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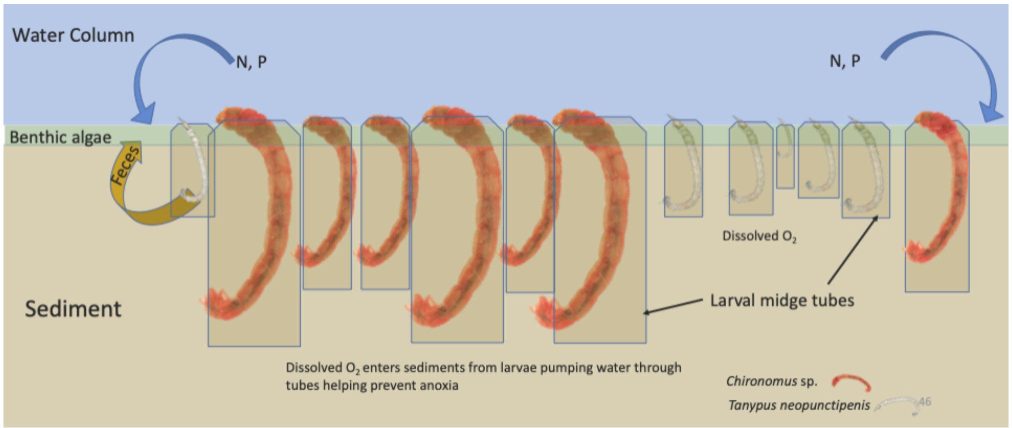
Chironomid Larvae: Under Appreciated but Essential Arbiters of Nutrient Mobilization and Cyanobacterial Bloom Dynamics in Utah Lake



Technical Report

To
Wasatch Front Water Quality Council

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Summary

Understanding nutrient fluxes between sediments and the water column in Utah Lake is critical to understanding causes of cyanobacteria blooms (HABs) and determining the most prudent management strategies for their control. Benthic invertebrates provide underappreciated but invaluable ecosystem services and are keystone taxa instrumental for the functioning of Utah Lake' ecosystem. Midge larvae 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 estimated to be from 700 to 3000 U.S. short tons that can be produced in just one summer month. By their sheer volume, biomass, secondary production, and ecology; midge larvae are the primary benthic/sediment ecosystem engineers responsible for much of the lake's benthic/sediment function and interaction with water column dynamics.

We calculated the rate of nutrient mobilization by midge larvae in Utah Lake using density estimates that we derived from data collected in 2016 and from published excretion rates for two dominant midge taxa, *Chironomus* sp. and *Tanypus* sp. The amount of nutrient mobilization by midge larvae as measured by excretion rates (tons yr^{-1}) was unexpectedly very high for both Utah Lake (without Provo Bay) and Provo Bay approaching estimates for entire lake sediment resuspension. Between ≈ 800 to 1000 tons of SRP and ≈ 3000 to 3700 tons of soluble N were mobilized (excreted) by midge larvae in Utah Lake in 2016.

In addition to nutrient mobilization, these tiny ecosystem engineers also affect whole lake ecosystem functions through several other mechanisms discussed in this report, including mutualistic- positive-feedback- loops between midge larvae, nutrients, and algae and trophic cascades. This simple analysis revealed that without a holistic knowledge of how the benthic ecosystem functions and interacts with nutrients, algal production, and the water column environment, there is no reason to believe that a prudent management strategy to control cyanobacteria blooms in Utah Lake can be achieved.

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Introduction

Understanding nutrient fluxes between sediments and the water column in Utah Lake is critical to understanding causes of cyanobacteria blooms (HABs) and determining the most prudent management strategies for their control (DWQ Utah Lake Science Panel, WFWQC scientists, and others). However, little or no research or consideration of the critically important role of benthic invertebrates in nutrient fluxes from sediments to water column cyanobacteria has been conducted other than the Wasatch Front Water Quality Council (WFWQC) and OreoHelix Ecological (Richards and Miller 2019, Richards and Miller 2017).

Benthic invertebrates provide underappreciated but invaluable ecosystem services and are keystone taxa instrumental for the functioning of Utah Lake' ecosystem (Richards and Miller 2019, Richards and Miller 2017). They are the major biological link between sediment and water column chemistry, nutrient cycling, benthic algae, phytoplankton, and Utah Lake's food web including carp, game fish, June suckers, waterfowl, shorebirds, etc. It has become clear that several dominant benthic taxa, primarily chironomids (midges) (Class Insecta, Family Chironomidae), can play a key role in the timing and intensity of harmful algal blooms (HABs) in the lake (Richards and Miller 2019, Richards and Miller 2017, Hölker et al. 2015).

Midge larvae 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 estimated to be from 700 to 3000 U.S. short tons that can be produced in just one summer month (Richards and Miller 2017). By their sheer volume, biomass, secondary production, and ecology; midge larvae are the primary benthic/sediment ecosystem engineers responsible for much of the lake's benthic/sediment function and interaction with the water column (Richards and Miller 2019, Hölker 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 nutrient recycling and consequently cyanobacteria blooms.

