2,181	0	0	115	0	230
Corral 4	5,510	0	125	1,879	125	1,002
Corral 5	6,885	459	0	9,180	0	0

Table 56. Densities (m^{-2}) of benthic invertebrate non-insects inside and outside of corrals on August 16, 2022.

		Oligochaeta	Oligochaeta	Lumbricidae	Bivalve
Site	Nematoda	Oligochaeta	Naididae	*Eiseniella* sp.	Bivalve
Lake 1	230	7,119	383	230	0
Lake 2	258	4,607	258	0	0
Lake 3	287	5,167	1,033	57	0
Lake 4	276	6,338	413	0	0
Lake 5	172	1,163	0	43	0
Corral 1	2,204	39,116	551	0	275
Corral 2	525	15,091	0	0	0
Corral 3	574	18,485	0	0	0
Corral 4	0	13,651	0	0	0
Corral 5	0	77,115	2,295	918	0

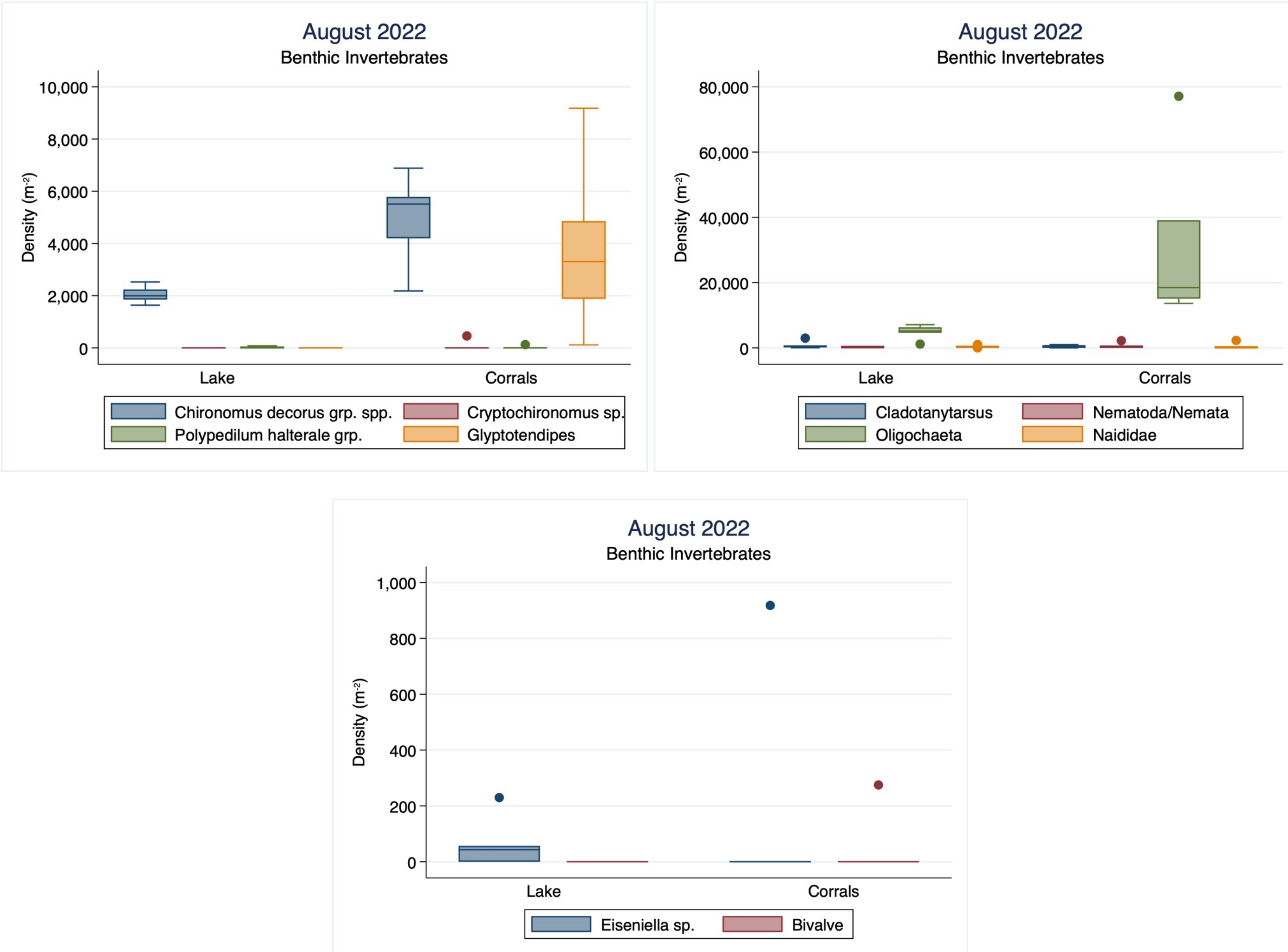


Figure 49. Comparisons of benthic invertebrate taxa densities (m^{-2}) inside corrals and in the lake August 16, 2022.

October

One of our most important findings of benthic invertebrate densities on October 11, 2022, was the very large densities of zooplankton taxa in Corral 7, the nutrient addition treatment, including *Acanthocyclops americanus*, *Ceriodaphnia dubia*, *Daphnia gaelata mendotae*, *Daphnia pulex* gr., *Pleuroxus aduncus*, and *Bosmina longirostris* complex that almost all exclusively occurred in Corral 7 (Table 57 to Table 62, and Figure 50). This was due to the high density of filamentous green algae in Corral 7 that provided structural (mostly diurnal) and potentially food resource habitat in the benthos for the zooplankton and likely increased production of phytoplankton (zooplankton food resource) due to nutrient addition.

Table 57. Densities (m^{-2}) of benthic invertebrate groups inside and outside of corrals on October 11, 2022.

Site	**Corixidae**	**Chironomidae**	**Tipulidae**	**Nematoda**	**Annelida**	**Bivalve**	**Ostracoda**	**Copepoda**	**Cladocera**	**Amphipoda**	**Total**
Lake 1	0	7,836	0	861	9,386	0	0	0	0	0	18,083
Lake 2	0	3,837	0	689	5,461	0	0	0	49	0	10,036
Lake 3	0	5,578	0	551	8,540	0	0	0	0	0	14,669
Lake 4	0	3,488	0	129	5,124	0	0	0	0	0	8,740
Lake 5	73	4,207	73	1,523	8,994	0	0	73	218	0	15,159
Corral 6	0	75	0	0	97	0	0	11	11	22	215
Corral 7	0	2,080	0	0	0	0	690	56,580	166,979	0	226,328
Corral 8	0	334	11	0	581	0	0	11	0	0	936
Corral 9	689	6,717	0	0	1,593	0	0	0	258	0	9,257
Corral 10	207	9,165	0	0	4,135	0	0	0	413	0	13,920

Table 58. Densities (m^{-2}) of benthic invertebrate insect taxa inside and outside of corrals on October 11, 2022.

	Corixidae	Corixidae	Corixidae	Corixidae	Chironomidae
Site	(immature)	*Corisella decolor*	*Corisella tarsalis*	*Tanypus neopunctipennis*	*Procladius* sp.
Lake 1	0	0	0	86	172
Lake 2	0	0	0	197	148
Lake 3	0	0	0	344	69
Lake 4	0	0	0	344	86
Lake 5	73	0	0	290	145
Corral 6	0	0	0	11	0
Corral 7	0	0	0	1	0
Corral 8	0	0	0	0	0
Corral 9	474	129	86	689	258

Corral 10	207	0	0	2,825	1,103

Table 59. Densities (m^{-2}) of benthic invertebrate insect taxa inside and outside of corrals on October 11, 2022. Continued.

	Chironomidae					Tipulidae
Site	*Chironomus* sp (pupae)	*Chironomus crassicaudatus*	*Chironomus decorus* grp. spp.	*Glyptotendipes* sp.	*Cladotanytarsus* sp.	*Antocha* sp.
Lake 1	0	5,709	1,869	0	0	0
Lake 2	0	2,226	1,267	0	0	0
Lake 3	0	2,808	2,357	0	0	0
Lake 4	0	2,328	729	0	0	0
Lake 5	0	2,891	881	0	0	73
Corral 6	22	32	11	0	0	0
Corral 7	0	1	0	8	2,070	0
Corral 8	0	161	161	0	0	11
Corral 9	43	5,169	342	172	43	0
Corral 10	207	2,568	877	1,585	0	0

Table 60. Densities (m^{-2}) of benthic invertebrate non-insects inside and outside of corrals on October 11, 2022.

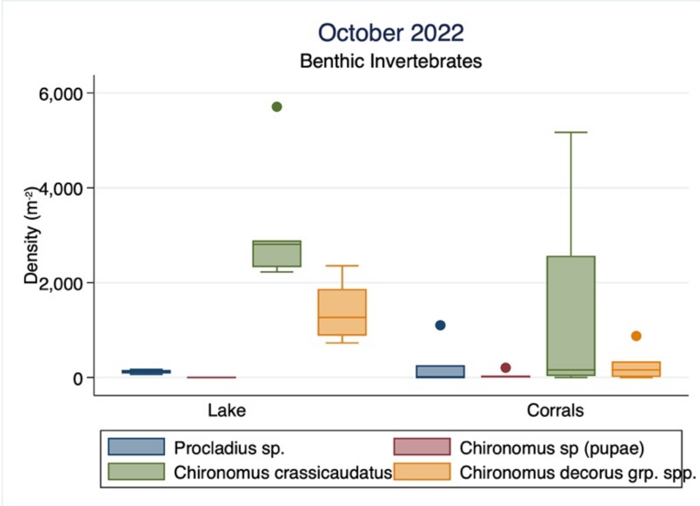
	Nematoda	Annelida	Annelida	Annelida	Mollusca	Crusteaceans
		Oligochaeta	Oligochaeta	Lumbricidae	Bivalve	Ostracoda
Site	Nematoda/Nemata	Oligochaeta	Naididae	*Eiseniella* sp.	Bivalve	Ostracoda
Lake 1	861	9,300	0	86	0	0
Lake 2	689	4,772	640	49	0	0
Lake 3	551	8,540	0	0	0	0
Lake 4	129	1,421	3,703	0	0	0
Lake 5	1,523	8,414	145	435	0	0
Corral 6	0	22	75	0	0	0
Corral 7	0	0	0	0	0	690
Corral 8	0	344	237	0	0	0
Corral 9	0	1,206	388	0	0	0
Corral 10	0	2,619	1,516	0	0	0

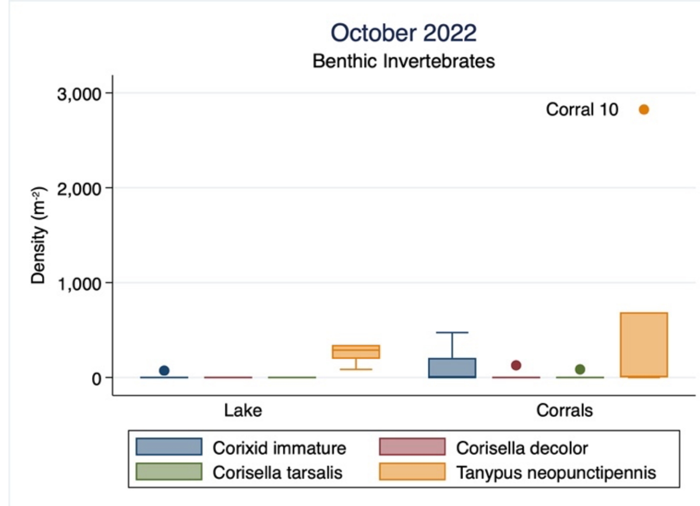
Table 61. Densities (m^{-2}) of benthic invertebrate non-insects inside and outside of corrals on October 11, 2022.Continued

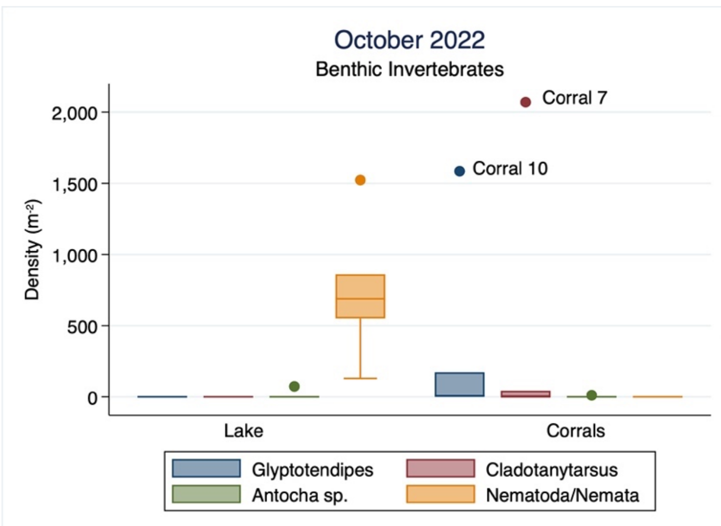
	Crusteaceans	Crusteaceans	Crusteaceans	Crusteaceans	Crusteaceans	Crusteaceans
	Copepoda	Copepoda	Copepoda	Copepoda	Cladocera	Cladocera
Site	Dioptomidae	*Acanthocyclops americanus* (imm)	*Acanthocyclops americanus*	*Attheyella* sp.	*Ceriodaphnia dubia*	*Daphnia* sp.
Lake 1	0	0	0	0	0	0
Lake 2	0	0	0	0	0	0
Lake 3	0	0	0	0	0	0
Lake 4	0	0	0	0	0	0
Lake 5	0	0	0	73	0	0
Corral 6	11	0	0	0	0	11
Corral 7	1,380	51,060	4,140	0	47,610	0
Corral 8	0	0	11	0	0	0
Corral 9	0	0	0	0	0	0
Corral 10	0	0	0	0	0	413

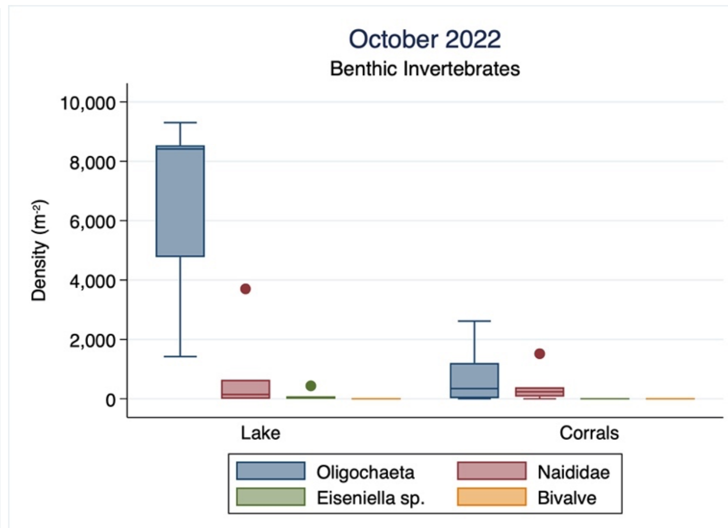
Table 62. Densities (m^{-2}) of benthic invertebrate non-insects inside and outside of corrals on October 11, 2022. Continued.

	Crusteaceans	Crusteaceans	Crusteaceans	Crusteaceans	Crusteaceans	Crusteaceans
	Cladocera	Cladocera	Cladocera	Cladocera	Cladocera	Amphipoda
Site	*Daphnia gaelata mendotae*	*Daphnia pulex* gr.	*Ilyocryptus sp.*	*Pleuroxus aduncus*	*Bosmina longirostris* complex	*Hyalella* sp
Lake 1	0	0	0	0	0	0
Lake 2	0	0	49	0	0	0
Lake 3	0	0	0	0	0	0
Lake 4	0	0	0	0	0	0
Lake 5	0	218	0	0	0	0
Corral 6	0	0	0	0	0	22
Corral 7	3,450	64,859	0	50,370	690	0
Corral 8	0	0	0	0	0	0
Corral 9	0	258	0	0	0	0
Corral 10	0	0	0	0	0	0


October 2022
Benthic Invertebrates
Density (m-2)
6,000
4,000
2,000
0
Lake
Corrals
Procladius sp.
Chironomus sp (pupae)
Chironomus crassicaudatus
Chironomus decorus grp. spp.


October 2022
Benthic Invertebrates
Density (m-2)
3,000
2,000
1,000
0
Corral 10
Lake
Corrals
Corixid immature
Corisella decolor
Corisella tarsalis
Tanypus neopunctipennis


October 2022
Benthic Invertebrates
Density (m-2)
2,000
1,500
1,000
500
0
Corral 7
Corral 10
Lake
Corrals
Glyptotendipes
Cladotanytarsus
Antocha sp.
Nematoda/Nemata


October 2022
Benthic Invertebrates
Density (m-2)
10,000
8,000
6,000
4,000
2,000
0
Lake
Corrals
Oligochaeta
Naididae
Eiseniella sp.
Bivalve

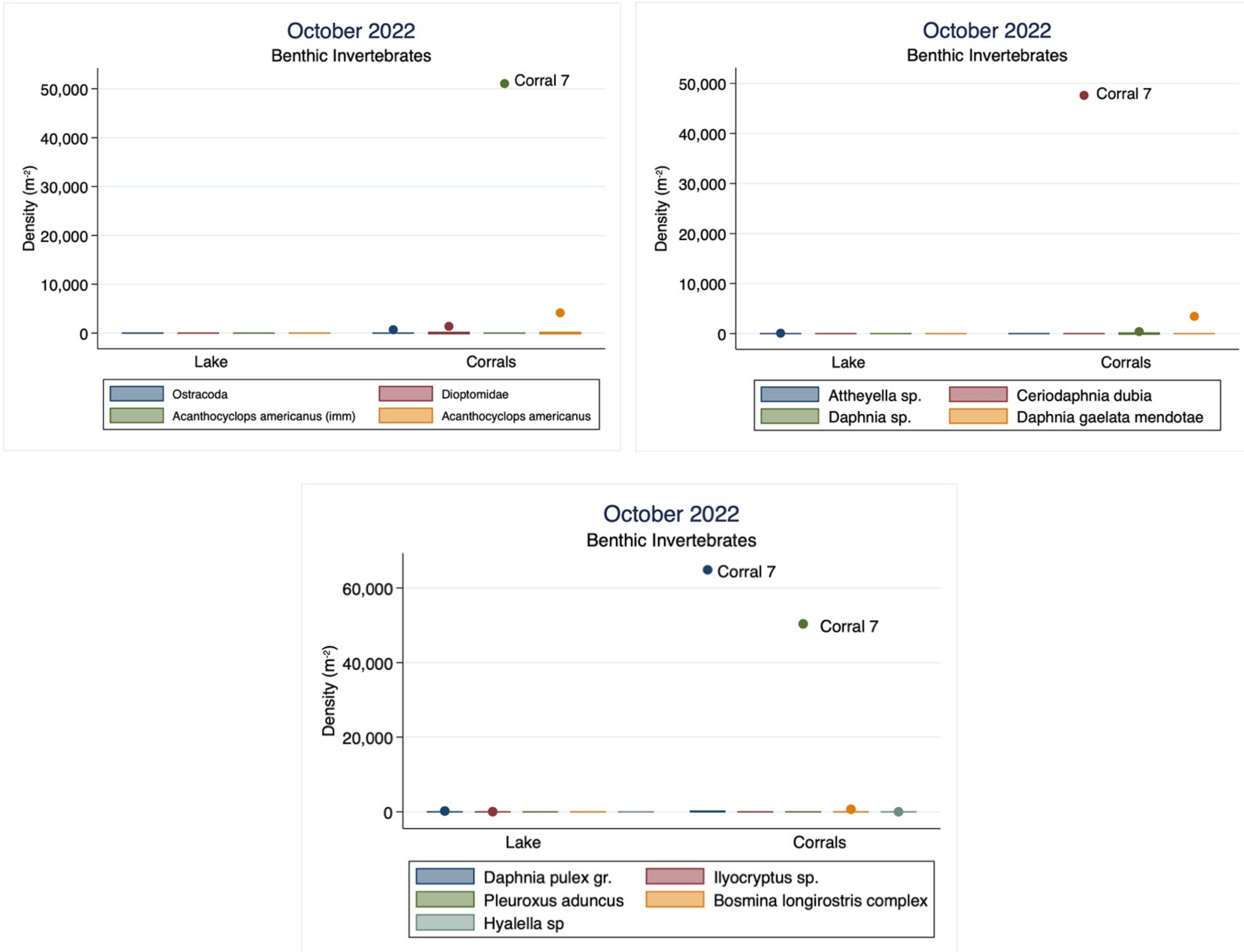


Figure 50. Comparisons of benthic invertebrate taxa densities (m^{-2}) inside corrals and in the lake October 11, 2022.

Attached algae, the periphyton community.

Attached algal growth that formed the periphyton[7] community on the bottom of corrals and on the sides of the corrals were abundant and, in some instances, luxurious particularly inside the deeper open water corrals later in the season (August through October) (Figure 52). Periphytic algae on the sides of corrals were observed to be denser with longer filaments on southern facing areas of the corrals, although it was much shorter in length than benthic filamentous green algae found on the bottom of several corrals.

Superficially the periphytic filamentous algae appeared to be composed of only one or two taxa however, on microscopic examination its community was often diverse with many other algal taxa found within their filaments (Table 63 and Table 64). Cell counts or biovolumes were not made for periphyton samples. There were at least six different filamentous green algae (Chlorophyta) taxa found within the corrals including, *Oedogonium* sp., *Cladophora* sp., *Mougeotia* sp. *Stigeoclonium* sp. *Microspora* sp., and *Spirogyra* sp.(Table 63, Table 64, and Figure 51).

Table 63. Periphytic algal taxa collected from inside of Corral 2 collected on July 28, 2022.

