Progress Report to Wasatch Front Water Quality Council

Factors Effecting the Ecological Health and Integrity of Utah Lake with a Focus on the Relationships between Water Column Regulators, Benthic Ecosystem Engineers, and CyanoHABs

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Cover photos:

Top photo: Utah Lake at Vineyard during low water in 2016. Clear water in foreground and up until pelicans visible in the distance is from abundant freshwater springs flowing off of the Wasatch Range that for the most part no longer flow directly into the lake but have lost their integrity due to unprecedented urban development.

Bottom photo: Utah Lake at Sandy Beach looking SW into Goshen Bay during low water in 2016. This was a relatively low water year and the mollusk hunter pictured would have been knee to waist deep in water at the same time period in 2019.

Summary

Utah Lake is the last large freshwater remnant of Lake Bonneville. It has undergone several primarily anthropogenically induced ecosystem shifts and hysteresis over the past 150 years resulting in alternative states in an analog environment. Subsequently, the lake has lost most of its ecological integrity. Utah Lake's ecological health has also been severely compromised with a concomitant reduction in its resistance and resilience to ongoing and future perturbations. A multitude of stressors have prompted this loss precluding its ability to self-regulate. These multiple stressors unshackle ecosystem constraints that provide competitive advantages to cyanobacteria, allowing for frequent blooms. Stressors that are discussed in this progress report include:

- Watershed diversions and water quality degradation
- Water level fluctuations
- Turbidity
- Near zero flush rates
- Changes to temperature regime
- Loss or reduction of aquatic vegetation and allelopathy
- Dominance by invasive fishes
- Watershed-wide pesticide use
- Metapopulation and metacommunity dynamics: Isolation
- Pharmaceuticals
- Urbanization, the most recent and ongoing catastrophic shift
- Loss of native zoological assemblages including mollusks
- Analog zooplankton assemblages
- Transition from native benthic ecosystem engineers to analog invasive engineers.

As a result, Utah Lake has become a poorly functioning analog of its former self. Our society has inadvertently created a much-simplified analog Utah Lake ecosystem that often favors a cyanobacterial lineage whose primordial ancestors evolved in simple, stressed systems billions of years ago.

Top-down biotic regulators, such as zooplankton, and benthic ecosystem engineers, including native mollusks and midges, have also lost most of their ability to regulate cyanobacteria blooms. Top-down regulators and benthic ecosystem engineers are the primary focus of this progress report and our research.

Almost no research has been conducted on zooplankton assemblages in Utah Lake and their life histories, ecology, importance to the functioning of the lake, and even their taxonomies are poorly documented. We are compiling and analyzing much needed research on zooplankton in the lake. Included in this progress report is our taxonomic evaluation and revision of zooplankton in the lake. Continued data collection will allow us to develop a definitive taxonomic key to be used by other researchers. We are also the only researchers that we are aware of, that conduct research on the importance of mollusks and midges to the functioning of Utah Lake, including their role in regulating cyanoHABs.

Our research group has collected environmental and ecological data and holistically examined many of the problems that face Utah Lake for almost a decade. We conclude that without such comprehensive and integrative knowledge of these synergistic intricacies, we could have thoughtlessly assumed that nutrient reduction alone will control cyanobacteria blooms in the future.

We also have determined that the best way to understand and monitor the biological health of Utah Lake is to develop a Multimetric Index of Biological Integrity (MIBI). This index contains dozens of important metrics (measures) and is an ongoing part of our Utah Lake research. The preliminary MIBI is included in this project report.

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Goals

The goal of our ecological research on Utah Lake is to increase our understanding of its ecological health and integrity, including environmental and ecological factors that can reduce its resistance and resilience and subsequently its ability to self-regulate cyanoHABs. We are doing this in a scientific holistic manner because we are well aware that focusing on only one or two stressors to the lake's ecosystem cannot possibly provide managers with enough understanding of how best to manage the lake into the future. As one major end point, we can use this knowledge to develop a suite of relevant metrics that can be used to monitor changes in Utah Lake' ecological health and address the causes.

Introduction and Background

Lake Bonneville: A Lake No More?

Utah Lake is one of the last remnant puddles of an ancient lake that until recently, in geologic time, spanned over 83,000 km^2 and at times was over 300 m deep; Lake Bonneville. Lake Bonneville was created when volcanic eruptions in southeast Idaho blocked an adolescent version of the Bear River and diverted its flow into central Utah, during the Pleistocene Epoch, between 130,000 and 30,000 years ago (Chronic 1990, Stokes 1986). Deep grabens[1] filled with diverted Bear River water and formed Lake Bonneville (Chronic 1990, Stokes 1986). At times, Lake Bonneville was as large as one of the largest of the Great Lakes, Lake Michigan and often was even deeper. Lake Bonneville and its remains sit on a limestone basin that in some locations is five miles thick. This limestone was deposited from highly productive, nutrient rich, shallow seas that ebbed and flowed in and out of existence starting in the Cambrian Period and lasted throughout the Pennsylvanian Period in the Paleozoic Era, some 540 to 250 million years ago (Chronic, 1990, Stokes 1986). Dozens of these ancient nutrient laden limestone layers deposited by marine life over the eons are clearly visible along the uplifted Wasatch Range (Figure 1).

Lake Bonneville water levels raised and lowered for thousands of years depending on climatic and geologic conditions, reaching its maximum height about 16,000 years ago. Then around 14,500 years ago, Lake Bonneville breached near Red Rock Pass, Idaho creating a cataclysmic flood into the Snake River, known as the Great Bonneville

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[1] Grabens are depressed blocks of the Earth's crust bordered by parallel faults formed by range-faulting.

Flood. The level of Lake Bonneville water then remained below its outlet due to a drying climate starting about 10,000 years ago, eventually resulting in remnant puddles; Great Salt Lake, Utah Lake, Sevier Lake, Rush Lake, and Parowan Lake (Chronic, 1990, Stokes 1986). Terminal Great Salt Lake became salty, Utah Lake remains fresh- slightly brackish because of its limited outflow into the Jordan River, and Sevier Lake is now a dry lakebed. Utah Lake and Great Salt Lake are the only large waterbodies that remain of Lake Bonneville, and Utah Lake is the only large bodied freshwater relict remaining.

Figure 1. Mt Timpanogos in the Wasatch Range near Utah Lake showing the many stratifications of nutrient rich, ancient shallow seas that formed in the Paleozoic Era before being uplifted.

Utah Lake

> "A lake that endured for millennia has been ecologically devastated within 150 years."
> (Janetski 1990)

The ecology of Utah Lake is tied to its past and the ecology of Lake Bonneville. Utah Lake is a slightly saline- eutrophic to hypereutrophic- alkaline-turbid- shallow-temperate lake with an average depth of about 1.5 to 2.8 m. It is about 40 km long by 21 km wide, with a surface area of about 384 km^2. Thirteen fish were native to Utah Lake, including the top predator, Bonneville cutthroat trout. Only two native fish species remain, the Utah sucker (*Catastomus ardens*) and the critically endangered June sucker

(*Chasmistes liorus*) (Carter 2005, Heckmann et al. 1981). Because it is shallow and has a large surface area, evaporation plays a key ecological role. Even though evaporation accounts for > 42% of its outflow; large amounts of evaporative losses are typical of shallow lakes residing within semi-arid to arid climates.

Although Utah Lake historically functioned as a natural shallow lake ecosystem, it has undergone what are known as ecological hysteresis[2] (Nikanorov and Sukhorukov 2008, Beisner et al. 2003) and catastrophic ecosystem shifts[3] (Scheffer et al. 2001, Beisner et al. 2003). This has resulted in what is known as 'alternative stable states'[4] and these dramatic transitions were primarily due to human economic activity. The most important factors that contributed to these shifts include; sedimentation, loss of submerged aquatic vegetation, abrupt transition from a native fishery to non-native fishery most notable the introduction of benthic feeding carp, loss of native fish and invertebrates including losses of critically important filter feeding bivalves and algal grazer snails, water diversions, increased nutrients and toxic metals, man-made water-level fluctuations, and multiple other types of pollution and pollutants[5] (Wakefield 1933, Petersen 1996, Crowl et al. 1998, Tan and Ozesmi 2006, Deseret News 1967, USFWS 2010, Carter 2005, Janetski 1990, Coops et al. 2003). Utah Lake is no longer a natural

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[2] Hysteresis "implies that communities and ecosystems might be easily pushed into some configurations from which it may prove much more difficult for them to recover" (Beisner et al. 2003). Hysteresis is "where the observed equilibrium of a system cannot be predicted solely based on environmental variables, but also requires knowledge of the system's past history". (Wikipedia accessed November 24, 2019).

[3] All ecosystems are exposed to gradual changes in climate, nutrient loading, habitat fragmentation or biotic exploitation. Nature is usually assumed to respond to gradual change in a smooth way. However, studies have shown that smooth change can be interrupted by sudden drastic switches to a contrasting state (see Footnote 4). Although diverse events can trigger such shifts, studies show that a loss of resilience usually paves the way for a switch to an alternative state. This suggests that strategies for sustainable management of such ecosystems should focus on maintaining resilience (Scheffer et al. 2001).

[4] Marten Scheffer (2009) provided a simple explanation for alternative stable states, "Suppose that you are in a canoe and gradually lean farther and farther over to one side to look as something interesting underwater. Leaning over too far may cause you to capsize and end up in an alternative stable state upside down. Although the details of the theory of alternative stable states may appear tricky, several key properties can be seen in this simple example. For instance, returning from the capsized state requires more than just leaning a bit less to the side. It is difficult to see the tipping point coming, as the position of the boat may change relatively little up until the critical point. Also, close to the tipping point resilience of the upright position is small, and minor disturbances such as a small wave can tip the balance.

[5] EPA's general definition of pollution is the man-made or man-induced alteration of the chemical, physical, biological, and radiological integrity of water. Whereas, pollutant is dredged spoil, solid waste, incinerator residue, sewage, garbage, sewage sludge, munitions, chemical wastes, biological materials, radioactive materials, heat, wrecked or discarded equipment, rock, sand, cellar dirt and industrial, municipal, and agricultural waste discharged into water (https://www.epa.gov/cwa-404/clean-water-act-section-502-general-definitions).

lake but is managed as an *operational water supply reservoir* because of a man-made dam at its outlet into the Jordan River built in 1872 and created to serve large water demands (USFWS 2010).

The Utah Lake ecosystem prior to Mormon settlement in the mid-1800s certainty was not at all what it is today. Utah Lake was arguably the most scenic and productive cold-water fishery in the western USA prior to Mormon settlement (Janetski 1990, Carter 2005, de Escalante 1776, Prat 1849, Bean 1854) and was a unique and ecologically important part of Utah's (and the nation's) natural heritage.

Bonneville cutthroat trout and twelve other fish species thrived by the millions. More species of freshwater mollusks called Utah lake home than anywhere in western North America and based on our understanding of freshwater mollusk ecology, they likely dictated most of its ecological functioning. Birds, wildlife, and Native Americans thrived in its enviros. In fact, historical records show that the first Mormon settlers likely would not have survived their first few winters in Utah if not for the tremendous native fishery in Utah Lake, particularly the Bonneville cutthroat trout fishery, and the generosity of Native Americans residing along its shores (Carter 2005, Heckmann et al. 1981). The following are a few excerpts from Janetski (1990) and Carter (2005) regarding Utah Lake prior to settlement:

> "... the valley and the borders of the lake of the Timpanogos (Utah Lake) ... is the most pleasant, beautiful and fertile in all of New Spain . . .. The lake and the rivers which empty into the lake abound in many kinds of choice fish; there are to be seen there very large white geese, many varieties of duck, and other kinds of beautiful birds never seen elsewhere; beavers, otters, seals, and other animals which seem to be ermines by the softness and the whiteness of their fur." (Escalante 1776).

> "I was at Utah Lake last week and of all the fisheries I ever saw, that exceeds all. I saw thousands caught by hand, both by Indians and whites. I could buy a hundred, which each weigh a pound, for a piece of tobacco as large as my finger. They simply put their hand into the stream and throw them out as fast as they can pick them up . . .. Five thousand barrels of fish might be secured there annually . . . "(Prat 1849).

> "Indeed, so great was the number of suckers and mullets passing continuously upstream that often the river would be full from bank to bank as thick as they could swim for hours and sometimes days together."— George Washington Bean, 1854.

Although Utah Lake continues to be highly productive and is sanctuary for thousands of migratory birds; its native fauna has all but disappeared and its waters are now primarily dominated by taxa such as cyanobacteria, algae, worms (oligochaetes), midges (chironomids), and introduced fishes. Utah Lake is now a highly regulated and abused reservoir ecosystem that has undergone human induced ecological hysteresis and catastrophic shifts and no longer resembles its natural self, pre-settlement. Consequently, Utah Lake is biologically impoverished and polluted. Understandably, Utah Lake is now severely underappreciated by naïve citizens and managers unfamiliar with its exceptional past.

In this progress report, we discuss historical and ongoing factors that cause(d) ecosystem shifts that degrade(d) and reduce(d) its resistance and resilience[6] to perturbation, its ecological health and integrity, and its inability to self-regulate cyanoHABs. We then discuss the relationships between water column regulators, benthic ecosystem engineers, and cyanoHABs[7] based on our ongoing research of Utah Lake's ecology. We submit that "absence of fundamental knowledge of the mechanisms driving harmful algal blooms frustrates most hope of forecasting their future prevalence" (Wells et al. 2015) or for developing relevant nutrient criteria. This progress report is an important addition to this limited knowledge.

Ecological Health and Integrity

The biological[8] and ecological integrity[9], of the majority of large temperature lakes throughout the world have been lost or severely compromised and the status of their ecological health is questionable. Although ecological integrity and ecological health are often used interchangeably, they are not the same (Karr 1993, 1996). According to Karr (1996):

> "Integrity implies an unimpaired condition or the quality or state of being complete or undivided; it implies correspondence with some original condition. Health, on the other hand, 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).

Regrettably, and despite its ancient lineage, Utah Lake is now a highly regulated and abused reservoir ecosystem and is consequently biologically impoverished. According to Karr (1996), "if biotic impoverishment is the problem, then protecting the integrity of"

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[6] Resistance is the property of communities or populations to remain "essentially unchanged" when subject to disturbance. Resilience is the capacity of a population/community of organisms or an ecosystem to respond to a perturbation or disturbance by resisting damage and recovering quickly.

[7] There is a misunderstanding that harmful algal blooms in Utah Lake are caused by algae. In fact, blooms in the lake are caused by cyanobacteria, not algae. We, therefore, refer to harmful algal blooms as cyanoHABs throughout this report.

[8] Biological integrity refers to the capacity to support and maintain a balanced, integrated, adaptive biological system having the full range of elements (genes, species, assemblages) and processes (mutation, demography, biotic interactions, nutrient and energy dynamics, and metapopulation processes) expected in the natural habitat … (Angermeier and Karr 1994, Karr and Dudley 1981, Karr et al. 1986).

[9] Ecological integrity is the sum of physical, chemical, and biological integrity (Karr 1993, 1996).

Utah Lake's "biological system(s) must be the goal". However, it is difficult to find and quantify any of Utah Lake's remaining ecological integrity, although as long as it is alive it must have some hidden shred of integrity.

The ecological health of Utah Lake on the other hand, given its age, genealogy, and historical and current abuse, appears to be quantifiable and salvageable. All lake ecosystems have limited and somewhat predictable lifespans (Wetzel 2001, Cole and Weihe 2016). All lakes evolve, grow old, and die. Because Utah Lake evolved with nutrient rich geological parent materials and is now for the most part a terminal reservoir with high surface area to depth ratio, severely limited flushing, in an arid environment with large evaporation rates; nutrient concentrations continue to increase. The lake is in the later stage of its life with increasing primary productivity (i.e. often eutrophic in spring and autumn). During summer it is regularly very productive (i.e. hyper eutrophic).

Utah Lake is not managed for its health or integrity but is principally managed for water use and consumption. Regulations have been established for Utah Lake to protect water quality 'designated beneficial uses' including 'warm water fisheries' and recreational use, however there is a large difference in how the lake is managed and how regulations are applied.

Dozens of measures (metrics) of Utah Lake's current ecological health derived from other lakes throughout the world are available from the literature and from ours and other's past and present research on the lake. Given our limited knowledge of Utah Lake's ecosystem function, these metrics can be accurately but imprecisely quantified and allow us to monitor changes to Utah Lake's ecological health.

In this progress report we review environmental factors that contribute(d) to ecosystem shifts in Utah Lake and that affect its health and integrity including self-regulation and resistance and resilience to cyanoHABs. We further evaluate important interactions between phytoplankton, zooplankton, and invasive fishes, and the importance of benthic ecosystem engineers for maintaining the lakes health. These results will allow us to greatly improve and refine scientifically valid metrics and indices urgently needed to monitor Utah Lake's ecological health.

Factors Affecting Utah Lake's Ecosystem Shifts, Integrity, Health, and CyanoHABs

Watershed Diversions and Degradation Favors CyanoHABs

One of the leading causes of Utah Lake's loss of ecological integrity, declining health, and vulnerability to perturbation has been and continues to be water diversions throughout the watershed, starting in its headwaters. Utah Lake resides in an arid to semi-arid environment, has a very large surface area to volume ratio, and loses a sizable portion of its water to evaporation. Utah Lake's ecosystem depends on the surrounding watershed for most of its water, predominantly from the Wasatch Range of the Middle

Rocky Mountains in the form of surface water and groundwater. However, much of this water is diverted before it reaches the lake and/or is polluted before entering the lake. Loss of a natural water regime has negative ecological effects that reverberate throughout Utah Lake's ecosystem, including its ability to self-regulate cyanoHABs. Again, Utah Lake is not a naturally functioning lake but a water supply reservoir. There is a large difference between how natural lake ecological function and reservoir ecological function that has been documented by countless research publications, white papers, and management agencies. Entire journals are devoted to this subject.

Rivers

The major tributaries to Utah Lake, including the Provo River, Spanish Fork, Beer Creek, Currant Creek, and American Fork River are all highly regulated. When their flows into Utah Lake are not completely curtailed and disconnected, they are severely reduced and do not follow a natural flow regime that a normally functioning lake would recognize. As with lakes, it is well documented that flow regulation degrades a river's integrity and threatens its health. In addition to flow regulations and unnatural flow regimes, all of these tributaries are also polluted by other types of pollutants and have had their ecologic integrity and health further conceded.

Figure 2. Timpanogos Creek a headwater tributary to the Provo River, the highly regulated main tributary to Utah Lake. This tributary originates on Mt Timpanogos (Figure 1) and flows through mostly limestone bedrock.

Spring Tributaries

The condition and health of spring tributaries and ground water inputs to Utah Lake is poorly understood. We are compiling information on these critically important water sources and have observed that most spring tributaries are in poor health. We have collected ecological data on one abused spring tributary near Vineyard and are currently analyzing this data and will be able to monitor any ecological changes in the future.

Fluctuating Water Levels Favor CyanoHABs

It is well known, that rapidly fluctuating lake (reservoir) levels, particularly unpredictable fluctuations, are detrimental to biota and ecological health, including resistance and resiliency (Thornton et al. 1990, Cowx 2008). Utah Lake levels fluctuate substantially both intra- and inter-annually, naturally and anthropogenically. The lake is nourished mostly by snow fed rivers and streams, springs, and ground water. Snowpack levels and rain events vary between years and effect Utah Lake levels. Utah Lake is a highly regulated reservoir and is principally managed for downstream agriculture use. Consequently, regulators have designated a lake compromise level[10] of 1368.4 meters. Utah Lake's tributaries are also managed for agriculture use and domestic use; much of the tributary water is diverted before it reaches the lake. Weather and climate related lake levels are exacerbated by ecologically unpredictable human demands.

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[10] As a result of the 1983-1984 flooding, a lawsuit was filed for compensation due to flooding based upon breach of contract of the previous compromise level. In 1985, a new compromise level was reached which governed the maximum level of the lake. The new level was chosen to be 4,489 feet (1,368 m) above sea level. When the water level in Utah Lake exceeds this level, the Jordan River pumps and gates are left open. The new compromise level also means that the lake's elevation was below Jordan River's stream bed (https://en.wikipedia.org/wiki/Utah_Lake).

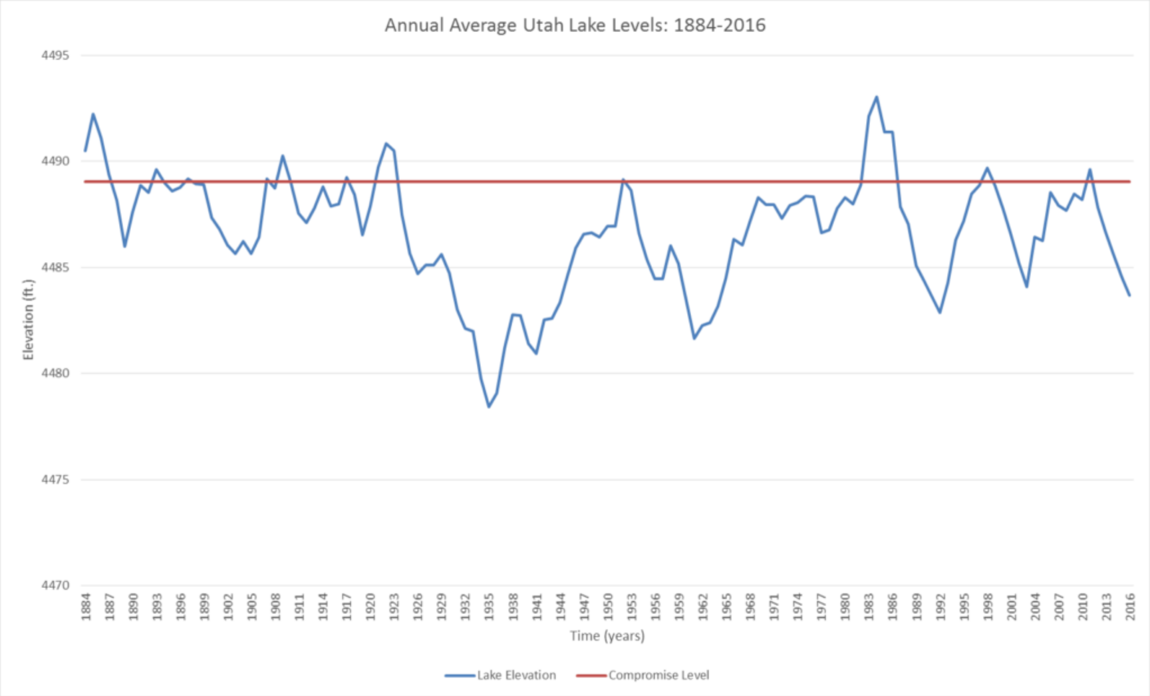

Figure 3. Utah Lake water elevations from 1884 until 2016. Note extreme low levels in 1935, which had catastrophic effects on the lake's biota. Red line is 'compromise' level = 1368 meters.

Low Lake Levels

In 2016, snowpack levels were low and water demand was high This caused lake levels to drop significantly. Utah Lake levels fell to about 2.13 ft below compromise level, the lowest it has been in over 23 years. The southern portion of Goshen Bay went completely dry in late summer for several months causing the clay and mud substrate to bake kiln-dry hard (Figure 4, Figure 5). Obviously, very few if any sessile, aquatic obligate organisms survived (e.g midge larvae, mollusks, oligochaetes, etc.) (Figure 6). Those that were able, moved to wetted habitats. It also takes many years for benthic macroinvertebrate assemblages to fully recolonize these large areas once water returns, which translates into a substantial loss of benthic secondary production and ecosystem function that resonates throughout the food web.

Figure 4. Exposed sun baked clay and mud substrate of southern Goshen Bay, 2016. Several square miles were affected. Obviously, very few if any benthic invertebrates survived, and complete recolonization will take several years.

Figure 5. Exposed sun baked clay and mud substrate of southern Goshen Bay, 2016. Several square miles were affected. A few early successional 'weeds' attempted to colonize these areas.

Figure 6. Invasive Asian Clam (*Corbicula* sp.) stranded during low water levels along the shoreline of Utah Lake near Vineyard, UT, summer 2016. Hundreds of these clams were observed stranded and eventually either perished due to desiccation or were preyed upon.

Low lake levels in 2016 revealed the existence and importance of large quantities of groundwater spring flows, particularly along the lake's eastern shores (Figure 7, and cover images).

Figure 8. Exposed springs flowing into Utah Lake, near Vineyard, UT 2016. The entire open areas behind the front row of cottonwood trees in foreground including those trees behind the front row have been lost to housing subdivisions. No open areas remain. The spring water sources are now mostly paved over and filled and any remaining ecological integrity destroyed.

Low lake levels also expose fine shoreline sediments that are highly erosional and only colonized by early succession plants (cover image 1), including invasive phragmites and tamarisk. Low water years can expose large amounts of habitat and large quantities of benthic macroinvertebrates (e.g. midge larvae, corixids, etc.) beneficial to wading shorebirds (Figure 9). Low water years also restrict adult fishes from competing with wading shorebirds for macroinvertebrates in shallow habitat a net benefit to wading birds and more importantly allowing macroinvertebrate populations to increase as a result of reduced fish predation. However, the clay content of the exposed habitat in some sections of the lake has been known to trap shorebirds and waterfowl, much to their demise (Richards and Miller, personal observations). Low water levels in Utah Lake can exacerbate cyanoHABs by increasing nutrient concentrations, increasing temperatures, and altering the food web, etc. or reduce cyanoHABs by allowing benthic invertebrate induced sediment aeration to continue or increase.

Figure 9. White faced ibis gorging itself on adult midges and ephydrid flies during the low water year, 2016. Low lake levels allow wading birds access to shallow sections of Utah Lake that otherwise would be inundated during high lake levels.

High Lake Levels

During high water years, near shore areas of Utah Lake are inundated and the water is too deep for wading shorebirds, which have to seek food resources and wading habitat elsewhere. 2019 was a relatively wet year and lake levels remained high and near compromise. Lake elevation at the time of this report was 1367.7 meter or about 30 cm below compromise. 2019 high waters inundated shoreline areas dominated by invasive phragmites and tamarisk and created wetlands that were hospitable to many organisms including zooplankton, macroinvertebrates, and frogs (primarily native Boreal Chorus Frogs and invasive American Bullfrogs). Inundated aquatic vegetation also provided fish spawning habitat and nurseries for native and invasive larval and juvenile fishes.

Zooplankton were able to take advantage of inundated phragmites in 2019. The following link to a YouTube video shows how abundant zooplankton can be within inundated phragmites stands:

Zooplankton in inundated phragmites video
https://youtu.be/orJ2_ILDb7I.

Flooded phragmites in 2019 also provided exceptional spawning habitat for invasive carp. Personal observations revealed in autumn 2019 to be a banner year for juvenile fish recruitment in inundated vegetation and we predict it to be a very strong year class for several species and will have food web effects for several years.

The following two links to YouTube videos provides an understanding of how important high lake levels are to sustaining large populations of this nuisance species:

Carp spawn video 1
https://youtu.be/kefBvIv5Fhw

Carp spawn video 2
https://www.youtube.com/watch?v=-HnwlZ1otH0

Any assessment of Utah Lake's ecological health needs to consider lake level fluctuations and their ecological impacts, for better or worse.

Note: The following sections on addition environmental conditions that favor cyanoHABs and in particular the following three sections; Turbidity Favors CyanoHABs, High Levels of Solar Radiation and Bouancy Favors CyanoHABs, and Limited Flush Rates Favor CyanoHABs are brief literature review synopses. There is a large and increasing amount of research being conducted on cyanobacteria ecology and the environmental conditions responsible for blooms in a response to ever increasing cyanoHABs, worldwide. Consequently, some of what we report in the following sections may become outdated or elaborated upon as our knowledge rapidly increases.

Turbidity Favors CyanoHABs

Sediments in Utah Lake are easily resuspended in the water column by even the slightest wind and wave action (DWQ Utah Lake Science Panel 2019, Randall et al. 2017). These suspended solids (total suspended solids = TSS = turbidity) can remain in the water column for several days or longer after strong wind events (Richards and Miller, personal observations) and dissolved solids constantly maintain turbidity in this eutrophic lake (see video below).

https://youtu.be/z07JTJfin7c

Turbidity significantly affects biological activity and productivity and directly influences the occurrence and abundance of cyanobacteria because they are considered superior competitors to green algae under low light conditions (i.e. high turbidity) (Smith 1986, Jensen et al. 1994, Scheffer et al. 1997). In addition to being superior light competitors, cyanobacteria also promote low light conditions by having a higher turbidity per unit of phosphorus than other phytoplankton, thus they increase shading starting at the onset of blooms (Scheffer et al. 1997). It is important to understand that this phenomenon occurs in eutrophic lakes regardless of water column nutrient levels (Scheffer et al. 1997)(Figure 10). Given Utah Lake's almost constant high turbidity, it is one of the more important mechanisms determining cyanoHABs in the lake.

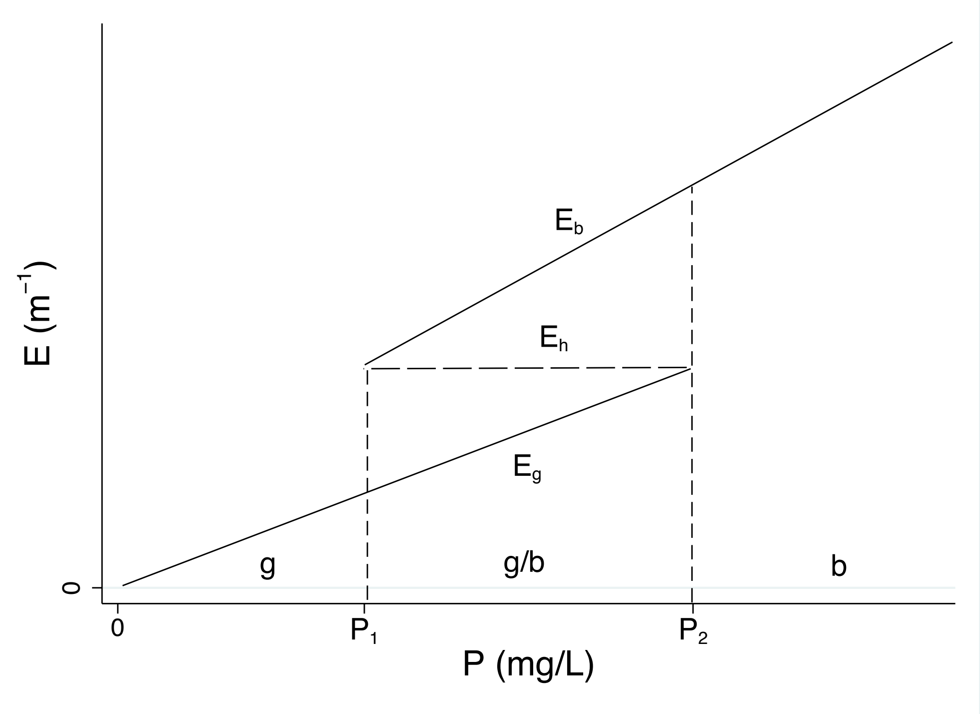

Figure 10. Green algae/cyanoHAB hysteresis as the response of turbidity, E (m^{-1}) with respect to phosphorus, P (mg/L) from Scheffer et al. 1997. "Starting in the region [b] where a cyanobacterial monoculture is the only stable state, a shift to the alternative state will only occur after the lower bifurcation line is passed. On the other hand, starting from the region [g] where the cyanobacterial monoculture is unstable, a switch to cyanobacteria will only occur after the upper bifurcation line is crossed. In the region [g/b] (P_1 to P_2) where two alternative equilibrium states are stable, the system will stay in its current equilibrium state, unless perturbations bring it within the basin of attraction of the alternative state." It can be seen from this diagram that a transition from blue- green to green dominance is always associated with a conspicuous drop in turbidity, and that in the vicinity of the breakpoints a small variation of a control parameter can be sufficient to induce the transition.