Justification

We reported how chironomid (midge) larvae can regulate cyanobacteria blooms in Utah Lake via oxygenation of sediments from their filtering actions within their tubes (Richards and Miller 2019, Richards and Miller 2017, Holker et al. 2015). We now present in this technical report estimates of midge larval sediment nutrient mobilization rates based on published excretion rates and density estimates made by us in 2016. We then discuss interactions between nutrient mobilization and our previous findings on midge larvae ecosystem function, and how these interactions can affect water column nutrients, and cyanobacteria blooms. A holistic understanding of nutrient fluxes between sediments and water column in Utah Lake, including its biological components, is critical to understanding causes of cyanobacteria blooms and for scientifically directing the most prudent management actions.

Methods

Sampling and Taxonomy

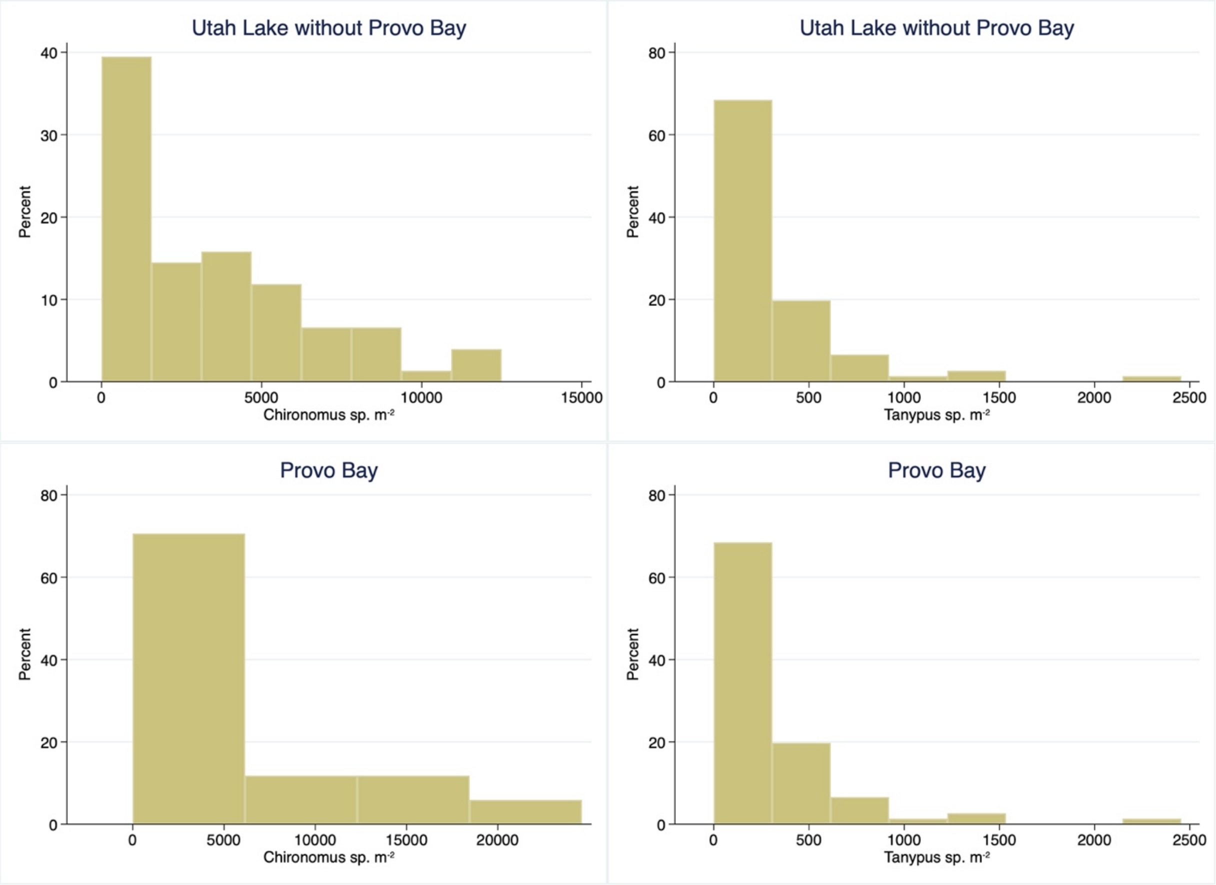
Ninety-three (93) benthic macroinvertebrate samples were collected between June and November 2016 at various locations in Utah Lake (see Richards and Miller 2019 for locations, dates, and sampling methods). Dr. Larry Gray (deceased), a leading expert on macroinvertebrates in Utah Lake, formerly at Utah Valley University, identified the taxa and estimated abundances and wet weight biomass. He also determined and grouped instar counts and biomass for two of the chironomid taxa, *Chironomus* sp. and

Tanypus sp. Density estimates were adjusted for all of Dr. Gray's results based on the sampling methods used. We have collected dozens more benthic invertebrate samples over the past several years however, those results have not been compiled and were not used in this analysis[1].

Statistical

Descriptive statistics and histograms of the densities of the larval stages of two midge taxa, *Chironomus* sp. and *Tanypus neopunctipeni*s were conducted (N = 93 benthic samples) separately for Provo Bay samples (N = 17) and for the other locations in Utah Lake (N = 76). Statistics and histograms were conducted separately for the two sections of the lake due to Richards and Millers (2017) results revealing that midge larval densities were significantly different between the two areas and our understanding that Provo Bay ecologically functions much differently than the rest of the lake.

Histograms showed that midge larval densities were not normally distributed for either taxa at each site grouping, and as often the case for benthic invertebrate densities, followed a negative binomial distribution[2] (Figure 1).