Taxon	Algal Division
Centric diatoms sp.	Bacillariophyta
Pennate diatoms	Bacillariophyta
Ankistrodesmus arcuatus Korshikov (= Monoraphidium arcuatum (Korshikov) Hindák)	Chlorophyta
Desmodesmus communis (Hegewald) Hegewald	Chlorophyta
Desmodesmus opoliensis (Richter) Hegewald	Chlorophyta
Dictyosphaerium ehrenbergianum Nägeli	Chlorophyta
Oocystis sp.	Chlorophyta
Pectinodesmus pectinatus (Meyen) Hegewald, Wolf, Keller, Friedl & Krienitz (= *Acutodesmus pectinatus* (Meyen) Tsarenko)	Chlorophyta
Pediastrum duplex Meyen (= Pediastrum duplex var. clathratum Meyen)	Chlorophyta
Scenedesmus sp.	Chlorophyta
Cryptomonas sp.	Cryptophyta
Aphanizomenon flosaquae Ralfs ex Bornet & Flahault	Cyanophyta
Dolichospermum circinalis (Brébisson) Wacklin, Hoffmann & Komárek (= *Anabaena circinalis* Rabenhorst)	Cyanophyta
Phacus sp.	Euglenophyta

Table 64.a) Periphyton and associated algae on the inside of Corral 7 October 11, 2022.

Taxon	Algal Division
Centric diatoms species	Bacillariophyta
Pennate diatoms	Bacillariophyta

[7] A periphyton community is comprised of an autotrophic assemblage made up of diatoms, green algae, and cyanobacteria, and a heterotrophic assemblage consisting of bacteria, protozoa, fungi, and other microorganisms (Wijewardene et al. 2022). We mostly focus on the autotrophs in this section.

Cladophora sp.	Chlorophyta
Oedogonium sp.	Chlorophyta

b) Periphyton and associated algae on the inside of Corral 1 October 11, 2022.

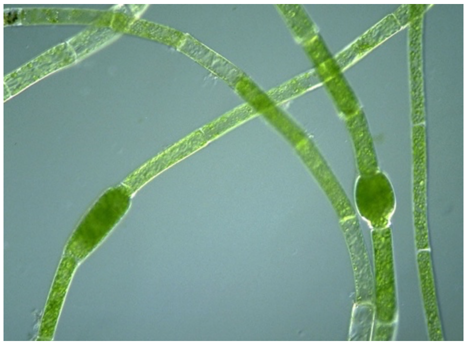
Taxon	Algal Division
Centric diatoms sp.	Bacillariophyta
Pennate diatoms	Bacillariophyta
Cladophora sp.	Chlorophyta
Microspora sp.	Chlorophyta
Mougeotia sp.	Chlorophyta
Scenedesmus sp.	Chlorophyta
Stigeoclonium sp.	Chlorophyta
Zygnema sp.	Chlorophyta
Chroococcus dispersus (Keissler) Lemmermann	Cyanophyta
Cylindrospermopsis sp.	Cyanophyta
Dolichospermum circinalis (Brébisson) Wacklin, Hoffmann & Komárek (= Anabaena circinalis Rabenhorst)	Cyanophyta
Phormidium species 5	Cyanophyta
Unknown filamentous cyanophyte	Cyanophyta
unknown filamentous cyanophyte 2	Cyanophyta

c) Periphyton and associated algae on the inside of Corral 3 October 11, 2022.

Taxon	Algal Division
Pennate diatoms	Bacillariophyta
Closteriopsis longissima (Lemmermann) Lemmermann	Chlorophyta
Cosmarium sp.	Chlorophyta
Mougeotia sp.	Chlorophyta
Pectinodesmus pectinatus (Meyen) Hegewald, Wolf, Keller, Friedl & Krienitz (= *Acutodesmus pectinatus* (Meyen) Tsarenko)	Chlorophyta
Spirogyra sp.	Chlorophyta
Aphanothece sp.	Cyanophyta
Coelosphaerium sp.	Cyanophyta
Cylindrospermum stagnale Bornet & Flahault	Cyanophyta
Dolichospermum sp.	Cyanophyta
Phormidium sp. 5	Cyanophyta
Pseudanabaena sp.	Cyanophyta

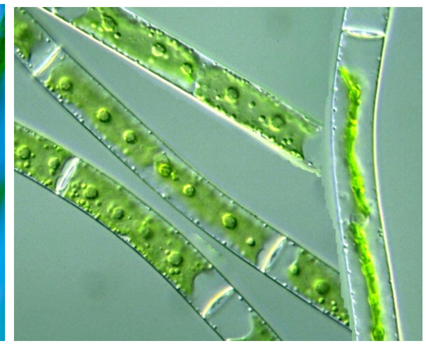
d) Periphyton and associated algae on the inside of Corral 5 October 11, 2022.

Taxon	Algal Division
Pennate diatoms	Bacillariophyta
Microspora sp.	Chlorophyta

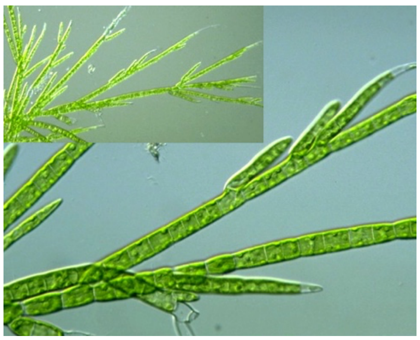


Oedogonium sp.

Cladophora sp.

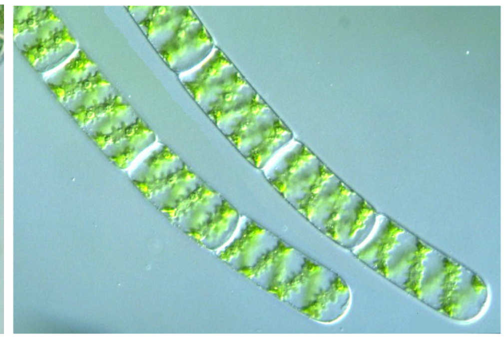


Mougeotia sp.

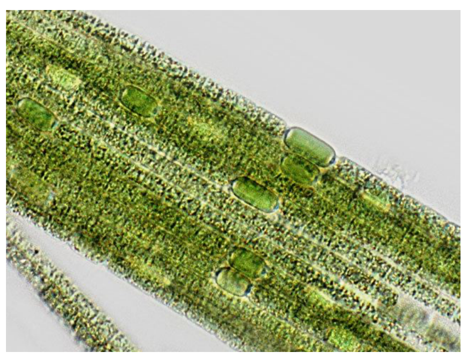


Stigeoclonium sp.

Microspora sp.



Spirogyra sp.



Aphanizomenon flosaquae

Figure 51. Major filamentous green algae (Chlorophyta) and blue green algae (Cyanophyta) found as periphyton on sides of corrals. All images were downloaded from the internet.

Growth of attached algae and the periphyton community on the sides and bottoms of corrals but not in the lake clearly demonstrated that suitable stable habitat for periphyton community establishment was nonexistent in our study area (Figure 52). It also demonstrates that these types of algae simply need stable substrates to compete with water column phytoplankton for nutrients and to add additional trophic level complexity (see Discussion: Trophic Transfer Efficiency). In addition, all filamentous algal samples were laden with fine sediments demonstrating that the autotrophic periphyton assemblages not only compete with nutrients with phytoplankton but also filter large amounts of suspended sediments. For a more detailed description of the importance of periphytic communities to foodwebs and ecosystem functioning see Vadeboncoeur and Steinman (2002) and Wijewardene et al. (2022).

Figure 52. Example of filamentous green algae complex growing in Corral 7 during August 2022 sampling.

Nutrients

Shallow water corrals 1 to 5

Corral nutrients tended to follow lake nutrient concentrations but at a lower amplitude with the exception of Corral 3 (macrophytes, bivalves, and carp treatment) which typically more closely followed lake nutrient concentrations. Spikes began around July 25, 2022, and started to drop somewhat in late August, early September (Figure 53).

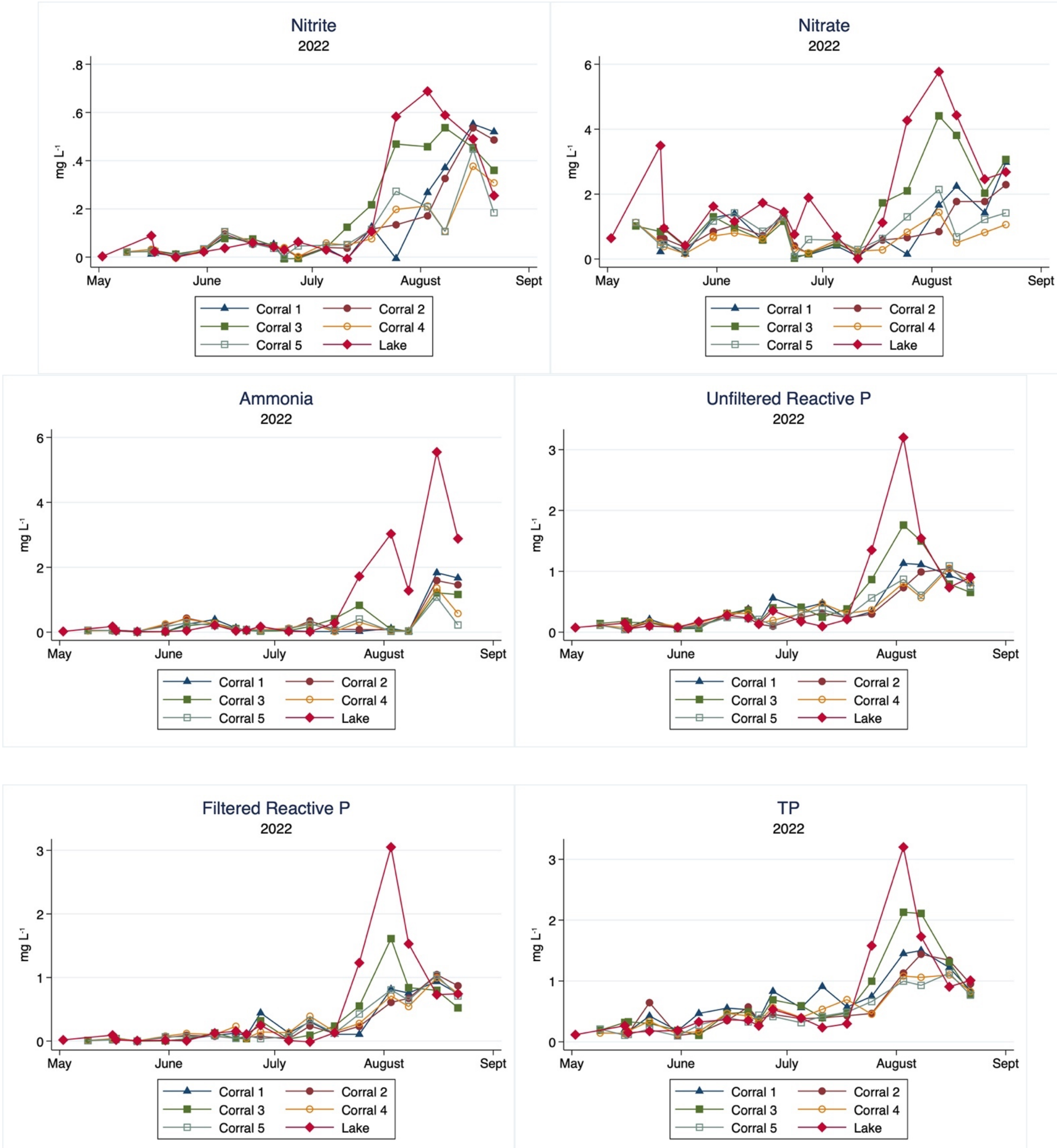


Figure 53. Nutrient levels in Corrals 1-5 and lake over the study period.

Deep corrals 6 to 10

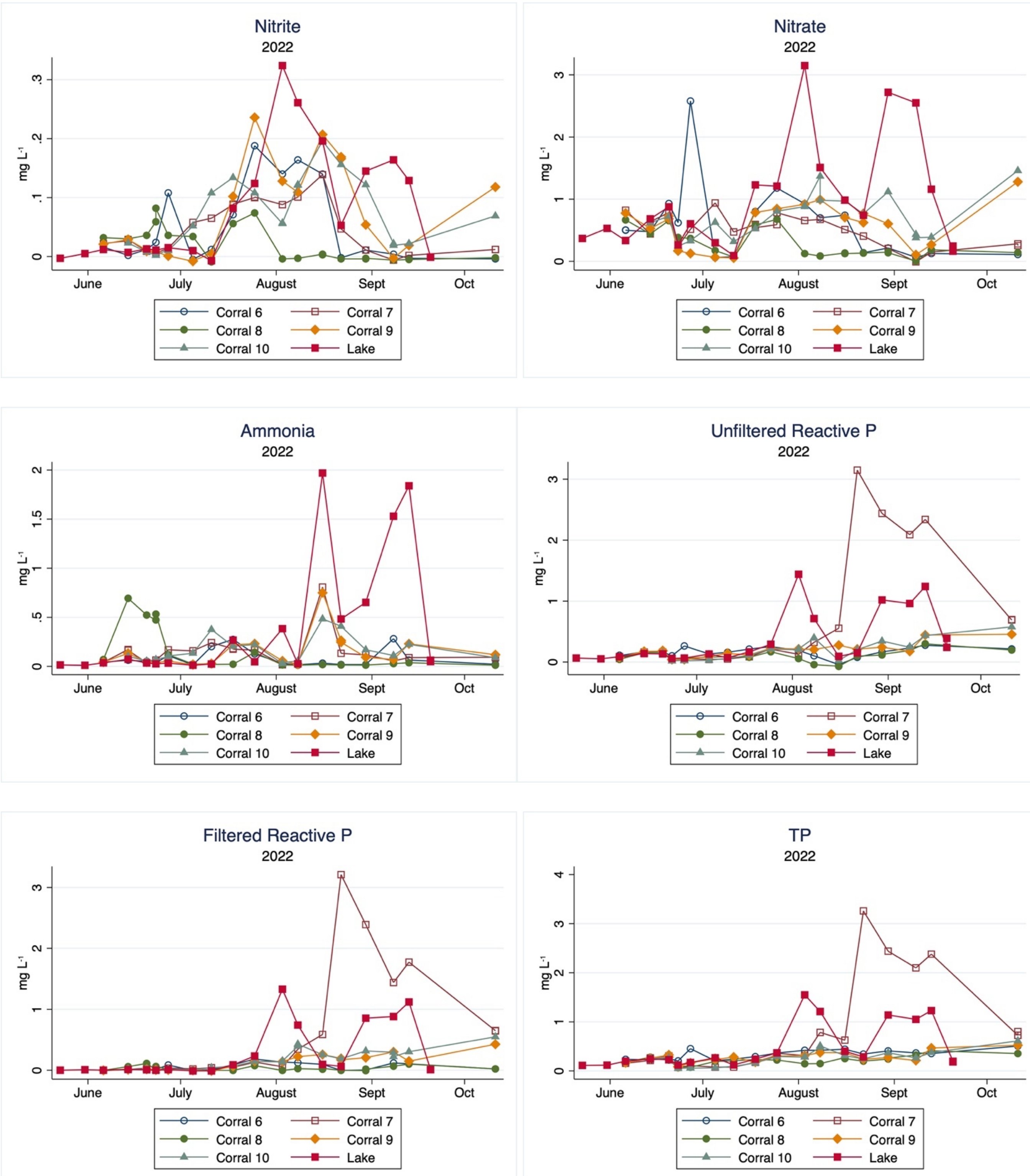


Figure 54. Nutrient concentrations in Corrals 6 through 10 and lake over durations of study. Notice spike in phosphorus fractions in Corral 7 after addition in mid-August.

Nutrients, Phytoplankton, and zooplankton

October Corrals 6 to 10

Table 65. Correlations between phytoplankton, zooplankton, and nutrients in Corrals 6 to 10 on October 11, 2022. N = 5; r = first value; p = second value in italics).

	zooplankton	nitrite	nitrate	ammonia	unfiltered reactive p	filtered reactive P	TP
nitrite	-0.27						
	0.65						
nitrate	-0.32	0.90					
	0.59	*0.03*					
ammonia	-0.58	0.83	0.76				
	0.30	*0.07*	*0.13*				
unfiltered reactive P	-0.64	0.38	0.46	0.80			
	0.23	*0.51*	*0.43*	*0.10*			
Filtered reactive P	-0.62	0.50	0.56	0.86	0.99		
	0.26	*0.39*	*0.32*	*0.05*	*0.00*		
TP	-0.82	0.12	0.18	0.62	0.90	0.85	
	0.08	*0.84*	*0.76*	*0.26*	*0.03*	*0.06*	
phytoplankton	0.34	-0.34	-0.60	-0.58	-0.82	-0.8	-0.61
	0.57	*0.56*	*0.27*	*0.29*	*0.08*	*0.07*	*0.27*

There was good evidence that phytoplankton biovolume was negatively related to filtered reactive P (Figure 55), given the small sample size (N = 5). No nutrient samples were collected from the lake on this date, therefore closest values were used.

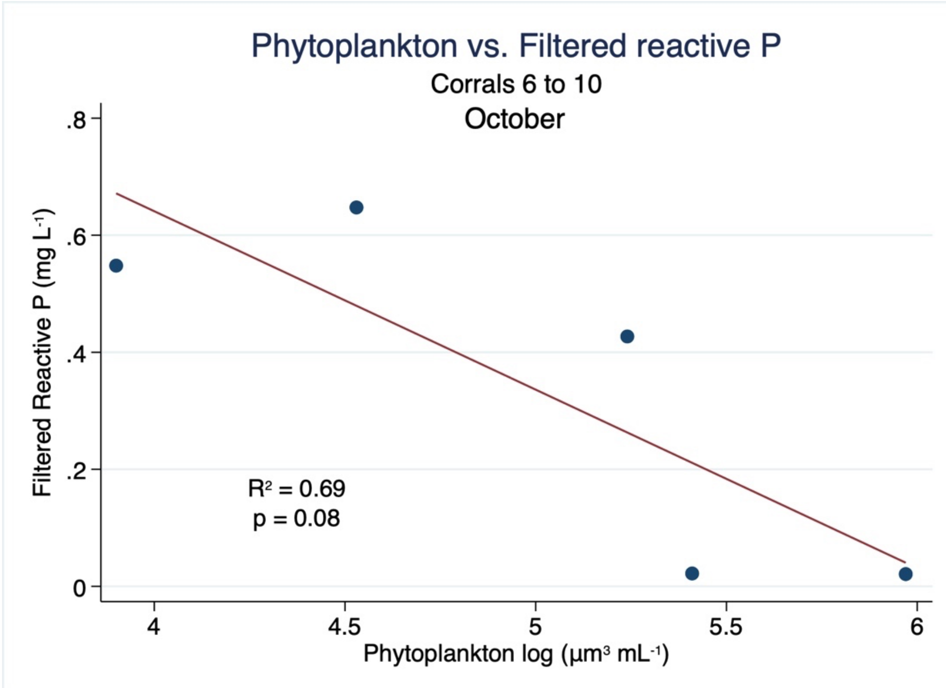


Figure 55. Relation between filtered reactive phosphorus and phytoplankton biovolume from October sampling event.

There was also weak evidence that phytoplankton biovolume (log (um^3 L^{-1})) was also negatively correlated with unfiltered reactive P (r = -0.83, p = 0.09) and that zooplankton abundance (individuals L^{-1}) were negatively correlated with TP (r = -0.82, p = 0.08). We interpret these findings as zooplankton are dependent on phytoplankton and phytoplankton consume reactive phosphorus.

Light

The simplest and most effective metric to measure changes in primary production from water column to benthic primary production is measuring photosynthetic active radiation (PAR), the light available for primary production at all wavelengths of the visible spectrum (Kelble et al. 2005). Traditionally light limitation for aquatic algal growth is considered when light intensity is 1% of surface irradiance (Sverdrup et al. 1954, Kelble et al. 2005, Kirk 2011). Factors causing light limitation in Utah Lake are numerous and are a primary blockade to restoration (see Discussion).

We analyzed several measures of light in this study including, turbidity (NTUs), Secchi disk depth, and light attenuation coefficients derived from Secchi disk readings inside and outside of corrals and in most instances found good to strong evidence of corral treatment effects. Shallow water corrals (Corrals 1 to 5) behaved differently that deeper, open water corrals (Corrals 6 to 10) and results are presented as such.

Shallow water Corrals 1 to 5

Turbidity

Turbidity was the least predictive measure of effects of corrals on light attenuation, except that turbidity was higher in Corral 3 than other corrals and the lake in May (Figure 56). Corral 3 treatment included a large carp (and macrophytes, bivalves) that obviously caused significant bioturbation especially in May during spawning season when carp "lose their minds" and are rambunctious.

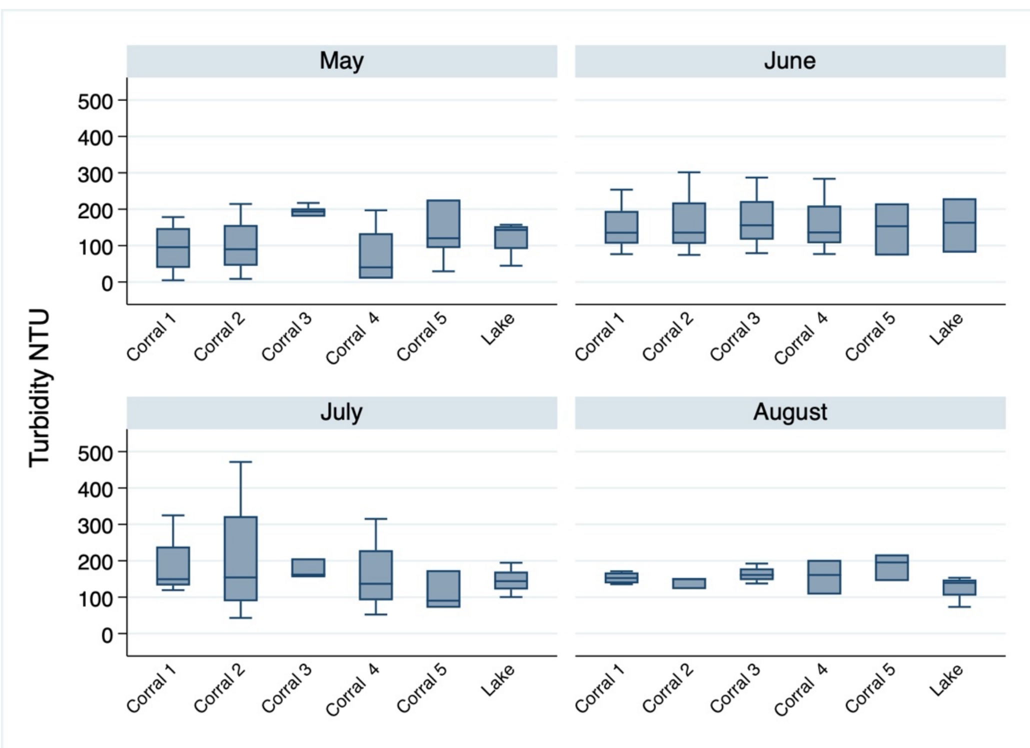


Figure 56. Boxplots comparing turbidity (NTU) between shallow water corrals by month.