Very preliminary data based on extremely limited samples sizes support the literature that phytoplankton blooms increase turbidity in Utah Lake (Figure 11, Figure 12). We are in the process of compiling and analyzing additional data from WFWQC and DWQ.

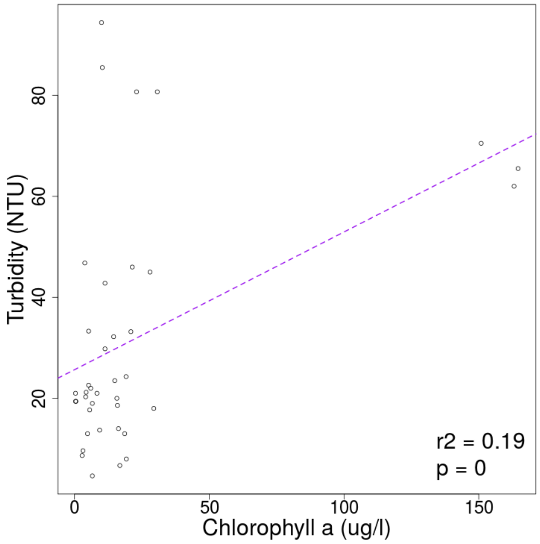

Figure 11. Very preliminary analysis of relation between Chlorophyll a and turbidity in Utah Lake. From UDWQ Shiny app (https://udwq.shinyapps.io/UtahLakeDataExplorer/). High turbidity at low *Chl-a* levels show sediment-based turbidity, whereas the three high turbidities at high *Chl- a* levels may show effects of phytoplankton bloom on turbidity. More analyses are required due to very low sample size, particularly in the Chlorophyll a range between 40 to 125 ug/l provided by UDWQ consequently the regression line and results should be considered irrelevant.

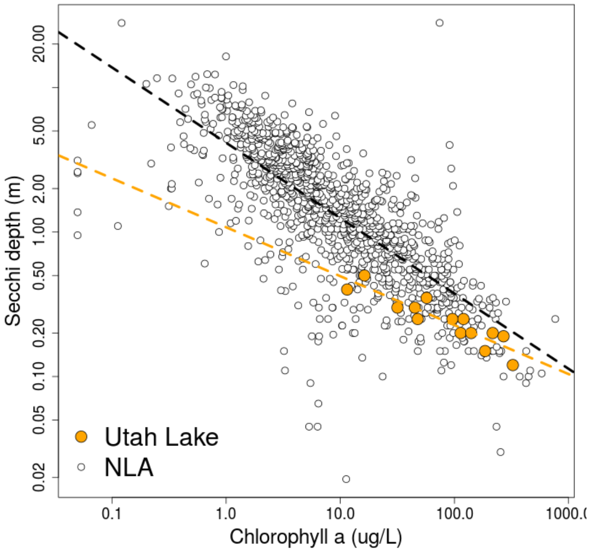

Figure 12. Very preliminary analysis of relation between Chlorophyll a and turbidity in Provo Bay. From UDWQ Shiny app (https://udwq.shinyapps.io/UtahLakeDataExplorer/). More analyses are required due to very small sample size. Yellow = data from Provo Bay; black open circles and line = data from National Lake Assessment Program. Provo Bay regression line (yellow dashed line) should be ignored and more relevant statistical analyses performed on this and future data.

The following figure, Figure 13, represents phosphorus levels (TP))(mg/L) in the water column of Utah Lake across all locations from 1989 to 2018 compiled by UDWQ and graphed by month. The red reference lines are 0.08 and 0.17 mg/L TP that represent hysteresis cutoffs of green algae/cyanobacteria relationships between turbidity and TP at a flush rate of 0.1/day (retention time of 10 days) based on Scheffer et al. 1997 (see Figure 10 above and Figure 9A in Scheffer et al. 1997). At TP ≅ 0.17 mg/L, cyanobacteria will dominate the lake even if turbidity is zero at a relatively high flush rate of 0.1/day. At lower flush rates, cyanobacteria will dominate even at lower TP levels. At TP ≅ 0.08 mg/L or higher, cyanobacteria will tend to dominate when turbidity is at moderate levels reported by Scheffer et al. (1997) (i.e. $E(m^{-1}) \cong 0.9$) at a flush rate of 0.1/day.

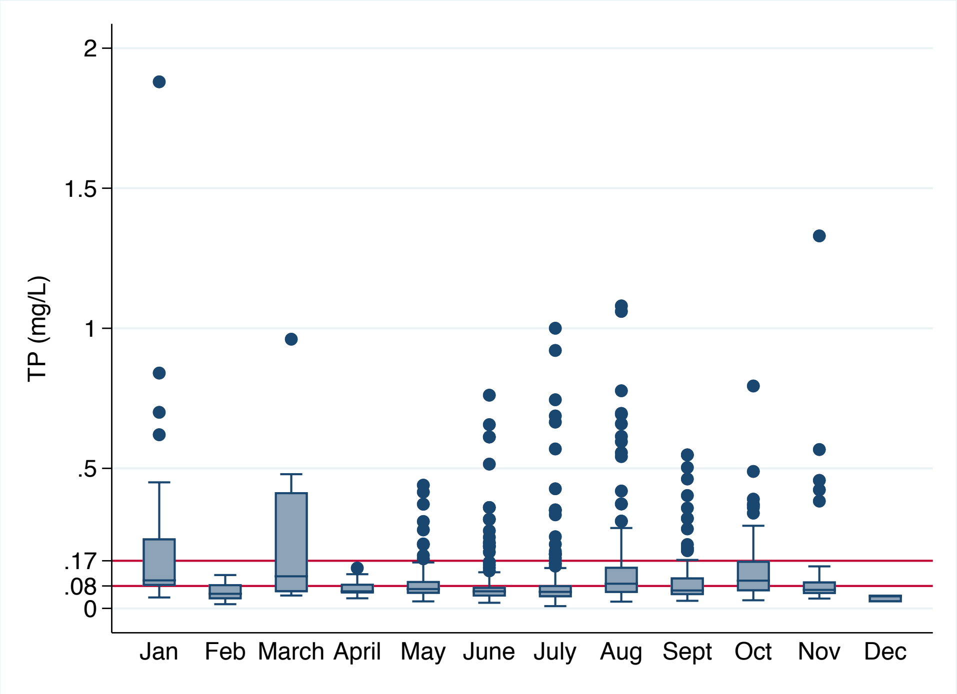

Figure 13. Monthly TP (mg/L) levels in Utah Lake based on UDWQ data from 1989 to 2018. Median, 25th, 75th, range, and outliers. Red reference lines are Scheffer et al. (1997) green/cyanobacteria hysteresis cutoffs at flush rate = 0.1/day (retention time = 10 days). N = 1112 TP recordings.

From Figure 13, we can see that much of the time, TP levels in Utah Lake favor cyanoHABs given its high turbidity and low flush rate (long retention time) and we can infer that lake wide TP reduction would have to be substantial to reduce cyanoHABs. However, other factors can influence cyanoHABs (see all sections of this report). At this time, we have not calculated retention times for Utah Lake, although we believe for most of the year, they are often much longer than 10 days. We also do not know turbidity and light extinction coefficient parameters for any of the green algae or cyanobacteria that cause blooms in Utah Lake but assume those values will be similar to those used by Scheffer et al. (1997).

Solar Radiation and Bouancy Favors CyanoHABs

Not only are many cyanobacteria species superior competitors for low light attenuation, they also are able to withstand high solar radiation and can regulate their buoyancy to maximize irradiance levels (Berg and Sutula 2015). After all, cyanobacteria have been present and evolving in aquatic ecosystems since the beginning of life on Earth and have easily withstood several mass extinctions. Cyanobacteria genera that occur in Utah Lake including Microcystis, Planktothrix and Aphenizomenon have the ability to regulate their buoyancy by a combination of gas vesicles and carbohydrate storage products (Berg and Sutula 2015). Gas vesicles allows positive buoyancy whereas carbohydrate storage products have the opposite affect (Walsby 1994, 2005) and the type and amount of carbohydrate storage products produced varies by species and irradiance level (Berg and Sutula 2015, Visser et al. 1997, Wallace and Hamilton 1999). Cyanobacteria can become neutrally buoyant and adjust upward lift by balancing gas vacuoles and carbohydrate storage products (Walsby et al. 2004), thus they can control their vertical position in the water column by regulating the amount of carbohydrate storage products consumed (Berg and Sutula 2015, Konopka et al. 1987, Wallace and Hamilton 1999). In order to maximize their growth potential, filamentous cyanobacteria can sink or float at speeds up to 0.3 m per day in order to position themselves at just the right depth (Walsby 2005). Obviously, nutrient availability affects carbohydrate production and buoyancy regulation; nitrogen starved cells have excess carbohydrate stores and tend to lose buoyancy more easily than nutrient sufficient cells (Brookes and Ganf 2001).

High irradiance levels are in part why cyanoHABs occur more frequently in summer. Adjusting buoyancy also allows many species of cyanobacteria to settle down on the benthic substrate at night., Cyanobacteria can acquire unoxidized iron and free phosphorus when the surface layer of sediments becomes hypoxic or anoxic. This transition between sediment anoxia and oxic conditions plays a very important role in whether green algae or cyanobacteria dominate in Utah Lake. We reported this important phenomenon in a section of our previous progress report (Richards and Miller 2019), which we have attached in **Appendix 1**, including how the presence or absence of chironomid larvae can influence these interactions.

Limited Flush Rates Favor CyanoHABs

High flush rates also reduce the probability of cyanoHABs because of their relatively slow growth rates (Scheffer et al. 1997, Figure 14). Alternatively, loss or reduction of flushing increases cyanoHABs (Jónasson and Adalsteinsson 1979, Einarsson et al. 2004). Unfortunately, Utah Lake rarely meets compromise level (see Figure 3) and unless lake water is actually physically pumped out of the lake, it most often functions as a terminal lake with near zero flush rate

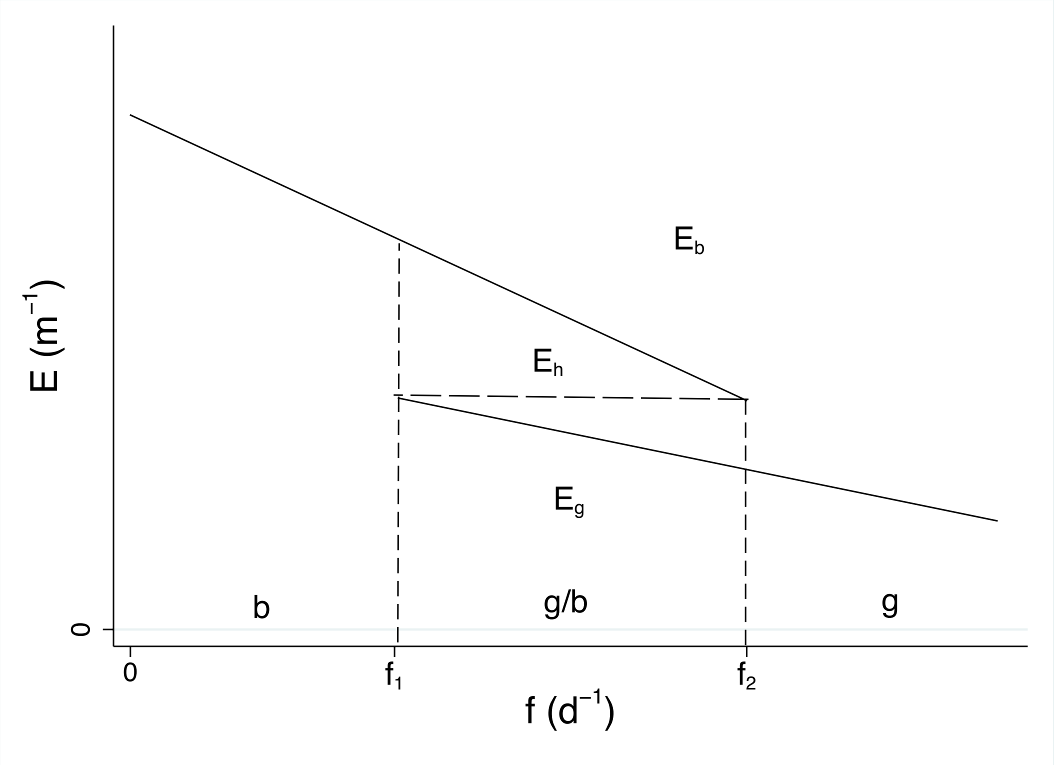

Figure 14. Green algae/cyanoHAB hysteresis as the response of turbidity, E (m^{-1}) with respect to phosphorus, flush rate, f(d^{-1}) from Scheffer et al. 1997. "Starting in the region [b] where a cyanobacterial monoculture is the only stable state, a shift to the alternative state will only occur after the lower flush rate bifurcation line is passed. On the other hand, starting from the region [g] where the cyanobacterial monoculture is unstable, a switch to cyanobacteria will only occur after the upper flush rate bifurcation line is crossed. In the region [g/b] (f_1 to f_2) where two alternative equilibrium states are stable, the system will stay in its current equilibrium state, unless perturbations bring it within the basin of attraction of the alternative state." It can be seen from this diagram that a transition from blue- green to green dominance is always associated with a conspicuous drop in turbidity, and that in the vicinity of the breakpoints a small variation of a control parameter can be sufficient to induce the transition.

Scheffer et al. (1997) noted in their study that beyond a flush rate of ≈18% lake volume per day, cyanobacteria were predicted to be absent irrespective of the nutrient level. Again, Utah Lake has flush rates much lower than 18% per day with rates that are often close to 0% per day.

The importance of flush rates controlling cyanoHABs in Utah Lake can be clearly shown by comparing environmental conditions between Utah Lake and downstream impounded wetland ponds in Great Salt Lake (GSL) within the same drainage (Table 1).

Table 1. Comparison of several environmental factors between Utah Lake and downstream Great Salt Lake (GSL) impounded wetland ponds that may be responsible for cyanoHABs in Utah Lake but not the ponds. All values are best estimates .....

	Utah Lake	GSL Impounded Wetland Ponds
Mean depth (m)	≈ 2	≈ 2
Water column TP[1] (mg/l) (mean and 95%CI)	0.11 (0.10; 0.12)	X
Estimated volume flush rates[2] (% day^{-1})	0 to << 18	≥ 18
Fish production/biomass	Very high	Very high
Aquatic vegetation cover	Sparse	Abundant
Water source	Utah Lake	Mostly Utah Lake during summer, POTWs, tributaries
CyanoHABs	Frequent in summer	Absent

[1] Utah Lake water column TP estimates from UDWQ online database. N = 1112 recordings.

[2] Lake volume flush rates estimated from Miller and Richards personal observations and needs quantification.

GSL wetland ponds receive much of their water from POTW discharge and Utah Lake via the Jordan River, especially in summer that transports large amounts of phytoplankton originating from Utah Lake, including cyanoHABs (Richards 2019). These ponds recieve X times as much P than what is in the water column in Utah Lake (Table 1). Interestingly, cyanoHABs have not been reported in GSL wetland ponds, whereas Utah Lake has frequent blooms in late summer. Flush rates are the only the major environmental difference between these water bodies provides strong evidence that low to nonexistent flushing of Utah Lake directly contributes to cyanoHABs within the lake. We have initiated a study comparing these two water bodies focusing on causal reasons for absence of cyanoHABs in wetland ponds and abundance of blooms in Utah Lake.

It appears that nutrient reduction alone cannot decrease cyanobacteria dominance in Utah Lake or unless strong management actions are implemented. For example, unrealistic efforts to reduce wind and wave derived ultra-fine sediment suspension turbidity via massive wind breaks and/or intensive pumping and flushing of water out of the system. Both inefficient and unconventional strategies. Alternatively, turbidity caused by benthic bioturbation can be mediated with careful planning as can implementation of other biomanipulation methods.

Even though turbidity, solar radiation, and flush rates in shallow lakes such as Utah Lake often supersedes nutrients in regulating cyanoHABs; recently extirpated top down (higher trophic level) regulators, such as native bivalves and zooplankton assemblages, reduced cyanoHAB frequency and intensity in the lake. However, Utah Lake is an out-of- balance analog with weakened resistance and resilience. Subsequently, cyanoHABs will continue to occur or may increase in frequency and intensity. It therefore becomes imperative to understand the current health of Utah Lake and in particular, the ecology and interactions between top down controllers of cyanoHABs in Utah Lake including, water column regulators and benthic ecosystem engineers. This understanding may then provide managers with more efficient alternative methods for reducing cyanoHAB frequency and intensity in the lake.

Temperature and CyanoHABs

Temperature is also an important environmental factor affecting cyanoHABs throughout the world and obviously in Utah Lake (Wells et al. 2015, Scheffer et al. 1997, Scheffer et al. 2001, Berger 1975, Reynolds 1988, Bissenger et al., 2008, Eppley 1972). In general, cyanoHABs increase with increased temperatures, although winter low temperatures also can influence cyanobacteria populations, including ice covered conditions. Climate change forcing will directly affect Utah Lake water temperatures and other key ecological variables and interactions that regulate cyanoHABs (Wells et al. 2015, Scheffer et al. 2001) (Figure 15).

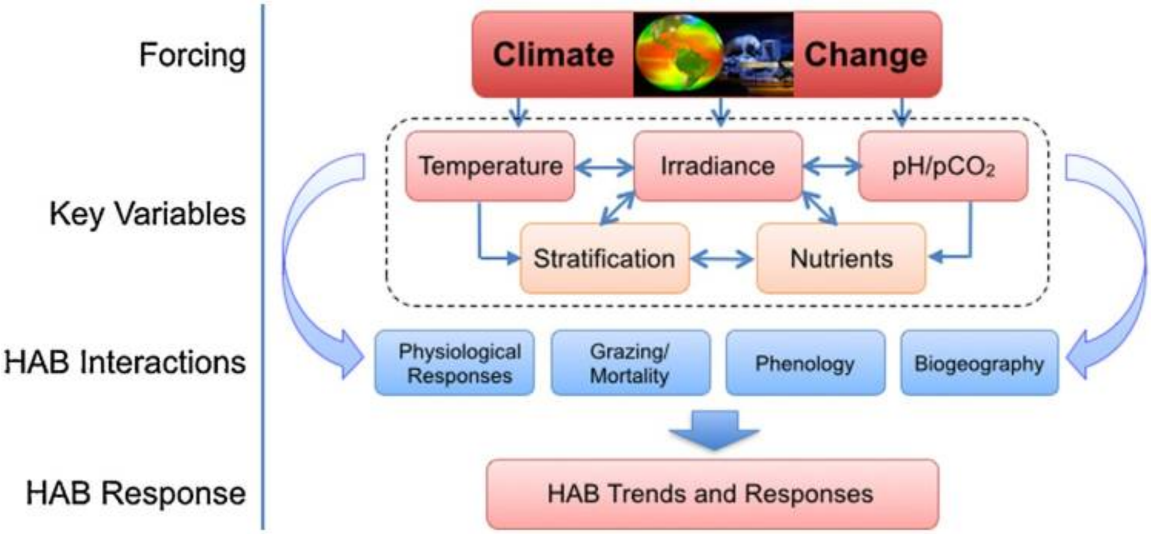

Figure 15. Generalized relationships between cyanoHAB trends and responses, interactions, key variables, and climate change forcing. Taken from Wells et al. 2015.

It is expected that warming water temperatures will increase potential growth rates of cyanoHABs (Wells et al. 2015). CyanoHAB motility (Kamykowski and McCollum, 1986), germination (Montresor and Lewis, 2006; Yamochi and Joh, 1986), nutrient uptake, photosynthesis, and other physiological processes (Beardall and Raven, 2004; Raven and Geider, 1988) are all influenced by temperature (Wells et al. 2015). For example, Li (1980) showed that the optimal temperature for phytoplankton photosynthesis is generally greater than the optimum for growth. The biogeographical breadth of phytoplankton species niches, including cyanoHAB species, is largely determined by temperature regimes (Longhurst, 1998; Okolodkov, 1999, 2005, Wells et al. 2015), including often underappreciated regulation by winter low temperatures (Scheffer et al. 1997, Berger 1975, Reynolds 1988).

The effects of winter low temperatures and duration of ice cover on cyanoHAB and other phytoplankton succession on the community level food web in Utah Lake has been grossly understudied. However, Richards and Miller (2019c) and Richards and Miller (2017) reported seasonal succession of phytoplankton in the lake in the recent past. The Wasatch Front Water Quality Council is increasing its winter ecological sampling efforts to better understand this phenomenon.

Obviously, cyanoHAB species, can show strong intraspecific differences in temperature tolerance and responses (de Boer, 2005, Wells et al. 2015). Ecological evolution prescribes that all phytoplankton species throughout the world, including Utah Lake, have “a temperature niche described by optimal, lethal and tolerable water temperatures at which cells do not grow well, but can survive” (de Boer, 2005; Fehling et al., 2004; Magaña and Villareal, 2006; Rhodes and O'Kelly, 1994, Wells et al. 2015).

Based on our research and knowledge of the Utah Lake ecosystem, we anticipate that temperature effects will cascade throughout the ecosystem as the climate changes including; affecting cyanobacteria and algal assemblages, likely increased bloom intensity and frequency, competition between phytoplankton grazer assemblages and their top down control, parasites, and planktivorous fish assemblages (Alheit et al., 2005; Edwards and Richardson, 2004; Hansen, 1991). Without a solid understanding and incorporation of the effects of changing temperature regimes, establishing nutrient criteria levels for Utah Lake will fall far short of any intended cyanoHAB management goals.

Figure 16. Unseasonably cold temperatures in October 2019 resulted in a rapid freeze of shorelines of Provo Bay, Utah Lake. Two days prior to taking this photo, air temperatures were 65^0 F and zoo biota, particularly juvenile fishes were abundant (https://youtu.be/5qYfa4_a_lk). Remaining emergent aquatic vegetation stands, including phragmites stands after aggressive control and removal projects provided some refugia for biota from the freeze. Note open water towards the center of the bay. One week later the ice was gone.

Allelopathy and CyanoHABs

An important but completely overlooked ecological factor that likely contributes to cyanoHABs in Utah Lake at least within the littoral zone, is the ecosystem- shifting reduction and loss of allelopathic chemical controls produced by submerged (SAV) and emergent (EAV) aquatic vegetation (aka macrophytes) (Scheffer et al. 1993). It is well known that most species of aquatic vegetation produce allelopathic chemicals, many of which negatively affect cyanobacteria (Hilt & Gross 2008; Al-Shehri 2010; Jasser 1995; Korner & Nicklisch 2002; Santonja et al. 2018; and others). According to Gross et al. (2007): “We now have ample evidence that low phytoplankton and epiphyte densities in shallow eutrophic lakes might be the result of complex abiotic and biotic feedback mechanisms, and allelopathy is considered as one alternative mechanism (Scheffer et al. 1993).”

It has been well documented that phytoplankton (including cyanobacteria) exhibit different, species specific and strain specific sensitivities to macrophyte allelochemicals (Gross 2003; Hilt & Gross 2008; Korner & Nicklisch 2002; Mulderij, Mooij, Smolders, & van Donk 2005; van Donk & van de Bund 2002; Al-Shehri 2010; Jasser 1995;

Santonja et al. 2018). For example, chlorophytes (green algae) appear to be less sensitive, whereas diatoms and cyanobacteria are often significantly inhibited by macrophyte allelochemicals (Hilt & Gross 2008; Al-Shehri 2010; Jasser 1995; Korner & Nicklisch 2002). Mulderij et al. (2005) reported a higher sensitivity of toxic than non-toxic *Microcystis aeruginosa* strains among cyanobacteria to aquatic vegetation allelochemicals. There is a general consensus among chemical ecologists that macrophyte derived allelochemicals can be strong drivers of phytoplankton communities (Santonja et al. 2018) and that invasive macrophytes can have differing effects on cyanobacteria than native species.

We have found no literature that evaluated allelochemicals produced by invasive *Phragmites* sp. on cyanobacteria, the dominant EAV along the shores of Utah Lake, although our review was only cursory. However, we have observed (and have limited unpublished data) that water clarity and zooplankton abundances are substantially greater in inundated *Phragmites* sp. stands in Provo Bay and other areas of Utah Lake compared with areas directly adjacent to the stands devoid of macrophytes and that wind disturbance does not appear to fully explain these differences. See the following YouTube video to see how water clarity is improved in Phragmites stands which allows zooplankton to prosper:

https://www.youtube.com/watch?v=orJ2_ILDb7I

The following video shows a green algal bloom on Provo Bay in June 2017 just outside of phragmites and cattail stands.

https://www.youtube.com/watch?v=Jqc44-EvzRA

Several more specific examples of allelochemicals effects on algae and cyanobacteria follow. *Myriophyllum* sp. (water milfoil) are known to produce polyphenols that play a major role in suppressing phytoplankton growth (Gross 2003b; Hilt 2006; Hilt et al. 2006; Bauer et al. 2009). *Myriphyllum spicatum*, a species of milfoil that grows in Utah, contains up to 30% polyphenols based on dry weight in apical meristems and exhibits a strong inhibitory action against various cyanobacteria and algae (Gross et al., 1996; Korner and Nicklisch, 2002; Bauer et al. 2009). Algicidal phenolic compounds produced by *Myriphyllum* sp. defensive use against phytoplankton has been shown in aquatic habitats and in situ experiments and may provide an advantage for submerged plants in the competition with phytoplankton for light and likely contribute to the stabilization of clear water states in macrophyte dominated shallow eutrophic lakes (Hilt and Gross, 2008; Bauer et al. 2009). Bauer et al. (2009) showed that crude extracts of apical meristems of *Myriphyllum* sp. always inhibited the growth of *Anabaena variabilis*, although the active chemical compounds were seasonally variable.

Santonja et al. (2018) found that allelopathic effects of aqueous leaf extracts of *Ludwigia hexapetala* (a South American species of water primrose) had strong effects on the photosynthetic activity of three target phytoplankton strains of cyanobacteria; *Scenedesmus communis*, a toxic *Microcystis aeruginosa* strain and a non-toxic *Microcystis aeruginosa* strain. They identified three flavonoid glycosides myricitrin, prunin and quercitrin as the main secondary compounds and suggested that these chemicals could favor the photosynthetic activity of toxic cyanobacteria in spring and reduce their photosynthetic activity in summer, potentially leading to drastic changes in the phytoplankton communities.

SAV and EAV macrophyte dominated conditions in shallow eutrophic Utah Lake may have been the norm, pre-settlement mid-1800's. Based on the literature and our limited personal observations, we posit that macrophyte allelochemical defenses helped control cyanoHABs in the lake in the past but at present their role has diminished. We also submit that observations of early explorers that documented Utah Lake as having clear water were based on shoreline observations that likely were influenced by SAV and EAV effects on water turbidity, including allelopathy.

Any holistic scientifically based management actions taken to reduce cyanoHABs in the lake must address SAV and EAV allelopathy and incorporate this knowledge. For example, there is an ongoing phragmites removal program along the shores of Utah Lake via several intrusive control methods, even though to our knowledge no rigorous BACI based monitoring program has or is being conducted that measures ecosystem effects of phragmites removal, including allelopathic control of cyanoHABs.

Watershed-wide Pesticide Use Favors CyanoHABs

The effects of pesticides on the environment have been well documented since Rachel Carson's 1962 book *Silent Spring*, the environmental text that "changed the world" (Carson 2002). Since 1962, we have come to understand that targeted and non-targeted application of pesticides within a watershed can have severe negative direct and indirect effects, and short-term pulse or chronic low-level effects on aquatic ecosystems (Van Dijk et al. 2013, Carson et al. 1962, countless others). The effects of pesticides can range from effects on individuals to populations to communities to entire ecosystems and their food webs, including ecosystem functions (Van Dijk et al. 2013, Englert et al. 2012). Community-level effects can occur even at low levels of toxicants (Liess and Beketov 2011).

Pesticides can act individually or synergistically and there are often large phylogenetic differences in toxicity. For example, freshwater ostracods had 48-h LC_{50}s for a pesticide that were 50–120 times lower than that of *Daphnia magna* (Sánchez-Bayo and Goka, 2006b) and the midge, *Chironomus tentants* LC_{50}s were four orders of magnitude lower than those for *D. magna*.

In addition, the inert components used in a pesticide formulation can also be toxic to aquatic organisms (Dunkel and Richards 1998). Aquatic organisms are constantly being exposed to residues of chemicals present in water, from which they cannot escape. The following figure (Figure 17) illustrates of modes of entry of pesticides into aquatic ecosystems.

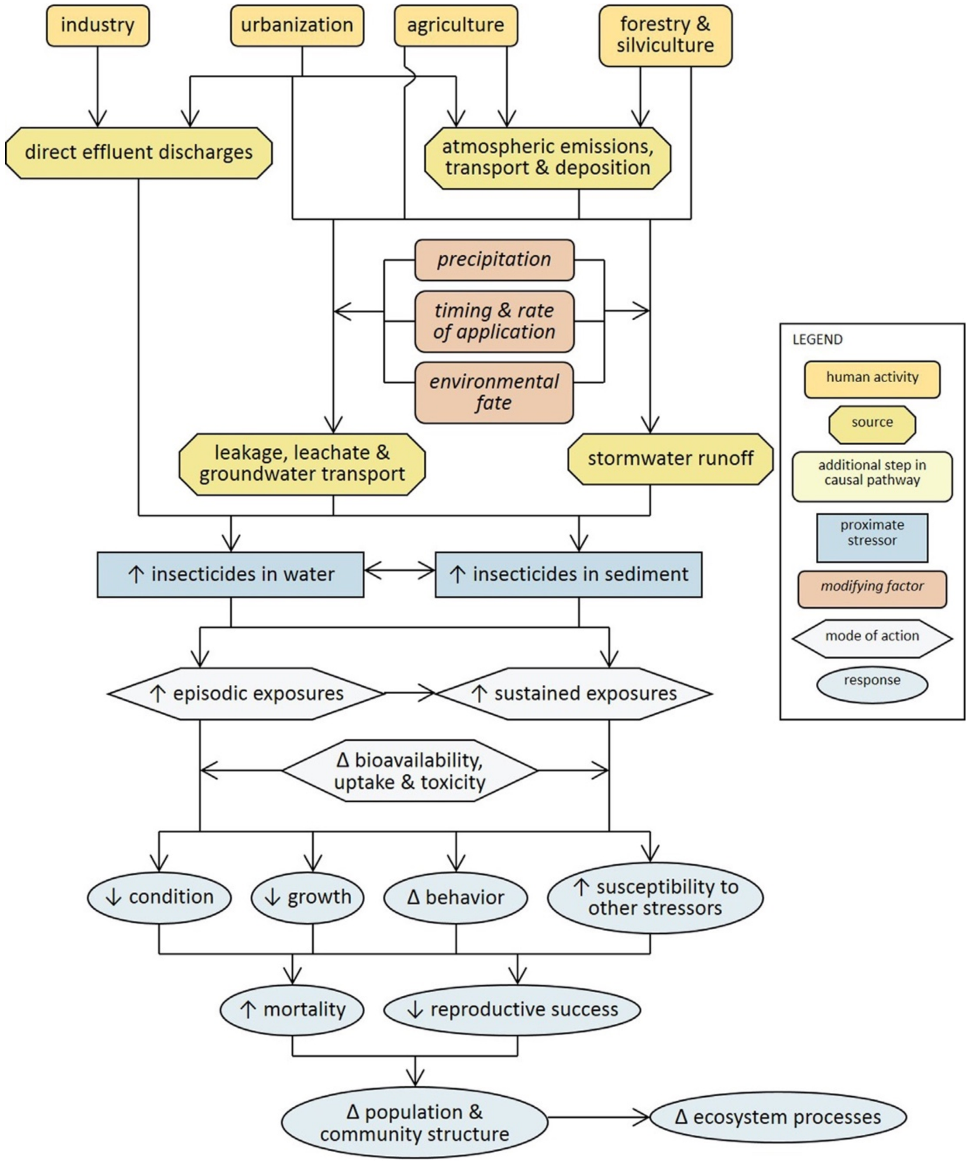

Figure 17. Conceptual model of mode of entry of pesticides into aquatic ecosystems from USEPA 2015.