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[1] Our 2016 benthic sampling was more extensive than subsequent years and provided a better understanding of spatial and temporal variation within a single year within the lake, however, midge population densities can vary by an order of magnitude or more from year to year (Herren et al. 2017), and we do not have sufficient sampling data to determine with certainty the variability between years. In addition, the urgency of presenting our findings to WFWQC, DWQ, ULSP, and others concerned with understanding factors involved in cyanobacteria blooms and their management in Utah Lake hastened these analyses and report.

[2] Densities are in fact count data, i.e., number (counts) of individuals per unit area. As such, standard statistical models based on Gaussian (normal) distributions should be used with extreme caution even after transformations. Statistical models that use Poisson or negative binomial distributions are more appropriate for count and density data.

Figure 1. Distribution of Chironomus sp. and Tanypus sp. densities (m^{-2}) in Utah Lake outside of Provo Bay and in Provo Bay. Distributions followed a non-normal, negative binomial distribution.

25th, 50th (median), and 75th centiles of densities were used in calculations for nutrient level mobilization rates because midge larval densities were not normally distributed. Herrren et al. (2017) calculated soluble nitrogen (combined $NH4^+$, $NO3^-$, and $NO2^-$) and soluble reactive phosphorus (SRP) excretion rates for *Chironomus* sp. and *Tanypus* sp. individuals. Their results estimated that *Chironomus* sp. excreted 1.05 µg/d ($\pm$ 0.19 SE) soluble nitrogen and 0.26 µg/d ($\pm$ 0.02) SRP. *Tanypus* sp. excreted 0.38 µg/d ($\pm$ 0.17) soluble nitrogen and 0.10 µg/d ($\pm$ 0.018) SRP. These values were used in the calculations presented in this report.

The following formula was used to estimate midge larval soluble nitrogen and SRP excretion rates in Utah Lake in 2016, reported as metric tons yr $^{-1}$:

$$\textbf{Nutrient excretion}_{n}\ \textbf{(tons yr}^{-1}\textbf{) = larval density}_{ij}\ \textbf{(m}^{-2}\textbf{) * excretion rate}_{ik}\ \textbf{(µg/d) * 1.0 x 10}^{-12}\ \textbf{(µg to metric tons) * surface area}_{l}\ \textbf{(m}^{2}\textbf{) *Days}_{m}$$

where,

n = nutrient type (soluble N or SRP),

i = midge taxon (*Chironomus* sp. or *Tanypus* sp.),

j = midge taxa specific densities for three estimates 25th, 50th, and 75th centiles,

k = taxon specific excretion rate estimates (-1 SE, mean, and +1 SE) from Herren et al. (2017),

l = estimated surface area[3], and

m = number of days (between 180 and 340 calculated at 10-day intervals).

This formula was applied to all combinations for each taxon separately, location separately and both taxa combined. Combined results for each subset of combinations (N = 153) were then bootstrapped 1000 times and means and 95% CIs were computed.

We used 180 to 340 days to estimate larval nutrient mobilization because larval activity occurs year-round, even under ice in Utah Lake. Although midge hatches (swarms) occur more often and at higher densities from spring to autumn during ice free days when air temps are at or above freezing on Utah Lake and water temperatures are more conducive to growth; larvae and adults are commonly active at subzero air temperatures (Carrillo et al., 2004). Adult midges have been observed swarming at -0.4 ^{0}C (Young 1969) and even at temperatures as low as -16 ^{0}C over Himalayan glaciers (Kohshima 1984). Dr. Richards has personally observed adult midge swarms on rivers at air temperatures well below freezing as long as there was open water. OreoHelix Ecological and WFWQC researchers have also observed successional growth changes in midge larval instars under ice cover in a Great Salt Lake wetland (unpublished data). The majority of ice cover came off of Utah Lake somewhere around January 15, 2021 (Dr. Richards personal observation), earlier than ever observed by either of the authors. We expect scattered midge (adult) hatches to start occurring within the next several weeks.

Adult hatches and swarms, and successional larval instar growth during winter months demonstrates that midge larvae are actively feeding, growing, and excreting nutrients throughout the year in the lake. Midge larvae only defecate while feeding and the length of interval between successive defecations is proportional to the amount of food eaten. We suggest that larval food resources are not limiting in hyper eutrophic Utah Lake at any time during the year. Subsequently, the range in days used in our calculations and nutrient mobilization rates should be considered conservative.

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[3] Estimated surface area for Provo Bay = 15,000,000 m^2 and 323,126,689 m^2 for Utah Lake minus Provo Bay using polygon area estimation from Google Earth Pro satellite image dated July 18, 2019.

Results

The amount of nutrient mobilization by midge larvae as measured by excretion rates (tons yr^{-1}) was unexpectedly very high for both Utah Lake (without Provo Bay) and Provo Bay (

) approaching estimates made by Hogsett et al. (2019), for entire lake sediment resuspension (≈1500 tons yr^{-1} P). Between ≈ 800 to 1000 tons of SRP and ≈ 3000 to 3700 tons of soluble N were mobilized (excreted) by midge larvae in Utah Lake in 2016 (

). Midge density estimates are in Table 2.

Table 1 Midge larvae nutrient mobilization (excretion) in Utah Lake (without Provo Bay) and Provo Bay in 2016. Values are in metric tons. N = 153 values for each estimate; Bootstrapped 1000 times. Mean and 95% CIs reported.