Secchi Depth and Derived Light Attenuation Coefficients

Secchi depth readings in corrals were recorded as true depth values even if the disk was visible at the bottom of the insides of corrals. In these instances, Secchi depths were underestimated because we did not know how much deeper readings could have been made. This limitation should be understood in the following results. Secchi depths also can give a rough estimate of light intensity at 1% surface. However, depth indices can vary from about 1.7 to 2.26 due to nonlinear light attenuation with depth (Padial and Thomaz 2008). Therefore, a simple crude estimate of 1% surface light intensity can be to multiply Secchi depth by 2.

Secchi depth measurements provide a much clearer picture of shallow water corral effects on light with Corral 3 and the lake having lower readings than the mean and the other corrals (Figure 57). The control corrals, Corrals 4 and 5 had the highest Secchi readings (Figure 57).

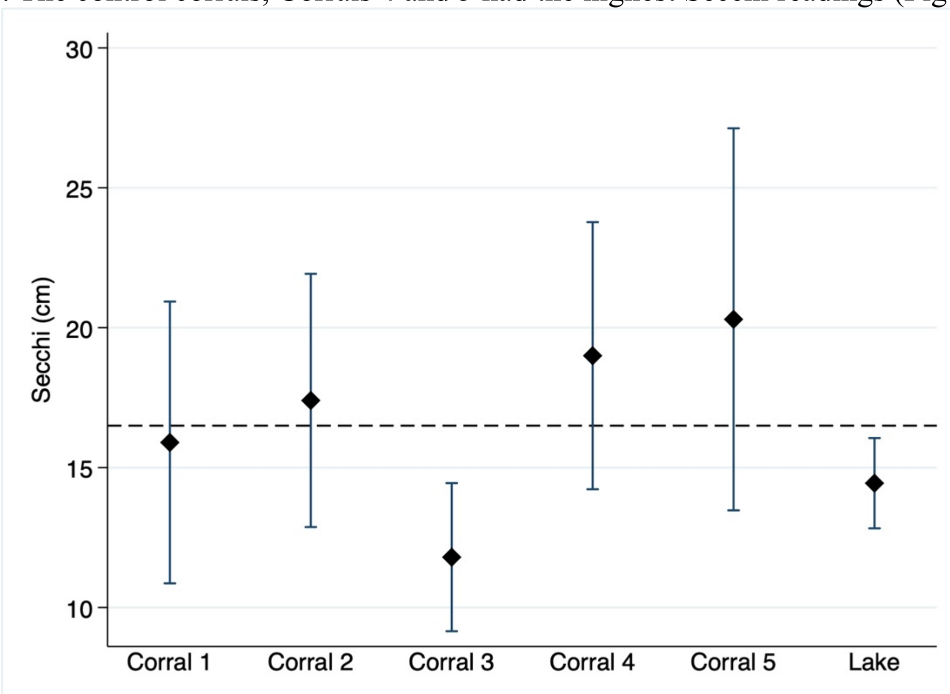


Figure 57. Secchi disk depth mean and 95% estimates between Corrals 1 to 5 and lake.

Because of the unknown but likely nonlinear light attenuation of light in Utah Lake, we used the nonlinear model for Secchi Disk depth index developed by Padial and Thomaz (2008):

$$k = 2.00 \text{ x } SD^{-0.76}$$

where k is the light attenuation coefficient.

Best fit fractional probit regression module for Secchi depth derived light attenuation coefficients in the shallow corrals 1 to 5 and lake. There was good evidence that Corral 3 had a higher coefficient than the lake (Figure 58, Table 66) due to the imprisoned rambunctious carp that was prevented from leaving the corral and joining its free ranging cohorts. Corrals 2, 4, and 5 had lower than mean coefficients and Corral 1 and the lake had about the same mean coefficient as the lake (Figure 58).

Table 66. Best fit fractional probit regression module of Secchi depth derived light attenuation coefficients (var13) vs. Corrals 1 to 5 and lake. Lake was baseline (var11).

```
Fractional probit regression                    Number of obs     =         59
                                                Wald chi2(5)      =       8.08
                                                Prob > chi2       =     0.1520
Log pseudolikelihood = -34.105854               Pseudo R2         =     0.0064
```

var13	Coef.	Robust Std. Err.	z	P>|z|	[95% Conf.	Interval]
var11						
1	.0158461	.075727	0.21	0.834	-.1325761	.1642682
2	-.0584777	.0732188	-0.80	0.424	-.2019838	.0850285
3	.2279167	.1241695	1.84	0.066	-.015451	.4712844
4	-.1052585	.0756348	-1.39	0.164	-.2534999	.0429829
5	-.0981305	.0853279	-1.15	0.250	-.2653701	.069109
_cons	-.6180266	.0377718	-16.36	0.000	-.6920579	-.5439953

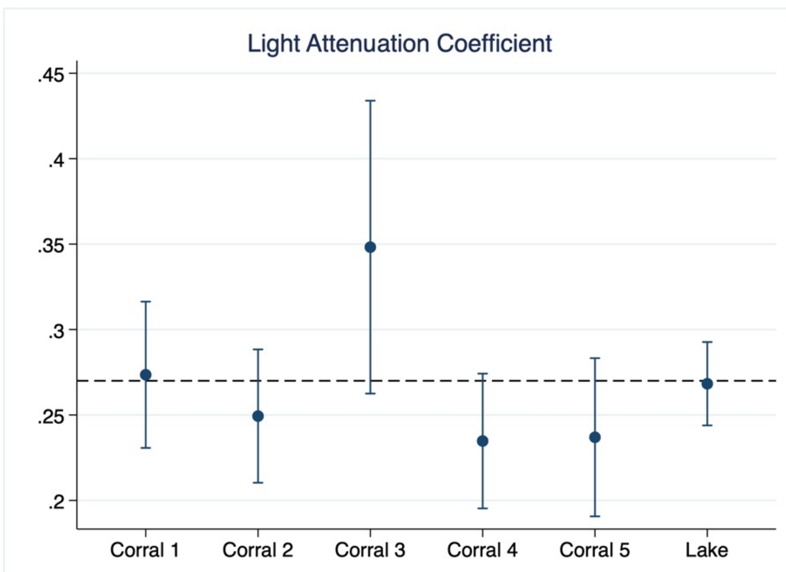


Figure 58. Best fit regression predicted Secchi disk depth light attenuation coefficients for Corrals 1 to 5 and lake. Mean and 95% CIs.

Deep, open water corrals 6 to 10

Turbidity

Turbidity varied temporally and due to corral affects, particularly in the deep open water corrals. A best fit linear regression model was made using turbidity as a function of corrals and months that gave and $R^2 = 0.46$, with evidence that corrals and months differed (Table 67, Figure 59). There was strong evidence that turbidity in Corral 6 was greater than Corrals 7 and 10 and some evidence greater than Corral 9 (Table 67, Figure 59). Corrals 6 and 8 had zooplanktivorous fishes that could have had trophic cascade effects discussed elsewhere in this report.

Table 67. Best fit linear regression of turbidity as a function of corral treatments and months. Corral 6 and May were baseline.

```
. regress turbidity i.corralcode i.Month

      Source |       SS           df       MS      Number of obs   =        94
-------------+----------------------------------   F(9, 84)        =      8.00
       Model |  148503.999         9  16500.4444   Prob > F        =    0.0000
    Residual |  173322.537        84  2063.36353   R-squared       =    0.4614
-------------+----------------------------------   Adj R-squared   =    0.4037
       Total |  321826.536        93  3460.50039   Root MSE        =    45.424

------------------------------------------------------------------------------
   turbidity |      Coef.   Std. Err.      t    P>|t|     [95% Conf. Interval]
-------------+----------------------------------------------------------------
  corralcode |
    Corral 7 |   -67.8764   17.61309    -3.85   0.000     -102.902   -32.85084
    Corral 8 |   -13.3592    17.1653    -0.78   0.439    -47.49427    20.77587
    Corral 9 |  -29.71164    16.8069    -1.77   0.081    -63.13401    3.710734
   Corral 10 |  -72.76624   17.64292    -4.12   0.000    -107.8511   -37.68135
        Lake |  -24.08905   17.90492    -1.35   0.182    -59.69495    11.51685
             |
       Month |
        June |    46.5438   35.43568     1.31   0.193    -23.92394    117.0115
        July |   31.95001   35.13716     0.91   0.366    -37.92409    101.8241
      August |   71.45379   34.94239     2.04   0.044     1.967021    140.9406
   September |   134.7348   37.27387     3.61   0.001     60.61162     208.858
             |
       _cons |   117.0241    36.7732     3.18   0.002     43.89652    190.1516
------------------------------------------------------------------------------
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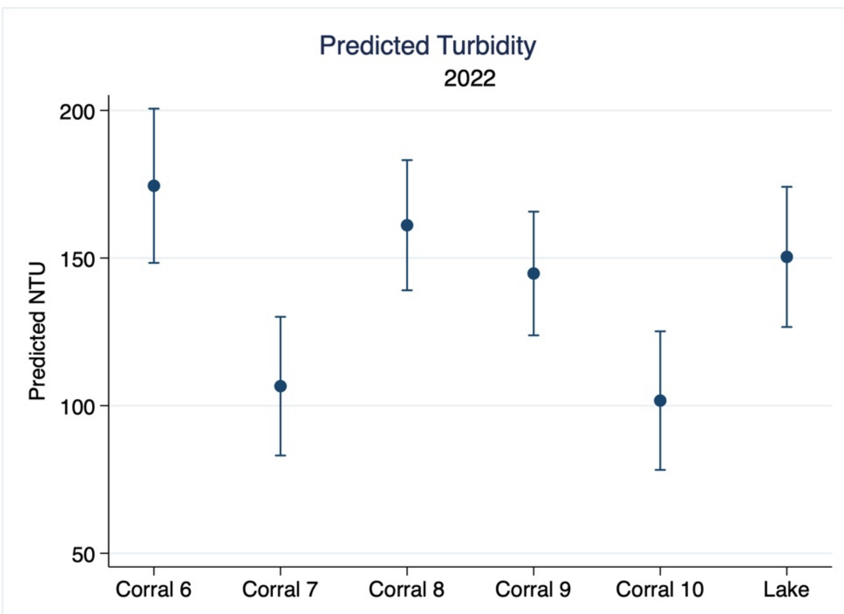

Figure 59. Predicted turbidity in Corrals 6 to 10 based on best fit model in Table 67. Mean and 95% CIs.

Secchi Depth and Derived Light Attenuation Coefficients

The best fit model for explain Secchi depth values in Corrals 6 to 10 was a Generalized Linear model vs. corrals that provided strong evidence that Secchi depths in all corrals except Corral 6 were greater than lake values (Table 68, Figure 60).

Table 68.Best fit generalized linear module (Poisson function) for Secchi depth vs. Corrals 6 to 10 and lake. Lake was baseline comparison.

Generalized linear models		Number of obs =	108
Optimization :	ML	Residual df =	102
		Scale parameter =	1
Deviance =	993.6321232	(1/df) Deviance =	9.741491
Pearson =	1079.212819	(1/df) Pearson =	10.58052
Variance function:	V(u) = u	[Poisson]	
Link function :	g(u) = u	[Identity]	
		AIC =	14.13621
Log likelihood =	-757.3555821	BIC =	516.0547

secchi2	Coef.	OIM Std. Err.	z	P>|z|	[95% Conf.	Interval]
Site2						
Corral 6	-.6286765	1.274219	-0.49	0.622	-3.1261	1.868747
Corral 7	20.97917	1.583118	13.25	0.000	17.87631	24.08202
Corral 8	14.25	1.612936	8.83	0.000	11.0887	17.4113
Corral 9	6.018382	1.41938	4.24	0.000	3.23645	8.800315
Corral 10	24.16964	1.630396	14.82	0.000	20.97413	27.36516
_cons	13.6875	.9249155	14.80	0.000	11.8747	15.5003

Corral 7, 8, and 10 Secchi depths based on the regression model were consistently greater than the mean, whereas Corrals 6, 9, and lake values were less than the mean (Figure 60).

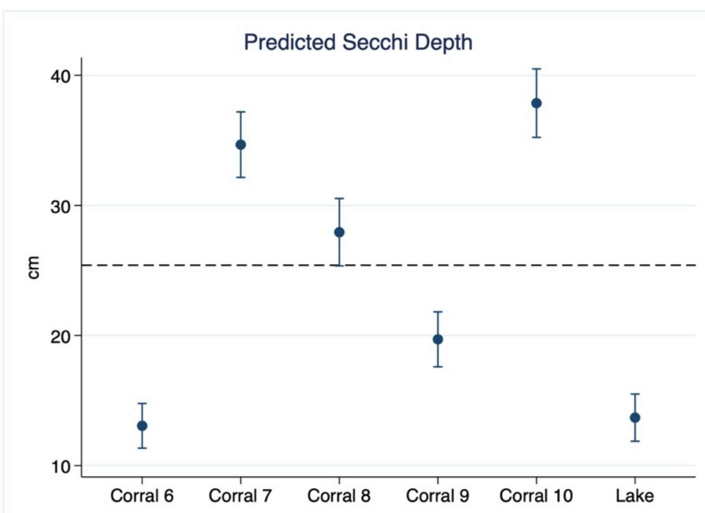

Figure 60. Best fit GLM regression predicted Secchi depths for Corrals 6 to 10 and lake. Mean and 95% CIs.

The best fit regression model was a fractional probit model that provide strong evidence that Secchi depth based light attenuation coefficients were lower in Corrals 7 and 10 than the lake but no evidence for Corrals 6, 8, and 9 coefficients lower than the lake (Figure 61, Table 69).

Table 69. Best fit fraction probit regression module for Secchi depth based light attenuation coefficients vs. Corrals 6 to 10 and lake. Lake was baseline comparison.

```
Fractional probit regression                    Number of obs     =        108
                                                Wald chi2(5)      =      31.07
                                                Prob > chi2       =     0.0000
Log pseudolikelihood = -58.341339               Pseudo R2         =     0.0165
```

lightattenuation	Coef.	Robust Std. Err.	z	P>|z|	[95% Conf.	Interval]
sitecode						
6	.0946171	.0974616	0.97	0.332	-.0964042	.2856384
7	-.3308644	.1077555	-3.07	0.002	-.5420614	-.1196675
8	-.1163178	.1068793	-1.09	0.276	-.3257974	.0931618
9	-.1179345	.0980387	-1.20	0.229	-.3100869	.0742179
10	-.4392922	.0985533	-4.46	0.000	-.6324531	-.2461312
_cons	-.5533662	.0490415	-11.28	0.000	-.6494857	-.4572467

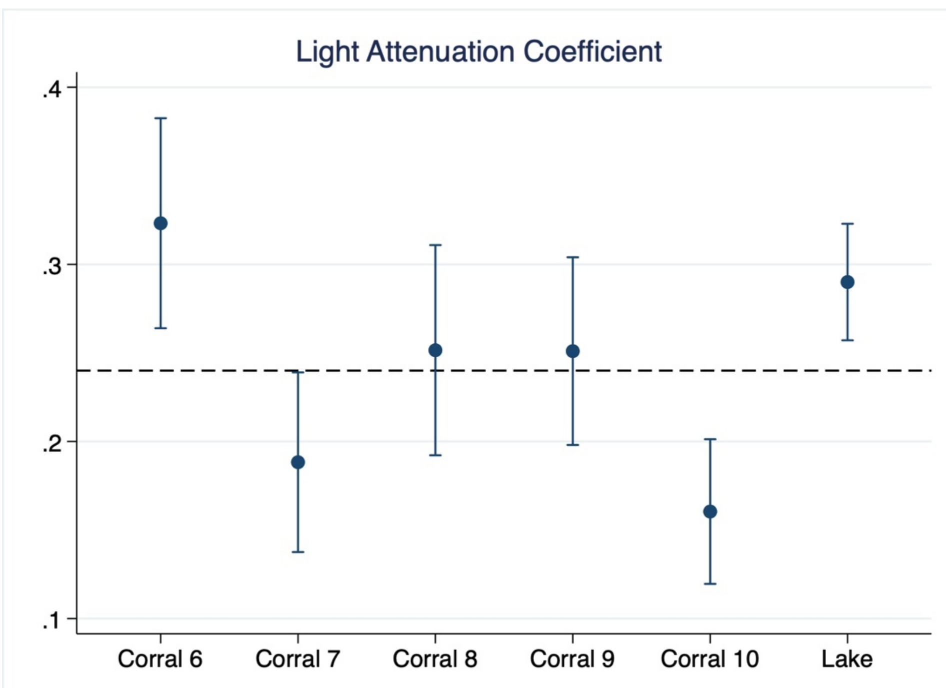

Figure 61. Light attenuation coefficients predicted means and 95% CIs based on best fit regression module.

August

On closer inspection, turbidity seemed to show a stronger relationship to corral effects in August (Figure 62, Table 70) and August data coincided with our mid-term biological sampling allowing us to make some inferences on the relation between light and biota in the food web including possible trophic cascade effects.

Table 70. Best fit linear regression of turbidity as a function of corral treatments in August 2022. Corral 6 was baseline.

```
. regress turbidity_01 i.corralcode_01
```

Source	SS	df	MS			
				Number of obs	=	33
				F(5, 27)	=	10.15
Model	37356.4159	5	7471.28317	Prob > F	=	0.0000
Residual	19881.1765	27	736.339872	R-squared	=	0.6527
				Adj R-squared	=	0.5883
Total	57237.5924	32	1788.67476	Root MSE	=	27.136

turbidity_01	Coef.	Std. Err.	t	P>|t|	[95% Conf.	Interval]
corralcode_01						
Corral 7	-71.6875	19.18775	-3.74	0.001	-111.0575	-32.31748
Corral 8	9.510004	17.00813	0.56	0.581	-25.38779	44.4078
Corral 9	-55.17	17.51594	-3.15	0.004	-91.10974	-19.23025
Corral 10	-69.47429	17.00813	-4.08	0.000	-104.3721	-34.57649
Lake	-12.478	18.2031	-0.69	0.499	-49.82768	24.87168
_cons	186.26	13.56779	13.73	0.000	158.4212	214.0988

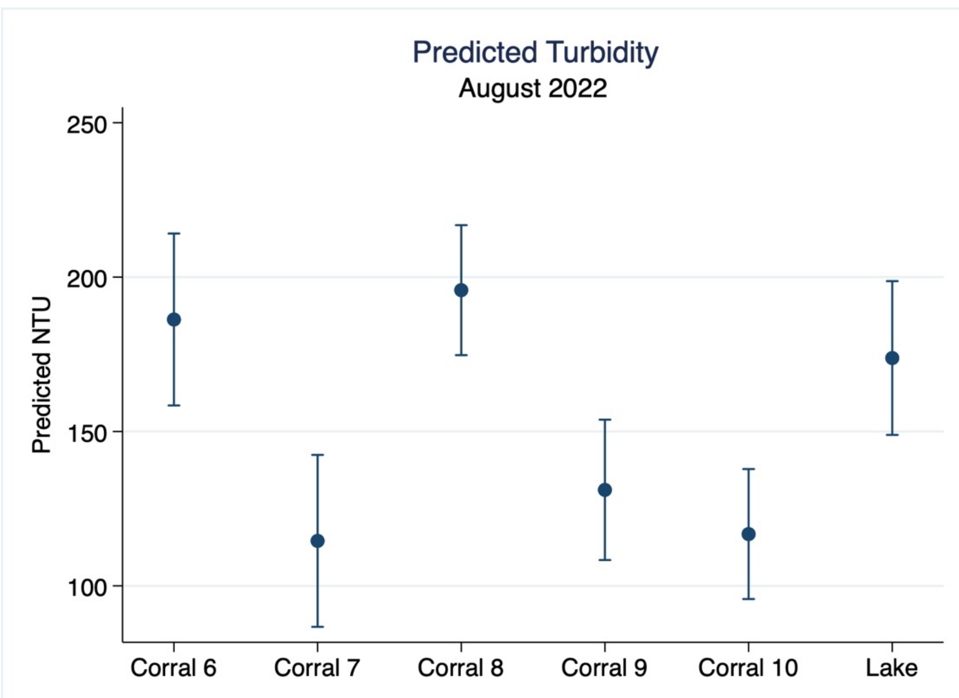

Figure 62. Predicted turbidity in corrals 6 to 10 in August based on best fit model in Table 70.

Turbidity was measured in August along with phytoplankton, zooplankton, and benthic invertebrates. Subsequently, we modeled relationships and found good evidence that turbidity was indirectly negatively related to zooplankton abundance (L^{-1}) suggesting to us and consistent with the literature that the more zooplankton there were the less phytoplankton biovolume there was due to grazing and consequently less turbidity due to less phytoplankton biovolume in the water column.

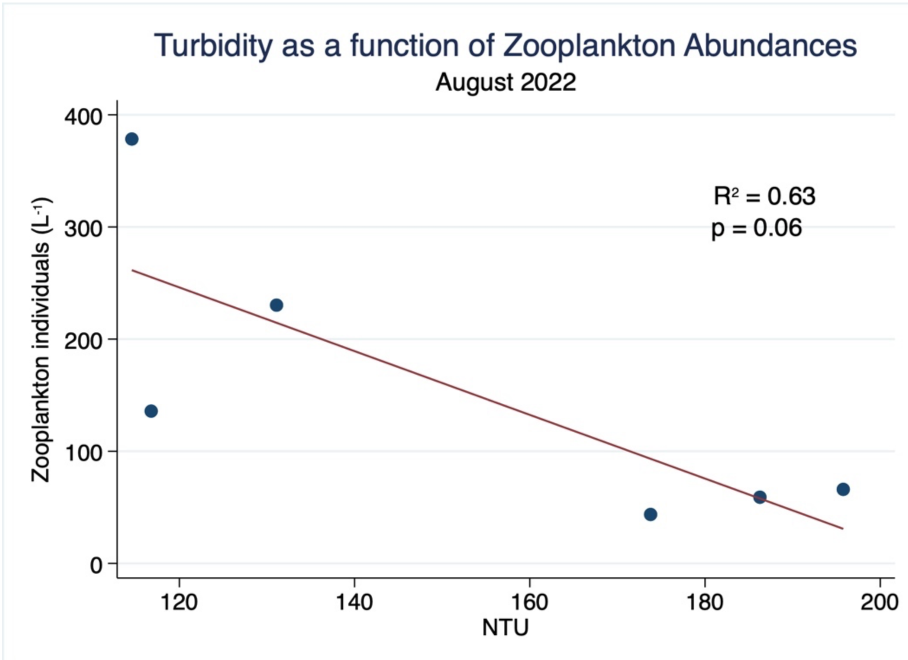

Figure 63. Turbidity as a function of zooplankton abundance in August 2022.

This apparent top down, trophic cascade was more pronounced using Secchi depths and associated light attenuation coefficients (Table 71,
Table 72, Figure 64). We found strong evidence that Secchi depth was affected by zooplankton abundance and that light attenuation coefficients were strongly affected by zooplankton abundance (Table 71,
Table 72, Figure 64).

Table 71. A linear regression model of the potential indirect effect of zooplankton on light availability as measured by Secchi depth. This model was not the most appropriate model but illustrates this relation.