Examples of the effects of pesticide use on aquatic organisms are voluminous. For example, long-term alterations in aquatic invertebrate community structure can occur after only a single pulse contamination of an aquatic ecosystem (Beketov et al. 2008, Van Dijk et al. 2013). Mohr et al. (2012) reported that negative effects on caddisflies occurred after a single pulse of the pesticide imidacloprid, and Diptera and Ephemeroptera larvae were affected after repeated pulses (Mohr et al. 2012, Van Dijk et al. 2013). This same pesticide caused zooplankton, benthic nekton and entire neuston communities to become significantly less abundant than non-treated controls (Hayasaka et al. 2011, Van Dijk et al. 2013).

Cumulative effects can act synergistically with other chemicals. For instance, Chen et al (2009) reported that eight days' exposure to a mixture of the nonylphenol polyethoxylate, R-11 and imidacloprid resulted in the crustacean *Ceriodaphnia dubia* population size that was three times smaller than with R-11 alone, and 13 times smaller than with imidacloprid alone (Van Dijk et al. 2013). Cumulative effects with exposure time become more relevant when organisms are constantly exposed to low levels of many contaminants (Tennekes and Sanchez-Bayo 2011). Even the lowest single pesticide concentrations can have toxic effects if sustained over a long period. For example, the difference in LC_{50} between only 2- and 5-day exposures was three orders of magnitude for freshwater ostracod *Cypridopsis vidua*, (Sánchez- Bayo, 2009). This trend toward lower LC_{50}s with increasing exposure time also occurs with other species including *Daphnia magna, Gammarus* amphipods, black fly larvae, alderflies, mayfly and dragonfly nymphs (Beketov and Liess, 2008a; Roessink et al., 2013, Van Dijk et al. 2013). Kunce et al. (2015) showed that survival of midge larvae (*Chironomus riparius*) was reduced in waters contaminated with mixtures of neonicotinoids (imidacloprid, thiacloprid) and pyrethroid insecticides (deltamethrin and esfenvalerate). Cumulative and synergistic effects do not always occur rapidly but may result in what is known as "delayed mortality" (Beketov and Liess, 2008a), which can occur many days, weeks, or even months after exposure.

Sublethal effects of pesticides also occurs and can reverberate throughout the food web (Desneux et al 2007, Van Dijk et al. 2013). Sublethal effects can affect neurophysiology, larval development, molting, adult longevity, immunology, fecundity, sex ratio, mobility, orientation, feeding behavior, and oviposition behavior (Desneux et al. 2007, Van Dijk et al. 2013). All of these sub-lethal effects have the potential to produce population level and community level impacts on ecosystems (Van Dijk et al. 2013).

Direct and indirect negative effects on individual species affects communities, food webs, and ecosystem function (Van Dijk et al. 2013). For example, direct negative effects on zooplankton species within the community can have indirect effects on growth suppression in fish feeding on the zooplankton species. Colombo et al. (2013) showed that the disappearance of chironomid larvae from pesticide use brought about increases in *Radix* sp. snails. Pestana et al. (2009) documented that the overall biodiversity of aquatic communities is negatively affected by pesticide use.

Many aquatic populations can be decimated by pesticides and recovery rates can be either slow or, if there is competition with other species, does not take place at all (Liess et al. 2013, Van Dijk et al. 2013). This is particularly true for univoltine or semivoltine species (Liess et al. 2013, Van Dijk et al. 2013). In addition, the structure of aquatic communities does not always revert to the original condition (i.e. hysteresis, resilience) because some species disappear while others increase in numbers (Beketov et al., 2008; Hayasaka et al., 2012a).

Hundreds of studies have shown that algae are particularly vulnerable to target and non-target herbicides. For example, several studies have shown that algae are particularly vulnerable to glyphosate-based herbicides because of their physiological and biochemical similarity with terrestrial plants (Annett, Habibi & Hontela, 2014; Tsui & Chu, 2003). Sáenz et al. (1997) showed that growth of green algae (*Scenedesmus acutus, S. quadricauda*) was inhibited by glyphosates and Tsui and Chu (2003) showed that the diatom species, *Skeletonema costatum* was more affected than green algae. Increased temperatures can also significantly reduce algal diversity exposed to herbicides. Obviously, benthic algae are also negatively affected by herbicides.

Cyanobacteria are much less susceptible to herbicides than are algae (diatoms and greens), which can result in their strong competitive advantage over other phytoplankton in Utah Lake. This competitive advantage combined with; 1) low light competitive advantage (see section Turbidity Favors CyanoHABs), 2) little or no lake water flushing competitive advantage (see section Flow Rates Favor CyanoHABs), 3) negative effects of pesticides on zooplankton grazers (this section), and 4) extinction prone populations and communities due to isolation (see following section Metapopulation and Metacommunity Dynamics: Isolation Favors CyanoHABs) allows cyanobacteria to dominate the Utah Lake ecosystem. Subsequently, cyanoHABs go virtually unchecked by other remaining compromised members of the lake's aquatic community.

Utah County has a long history of pesticide use and is one of the leading pesticide applicators in Utah with an extensive list of pesticides used (Eisele et al. 1989). Pesticides have been heavily applied near Utah Lake for decades (including DDT), particularly on its southern end with intensive agricultural land use. Tributaries that transport pesticides to Utah Lake from agricultural southern lands include Beer Creek, Spanish Fork, Currant Creek, etc. Forested lands and silvicultural lands within the watershed are also sources of pesticides to the lake, as well as unmonitored urban industrial and household sources and atmospheric drift. A very short list compiled by the author in a 1998 publication of several pesticides that have been used in agricultural and forested land and their effects on macroinvertebrates is in

Table 2.

Table 2. Effects of several pesticides on aquatic macroinvertebrates frequently applied to agricultural and forested areas. From Dunkel and Richards 1998.

Pesticide Name	Type	Aquatic invertebrate tested	Lethal Concentration	Duration	Citation

2,4-D	Systemic Pyridine herbicide	Amphipods	LC$_{50}$ 2.1-6.8 ppm	24h	1
Picloram	Systemic Pyridine herbicide	*Gammarus lacustris* (Amphipod)	LC$_{50}$ 2.1-6.8 ppm	24h	2
Fenvalerate	Synthetic pyrethroid	*Gammarus lacustris* (Amphipod)	LC$_{50}$ 0.00003 ppm to 0.000093 ppm	96h and 24h	3
Diflubenzuron	Growth regulator	*Skwala* sp. (Plecoptera)	LC$_{50}$ 57.5 ppm	96h	4
Malathion	Organophosphate	Various macroinvertebrates	LC$_{50}$ 0.000069 to 3.0 ppm	96h	5
Carbaryl	Carbamate	Various macroinvertebrates	LC$_{50}$ 0.0048 to 0.28 ppm	96h	6
Azinphosmethyl	Organophosphate	Various macroinvertebrates	LC$_{50}$ 0.00015 to 0.021 ppm	96h	7
Glyphosate R		amphipod	LC$_{50}$ 43 ppm	96h	8
Flucythrinate	Synthetic pyrethroid	amphipod	LC$_{50}$ 0.00022 ppm	96h	9
Flucythrinate	Synthetic pyrethroid	*Brachycentrus americanus* (Trichoptera)	40 to 80% immobilization	Almost immediately	10
Flucythrinate	Synthetic pyrethroid	*Pteronarys dorsata* (Plecoptera)	LC$_{50}$ > 0.0000007 mg/liter	12d	11

[1,4,5,6,7,8]Meehan 1991; [2,3] Anderson 1982, Smith and Stratton 1986; [9,10, 11] Anderson and Shubat 1984

There is ongoing use and misuse of pesticides to control mosquitos and phragmites directly adjacent to the shores of Utah Lake. Several dozen pest control businesses advertise aquatic insect control using pesticides, including at least one company that promotes controlling midges and mayflies (D.C. Richards, personal observation, see https://www.orkin.com/other/mayflies for a leading pest control business view on mayflies as pests). These applications certainly have a negative indirect on non-target organisms including midges and green algae, two important regulators of cyanoHABs in Utah Lake. As documented in this report and other reports (Richards and Miller 2019b, 2019c, 2017, Richards 2019a, 2019b, 2018, 2018b, and 2016), zooplankton are the top down regulators of phytoplankton and midge larvae are the dominant benthic ecosystem engineers in Utah Lake. Both these groups, as well as algae (excluding cyanobacteria) are highly susceptible to pesticides entering the lake and any negative effects restrict their important contributions to Utah Lake's food web, maintaining its ecosystem function, resistance and resilience, and as natural controls of cyanoHABs.

Metapopulation and Metacommunity Dynamics: Isolation Favors CyanoHABs

Ecological integrity as noted earlier, is the sum of physical, chemical, and biological integrity (Karr 1993, 1996). Biological integrity includes the full range of elements that specifically include metapopulation and metacommunity processes (Angermeier and Karr, 1994; Frey, 1975; Karr and Dudley, 1981; Karr et al., 1986).

Metapopulations and metacommunities are not completely isolated nor completely connected with other populations or communities but are those that 'blink in and out of extinction' due to limited dispersal and connectivity. They rely on rescue from nearby populations and communities for their survival. Therefore, limited amounts of dispersal and connectivity decrease the extinction risk of isolation. In addition, environmental stochasticity is not completely correlated between metapopulations and metacommunities such that individual populations or communities do not have the same extinction risk.

Dispersal, connectivity, and the level of demographic and environmental stochasticity correlation determines metapopulation and metacommunity viability (Altermatt 2011, Oliver et al. 2013). Isolated populations and communities on the other hand, are those that have no dispersal and connectivity to other populations or communities resulting in much higher extinction probabilities either through demographic or environmental stochasticity (Hanski 1999, MacArthur and Wilson 1967, Fagan et al. 2002, Strayer 2008).

Metapopulation viability is also determined by the relationship between suitable and unsuitable habitat. Suitable habitat can be occupied or unoccupied by populations and communities, likewise unsuitable habitat may be occupied or unoccupied. The proportion of suitable habitat that is occupied is a major driver in population and community viability. Suitable habitat may be unoccupied solely due to lack of dispersal and connectivity from other populations or communities (Strayer 2008). For example, water quality conditions that became unsuitable in the recent past from human activities may now be or may become suitable in the future but if there no dispersal and connectivity between populations and communities these suitable habitats will remained unoccupied. Habitat connectivity is key to ecosystem resistance and long-term resilience, as is biodiversity (Oliver et al. 2015).

It is likely that many extant populations once occupied most of the suitable habitats in Utah Lake prior to settlement but now have near- zero occupancy rates due to loss of connectivity and dispersal from other systems. Loss of habitat also increases dispersal distances between populations, which causes a loss in the proportion of unoccupied suitable habitat and therefore increases the extinction debt (Strayer 2008). Loss of dispersal ability and loss of suitable habitat are not additive but multiplicative (Strayer 2008). For example, if only 30% of suitable habitat remains and only 60% remains occupied due to reduced migration for example, then only 18% of the previously suitable habitats that were once occupied are now unoccupied.

Some of the native specie's populations in Utah Lake may be at such critically low densities that they may also have entered what is known as the 'extinction vortex' (Gilpen and Soule 1986), where in addition to the factors just described; genetic factors such as inbreeding depression, genetic drift, and 'mutational meltdown' (Lynch and Burger 1993) and demographic and environmental stochasticity combine in positive feedback loops that accelerate their extinction probabilities (Lynch et al. 1993, and Lynch and Gabriel 1990, Mock et al. 2004, Fagen and Holmes 2006).

Utah Lake for the most part can be considered to be isolated from other suitable habitats; thus, its populations and communities are isolated. As a remnant of Lake Bonneville, Utah Lake's biological community evolved in relative isolation from other lakes its size and has gradually adapted and evolved during the environmental and ecological transition from Lake Bonneville to Utah Lake. The only slightly similar large water body in proximity and connectivity to Utah Lake is downstream Farmington Bay of Great Salt Lake, a recently transitioned saltwater water body to fresh/brackish water body. Any aquatic dispersal and rescue of populations and communities in Utah Lake from Farmington Bay would have to be upstream through the Jordan River, which is often not physically connected to Utah Lake due to a dam and low lake water levels or via aerial dispersal of adult insects, although winds are typically from the south in summer when aerial insect adults are present. Because Utah Lake is now a lentic warm water system during summer, very few upstream connections exist because most upstream communities are lotic, cold water adapted. Consequently, population and community extinction risks are highly elevated in the lake.

As one example, Utah Lake's fish assemblage is now dominated by invasive species. Its benthic invertebrates and zooplankton have evolved with the community level effects of these invasive species without the support of rescue populations. Given all of the other stresses imposed on the lake, Utah Lake is now a poor analog of its former self. Utah Lake's simplified, depauperate, isolated, analog biological community cannot function properly enough to self-control cyanoHABs.

Urbanization: Most Recent and Ongoing Catastrophic Shift Favors CyanoHABs

Utah is experiencing a burgeoning exponential human population growth; Utah County is ground zero (Coon 2017). Utah's population was recorded at 11,380 in 1850, ten years later it was 40,273, a 250% increase and by 1900 it had grown to 276,749. Utah's population is roughly 3.22 million as of 2019 and by 2060 it is projected to have 6.84 million people (World Population Review 2019a). Utah County's human population was 2,206 in 1850. Today it is 606,503, a 27,500% increase and rapidly growing (Figure 18) (World Population Review 2019b).

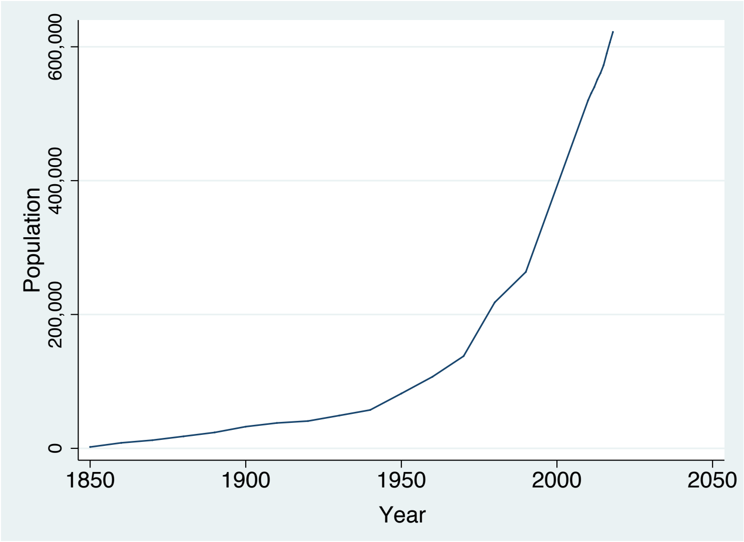

Figure 18. Exponential human population growth since Mormon settlement in 1850s in Utah County, UT (data extracted from World Population Review 2019b).

The following is a YouTube link to a video of the unprecedented urban development occurring along the shores of Utah Lake at Vineyard, UT. This area had dozens of spring feed groundwater tributaries feeding the lake whose fate is now unknown:

https://youtu.be/88CWhlhBc-8

The last remaining old growth cottonwood 'parks' are also being cleared to make room for subdivisions (Figure 19).

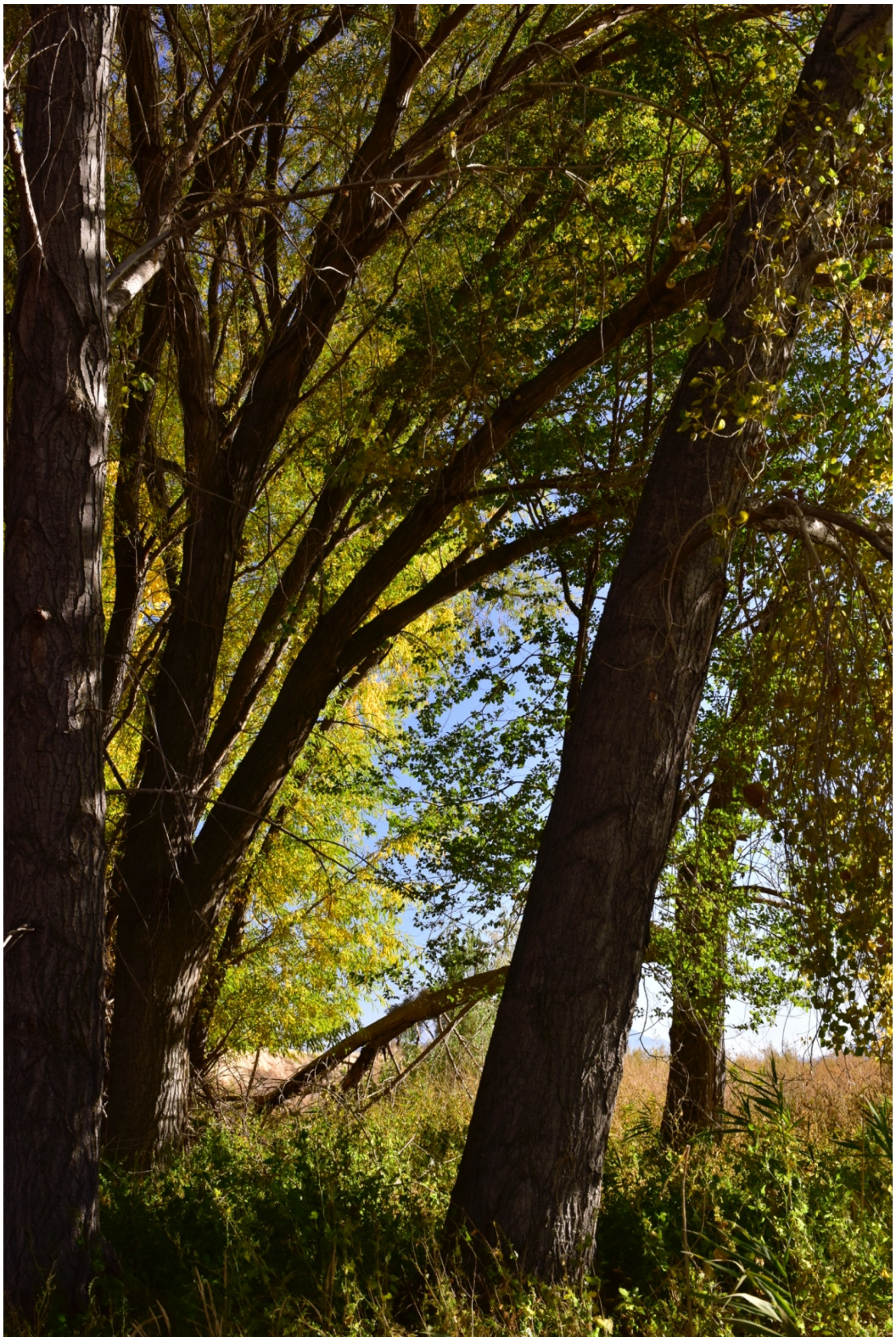

Figure 19. One of last remaining native Fremont cottonwood groves along the shores of Utah Lake, near Vineyard, UT. Acres of these groves have been recently removed to make room for housing and industrial development to support Utah County's burgeoning human population. These riparian forests were instrumental in maintaining Utah Lake's health and integrity and their role is now likely insignificant and they can be considered relict or ghost species and ecosystems due to compounding extinction debt.

Freshwater springs along the shores of Utah Lake and their wetlands are now being lost to urbanization. The following YouTube video documents one of the few remaining springs that has been polluted by urbanization but may still have some remaining health, resistance, and resilience.

https://youtu.be/7PZe-HQFzmI

This spring has been further polluted after increased housing development since the video was recorded.

Utah is the second driest state in the U.S., consequently water demands are high, particularly in the metropolitan areas surrounding Salt Lake City and Utah County. With projected population growth estimated to be in the millions in the next few decades; water demands are only expected to get higher and perhaps unsustainable. Urbanization, industrialization, housing development, and agriculture are all putting unprecedented pressure on water resources on Utah Lake's watershed. In addition, unregulated and unenforced pollutants and pollution are entering its waters via urban runoff, agriculture, household, and industrial wastes.

Unmeasured amounts of oil based industrial chemicals enter the lake via non-point urban surface and groundwater runoff during and after housing, business, and industrial construction. Pesticides enter via non-point agricultural runoff from increased agricultural production (see Pesticide section). Pharmaceutical chemicals mostly enter the lake via POTW effluent.

Pharmaceuticals: An underestimated disruptor of Utah Lake's ecosystem.

It is estimated that aquatic macroinvertebrates can have at least sixty-one kinds of multi-class pharmaceuticals in their tissues (Richmond 2018, Rodríguez-Mozaz 2015). The bugs are on drugs. According to Richmond et al. (2015):

> "Although we do not yet understand the direct and indirect effects of these compounds, either singly or in complex mixtures, on fish and wildlife, a growing body of research demonstrates that many pharmaceuticals disrupt ecological interactions, functions and communities (Richmond et al. 2017). For example, amphetamines and antidepressants in stream water can disrupt the timing of emergence of aquatic insects (Lee et al. 2016, Richmond et al. 2016); psycholeptics such as Valium™ and the illicit drugs amphetamine and LSD can compromise the web-building ability of spiders (Witt 1971); and fish behaviour is altered when consuming prey contaminated with an antidepressant (Brodin et al. 2014). While pharmaceuticals have been detected in trace amounts (part per trillion concentrations) in surface waters around the world for over two decades, it was widely assumed that these concentrations pose little risk to the aquatic biota because environmental concentrations are usually well below lethal concentrations, and many of these compounds degrade rapidly in the environment, suggesting low risk of persistence and biomagnification potential (reviewed by Richmond et al. 2017). In light of these assumptions, it was surprising that we detected such a diverse suite of pharmaceuticals in aquatic invertebrates and at such high concentrations (part per million concentrations of total pharmaceuticals in invertebrates at the most contaminated sites)."

It's fairly common knowledge that Utah is one of the top states among prescription drug use and abuse in the U.S (https://turningpointcenters.com/2012/10/29/prevalence-of-prescription-drug-abuse-in-utah/, https://www.recoveryconnection.com/substance-abuse-statistics-by-state/utah/). Although unmeasured, it should come as no surprise that many of these chemicals are entering Utah Lake's food web and like other waterbodies throughout the world are having a negative effect on ecosystems. It is apparent that Utah Lake's ecosystem in its present state cannot hope to cope with urbanization and all of the other stressors discussed throughout this introduction and that most likely, Utah Lake has lost its ability to self-regulate cyanoHABs, and its resilience to future perturbations weakened.

Wetlands and Phragmites

Utah Lake wetlands are an integral part of the healthy functioning of the lake. They provide invaluable ecosystem services including improving water quality, however most of these wetlands have been lost to development and are continuing to be lost. As is with the rest of Utah Lake's ecosystem, wetlands health has been compromised. We have not quantitively evaluated any wetland data for inclusion in this progress report but provide a brief anecdotal discussion on our observations focusing on the invasive strain of the common reed, *Phragmites australis*.

The invasive subspecies (or strain depending on which authority cited) of the common reed, *Phragmites australis australis* plays a critical role in Utah Lake's wetland ecology. Although, it is thought by many to be a devastating ecological threat, as it is now the dominant analog wetland emergent plant species; Phragmites provides important ecosystem services that native species are currently challenged to do including; shoreline protection from wind and waves that are all too common on Utah Lake, shelter and habitat for zooplankton and juvenile fishes, reduced turbidity, and switching algal assemblages from water column phytoplankton to sediment surface periphyton, etc. Utah Lake historically supported vast stands of native Phragmites, and every effort should be made to reintroduce and promote their recovery.

Native phragmites, bulrush, cattails (*Typha* sp.), and other species gave way to invasive phragmites and Salt Cedar (*Tamarix* sp.), etc. in Utah Lake's wetlands over the last 150 years or so. Recently, there is an intensive phragmites management control/removal effort ongoing along the shores of Utah Lake. However, as far as we know, no formal BACI type quantitative monitoring or evaluation of the effects of phragmites removal on the wetland's ecological functioning, food web or role in regulating cyanoHABs has occurred or is planned. Without such monitoring there is no scientific possibility of evaluating ecological benefits or impacts of phragmites removal.

We have observed what we conclude are important ecological benefits of phragmites stands in Utah Lake some of which were briefly discussed in this report. The following two videos demonstrate how phragmites can protect shorelines from wave action on the lake:

https://youtu.be/gUnh2QnMOSo

https://youtu.be/ihI0gj1A8s8

Appendix 5 is a nine-page opinion report that Dr. Richards was asked to provide to members of the USDA, APHIS Technical Advisory Group for Field Release for Biological Control Agents of Phragmites, early 2019. Dr. Richards has past scientific experience developing and using biocontrols on weeds and field experience observing phragmites ecology and habitat on Utah Lake. The opinion report is titled, “A Case for Adaptive Holistic Management of Phragmites in the Jordan River Drainage and Southern Utah”.

Obviously, much more research is needed to evaluate the importance of remaining wetlands and their plant communities to the healthy functioning of Utah Lake ecosystem.

Water Column Regulators and the Ecosystem Engineers

Water column and benthic sediments in shallow lakes, unlike deep lakes, are in close proximity, intimately linked, and do not function in isolation from each other (Scheffer 1998). However, water column and benthic environs operate under different sets of ecological conditions and guidelines. For example, water column nutrient cycling interacts directly with atmospheric deposition, whereas nutrient cycling within the benthos is dependent on nutrient obtained from the sediments and nutrients ‘falling’ out of the water column. Benthos are also more likely to experience anoxic conditions more frequently than the water column. Biotic assemblages also differ between these habitats and conditions.

Zooplankton and pelagic fishes are the most important top down regulators of nutrients and phytoplankton (including cyanoHABs) within the water column. Grazing by zooplankton on phytoplankton and predation of fishes on zooplankton recycle nutrients within the water column, often within a matter of minutes (Sailey et al. 2015). Zooplankton assemblages in Utah Lake are spatially and temporally heterogenous and exhibit a somewhat predictive seasonal succession that is directly and indirectly related to phytoplankton dynamics (see all Richards reports in Literature Cited section, this report, and Sailey et al. 2015). Zooplankton assemblages in the lake are also apparently strongly influenced by planktivorous fishes, predominately invasive species such as carp and the juvenile stages of most other species. Predation on zooplankton likely has reduced their ability to regulate phytoplankton assemblages in Utah Lake (Richards and Miller 2019b, Richards 2019b, Sondergaard et al. 2008; Wetzel 2001; Cole and Weihe 2016; Havens et al. 2015a, 2015b; Gophen 1990; Cooke et al. 2016).

Ecosystem engineers are species that have disproportionate influences on their ecosystems (Paine 1966). A single species of ecosystem engineer can alter the physical environment, which can have cascading consequences for the whole system (Jones et al. 1994, Bertness and Leonard 1997, Wright and Jones 2006). They also have other direct and indirect effects within a community through competition, herbivory, predation, etc. (Jones et al. 1997, Bertness et al. 1999, Hastings et al. 2007, Largaespada et al. 2012, Phillips et al. 2019). Three benthic ecosystem engineers have had a disproportionate influence on the ecology of Utah Lake and have transitioned in importance over recent times due to human induced impacts: mollusks- to chironomids (midges)- to invasive fishes, particularly carp and catfish (see Richards reports in Literature Cited section, and this report). More details of ecosystem effects of these engineers are presented in following sections.

Water column regulators and nutrient cycling

Nutrient cycling and recycling occur rapidly in the water column portion of the food web consisting of phytoplankton, zooplankton, and fishes (Sailley et al. 2015). Nutrients also enter the water column via atmospheric deposition, wastewater treatment facilities, surface water, groundwater, and sediments. Because Utah Lake has a large surface area, is shallow, has frequent local inversions (Figure 20), and strong wind storms that deliver nutrients to the lake from surrounding nutrient rich soils; the amounts and effects of atmospheric nutrient deposition can be substantial and are presently being quantified by researchers at Wasatch Front Water Quality Council. The shallow nature and high amounts of background nutrients in the lakebed results in a substantial and important influx of nutrients from benthic sediments into the water column (Scheffer 1998, Hogsett and Goel 2013, Hogsett et al. 2019). In fact, Hogsett et al. (2019) reported that sediment phosphorous loading in Utah Lake was 5 time higher than external loading and was estimated at 1500 tons/year. For the most part, nutrient limitation does not seem to be a problem in Utah Lake due to continuous release from sediments, except perhaps during summer cyanoHABs (Hogsett et al. 2019).

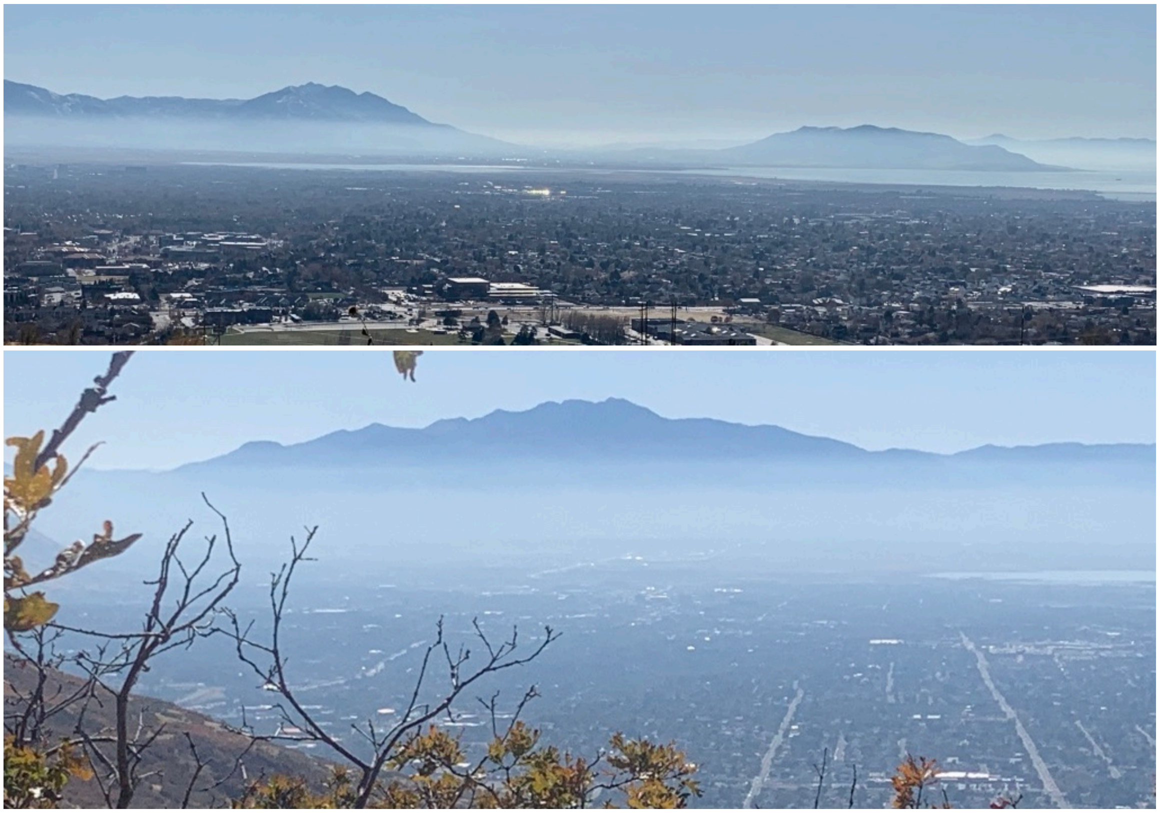

Figure 20. Common inversion layer over Provo Bay and southern Utah Lake. High concentrations of nutrient and other pollutants can enter the surface water of the lake during these times. Atmospheric deposition of nutrients into Utah Lake are presently being quantified by WFWQC scientists.