Provo Bay			
	***Chironomus* sp.**	***Tanypus* sp.**	**Total**
SRP	30 (26, 33)	11 (10, 12)	41 (36, 45)
Soluble N	119 (106, 133)	28 (25, 32)	147 (130, 165)
Utah Lake			
	***Chironomus* sp.**	***Tanypus* sp.**	**Total**
SRP	636 (563, 709)	235 (206, 264)	872 (767, 977)
Soluble N	2570 (2258, 2881)	612 (535, 690)	3183 (2806, 3558)

Table 2. Chironomus sp. and Tanypus sp. density estimates (25th, 50th, and 75th centiles) from 93 samples collected in Utah Lake in 2016 (see Richards and Miller 2017 for more detailed information).

	Utah Lake		**Provo Bay**	
	Chironomus sp.	*Tanypus* sp.	*Chironomus* sp.	*Tanypus* sp.
50th	2605	200	3531	861
25th	646	43	528	344
75th	5489.5	379.5	6458	3600

Discussion

Our estimates of nutrient mobilization from midge larval excretion were based on several simplifying assumptions including constant excretion and flux rates, as estimated from the Herren et al. (2017) excretion assays, and that chironomid densities (and size structure) remain relatively constant. Midge larval densities used in this report are likely low-end accurate but not precise because midge densities can vary by several orders of magnitude annually in Utah Lake. For example, Thorbergsdóttir et al. (2004) reported that chironomids occurred at densities >500,000 m^{-2} in the benthos of Lake Mývatn (Midge Lake), Iceland that has an abundant and diverse food web (Einarsson et al. 2002) and that the lake's midge densities fluctuated over 3–4 orders of magnitude but routinely reached very high densities, comprising >90% of secondary production (Einarsson et al. 2002, Ives et al. 2008). Herron et al. (2017) reported that it was evident that, in supporting this large amount of chironomid biomass, algal growth rates were able to keep pace with the grazing pressure of these primary consumers in Lake Mývatn. Our estimates of midge larval density in Utah Lake in 2016 of a median of 7197 m^{-2} (1561 to 15,927) (

) is about 70 times less than that reported for Lake Mývatn, even though Utah Lake is eutrophic to hyper eutrophic with extremely high primary production rates that occur over longer periods throughout the year than does high latitude Lake Mývatn that has a much shorter growing season. Given the low-level intensity and inconsistency of benthic invertebrate surveys in Utah Lake, we do not know if 2016 was an abnormally poor year for midge populations or if these densities are typical. Several reasons can explain why midge population densities appear to be low compared to other eutrophic lakes: 1) high densities and biomass of benthivorous fish (i.e., carp, catfish, etc.) feeding on midge larvae and bioturbation from these fishes, 2) wind driven sediment disturbance (turbidity) due to the lake's shallow condition, 3) shading of benthic algae from phytoplankton blooms, 4) Utah Lake is a highly regulated reservoir and cannot function naturally, and 5) low abundance point in midge population cycle in 2016, 6) other unmeasured pollutants entering the lake. Still, our nutrient mobilization estimates further demonstrate the potential for chironomids to influence whole-ecosystem processes within Utah Lake (Hölker et al. 2015, Herron et al., 2017). Similarly, prior research has found that chironomids may have a substantial impact on benthic nutrient cycling even at densities of only 1,000 m^{-2} (Tátrai 1988).

The following is an illustration of how Utah Lake's ecosystem components interact to regulate turbidity (Hölker et al. 2015).