```
. regress secchi zooplankton

      Source |       SS           df       MS      Number of obs   =        12
-------------+----------------------------------   F(1, 10)        =      7.34
       Model |  707.585815         1  707.585815   Prob > F        =    0.0219
    Residual |  963.523386        10  96.3523386   R-squared       =    0.4234
-------------+----------------------------------   Adj R-squared   =    0.3658
       Total |   1671.1092        11  151.919018   Root MSE        =    9.8159

------------------------------------------------------------------------------
      secchi |      Coef.   Std. Err.      t    P>|t|     [95% Conf. Interval]
-------------+----------------------------------------------------------------
 zooplankton |   .0713069   .0263132     2.71   0.022     .0126775    .1299364
       _cons |     16.528   5.066073     3.26   0.009     5.240082    27.81591
------------------------------------------------------------------------------
```

Table 72. Best fit regression model was a fractional probit model for light attenuation coefficient vs. zooplankton abundance (L^{-1}).

```
Fractional probit regression                    Number of obs     =         12
                                                Wald chi2(1)      =       7.60
                                                Prob > chi2       =     0.0058
Log pseudolikelihood = -5.7790998               Pseudo R2         =     0.0174
```

lac	Coef.	Robust Std. Err.	z	P>|z|	[95% Conf.	Interval]
zooplankton	-.001805	.0006549	-2.76	0.006	-.0030885	-.0005215
_cons	-.596259	.1481624	-4.02	0.000	-.8866521	-.305866

Corrals 6 and 8 housed zooplanktivorous fish and Corral 3 had a large boisterous carp, a species whose adult diets often consists of zooplankton. These three corrals had the lowest zooplankton abundances and lowest Secchi depths closely resembling lake conditions (Figure 64). Other corrals including control corrals (Corrals 4, 5, and 10) had higher zooplankton abundances and greater Secchi depths. Corral 7 (nutrient addition with the most observed periphytic algae) was somewhat of an anomaly with the highest zooplankton abundances and very high Secchi depth readings. Corrals 1 and 2 had low zooplankton abundance and low light attenuation (large Secchi depth) (See next section: Macrophytes).

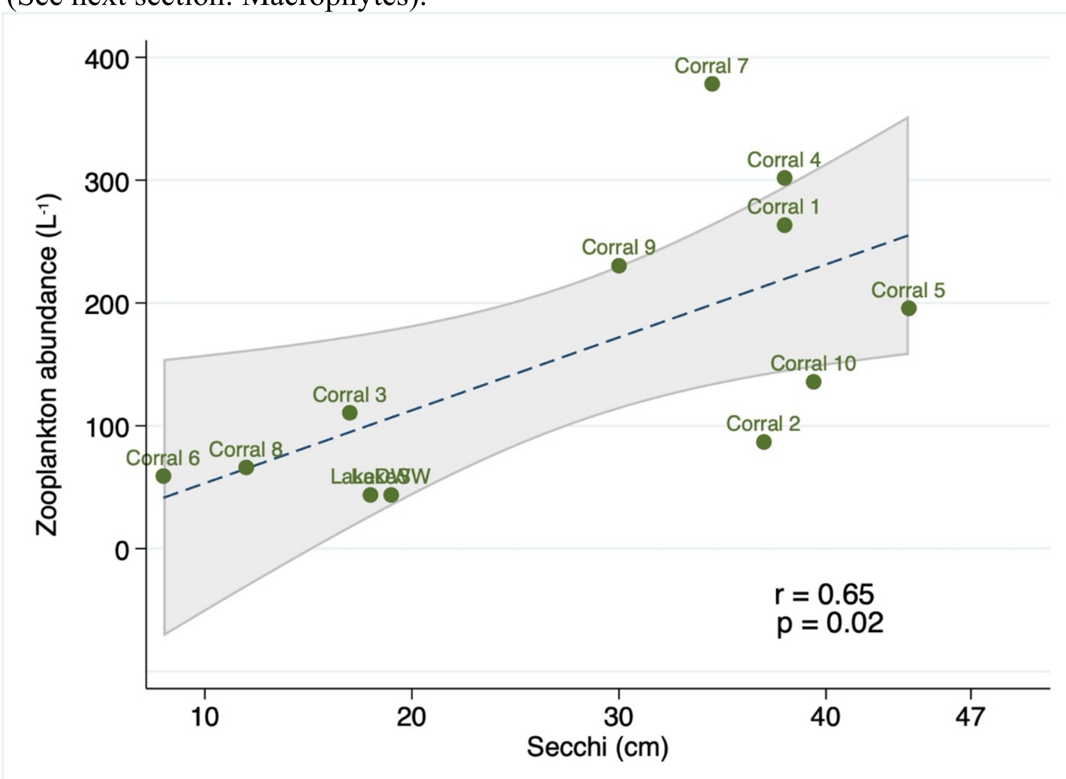

Figure 64. Relation between zooplankton abundance and Secchi depth for Corrals 1-10 and lake samples collected on August 16, 2022. Secchi depths were not collected on August 16, 2022; therefore, the closest dates were used.

Although other factors could have been responsible for these results the most logical and consistent with the literature suggests top down, trophic cascade effects where zooplanktivores reduced zooplankton abundance that allowed phytoplankton to proliferate, thus increasing light attenuation. Subsequently, zooplankton can be instrumental in keeping water clear.

The following photo (Figure 65) taken in June 2022 demonstrates how quickly water clarity in the lake can improve when bioturbation from carp and wave action induced turbidity are eliminated. Mesocosms (aka limnocorrals) were established several weeks prior to when photo was taken for a collaborative multiyear research study designed to understand causes of and remedies for algal blooms focusing on ecosystem restoration. Water clarity within three of the mesocosms allowed light to penetrate to the bottom of the mesocosms (approximately 0.8-to-1.0-meter depth). Secchi disk was visible at the bottom of these three mesocosms demonstrating that light attenuation (availability) was at least 1.6 to 2.0 meters depth and available to benthic algae simply by eliminating carp and wave action. Contrarily, light attenuation (availability) was < 0.2 m directly outside of the mesocosm. One female carp in spawning condition inadvertently entered the middle mesocosm a week or so prior to photo and reduced light attenuation to approximately 0.4 m via bioturbation.

Figure 65. Mesocosms (limnocorrals) demonstrating the effects of removing carp and wave action on water clarity and light attenuation. Mesocosms 1,2, and 4 from left to right were carp and wave action free with light attenuation at least to 2.0 m depth. Mesocosm 3 from left had at least one carp that caused light attenuation to be reduced to approximately 0.4 m. Light attenuation outside of mesocosms was < 0.2 m. Photo courtesy Rich Mickelson, Timpanogos Special Service District.

Bivalves

We found limited evidence that bivalves had an effect on the ecology within corrals compared to the lake mostly because bivalves were added to corrals that also had other treatments including macrophytes (Corral 1) and macrophytes and a carp (Corral 3) in an effort to demonstrate the synergistic effects of macrophytes and bivalves (Corral 1) (see Discussion) and how these synergistic effects could be mitigated by benthivorous fish (Corral 3). This limited evidence was disappointing because there is overwhelming evidence that bivalves have a strong ecosystem engineering effect wherever they occur (see Discussion sections).

In addition, at the end of the experiments we found very few live bivalves mostly because of immense sediment accrual (compared to their body size) that buried them, and they were likely unable to survive. However, they did survive within Corral 1 long enough to reproduce with several very small live juveniles found on August 16, 2022 (Figure 66). This finding suggests that in addition to nutrient and turbidity pollutants fluxing from fine unconsolidated sediments affecting the water column, these sediments also have a negative effect on the benthic invertebrates including bivalves that are essential for restoring Utah Lake. Constant sediment movement, deposition, and accrual in areas of Utah Lake may partially explain low densities of bivalves (see Discussion).

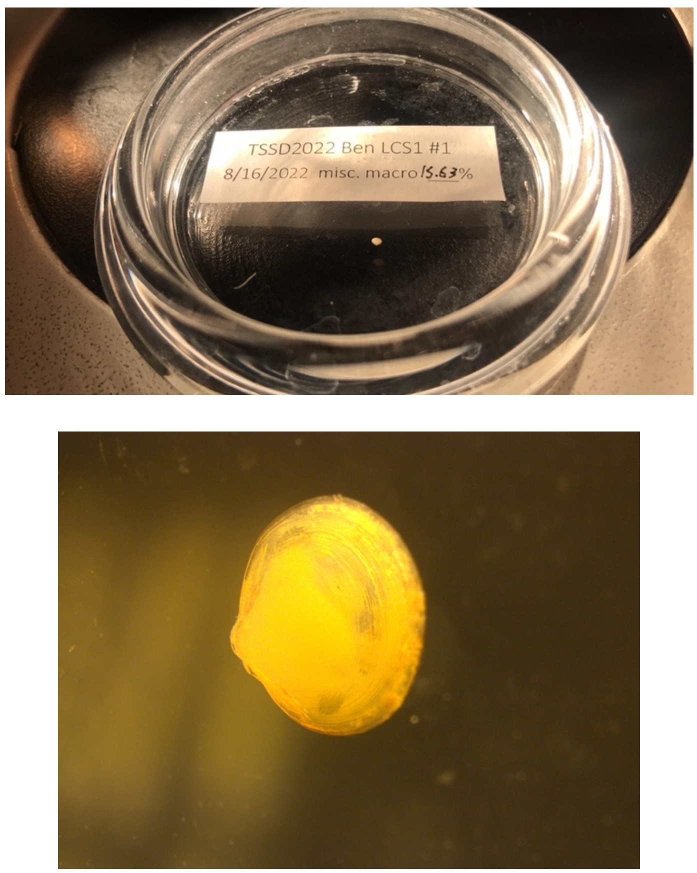

Figure 66. Image of live juvenile bivalve that was born in Corral 1 and collected on August 16. 2022.

We are scheduled to deploy two bivalve treatment corrals in Spring 2023, using specially designed suspended cages that will eliminate the negative effects of sediment burial and allow us to measure their contribution to improving water quality and potential restoration of Utah Lake.

Macrophytes

We stocked three corrals (Corrals 1, 2, and 3) with several macrophytes [submerged aquatic vegetation (SAV) and emergent aquatic vegetation (EAV]) that included Hardstem Bullrush (*Schenoplectus acutus*), Broadleaf Cattail (*Typha latifolia*), Water Smartweed (*Persicaria amphibia*) and Water crowfoot (*Ranunculus aquatilis*) in spring/early summer 2022 (Figure 68, Figure 69). This was in addition to two exclosures stocked with the same species in 2021 (Figure 73, Figure 74, Figure 75). Establishment in the corrals was quite successful, however in Corral 3 our rambunctious large carp tore up on plug of vegetation that was then reestablished. As of the end of the study macrophytes were well established within corrals (Figure 70, Figure 71) and valuable information was obtained including their positive effects on light attenuation reduction, sediment stabilization, and structural habitat for periphytic algae, invertebrates, and perching birds.

Macrophyte corrals also affected zooplankton assemblages. For example, Cyclopidae (copepods) abundances were greater in Corrals 1 and 2 than other corrals and the lake on July 28, 2022, and August 16, 2022, as were Daphniidae (Cladocera) (see Results: Zooplankton) (Figure 67).

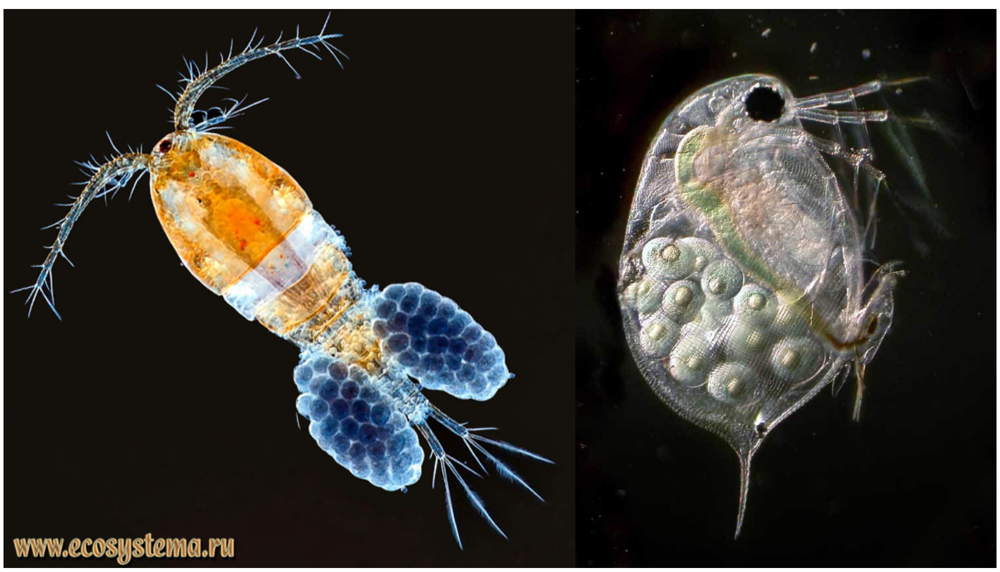

Figure 67. Cyclopidae (copepod)(left) and Daphniidae (Daphnia pulex) (cladoceran) (right) were more abundant in Corrals 1 and 2 that had macrophytes but not carp in July and August 2022 than other corrals and our lake samples. Images downloaded from internet.

These zooplankton taxa typically have greater abundances in protected habitat, which the macrophytes provided in abundance.

As briefly discussed in a previous section, Corrals 1 and 2 had higher zooplankton abundance and greater Secchi depth readings (lowered light attenuation) (Figure 64). We attribute this to zooplankton grazing on phytoplankton subsequently reducing phytoplankton biovolume effects on light attenuation. Bivalves in Corral 1 may have also reduced phytoplankton via filter feeding but the problems with bivalve survival presented in the Bivalve results section made it difficult to discern. Macrophytes likely also blocked wave action induced sediments flux contributing to improved light penetration often to the bottom of corrals.

Stems of all macrophytes in Corrals 1, 2, and 3 were thickly covered in epiphytic algae, what we describe as BDS, a mixture of bacteria, diatoms, and sediment (Hoven 2015; Hoven, Richards, and Johnson 2014; Hoven and Richards 2015). Thick BDS on macrophyte stems is indicative of excessive and underutilized nutrients and other impairments (Hoven 2015; Hoven, Richards, and Johnson 2014; Hoven and Richards 2015). Epiphytic algae most likely competed with phytoplankton for nutrients. Filtered reactive phosphorus was often lowest in Corrals 1 and 2 during summer months (see Results: Nutrients).

Figure 68.Blake Wellard (right), Jason Baker (second from right) and two volunteers digging up emergent vegetation from local source for stocking in corrals and exclosures on June 11, 2022. Notice how tall and dense vegetation wall is. This is precisely what we suggest needs to be accomplished within shallow areas of Utah Lake, a wall of tall emergent vegetation that will block wave action, reduce turbidity, increase habitat, and stabilize sediment.

Figure 69. Blake Wellard (co-author) hauling a heavy sled full of emergent vegetation across the wetland to stock corrals, June 11, 2022.

Figure 70. Corrals 1,2, and 3 (upper right) stocked with native aquatic vegetation, September 2022. Exclosure (left) with aquatic vegetation established in 2021. Notice how tall and good condition exclosure vegetation is after 2 years exposed to lake level fluctuations including ice scouring. Notice also how surrounding vegetation has had limited growth demonstrating that native plants will take years to establish and become as luxuriant and important as wave breaks and sediment stabilization unassisted.

Figure 71. Corrals 1 and 2 stocked with emergent aquatic macrophytes, September 2022. Utah Lake level was < 50% at time of photo. Corrals were in about 1 meter of water depth at beginning of study in May 2022.

Figure 72. Corral 3 stocked with macrophytes and after corral was removed September 2022. Deeper water corrals can be seen in upper right of photo.

Figure 73. Emergent aquatic macrophytes in two exclosures (far right and middle left) after two years of establishment. Both corrals were under water when stocked in spring of 2021. Notice how surrounding vegetation has had limited growth demonstrating that natura reestablishment could take years or decades without active restoration.

Figure 74. On April 15, 2022, this was the shallow water flow-through exclosure stocked with macrophytes in 2021. This is the same exclosure shown on the far right of photo in Figure 73. Hardstem Bullrush (Schenoplectus acutus), Broadleaf Cattail (Typha latifolia), and even Water Smartweed (Persicaria amphibia) were beginning to green-up much faster than surrounding shoreline vegetation (upper area).

Figure 75. On April 15, 2022, this was the deeper water flow-through mesocosm stocked with macrophytes in 2021 (foreground exclosure). This was the same exclosure shown in Figure 73 on left side of photo. Shallow water exclosure can be seen in upper left of photo. Hardstem Bullrush (Schoenoplectus acutus), Broadleaf Cattail (Typha latifolia) were beginning to green-up much faster than surrounding shoreline vegetation (upper area). Shallow water mesocosm (Figure 74) can be seen in upper left area of this photo. This illustrates how water level fluctuations can change dramatically from season to season and year to year in Utah Lake (reservoir).

See Richards et al. (2021) mesocosm progress report for details of macrophyte success story including that planted macrophytes in exclosure cages survived ice flows, strong wind, and wave action, and appear to flourish if carp are not allowed to disturb them. Results from our macrophyte treatments (including exclosure cages) clearly demonstrated the benefits and need for native aquatic vegetation restoration in Utah Lake (see following discussions).

Discussion

Results from our 2022 mesocosm (limnocorral) ecological studies confirmed our premise (hypotheses) that wave and to a lesser extent carp induced turbidity, as well as planktivorous fish predation can have direct and indirect effects on phytoplankton, zooplankton, benthic invertebrates, benthic algae and periphyton, and light availability in Utah Lake. Reducing wave action and zooplanktivorous fish predation can allow for increased zooplankton abundance particularly larger sized individual taxa such as daphniids to prosper. Increased abundance of large-sized zooplankton should be able to graze and reduce phytoplankton biovolume and likely alter the phytoplankton assemblage's relative abundances and dynamics that will reverberate throughout Utah Lake's foodweb and ecosystem. Wave and carp induced turbulence is mostly responsible for nutrient flux from easily suspended fine sediments. Subsequently, turbulence reduction can increase light penetration to the substrate allowing benthic algae to increase in biovolume and compete with phytoplankton, including potential reduction of harmful algal blooms. Given the dominance of sediment nutrients flux to Utah Lake's water column, we suggest that external nutrient reduction alone will likely have little effect on improving the lake's ecosystem (Richards 2022d).

All results in this study are consistent with over a century of aquatic ecological findings from other ecosystems worldwide; Utah Lake was not expected to be an exception. These findings also show that restoration of Utah Lake is straight forward and not beyond are capability. Successful science based aquatic ecosystem restoration is being conducted worldwide (see the many Restoration Ecology journal articles published by the Society for Ecological Restoration). For example, Jin et al. (2021) documented a successful lake restoration project Marker Wadden in the Netherlands, an ecosystem similar to Utah Lake and one that can act as a template of what can be accomplished in Utah Lake. More detailed discussion on the relevance of our mesocosm findings in relation to aquatic ecosystem science and restoration follows. It should be noted that the following sections have substantial overlap due to the many interactions they invariably have within the ecosystem.

Light Limitation

The littoral zone is the area of a lake where rooted aquatic macrophytes (plants) are established. The limnetic zone is where rooted plants do not exist. Utah Lake currently has a very poorly functioning littoral zone primarily due to the lake being managed as a reservoir with unpredictable shoreline water level fluctuations, wind and wave action scouring, high suspended solid and algal turbidity, and to a lesser extent carp bioturbation. Our mesocosm results unmistakably demonstrated that Utah Lake is light limited; a finding that has been well known for several decades (L. Merritt, Professor Emeritus, BYU, and Rushforth Phycology, Richards 2021b).

Reduced light availability in the water column from sediment resuspension also decreases benthic algae that depend on light reaching the sediment surface. Consequently, reduction in benthic algal production can further increase nutrient availability in the water column resulting in a net positive effect on phytoplankton production. When light reaches the sediment surface, benthic algae can directly take up nutrients from both the water column and the sediment (Spears et al. 2008, Zhang et al. 2014), and can reduce nutrient release rates from the sediment by oxidizing the sediment through their photosynthetic activity (Carlton and Wetzel 1988). Benthic algae also stabilize the sediment surface through excretion of extra-cellular polymers (Paterson 1989) and mat formation (Dodds 2003), further reducing resuspension and thus becoming dominant over phytoplankton (Jäger and Diehl 2014). Benthic algae may be unable to colonize exposed habitat due to sediment resuspension and unstable sediment (Jorge and Beusekom 1995).

Trophic cascades and top-down control

Inorganic chemistry is relatively simple compared to biology systems (and biochemistry), which are considerably more complex. Ecosystems are even more complex, have higher exergy and ascendency, and lower entropy (see section: State, Structure, and Function of Utah Lake's Ecosystem). As an example, there are likely more types (diversity) of biochemical reactions and chemical compounds in a single 3 mm midge larvae than all the inorganic chemical compound interactions in the entirety of Utah Lake water, and ecological interactions are orders of magnitude more complex than either biology or chemistry alone. Take for example nutrient flux from sediments to water column. Simple diffusion models explain very little of this phenomenon in ecosystems such as Utah Lake. A somewhat more realistic model of nutrient flux that only include the role of one biological group of organisms, periphyton in phosphorus retention are shown in Figure 76.

ROLE OF PERIPHYTON IN PHOSPHORUS RETENTION 841

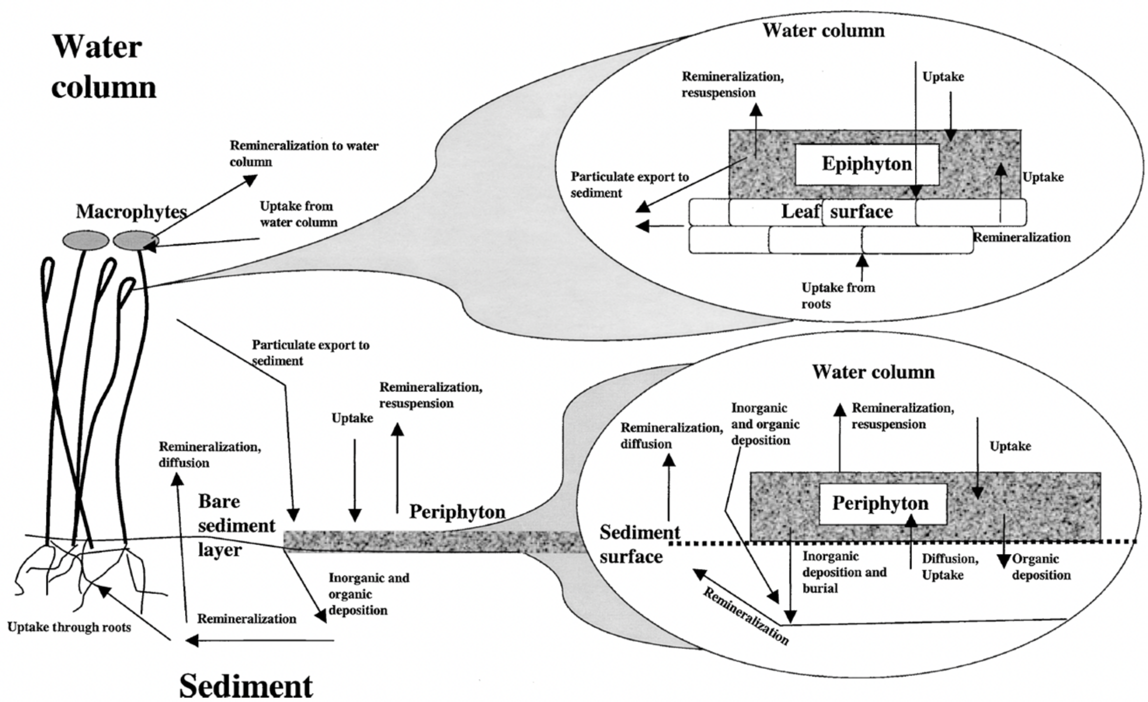

FIG. 1. Conceptual diagram of nutrient flux to and from sediments as modified by periphyton. The inset on the top-right details processes occurring at the surface of macrophytes, the inset at the lower right details processes at the sediment-periphyton interface.

Figure 76. Nutrient flux to and from sediments and water column as modified by periphyton and epiphyton. Taken from Dodds (2003).

The model shown in Figure 76 does not include other biota nor their ecological interactions within the food web including benthic invertebrates, microbial loop, or benthic feeding fishes, etc.

Although nutrients are critical for algae growth, nutrients typically explain substantially less than half the variability of algal blooms (Chl *a* as surrogate) in lakes. Carpenter and Kitchell (1993) stated that algal concentrations (production) can differ among lakes by an order of magnitude or more at any given level of nutrient loading or concentration. Obviously, something else affects algal growth. In addition, Carpenter and Kitchell (1993) found that just one simple component of the food web, *zooplankton mean length* (an indicator of size-selective predation and the intensity of grazing) explained 45% of the variability in summer mean chlorophyll *a* in their study lake, more than did nutrient levels. It is obvious that there are thousands of ecological interactions other than *zooplankton mean length* that affect chlorophyll *a* (e.g., algal blooms, phytoplankton assemblages and biomass) in lakes. These other factors dwell in the realm of trophic cascades or top-down controls[8].

[8] Trophic Cascades, Top-down controls are a well-known ecological concept and are triggered by the addition or removal of top predators and involving reciprocal changes in the relative populations of predator and prey through a food web, which often results in dramatic changes in ecosystem structure and nutrient cycling.