Water Column Regulators: Zooplankton and Invasive Fishes

Zooplankton

Zooplankton grazers are the number one water column regulator of phytoplankton, including cyanoHABs (Iglesias et al. 2007, Scheffer 1998). Zooplankton frequently move between habitats including daily horizontal migration; subsequently zooplankton are a vital linkage between the pelagic, benthic and littoral zones (Vander Zanden and Vadeboncoeur 2002, Jones and Waldron, 2003). However, very little is known about the spatial and temporal patterns of zooplankton in Utah Lake despite their critically important relationships with: nutrient cycling, phytoplankton (including cyanoHABs) ecology and population dynamics, and other food web components in the lake (Richards and Miller 2017, Richards 2018).

Zooplankton obviously have top down 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. have the ability to 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).

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 cyanoHABs 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, Vehmaa et al. 2013, Gorokhova and Engstrom-Ost 2009, Hogfors et al. 2014, Ger et al. 2016).

Utah Lake supports a rich and diverse zooplankton assemblage that varies spatially and temporally (Richards and Miller 2017). There are >> 20 zooplankton taxa occurring in Utah Lake including; cladocera, copepod, 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 (see Appendix 4). It is of utmost importance to correctly identify zooplankton taxa in the lake.

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 that may no longer be able to regulate cyanoHABs. 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.

Invasive Fish Predation on Zooplankton Favors CyanoHABs

Planktivorous 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 & Dodson, 1965) or behavioural shifts (Timms & Moss, 1984; Schriver et al., 1995; Lauridsen & Lodge, 1996; Burks et al., 2002; Romare & 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).

We have conducted preliminary analysis of zooplankton body sizes in Utah Lake and found that they are substantially smaller than expected, indicating that invasive planktivores have altered the zooplankton assemblages in the lake, which could be contributing to cyanoHABs. See Appendix 3: *Spatial and Temporal Variability of Zooplankton Body Lengths in Utah Lake*, *Technical Memo* for results of this analysis. We are also incorporating zooplankton body size metrics into our Multimeric Index of Biological Integrity for Utah Lake (Appendix 2) 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. See video:

https://youtu.be/5qYfa4_a_lk

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 cyanoHABs (see following section). 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. cyanoHABs). (Marroni et al. 2016, Caraco et al. 1997, Prins and Escaravage 2005, Newell et al. 2007).

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 & 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) (Raposeiro et al. 2017). Furthermore, resuspension of sediment particles can interfere with the filtering apparatus of cladocerans (Kirk & Gilbert, 1990), and bioturbation may also affect zooplankton dormant stages in sediments, negatively effecting emergence patterns (Angeler et al., 2002) (Florian et al. 2016).

As we have reported in Richards and Miller (2019b) (see Appendix 2), many studies have shown that removal or reduction of planktivorous fish populations could be used to enhance zooplankton grazing on algae, including reduction of cyanoHABs and thereby creating a clearwater state (Gulati, 1990; Hansson et al., 1998a; Søndergaard et al., 2007, 2008). This has led many researchers and managers to recommend biomanipulation as a relatively inexpensive remedy for controlling algal blooms compared to attempts at whole drainage nutrient control (Riedel-Lehrke 1997; Cooke 1986; Jeppesen et al. 2007; Richards 2019a).

Phytoplankton and Zooplankton Relationships

TBD

Transition of Benthic Ecosystem Engineers: Bivalves to Midges to Invasive Fishes

Each has a different method of engineering sediments with differing results
Describe

Mollusks

Freshwater mollusks include bivalves (mussels and clams) and gastropods (snails). Their diversity and abundances in the depauperate western USA peak in the Utah Lake-Jordan River drainage and the surrounding area (Richards 2017, Richards 2014). Utah Lake's mollusk diversity and abundances are due to a Lake Bonneville heritage, abundant nutrients, high pH and high $CaCO_3$ levels originating from the thick limestone base rock in the watershed which they require (see Introduction and Background: *Lake Bonneville: A Lake No More?)*.

Native mollusks were the dominant benthic ecosystem engineers in Utah Lake when early explorers and Mormon settlers first arrived in the 1800s. Native mollusks were also responsible for much of the water column functioning (Richards 2014, 2017, 2018b, and 2019a). Unfortunately, their role as keystone species and ecosystem engineers has been eliminated.

Historically, there were two species of mussels native to Utah Lake, the now 'critically imperiled' *Margaritifera falcata,* common name Western Pearlshell (Figure 21) and the 'imperiled' *Anodonta californiensis/nutalliana,* common name Floater (Figure 22). Both species are extinct in the lake, however small, isolated, remnant, imperiled populations of *A. californiensis/nutalliana* still occur in upstream creeks (Richards 2017). Highly weathered shells of *A. californiensis/nutalliana* can still be found along Utah Lake shores (Figure 25) but no shells of *M. falcata* have been found in more than one hundred years. Both species were abundant and large enough sized to be important food items to Native Americans and early settlers. Native mussels were an important part of Utah Lake's fisheries, although *M. falcata* was usually not eaten (Chamberlain and Jones 1929, Janetski 1990). Native mussel and other bivalve and snail shells from the region were highly prized and traded throughout the west. Thus, Utah Lake's native mollusk fisheries[11] were a critical component of Native American

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[11] In fisheries – the term fish is used as a collective term, and includes **mollusks**, crustaceans and any aquatic animal which is harvested. Fishery is defined as: The industry or occupation devoted to the catching, processing, or selling of fish, **shellfish**, or other aquatic animals. Shellfish include mussels, clams, and snails.

economies and an important part of the early settler economy. Utah Department of Natural Resources (2007) reported that Utah Lake likely had the largest population of *A. californiensis/ nutalliana* in the entire state but have now been extirpated from the lake. One likely reason for their disappearance from Utah Lake was predation by the apex predator, the introduced European carp (*Cyprinus carpio*), which still occurs in the lake by the tens of millions and will likely not be completely eliminated into the foreseeable future.

Native clams (Family Sphaeriidae) population data is completely lacking from Utah Lake. However, we have found hundreds of weathered native clam shells throughout the lake and tributary sediments (Figure 24). Regrettably, we have not found any live native clams. Their abundances in Utah Lake were likely as great or greater than native mussels because unlike native mussels, native clams do not require secondary fish hosts to complete their life cycle. We suspect that similarly to native mussels, Utah Lake's native clam populations are either extinct or very close to extinction.

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 of these taxa are extinct in Utah Lake including; several species of springsnails in the genus, *Pyrgulopsis*, the pebble snail, *Fluminicola coloradoensis* (Figure 28), 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 (take and add photo), and the iconic *Helisoma newberryi newberry*, the Great Basin Ramshorn (Figure 26, Figure 27). Utah Lake probably supported he largest population of *Planorbella binney* in Utah (Oliver and Bosworth 1999). Several other tolerant snail species still exist in the lake, including those in the families Lymnaeidae and Physidae. We continue to find thousands of the now extinct snail shells along Utah Lake's shorelines and in benthic sediments during routine benthic sampling.

We have documented that native mollusk shells form a layer about 1 to 3 cm thick within the benthic sediments just under an organic layer, especially in Provo Bay. We are currently estimating relative abundances of these extant and extinct species from several locations in the lake in an effort to understand recent past environmental spatial patterns in Utah Lake. We are also collaborating with several researchers examining sediment core samples from the lake to estimate when most of these mollusk species went extinct.

Figure 21. *Margaritifera falcata* from Big Cottonwood Creek, Salt Lake County, UT, circa 1880. These specimens are housed in the Natural History Museum of Utah, Salt Lake City, collected by Dr. Orson Howard, Professor Biology at University of Utah, in the late 1880's and were apparently fairly common (Richards personal examination of museum specimens) however, the exact location of collection in Big Cottonwood Creek was not documented. These historical specimens were identified by Dr. Howard as *Margaritana margaritifera*, which was later revised to *Margaritifera. falcata*.

Figure 22. One of the few remaining live adult Anodonta found lying on the surface of what was mostly comprised of thousands of invasive Asian clams, Corbicula, in Currant Creek, a former tributary to Utah Lake, August 2016.

Figure 23. Weathered Anodonta shell exposed during low water levels in Utah Lake near SW corner of Provo Airport, July 29, 2016.

Figure 24. Remnants of the diverse, abundant, and unique bivalve assemblage of Utah Lake exposed in the substrate of a spring creek entering the lake near Vineyard, UT in 2016. At least three species of bivalves are visible, two species of fingernail clams and the mussel *Anodonta* sp., which is considered extinct in Utah Lake. Native fingernail clams may also now be extinct in the lake and its tributaries.

These biofilterers are presumed to have occurred in such high abundance that they regularly filtered the entire water column of the lake in a few days and thus were instrumental in controlling cyanoHABs. This spring creek has now been polluted by urban development and these shell fragments are now covered in thick sediment.

Figure 25. 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.

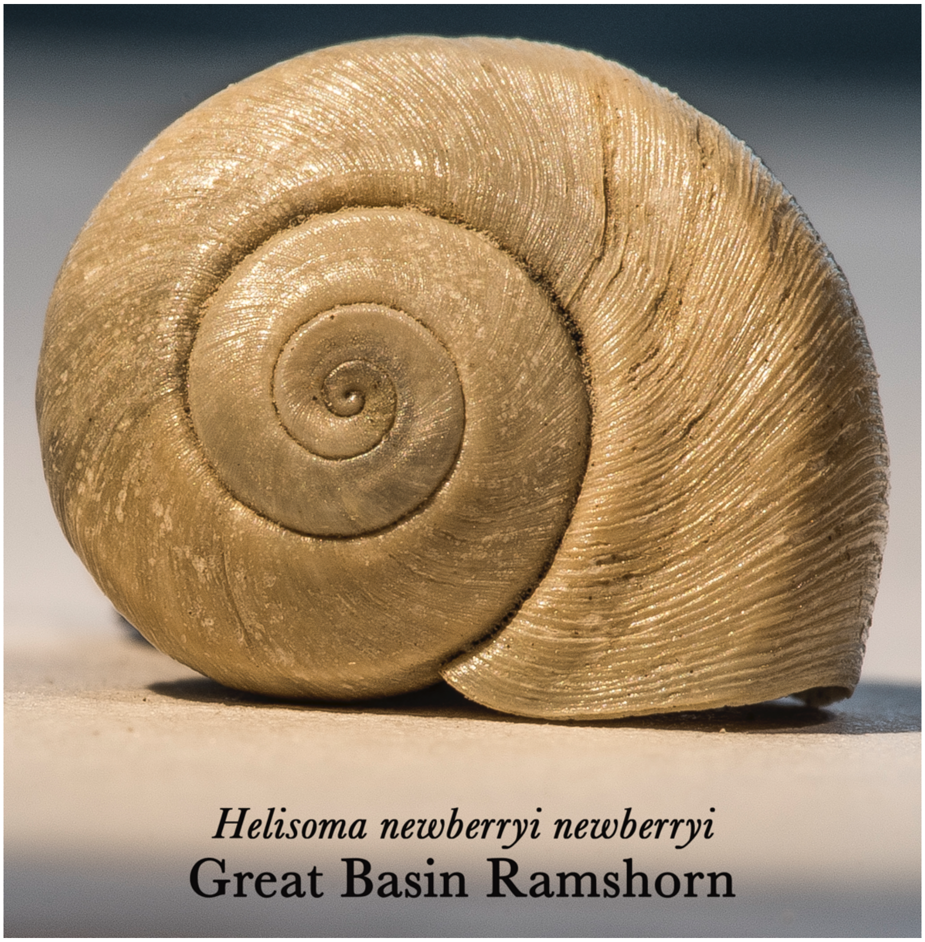

Figure 26. Shell of *Helisoma newberryi newberry*, the Great Basin Ramshorn, a former abundant resident of Utah Lake. No live specimens of this subspecies have been found in the lake for many years and its viability in Utah is questionable but presumably it is extinct. Snail assemblages in Utah Lake were instrumental in regulating benthic algal assemblages and nutrient transfer into the food web and their past role in the ecosystem is now vastly diminished. Presently, only two or three pollution tolerant species survive.

Figure 27. Remnant shells of *Helisoma newberryi newberry*, The Great Basin Ramshorn and *Valvata utahensis*, the Utah Round Mouth Snail or Desert Snail collected from Utah Lake in 2019.

Figure 28. Empty shells of the prosobranch snail, *Fluminicola coloradoensis,* Green River Pebblesnail found in several locations in Utah Lake during our mollusk surveys. Scale lines are 1 mm.

Native mollusks were the consummate ecosystem engineers in Utah Lake and until recently (200 to 150 years ago) governed almost all of its ecosystem functions. Due to human economic activities, however, most native mollusks in Utah Lake have been extirpated and no longer provide those critical ecosystem services, including the regulation of cyanoHABs.

Utah Lake's two native mussel species and several clam species 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 two native mussels and several species of clams were likely able to filter the entire lake's water column in just a few days (Richards 2014, 2017, 2018b, and 2019a).

Native freshwater mollusks likely constituted the largest portion of benthic standing crop biomass in Utah Lake. 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).

As most of us know, mollusk shells are mostly composed of $CaCO_3$ and it is reported that shell composition in freshwater mollusks is typically > 0.95 g $CaCO_3$ g^{-1} shell (Richards 2018; Ademolu et al. 2016; Malathi and Thippeswamy 2013; Mann, 1964; Negus, 1966; Cameron et al. 1979; Liu et al. 2010; Cameron et al. 1979). Mollusks also incorporate minerals into their body tissue. For example, Malathi and Thippeswamy (2013) reported mineral contents of body tissue in the freshwater mussel *Parreysia* *corrugata* and showed that mineral contents were substantial and varied seasonally. Liu et al. (2010) found that soft tissues of *Anodonta* sp. contained 19 g Mn kg^{-1} tissue dry weight and ≤ 19 g Fe kg^{-1} tissue dry weight.

We have documented the substantial ecosystem effects that invasive *Corbicula* and *Potamopyrgus* can have in the Jordan River, including their influence on Ca, CO_3, nutrients, and mineral cycling and infer that native mollusks had similar effects in Utah Lake in the past (Richards 2018). Mollusks in Utah Lake could have also had substantial effects on phosphorus cycling. For example, it is becoming more common for water treatment facilities to use powdered mollusk shells to remove aqueous P from wastewater (Abeynaiike 2011; Xiong et al. 2015). Abeynaiike (2011) found that with excess of partially calcined pyrolysed mussel shells, at a concentration of 5 g L^{-1}, more than 95% phosphate removal can be achieved.

Our basic understanding of mollusk chemical interactions with their environment suggests that in the past, native mollusks in Utah Lake strongly influenced sediment chemistry in the lake and that sediment, pore-water, and water column chemistry now observed in the lake is a direct result of the loss of native mollusks (Richards et al. 2019). This is particularly important for understanding phosphorus chemistry levels and interactions in the lake as they may relate to cyanoHABs. We cite Randall et al. (2019) for a detailed description of current sediment P in Utah Lake to help illustrate our concern that in the past, native mollusks regulated P and other chemical conditions including pH, $CaCO_3$, and indirectly regulated cyanoHABs but due to extirpation, are no longer able to do so.

Randall et al. (2019) reported that sediment P in Utah Lake:

> "… was primarily bound to oxidized Fe/Mn compounds (BD fraction) and Ca phosphate minerals or acid-soluble organic P (HCl fraction). On average, 49.1% ± 1.8% of TN was associated with the BD fraction (range: 41–61%) and 38.6% ± 2.1% with the HCl fraction (range: 25–47%). Given low Mn concentrations in Utah Lake sediment (.0.06 wt. %), the BD fraction likely represents P associated with Fe rather than Mn. Likewise, given that the sediments are calcite-rich, the HCl fraction is likely dominated by P from calcium phosphate minerals rather than organic P."

And that,

> "The association of P with different minerals affects the subsequent mobility in sediments and potential flux to the water column. Phosphorus was primarily associated with Fe (Fe (OOH)) and Ca ($CaCO_3$ or $Ca_{10}(PO_4)_6(OH,F,Cl)_2 \approx P$) from the BD and HCl fractions. These minerals act as sinks to sequester P from water column to the sediment. Coprecipitation of P with calcite and apatite minerals is strong at neutral to alkaline pH. Utah Lake is an alkaline lake with pH values typically over 8 and is buffered by high bicarbonate concentrations. The Ca-associated P is likely precipitated with calcite ($CaCO_3 \approx$ P) or apatite ($Ca_{10}(PO_4)_6(OH,F,Cl)_2$) minerals. Although sediment chemistry is not kinetically conducive to precipitation of apatite, authigenic apatite mineral precipitation may occur as diatoms store polyphosphates inside their cells and form Ca phosphate minerals [35]. The majority of Ca-associated P may act as a permanent sink for P in Utah Lake with alkaline pH values. In

> contrast, the Fe-bound P pool is mobile as P may be released from sediments under anoxic conditions with the reductive dissolution of Fe-oxide minerals. Anoxic conditions may develop locally near the sediment-water interface, particularly during summer when microbial activity is high. Although we did not evaluate seasonal differences in P fractionation in this study, it is possible that the Fe-bound fraction may decrease as P is released under summertime anoxic conditions. While flux rates from the sediment to overlying water column are unknown, the sediment-water interface is potentially a major controlling factor of P cycling in Utah Lake."

This remarkable similarity between sediment chemistry in Utah Lake reported by Randall et al. (2019) and mollusk chemical interactions with their environment strongly suggests that native mollusks were instrumental in regulating nutrient cycling and sediment chemistry in Utah Lake. We suggest that mollusks also regulated alkalinity in the lake via their sequestration of $CaCO_3$. These strong and synergistic associations between sediment chemistry and mollusks in Utah Lake requires further analyses perhaps starting with conceptual models and is especially important for understanding the regulation of cyanoHABs in the lake.

Midges

After the inevitable decline and demise of Utah Lake's native molluscan fishery over the past 100 years or so, remaining non-molluscan benthic invertebrates became the dominant native benthic ecosystem engineers, especially chironomids (midges) and oligochaetes (aquatic worms). Non-molluscan benthic macroinvertebrates are now one of the most critical components of the ecology and ecosystem functioning of Utah Lake. They are a major link between sediment chemistry, water column chemistry, nutrient cycling, benthic algae, phytoplankton, and Utah Lake's food web including non-game and game fish, June suckers, waterfowl, shorebirds, etc. Benthic invertebrates provide underappreciated but invaluable ecosystem services and are keystone taxa instrumental for the functioning of Utah Lake' ecosystem.

Midge larvae (Family Chironomidae; Class Insecta) dominate the benthic ecosystem in Utah Lake and can often comprise 80-90% of the benthic invertebrate biomass with a standing crop wet weight biomass of 700 to 3000 U.S. short tons, which can be produced in one summer month (Richards and Miller 2019c). By their sheer volume, biomass, secondary production, and ecology; midge larvae are the benthic/sediment ecosystem engineers responsible for much of the lake's benthic/sediment function and interaction with the water column (Richards and Miller 2019c, Holker et al. 2015); and has been reported by Randal et al. (2017) and Hogsett et al. (2019), the sediment water interface appears to be a major controlling factor of P recycling.

Adult midges also transfer energy and nutrients out of Utah Lake into surrounding wetlands after larval pupation and adults become airborne. Midge swarms along the shoreline of Utah Lake are often intense with tens of thousands of adults participating in their mating rituals. The following two videos show such swarms along the lake's shores:

https://www.youtube.com/watch?v=vVSgmNQS9YI
and
https://youtu.be/aE4nThbiY6s

Adult midges also rest in shoreline vegetation between mating (Figure 29) and before females release eggs back into the lake.

Figure 29. Adult male midge (Chironomidae) resting on a wild iris in wetlands along the eastern shore of Utah Lake, July 2019. This stand of wild irises was destroyed in 2019 during the phragmites removal program.

Although midge densities are extremely high in Utah Lake, they are often much higher in Farmington Bay (Figure 30) and are nothing compared to densities and swarms that can occur in Lake Myvatn, Iceland[12].

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[12] Lake Myvatn literally translates to Midge Lake.

Figure 30. Adult midge swarm at Farmington Bay, Great Salt Lake wetland ponds. Swarms appear to be dark funnel clouds along the wetland horizon and are not controlled burning.

The following video shows a typical midge swarm in Lake Myvatn:

https://www.youtube.com/watch?v=E0BhQm27RA4.

It has become clear that several dominant benthic taxa, primarily chironomids (midges), can alter benthic ecosystem function and play a key role in the timing and intensity of cyanoHABs in lake ecosystems. However, this relationship has received very little attention, particularly in Utah Lake. For refresher, the section on the relation between midge larvae and cyanoHABs that we reported in our 2016 Progress Report has been added in Appendix 1. In the following section, we discuss our latest literature findings on just how important midge larvae can be to benthic ecosystem functions, including cyanoHABs in Utah Lake.

Substrate Stabilization and Structure, Net Ecosystem Production, and cyanoHABs

Larval midge tubes are constructed from silk similar to the kind of silk produced by spiders, which has very strong tensile strength and ductility. Midge larvae also produce connecting networks of silk that stabilizes the substrate and provides three-dimensional structure to the sediment (Olafsson and Paterson 2004, H€olker et al. 2015). Midge larvae can reach very high densities in Utah Lake, which certainly helps stabilize the substrate and increases structure (Figure 31).

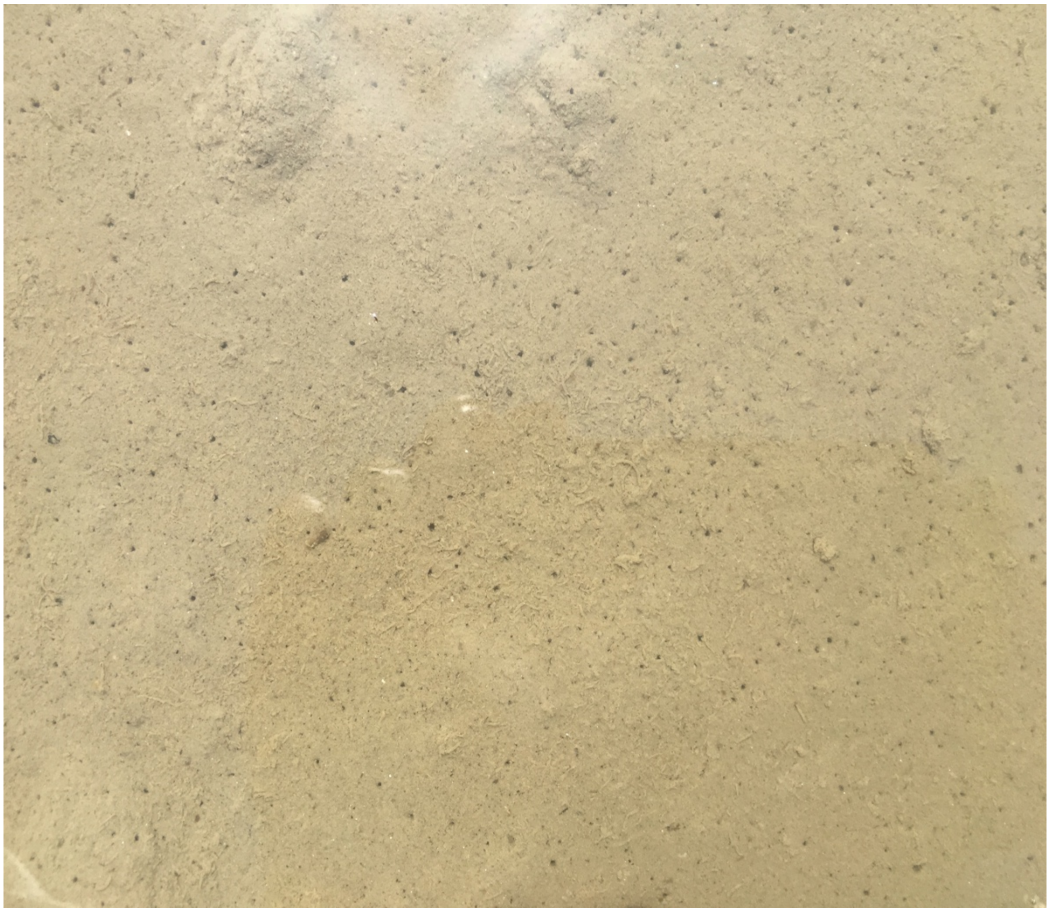

Figure 31. Thousands of different midge larval instar tubes in Provo Bay, Utah Lake. These larvae help stabilize the easily disturbed substrate, provide three-dimensional structure, and the larvae actively oxygenate the sediments including Fe near the sediment water boundary layer. Tubes are likely either *Chironomus* sp. or *Tanypus* sp. or both. This photo was taken during a low water year when water levels were shallow enough that large insectivorous fish were excluded, and predation was reduced allowing midge populations to maintain high densities and to continue to provide valuable ecosystem services other than just as fish food.

Midge larval tubes increase sediment shear strength subsequently reducing resuspension and turbidity. Ólafsson and Paterson (2004) documented that *Tanytarsus gracilentus* (midge) larvae in Lake Myvatn, Iceland modified the surface sediment by tube building and showed that shear strength of the sediment surface, and hence resistance to erosion, increased significantly with increased densities of *T. gracilentus* larvae (Phillips et al. 2019).

Sediment stabilization is critical for Utah Lake because among other things, sediments and nutrients are easily suspended and affect turbidity and nutrient availability, which often favors cyanoHABs (see the previous section on Turbidity). Midge larval tubes provide three-dimensional structure that also increases habitat for small microorganisms and algae. By providing stable substrate for algae, larval midge tubes indirectly increase gross primary production (GPP) in the sediment, although by consuming algae, midges may inhibit GPP. Midge larvae can also stimulate microbial respiration (RESP) by oxygenating the sediment. (Phillips et al. 2019, Holker et al. 2015). Therefore, the overall effect of midge larvae on net ecosystem production (NEP) depends on the balance between their effects on GPP and RESP, which is also affected by light conditions (Phillips et al. 2019) (Figure 32).

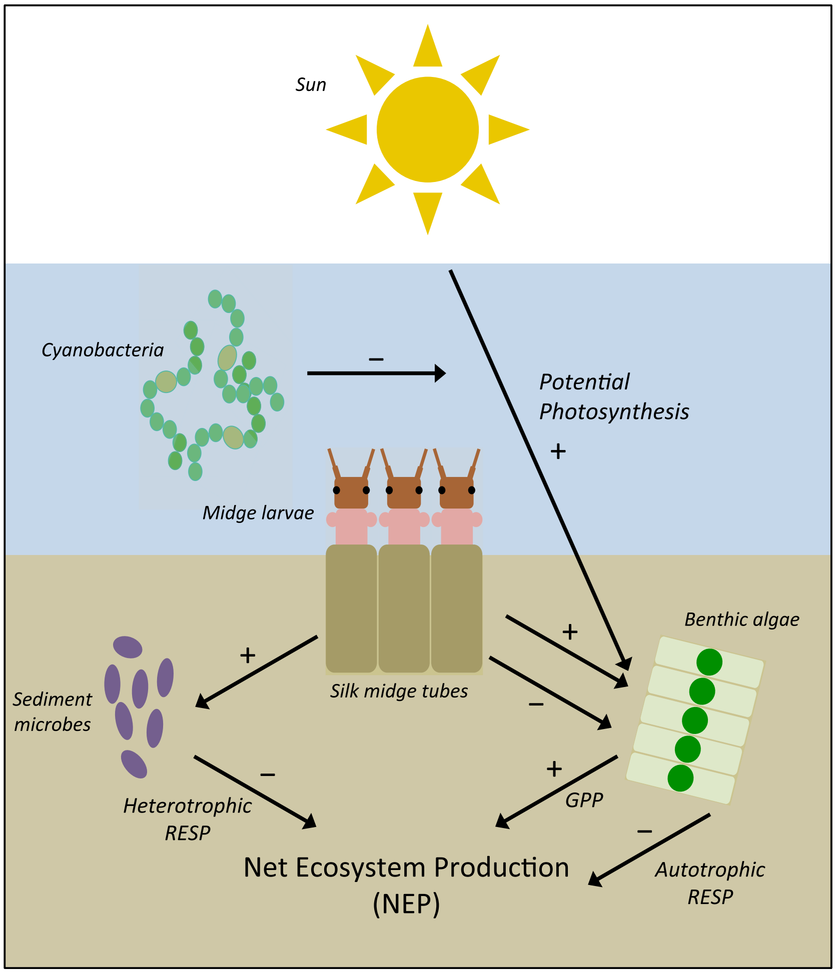

Figure 32, Midge larvae alter benthic ecosystem function. This figure and caption were taken from Philipps et al. 2019. "Midges can alter benthic ecosystem function. Larval midges build silk tubes that provide a substrate for algal growth and increase gross primary production (GPP) in the sediment. However, midges may inhibit GPP through consumption of algae. Furthermore, midges can stimulate microbial respiration (RESP) by oxygenating the sediment. Gross primary production and RESP have opposite effects on net ecosystem production (NEP), so the effect of midges on NEP depends on the balance between their effects on GPP and RESP. We hypothesized that light mediates this balance, because the positive effects of midges on GPP would decline as photosynthesis became more limited by light. Episodic cyanobacterial blooms have a negative effect on benthic light levels, which could result in spatiotemporal variation in the net effects of midges on benthic production."

Midge larvae and cyanoHABs

We briefly reported how midge larvae could affect cyanoHABs in Utah Lake in our Utah Lake 2016 Progress Report, including how circumstantially, cyanoHABs appeared to cycle out of sync with larval abundance (Richards and Miller 2019c, and Appendix 1 of this report). Philips et al. (2019) further elaborated on these effects more recently (Figure 32). Einarsson and Örnólfsdóttir (2004) also reported that intense cyanoHABs blooms (*Aphanizomenon flos-aquae*) always occurred in years of low chironomid populations but sometimes developed in other years in Lake Myvatn and similar to our current findings; cyclic patterns of dominant midges varied several orders of magnitude. Einarsson and Örnólfsdóttir (2004) also suggested that cyclic patterns of midges were not likely due to climate. *Tanytarsus gracilentus* in Lake Myvatn showed cyclic population fluctuation with three peaks occurring during a 20-year period. Body size of *T. gracilentus* fluctuated with population size but in an opposite fashion and with a time lag in Lake Myvatn again, similar to our findings in Utah Lake (Richards and Miller 2019). *T. gracilentus* body size and abundance and predator abundance in Lake Myvatn suggested that the population fluctuations were driven by interaction with resources and not by predator-prey interactions (Einarsson et al. 2002). However, there are only two major predacious fish in Lake Myvatn, three-spined stickleback (*Gasterosteus aculeatus*) and Arctic charr (*Salvilinus alpinus*) (Einarsson et al. 2004), whereas there are several invasive fish species in Utah Lake that are avid midge larvae hunters; common carp (*Cyprinus carpio*), white bass (*Moron chrysops*), channel catfish (*Ictalurus puntatus*), and black bullhead (*Ameiurus melas*), to name a few. Common carp biomass is measured in the tens of tons in Utah Lake and this species alone can regulate or decimate midge populations within the lake.