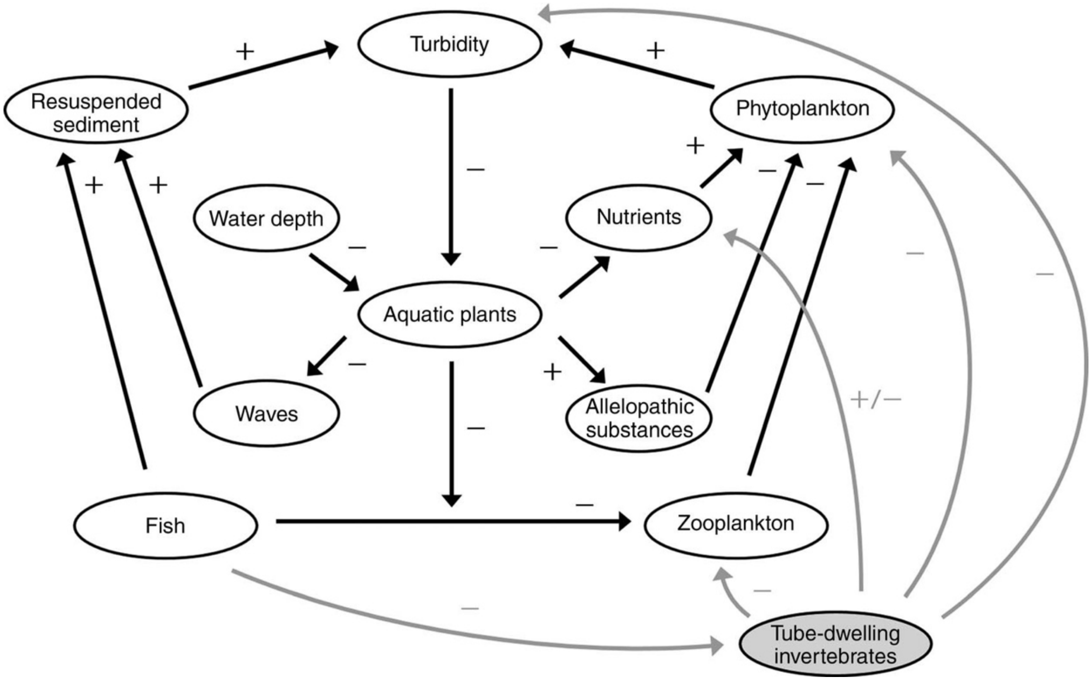

Figure 2. Interactions and feedbacks in a lake ecosystem concerning water turbidity, including the (partly unknown) effects of tube-dwelling invertebrates (in gray) that may cause alternative equilibria. Both turbidity and aquatic plants have a positive effect on themselves through different feedback loops, of which several are influenced by tube-dwelling invertebrates (figure modified from Scheffer et al. [1993]).

Cyclic patterns of midge populations also can affect zooplankton assemblages and subsequently cyanobacteria blooms. Einarsson and Örnólfsdóttir (2004) concluded that by over exploiting the detrital resource, midge larvae not only cause their own population declines (e.g., initiating a decadal population cycle) but can also alter exploitative competition between small-bodied zooplankton and juveniles of large-bodied zooplankton leading to the suppression of the latter, which subsequently may lead to increased cyanobacteria blooms. Ersoy et al. (2017) concluded that, highly variable cyclic and semicyclic occurrences of cyanobacteria blooms in Lake Mývatn (Einarsson et al., 2004) concurred with the cycles of zoobenthos and that blooms appeared during years when the chironomid population collapsed that triggered high internal loading of phosphorus from the sediment (Einarsson and Örnólfsdóttir 2004).

Chironomid larvae not only consume benthic algae, but also consume detritus, typically comprising 30–50% of their diet (Einarsson et al. 2004, Ingvason et al. 2004) subsequently also mobilizing nutrients stored in decaying organic matter and diatom fragments (Herren et al. (2017).

We suggest that benthic algal production is light limited at certain times of year within Utah Lake. Light limitation can affect midge diets, nutrient sediment-water column fluxes and interactions with cyanobacterial blooms. We cited Scheffer et al. (1993) in several of our reports showing that cyanobacteria blooms can shade other phytoplankton and dominate algal assemblages. Algal blooms also shade benthic algae and reduce benthic algal production. Light penetration (as measured by Secchi depth) is insufficient to reach benthos in the lake even in shallow Provo Bay for a large portion of the year (unpublished data). This is due to overabundance of easily suspended fine sediments and heavy algal blooms. Midge larvae likely switch a portion of their diets away from benthic algae to detritus and to diurnal phytoplankton that migrate to the bottom of the lake during these times. Midge larvae are excellent filter feeders and actively pump phytoplankton through their tubes ((Hölker et al. 2015, Herron et al., 2017, Richards and Miller 2019, Richards and Miller 2017). The combination of phytoplankton filter feeding, benthic algal consumption, and sediment nutrient mobilization by midge larvae results in what has been described as a mutualistic- positive- feedback- loop (Hölker et al. 2015, Herron et al., 2017, Richards and Miller 2019, Richards and Miller 2017).

One of our most important findings for a Farmington Bay wetlands food web was that it consisted of mutualistic positive feedback loops between the consumers (i.e., midge larvae) and the producers (benthic algae and phytoplankton) (Richards et al., 2020). These insights were edified by Herren et al. (2017) in the journal Ecology and were cultivated by our research. These same loops also likely occur in Utah Lake.

The positive feedback loop in Utah Lake is primarily the mutualism between midge larvae and benthic algae (Figure 3). Midge larvae were by far the most dominant benthic invertebrate in the Utah Lake as measured by density and biomass in 2016. This positive mutualistic feedback loop between nutrients, benthic algae, and midge larvae is essential. Herren et al. (2017) showed that as midge larvae densities increase, algal production increases and consequently larval growth rates increase as their densities increase, likely because of the increase in algae, i.e., the positive feedback loop. We suggest that cyanobacteria blooms would likely occur more frequently and at higher densities without this positive feedback loop controlling mechanism in the lake.

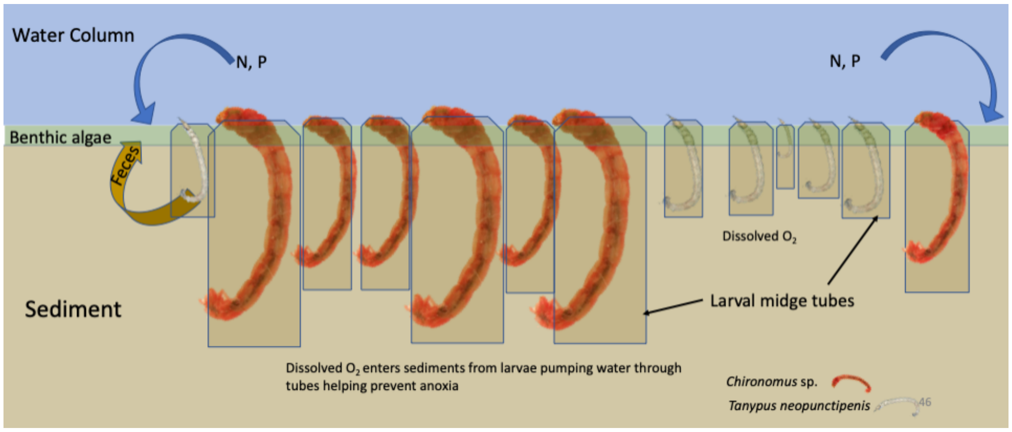

Figure 3. Simplified illustration of the hypothesized mutualistic positive feedback loop between midge larvae, benthic and water column algae, and nutrients in Utah Lake. Please review Herron et al. (2017) for a detailed description of how this loop functions.