Trophic cascades (top-down controls in food webs) are not new to science. This concept has been well established in the ecological literature for almost a century (Elton 1927, Lindeman 1942, Paine 1980, others) and in many respects since Darwin's (1859) view that plants and animals 'are bound together by a web of complex relations.' In general, "the trophic cascade hypothesis states that nutrient input sets the potential productivity of lakes and that deviations from the potential are due to food web effects "(Carpenter et al., 1985, Carpenter and Kitchell 1993), i.e., trophic cascades/top-down control.

Wave driven turbulence, turbidity, and other effects.

Utah Lake suffers from high turbidity due to several factors including,

- its shallow nature,
- strong winds and waves,
- easily suspended fine sediments,
- bioturbator fishes (primarily carp but also other non-indigenous species in the catfish family),
- transition from benthic and macrophyte primary producers that stabilized sediments to phytoplankton dominated primary production,
- loss of mollusks that also stabilized sediments, and
- regulation as a reservoir that resulted in unnatural lake level fluctuations, etc. (Richards reports)

Turbidity in Utah Lake is now primarily caused by wind and wave driven sediment resuspension that directly affects light penetration and nutrient levels in the water column. Although bioturbators (e.g., carp, catfish) also contribute to sediment resuspension but likely to a lesser extent. Light and nutrient levels can have many anticipated and unanticipated indirect effects on Utah Lake's foodweb including the transfer of nutrients and energy from the base of the foodweb (primary producers), to grazer consumers (zooplankton), to higher level trophic organisms including fishes and birds.

Figure 77 illustrates the optimal production 'window' a balance between benthic algae and macrophyte driven production and phytoplankton driven production as affected by turbulence. This figure was taken from Jin et al. (2021) who documented successful restoration of a eutrophic aquatic ecosystem in the Netherlands and can be a model of how to restore Utah Lake.

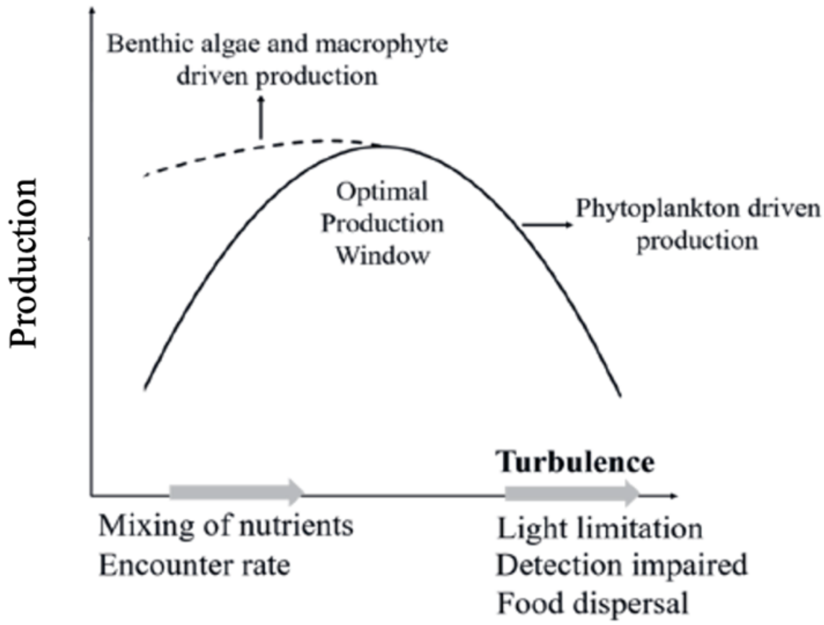

Figure 77. Response of primary, secondary, and tertiary production to turbulence (e.g., sediment resuspension, turbidity). From Jin et al. (2021).

Trophic transfer of energy and matter from primary producers to higher trophic levels is a fundamental aspect of food web functioning (Jin et al. 2021, Richards 2022a). A reduction in trophic transfer due to wind induced turbulence can potentially lead to declines of higher trophic levels in aquatic food webs including fish and waterbirds, but is generally understudied (Jin et al. 2021, Richards 2022a). A draft Utah Lake foodweb model created by Richards (2022b) suggested that trophic transfer efficiency in the lake was out of balance with Lindeman's (1942) 10% 'rule'. Richards (2022b) also found that zooplankton grazers in the lake did not appear to be able to utilize a large portion of the phytoplankton biomass mostly during summer months (i.e., low ecotrophic efficiency) and that much of the phytoplankton biomass was unconsumed and fell as detrital 'rain'. These findings suggest that the effects of sediment resuspension, turbulence, and turbidity on light and nutrient levels in Utah Lake likely play a significant role in retaining Utah Lake in an unbalanced poorly functioning state, but the lake is redeemable.

In large shallow lake ecosystems such as Utah Lake, phytoplankton primary productivity generally increases with nutrient availability but then becomes light limited by wave induced turbidity (Quinlan et al. 2021, Edwards et al. 2016, Scheffer 1998, Scheffer et al. 2001, Richards 2022b). Resuspension enhances release of sediment bound particles into the water column making them available to phytoplankton (Tammeorg et al. 2013, Tang et al. 2020, Zhang et al. 2020). However, large amounts of suspended solids entering the water column from resuspension interferes with nutrient and light availability for phytoplankton production (Schallenberg and Burns 2004).

Wind and wave action induced turbidity is a major impediment for all members of the food web. High turbidity makes it extremely difficult for visual predators (e.g., piscivorous fishes) to feed and in most of the lake when wave action is strong fish may not even attempt feeding. Turbidity acts as a cover for planktivorous fishes (e.g., all juvenile fishes in Utah Lake) allowing them to feed on zooplankton that would have helped control phytoplankton (Trochine et al 2022). Sediment resuspension from strong waves can last for many days after a storm event. Strong wave action also dislodges benthic invertebrates, including the most abundant taxon, midge larvae and is in part one of the reasons why midge larvae densities are not higher. Filter feeding invertebrate including remaining bivalve clams cease to feed when total suspended solids (TSS) reach concentrations of as little as 20 mg l^{-1} (Hornbach et al. 1984, Way et al. 1990). Even relatively pollution tolerant invasive Asian clams (*Corbicula* sp.) and less tolerant fingernail clams (Sphaerium) initiate pseudofeces[9] production at 17 to 20 mg l^{-1} TSS (Fuji 1979, Hornbach et al. 1984, Way et al. 1990). Increasing rates of suspended solids from sediment resuspension, calcium precipitate, and increasing algal concentrations may have been partly responsible for the demise of native mussels and severe reduction in native clam populations. The invasive Asian clam, *Corbicula* sp. occurs at very high densities in most tributaries and the Jordan River but at low densities in the lake. High levels of suspended solids may be partially responsible.

In addition, Jin (2021) experimental results clearly showed that under unsheltered wave driven turbid conditions, phytoplankton was the dominant primary producer, while in sheltered conditions submerged macrophytes became dominant. Jin (2021) also suggested that macrophyte establishment may directly be inhibited from wave action due to stem breakage, uprooting, or limitations in establishment of their propagules (Jupp and Spence 1977, Keddy 1983, Schutten et al. 2005, Van Zuidam and Peeters 2015). In our study, it appears that macrophytes are able to withstand stem breakage and uprooting and is dependent on densities and extent of macrophyte coverage. Jin (2021) also suggested that wind-induced disturbances may favor phytoplankton dominance by releasing it from competition by other primary producers (Sand- Jensen and Borum 1991, Hansson et al. 2020).

Beyond direct wind effects, wind also has indirect effects on shallow lake ecosystem functioning. A key indirect effect of wind in shallow lakes is its effect on sediment resuspension, which can alter relative resource availabilities for distinct primary producers (Tammeorg et al. 2013). For example, sediment resuspension typically leads to higher nutrient concentrations in the water column coupled with decreased light availability (Blottière et al. 2017, Tang et al. 2020). Consequently, high nutrient availability in the water facilitates the growth of phytoplankton, while low light availability created by high phytoplankton abundance and suspended sediments inhibits or restricts the growth of submerged macrophytes or benthic algae (Jäger and Diehl 2014). Sediment resuspension often brings nutrients up into the water column and boosts phytoplankton growth by enhancing nutrient availability (Jin et al. 2021). This has been shown in shallow lakes (Tammeorg et al. 2013, Tang et al. 2020) and in mesocosms (Jin et al. 2021, Ding et al. 2017, Zhang et al. 2020) and it appears that Utah Lake is the rule, not the exception. Jin et al. (2021) showed that in microcosm experiments sediment resuspension had positive effects on phytoplankton biomass and negative effects on benthic algae and this effect became stronger with increasing resuspension intensity. Jin et al. (2021) also showed that

[9] Pseudofeces are a specialized method of expulsion that filter-feeding bivalve mollusks (and filter-feeding gastropod mollusks) use to expel suspended particles that cannot be used as food, and which have been rejected by the animal. The rejected particles are wrapped in mucus and are then expelled without having passed through the digestive tract. Thus, although they may closely resemble the mollusk's real feces, they are not actually feces, hence the name pseudofeces, meaning false feces.

sediment resuspension significantly reduced zooplankton biomass where zooplankton biomass in middle and high resuspension treatments varied from 0 - 1.7 µg L^{-1}, whereas without resuspension this was 45.3 - 109.3 µg L^{-1}.

Water clarity and turbidity

The photic zone (also known as euphotic zone) is the depth at which light penetration is sufficient for photosynthesis and the aphotic zone is the zone below the photic zone and insufficient for photosynthesis. The lower limit of the photic zone is almost universally considered as the depth at which < 1% light energy occurs (Kirk 2011). Utah Lake has a very shallow photic zone due to suspended solid (predominantly silt and calcium precipitates) and algal turbidity that varies spatially and temporally. Estimated photic zone depth using Secchi disk measurement has shown that it is often much less than 30 cm and often less than 10 cm. Except for the very shallowest locations on the lake (or sometimes under ice cover) photosynthetically available light does not penetrate to the benthos to allow for benthic primary production in which case, only heterotrophic bacterial production occurs in the benthos (Richards and Miller unpublished data).

Although Utah Lake is naturally prone to turbid conditions, likely it was much less turbid prior to settlement (Janetski 1990). This is because of past abundance of macrophytes, mollusks, and the major contribution of benthic algae to filter and stabilize the substrate compared to present day dominance by water column phytoplankton, bioturbation by invasive carp, and cessation of natural flow and water level regime.

Macrophyte and Bivalve Synergy

Results of these mesocosm studies also demonstrated that aquatic plants (macrophytes) and bivalves (when they survived) contribute significantly to improving conditions in Utah Lake. Macrophytes (aquatic vegetation) and bivalves (mussels, clams) historically provided critical ecosystem services to Utah Lake up until their concurrent and rapid evolutionarily- time- scale decline, post Mormon settlement @ late 1800's. Cross-phylum facilitation of substrate stabilization by autogenic ecosystem engineer macrophytes (Phylum Plantae) and bivalves (clams and mussels)(Phylum Animalia) likely was the primary factor that maintained Utah Lake's integrity, stability, resistance, and resilience. Within the much larger littoral zone areas of the lake than remain today, macrophytes and bivalves fostered an aquatic ecosystem governed more by benthic primary production than water column primary production. Macrophytes and bivalves thus controlled nutrient cycling within the lake that regulated and reduced algal bloom intensity and duration.

Ecosystem services provided by macrophytes and bivalves in Utah Lake included:

- Habitat structure that reduced abiotic and biotic stress (Gagnon et al. 2021),
- Maintenance and increased biodiversity (Nordlund et al. 2016; Hyman et al. 2019; Ysebaert et al. 2019, Gagnon et al. 2021),
- Shoreline protection from wind, waves, and ice (Fonseca & Cahalan 1992; van der Zee et al. 2012, Richards papers),
- Carbon sequestration (Fourqurean et al. 2012; Rohr et al. 2018, Richards 2018),

- As allogenic ecosystem engineers, bivalves reduced turbidity and increased light penetration though filtration (Wall et al. 2008, Richards papers) and increased sediment nutrient availability through biodeposition via pseudo-feces (Worm & Reusch 2000; Vinther & Holmer 2008, Richards 2018, Ysebaert et al. 2019),
- Macrophytes facilitated bivalves via protection from physical disturbances (Reusch & Chapman 1995, Richards), promoted larval settlement (Reusch 1998), and increased food availability (Ruckelshaus et al. 1993).
- See Richards reports in Literature Cited for additional ecosystem services.

Utah Lake's past ecological integrity depended on the unique facilitative interactions, self-sustaining positive feedbacks, and possibly co-dependencies between Phyla (Plantae and Animalia) and Classes (Bivalvia and Gastropoda). Although gastropods (snails) were not manipulated in any of our treatments, epiphytic and periphytic grazing gastropods (snails) most certainly maintained the health of macrophytes and controlled benthic algal assemblages in the lake (Richards 2018, and other Richards reports).

As ecologists are aware, catastrophic (regime) shifts as described by Scheffer et al. (2001) invariably result in an ecosystem functioning at a lower stable state that makes it difficult or impossible to return to its previous state. This is also true for loss of macrophytes and mollusks in Utah Lake. The loss of these taxa and their facilitative interactions now makes it very challenging for natural unassisted reestablishment for several reasons:

- Unstable substrate due to loss of belowground macrophyte root structure (Gagnon et al. 2021, Richards reports)
- Unstable sediment resuspension subsequently reducing light availability (Adams et al. 2016, Carr et al. 2016)
- Unstable sediment reduces suitable habitat for bivalve recruitment (Wilcox et al. 2020, Gagnon et al. 2021).

We contend that improving and maintaining the health of Utah Lake ecosystem, including reduction of algal blooms, depends on the presence and coexistence of macrophytes and mollusks. By incorporating facilitative interactions between macrophytes and mollusks necessary to overcome negative feedbacks under its impaired stressed condition [e.g., stress gradient hypothesis (Stachowicz 2001, Reeves et al. 2020)], future restoration successes in the lake are more likely (Gagnon et al. 2021, Halpern et al. 2007). Contrarily, if these facilitative interactions are ignored during restoration, failure becomes more probable (Halpern et al 2007).

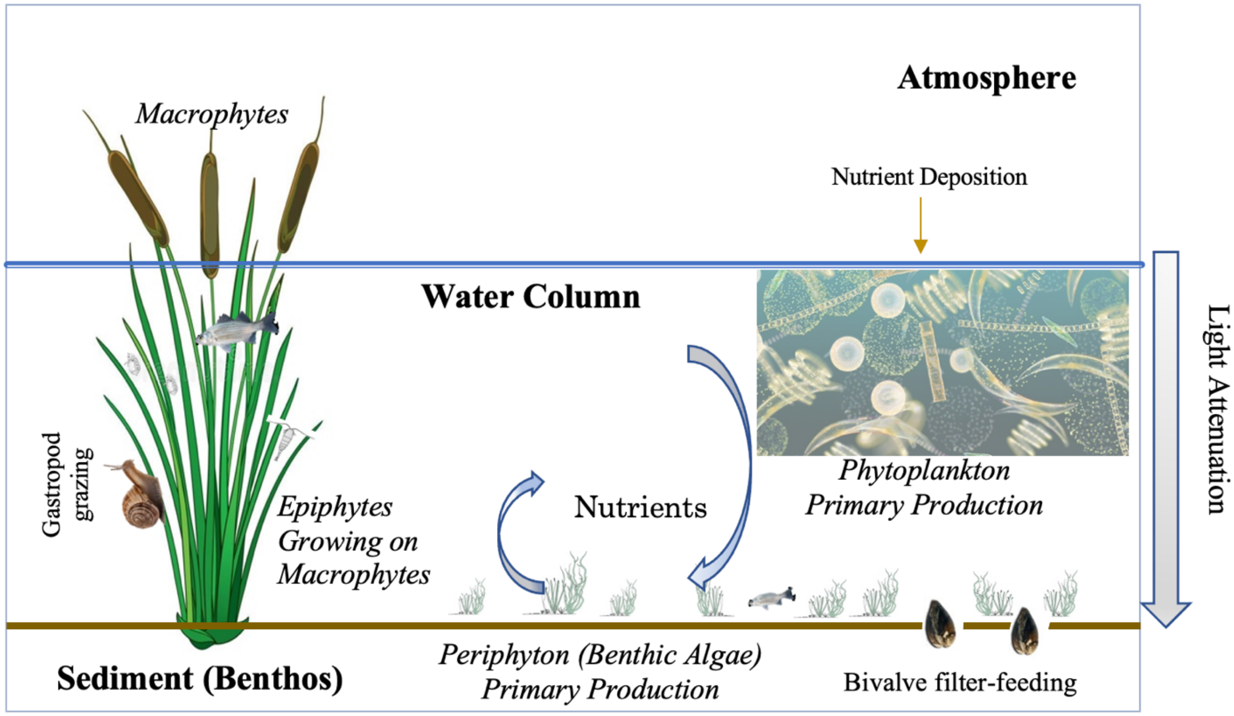

Figure 78. Although nutrients are the primary cause of algal blooms in Utah Lake, it is the state of the system which determines the result of this process. "The basic mechanism is that cyanobacteria are the superior competitors under conditions of low light, but also promote such conditions, as they can cause a higher turbidity per unit of phosphorus than other algae. This mechanism of hysteresis explains the resistance of cyanobacteria dominance in shallow lakes to restoration efforts by means of nutrient reduction alone." (Smith et al., 1987, Scheffer et al. 2007, Dokulil and Teubner 2000).

Wu and Yu (2001) demonstrated that by establishing and restoring macrophytes in a eutrophic lake there was an increase in water transparency, decreased algae, and that eutrophication transformed from water column phytoplankton dominated primary production to benthic macrophyte dominated primary production and they concluded that macrophyte establishment was an effective method to control eutrophication. It is uncertain if macrophytes are increasing in Utah Lake post reduction of carp abundances and biomass circa 2009, as macrophyte abundance and diversity is highly variable between years due to several other environmental factors (Landom and Walsworth 2021, Walsworth and Landom 2021). Macrophyte diversity and abundance and their much-needed contribution to Utah Lake's ecosystem functioning is delegated to small, localized patches. Even though macrophytes contribute disproportionately to ecosystem functioning and the food web, the small area they occupy appears to have little overall benefit to the large area of nonexistent macrophyte habitat within the lake. Our mesocosm studies conclusively demonstrate that native aquatic plants (macrophytes) can be successfully established in the lake and that they will likely not be able to reestablish unaided. Subsequently, well planned restoration of native macrophytes will substantially contribute to improving the health and ecosystem function of Utah Lake.

Mollusks, the Catastrophic Loss of Utah Lake's Penultimate Ecosystem Engineers

In the most well-known case of mussels affecting ecosystems, invasive zebra mussels in Lake Erie caused dramatic improvements in water clarity and comprised most of the whole lake invertebrate production that occurs in the benthos (Johannsson et al. 2000). Loss of native mollusks, the unheralded ecosystem engineers, in concert with cultural eutrophication in Utah Lake likely contributed to the shift from benthic primary production to water column primary production. This important negative ecological shift has had grave consequences for Utah Lake ecosystem. The transfer ratio of primary production from benthic to water column and back can be used as a metric for monitoring water quality improvement in the lake and is highly recommended.

Mollusk (mussels, clams, and snails) diversity and abundances peak in the Utah Lake-Jordan River drainage and the surrounding areas in the depauperate western USA (Richards 2017, Richards 2014). Utah Lake's historic mollusk diversity and abundances were due to its Lake Bonneville heritage of abundant nutrients, relatively high pH and high $CaCO_3$ levels originating from the > 1-mile-thick limestone base rock within the watershed (Richards and Miller 2019).

Native mollusks were the dominant benthic ecosystem engineers in Utah Lake when early explorers and Americans of European descent first arrived in the 1800's. Native mollusks were also responsible for much of the water column functioning (Richards 2014, 2017, 2018b, and 2019a) and until recently likely governed almost all its ecosystem functions. Unfortunately, their role as keystone species and ecosystem engineers has been eliminated.

Native freshwater mollusks likely constituted the largest portion of benthic invertebrate standing crop biomass in Utah Lake. Consequently, mollusks were the primary contributors to calcium and carbonate cycling in the lake, both critical for regulating phosphorus in the water column (Toner and Catling 2020) and other nutrients and trace metals (Malathi and Thippeswamy 2013; Mann, 1964; Negus, 1966; Cameron et al. 1979; Liu et al. 2010). Mollusks in Utah Lake bio-actively removed large quantities of $CaCO_3$ in the water column to grow their shells. Their living and empty shells bound $CaCO_3$ for perhaps hundreds of years in Utah Lake and thousands of years prior as Lake Bonneville. By actively removing $CaCO_3$ from the water column, mollusks allowed phosphate to precipitate from the water column as apatite further chemically reducing phosphorus from the water column and subsequently reducing the amount of phosphorus available to phytoplankton (water column algae). This biochemical reaction by mollusks also reduced pH (Toner and Catling 2020). Thus, the loss of native mollusks was in a large part responsible for increased phosphorus in the water column and current algal blooms. This loss was exacerbated by Americans of European decent induced reduction in tributary flows to the lake that had much more Ca^{2+} than the resulting closed basin Utah Lake, which then began to concentrate phosphate even more (Toner and Catling 2020).