We agree with the midge researchers on Lake Myvatn that the underlying mechanisms for midge cycles are not fully understood and that further investigation is required and that by sheer abundance, midges may be one of the major regulating factors in the long-term dynamics of Lake Myvatn and Utah Lake ecosystems. We also agree with our Icelandic colleagues that “for effective conservation, the only sound strategy seems to be to avoid interfering with the basic components of the ecosystem” (Phillips et al. 2019).

The effects of midge larval on ecosystem respiration (RESP) and GPP vary seasonally with greater effects in summer during increased temperatures. Baranov et al. (2016) showed that RESP in sediments with and without chironomids did not differ at 5^0 C, but at 30^0 C sediment respiration in microcosms with 2000 chironomid larvae per m^2 was 4.9 times higher than in uninhabited sediments. This is a somewhat lower density of larvae than what we typically find in Utah Lake and compared to their results suggest that midge larval effects on RESP may be higher in Utah Lake.

Warm summer water temperatures result in faster midge larval development, shorter life cycles, additional generations per year and higher reproduction rates—all resulting in higher larval densities and intensified ecosystem effects (Hamburger et al. 1995;

Eggermont and Heiri 2012). With large densities, especially in eutrophic water bodies with warm water, midge larvae burrowing, and ventilation activities can dramatically impact freshwater biogeochemistry (Morad et al. 2010). For example, in shallow Lake Muggelsse in Germany (mean depth 5 m, relatively similar to Utah Lake mean depth) a volume equivalent to the total water column of the lake is pumped by chironomids through their burrows, once a week (Morad et al. 2010). This rate is likely similar to Utah Lake. That is, during certain times of year when midge larvae are at relatively high densities and are active, they can pump the entire water column of Utah Lake through the sediments, perhaps weekly or less. Baranov et la. (2016) concluded that high densities of chironomids in shallow lakes can significantly intensify sediment respiration, especially in warm and well-oxygenated systems. This effect is most pronounced in shallow, non-stratified lakes such as Utah Lake and is consistent with sediment chemistry findings by Hogsett et al. (2019).

Very few studies have been conducted on the benthic invertebrate assemblages in Utah Lake (Barnes and Toole 1981, Spencer and Denton 2003, Shiozawa and Barnes 1977) and none were conducted at the level and intensity that is presently being accomplished by this group. No study has ever examined the role of benthic invertebrates on HABs in Utah Lake, this is the first. Our research is also an important element of sediment chemistry, nutrients, and food web models that are presently being conducted by us and others on Utah Lake. Preliminary results of our research are leading to valuable insights on the role of benthic macroinvertebrates in the ecology and ecosystem functioning.

Invasive Fishes: Benthic Ecosystem Disruptors

Invasive benthivorous fish can alter the benthic sediment ecosystem more drastically than did mollusks and midges in Utah Lake. It is well known that common carp (*Cyprinus carpio*) are one of the most important pelagic and benthic ecosystem disrupters in Utah Lake. Carp are omnivorous and feed largely on macrophytes and invertebrates. In Utah Lake, feeding activity by adult carp and catfish involves rooting in the sediment and disrupting and destabilizing natural processes, causing large amounts of bioturbation. Native mollusks and midge larvae on the other hand, stabilized sediments and reduced turbidity. Benthic feeding invasive fishes also destabilize Utah Lake sediments in other ways that have not been fully documented or quantified. However, others researchers have reported that in general, the net impact of ecosystem engineers depends on the balance between diverse and potentially conflicting effects, which itself can depend on the environmental context and the species involved (Bertness et al. 1999, Norkko et al. 2006, Daleo and Iribarne 2009, Brown and Lawson 2010, Lathlean and McQuaid 2017). The context dependence of ecosystem engineering means that environmental variation can produce large differences in engineer effects through space and time (Wright et al. 2006, Hastings et al. 2007). Ecosystem responses of engineering to environmental conditions are likely nonlinear (as is true for many ecological processes) and the shape of this nonlinearity could have large consequences for the overall effects of analog engineering in variable environments (Ruel et al. 1999), such as Utah Lake. We strongly suggest that additional research is needed comparing the now analog benthic ecosystem engineer invasive fishes with past molluskan engineers and remaining midge engineers in Utah Lake.

Invasive Dojo: Game Changer

The occurrence of Oriental Weatherfish, *Misgurnus anguillicaudatus* (a.k.a. Dojo) in the Utah Lake drainage is also very concerning. We recently documented this invasive species in the Jordan River just downstream of Utah Lake (Richards 2019). Dojo were common throughout the upper Jordan River in our 2019 electrofishing survey and occurred in mostly in silty, heavily vegetated habitat in slower sections of the river.

Figure 33. Image of Invasive Dojo (Misgurnus anguillicaudatus) from nas.er.usgs.gov. Zachary Randall, Florida Museum (UF 236274) ©.

Dojo life history and ecology are poorly documented in North America, including ELS. However, multiple authors have found that this species has caused reductions in macroinvertebrate populations, altered aquatic habitats, and are vectors for certain fish parasites (https://www.fws.gov/Fisheries/ANS/erss/highrisk/Misgurnus-anguillicaudatus-WEB-8-21-12.pdf). Dojo are considered r-selected organisms that mature quickly, reproduce multiple times in their lifetimes and throughout the year and produce a great number of offspring. In their native range, these fish spawn multiple times per year during a spawning season that lasts from mid-April until mid-October and appear to be altering their breeding season based on different environmental conditions in their non-native ranges (Frable 2008). Dojo tolerate and thrive in a very wide range of temperature and oxygen conditions and their thermal tolerances range from 3.7 ^{0}C to 19.3 ^{0}C (Logan et al. 1996). They are able to survive in low oxygen and hypoxic conditions and are known hosts of non-native digenean trematode flukes and viral pathogens (Lintermans et al. 1990; Frable 2008). Keller and Lake (2007) demonstrated in the laboratory that oriental weatherfish caused significant levels of increased turbidity and water column nitrogen. Dojo are likely altering the Jordan River ecosystem and will continue to do so as their population increases. These ecological and life history factors could contribute heavily in the facilitation of harmful algal blooms and eutrophication of many water bodies. Dojo could become a severe problem in Utah Lake, if and when they become established; if they haven't done so already. It is our opinion that Dojo will inevitably become established and will thrive in Utah Lake and will cause major ecosystem shifts that could exacerbate cyanoHABs.

Recommendations

TBD

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Appendices

Appendix 1. Midge larvae and cyanoHABs section from Richards and Miller 2019.

Benthic Macroinvertebrates and HABs

The relationship between benthic macroinvertebrates, particularly worms and midges, and harmful algal blooms has received very little attention. In this section, we discuss the latest science on just how important these interactions are to Utah Lake HABs.

For several decades it has been recognized that anoxia is a pre-condition for cyanobacteria blooms in eutrophic waters (Trimbee and Prepas 1988) and that warm temperatures and stable water columns promote anoxia (Paerl, 1988; Zhang & Prepas, 1996). However, the role of Fe in cyanobacteria blooms has been severely underappreciated and the role of midge (Chironomidae) larvae in regulating Fe availability has been even less so.

Anoxia and Fe

Molot et al. (2014) proposed that the role of anoxia and ferrous iron was critical for cyanobacteria bloom formation. Their model can be summarized as follows:

> "The model has several critical concepts: (i) P regulates biomass and productivity in fresh waters until excessive loading renders a system N-limited or light-limited, but it is the availability of ferrous ions (Fe^{2+}) that regulates the ability of cyanobacteria to compete with its eukaryotic competitors; (ii) Fe^{2+} diffusing from anoxic sediments is a major Fe source for cyanobacteria, which acquire it by migrating downwards into Fe^{2+}-rich anoxic waters from oxygenated waters; and (iii) subsequent cyanobacterial siderophore production provides a supply of Fe^{3+} for reduction at cyanobacteria cell membranes that leads to very low Fe^{3+} concentrations in the mixing zone.
>
> When light and temperature are physiologically suitable for cyanobacteria growth, bloom onset is regulated by the onset of internal Fe^{2+} loading which in turn is controlled by anoxia, reducible Fe content of surface sediments and sulphate reduction rate."

Figure 34 (taken from Molot et al. 2014) illustrates this concept.

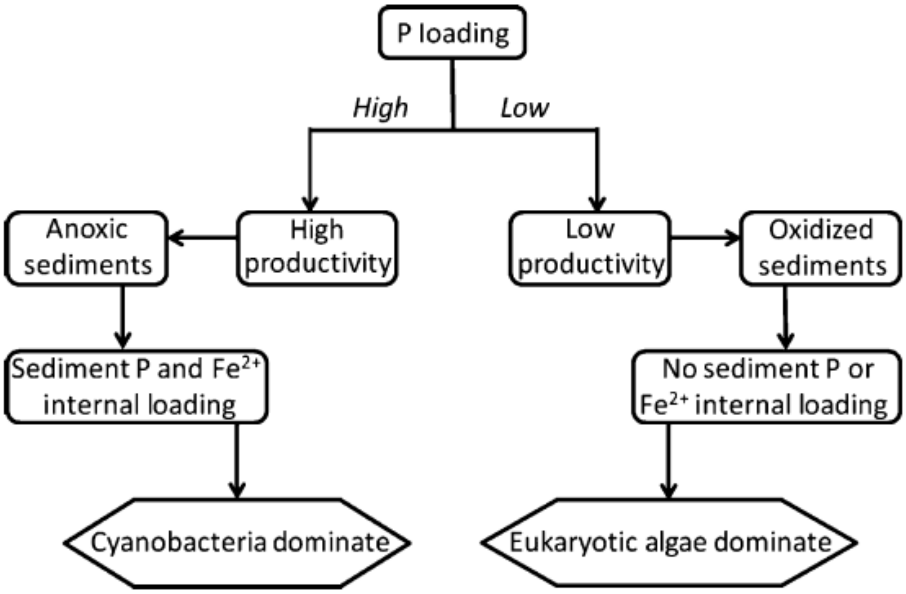

Figure 34. Simplified conceptual diagram of the modified phosphorus eutrophication model of cyanobacteria bloom formation for systems lacking naturally anoxic surficial sediments. The only factor controlling Fe^{2+} production shown here is anoxia at the sediment water interface.

Figure 35 (taken directly from Molot et al. 2014) illustrates the processes that promote Fe delivery to cyanobacteria and thereby promote cyanobacteria dominance in lakes.

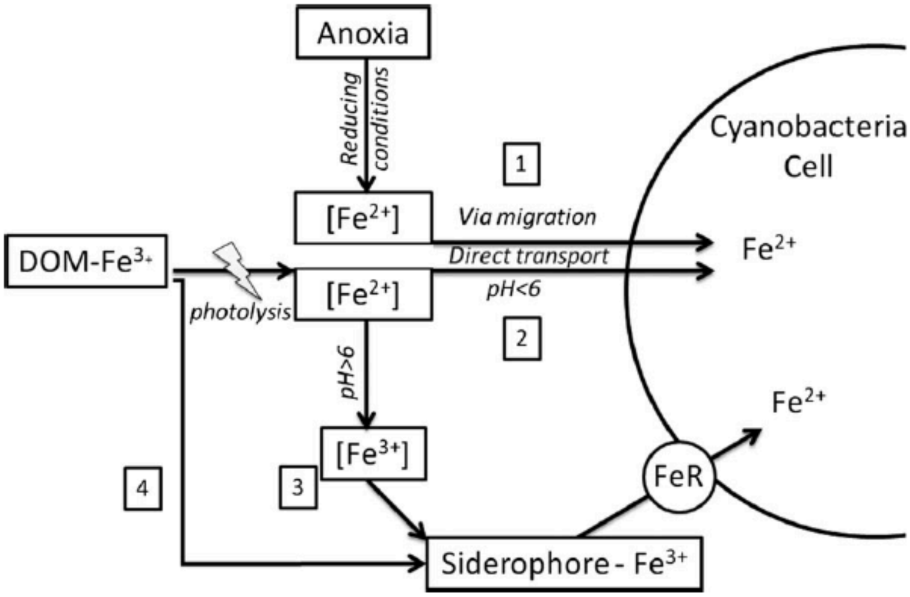

Figure 35. Anoxia: systems with anoxic sediments will experience Fe^{2+} flux into anoxic waters. Migrating cyanobacteria can acquire Fe^{2+} for direct transport into cells. (2) Photoreduction: DOM-Fe^{3+} can be photo-reduced, giving rise to Fe^{2+} that is available for direct Fe^{2+} transport into phytoplankton cells, but the transport rate is pH dependent. Acidity affects rates of abiotic oxidation by dissolved O_2 and at pH <6 Fe re-oxidation may be low enough to give rise to a pool of transportable Fe^{2+}. At higher pH, much of it is probably re-oxidised before transport. (3) and (4) Fe-scavenging (or acquisition) system: siderophores are produced by cyanobacteria that can (3) bind free soluble Fe^{3+} and (4) cleave Fe^{3+} from DOM complexes. Scavenged Fe^{3+} is then delivered to the cell membrane, creating a pool of Fe only accessible by cyanobacteria. Fe^{3+} is reduced by the Fe reducing system (FeR) before transport across the inner membrane. The Fe^{2+} pool is shown as two separate pools – in anoxic waters (internal loading) and in the mixing layer (photo-reduction).

Midge larvae

Midge larvae can actively oxygenate the sediments near the sediment/water boundary, including converting Fe^{2+} to Fe^{3+} (Holker et al. 2015) (Figure 36). Midge larvae are extremely abundant in Utah Lake sediments and can thus have a tremendous effect on Fe conversion. However, midge larvae pupate and then leave the lake as adults and are therefore not always present actively aerating the sediment. Subsequently, when larvae pupate and leave sediments as adults, larval tubes collapse and Fe^{3+} reduces to Fe^{2+} (Figure 36).

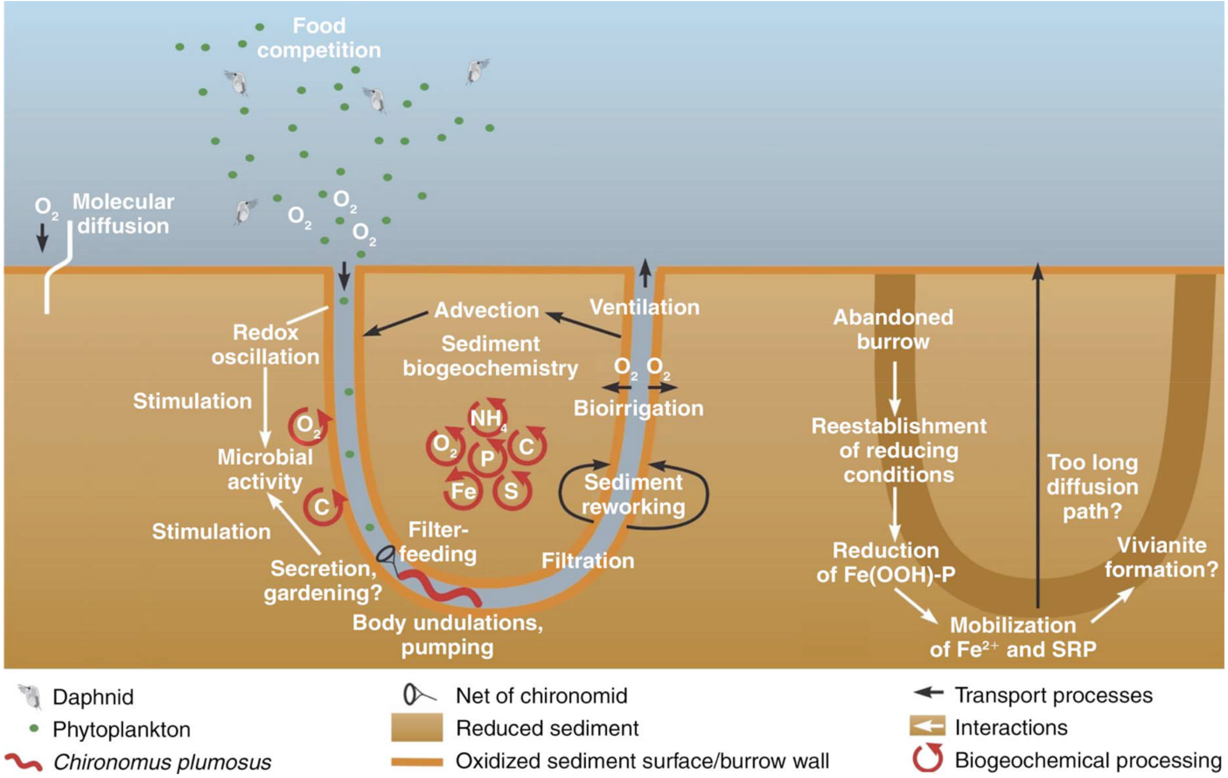

Figure 36. From: Holker et al. 2015. Tube-dwelling invertebrates: tiny ecosystem engineers have large effects in lake ecosystems

Appendix 2. A provisional multivariate index to monitor water quality in Utah Lake based on regulatory directives. Version 1.3.2

A Provisional Multi-Metric Index of Biological Integrity (MIBI) to Assess Water Quality in Utah Lake centered on Regulatory Directives

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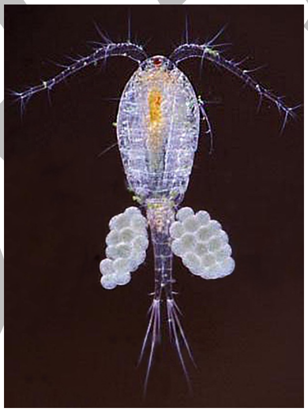
Draft Technical Report



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Regarding society's poor track record of environmental protection:
"*The complex reasons for failure center on the hubris of a society that behaves as if it could repeal the laws of nature. Plans generated by economists, technologists, engineers, and ecologists have too often assumed that lost or damaged components of ecological systems are unimportant or can be repaired or replaced."* J. R. Karr, 1996

Cover image: Female cyclopoid copepod.
http://www.ulrichhopp.de/bilder/kleinkrebse/Kleink_03_Mesocyclops_leuckarti_003.jpg

Table of Contents

Introduction

Multimetric indices of biological integrity (MIBIs) are a type of bioassessment that rely on empirical knowledge of how a wide range of biological attributes respond to varying degrees of human influence (Karr 1993, Karr and Chu 1997). The most useful MIBIs explicitly embrace several attributes of the biotic assemblages, including; taxa richness (diversity) and composition, indicator taxa (e.g., tolerant and intolerant groups), population dynamics, production, and an assessment of processes that include trophic structure, feeding strategies and other functional traits (Allen and Polimene 2011; Calow 1987; Cao and Hawkins 2019). The goal of a MIBI is to measure and evaluate the consequences of human actions on biological systems (Karr 1993, Karr and Chu 1997) however, it should be emphasized that bioassessments, including MIBIs, are not science but are the link between scientists and managers, and thus some level of subjectivity (e.g. professional judgment and management objectives) is inherent and cannot be completely avoided. MIBIs are evaluative precursors to more intensive, stressor specific, monitoring programs. They are assessment tools not monitoring tools and should not be used as such, although more comprehensive MIBIs such as the one presented in this report can help guide managers as to the types and causes of impairment.

Utah Lake

Utah Lake is an underappreciated, unique, and ecologically important part of Utah's (and the nation's) natural heritage. It is one of the few freshwater remnants of pluvial Lake Bonneville, that likely outsized Lake Michigan in size and volume. Utah Lake has until recently supported one of the most diverse and productive molluscan faunas in the western USA with perhaps twenty snail, clam, and mussel taxa. These mollusks likely dictated much of Utah Lake's ecosystem function (Richards and Miller 2017; Richards and Miller 2019; Richards 2016, 2018, 2019). Unfortunately, the majority of these molluscan taxa have been extirpated from the lake and their populations have been drastically reduced throughout most of its drainage (Richards and Miller 2019; Richards and Miller 2017; Richards 2016,2017, 2018, 2019a). Utah Lake was also once home to at least a dozen native fishes, including the Bonneville Cutthroat Trout (extirpated), Utah Lake Sculpin (extinct), and June Sucker (endangered) due to in part its ancient lineage and isolation from other large bodied freshwater lakes. Most native fishes have been extirpated from Utah Lake.

Regrettably, Utah Lake is now a highly regulated and abused reservoir ecosystem that has undergone human induced ecological hysteresis and catastrophic shifts and no longer resembles its natural self, pre-Mormon settlement. Consequently, Utah Lake is biologically impoverished. According to Karr (1996), "if biotic impoverishment is the problem, then protecting the integrity of" Utah Lake's "biological system(s) must be the goal".

Sections 101(a) of the Clean Water Act (1987) legally mandates USEPA to protect the physical chemical, and ***biological integrity***[13],[14] of our nation's waters. In addition, the Clean Water Act necessitates protection and enhancement of shellfisheries[15], which many managers fail to realize, includes freshwater mollusks (mussels, snails, clams).

Under the provision of the Clean Water Act, the Utah Division of Water Quality (UDWQ) is mandated to protect Utah Lake's three designated biological beneficial uses:

1. Warm-water fisheries,
2. other aquatic life (e.g. bird populations), and the
3. aquatic life they depend on (UDWQ 2019).

UDWQ is also required to protect for recreational beneficial use of Utah Lake; the main impairment is considered toxin-producing cyanoHABs, and for agricultural uses[16].

Because Utah Lake: 1) is the last freshwater remnant of pluvial Lake Bonneville, 2) its large size (surface area ≈ 100,000 acres) in an semi-arid climate, 3) its unique molluscan and fish diversity heritage, and 4) no other 'reference' water bodies with which to compare; the index of metrics (MIBI) and baseline values presented in this report are site specific for Utah Lake. The index can, however, be modified for other lentic waters and will be for Farmington Bay of Great Salt Lake.

Metrics

Primary Metrics

The Utah Lake MIBI is composed of relatively easy to measure primary metrics specifically targeting designated beneficial uses (fisheries, shell fisheries (e.g. mollusks), birds, and the aquatic life they depend (e.g. zooplankton, benthic invertebrates) including:

1. Benthic macroinvertebrate diversity,

---

[13] We adhere to the following definition of biological integrity throughout this document and during all of our research endeavors: ***Biological integrity*** refers to the capacity to support and maintain a balanced, integrated, adaptive biological system having the full range of elements (genes, species, assemblages) and processes (mutation, demography, biotic interactions, nutrient and energy dynamics, and metapopulation processes) expected in the natural habitat … (Angermeier and Karr, 1994; Frey, 1975; Karr and Dudley, 1981; Karr et al., 1986).

[14] The combination of physical, chemical, and biological integrity = ecological integrity (Karr 1996).

[15] The Clean Water Act (1987) states that: "It is the national goal that wherever attainable, an interim goal of water quality which provides for the protection and propagation of fish, ***shellfish***, and wildlife and provides for recreation in and on the water be achieved."

[16] UDWQ (2019) documents that, "The state classifies waters based on their uses and develops water quality standards to protect those uses. Utah's designated uses include drinking water, recreation, aquatic wildlife, and agriculture. Utah Lake is protected for the following designated uses:

2B: Infrequent primary contact recreation such as boating, wading, or similar uses
3B: Warm-water species of game fish, including the necessary aquatic organisms in their food chain
3D: Other aquatic wildlife.
4: Agricultural uses including irrigation of crops and stock watering" (UDWQ 2019).

2. Benthic macroinvertebrate secondary production (biomass as a substitute),
3. Zooplankton diversity,
4. Zooplankton secondary production (biomass as a substitute),
5. Mollusk diversity,
6. Mollusk densities,
7. Fish condition index.

An easy to measure metric for recreational beneficial use (e.g. swimmable) will be:

1. Creation of a DNA identification code of toxin producing cyanoHABs and develop metric baseline values.

The MIBI emphasizes the importance of Utah Lake's unique molluscan fauna, the importance of benthic invertebrates, particularly chironomids to its fisheries and birds, and the importance of zooplankton to its fisheries. Present values of each metric reported by Utah Lake researchers (e.g. Richards and Miller 2017; Richards 2016, 2018, 2019, UDWQ, and others) and/or those reported in the literature will be used as baseline values in which to compare future changes.

Secondary Metrics

There are also several dozen secondary metrics, including functional trait based metrics that are increasingly recognized as equally important or superior to taxa based metrics (Allen and Polimene 2011; Calow 1987; Dehling and Stouffer 2018; Monteiro and Faria 2018; Hayden et al. 2019), that will help fine tune and support the primary metrics and allow managers to better understand the levels and types of impairments affecting the lake.

A brief summary of secondary metrics includes:

- Phytoplankton, zooplankton, benthic invertebrate, mollusk, and fish taxa diversity indices, e.g. evenness, effective number of taxa,
- Zooplankton family relative abundances and ratios,
- Zooplankton, benthic invertebrate, mollusk, and fish functional traits indices: Particularly for zooplankton e.g. body size; mesotrophic vs. eutrophic zooplankton taxa ratio, taxonomic group changes (Cladocera, copepods, rotifers, etc.).

The use and validity of all of the primary and secondary metrics included in the MIBI (Table 1) are well grounded in the ecological and bioassessment literature (see Unabridged Literature Cited and References section).

Baseline Values

All of the metrics listed in Table 1 (Provo Bay specific as an example) will be populated from values based on recent and present conditions. These will be considered baseline scores to evaluate changes. Some metrics will increase or decrease depending on changes in water quality. No overall score(s) will be derived as is frequently done in other MIBIs. We contend that there is no statistical or ecological rational for weighting each metric and then subjectively combining them into a final score, therefore, we consider each metric as stand-alone. Each metric will either respond separately to different types and levels of impairment or compliment or add support to other metrics. Avoiding an overall score will allow researchers and managers the ability to observe more subtle changes in conditions and act accordingly.

Less Eutrophic Utah Lake Goal

Many of the metrics values will directly or indirectly change if and when Utah Lake moves along the primary production gradient from the current highly productive 'hyper eutrophic' condition to a lesser productive hyper eutrophic to eutrophic condition, as is the management goal of several agencies, including USEPA and UDWQ. Some metrics may have already exceeded a productivity threshold. For example, Utah Lake benthic invertebrate secondary production may or may not have exceeded a threshold value due to hyper-eutrophic conditions and could increase when primary production (e.g. eutrophication) is lowered. The appropriate value for benthic invertebrate secondary production would therefore be its maximum obtainable to protect for the designated beneficial uses of warm-water fisheries and bird populations.

Spatially and Temporally Derived MIBIs

We have confirmed that biological components including phytoplankton, zooplankton, benthic invertebrates, and fisheries, etc. vary both spatially and temporally in the lake (Richards and Miller 2017; Richards 2016, 2018, 2019, unpublished data and observations). MIBI baseline scores presented in the Table 1 example will therefore be provided for three locations that are mostly ecologically distinct based on others and our research:

1) Provo Bay,
2) Goshen Bay, and
3) Utah Lake proper.

That is, separate MIBIs will be required for each of the three sections of the lake.

Although marinas including Lindon Marina, Utah Lake State Park Marina, and Lincoln Marina experience quite different ecologies and baseline metric values compared to the other two locations, they will not have separate MIBIs. It is apparent that marinas function as a type of pollutant and should be treated as such.

The example MIBI presented in Table 1 includes metrics that reflect the temporal component of Provo Bay's ecology. Recommended times of year such as annual, seasonal, or monthly metric measurement are included in the MIBI.

Focus on Zooplankton Metrics

Zooplankton are a main focus of this MIBI. Zooplankton are in the pivotal position of transferring nutrients throughout aquatic food webs (bottom-up, top-down, trophic cascades) (Caroni and Irvine 2010; García-Chicote et al. 2018) and thus play an essential ecological role within Utah Lake. Zooplankton have a proportionally high indicator value that cannot be encompassed by phytoplankton or fish metrics (Carpenter et al. 1985;

Jeppesen et al. 2011; García-Chicote et al. 2018; Naselli-Flores and Rossetti, 2010; Barnett and Beisner 2007). In addition, the response of zooplankton assemblage structure metrics can be both to specific disturbances and chronic changes ((Attayde and Bozelli, 1998; Cairns et al., 1993; García-Chicote et al. 2018). Subsequently, these ecological roles of zooplankton in Utah Lake are explicitly and implicitly captured in the MIBI.

Zooplankton Taxonomy

There are only about twenty or so zooplankton taxa in Utah Lake (Richards 2019; Marshall 2019), which makes species level identification relatively easy for trained taxonomists or geneticist using DNA barcoding. We consider the Marshall (2019) report to be the definitive taxonomic reference for Utah Lake zooplankton until further modified. This reference was used to develop baseline zooplankton metric scores presented in the MIBI (Table 1 example for Provo Bay).

Fish Assemblage Imbalance

Utah Lake's native fish assemblage no longer exists. Thirteen native species occurred in the lake upon arrival of Mormon settlers in the mid 1800s. The Bonneville Cutthroat Trout, Bonneville Redside Shiner, Mottled Sculpin, Utah Lake Sculpin, Leatherside Chub, Utah Chub, Speckled Dace, Longnose Dace, Mountain Whitefish, and Mountain Sucker no longer exist in Utah Lake. The analog Utah Lake fish assemblage is now dominated by introduced species including Carp, Largemouth Bass, White Bass, Black Bullhead, Channel Catfish, Walleye, Goldfish, Yellow Perch, Blue Gill, and Black Crappie. The fish assemblage in the lake is most certainly out of balance.

We have incorporated several metrics that reflect this imbalance directly and several indirectly. It is well known that planktivorous fish can alter entire lake food webs primarily by preferentially consuming larger bodied zooplankton which in turn preferentially prefer feeding on larger phytoplankton including cyanophytes (Sondergaard et al. 2008; Wetzel 2001; Cole and Weihe 2016; Havens et al. 2015a, 2015b; Gophen 1990; Cooke et al. 2016). All of the fish species currently residing in Utah Lake are planktivorous at least during their juvenile stages. Many studies have shown that removal or reduction of planktivorous fish populations improves water quality including reduction of cyanoHABs leading many researchers and managers to recommend biomanipulation as a relatively inexpensive remedy for controlling algal blooms compared to attempts at whole drainage nutrient control (Riedel-Lehrke 1997; Cooke 1986; Jeppesen et al. 2007; Richards 2019a). We have shown that at least one metric, *zooplankton body length* is reduced in Utah Lake compared to other temperate lakes and that body lengths of zooplankton in the lake vary temporally and spatially in a pattern consistent with planktivore feeding (Appendix 1). Several of the zooplankton metrics in the example MIBI (Table 1) will respond to changes in fish assemblage composition especially if a fisheries biomanipulation program is initiated in Utah Lake.