Conclusion

The Utah Lake ecosystem is obviously impaired and out of balance. It is a shallow, eutrophic, highly regulated reservoir whose sediment and water column ecosystem functions and interactions cannot be separated. Without a holistic knowledge of how the benthic ecosystem functions and interacts with nutrients, algal production, and the water column environment, there is no reason to believe that a prudent management strategy to control cyanobacteria blooms can be achieved. This simple analysis presented in this report showed how the underestimated importance of tiny ecosystem engineers, chironomid (midge) larvae, are to sediment and water column nutrient mobilization via excretion, their role in phosphorus release from sediments into the water column, and how they can affect cyanobacteria blooms in mutualistic positive feedback loops throughout Utah Lake.

Recommendations

1. It is imperative to increase benthic invertebrate sampling to 2016 levels in order to determine densities that can vary several orders of magnitude annually. This technical report was only based on one year's data and may not be fully representative of benthic invertebrate population abundances and densities.

2. Conduct laboratory studies to measure excretion rates at different temperatures and nutrient levels. Compare with rates from ongoing foodweb studies on the North Davis Sewer District effluent dominated Farmington Bay wetland.

3. Incorporate findings into ongoing food web model development and compare with FB wetland food web.

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Appendices

Appendix 1. Midge larvae ecosystem function and cyanoHABs sections 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 and 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 4 (taken from Molot et al. 2014) illustrates this concept.

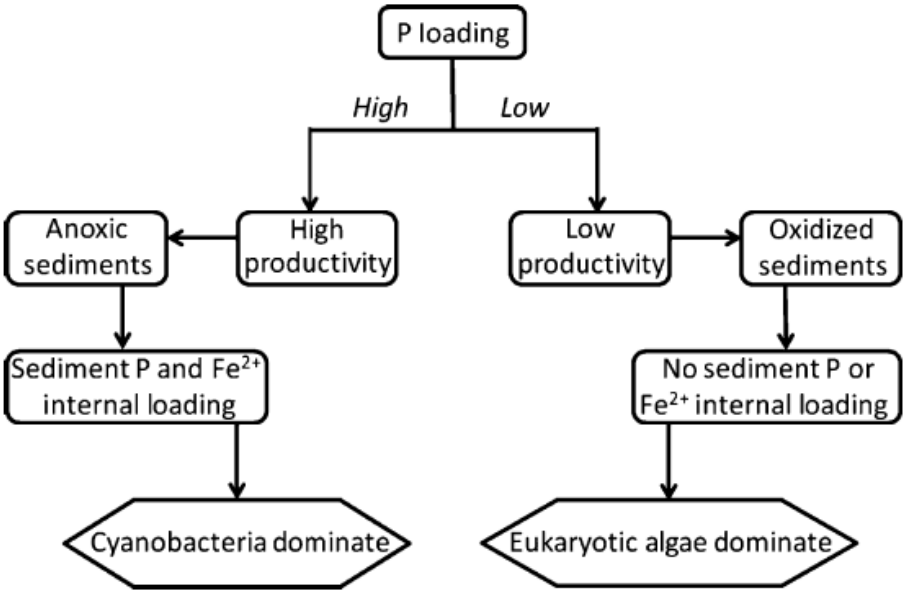

Figure 4. Simplified conceptual diagram of the modified phosphorus eutrophication model of cyanobacteria bloom formation for systems lacking naturally anoxic surficial sediments. The only factor controlling Fe^{2+} production shown here is anoxia at the sediment water interface.

Figure 5 (taken directly from Molot et al. 2014) illustrates the processes that promote Fe delivery to cyanobacteria and thereby promote cyanobacteria dominance in lakes.