At least one species of native mussel dominated the lake, the 'imperiled' *Anodonta californiensis/nutalliana*. Several species of fingernail clams (Family Sphaeriidae) also occurred at very large densities. Examination of relict snail samples from the shoreline of eastern Goshen Bay, Utah Lake resulted in identification of eleven highly abundant taxa (Holcomb et al. 2020). Many of these species required cool-cold, well oxygenated water (e.g., pebble snail, *Fluminicola coloradoensis)* or thick stands of aquatic vegetation and ample benthic algal primary production (e.g., *Valvata* spp.).

Unfortunately, due to human activities, Utah Lake's native mollusk assemblage has all but been annihilated. The native mussel, *A. californiensis/nutalliana* is extinct in the lake even though the lake was home to more mussels than any other water body in Utah (Richards 2014). Fingernail clams, primarily *Sphaerium* sp. are almost extinct in Utah Lake and may now be below viable population levels and extinction prone (Richards personal observations). One invasive clam, the Asian clam, *Corbicula* sp. exists in the lake but even this highly invasive and tolerant species only occurs at relatively low densities due to degraded conditions (Richards unpublished data). Of the eleven native snail taxa that historically occurred in the lake, only two tolerant taxa, *Physella* sp. and *Stagnicola* sp. remain (Holcomb et al. 2020, Richards unpublished data).

Utah Lake's native bivalves likely dominated the benthic invertebrate community responsible for water column nutrient cycling in Utah Lake both numerically and in terms of biomass ≥150 years ago. They performed both the function of particle removers from the water column and regulated other biota involved in water purification, including algae, bacteria, and fungi in the sediments (Ostroumov 2002a; Newell 1988; Newell & Ott 1998). They also controlled the key process of oxidation of organic matter particularly the major oxidizer, bacteria (Wetzel 2001; Sorokin et al. 1997; Ostroumov 2005). Native mussels likely directly reduced the amount of particulate organic matter (POM) available to be remineralized by pelagic consumers and bacterioplankton in the lake (Cloern 1982; Officer et al. 1982; Newell et al. 2005). Bivalves are world renowned for the ability to filter large volumes of water and Utah Lake's native bivalves were likely able to filter the entire lake's water column in just a few days (Richards 2014, 2017, 2018b, and 2019a) (Figure 79).

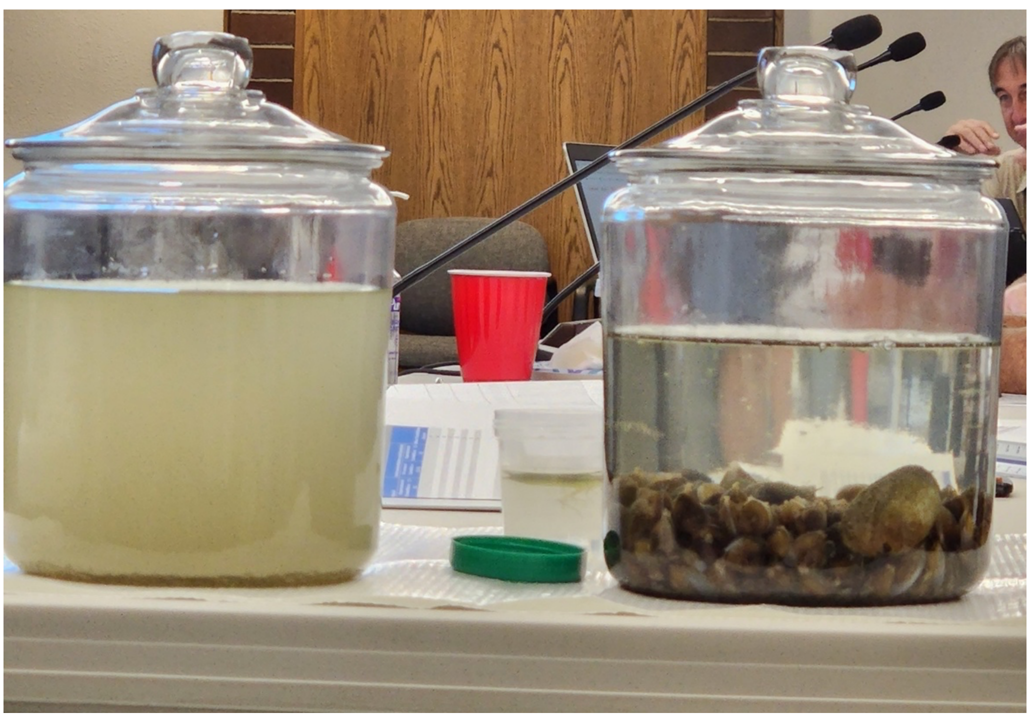

Figure 79. In this photo, both jars were filled with Utah Lake water. The jar on the right had a few dozen clams added and within twenty minutes water clarity was as shown, whereas the jar on the left still remained turbid. This demonstration occurred at a TSSD stakeholders meeting in 2022 and all that attended were impressed by the ability of clams to remove suspended sediments from lake water.

Native freshwater mollusks likely constituted the largest portion of benthic invertebrate standing crop biomass in Utah Lake (Figure 80). Consequently, mollusks were the primary contributors to Ca and CO_3 cycling in the lake. They were also major regulators of other nutrients, including phosphorus, and trace metals (Malathi and Thippeswamy 2013; Mann, 1964; Negus, 1966; Cameron et al. 1979; Liu et al. 2010).

Figure 80. Mollusk shell remnants (two white bands) piled along the eastern shoreline of Goshen Bay, Utah Lake. Shells are mostly native snails, but native clams and mussels occur as well. These remnants show that mollusks in Utah Lake were much more diverse, abundant, and unique than at present and were the dominant benthic ecosystem engineers of Utah Lake until the recent past.

Gastropods, snails, The Grazers

Although not added as a treatment factor in our 2022 mesocosm study, the importance of restoring native gastropods (snails) requires discussion. It is well known that grazers (herbivores) are critical to the health and integrity of ecosystems worldwide (Joern and Raynor 2018). Zooplankton are the water column phytoplankton grazers in Utah Lake, whereas, where abundant, snails are the dominant benthic algae, periphyton, and epiphyte grazers.

Lake primary production typically responds positively to grazing (McNaughton 1979, Frank et al. 1998). Snails facilitate primary production by preventing self-shading, facilitate nutrient flux to the algae (periphyton/epiphyton), and recycling limiting nutrients (Lamberti and Resh 1983).

Snail grazing causes periphyton and epiphyton to increase production consequently taking up more nutrients from the water column than would occur in the absence of snail grazers. Snail diversity and abundance was perhaps greater in Utah Lake than any other aquatic ecosystem in the western USA. (Richards and Miller 2019). The loss of snail herbivory (grazing) in Utah Lake is thus linked to the transition from clear water state with high levels of submerged vegetation to a turbid state with little to no submerged vegetation and super abundant phytoplankton (Jeppesen et al. 1997).

Utah Lake’s native snail populations likely consisted of more than a dozen species, all of which had a different ecological niche and provided vital ecosystem functions in the lake (Richards 2014, 2017, 2018b, and 2019a). Almost all these taxa are extinct in Utah Lake including several species of springsnails in the genus, *Pyrgulopsis*, the pebble snail, *Fluminicola coloradoensis*, two valvata species, *Valvata humeralis*, the glossy valvata, and *Valvata utahensis*, the Utah round mouth snail or desert snail, *Planorbella binney,* the Coarse Rams-Horn, and the iconic *Helisoma newberryi newberry,* the Great Basin Ramshorn. Utah Lake probably supported the largest population of *Planorbella binney* in Utah (Oliver and Bosworth 1999). Richards (personal observations) continue to find thousands of shells from the now extirpated snails along Utah Lake’s shorelines and in benthic sediments during routine benthic sampling.

Gastropods, snails are the penultimate grazers in lakes worldwide primarily feeding on periphyton and epiphytes that grow on macrophytes. They too can be considered ecosystem engineers (Richards 2018, vast literature papers). Our mesocosm study 2022 did not incorporate gastropod treatment, however based on our understanding of their importance to lake function, we recommend reestablishing their populations to Utah Lake.

Utah Lake’s Unbalanced Fishery

Our mesocosms study showed that zooplanktivorous fish can have a substantial top-down trophic cascade effect. Utah Lake’s fisheries is out of balance (Richards 2022b). Utah Lake once supported 13 species of native fish. Ten of which have been extirpated or gone extinct. The lake currently only supports three of its native species including the threatened June Sucker (*Chasmistes liorus*), Utah Sucker (*Catastomus ardens*), and Utah Chub (*Gila artraria*) that account for less than 2% relative abundance. Twelve non-native and highly invasive species now account for 98% relative abundance (Richards 2022d). The introduction of non-native fishes has disrupted the lake’s food web and in combination with the loss of its natives has severely impaired the lake’s biological and ecological integrity.

Common carp (*Cyprinus carpio)* have played a major role in the reduction of aquatic vegetation and unmeasured but likely substantial impact throughout the food web from juveniles to adults. Carp ecosystem effects have been documented worldwide including their effects on turbidity, transition from clear to turbid water state, and declines and other detrimental effects on aquatic vegetation. Estimated Carp biomass values where these effects are likely to impact Utah Lake are in Table 73.

Table 73. Carp Densities (Tons Km^{-2}) Ecosystem Effects of Carp. Derived From Koehn Et Al. 2016

Ecosystem Effect	Carp biomass (tons km^{-2})
Significant increase in turbidity[1]	5 to 7.5

Noticeable shift clear to turbid[2]	20 to 30
Decline and detrimental effects on aquatic vegetation[3]	6.8 to 45
Management threshold density[4]	10 to 17.4

[1] Zambrano and Hinojosa 1999, Vilizzi et al. 2014
[2] Williams et al. 2002, Parkos et al. 2003, Haas et al. 2007, Matsuzaki et al. 2009
[3] Hume et al. 1983, Fletcher et al. 1985, Osborne et al. 2005, Pinto et al. 2005, Bajer et al. 2009, Vilizzi et al. 2014
[4] Haas et al. 2007, Bajer et al. 2009, Matsuzaki et al. 2009

Walsworth et al. (2022) estimated carp biomass in Utah Lake in 2021 at approximately 91 (50 to 150) tons km^{-2}. This is far greater biomass than the minimum ecosystem effects and management threshold densities shown in Table 1 demonstrating that carp biomass needs to be drastically reduced from current levels to have any restorative effects on the Utah Lake ecosystem. In addition, Scheffer et al (2001) clearly showed that returning to a clear water state requires a substantially greater reduction in the perturbation (i.e., carp densities) that caused the transition from turbid to clear. Researchers have shown that carp populations have been increasing since 2013 despite an intense carp removal program initiated in 2009 (Landom and Walsworth 2021). Consequently, carp are likely to continue to be a prime factor in maintaining the lake's degraded and resistant trophic state.

Although millions of dollars have been spent on improving June Sucker populations and habitat over the last decade and reducing its status from federally Endangered to Threatened, this species continues to struggle. It appears that insuring population viability is not forthcoming without regular hatchery supplementation and continued management intervention (Walsworth and Landom 2021, Landom and Walsworth 2021).

In addition, Richards (2022b) food web model showed that size/age classes of predatory fish diets that should be focused on preying on smaller fishes (piscivory) are focusing on benthic invertebrates (Richards unpublished results obtained from Ecology Center and Watershed Sciences Department, Utah State University). This further demonstrates an out of balance fishery and food web.

Zooplanktivory and Zooplankton

Zooplanktivorous fish predation has strong deleterious effects on zooplankton prey. Planktivory also negatively affects entire zooplankton assemblages and often initiates trophic cascades throughout the food web (Carpenter and Kitchell, 1996, Scheffer and Jeppesen, 1998; Jeppesen et al., 1998; Moss et al., 1998, Iglesias et al. 2007). This can be especially catastrophic if planktivorous fish are invasive and the native zooplankton assemblages haven't evolved with invaders.

Planktivory is thought to be the main factor controlling the spatial distribution, abundance and body size of zooplankton in shallow lakes (e.g. Scheffer, 1998; Burks et al., 2002, Iglesias et al. 2007) and often induces major shifts in the size distribution of zooplankton (Hrbáček et al., 1961; Brooks and Dodson, 1965) or behavioral shifts (Timms and Moss, 1984; Schriver et al., 1995; Lauridsen and Lodge, 1996; Burks et al., 2002; Romare and Hansson, 2003). For example, in Lake Blanca, Uruguay, the small size of the dominant cladocerans and the dominance by copepods and rotifers likely reflect the extremely high abundance of planktivorous fish predators (Iglesias et al. 2007). The effect of planktivory on decreased zooplankton size can increase the likelihood of cyanoHABs. This is because larger sized zooplankton are often better at feeding on larger strands of algal particularly cyanobacteria (Carpenter and Kitchell 1988, Caroni 2010, Jeppesen et al. 2011, Attayde and Bozelli 1998, Carpenter et al. 1985, Jeppeson et al 2000, Jeppesen et al 2003, Lamper et al 1986, Gannon and Stemberger 1978, others). Sarnelle (2007) also reported that high abundances of generalist grazers (i.e., *Daphnia*) may control blooms when released from planktivorous fish predation (Ger et al. 2016). Our results are consistent with this.

Richards et al. (2019b) conducted preliminary analysis of zooplankton body sizes in Utah Lake and found that zooplankton were substantially smaller than expected, indicating that invasive planktivores have altered the zooplankton assemblages in the lake, which could be contributing to cyanobacteria blooms (See Appendix 3: *Spatial and Temporal Variability of Zooplankton Body Lengths in Utah Lake*, *Technical Memo* in Richards (2019b) for results of this analysis. Richards et al. (2019b) also incorporated zooplankton body size metrics into their Multimeric Index of Biological Integrity for Utah Lake because of its importance to the lake's ecological health.

Zooplankton survival often depends on heterogenous habitat to avoid planktivores. Consequently, zooplankton assemblages and abundances often differ between littoral submerged and emergent aquatic vegetated habitat and open water habitat; planktivory will have different effects depending on type of habitat. Almost all small juvenile fish in Utah Lake are planktivores and tend to seek refuge in aquatic vegetation from larger piscivorous fish, subsequently increasing planktivory. However, aquatic vegetation is also a refuge for zooplankton. Aquatic vegetation also decreases turbidity and improves clarity and visibility, either through decreased sediment turbulence or phytoplankton allelopathy or both. Clearer water in vegetated habitat also has less phytoplankton abundance food resources for zooplankton, either through increased grazing by zooplankton or allelopathy or both. In Utah Lake, open water habitat is defined by turbidity and can provide zooplankton cover from visual planktivores and an abundance of phytoplankton food resource. Tradeoffs are inevitable. However, given the very high seasonal abundance of juvenile planktivorous fishes, no habitat may provide significant refuge for zooplankton in the lake at those times (Iglesias et al. 2007). It has been our observation that the most devastating impact of non-native juvenile fish planktivores occurs during clear water conditions in autumn in shallow habitats where phragmites and other aquatic vegetations have been physically removed and juvenile fishes are schooling.

Fish planktivory on zooplankton obviously occurred with native fishes (i.e., June Sucker) in Utah Lake in the past. However, in the past, mussels and clams were likely another dominant predator (via filtration) of phytoplankton, particularly during times when zooplankton abundances were reduced by fish planktivory and these bivalves likely helped control cyanobacteria blooms (see other sections). Bivalves also eat smaller sized zooplankton which results in an average larger size zooplankton assemblage, which in turn eat more phytoplankton especially the larger size phytoplankton (e.g., cyanophytes). (Marroni et al. 2016, Caraco et al. 1997, Prins and Escaravage 2005, Newell et al. 2005, Newell 1988, Newell and Ott 2013).

Invasive common carp (*Cyprinus carpio*) are a major disruptor of Utah Lake's ecosystem including their impacts on zooplankton. Meijer et al. (1990), Khan (2003), and Britton et al.

(2007) reported that up to 25% of the biomass ingested by carp can consist of zooplankton in other lakes. Carp can therefore affect the zooplankton assemblages in many ways, by direct predation (Miller and Crowl, 2006), by consuming macroinvertebrates that themselves are zooplankton predators (Khan, 2003), through loss of macrophytes that provide shelter, and by increasing phytoplankton biomass and promoting cyanobacterial blooms (Parkos et al., 2003). Furthermore, resuspension of sediment particles can interfere with the filtering apparatus of cladocerans (Kirk and Gilbert, 1990), and bioturbation may also affect zooplankton dormant stages in sediments, negatively effecting emergence patterns (Angeler et al., 2002a, 2002b, 2007) (Florian et al. 2016).

As Richards and Miller (2019a) reported, many studies have shown that removal or reduction of planktivorous fish populations could be used to enhance zooplankton grazing on algae, including reduction of cyanobacteria blooms, and thereby helping to create a clearwater state (Gulati 1978, Hansson et al., 1998, 2020, Søndergaard et al., 2007, 2008). This has led some researchers and managers to recommend fish biomanipulation as a relatively inexpensive remedy for controlling algal blooms compared to attempts at whole drainage nutrient control (Riedel-Lehrke 1997, Richards 2019a).

The strong evidence for greater zooplankton abundances in corrals vs lake throughout this study demonstrates that wave reduction and predation pressure reduction alone can allow for vast increases in zooplankton abundance, biomass, and probably secondary production in the lake that effects all trophic levels within the foodweb. Increased zooplankton abundance can reduce phytoplankton and indirectly cause phytoplankton to increase production due to less intraspecific competition with other phytoplankton and in turn can indirectly increase nutrient concentrations from the water column due to increased consumption from phytoplankton. Wave action can be alleviated by wave breaks preferably by restoring and increasing native aquatic plants, macrophytes. Alternatively, the installation of other types of wave break dikes or islands can also have similar effects.

Utah Lake supports a zooplankton assemblage that varies spatially and temporally (Richards and Miller 2017). There are approximately 20 zooplankton taxa occurring in Utah Lake including cladocerans, copepods, and rotifer taxa from several functional groups, each with different life history and feeding strategies (Richards and Miller 2017, Richards 2019, Marshall 2019, and unpublished data). The taxonomy of Utah Lake's zooplankton has never been fully documented and verified. Because of this gap, zooplankton taxonomy is under revision by OreoHelix Ecological and River Continuum Concepts, Manhattan, MT. It is of utmost importance to correctly identify zooplankton taxa in the lake. Our mesocosm study continues to add to this knowledge.

Unfortunately, zooplankton assemblages in Utah Lake have also undergone bottlenecks and assemblage shifts, including those stressors discussed in the previous sections that have resulted in Utah Lake's zooplankton assemblages becoming analogs of past natural assemblages and are unable to help regulate cyanobacteria blooms in its current state. One of the most important factors not discussed so far has been and continues to be predation on zooplankton by planktivorous invasive fish and how this affects cyanoHABs.

Richards and colleagues have conducted the most extensive zooplankton diversity, abundance, and spatial and temporal dynamics research in Utah Lake to date, including those in this study. Richards (years) found that diversity (approximately 20 taxa) was quite low compared to other lakes in North America (Richards 2019) and that the effective number of taxa was only 3 to 4. They also found that overall body size was lower than expected suggesting selective pressure from planktivorous fishes in the lake (Richards and Miller 2019). All the fish species in Utah Lake are planktivorous at least during juvenile stages. USU researchers have suggested that zooplankton body lengths have increased after the carp removal project was initiated but time will tell if this trend continues due to apparently increasing carp densities post 2013 (Walsworth et al. 2020, Walsworth and Landom 2021, Landom and Walsworth 2021). Our mesocosm findings show that larger sized zooplankton still exist in the lake and can increase in abundance under restorative conditions.