Species Variability as a Function of Ecosystem Stability

Individual plankton species abundances and assemblage composition variability increases disproportionally to other commonly measured environmental variables as ecosystems become more and more out -of -balance and unstable (e.g. loss of diversity; increased nutrients; other pollution and pollutants; trophic cascades; altered food webs; etc.) (Cottingham et al. 2000; Ptacnik et al. 2008; Zohary 2004; Thomas et al. 2018). The well-established population dynamics literature shows that widely fluctuating populations are a good indicator of disturbance and that at low population levels, extinction risk increases with increased variability (e.g. demographic stochasticity, environmental stochasticity) (Melbourne and Hastings 2008; Vucetich et al. 2000; Pimm et al. 1988). Many phyto- and zooplankton taxa in Utah Lake occur at low abundances that are highly variable (see relevant Richards citations). These taxa are more susceptible to extinction and are inherently useful indicators of impaired conditions. Several metrics in Table 1 reflect low taxa abundance and variability (e.g. CV metrics reflect the well-known theoretical predictions that extinction risk increases with an increase in temporal coefficient of variation in population size (CV) (Pimm et al. 1998)).

The development and refinement of this MIBI is designed to be a collaborative effort between agencies including UDWR fisheries program, UDWQ, WFWQC, and others.

The following table, Tables 1 is our proposed MIBI for Provo Bay and functions as a working guideline for Wasatch Front Water Quality Council researchers and their contractors who are collecting data on Utah Lake.

Table 3. Example of proposed multimetric index of biological integrity (MIBI) template for monitoring Utah Lake. Provo Bay MIBI. Justification of metrics used in this MIBI can be found in Unabridged Literature Cited and Selected Reference Section. Metric values are in the process of being populated in this MIBI. TBD = To Be Determined.

Provo Bay	Metric	Baseline Value	Improvement Change
Phytoplankton	All Divisions		
	Chl A[9] (monthly mean and 90% CI)	Jan: Feb: March: April: May: June: July: Aug: Sept: Oct Nov: Dec:	Decrease
	Total biovolume (cells L^{-1}) (monthly mean and 90% CI)[11]	Jan: 326 (91; 561) Feb: 2945 (1,989; 3,900) March: 7,333 (4,239; 10,427) April: 10,988 (6,024; 15,952) May: 75,806 (unk.; 179,259) June: 93,746 (unk.; 190,318) July: 2,289,270 (597,856; 3,980,684) Aug: 606,535 (397,855; 815,215)	Decrease

		Sept: 668,899 (407,730; 930,068) Oct/Nov: 423,521 (290,408; 556,634) Dec: unknown	
	Total biovolume CV	Jan: Feb: March: April: May: June: July: Aug: Sept: Oct Nov: Dec:	Decrease
	Toxin level (μg L^{-1}) [12] (monthly mean and 90% CI)	Jan: Feb: March: April: May: June: July: Aug: Sept: Oct Nov: Dec:	Decrease
	Mean cell size (V) (μm^3 cell^{-1}) (monthly mean and 90% CI)	Jan: Feb: March: April: May: June: July:	Decrease

		Aug: Sept: Oct Nov: Dec:	
	Mean cellular C content (pg C cell^{-1}) (monthly mean and 90% CI)	Jan: Feb: March: April: May: June: July: Aug: Sept: Oct Nov: Dec:	Increase
	Mean C content/mean cell volume (C/V) (pg C µm^{-3}) (monthly mean and 90% CI)	Jan: Feb: March: April: May: June: July: Aug: Sept: Oct Nov: Dec:	Increase
	Taxa Based Diversity[15]		
	Richness (seasonal mean and 90% CI)	Winter Spring: Summer: Autumn:	Increase
	Evenness	Winter	Increase/Decrease[17]

	(seasonal mean and 90% CI)	Spring: Summer: Autumn:	
	ENT [13] (seasonal mean and 90% CI)	Winter Spring: Summer: Autumn:	Increase/Decrease[17]
	Division Based Biovolume[11]		
	Proportion biovolume Cyanophytes (cells L^{-1}) (monthly mean and 90% CI) [11]	Jan: 0.00 Feb: 0.08 (0.00, 0.16) March: 0.09 (0.00, 0.18) April: 0.09 (0.04, 0.14) May: 0.21 (0.00, 0.44) June: 0.69 (0.59, 0.79) July: 0.87 (0.80, 0.95) Aug: 0.54 (0.46, 0.62) Sept: 0.68 (0.53, 0.83) Oct/Nov: 0.14 (0.05, 0.24) Dec:	Decrease
	Proportion biovolume Chlorophytes (cells L^{-1}) (monthly mean and 90% CI) [11]	Jan: 0.08 (0.00, 0.017) Feb: 0.10 (0.00, 0.24) March: 0.11 (0.05, 0.18) April: 0.44 (0.33, 0.54) May: 0.34 (0.10, 0.58) June: 0.22 (0.15, 0.29) July: 0.11 (0.04, 0.19) Aug: 0.40 (0.32, 0.49) Sept: 0.24 (0.13, 0.36) Oct/Nov: 0.83 (0.73, 0.94) Dec: unknown	Increase in summer months
	Proportion biovolume Bacillariophytes (cells L^{-1}) (monthly mean and 90% CI) [11]	Jan: 0.90 (0.82, 0.99) Feb: 0.82 (0.66, 0.98) March: 0.79 (0.69, 0.89) April: 0.45 (0.34, 0.55) May: 0.44 (0.18, 0.71)	Increase

		June: 0.08 (0.03, 0.13) July: 0.01 (0.00, 0.02) Aug: 0.05 (0.03, 0.06) Sept: 0.08 (0.02, 0.14) Oct/Nov: 0.02 (0.01, 0.03) Dec: unknown	
	Proportion biovolume other Divisions (cells L^{-1}) (monthly mean and 90% CI)[11]	Jan: 0.01 (0.00, 0.04) Feb: 0.00 March: 0.01 (0.00, 0.01) April: 0.03 (0.01, 0.05) May: 0.01 (0.01, 0.02) June: 0.01 (0.00, 0.01) July: 0.01 (0.00, 0.01) Aug: 0.01 (0.00, 0.02) Sept: 0.00 Oct/Nov: 0.00 Dec: unknown	Increase
	Division Based Diversity		
	Proportion Cyanophyte Taxa (seasonal mean and 90% CI)	Winter Spring: Summer: Autumn:	Decrease
	Proportion Chlorophyte Taxa (seasonal monthly and 90% CI)	Winter Spring: Summer: Autumn:	Increase
	Proportion Bacillariophyte Taxa (seasonal mean and 90% CI)	Winter Spring: Summer: Autumn:	Increase
	Proportion other Divisions Taxa (seasonal mean and 90% CI)	Winter Spring: Summer: Autumn:	Increase

Zooplankton	Assemblage Level Body Size		
	Length (mm) (seasonal mean and 90% CI)[5]	Winter: 0.66 (0.38, 0.95)[1] Spring: 0.68 (0.60, 0.75) Summer: 0.77 (0.72, 0.82) Autumn: 0.89 (0.72, 1.06)	Increase
	CV length[5] (seasonal)	Winter: 0.55 Spring: 0.30 Summer: 0.15 Autumn: 0.18	Decrease
	Body mass (mg) (seasonal mean and 90% CI)	TBD[10]	Increase
	Biovolume (mm^3) (seasonal mean and 90% CI)	TBD[10]	Increase
	Assemblage Level Production		
	Biomass (mg L^{-1}) (seasonal mean and 90% CI)	Winter: Spring: Summer: Autumn:	Increase
	Biomass (mg L^{-1}) *CV* (seasonal)	Winter: Spring: Summer: Autumn:	Decrease
	Assemblage Level Growth/Reproduction		
	Potential Growth Rate (seasonal mean and 90% CI)	TBD from Literature[4]	
	Reproduction Type/Frequency (seasonal mean and 90% CI)	TBD from Literature[4]	
	Offspring Size/Number (seasonal mean and 90% CI)	TBD from Literature[4]	
	Assemblage Level Consumption		
	Clearance Rate (seasonal mean and 90% CI)	TBD from Literature[4]	
	Food Size Range (seasonal mean and 90% CI)	TBD from Literature[4]	

	Sloppy Feeding (seasonal mean and 90% CI)	TBD from Literature[4]	
	Assemblage Level Predator Avoidance		
	Vertical Migration (seasonal mean and 90% CI)	TBD from Literature[4]	Decrease
	Escape Response (seasonal mean and 90% CI)	TBD from Literature[4]	
	Transparency (seasonal mean and 90% CI)	TBD from Literature[4]	Decrease
	Cyclomorphosis/Defense (seasonal mean and 90% CI)	TBD from Literature[4]	Decrease
	Assemblage Level Waste/Loss		
	Egestion Rate (C, N, P) (seasonal mean and 90% CI)	TBD from Literature[4]	
	Fecal Pellet Sedimentation Rate (C, N, P) (seasonal mean and 90% CI)	TBD from Literature[4]	
	Excretion Rate (NH_4, PO_4) (seasonal mean and 90% CI)	TBD from Literature[4]	
	Assemblage Level Metabolism		
	Respiration Rate (seasonal mean and 90% CI)	TBD from Literature[4]	
	Digestion (seasonal mean and 90% CI)	TBD from Literature[4]	
	Assimilation (seasonal mean and 90% CI)	TBD from Literature[4]	
	Diversity[2]		
	Taxa Richness (annual)	6.79 (6.30, 7.29)	Increase
	Taxa Evenness (annual)	0.59 (0.55, 0.64)	Increase/Decrease[17]
	ENT (annual)	3.18 (2.95, 3.40)	Increase/Decrease[17]
	Group Relative Abundance		

	Proportion Rotifera (seasonal)	Winter: 0.14 (0.05; 0.22) Spring: 0.13 (0.09; 0.17) Summer: 0.10 (.06; 0.14) Autumn: 0.03 (0.00; 0.06)	
	Proportion Rotifera CV (seasonal)	Winter: 0.99 Spring: 1.02 Summer: 1.00 Autumn: 1.62	Decrease
	Proportion Cladocera (seasonal)	Winter: 0.27 (0.24; 0.30) Spring: 0.33 (0.30; 0.36) Summer: 0.35 (0.31; 0.39) Autumn:0.34 (0.29; 0.38)	
	Proportion Cladocera CV (seasonal)	Winter: 0.20 Spring: 0.33 Summer: 0.30 Autumn: 0.30	Decrease
	Proportion Calanoida (seasonal)	Winter: 0.15 (0.08; 0.22) Spring: 0.10 (0.08; 0.13) Summer: 0.05 (0.02; 0.07) Autumn: 0.12 (0.04; 0.21)	
	Proportion Calanoida CV (seasonal)	Winter: 0.73 Spring: 0.91 Summer: 1.47 Autumn: 0.84	Decrease
	Proportion Cyclopoida (seasonal)	Winter: 0.22 (0.16; 0.28) Spring: 0.28 (0.23; 0.30) Summer: 0.32 (0.25; 0.39) Autumn: 0.29 (0.12; 0.45)	
	Proportion Cyclopoida CV (seasonal)	Winter: 0.42 Spring: 0.29 Summer: 0.58 Autumn: 0.70	Decrease
	Proportion Harpacticoida (seasonal)	Winter: 0.03 (0.00; 0.06) Spring: 0.01 (0.00; 0.01) Summer: 0.02 (0.00; 0.03)	

		Autumn: 0.05 (0.00; 0.10)	
	Proportion Harpacticoida CV (seasonal)	Winter: 1.61 Spring: 4.1 Summer: 2.15 Autumn: 1.16	Decrease
	Proportion Daphnia sp. (seasonal)	Winter: 0.19 (0.13; 0.24) Spring: 0.16 (0.14; 0.18) Summer: 0.17 (0.14; 0.19) Autumn: 0.18 (0.10; 0.26)	Increase
	Proportion Daphnia sp. CV (seasonal)	Winter: 0.49 Spring: 0.49 Summer: 0.43 Autumn: 0.55	Decrease
	Zooplankton-phytoplankton relationships		
	Z:P ratio (zooplankton biomass to phytoplankton biomass) (seasonal mean and 90% CI)	Winter: Spring: Summer: Autumn:	Increase
Non-Molluscan Benthic Invertebrates	Diversity		
	Taxa Richness (seasonal)	Winter: Spring: Summer: Autumn:	Increase
	Taxa Evenness (seasonal)	Winter: Spring: Summer: Autumn:	Increase
	ENT (seasonal)	Winter: Spring: Summer: Autumn:	Increase
	Production		
	Total biomass (mg dry weight m^{-2})	Winter: na	Increase

	(seasonal)	Spring: na Summer: 10,546 (Autumn. 10,961 (	
	Total biomass CV (seasonal)	Winter: na Spring: na Summer: 0.84 Autumn: 0.89	Decrease
	Chironominae biomass (mg dry weight m^{-2}) (seasonal)	Winter: na Spring: na Summer: 3,304 (Autumn: 8,827 (	Increase
	Chironominae biomass CV (seasonal)	Winter: na Spring: na Summer: 1.23 Autumn: 1.01	Decrease
	Tanypodinae biomass (mg dry weight m^{-2}) (seasonal)	Winter: na Spring: na Summer: 6975 (Autumn: 1372 (	Increase
	Tanypodinae biomass CV (seasonal)	Winter: na Spring: na Summer: 1.23 Autumn: 1.03	Decrease
	Oligochaete biomass (mg dry weight m^{-2}) (seasonal)	Winter: na Spring: na Summer: 267 (Autumn: 761 (	Increase
	Oligochaete biomass CV	Winter: na Spring: na Summer: 1.28 Autumn: 0.66	Decrease
	Corixid biomass (mg dry weight m^{-2}) (seasonal)	Winter: na Spring: na Summer: na Autumn: na	Increase

	Corixid biomass CV (seasonal)	Winter: na Spring: na Summer: na Autumn: na	Decrease
Mollusks	Diversity[16]		
	Native gastropod richness	Autumn: 2	Increase
	Invasive gastropod richness	Autumn: 0	Maintain
	Pulmonate richness	Autumn: 2	Increase
	Non-pulmonate richness	Autumn: 0	Increase
	Native bivalve richness	Autumn: 0	Increase
	Invasive bivalve richness	Autumn: 1	Decrease
Fishes	Condition		
	Biological Condition Index[3] (seasonal)	TBD	Increase
	Diversity		
	Proportion planktivore taxa (yearly)	TBD[3]	Decrease
	Proportion piscivore taxa (yearly)	TBD[3]	Increase
	Proportion benthic taxa (yearly)	TBD[3]	Decrease
	Proportion invasive taxa (yearly)	TBD[3]	Decrease
Submerged Aquatic Vegetation	Abundance[7]		
	Proportion substrate cover (yearly)	TBD	Increase
	Diversity[7]		
	Taxa Richness (yearly)	TBD	Increase

[1] More data needed to reduce variability estimates

[2] Taxa diversity metrics S, E, and ENT use annual value because there were no significant differences between seasons using bootstrapped (N = 500) mean and 90% CIs.

[3] Consultation with UDWR fisheries biologists needed for metric values

[4] Metric values need to be determined from literature and then confirmed with Utah Lake empirical values

[5] Zooplankton body lengths and CV metrics derived from Richards 2019 literature review and need to be confirmed with empirical data from future samples.

[6] Further refinements and justification of seasonal body length sub- metrics are in Appendix 1.

[7] Collaborative research needs to be initiated asap to estimate SAV metrics at all three locations

[8] Temperature data to be acquired from UDWQ Utah Lake database

[9] Data to be compiled from WFWQC and UDWQ Utah Lake database

[10] To be determined empirically

[11] Monthly means and 90% CIs based on lake wide values for 2017 only. Need to compile data from WFWQC and UDWQ and re analyzed

[12] A DNA based measure of toxin level detection is suggested

[13] ENT = effective number of taxa = exponentiated Shannon Diversity Index (*H*) (Jost 2006; Chao et al. 2010)

[15] Phytoplankton taxa diversity metric means and 90% CI values will be derived from UDWQ database from Rushforth Phycology and after taxonomic status and synonymies are accounted and adjusted for (see Richards 2018b for taxonomic updates).

[16] Utah Lake mollusk diversity metric values derived from Richards 2017 and unpublished data

[17] Evenness and ENT may either increase or decrease with changes in conditions and need to be evaluated based on baseline values (Cao and Hawkins 2019)

Discussion

This is a provisional MIBI illustrating metrics specific to Provo Bay but will include Goshen Bay and Utah Lake proper metric values (presently being populated). More literature review, data compilation, and consultation with fisheries biologist and other Utah Lake researchers will be essential to modify, evaluate, and complete it. Once metric values are populated for each location, researchers and managers will be able to confidently evaluate changes to the biological and ecological condition of Utah Lake as opposed to depending on professional judgment or highly simplified indices comprised of only a few easy to measure generalized metrics. Utah Lake is a unique body of water in the western USA with a remnant unique native biota that deserves our best efforts to assess and then monitor its present state. It is our responsibility to maintain and improve Utah Lake's condition and protect its biological and ecological integrity, including its beneficial uses for this and future generations.

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Appendix 3. Spatial and Temporal Variability of Zooplankton Body Lengths in Utah Lake

Spatial and Temporal Variability of Zooplankton Body Lengths in Utah Lake

Technical Memo

By
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OreoHelix

To:
Wasatch Front Water Quality, Council, Salt Lake City, UT

April 16, 2019

Introduction

Body lengths of zooplankton are a widely used metric for evaluating conditions in lakes. Zooplankton body lengths typically decrease with increased; temperature, eutrophication, DIN:DP ratio, pollutants, fish predation, and interactions between these factors (Havens and Hanazato 1993; Havens et al. 2015; Havens and Beaver 2011;Trommer and Stibor 2019; Barnett and Beisner 2007; Gliwicz and Lampert 1990; Richman and Dodson 1983; Gillooly and Stanley 2000; others). Body size is extremely important in algal bloom dynamics because larger sized zooplankton are often better at feeding on larger strands of algal particularly cyanobacteria, therefore the loss of larger sized zooplankton may result in cyanoHABs (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). Richards (2019a) is developing a multi-metric index of biological integrity to monitor water quality in Utah Lake and Farmington Bay using zooplankton body length as an important metric.

Even though water quality managers are very concerned about cyanoHABs in Utah Lake, there have been no estimates of zooplankton body length spatial and temporal patterns in in Utah Lake, despite their well-known importance as a metric for monitoring water quality. We have remedied this situation by conducting statistical analyses on spatial and temporal patterns of zooplankton body lengths in Utah Lake with results presented in this memo and Richards (2019a in progress).

Methods

We used zooplankton data collected from Wasatch Front Water Quality Council and OreoHelix Consulting over the last several years as was presented in Richards 2019b. We then determined sample weighted zooplankton body lengths based on abundance data and lengths reported in Richards (2109b). We then conducted best-fit regression analyses, marginal analyses, and predicted mean and 95% CI body lengths for each location and month in Utah Lake.

Results

Zooplankton body lengths significantly varied spatially and temporally in Utah Lake with a relatively small to medium- small mean length = 0.85 mm (std. dev. = 0.19). Overall, body lengths were smallest from March through August and mostly significantly smaller than the mean (Figure 37). Body lengths were also significantly smaller than average in Provo Bay, Lindon Marina, and Utah Lake State Park Marina and significantly larger than average in the mid sections of the lake (labeled LP) (Figure 38).

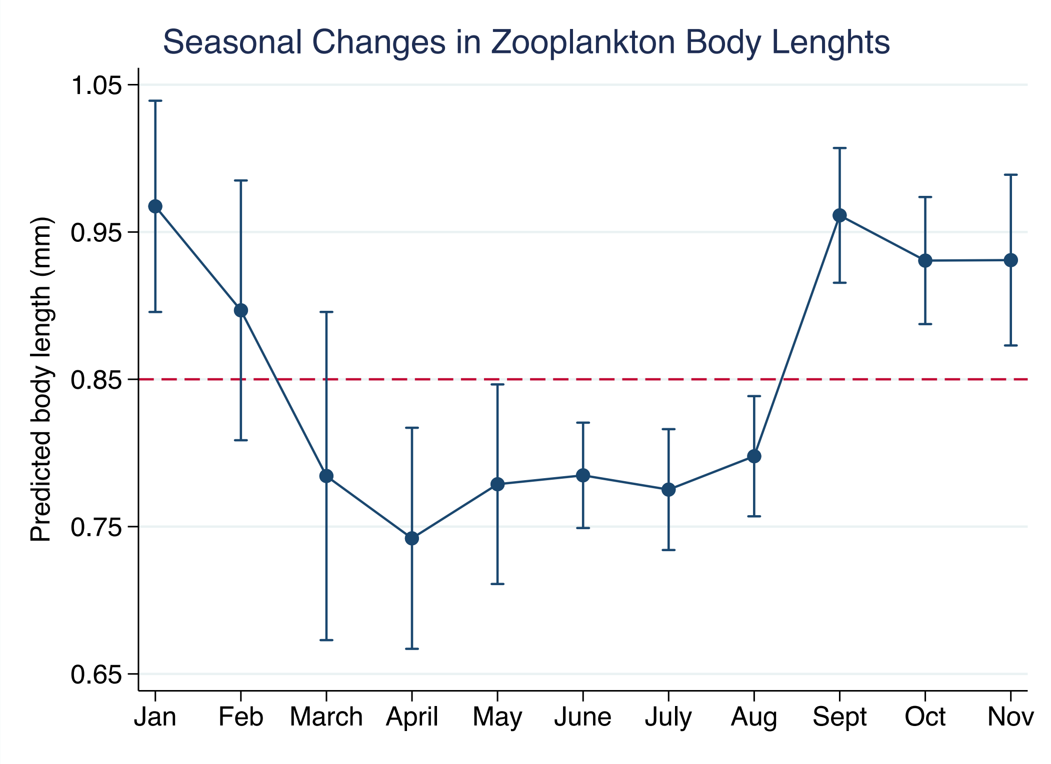

Figure 37. Predicted mean and 95% CIs for zooplankton body lengths from best fit regression models in Utah Lake seasonally.

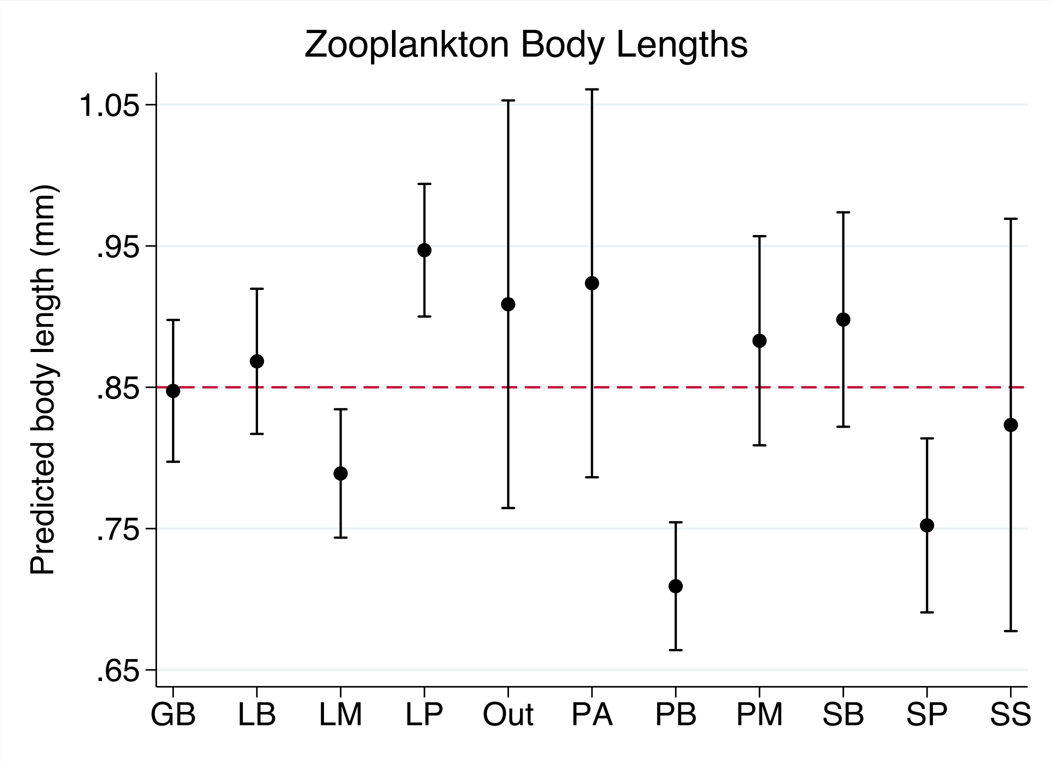

Figure 38. Predicted mean and 95% CIs for zooplankton body lengths from best fit regression models in Utah Lake by location.

Zooplankton body lengths were relatively uniformly small in Lindon Marina throughout the seasons (Figure 39) but significantly smaller than average in Provo Bay in March and April (Figure 40) and smaller than average from May to August at Utah Lake State Park Marina (Figure 41).

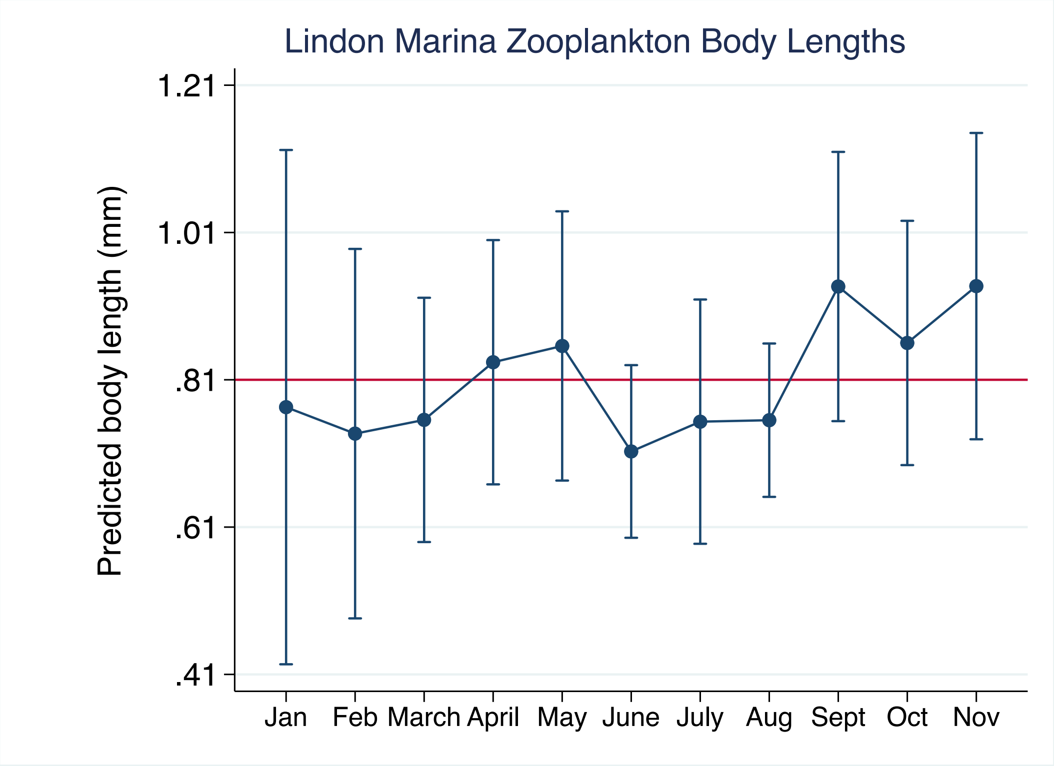

Figure 39. Predicted mean and 95% CIs for zooplankton body lengths from best fit regression models in Lindon Marina.

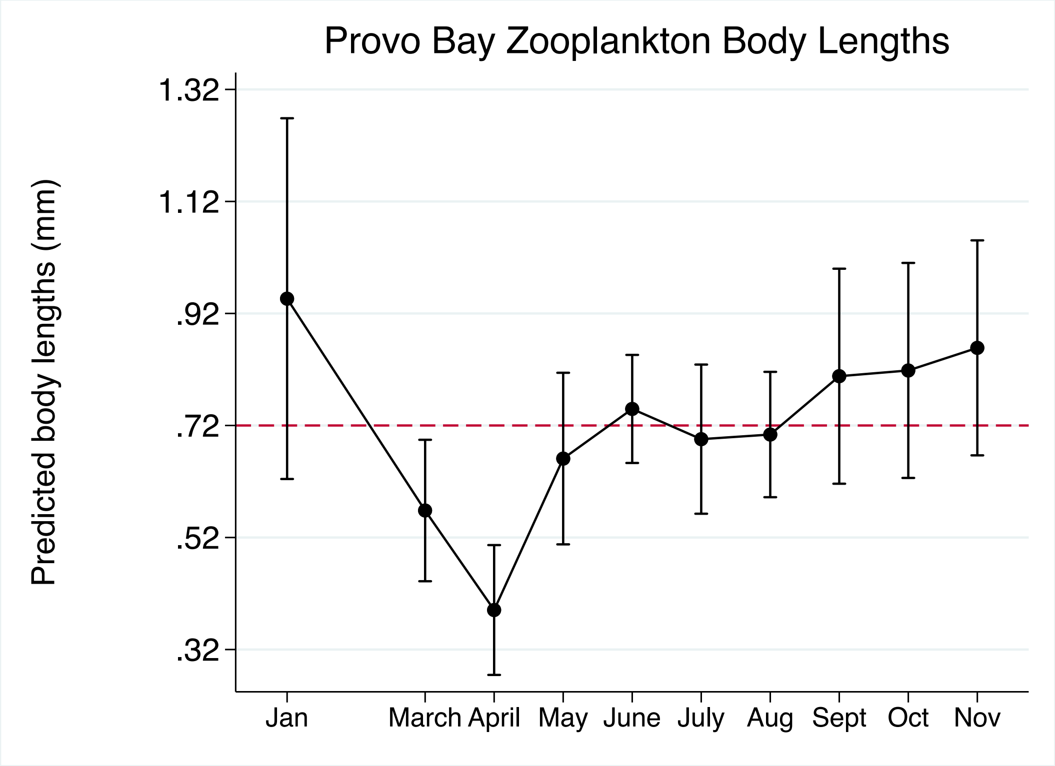

Figure 40. Predicted mean and 95% CIs for zooplankton body lengths from best fit regression models in Provo Bay.

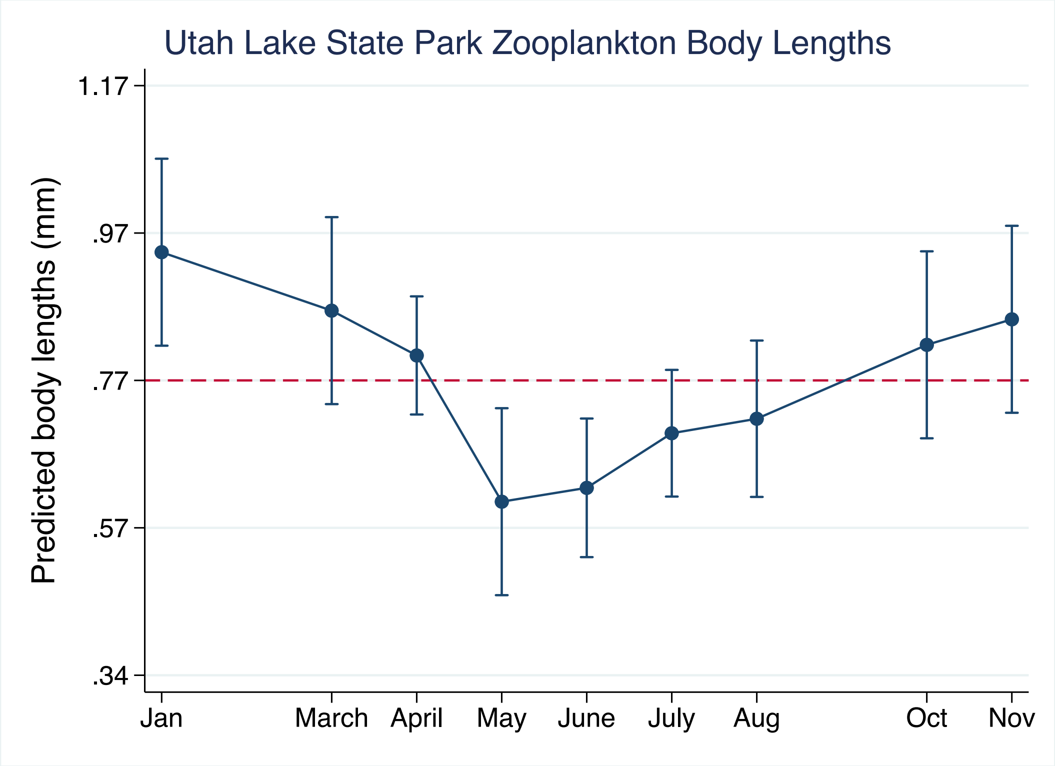

Figure 41. Predicted mean and 95% CIs for zooplankton body lengths from best fit regression models in Utah Lake State Park marina.