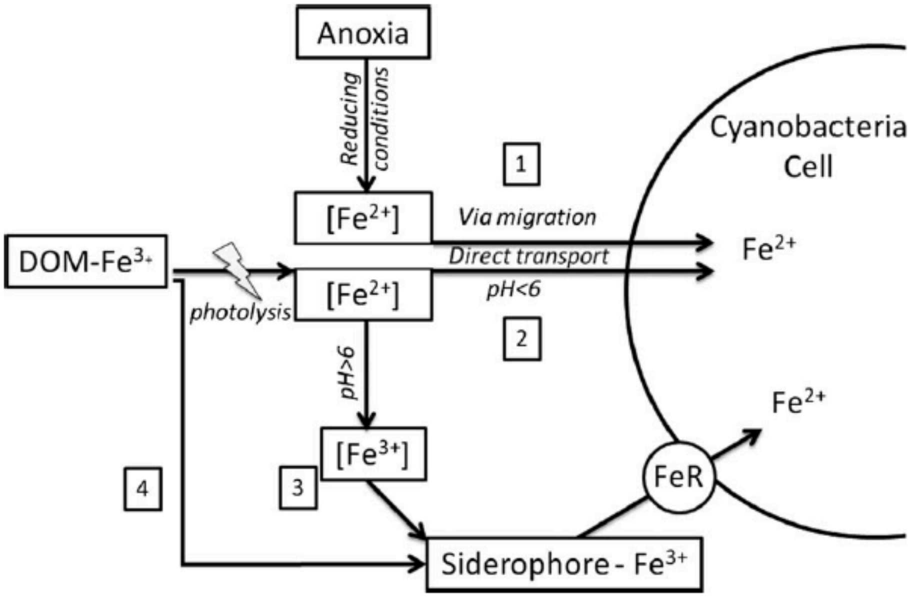

Figure 5. Anoxia: systems with anoxic sediments will experience Fe^{2+} flux into anoxic waters. Migrating cyanobacteria can acquire Fe^{2+} for direct transport into cells. (2) Photoreduction: DOM-Fe^{3+} can be photo-reduced, giving rise to Fe^{2+} that is available for direct Fe^{2+} transport into 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 6). 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 6).

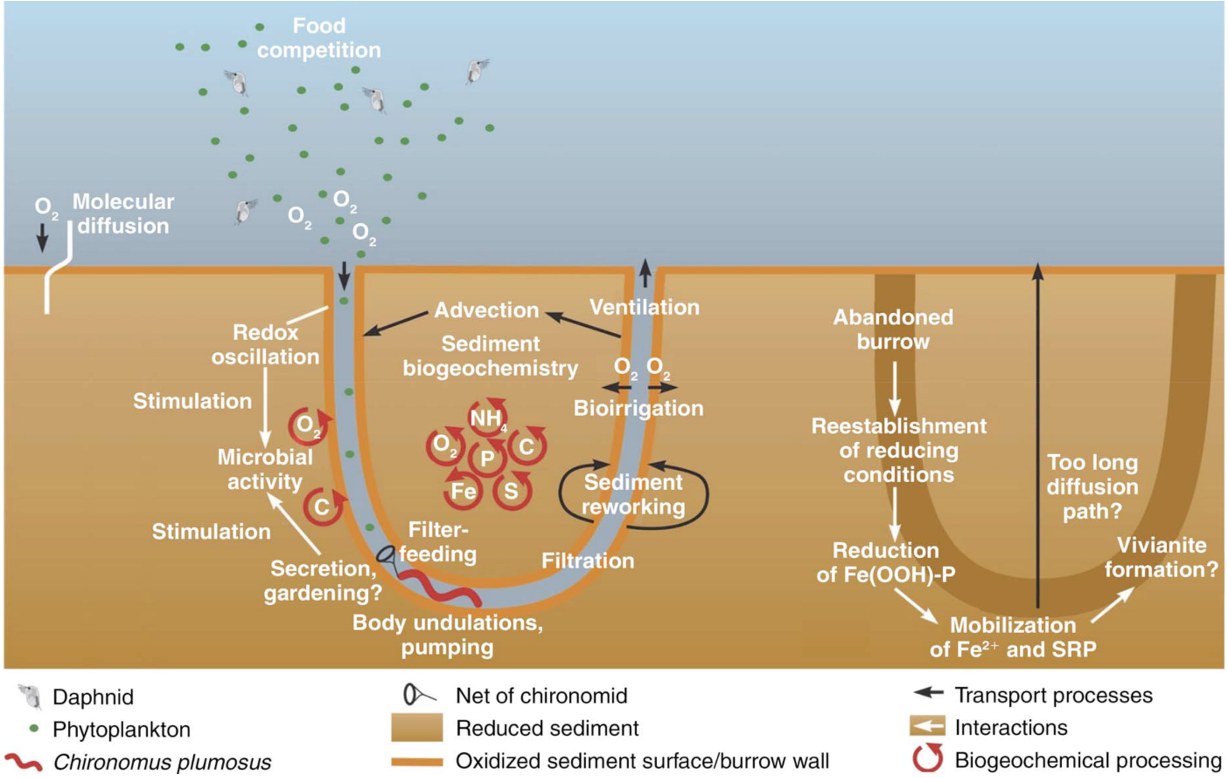

Figure 6. From: Holker et al. 2015. Tube-dwelling invertebrates: tiny ecosystem engineers have large effects in lake ecosystems

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 7) and before females release eggs back into the lake.

Figure 7. 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 8) and are nothing compared to densities and swarms that can occur in Lake Myvatn, Iceland[4].

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[4] Lake Myvatn literally translates to Midge Lake.

Figure 8. 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 9).