In addition, zooplankton now appear to have limited control of phytoplankton densities in Utah Lake, other than within our artificially protective mesocoms. The zooplankton to phytoplankton biomass ratio, Z/P is often used as a metric evaluating trophic status of a water body and ecosystem functioning, and as a component of food web models. Z/P typically decreases with increased eutrophication (Gulati, 1983; Andronikova, 1996; Jeppesen et al., 1999, 2000, 2005; Haberman & Laugaste, 2003, Blank et al. 2010). Richards (2022) calculated that Utah Lake Z/P varied seasonally with higher values in winter vs. summer. The highest Z/P was in March = 0.18, lowest in September and order of magnitude lower at 0.018 (annual mean = 0.07). Z/P showed that zooplankton grazing was very inefficient from June through November when harder to digest phytoplankton were dominant and infers that much of the unconsumed phytoplankton (and dead zooplankton) falls as detrital 'snow' to the sediments. Large amounts of detrital snow alter the benthic portion of the food web from past benthic algae autotrophic to heterotrophic and signify a food web much out of balance. It also emphasizes that the microbial loop in Utah Lake likely contributes disproportionately more to the food web than typical, although there have been no studies on this important component in the lake's function. Results from this mesocosm study suggests that restoration efforts directed towards turbulence reduction and a more balanced fisheries can allow zooplankton assemblages to adjust and steer the lake to a more functioning ecosystem.

Zooplankton grazers are the number one water column regulator of phytoplankton, including cyanobacteria in Utah Lake (Iglesias et al. 2007, Scheffer 1998, Richards and Miller reports). Zooplankton frequently move between habitats including daily horizontal migration. As we have shown in this study, zooplankton can occur in very high abundances in benthic filamentous algae, at least during daylight hours when we sampled. Subsequently, zooplankton are a vital linkage between the pelagic, benthic, and littoral zones (Vander Zanden and Vadeboncoeur 2002, Jones and Waldron, 2003). Zooplankton are the main consumers of phytoplankton and are in turn consumed by small fish, including all juvenile fishes and all juvenile and adult June Suckers in Utah Lake (Richards et al. 2019). They are the chief intermediaries between primary production and higher trophic levels, and thus play a critical role in Utah Lake food web dynamics (Richards et al. 2019).

Zooplankton obviously have top-down (trophic cascade) grazing effects on phytoplankton and cyanobacteria and in turn are affected by these (bottom- up effects) (Iglesias et al. 2007).

Zooplankton also have different modes of feeding including grazing and predation, some of which prey upon other zooplankton. Most zooplankton are selective feeders. All of these complex interactions directly and indirectly influence nutrient cycling in the water column. Zooplankton excretion and respiration of nitrogen, phosphorus, and ammonia is immediately available and consumed by phytoplankton, often within minutes. This phytoplankton-zooplankton component of water column nutrient cycling has been well documented and known by limnologists and ecologists for several decades and is likely an important driver of cyanobacteria blooms in Utah Lake (Iglesias et al. 2007, Scheffer 1998). Medium- and large-sized cladocerans, typically *Daphnia* spp. can markedly reduce phytoplankton biomass (Jeppesen et al. 1990, Scheffer 1998), even in communities dominated by cyanobacteria (Jeppesen et al. 2003, Lampert et al. 1986, Brooks and Dodson 1965, Gorokhova and Engstrom-Ost 2009, and Hogfors et al. 2014). *Daphnia* spp. can feed on bacteria, protozoa, phytoplankton and even some small zooplankton, highlighting their important role in freshwater food webs (Yin et al. 2010). It has been demonstrated that intensive zooplankton grazing can promote a clear-water state (Scheffer 1998). For example, grazing by *Daphnia* sp. has been reported to be responsible for spring clearing in temperate lakes (Meijer et al. 1999). Our results suggest that *Daphnia* sp. and others consume cyanophytes.

Phytoplankton assemblages can have a bottom-up control on zooplankton assemblages via several mechanisms, including relative abundance, digestibility, nutrient content, etc. Conversely, zooplankton assemblages can have a top-down control on phytoplankton assemblages via selective and non-selective grazing and contrary to past assumptions, it has become apparent that zooplankton routinely and selectively rely on cyanobacteria in their diets. Consequently, zooplankton assemblages can shift phytoplankton assemblages toward better adapted cyanobacteria consumer species (Motwani et al. 2017, Woodland et al. 2013, Koski et al. 2002, Gorokhova and Engstrom-Ost 2009, Hogfors et al. 2014, Ger et al. 2016).

Jin (2021) reported that zooplankton are often hindered by filtering sediment laden water and do not have the ability to prevent ingesting sediment. This can limit their intake of phytoplankton and sediment excretion is energetically costly (Koenings etal. 1990, Kirk and Gilbert 1990, Penning et al. 2013). Turbulence may also inhibit growth of large-sized zooplankton species with body sizes that exceed Kolmogorov length scale because they are more affected by eddy motion (Peters and Marrasé 2000, Jin 2021). This can impair food detection or capture, or directly lead to body damage (Visser et al. 2009, G. -Tóth et al. 2011, Zhou et al. 2016, Jin 2021). We suggest that reducing wave induced turbulence can be effective to stimulate higher trophic production in Utah Lake (Jin 2021). Sediment resuspension may also cause physical damage to zooplankton by abrasion and turbulent shear forces which may lead to decreases in zooplankton biomass (Peters and Marrasé 2000).

Benthic invertebrates, midges dominate

After the inevitable demise of the keystone ecosystem engineering mollusks and associated ecological shift to a lower trophic state in Utah Lake, remaining benthic invertebrate species endeavored to fill vacant functional roles. Benthic substrate conditions shifted from a substrate stabilized by mussels and clams, macrophytes, and benthic algae to a mostly unconsolidated mud-clay-silt unstable substrate that occupies most of the top layers of the lake substrate today. The dominant benthic invertebrates in the lake presently consist of just a handful of taxa, predominantly pollution tolerant chironomid (midge) larvae and segmented (oligochaetes) and non-segmented (nematode) worms. As a result, much of the lake exists as profundal and can be considered chronically impaired (Richards 2022). However, some areas of the lake including areas in Provo Bay and the limited macrophyte habitats outside of the bay have a greater diversity, albeit lower overall abundance and biomass, of benthic invertebrates including corixids (bugs) and coleoptera (beetles) as well as odonates (dragonflies) and isopods and amphipods, etc. (Landom and Walsworth 2021). Out of approximately twenty macroinvertebrate taxa found Richards et al. (2016) research that included 93 benthic samples, only three taxa dominated the invertebrate biomass, *Chironomus* sp. (midge), *Tanypus* sp. (midge larvae), and oligochaete worms. These three pollution tolerant indicators comprised 99% of the biomass (Richards and Miller 2019) and continue to do so, although it appears that midge larvae densities in the lake fluctuate greatly from year to year and may be decreasing (Richards and Miller 2019, and unpublished data).

This extreme low effective number of benthic invertebrate taxa is of great concern because it reflects the degraded condition of Utah Lake's benthic environment. Dominance by only three pollution tolerant taxa is a red flag in all biological assessments of water quality throughout the world. However, these remaining three dominant taxa are now the default keystone ecosystem engineers that struggle to maintain the lake's present ecological state and are a crucial component of the lake's food web (Richards and Miller 2019). Their presence and role in Utah Lake's ecosystem should not be underestimated nor undervalued. Midge larvae are responsible for much of the lake's benthic/sediment function and interaction with the water column given their sheer volume, biomass, secondary production, and ecology (Richards and Miller 2019c, Holker et al. 2015); and as been reported by Randal et al. (2017) and Hogsett et al. (2019), the sediment water interface appears to be a major controlling factor of phosphorus recycling and subsequent algal blooms. Although midge larvae densities often exceed 10,000 m^{-2} in the lake, primary production estimates suggest that their numbers should be substantially greater (Richards 2022). For example, in Lake Myvatn (Midge Lake), Iceland, midge larval density often exceeds 500,000 m^{-2}. The reason for the relatively low density of midge larvae in Utah Lake can be attributed to heavy predation from fishes and to a lesser extent unsuitable conditions. Midge larvae are the most common prey item of all fish species in the lake, including those fishes that typically should focus their diets on other smaller fishes (Richard 2022). This conundrum of low biomass and preferred food item of large numbers of fish suggest that midge larvae secondary production is very high (i.e., the production to biomass ratio could be near 100 or more) and that Utah Lake's foodweb is severely out of balance. Science based restoration is needed.

Benthic Algae, Periphyton and Epiphytes

Shifts from benthic algal production to phytoplankton production in shallow lakes including Utah Lake is primarily a result of eutrophication, however many other factors are involved (Vadeboncoeur et al. 2002, 2003, 2008, Dodds 2003). This shift from benthic algal primary production to water column primary production is likely the single most important metric demonstrating the degradation of Utah Lake's ecosystem over the last 150 years.

Our observed increase in benthic algae on the inside bottoms and sides of the corrals in this mesocosm study clearly demonstrated that two limiting factors were removed, limited light to the benthos and chronic sediment resuspension. Restoration of these two key factors alone will allow for a measurable transition from water column dominated primary production to benthic primary production and less nutrient availability to phytoplankton including HABs. Additional benthic periphyton benefits (i.e., functions) are numerous and described herein.

Benthic periphyton (algae) ecosystem functions include significant contributions to gross primary production (Velasco et al. 2003, Vadeboncoeur et al. 2002), trophic interactions (Moulten et al. 2004), ecosystem engineering (e.g., biostabilization of sediments; Dodds 2003; Droppo et al. 2007; Spears et al. 2007b) and regulation of nutrient cycling across the sediment–water interface (Dodds 2003, Poulickova et al. 2008, Vadeboncoeur et al., 2003). Benthic algae are also vastly underappreciated contributors to pelagic fisheries (Vadeboncoeur et al. 2002) and also increase retention of nutrients. According to Dodds (2003), periphyton can:

- Remove nutrients from the water column and cause a net flux of nutrients toward the sediments,
- slow water exchange across the sediment/water column boundary thus decreasing advective transport of P away from sediments,
- intercept nutrients diffusing from the benthic sediments or senescent macrophytes,
- cause biochemical conditions that favor P deposition and can,
- trap particulate material from the water column (Adey et al. 1993).

Vadeboncoeur and Steinman (2002) suggested that the balance between phytoplankton and periphyton primary production can be affected by differences in grazing pressure (e.g., zooplankton), habitat suitability, disturbance, and pelagic trophic structure (e.g., a balanced fishery). Benthic (epiphytic and periphytic) algae are still present in Utah Lake but are limited by a paucity of available stable substrate attachment surfaces. The vast majority of the lake's substrate is a loose, unconsolidated mixture of silt, clay, and organic matter. Our study showed that benthic algae are present and just waiting for stabilization of sediment habitat to help balance the nutrient cycle and improve the lake's foodweb.

State, Structure, and Function of Utah Lake's Ecosystem

Understanding the state, structure, and function of Utah Lake's ecosystem is of paramount importance if we are to manage and restore it based on a scientific ecological perspective. Several metrics that are used to measure ecosystem health, integrity, maturity, robustness, resistance, resilience, state, structure, and function include: Trophic transfer efficiency (TTE), ecoexergy, ascendency, overhead, and redundancy, to name a few (Christensen et al 2005, Nielson et al. 2020, Richards 2022b, Jørgensen 2005, 2007). These measures are used by ecosystem ecologists as more informative quantitative metrics than the latent buzz words used primarily by managers, health and integrity. These will be discussed briefly in relation to our mesocosm 2022 findings.

Trophic Transfer Efficiency

Results from our study indirectly demonstrate improvement of trophic transfer efficiency (TTE), how efficiently energy is transferred up to higher trophic levels (i.e., the foodweb). TTE is a direct measure of an ecosystem's health and is widely used in aquatic foodweb models. Richards (2022b) foodweb model showed that Utah Lake has major trophic level transfer problems.

Results from our 2022 mesocosm study showed that allowing for the recovery of benthic and periphytic algae can pave the way for the re-establishment of submerged macrophytes (Vasconcelos et al. 2016, Hansson et al. 2020, Jin 2021), and improve TTE. Obviously, the increased zooplankton biomass within protected mesocosms showed that reducing wave turbulence can in turn support higher trophic levels (i.e., fishes) in the lake. Trophic transfer from phytoplankton to zooplankton is directly affected by sediment resuspension (Pécseli et al. 2014) and indirectly by nutrient availability (Hessen et al. 2013). However, trophic transfer efficiency can become impaired because high concentrations of suspended sediment in the water column can interfere with zooplankton filter feeding (Koenings et al. 1990, Kirk and Gilbert 1990) as well as other effects. This low transfer efficiency between phytoplankton and zooplankton may also be explained by reduced quality of the seston, indicated by higher C:N ratio, suggesting a reduced nutritional value that limit zooplankton growth (Hessen et al. 2013).

Increased benthic and periphytic algae can support increased grazers, such as gastropods that also contribute to food web transfer efficiency. In contrast, phytoplankton will continue to dominate areas in the lake exposed to strong wind and wave effects, i.e., most of the lake, at reduced efficiency. Without intervention, phytoplankton will continue to maintain their dominance because wind and wave-induced sediment resuspension will provide almost unlimited nutrient availability for their growth (Jin 2021). Unhindered, turbulence will continue to decrease competition from macrophytes and benthic algae by decreasing light availability and through the mechanic forces waves exert on macrophytes and their propagules, as well as prevention of early establishing benthic algal communities (Jupp and Spence 1977, Keddy 1983, Jin 2021). Without wave reduction, the recolonization of both macrophytes and benthic algae will be limited. Results from the Marker Wadden project in the Netherlands supports our conclusions that for shallow lakes, such as Utah Lake suffering from wind and wave effects, reducing sediment resuspension can be effective in restoring the trophic transfer efficiency.

Ecological Succession and Ecoexergy

Richards (2022b) foodweb model also showed that Utah Lake is now stalled at an 'immature' early ecological successional stage. Richards (2022b) suggested that this was primarily because of chronic wave action and unnatural water level fluctuations that consistently disturb unconsolidated sediments and reset the food web, thus preventing maturation and stability of the system.

Exergy has been proposed as a useful indicator of the state, structure, and function of an ecosystem (Nielsen et al. 2020). Ecoexergy is the term used for ecosystem exergy. Ecoexergy is the amount of inherent workable energy of an ecosystem when it maintains equilibrium within its living environment. The concept has been suggested by Jørgensen (2005, 2007) and reviewed by Nielsen et al. (2020). When ecosystem is at maximum distance from thermodynamic equilibrium, it possesses the highest value of ecoexergy (Jørgensen 2007). Therefore, ecoexergy measures the distance from thermodynamic equilibrium (Jørgensen 2005)[10]. Higher group

[10] Ecoexergy is often explained as a translation of Darwinian survival of the fittest. The fittest ecosystem is the one able to use and store fluxes of energy and materials in the most efficient manner i.e., it has the highest ecoexergy. Ecoexergy can also be considered reverse entropy or 'negentropy' (Nielsen et al. 2020). Exergy may then constitute

organisms possess more exergy value than the simpler organisms, and in a complex system, the ecoexergy level is high. Living systems have a particular high ecoexergy mostly due to their high information content (Jørgensen 2005). The theory is that biological systems including ecosystem should evolve in a way that they optimize their thermodynamic efficiency (Nielsen et al. 2020). Ecoexergy can be considered one of the major functional parameters of the ecosystem, as it reflects the components' energy level to maintain the normal functioning of the ecosystem (Zhang et al., 2010). Lake Mendota, Wisconsin one of the most studied lakes in the world, was shown to have an increase in entropy (decrease ecoexergy) due to eutrophication (Aoki 1989, Nielsen et al. 2020). Margues et al. (1997) found exergy and species richness decreased as a function of increased eutrophication. Flindt et al. (1997) showed that ecoexergy differed with different degrees of organic pollution.

Ascendency is the measure of the average mutual information in a system. It is a product of total throughput (TST) and average mutual information (AMI) of a system (Ulanowicz and Puccia, 1990). A system with high ascendency is more developed and diversified and contains efficient pathways of energy flow in an unperturbed condition (Ulanowicz, 1986). Ecosystem information is a concept primarily based on functional DNA; the amount of DNA responsible for the part of the genome which is believed to be expressed during the life history of the organism (Nielsen et al. 2020). More complex organism (e.g., fish vs. algae) have more DNA information, and more complex ecosystems have more information than less complex ecosystems. Subsequently, the amount of DNA information an ecosystem stores is a measure of ecoexergy and reverse entropy.

Overhead, *O* also known as the "system reserve" to counter the external perturbation (Ulanowicz, 1986), is complementary to ascendancy. It describes the parallel (unrecognized) path of energy in a system (Feng et al., 2018). Unlike ascendency, overhead is asymmetrical, i.e., the values from input and output are different (Christensen et al., 2008). Among the four components of overhead (i.e., export, import, internal flow and respiration), overhead in internal flow or redundancy is a sensible attribute to measure the system stability by indicating the number of parallel ways for energy flow between two components (Christensen et al., 2005; Heymans et al., 2007). Overhead and the redundancy are measures of the resilient capacity of any system; a high overhead bearing system is more resilient and has more reserve strength (Odum, 2014). Functional redundancy is the major aspect of the resilient capacity and is considered the integral part to maintain robustness so that a system can overcome any stress factor to maintain its function (Mumby et al., 2014).