Discussion

Results presented in this memo show that zooplankton body lengths were relatively small compared to other temperate lakes (see References) and are a highly useful metric for monitoring water quality in Utah Lake. Body lengths significantly varied spatially and temporally. We suggest that other than the typical seasonal progression of zooplankton assemblages, was also due to the effects of planktivorous fish predation. Body lengths were typically smallest from spring through summer when fish are most actively feeding and when water clarity was often the best for visual planktivore feeding. The reason zooplankton body size was smallest in Provo Bay compared to most other sites was likely because this bay has the greatest planktivorous fish densities in the entire lake. Planktivorous fish prefer larger sized zooplankton.

2019 was a relatively high-water year in Utah Lake that resulted in a highly successful carp spawn and subsequently a boom in YOY juvenile carp production (Richards personal observation). Planktivorous juvenile carp require substantially more energy/individual body mass during growth than do larger adult carp maintaining body mass, thus zooplankton consumption rates should be higher in 2019 and subsequent years until the 2019 carp age class reaches adulthood than in previous less successful spawn years. Other planktivorous fish in the lake may have also produced more YOY than previous years. This phenomenon may alter zooplankton biomass and assemblage structure and requires careful monitoring.

Increased body sizes in late summer reported here were possibly due to increased algal bloom induced turbidity in mid-summer, which reduced visual ability of planktivores to find larger zooplankton, and subsequently allowed larger zooplankton such as *Daphnia* sp. to be able to consume larger sized phytoplankton, which then was partially responsible for decreased algal blooms in late summer/early autumn (Carpenter 1988; Chislock et al. 2019; Richards 2019b). Other causal factors for reduced zooplankton body size in Utah Lake are under investigation, including relationships between zooplankton body size and phytoplankton traits, pollution effects, and temperature effects. Results of these analyses will be directly applicable to the MIBI that is being produced by Richards (2019a).

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Appendix 4. Laboratory Observations Regarding Identifications and likely Synonymies among Zooplankton from Utah Lake (2017-2018)

Laboratory Observations Regarding Identifications and likely Synonymies among Zooplankton from Utah Lake (2017-2018)

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March 29, 2019

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Cover Photo:

Daphnia galeata mendotae from Utah Lake. Although the specimen has a pointy, extended, and partially re-curved head, the clearly visible ocellus, positioned midway down the head, clearly separates this (and several other) species from *Daphnia retrocurva*—the only previously reported *Daphnia* from this "group" (see report) in Utah Lake.

> "The beginning of wisdom is to call things by their proper name."
>
> — Confucius

Laboratory Observations Regarding Identifications and likely Synonymies among Zooplankton from Utah Lake

March 29, 2019

Brett D. Marshall, MSc.

River Continuum Concepts, Inc.

Abstract

We identified 106 zooplankton samples collected from Utah Lake, UT by David Richards (OreoHelix Consulting). There were some conflicts among the historic taxa lists provided by two morphological taxonomists and genetic taxonomy. Here we detail our notes to provide insights on how to best optimize the operational taxonomic units for working with data describing zooplankton assemblages of Utah Lake, including the most defensible method combining of data from multiple sources.

Suggested citation:

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Introduction

One of the great challenges of ecological science is minimizing unwanted sources of uncertainty so that our studies can be used to elucidate the causes of variation and covariation within and among biological populations interacting with their abiotic environment. The uncertainty of observations is exacerbated when two (or more) different taxonomists yield different species lists; did the species composition change between sampling events or are the differences simply artefacts of different methods in sample processing?

In this report, we provide information critical to the effective and defensible analysis of zooplankton data from Utah Lake. The species lists from four data-sources are in conflict and this report recommends which taxa should be synonymized and which should be retained as operational taxonomic units based on practical applications of microscopy, laboratory processing, and practical taxonomic effort. The results balance the current taxonomic literature vs. practical aspects of taxonomy and ecology to ensure the same taxonomic standards can be effectively used for processing samples in future years.

Methods

Data sources were from Richards and Miller (2017), Richards (2017a), and Richards (2017b). Richards 2016 used data provided by Larry Gray (the Gray data hereafter) and were sometimes in conflict with the taxa list provided by another taxonomist from LimnoPro (Richards 2017a (the LimnoPro dataset hereafter)). Both of these sources were sometimes in conflict with the taxa list comprised by the analysis of DNA Barcodes (Richards 2017b). Our focus was to ensure our taxonomic laboratory effort reconciled these sources and to understand why the differences occurred so that synonymies among the datasets are credibly and responsibly addressed. Thus, the taxonomy involved multiple keys and sometimes primary literature on taxonomic revisions and species description—much more effort than a routine bench taxonomy project. The Results Section of this report details some likely sources of variation in taxonomy referring to data from Gray, LP (LimnoPro), DNA, and RCC (our current accompanying dataset). The first data source, compiled by Gray, consisted of 4 copepod taxa, 10 cladoceran taxa, and 3 rotifer taxa (Table 1). Gray's dataset was the basis for the LimnoPro dataset (Table 2), which consisted of 4 copepod taxa, 11 cladoceran taxa, and 3 rotifer taxa. The taxa lists were similar to each other but may not have been completely independent. Both datasets deviated considerably from the DNA dataset (Table 3) which consisted of 6 copepod taxa, 23 cladoceran taxa, 3 rotifer taxa. However, it should be noted that only a sub-sample of samples sent to LimnoPro were included in the taxa list.

Table 1. Data from the Gray dataset (Richards 2016) included the following taxa.

Order	Family	Gray Taxa
Cyclopoida	Cyclopidae	*Eucyclops agilis*
Cyclopoida	Cyclopidae	*Acanthocyclops robustus*
Calanoida	Diaptomidae	*Leptodiaptomus sicilis*
Harpacticoida	Canthocamptidae	*Attheyella*
Cladocera	Daphniidae	*Ceriodaphnia quadrangula*
Cladocera	Daphniidae	*Daphnia pulex*
Cladocera	Daphniidae	*Daphnia retrocurva*
Cladocera	Chydoridae	*Pleuroxus striatus*
Cladocera	Chydoridae	*Chydorus sphaericus*
Cladocera	Chydoridae	*Leydigia leydigi*
Cladocera	Sididae	*Diaphanosoma* sp.
Cladocera	Bosminiidae	*Bosmina longirostris*
Cladocera	Ilyocryptidae	*Ilyocryptus* sp.
Cladocera	Leptodoridae	*Leptodora kindti*

Plioma	Brachionidae	*Brachionus*
Plioma	Brachionidae	*Keratella*
Plioma	Asplanchnidae	*Asplanchna*

Table 2. Data from the LimnoPro dataset (Richards 2017a) included the following taxa.

Order	**Family**	**LimnoPro Taxa**
Cyclopoida	Cyclopidae	*Microcyclops rubellus*
Cyclopoida	Cyclopidae	*Acanthocyclops robustus*
Calanoida	Diaptomidae	*Leptodiaptomus sicilis*
Harpacticoida	Canthocamptidae	*Cletocamptus* sp.
Cladocera	Daphniidae	*Ceriodaphnia quadrangula*
Cladocera	Daphniidae	*Daphnia pulex*
Cladocera	Daphniidae	*Daphnia retrocurva*
Cladocera	Daphniidae	*Simocephalus vetulus*
Cladocera	Chydoridae	*Pleuroxus aduncus*
Cladocera	Chydoridae	*Chydorus sphaericus*
Cladocera	Chydoridae	*Leydigia leydigi*
Cladocera	Moinidae	*Moina macrocarpa*
Cladocera	Sididae	*Diaphanosoma brachyurum*
Cladocera	Bosminiidae	*Bosmina longirostris*
Cladocera	Leptodoridae	*Leptodora kindti*
Plioma	Brachionidae	*Brachionus plicatilis*
Plioma	Brachionidae	*Brachionus calyciflorus*
Plioma	Asplanchnidae	*Asplannchna* sp.

Table 3. Data from the DNA dataset (Richards 2017b) included the following taxa. The list was modified to only include zooplankton.

CLASS	Family	Species
c__Branchiopoda	f__Artemiidae	s__Artemia franciscana
c__Branchiopoda	f__Bosminidae	s__Bosmina sp. BOLD:AAV0686
c__Branchiopoda	f__Bosminidae	s__Bosmina liederi
c__Branchiopoda	f__Chydoridae	s__Chydorus brevilabris
c__Branchiopoda	f__Chydoridae	s__Leydigia lousi
c__Branchiopoda	f__Daphniidae	s__Daphnia magna
c__Branchiopoda	f__Daphniidae	s__Ceriodaphnia dubia
c__Branchiopoda	f__Daphniidae	s__Simocephalus sp. BOLD:AAB1538
c__Branchiopoda	f__Daphniidae	s__Simocephalus cf. punctatus 3 NA
c__Branchiopoda	f__Daphniidae	s__Daphnia galeata
c__Branchiopoda	f__Daphniidae	s__Ceriodaphnia cf. acanthina AS29b3
c__Branchiopoda	f__Daphniidae	s__Ceriodaphnia cf. laticaudata ZMXII-611
c__Branchiopoda	f__Daphniidae	s__Ceriodaphnia sp. BOLD:AAB6934
c__Branchiopoda	f__Daphniidae	s__Simocephalus cf. punctatus 1 NA
c__Branchiopoda	f__Daphniidae	s__Ceriodaphnia cf. laticaudata BOLD:AAB5055
c__Branchiopoda	f__Daphniidae	s__Ceriodaphnia sp. BOLD:AAB5055
c__Branchiopoda	f__Daphniidae	s__Ceriodaphnia sp. HE-627
c__Branchiopoda	f__Daphniidae	s__Ceriodaphnia cf. laticaudata AS43e4
c__Branchiopoda	f__Daphniidae	s__Ceriodaphnia cf. laticaudata HE-615.1
c__Branchiopoda	f__Daphniidae	s__Daphnia ambigua
c__Branchiopoda	f__Daphniidae	s__Simocephalus punctatus
c__Branchiopoda	f__Moinidae	s__Moina mongolica
c__Branchiopoda	f__Sididae	s__Diaphanosoma cf. heberti BOLD:AAB9853
c__Branchiopoda	f__Sididae	s__Latonopsis cf. australis AS40c3
c__Maxillopoda	f__Cyclopidae	s__Acanthocyclops americanus
c__Maxillopoda	f__Cyclopidae	s__Cyclopidae sp. BOLD:AAG9780
c__Maxillopoda	f__Diaptomidae	s__Leptodiaptomus cf. sicilis JAAR-2015
c__Maxillopoda	f__None	s__Calanoida sp. HE-071
c__Maxillopoda	f__None	s__Cyclopoida sp. HE-241

c__Maxillopoda	f__None	s__Calanoida sp. HE-073
c__Monogononta	f__Brachionidae	s__Brachionus sp. Almenara
c__Monogononta	f__Brachionidae	s__Brachionus plicatilis group sp. MEG-2012
c__Monogononta	f__Brachionidae	s__Brachionus urceolaris

Results

General

Our analysis of 106 zooplankton samples from Utah Lake included 7 copepod taxa, 16 cladoceran taxa, and 4 rotifer taxa—in addition to some aberrant species such as insects (Table 4). This is the RCC dataset. Our dataset found more taxa than either of the other datasets because, we were driven to understand and reconcile the differences among the other sites; we made many slides, used multiple keys, and where keys failed went to primary taxonomic literature, including taxonomic revisions and species descriptions (Table 4). Thus, the effort was above and beyond routine standard bench taxonomy. However, the effort will allow for better[17] routine standard bench taxonomy in the future.

Table 4. Taxa list from the analysis by the River Continuum Concepts (RCC dataset hereafter) from samples collected in 2017-2018, and processed in late 2018.

Order	Family	RCC Taxa
Cyclopoida	Cyclopidae	*Microcyclops rubellus*
Cyclopoida	Cyclopidae	*Acanthocyclops americanus*
Calanoida	Diaptomidae	*Leptodiaptomus sicilis* female
Calanoida	Diaptomidae	*Leptodiaptomus sicilis* male
Harpacticoida	Harpacticoida	Harpacticoida
Harpacticoida	Canthocamptidae	Canthocamptidae
Harpacticoida	Canthocamptidae	*Attheyella* sp.
Harpacticoida	Laophontidae	*Onychocamptus mohammed*
Cladocera	Daphniidae	*Ceriodaphnia* sp.
Cladocera	Daphniidae	*Ceriodaphnia dubia*
Cladocera	Daphniidae	*Daphnia* sp.
Cladocera	Daphniidae	*Daphnia mendotae*
Cladocera	Daphniidae	*Daphnia retrocurva*

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[17] Better: more resolute, more consistent, more reproducible, and more efficient.

Cladocera	Daphniidae	*Daphnia ambigua*
Cladocera	Daphniidae	*Daphnia magna*
Cladocera	Daphniidae	*Simocephalus* sp.
Cladocera	Chydoridae	*Leydigia louisi*
Cladocera	Chydoridae	*Alona setulosa*
Cladocera	Moinidae	*Moina micrura*
Cladocera	Sididae	*Diaphanosoma* cf. *heberti*
Cladocera	Bosminiidae	*Bosmina longirostris* complex
Cladocera	Macrothricidae	*Macrothrix* sp.
Cladocera	Ilyocryptidae	*Ilyocryptus* sp.
Cladocera	Leptodoridae	*Leptodora kindti*
Plioma	Brachionidae	*Brachionus calyciflorus*
Plioma	Brachionidae	*Brachionus variabilis*
Plioma	Brachionidae	*Brachionus* sp. Almenara
Plioma	Asplanchnidae	*Asplanchna* sp.

Copepoda

Cyclopoda: Acanthocyclops

The case of *Acanthocyclops* presents a significant conundrum in taxonomic synonymies for the Utah Lake zooplankton dataset. The Gray and LimnoPro datasets reported the presence of *A. robustus,* whereas the DNA assessment of samples from Utah Lake reported only *A. americanus.*

In our initial identifications of *Acanthocyclops* using keys of Thorpe and Rogers (2016), we agreed with datasets provided by Gray and by LimnoPro that the *Acanthocyclops* in Utah Lake appeared to be *A. robustus*. However, Thorpe and Rogers (2016) and several other sources (e.g., Haney et al. 2013) do not list *A. americanus* among the fauna of North America even though the worldwide consensus is that the species occurs here. The story of this species is an interesting mix of history and biology. In the late 1800s, the "*Acanthocyclops robustus* group" was comprised of three highly varied (among species) and variable (within species) species: *A. vernalis, A. robustus, and A. americanus*. *A. americanus* was newest of the three species and the only species originally described in the USA, whereas the other two species were described from Europe. In the 1920s, *A. americanus* was found in Europe and the whole idea of geographic isolation as the basis of taxonomy came into question. Over the next half century, systematists worked with an extensive network of subspecies designations of the *A. robustus* group, that ultimately columnated with Kiefer (1976) combining *A. americanus* and *A. robustus* into a single species— with *A. robustus* having seniority by a few months. Thus, all *A. americanus* became *A. robustus* and all records of *A. americanus* gradually disappeared. In the 1990s, a resurgence of 'dividing' taxonomy began as European biologists began separating the species of the group again. Over time, the ecological differences among the species-complex had been noticed by biologists. This eventually led to Miracle et al. (2013) publishing their molecular-genetic assessment of the *Acanthocyclops robustus* group, along with the definitive physical characteristics to separate the species. This allowed major ecological differences among the species of the *A. robustus* group to be further elucidated. Miracle et al. (2013) report that these three species (*A. vernalis, A. robustus, A. americanus*) remain valid, while they synonymized several newer European species back into *A. americanus*.

For the study of zooplankton in Utah Lake, the differentiation of *A. robustus* from *A. americanus* is especially important because they usually occupy different ecological niches, with the former preferring a more littoral-zone habitat, and the later preferring pelagic/limnetic habitat (e.g., Miracle et al.2013). Thus, changes in the distribution, abundance, and production of these species would probably be important in describing the changing ecology of Utah Lake. Although the datasets of Gray and LimnoPro were not incorrect in their determination of *A. robustus* (because there are no published keys of North American fauna that include *A. americanus*), using the morphological characters defined by Miracle et al.
(2013) we were clearly able to associate these specimens to the currently recognized species of *A.*
americanus and bring these dataset into the modern standards of taxonomy.

We believe the two names *A. americanus* and *A. robustus* should be synonyms in the current datasets from Utah Lake because (1) the DNA taxa-list was generated using subsamples of the samples processed by LimnoPro, but did not find any trace of *A. robustus*, and (2) because the limitations in the keys to North
American fauna prevented LimnoPro and Gray from arriving at the determination of *A. americanus* (Table 5). I usually do not promote following nouveau taxonomy because changing names for the sake of changing names is detrimental to the long-term integrity of datasets. However, the taxonomy of this group has followed a long process over the last century and it also corresponds to differences in ecological niche that might be important for understanding the changing ecology of Utah Lake. Regardless of the name used, I believe that both names (*A. americanus* and *A. Robustus*) describe the same taxon—at least usually.

Table 5. Synonymies in the genus *Acanthocyclops*. 'X' marks determinations in each of the datasets considered. The final recommended taxon (O.T.U.) is in the bottom row highlighted.

Species	**Gray**	**LimnoPro**	**DNA**	**RCC**
A. vernalis				
A. robustus	X	X		
A. americanus			X	X

Recommend: *A. americanus*				

Cyclopidae: Eucyclops agilis

Gray reported the species *Eucyclops agilis* from Utah Lake. This was not found in any other dataset.

However, the taxon is superficially similar to *Microcyclops rubellus* that was found by LimnoPro, RCC and DNA. Moreover, not only is the size and shape similar, the course antennal morphology (that would have been used under a dissecting scope to 'morpho-type' *Microcyclops rubellus* incorrectly as *Eucyclops agilis)* is similar for both species (Table 6).

Table 6. Synonymies in the genera *Eucyclops* and *Microcyclops*. 'X' marks determinations in each of the datasets considered. The final recommended taxon (O.T.U.) is in the bottom row highlighted

Species	**Gray**	**LimnoPro**	**DNA**	**RCC**
Microcyclops rubellus		X	X	X
Eucyclops agilis	X			
Microcyclops rubellus				

Calanoida: Leptodiaptomus sicilis

The only Calanoida among the Gray and LimnoPro datasets was the species *Leptodiaptomus sicilis*. The DNA dataset found *Leptodiaptomus sicilis* but also several hits for a vague order-level taxon "Calanoida sp.." The only Calanoida species we found was *Leptodiaptomus sicilis* (Table 6). We differentiated the sex of the species because different keys were used. This may ultimately be useful information.

Table 6. Synonymies in the genera *Eucyclops* and *Microcyclops*. 'X' marks determinations in each of the datasets considered. The final recommended taxon (O.T.U.) is in the bottom row highlighted

Species	**Gray**	**LimnoPro**	**DNA**	**RCC**

Leptodiaptomus sicilis	X	X	X	X
"Calanoida sp."			X	
Leptodiaptomus sicilis				

Harpacticoid copepods

The harpacticoids were represented by only one taxon in the Gray dataset (*Attheyella* sp.), and only one taxon (and only a few individuals (~5/10,000)) in the LimnoPro dataset (*Cletocamptus* sp.). Although both datasets reported a different taxon, it would be presumptuous to assume that both taxonomists were looking at the same species and arrived at different names. These are uncommon constituents of plankton samples and the DNA dataset reported zero harpacticoids. In truth, the specimens were under represented to provide meaningful analysis because they are usually benthic-zone inhabitants. There are too few of them for conventional statistics, and the underlying assumption of multivariate statistics is that samples not containing a taxon are from habitats not suitable for that taxon; their occurrence is aberrant in plankton samples. Subsampling may further omit harpacticoid specimens from the taxa list. The most efficient way to deal with these aberrations is to either lump them up into a more inclusive taxon (e.g., Harpacticoida) or to exclude them from analysis all together. We favor inclusion in the dataset because their occurrence in plankton could indicate a benthic disturbance or ecological event. However, their use as such an indicator is probably best at the level of Harpacticoida. Incidentally, they were only identified as harpacticoida sp. in the DNA dataset also.

Cladocerans

Daphnia

The *Daphnia* were reported as from two groups of morphologically similar taxa. The groups were arbitrarily assigned as Group-1 and Group-2 to facilitate discussion of likely synonymies, which was important because we found some serious problems among the identities assigned to *Daphnia*—these problems are best addressed by dealing with different groups separately. Group-1 was comprised of *Daphnia* specimens with different degrees of expanded head capsule (i.e., 'helmet') and included *D. retrocurva, D. galeata,* and *D. mendotae*. Group-2 included taxa without as expanded of a helmet though occasionally a point of variable size occurred off the head. The Group-2 taxa were *D. pulex, D. magna,* and *D. ambigua*. Both groups had conflicts among the morphology datasets and the DNA dataset.

Daphnia: Group-1

Both the Gray and the LimnoPro datasets reported *Daphnia retrocurva* as the sole member of this group, whereas the DNA dataset reported *D. galeata* as the only member of this group. Most of the specimens processed in the RCC dataset were identified as *Daphnia mendotae*. *D. mendotae* is a synonym for *Daphnia galeata mendotae*. The North American subspecies *D. g. mendotae* is the sibling to the European *D. galeata galeata* (historically *D. galeata*). Thus, the specimens identified as *D. mendotae* in the RCC dataset is congruent with specimens called *D. galeata* in the DNA dataset, which recognized the eventual synonymy of *D. mendotae* and *D. galeata,* but not the subspecies differentiation of continental populations.

D. g. mendotae is a highly variable species, and there is some curvature in the head that superficially resembles that of underdeveloped *D. retrocurva*. However, finer examination of the head curvature and the presence of an ocellus that is clearly visible under higher magnification and on slide-mounted specimens assigns these specimens clearly to *D. g. mendotae*--not *D. retrocurva*. The *D. g. mendotae* are clearly separable from *D. retrocurva* even when the head is curved (or the *D. retrocurva* is under developed) by the presence of an ocellus below the compound eye, which is lacking in *D. retrocurva.* Unfortunately, the key of Thorpe and Rogers (2016) incorrectly suggest that *D. retrocurva* has an obvious ocellus, further confounding taxonomists using this key.

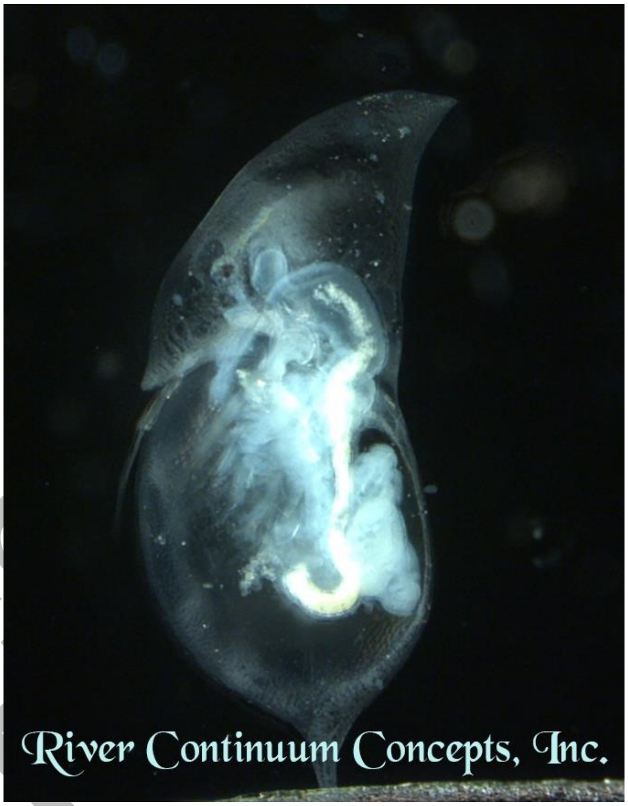

Figure 1. *Daphnia retrocurva* from Utah Lake.

Our impression is that most of the specimens identified by LimnoPro and Gray as *D. retrocurva* were probably mostly misidentified specimens of *D. g. mendotae*—the dominant *Daphnia* in our samples. However, we eventually found several true specimens *D. retrocurva* (Fig. 1) among the samples processed at RCC. Since these were less abundant in many samples that we processed, the species was probably omitted from the DNA dataset simply because of subsampling. Datasets from Gray and LimnoPro probably overestimated the abundance of *D. retrocurva* while omitting the occurrence of *D. g. mendotae* (Table 7).

For combining datasets, consider calling them *Daphnia* Group-1. Alternatively, accept the fact that *D. retrocurva* was uncommon, and call them all *D. galeata mendotae*—accepting the fact that an unknown (and variable) error increases the abundance of the taxon historically from (0-50%). To be clear, we would continue to differentiate *D. retrocurva* from *D. galeata mendotae* in future datasets, but to compare with historical datasets, investigators will need to group them.

Table 7. Synonymies in the genus *Daphnia* (Group-1). ‘X’ marks determinations in each of the datasets considered. The final recommended taxon (O.T.U.) is in the bottom row highlighted.

Species	Gray	LimnoPro	DNA	RCC
D. retrocurva	X	X		X

D. galeata			X	
D. mendotae				X
Recommend: *D. galeata mendotae (D. retrocurva* separate*)*				

Daphnia: Group-2

The datasets from Gray and LimnoPro both identified the Group-2 *Daphnia* species as *Daphnia pulex* whereas the DNA dataset found no *D. pulex*, but rather *D. magna* and *D. ambigua* (Table 8). Although the separation of these species should be routine, the keys of Balcer et al. (1984) do not include *D. magna*, which prefers more eutrophic waters than the Great Lakes of the northcentral USA and Canada. Therefore, Balcer et al.'s (1984) key would incorrectly identify any *D. magna* specimens to the species of *D. pulex* because of the spatial intent of the key. Microscopic differentiation of *D. magna* from *D. pulex* requires slide mounting for smaller specimens, but larger *D. magna* specimens jump out from other species, especially in slide-mounted specimens (but also under ~80-100x on dissecting scopes), because of the sigmoid structure of the postabdomen. The direction and angle of the carapace-head union separates *D. magna* from *D. ambigua*. Had the investigators (Gray, LimnoPro) used slide-mounted specimens and used a broad taxonomic key, this determination should have been straight forward.
For combining datasets, consider *D. magna*, *D. ambigua*, and *D. pulex* synonymous with *Daphnia* Group-2 or 'D. magna / D. ambigua.'

Table 8. Synonymies in the genus *Daphnia* (Group-2). 'X' marks determinations in each of the datasets considered. The final recommended taxon (O.T.U.) is in the bottom row highlighted.

Species	**Gray**	**LimnoPro**	**DNA**	**RCC**
D. pulex	X	X		
D. magna			X	X
D. ambigua			X	X
Recommend*: D. magna / D. ambigua*				

Ceriodaphnia

The *Ceriodaphnia* of Utah Lake were identified by both the Gray and LimnoPro datasets as only *C. quadrangula*. However, this taxon was not validated by DNA evidence, and although we reviewed many *Ceriodaphnia*, we were unable to find any *C. quadrangula* in the samples. This includes not only thousands of *Ceriodaphnia* from Utah Lake, but also thousands from Farmington Bay of Great Salt Lake— no *C. quadrangula.* We believe this maybe from sloppy taxonomic error because you cannot possibly determine a specimen to be *C. quadrangula* if it has a fenestra. All the specimens we observed had a fenestra, and therefore could not be keyed to *C. quadrangula* by anyone carefully examining the specimens—though this usually requires slide mounting.

The DNA dataset, included *C. dubia*, *C. acanthina*, *C. laticaudata*, and *Ceriodaphnia* sp.. These species can only be identified by microscopic analysis at high magnification (i.e., slide mounting). The specimens we identified in the RCC dataset included *C. dubia* and when occasionally specimens that could not be identified because of their maturity or condition (*Ceriodaphnia* sp.). Upon cursory examination, the shape of these *Ceriodaphnia* gestalts similar to *C. quadrangula,* and the body appears to lack reticulations (as per *C. quadrangula).* However, microscopic examination of finer features indicates that (in addition to fenestra mentioned above) they have a light and variable reticulation of the carapace that also matches *C. dubia*. It is possible that a few other species were present and that we found them as *Ceriodaphnia* sp..
One answer to this problem is simply to call all *Ceriodaphnia* the single genus-level taxon, *Ceriodaphnia* sp., as recommended in the table below (Table 9).

Table 9. Synonymies in the genus *Ceriodaphnia*. 'X' marks determinations in each of the datasets considered. The final recommended taxon (O.T.U.) is in the bottom row highlighted.

Species	**Gray**	**LimnoPro**	**DNA**	**RCC**
C. quadrangula	X	X		
C. dubia			X	X
C. cf. *acanthina*			X	
C. cf. *laticaudata* (x3)			X	
Ceriodaphnia sp. (x3)			X	X
Recommend: *Ceriodaphnia* sp.				

Diaphanosoma

The dataset from Gray used the ambiguous *Diaphanosoma* whereas, LimnoPro identified all *Diaphanosoma* as *D. brachyurum*. However, the DNA dataset found zero *D. brachyurum*, rather relating the DNA sequences to a different species, *D.* cf. *heberti*; this is a species not represented in any North American key (e.g., Thorpe and Rogers 2016, Haney et al. 2013, Pennak 1978, etc.). Thus, it was impossible for taxonomists in North America to identify this species using standard bench references. Additionally, the species *D. heberti* was not listed as a taxon on ITIS, or WORMS (lists of current taxa). When systematic study determines that an ITIS-listed species is determined to be invalid, or a synonym for another species, they remain listed but are flagged as invalid taxa. Thus, when we find a taxon completely omitted from these species lists, it usually means they were missed simply as an oversight. We have reached out to several authors on the topic Including the original author that described *D. heberti* (Korovchinsky 2002).
When we found these specimens, we understood why they called them *D. brachyurum*; but we also disagreed with their final determination because the fit just wasn't right. First, the most-current key to North American *Diaphanosoma* (Thorpe and Rogers 2016) is broken. Page 458, couplet 5, "posterioventral margin of valves with denticles," vs. couplet 5', "posterioventral margin of valves with denticles…." One of the coupling choices is a typographical error). Additionally, the prior coupling (4) states that the dorsal antennal ramus [has] 7 or 8 setae—so the extension of coupling 5' continuing, "…distal antennomere [=ramus] with 7 or 8 setae," is redundant, and self-validating. Every species with 7 or 8 setae on dorsal antennal ramus will key (ambiguously) to this one species.