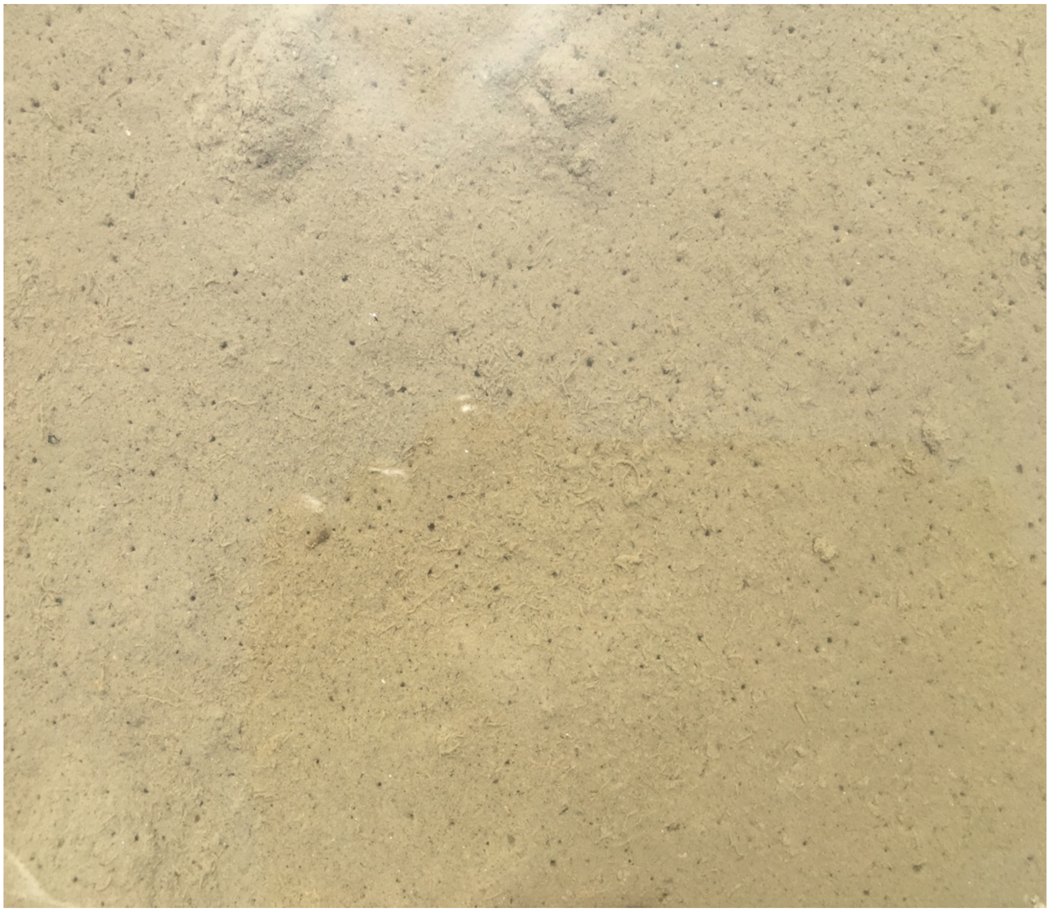

Figure 9. Thousands of different midge larval instar tubes in Provo Bay, Utah Lake. These larvae help stabilize the easily disturbed substrate, provide three-dimensional structure, and the larvae actively oxygenate the sediments including Fe near the sediment water boundary layer. Tubes are likely either 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 10).

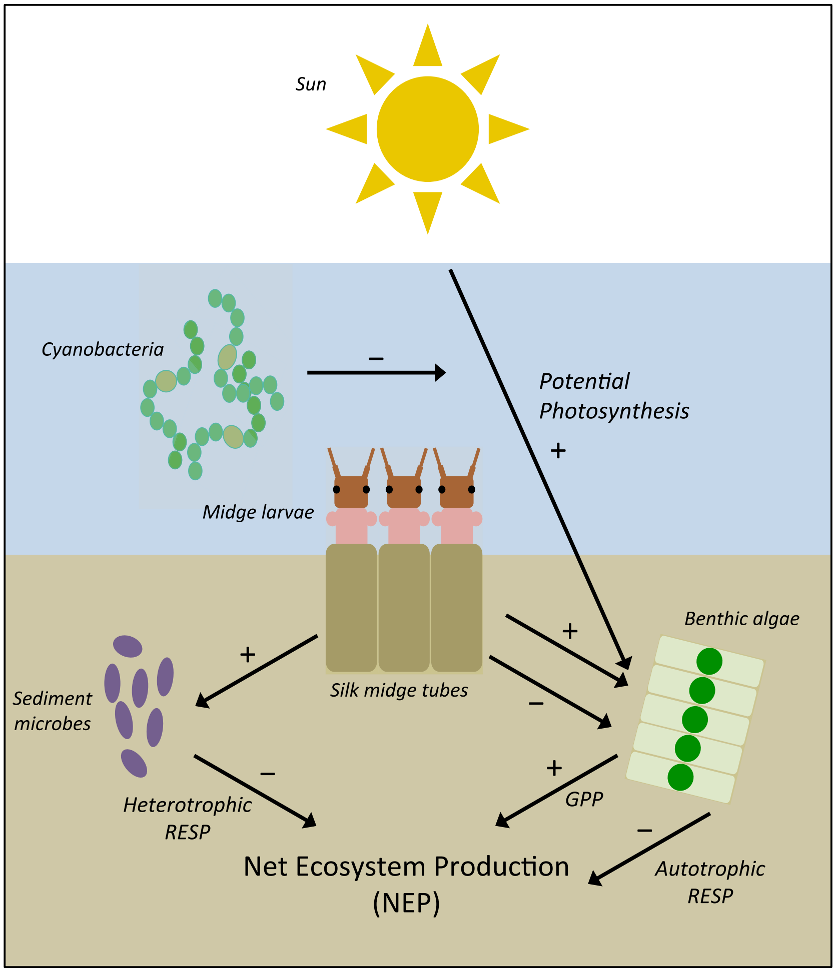

Figure 10, Midge larvae alter benthic ecosystem function. This figure and caption were taken from Philipps et al. 2019. "Midges can alter benthic ecosystem function. Larval midges build silk tubes that provide a substrate for algal growth and increase gross primary production (GPP) in the sediment. However, 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 10). 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.