Although not measured in our mesocosm 2022 study but based on our findings, measurable TTE, ecoexergy, ascendency, overhead, and redundancy metrics should improve in Utah Lake if:

- wave induced nutrient loading is reduced allowing for benthic primary production to increase,
- decrease in light limitation,
- zooplankton grazers increased in abundance and diversity, particularly larger sized *Daphnia* sp.,
- a more diverse and balanced fishery that reduces zooplanktivore abundance and increases ability of piscivorous fishes to top down regulate,

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not only a suitable system-oriented characteristic to express natural tendencies of ecosystems evolution, but also a good ecological indicator of ecosystems health Marques et al. (1997).

- macrophyte reestablishment that will provide much needed structural habitat,
- and other responses outlined in this discussion.

Nutrient Loading Utah Lake

Hogsett and Goel (2013) and Hogsett, Hanyan, and Goel (2019) reported that the internal loading[11] of phosphorus from Utah Lake sediments to water column was estimated to be near 1500 tons annually (roughly 85% of total (Richards 2022)). This internal P loading far exceeds all other external sources of phosphorous loading including tributaries, wastewater treatment facilities, and atmospheric deposition combined (Richards 2022). Tributaries and wastewater treatment facilities combined perhaps only contribute 5 to 7% (roughly 100 tons) of the phosphorus load to the lake. Atmospheric deposition can contribute almost as much as tributaries and wastewater treatment facilities (Utah Lake Science Panel estimates in progress). The only major export of nutrients from the lake is downstream via the Jordan River with TP exports estimated to be < 20 tons/year which might only be about 5 to 10% of total imports. Without controlling sediment nutrient resuspension, the road to recovery for Utah Lake is blocked.

Sediment Removal

For many decades, sedimentation was considered the number one EPA designated impairment for water bodies in the Western USA. Then came nutrient concerns that diverted the focus of water quality management agencies away from sedimentation. However, sedimentation continues to be one of the most important types of impairment despite this focal shift toward nutrients and sedimentation and nutrient issues are often inseparable as is the case for Utah Lake.

Sedimentation is a major water quality impairment in Utah Lake. Human caused increases in sedimentation over the last 150 years along with the lake’s inability to flush sediments due alterations in watershed inputs to the lake as well as the lake being regulated as a reservoir have caused many areas within the lake to accumulate loose sediments often > 0.5 m. Buildup of sediment deposits in reservoirs (i.e., Utah Lake) is a long-standing problem with serious consequences on a reservoirs’ functionality (Kantoush et al. 2021), including Utah Lake.

Results from Richards (2022) draft food web model suggest that Utah Lake remains in a depauperate, immature, early successional, and poorly resilient condition. This is in part due to wave action and near constant sediment resuspension.

Findings from our ongoing mesocosm studies support the assumption that sedimentation can be detrimental to the recovery of Utah Lake. Loose sediment comprised of sand/clay/silt and organic matter was easily redistributed in our study area by wave action and ranged from 15 to 40 cm thick. Sediment also appeared to increase within several of the mesocosms despite being isolated from strong wave action. Benthic assemblages including periphyton, macroinvertebrates, and bivalve mollusks may subsequently be severely restricted by sedimentation, as our analyses suggest. For example, mortality rates of clams in the two mesocosm stocked with clams was $\geq$ 90% when examined in September, which we attribute to their inability to cope with

[11] Internal loading is a widely accepted cause of lake eutrophication by scientists worldwide. “It has become increasingly clear that external changes in nutrient loads alone cannot explain severe eutrophication of surface waters” (Smolders et al. 2006)

sedimentation. All clams were buried in several cm of fine sediment. These findings support the knowledge accrued in the ecological restoration discipline and malacological knowledge that sedimentation in Utah Lake, at least in the area we are studying, is detrimental to water quality in the lake and that sedimentation will impede lake restoration efforts, including among other biota, native bivalve recovery. We posit that turbidity and nutrient resuspension from fine sediments is the limiting factor in Utah Lake recovery.

One of the most widely used and successful methods for restoration of lakes, larger rivers, and estuaries worldwide is sedimentation removal, often by use of suction dredging (Chen et al. 2019; Brookes, 1987; DeCoursey and Vernberg, 1975; Howarth et al., 1982; Lewis et al., 2001; Lohrer and Wetz, 2003; Nayar et al., 2004; Spencer et al., 2006, Lohrer and Wetz, 2003; Spencer et al., 2006; Zhong and Fan, 2007; Jeppesen et al. 2009; Hupfer and Hilt 2008). Dredging removes the top nutrient rich layers of the sediment and can reduce internal nutrient loading subsequently reducing algal blooms (Wan et al. 2020, Zhi-yng et al. 2008, Nijman et al. 2022; Jeppesen et al. 2009). For example, sediment dredging is widely used to treat hyper-eutrophic lakes in China. Zhang et al. (2009) demonstrated that suction dredging in a shallow eutrophic lake decreased phosphorus, organic matter, total suspended solids, and Chlorophyll *a,* and shifted the zooplankton assemblage to a less eutrophic composition. Their finding of a significant decrease in Chl-*a* indicated a marked decline in algal biomass likely due to a decrease in phosphorous levels and subsequent P limitation to primary production. Suction dredging also led to a shift from rotifer to larger size crustacean zooplankton (Zhang et al 2009), which has ecological benefits to food webs (Richards 2022a, 2022b) including as we have shown in this study, Utah Lake. Zhang et al. (2009) concluded that suction dredging was an effective method of environmental improvements for shallow, eutrophic lakes. In another study, Zhiying et al (2008) showed that the N and P content in the sediment were decreased after dredging a shallow eutrophic lake and that the water quality obviously improved. They also showed that phytoplankton community density and chlorophyll-*a* concentrations decreased, and that the phytoplankton trophic level compartment also had decreased. Wenjie et al. (2020) showed that dredging changed the association between the bacterioplankton assemblage and sediment biogeochemistry indicating that dredging is an effective method for mitigating cyanobacteria blooms via changing the association between the bacterioplankton assemblage and sediment biogeochemistry. In addition, exposing more stable sediment is expected to produce a more diverse benthic community than the current one dominated mostly by dipterans and worms in Utah Lake. Dredging offers a more permanent solution to internal P loading in shallow lakes such as Utah Lake than chemical treatments such as alum treatment because sediments, the actual source of the P loading, are removed from the system (Lembi 2003). Given this situation, it is most certain that algal blooms will continue to occur in the lake unimpeded without controlling sediment flux of nutrients into the water column either through biomanipulation (e.g., macrophytes and mollusks, foodweb modifications) and/or mechanical removal (e.g., dredging).

Conclusion

Results from our 2022 mesocosm study clearly showed the negative effects of wave induced light limitation, nutrient flux from sediments, and the impacts of carp and zooplanktivorous fishes, and the positive effects of increased zooplankton abundance and diversity, macrophyte establishment and to a lesser extent bivalve establishment on Utah Lake's ecosystem. Restorative measures based on these findings especially native aquatic plant reestablishment, and what is known and practiced throughout the world can be prudently and expeditiously used to improve Utah Lake's foodweb, including its health, integrity, and resilience to future perturbation.

Recommendations

Although much valuable information was generated from this mesocosm study, no replication of treatments was performed. Consequently, statistical rigor was lacking. Based on this study the following are recommended:

- Future mesocosm treatments need to be replicated focusing on wave, carp, and mollusk effects.
- More detailed analyses of response variables such as
  - mollusk growth, diets, fitness,
  - zooplankton size distributions, diets, and diversity,
  - fish fitness, diets, growth,
- Initiation of reestablishment of native aquatic macrophytes, particularly emergent vegetation throughout the lake.
- Installation of temporary wave breaks at select locations.
- Consideration of sediment removal via suction dredging.
- Reintroduction of native mollusks.

Acknowledgements

We gratefully acknowledge the students at BYU, especially Kaylee Tanner, Rachel Valek, and their major professor Dr. Gus Williams for their tireless contributions to this project without which we could not have accomplished our goals. Also, Rich Mickelson and his staff at TSSD for their major efforts of making sure mesocosms (corrals) were installed, removed, maintained, and their often-needed encouragement intellectual inputs. We also shout out a big thanks to the staff at Wasatch Front Water Quality Council for their assistance in corral installation and removal and on occasion ecological sampling, at to Dr. Theron Miller at WFWQC for his valuable scientific expertise suggestions that made this project much more successful. Thanks also to Jeff Den Bleyker at Jacobs Engineering for project management and direction. Also, to anyone else we forgot to mention, many, many, thanks!

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Appendices

Appendix 1. Monthly biovolumes (log µm^3 mL^{-1}) of phytoplankton taxa inside and outside of corrals that occurred in our mesocosms study in 2022. Taxa names are in Table 3.

May

Site	ANAR	ANFA	APCSP	AUGR	BOSP	CD2	CDSP	CHDI	CHSP	COSP	CRSP	CYPL	DECO	DEIN	EUSP	FRCR	GRLA
Corral 1	3.55	0.00	3.74	0.00	0.00	6.88	5.16	4.28	9.45	0.00	5.63	4.13	3.92	4.31	4.97	5.78	0.00
Corral 2	0.00	3.23	0.00	0.00	0.00	6.60	4.61	0.00	5.58	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Lake 1	2.77	0.00	0.00	0.00	0.00	6.83	5.57	3.97	5.12	0.00	0.00	0.00	4.23	0.00	4.49	0.00	3.75
Lake 2	3.75	2.92	5.33	4.44	6.53	6.39	5.27	4.28	5.38	5.79	5.85	0.00	4.53	4.31	5.19	0.00	0.00
Lake 3	0.00	0.00	0.00	0.00	0.00	6.58	5.46	0.00	5.38	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Lake 4	0.00	0.00	0.00	0.00	0.00	0.00	6.37	4.28	0.00	0.00	0.00	0.00	4.23	4.31	0.00	0.00	0.00
Lake 5	3.75	0.00	0.00	0.00	0.00	6.23	5.57	0.00	5.46	0.00	0.00	0.00	4.23	4.33	0.00	0.00	0.00

Site	KILU	LILI	MOCO	OOBO	OOSP	PD	PLAG	SCAR	SCSE	SNLA	SNSP	SPSC	TRSE	WICR	WIRE
Corral 1	4.25	4.40	2.96	5.32	5.33	5.85	6.28	0.00	3.78	0.00	0.00	0.00	0.00	0.00	4.95
Corral 2	0.00	0.00	3.20	0.00	5.28	5.73	0.00	0.00	0.00	6.15	0.00	0.00	0.00	0.00	5.25
Lake 1	0.00	0.00	0.00	0.00	5.38	5.34	6.28	0.00	0.00	5.37	0.00	0.00	0.00	4.35	4.73
Lake 2	4.35	0.00	3.80	5.93	0.00	5.84	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.49	5.98
Lake 3	0.00	0.00	3.27	0.00	5.63	5.73	0.00	4.25	0.00	0.00	0.00	5.67	0.00	4.35	4.86
Lake 4	0.00	0.00	3.50	0.00	5.59	5.39	0.00	0.00	4.95	0.00	4.98	0.00	3.92	0.00	4.55
Lake 5	0.00	0.00	0.00	5.32	0.00	5.89	0.00	4.55	0.00	0.00	0.00	5.67	0.00	4.65	5.31

June

SiteCode	ACGR	ACHA	ANAR	APIN	APSP	CD2	CDSP	CHDI	CHLSP	CHTU	COPL	CRFE	CRQU	CRRI	CRSP	DECO	DEIN	DEOP	DOCI
622c10	0.00	0.00	0.00	0.00	4.63	4.25	0.00	0.00	3.98	4.30	0.00	0.00	0.00	0.00	5.83	3.23	0.00	3.23	0.00
622c6	0.00	0.00	0.00	0.00	5.63	5.59	5.01	0.00	5.16	0.00	4.99	0.00	0.00	0.00	5.63	4.62	0.00	0.00	5.34
622c7	0.00	0.00	2.77	0.00	5.16	5.66	4.61	3.91	4.38	0.00	0.00	0.00	0.00	0.00	5.45	0.00	4.03	0.00	0.00
622c8	0.00	0.00	0.00	0.00	4.46	4.20	4.22	0.00	3.38	0.00	0.00	0.00	0.00	0.00	4.75	0.00	0.00	0.00	0.00
622c9	0.00	0.00	2.77	0.00	5.40	5.44	5.16	4.21	5.03	0.00	0.00	0.00	0.00	0.00	6.00	4.53	4.33	0.00	4.81

622out1	0.00	0.00	3.25	0.00	6.11	5.93	5.54	3.91	4.38	0.00	0.00	0.00	4.11	0.00	5.75	4.40	4.33	4.23	5.64
622out2	0.00	3.49	0.00	0.00	5.25	6.53	4.61	0.00	4.08	0.00	0.00	5.18	0.00	0.00	6.00	3.92	4.33	3.92	5.34
622out3	4.20	0.00	2.77	0.00	5.16	5.49	4.61	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.45	0.00	4.21	0.00	0.00
622out51	0.00	0.00	2.77	0.00	5.51	5.82	4.79	0.00	4.08	0.00	0.00	0.00	0.00	0.00	5.75	0.00	3.73	0.00	5.33
622out52	0.00	0.00	3.07	0.00	5.56	5.65	5.22	4.38	4.78	5.47	0.00	5.00	0.00	3.75	0.00	4.23	4.03	4.40	5.34

SiteCode	ERGI	EUSP	GLSP	GOSP	KILU	KISP	KOSP	LASP	LESP	MEGL	MESP	MOCO	OOBO	OOSP	PD	PEPE	QUSP	SCAR	SCEL
622c10	0.00	4.27	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.73	2.20	4.00	4.81	4.39	0.00	0.00	0.00	4.46
622c6	0.00	4.97	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.13	0.00	0.00	5.13	5.29	0.00	0.00	0.00	0.00
622c7	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.62	4.92	0.00	3.43	0.00	4.70	5.27	5.79	0.00	0.00	0.00	5.16
622c8	0.00	3.79	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.21	0.00	4.00	4.43	5.63	0.00	0.00	0.00	0.00
622c9	0.00	4.49	0.00	0.00	0.00	4.03	3.92	3.92	0.00	0.00	3.73	0.00	5.00	5.33	5.47	0.00	0.00	0.00	0.00
622out1	0.00	5.09	0.00	5.25	0.00	4.03	0.00	3.62	4.92	0.00	4.43	0.00	4.70	5.63	6.30	4.15	0.00	3.95	5.16
622out2	0.00	4.49	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.89	0.00	5.54	5.57	4.15	0.00	0.00	0.00
622out3	0.00	4.79	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.13	0.00	0.00	5.21	5.57	0.00	0.00	4.55	0.00
622out51	0.00	4.79	0.00	0.00	0.00	4.03	0.00	0.00	0.00	0.00	3.43	2.89	0.00	5.21	5.89	0.00	4.23	4.25	4.86
622out52	0.00	4.79	4.45	0.00	4.00	0.00	0.00	0.00	0.00	4.02	0.00	0.00	0.00	5.61	6.03	0.00	4.53	3.95	4.86

SiteCode	SCSE	SNSP	SPSC	TRSP	UNCCY	UNDI	UNSPCH3	WICR	WIRE
622c10	3.01	4.47	0.00	0.00	3.89	0.00	2.53	0.00	4.16
622c6	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
622c7	3.71	0.00	0.00	0.00	0.00	0.00	3.23	0.00	4.55
622c8	0.00	0.00	0.00	0.00	0.00	0.00	2.53	0.00	3.86
622c9	0.00	0.00	5.37	0.00	0.00	4.23	2.92	0.00	4.55
622out1	4.19	0.00	0.00	0.00	0.00	0.00	3.77	4.35	5.16
622out2	4.31	0.00	0.00	4.01	0.00	4.70	2.92	0.00	0.00
622out3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.25
622out51	4.01	0.00	0.00	0.00	0.00	0.00	3.53	0.00	4.25
622out52	3.71	0.00	0.00	0.00	0.00	0.00	3.40	0.00	4.86

July

SiteCode	ACHA	ANAR	ANFA	APCSP	APFL	AUGR	CD2	CDSP	CHMI	COMSP	COPL	CRSP	DEBI	DECO	DEIN	DEOP	ERGI	GLSP	KISP
Corral 2	0.00	0.00	0.00	5.46	0.00	0.00	4.23	5.35	0.00	0.00	4.99	5.63	0.00	4.23	4.03	3.92	0.00	0.00	3.73
Corral 3	0.00	2.77	3.20	5.60	4.70	0.00	0.00	5.68	0.00	0.00	0.00	5.45	0.00	0.00	0.00	0.00	0.00	0.00	3.55
Corral 4	3.79	3.77	3.20	0.00	0.00	4.27	0.00	10.79	4.57	0.00	5.59	5.75	0.00	4.23	4.33	4.23	5.23	0.00	4.46
Corral 5	4.09	4.07	3.81	5.94	0.00	5.04	4.89	7.13	6.53	5.59	5.29	6.36	4.65	4.92	4.63	4.92	5.23	5.05	4.93

SiteCode	KOSP	MASP	MEGL	OOBO	OOSP	PD	PEAN	PEDU	PLSP	SCSE	SPSP	TECA	UNSPCH
Corral 2	0.00	0.00	0.00	0.00	0.00	6.17	0.00	5.45	5.54	0.00	3.47	0.00	0.00
Corral 3	3.92	0.00	0.00	0.00	0.00	6.07	0.00	5.13	0.00	0.00	0.00	0.00	4.05
Corral 4	0.00	0.00	0.00	0.00	5.03	6.69	4.75	5.45	0.00	4.01	0.00	0.00	0.00
Corral 5	0.00	4.75	3.72	5.00	5.73	6.57	5.59	6.28	0.00	4.01	0.00	3.62	0.00

August

SiteCode	ACHA	ANAR	ANFA	APCSP	APFL	APIN	APSP	AUGR	CD2	CDSP	CHDI	CHGL	CHLSP	CHMU	CHSP	CHTU	CRSP	CYPL	DEBI
822c1	0.00	3.25	0.00	0.00	6.56	4.89	0.00	0.00	3.75	6.73	0.00	3.76	4.08	4.92	0.00	5.77	5.45	0.00	4.05
822c2	0.00	3.47	0.00	0.00	0.00	0.00	5.16	0.00	6.27	4.92	4.51	0.00	0.00	0.00	5.92	0.00	0.00	3.83	0.00
822c3	0.00	3.07	3.20	0.00	0.00	0.00	0.00	0.00	6.51	4.61	0.00	0.00	0.00	0.00	5.74	0.00	5.75	4.43	0.00
822c4	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	6.45	4.92	0.00	0.00	0.00	0.00	5.92	0.00	0.00	0.00	0.00
822c5	3.79	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.96	5.22	0.00	0.00	0.00	0.00	5.28	0.00	0.00	0.00	0.00
822out1	0.00	0.00	0.00	4.86	7.10	0.00	0.00	4.14	4.53	5.90	0.00	0.00	4.08	0.00	0.00	5.30	0.00	0.00	0.00

SiteCode	DEBIC	DECO	DEIN	DEOP	DOCI	EUSP	GLSP	KILU	KISP	KOSP	LILI	MESP	MISP	MOCO	MOCOV	OOBO	OOSP
822c1	3.52	4.23	0.00	4.23	5.34	0.00	4.45	0.00	0.00	3.92	0.00	3.73	5.25	0.00	2.89	0.00	4.43
822c2	0.00	0.00	4.03	3.92	0.00	5.09	0.00	0.00	4.21	0.00	0.00	0.00	0.00	3.37	0.00	5.00	5.43
822c3	0.00	4.23	4.03	0.00	0.00	5.27	0.00	0.00	4.03	0.00	4.51	0.00	0.00	3.50	0.00	0.00	5.33
822c4	0.00	0.00	0.00	0.00	0.00	5.57	0.00	0.00	4.03	0.00	5.17	0.00	0.00	3.20	3.26	5.00	5.33
822c5	0.00	0.00	4.03	0.00	0.00	4.79	0.00	0.00	0.00	0.00	5.00	0.00	0.00	0.00	0.00	0.00	5.43
822out1	0.00	0.00	3.73	0.00	5.34	0.00	0.00	3.40	0.00	3.92	0.00	0.00	0.00	0.00	0.00	0.00	4.43

SiteCode	OOSP	PD	PEAN	PEDU	PSBO	QUSP	SCAR	SCEL	SCSE	SNLA	UNDI	WICR
822c1	4.43	5.77	4.75	5.13	5.66	0.00	0.00	4.86	3.71	0.00	0.00	0.00

822c2	5.43	5.73	0.00	0.00	0.00	0.00	0.00	0.00	3.71	5.07	4.23	0.00
822c3	5.33	5.73	0.00	0.00	0.00	0.00	0.00	0.00	4.01	0.00	0.00	4.83
822c4	5.33	6.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
822c5	5.43	5.80	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.37	0.00	4.83
822out1	4.43	5.71	0.00	0.00	0.00	0.00	0.00	0.00	3.71	0.00	0.00	0.00

October

Site	ACHA	ANFA	APCSP	APFL	APIN	AUGR	CD2	CDSP	CHLSP	COSP	CRSP	DECO	DEIN	DEOP	DOCI	EUSP	KILU	KISP	MASP
Corral 6	0.00	2.90	0.00	0.00	0.00	0.00	5.29	5.01	5.08	0.00	0.00	0.00	4.03	0.00	0.00	4.49	0.00	0.00	0.00
Corral 7	0.00	0.00	0.00	0.00	4.20	0.00	3.53	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Corral 8	2.79	0.00	0.00	0.00	0.00	0.00	4.93	4.61	0.00	0.00	0.00	0.00	0.00	0.00	4.35	3.79	0.00	3.03	3.45
Corral 9	0.00	0.00	0.00	0.00	0.00	0.00	4.39	0.00	4.16	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Corral 10	0.00	0.00	0.00	0.00	0.00	0.00	3.75	0.00	3.38	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Lake 1	0.00	2.90	0.00	0.00	4.89	0.00	5.21	0.00	0.00	0.00	0.00	0.00	4.03	0.00	0.00	0.00	3.70	0.00	0.00
Lake 2	0.00	2.90	0.00	6.09	4.59	4.44	0.00	6.25	0.00	0.00	0.00	3.92	0.00	0.00	5.34	0.00	3.88	3.43	0.00
Lake 3	0.00	0.00	4.86	0.00	0.00	0.00	0.00	5.73	0.00	0.00	0.00	0.00	0.00	4.23	0.00	0.00	0.00	0.00	0.00
Lake 4	0.00	3.20	0.00	0.00	5.20	0.00	5.16	5.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Lake 5	0.00	0.00	0.00	0.00	4.89	0.00	5.87	0.00	5.28	4.67	5.45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Site	MEGL	MESP	OOSP	PD	PEDU	PESP	PHSP	SNLA	UNFC	UNSC	WIRE
Corral 6	0.00	0.00	4.43	5.09	0.00	5.30	4.16	5.07	0.00	0.00	0.00
Corral 7	0.00	0.00	3.73	3.99	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Corral 8	0.00	0.00	0.00	4.87	0.00	0.00	0.00	0.00	4.40	0.00	0.00
Corral 9	0.00	0.00	4.88	4.77	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Corral 10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Lake 1	3.42	0.00	4.43	5.39	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Lake 2	0.00	3.91	5.03	5.89	0.00	0.00	0.00	0.00	0.00	0.00	4.25
Lake 3	0.00	0.00	5.33	0.00	5.59	0.00	0.00	0.00	0.00	4.29	4.55
Lake 4	0.00	0.00	4.73	4.69	0.00	0.00	0.00	0.00	0.00	0.00	4.55
Lake 5	0.00	4.03	5.21	5.54	0.00	0.00	0.00	0.00	0.00	0.00	0.00