In Pennak (1978), these specimens are clearly identified as the now defunct species, *D. leuchtenbergianum,* which was synonymized (and then split into several other species) with *D. bergei* (Kořínek 1981). But working through the Pennak (1978) key may have revealed why the Gray and Limnopro datasets designated Utah Lake *Diaphanosoma* to the species *D. brachyurum*. Pennak (1978) differentiates *D. brachyurum* from *D. leuchtenbergianum* (=*D. bergei* et al.) by the eye being near the <u>anterior</u> margin of the head, whereas the key by Haney et al. (2013) specifies only that they eye is near the margin of the head. Thus, the key of Haney et al. (2013) would (incorrectly) take specimens from Utah Lake, with eyes near the <u>ventral</u> margin of the head to species *D. brachyurum*. The key by Balcer et al. (1984) did not provide species level keys, deferring to Kořínek (1981).

The most recent functional key (given that the key of Thorpe and Rogers (2016) is broken) to United States *Diphanosoma* is by Haney et al. (2013) who separated the two similar species based on the "proximity of the eye to the margin of the head" for *D. brachyurum*. This was presented and interpreted in one important coupling to mean near <u>any</u> margin of the head, but in species descriptions at the end of the key, *D. brachyurum* should have a very large eye, near the anterior margin of the head, vs. *D. bergei* which has a smaller eye (Fig. 2), located more centrally or ventrally-marginally (Kořínek 1981, Haney et al. 2013).

If not for DNA evidence for another species, we would have left these taxa and the *D. brachyurum / D. bergei* complex in the RCC dataset also. But to understand the validity of this observation, we needed to know the rationale for the difference in the DNA dataset, which found *D. heberti* but zero *D. Brachyurum.* The original species description of *D. heberti* (Korovchinsky 2002) considers the morphology antennal spines and they are quite different between species. Specifically, *D. heberti* has a single short and stout spine where all others have a long skinny one. Barcoding for this species has been done in Mexico and Canada, but since North American keys excluded the species, no American biologists report it; the distribution is an arc ending at the US border. Korovchinsky (pers comm) verified that this is still a valid taxon (Table 10).

Table 10. Synonymies in the genus *Diaphanosoma*. 'X' marks determinations in each of the datasets considered. The final recommended taxon (O.T.U.) is in the bottom row highlighted. Asterisks indicate that using different references produced different results. Thorpe and Rogers (2016) placed these specimens in the *D. bergei* complex. Whereas Pennak (1978) placed them in the defunct species *D. leuchtenbergianum*.

Diaphanosoma sp.	X			
Diaphanosoma brachyurum		X		
Diaphanosoma herberti			X	X
Diaphanosoma leuchtenbergianum				*
Diaphanosoma bergei				*
Recommend: *D.* cf. *heberti*				

Figure 2. *Diaphanosoma* cf. *heberti* from Utah Lake. Note that truncated head is not typical—specimen was damaged by handling.

Moina

The dataset of Gray reported no *Moina* species at all. Given the abundance of this species, they were probably grouped with another taxon through error in the Gray dataset. *Moina* and *Ceriodaphnia* both have a notch behind the head that could cause some confusion. However, the gestalt body form of *Moina* is more similar to *Diaphanosoma* in that the shape of the carapace and head is comparable. Additionally, the carapace is often parted wide at the ventral side, reminiscent of the wing-like appearance of the *Diaphanosoma* carapace. Moreover, since the ultimate determination of *Moina* was *M. micrura*, which is very small, specimens may have been thought to be immature *Diaphanosoma*—explaining why the taxon '*Diaphanosoma* sp.' was used by Gray. Given the high densities and importance of the species, this taxonomic error should be addressed.

The dataset from LimnoPro reported 380 *Moina macrocarpa*. *Moina macrocarpa* is not, a valid taxon. It is however, a very popular misspelling, so popular that the misspelling has made it into journal articles, magazine articles and web pages. The valid species is *M. macrocopa* (q.v., Goulden 1968, Haney 2013, Thorpe and Rogers (2016), ITIS (2018), and WORMS (2018)). Since it is cultured for fish culture, popular magazines help propagate the misspelling. However popular, *M. macrocopa* is a relatively large and hairy beast of a *Moina*. Those observed in Utah Lake are much smaller and delicate.

The RCC dataset reports these as *M. micrura*. The specimens of Utah Lake key to this taxon by multiple keys, including: Thorpe and Rogers 2016, Haney 2013, and the original systematic revision of worldwide *Moina* taxonomy by Clyde Goulden (1968) at the Academy of Natural Sciences. It is necessary to view slide-mounted specimens at high magnification to differentiate these specific *Moina* species; we do not believe that Gray or LimnoPro prepared slides for most specimens, but rather rolled the dice using the pop culture supposition that all *Moina* are *M. macrocarpa* [sic]. In addition to being larger and hairier, *M. macrocopa* has large spines on the first leg. Whereas, *M. micrura* have plumose setules on the last and penultimate articles of the first leg. This is relatively easy to distinguish *IF* slides are prepared (Table 11).

The case of Utah Lake *Moina* is more interesting in that it highlights one of the pitfalls of DNA taxonomy. Specifically, the DNA dataset found no *M. micrura* but did find an occurrence of *Moina mongolica*, which is strictly an Old-World halophile (saltwater-dweller). In the systematic revision of Moinidae (Goulden 1968) the history of taxonomy was considered briefly. Goulden (1968) described how several other OldWorld species were synonymized into *Moina micrura*, those of the USA are typically the *M. m. typica* subspecies. However, many of the records of *Moina mongolica* from fresher waters in central Russia (late 1800s-early1900s) were very likely misidentified *M. micrura* (Goulden 1968). Thus, there are two possible paths whereby the DNA database would identify *M. mongolica*. First and most likely, *M. micrura* specimens from old museum collections (improperly identified as per Goulden 1968) were incorrectly barcoded as *M. mongolica*, and this code persisted in the DNA database based on erroneous taxonomy. Another (less-likely) scenario could occur whereby *M. mongolica* had come as an invader to Great Salt Lake and spread to other regional aquatic systems. In our Review of Farmington Bay zooplankton, we found that *Moina micrura* was the only Moinidae species present (so far). If halophile *M. mongolica* were to invade Utah's waters, Great Salt Lake would be the most likely epicenter of the invasion—and our analysis of zooplankton there also only found *M. micrura*. Therefore, we believe the correct identity of *Moina* in Utah Lake to be *M. micrura* despite DNA evidence. This identity is confirmed up by every taxonomic key we examined (e.g., Goulden 1968, Pennak 1978, Haney 2013, Thorpe and Rogers 2016). Regardless of the nature of the error, the moinid specimens we have observed differ from *M. macrocopa* (or *M. marcocarpa* [sic]) in many ways. The over use of historic local species-lists developed without mounted specimens, and cavalier taxonomy without slide validation caused a taxonomic (and indeed typographic) error to have persisted among zooplankton datasets of the region for many years.

Table 11. Synonymies in the genus *Moina*. 'X' marks determinations in each of the datasets considered. The final recommended taxon (O.T.U.) is in the bottom row highlighted. *Gray probably added these to *Diaphanosoma* sp., which is (likely) why he used the ambiguous genus identity.

Moina Taxonomic Synonymies				
Species	**Gray***	**LimnoPro**	**DNA**	**RCC**

Moina marcrocarpa [sic]		X		
Moina mongolica			X	
Moina micrura				X
Recommend: *Moina* cf. *micrura*				

Bosminidae: Bosmina longirostris.

All the morphological taxonomic determinations of Bosminidae resulted in the same conclusion: the ubiquitous *Bosmina longirostris*. However, the DNA dataset called all *Bosmina* sp. the single species *Bosmina leideri*. Thorpe and Rogers (2016) note that the determination of *B. longirostris* is actually a complex of cryptic species *B. longirostris*, *B. freyi*, and *B. leideri*—species that cannot currently be morphologically separated. We do not believe these taxonomic units to be in any conflict. The ambiguity of this species complex should be acknowledged by including the 'complex' after the species name. However, since the species apparently can not be separated, one wonders how a DNA database record for *B. leideri* came into existence. We prefer the more ambiguous "*Bosmina longirostris* complex" because it accommodates the future resolution of these species, while being independently replicable by other investigators (Table 12).

Table 12. Synonymies in the genus *Bosmina*. 'X' marks determinations in each of the datasets considered. The final recommended taxon (O.T.U.) is in the bottom row highlighted.

Species	**Gray**	**LimnoPro**	**DNA**	**RCC**
Bosmina longirostris	X	X		X
Bosmina leideri			X	
Recommend: *Bosmina longirostris* complex				

Chydoridae*: Leydigia* sp.

Gray and LimnoPro both identified *Leydigia* to the species *Leydigia leydigi*. However, this species was not identified by DNA, which instead found *L. lousi* [sic.], which was misspelled in the database (L. louisi). The most current key (Thorpe and Rogers 2016) supposedly separates *L. leydigi* from *L. louisi mexicana*. However, the key uses only the characters that Kotov (2003) used to separate *L. leydigi* from *L. louisi* in general (including all subspecies), completely ignoring the characters of Kotov et al. (2003) that separate *L. louisi louisi* from *L. louisi mexicana*. Thus, the key of Thorpe and Rogers (2016) is incomplete and erroneous. We recommend that the best taxon for this group is to ignore the sub-species designation in the key of Thorpe and Rogers (2016) because this will allow independent validation / confirmation / replication of taxonomic effort without referring investigators to the ever-changing sea of primary systematic literature (Table 13).

The actual current separation of *L. l. mexicana* from *L. l. louisi* involves the location of chitinous insertions within the swimming setae (far from bases in *L. l. mexicana*, near bases in *L. l. louisi*). Additionally, the shape of ocelli differs markedly between the two different sub species. Thus, it is possible to separate these subspecies relatively reliably, under high magnification. We will continue to report the subspecies, but for combining datasets, investigators should assume that historical *L. leydigi* are probably *L. louisi*—and further they are probably *L. louisi louisi*.

As to the nature of the errors from *Leydigia leydigi*, we believe that taxonomists (Gray, LimnoPro) saw the large, swooping circular postabdomen under dissecting scope, and assumed that the lateral spines (which they could not see) were small (*Leydigia leydigi*) when in fact they were, proportionally large (*Leydigia louisi*).

Table 13. Synonymies in the genus *Leydigia*. 'X' marks determinations in each of the datasets considered. The final recommended taxon (O.T.U.) is in the bottom row highlighted.

Species	**Gray**	**LimnoPro**	**DNA**	**RCC**
Leydigia leydigi	X	X		
Leydigia lousi [sic.]			X	
Leydigia louisi mexicana				
Leydigia louisi louisi				X
Recommend: *Leydigia louisi louisi*				

Chydoridae: Pleuroxus

We did not find any *Pleuroxus* from Utah Lake in the 2017-2018 samples we identified, but both Gray and LimnoPro did find this genus—though they disagreed on the species determination. Since we did not see their specimens, thoughts presented here are more conjecture than in the other taxonomic groups where we were pretty sure that we were talking about the same specimens. *Alona* (RCC dataset) could have been included here in Gray and LimnoPro.

Chydoridae: Chydorus spaericus

Both Gray and LimnoPro identified *Chydorus spaericus* from Utah Lake. We did not find any *Chydorus* in the RCC 2017-2018 data, but the DNA dataset found *Chydorus brevilabris*. Both are small and roundish. Belyaeva and Taylor (2008) reported many cryptic species, recognized by molecular markers and ontology, occur in the '*Chydorus spaericus* complex.'

Chydoridae: Alona setulosa

We found 20 specimens of *Alona setulosa* (out of more than 23,000 identified specimens we examined for the Utah Lake dataset). It makes sense that this species was omitted from DNA analysis due to subsampling and splitting. If the other datasets included *A. setulosa*, it would be difficult to imagine how they might have misclassified it. However, it has a superficial appearance to other Chydoridae. It is especially similar to *Leydigia* sp.—both *Alona* sp. and *Leydigia* sp. are in the subfamily Aloninae—if a few specimens were in the older datasets, they were probably added to the more common *Leydigia*. The effect of this error is probably small, since among our samples, *Alona* comprised only about 0.08% of the annual community of zooplankton. Or *Alona* (some or all) may have been included with *Pleuroxus* sp..

Rotifera

Rotifers were generally under sampled or at least under represented. It might be best to lump them into a very wide taxon, perhaps Rotifera. Regardless of how they are dealt with, we did not have enough specimens to make recommendations on the taxonomy of the group.

Results: Recommended Tabulated Synonymies by Dataset

We summarized the synonymies from the previous section, to recommend the best practical grouping for each dataset. Taxa shaded in orange require taxonomic reclassification with other datasets.

1. Gray Data required the most changes (below).

Family	Gray Taxa	New Recommended O.T.U.
Cyclopidae	*Eucyclops agilis*	*Microcyclops rubellus*
Cyclopidae	*Acanthocyclops robustus*	*Acanthocyclops americanus*
Diaptomidae	*Leptodiaptomus sicilis*	*Leptodiaptomus sicilis*
Canthocamptidae	*Attheyella*	Harpacticoida

Daphniidae	*Ceriodaphnia quadrangula*	*Ceriodaphnia* sp. / *Ceriodaphnia dubia*
Daphniidae	*Daphnia pulex*	*Daphnia magna / Daphnia ambigua*
Daphniidae	*Daphnia retrocurva*	*Daphnia galeata mendotae / D. retrocurva*
Chydoridae	*Pleuroxus striatus*	*Pleuroxus* sp.
Chydoridae	*Chydorus sphaericus*	*Chydorus brevilabris* (per DNA only)
Chydoridae	*Leydigia leydigi*	*Leydigia louisi / (also Alona* sp*).*
Sididae	*Diaphanosoma* sp.	*Diaphanosoma* cf. *heberti* / Also: *Moina micrura*
Bosminiidae	*Bosmina longirostris*	*Bosmina longirostris* complex
Ilyocryptidae	*Ilyocryptus* sp.	*Ilyocryptus* sp.
Leptodoridae	*Leptodora kindti*	*Leptodora kindti*

Brachionidae *Brachionus* Rotifera? Brachionidae *Keratella* Rotifera? Asplanchnidae *Asplanchna* Rotifera?

2. Data From LimnoPro (below)

Order	**Family**	**LimnoPro Taxa**	**New Recommended O.T.U.**
Cyclopoida	Cyclopidae	*Microcyclops rubellus*	*Microcyclops rubellus*
Cyclopoida	Cyclopidae	*Acanthocyclops robustus*	*Acanthocyclops americanus*
Calanoida	Diaptomidae	*Leptodiaptomus sicilis*	*Leptodiaptomus sicilis*
Harpacticoida	Canthocamptidae	*Cletocamptus* sp.	Harpacticoida
Cladocera	Daphniidae	*Ceriodaphnia quadrangula*	*Ceriodaphnia* sp. / *Ceriodaphnia dubia*
Cladocera	Daphniidae	*Daphnia pulex*	*Daphnia magna / Daphnia ambigua*
Cladocera	Daphniidae	*Daphnia retrocurva*	*Daphnia galeata mendotae / D. retrocurva*
Cladocera	Daphniidae	*Simocephalus vetulus*	*Simocephalus* sp.
Cladocera	Chydoridae	*Pleuroxus aduncus*	*Pleuroxus* sp.
Cladocera	Chydoridae	*Chydorus sphaericus*	*Chydorus brevilabris* (per DNA only)

Cladocera	Chydoridae	*Leydigia leydigi*	*Leydigia lousisi*
Cladocera	Moinidae	*Moina macrocarpa*	*Moina micrura*
Cladocera	Sididae	*Diaphanosoma brachyurum*	*Diaphanosoma* cf. *heberti*
Cladocera	Bosminiidae	*Bosmina longirostris*	*Bosmina longirostris* complex
Cladocera	Leptodoridae	*Leptodora kindti*	*Leptodora kindti*
Plioma	Brachionidae	*Brachionus plicatilis*	Rotifera?
Plioma	Brachionidae	*Brachionus calyciflorus*	Rotifera?
Plioma	Asplanchnidae	*Asplannchna sp.*	Rotifera?

Conclusions

We documented a rationale for the systematic and defensible integration of data from different sources for Utah Lake and beyond. Without this information, the underlying assumptions of grouping taxa might appear arbitrary. This document provides a framework for discussing potential taxonomic synonyms and Operational Taxonomic Units (O.T.U.s) without each and every Utah Lake study requiring a comprehensive literature review to support laboratory operations; investigators can simply cite this document and explain why they agree or disagree with our recommended taxonomic units. Similarly, changes and deviations from procedure can refer to this document for context.

We also found numerous apparent taxonomic errors. Some were due to observer error, and some might be due to using inappropriate regional keys, but many were due to the quality of taxonomic keys not keeping pace with the changing state of the science. Therefore, in addition to providing a framework for systematic grouping of animals, we also have worked out the current ideal taxonomic effort for Utah Lake zooplankton studies. This will streamline our laboratory work in the future. Furthermore, we have found that many of the same issues may apply to other regional waterbodies, such as Farmington Bay. This allows for broader application of our findings.

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Appendix 5. A Case for Adaptive Holistic Management of Phragmites in the Jordan River Drainage and Southern Utah

A Case for Adaptive Holistic Management of Phragmites in the Jordan River Drainage and Southern Utah

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Figure 42. Phragmites along the shore of Utah Lake, UT photo courtesy of the Utah Lake Commission.

Background

Wetlands in the Jordan River drainage, Utah include those surrounding Utah Lake, the fourth largest freshwater lake in the western U.S. and those surrounding the southern portion of Great Salt Lake, primarily Farmington Bay. Phragmites has invaded all of wetlands in the drainage and it impacts are substantial. I have been conducting ecological research on Jordan River drainage Utah wetlands for about 9 years, including phragmites research. My expertise includes ecological studies on; phytoplankton, zooplankton, aquatic macroinvertebrate assemblages, fisheries, nutrients, and invasive species, as well as serving as a consultant for management of these critical wetlands. Invasive species research that I have conducted includes impacts on native aquatic threatened and endangered species and ecosystems (see Richards, Richards et al., and Hoven and Richards in Literature Cited) and developing biocontrol agents including chrysomelid beetles, the weevil (*Rhinocyllus conicus*) and hawk moths (Family Sphingidae) for controlling St John's wort (*Hypericum perforatum*), leafy spurge (*Euphorbia esula*), Spotted Knapweed (*Centaurea maculosa*), and Canadian musk thistle (*Carduus nutans*).

Wetlands in the Jordan River drainage are some of the most important and last remaining wetlands in the Central Flyway and are designated World Natural Heritage sites, primarily because of the importance to shorebirds and waterfowl. Not surprisingly, the vast majority of managers in the area consider invasive phragmites to be a major problem. One of these negative effects that I am analyzing with several other researchers is the loss of shorebird nesting habitat due to expanding phragmites stands.

All managers of these wetlands also agree however, that the number one problem facing these wetlands is chronic lack of water. Most suggest that the second most important problem is excessive nutrients.

Having had the privilege of spending much time researching these wetlands, I have a much different opinion on phragmites than most and will discuss some of its vastly underappreciated ecological benefits. I will also discuss some of the best ways to manage this invasive grass focusing on Provo Bay, Utah Lake and Farmington Bay, Great Salt Lake.

Ecological benefits of invasive Phragmites

Both Provo Bay and Farmington Bay are paltry analogs of a once incomparable and incredibly diverse Jordan River drainage ecosystem, pre-Mormon settlement, mid-1800s (Richards 2018a). At present, during years with normal precipitation, both bays have enough water to flood invasive phragmites stands up to about one meter in depth that lasts throughout most of the year. However, in summer both bays typically dry and phragmites stands are elevated on dry ground several inches above water level. Cattails (*Typhus* sp.) and submerged aquatic vegetation (e.g. *Stuckenia* sp., *Ruppia* sp., etc.) cannot survive in these drying conditions. Therefore, many natives, including cattails, are not losing habitat as much to phragmites invasion but to increasingly drying conditions from chronic dewatering and now, climate change.

Phragmites and soil conditions

Stands of this invasive grass provide shading that cools and helps maintain damp soils and cools surface water during summer when daytime air temperatures regularly exceed 100^0 F. Surface ground temperatures reach or exceed air temperatures, soils quickly dry, and top soil layers are lost to wind action in locations where phragmites stands have been physically removed by managers. In stands of phragmites, soil temperatures remain cooler and moister (Richards unpublished data). Of real concern to citizens in the Greater Salt Lake City Metropolitan Area is degradation of air quality due to wind born particles from exposed Great Salt Lake sediments, most of which contain toxic metals including zinc, cadmium, lead, and mercury that can easily become windborne. Although not quantified, phragmites stands likely help prevent some of this loss and help protect air quality. More research is needed to evaluate transpiration loss from phragmites vs. evaporative loss without such stands including soil loss and changes in air quality.

Phragmites and Aquatic Faunal Assemblages

Provo Bay and Farmington Bay wetlands provide crucial habitat for aquatic species, typically starting from shortly after ice out (Provo Bay) and continuing throughout spring into early-mid summer when they are inundated. Utah Lake and Farmington Bay waters are eutrophic to hypereutrophic. Utah Lake is one of the most productive warm water fisheries in the western USA and is the most productive lake in Utah. Provo Bay has the highest primary and secondary production in Utah Lake. Hundreds of acres of phragmites in Provo Bay contribute to this productivity. When inundated, phragmites stands provide premier habitat for; zooplankton, free swimming and benthic macroinvertebrates (e.g. midges, snails, beetles, bugs, etc.), and act as nurseries for small fishes including larvae, juveniles, and minnows. Large predatory fish cannot penetrate the stands, although several broadcast spawners (i.e. White Bass, Carp, Channel Catfish etc.) utilize phragmites for egg laying. We have collected dozens of biotic samples within these stands and directly outside of the stands and estimate that invertebrate and small fish densities and biomass are at least an order of magnitude greater in phragmites stands than outside. Loss of these stands would dramatically reduce fisheries productivity in Provo Bay and Utah Lake. Because Farmington Bay is more saline than Provo Bay it does not sustain a warm water fishery, other than invasive carp, but does support one of the greatest concentrations of shorebirds, wading birds, and waterfowl in the western USA, all of which depend on its aquatic invertebrate food base.

I have estimated that Utah Lake produces 1000 to 6000 tons of chironomids (midge) biomass seasonally and that Provo Bay often produces 20,000 midge larvae/m^2 of lake bottom (Richards 2017). Likewise, Farmington Bay. Midges are the dominant food source for higher trophic levels including aquatic and terrestrial. Migratory cliff swallows and barn swallows almost exclusively feed on adult midges during late summer/early autumn. Dozens of other bird species also depend on this harvest. Adult midge swarms in Provo Bay and Farmington Bay are spectacular. These mating swarms are often misidentified as smoke from fires and can contain tens of millions of male and female midges per swarm with dozens of swarms occurring at once, each rising from the shoreline up to perhaps 100 to 200 feet in altitude (D.C. Richards personal observations). Adult midges rely on the thick stands of phragmites as shelter after emerging from the bays and as resting substrate between mating. I have begun measuring and comparing midge densities in phragmites and other plants including cattails, bulrush, and invasive salt cedar. Midge densities are greatest per surface area on salt cedar due to its many branches and surface area but phragmites stands support the greatest midge density per unit land area due to its height and density (unpublished data). I postulate that midge densities would be much lower in Provo Bay and Farmington Bay without stands of phragmites to provide shelter to adults. This would have severe negative consequences on fish and bird populations dependent on these aquatic insects. Other invertebrate species in Provo Bay and Farmington Bay also depend on phragmites, including several Odonata taxa (dragonflies and damselflies), aphids, spiders, beetles and bugs, to name a few (personal observations).

Phragmites allelopathic chemicals can reduce algal blooms

Phragmites is known to produce allelopathic chemicals that reduce interspecific competition from other plants, including algae. Provo Bay and Farmington Bay have massive algal blooms during summer, including potentially harmful cyanobacteria blooms. Algal blooms are often non-existent within phragmites stands except during the most severe blooms. Water clarity is much better within stands than out, which I attribute more to allelopathic chemicals than to reduced wind induced sediment disturbance and have much lower levels of algae within (unpublished data).

Phragmites and Other Wildlife

The thick stands of phragmites in Provo Bay and Farmington Bay cover hundreds of acres and provide shelter and cover for many mammals, small and large. Native mule deer populations in Utah and throughout the west are in decline and what was once prime mule deer habitat in these highly urbanized areas now supports relatively few and small populations. However, mule deer survive in Provo Bay and Farmington Bay wetlands in part due to the security provided by dense stands of phragmites. Remaining agriculture lands near the bays provide food resources for mule deer, while phragmites provides visual shelter from hunters. Utah is a recreational hunting culture. These small deer populations would be eradicated without this shelter. Several agencies are involved in restoration projects along the Jordan River that joins Utah Lake and Great Salt Lake and one of their goals is to provide habitat for mule deer. I have observed dozens of deer using phragmites on Provo Bay and Farmington Bay to safely move between other habitats. There are deer trails through all but the thickest stands. I have personally observed other mammals utilizing phragmites include; beaver, muskrat, skunk, coyote, mink, voles, and other rodents. Amphibians also thrive in phragmites stands in the bays. Boreal Chorus Frogs occur by the millions and use the stands for mating and egg laying; their croaking during mating gets so loud at times that it can drown out the sounds of low flying commercial jets at Salt Lake City airport. Threatened Columbia Spotted Frog and the invasive American Bullfrog also thrive in phragmites during high water. Hundreds of flocking birds such as grackles and starlings utilize the thick phragmites stands to feed and avoid harriers, falcons, and other raptors, even during the coldest winter days. Several species of waterfowl rely on security and food resources provided by phragmites stands to nest and raise young including; American coots, Canada geese, and mallards. Great Horned owls and other owl species patrol phragmites at night for small rodents in Provo Bay and Farmington Bay. Even though it is virtually a monoculture within phragmites stands; the ecosystem is alive with life.

Phragmites and Nutrient Removal

The second biggest threat to the Provo Bay and Farmington Bay ecosystems, real or perceived, is nutrients. Water quality agencies including Utah Division of Water Quality and USEPA have been focusing their attention on reducing nutrient inputs into these bays. However, phragmites is the number one reducer of nutrients into the bays. We have documented at least a tenfold reduction of phosphorus in water treatment effluent as it passes through phragmites wetlands and enters into Provo and Farmington Bays. Phragmites also uptakes excessive nutrients from the soil and stores them as plant material. Point and non-point sources of nutrients may be contributing to algal blooms in the bays and phragmites is by far the most cost-effective method of reducing these sources of nutrients.

Adaptive Phragmites Management: A Holistic Approach

Poorly planned, poorly enacted, poorly coordinated, and myopic phragmites management in the Jordan River drainage is a problem. Multiple government agencies from city to county to state to federal and numerous 'commisions' have differing agendas when it comes to managing phragmites. The most common methods used in the drainage are mowing, crushing, spraying with herbicides, and grazing by cattle with very little coordination between agencies and with no formalized plan as to how best revegetate with native species. The mantra by government agencies in Utah is; 'phragmites is bad and it must be eliminated'. Most citizens that I discuss phragmites with tend to think phragmites is not a problem and actually is esthetically pleasing, unless of course they are allergic to it. Obviously, the truth is somewhere in between.

Several promising approaches to managing phragmites include but are not limited to: grazing by cattle, harvesting as food resource for livestock, harvesting for cultural use by Native Americans, and boutique paper. Managers at the Farmington Bay Waterfowl Management Area near Salt Lake City are using cattle grazing to remove phragmites to improve shorebird and waterfowl habitat. Results are promising and it appears that once cattle have been introduced to Phragmites, they prefer it to other forage. It has been estimated that phragmites contains 18% protein which is higher than the most widely used cattle forage crop, alfalfa. Phragmites however is harder to digest than alfalfa and a simple remedy would be to harvest and produce easier to digest pellets. A business opportunity waiting to be implemented.

Continued harvesting of phragmites either by direct grazing or as a sustainable crop would remove nutrients tied up in the plants and thus remove nutrients from the soil and eventually reduce the impacts of nutrients on water quality and possibly reducing the intensity of harmful algal blooms. An estimated 1500 tons of ortho phosphates are released into Utah Lake annually from lakebed sediments alone (Hogsett et. al. 2019). Unpublished data from the Wasatch Front Water Quality Council has estimated that perhaps up to 500 tons or more are deposited annually on the lake from the atmosphere. There is also a legacy of natural and anthropomorphic nutrient overload in these wetlands. Sustainable harvest of phragmites is the most prudent management option for reducing nutrients in the wetlands and the waters of Utah Lake and Great Salt Lake.

Southern Utah continues to experience drought conditions, with the exception of 2019. Global climate change models predict continued and intensifying drought into the foreseeable future in southern Utah and the southwest. Native Americans, including Navajo, Ute Mountain, and Hopi Tribes are particularly hard hit by these droughts and often do not have enough water to grow forage for their livestock. Harvesting phragmites from Utah Lake and Great Salt Lake wetlands could easily meet Native American livestock needs. I have been in conversations with members of this tribe and they support this idea. In addition, Native Americans have used and continue to use native phragmites and other grasses for many items including baskets, housing material, food, medicine, and other uses. Adobe building material is composed of grass and mud and phragmites is an excellent adobe building material, including traditional Navajo hogans. Indeed, several Native Americans regularly make the trip from southern Utah to Provo Bay to harvest pickup truck loads of phragmites for multiple uses. Every effort should be made to increase these uses to benefit tribes and reduce impacts of invasive phragmites in wetlands.

Of course, phragmites has been used for centuries throughout the world to make paper. Boutique paper made from unique plant materials is a thriving business and phragmites harvested from Utah Lake and Great Salt Lake wetlands would be ideal start up to one or more entrepreneurial business minded citizens.

It is time for us to stop considering invasive phragmites as a nuisance and begin to utilize it as a crop to help meet the needs of our now universally altered analog ecosystems and promote sustainable economies where it has become established. Adaptive and holistic management of phragmites will require a landscape ecology perspective (e.g. patch dynamics vs. mono single species stands) and an unbiased understanding of its negative impacts and more importantly its beneficial ecosystem services that it now provides (Kiviat 2013).

Remaining Native Phragmites Stands and Unnecessary Introduction of Biocontrol Agents

There are very few remaining stands of native phragmites in the Jordan River drainage and southern Utah. They are ecologically, culturally, and esthetically important. These remaining stands need protection including that from invasive phragmites. However, introducing biocontrol agents to control invasive phragmites is not a rational idea given the management options that I have listed above and more importantly because: The literature is ripe with instances where introduced biocontrol agents either failed to control targeted invasives or had severe direct or Indirect negative effects on ecosystems (Simberloff and Stiling 1996a; 1996b; Strong and Pemberton 2000; Louda et al 2003; Louda 1997; Boettner 2000; Henneman and Memmott 2001; Louda and O’Brian 2002; Pearson and Callaway 2003). Once established it is near impossible to eliminate invasive species, including those used for biocontrol.

Managers consistently consider biocontrols as alternatives to controlling invasive species, including insect predators on wetland invasive plants. Introduced tamarisk beetles have had limited impact on invasive salt cedar in Utah, primarily due to misapplication and a poor understanding of the biocontrols ecology (Dr. Tim Graham, Moab, UT). In the case of releasing phragmites biocontrols, what is going to keep the biocontrols from spreading to native phragmites? (nothing). The Jordan River drainage and other parts of Utah where both native and invasive phragmites occur often get extremely windy and also have long periods of time with little or no winds. Given enough time, it is inevitable that insect biocontrols will be transported to native stands and their populations will become established in native phragmites stands, if they are released. Functional extinction of native phragmites would be a tragic loss to Utah's native ecological and cultural heritage. Much better options are available.

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