Spatial and temporal trends of Minnesota River phytoplankton and zooplankton

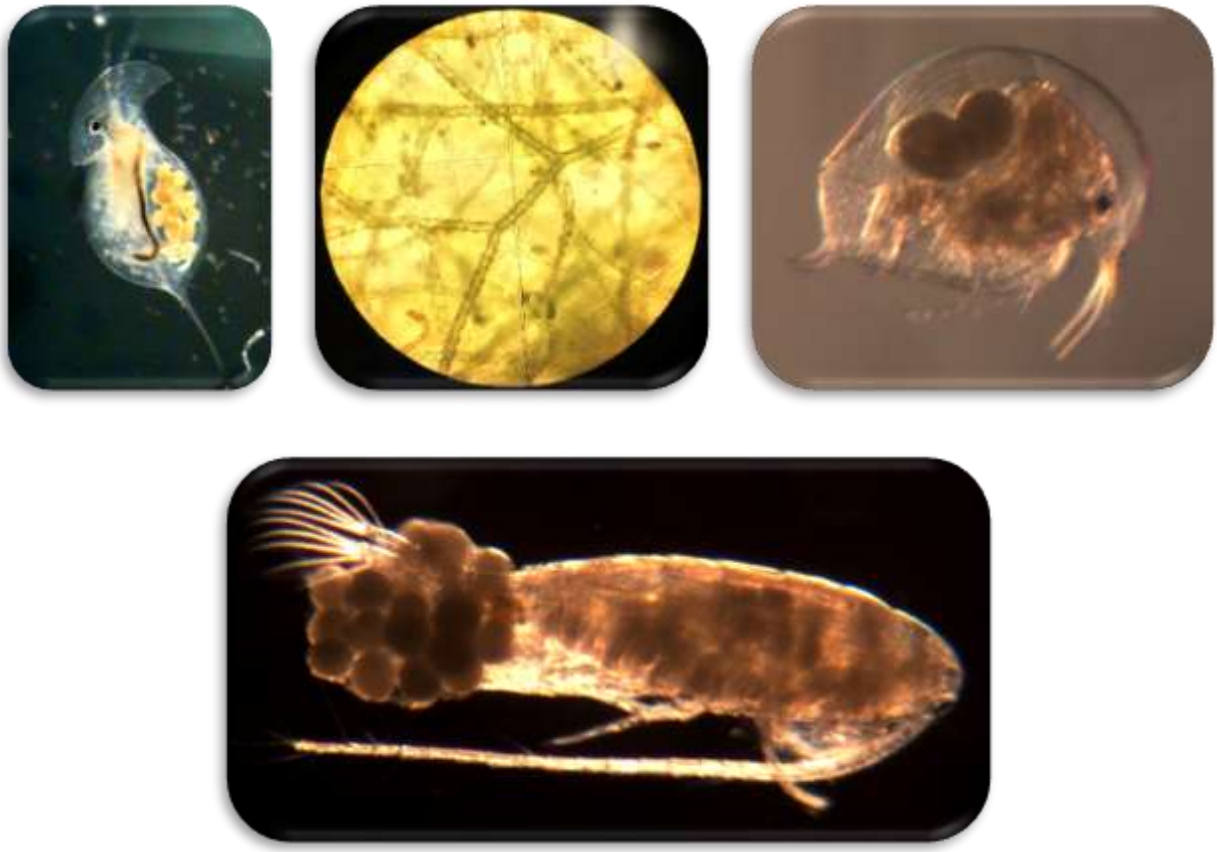

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Table of Contents

Executive Summary

Activity 1: Accelerate collection of baseline Minnesota River lower trophic data.

Project Objectives

- Establish baseline understanding of Minnesota River phytoplankton and zooplankton communities.
    - Quantify spatial and temporal trends in plankton communities.
    - Identify relationships between plankton communities and environmental parameters (e.g., water chemistry, discharge).

Significant Outcomes

- Minnesota River phytoplankton biovolume and zooplankton biomass significantly differs among months (temporally) and river kilometers (spatially).
    - Total zooplankton biomass and crustacean zooplankton biomass is greater at upstream sites than downstream sites.
    - We observed peak phytoplankton biovolume during July–October, primarily influenced by abundant blue-green algae.
    - We observed the greatest peaks in rotifer and copepod biomass during May and in daphnid biomass during October.
- Combining months and sites, mean phytoplankton biovolume was 20.4 mm^3 l^{-1}, mean cladoceran biomass was 26.4 µg l^{-1}, mean copepod biomass (excluding nauplii and copepodites) was 17.1 µg l^{-1}, and mean rotifer biomass was 6.1 µg l^{-1}.
- The Minnesota River has diverse plankton communities similar to other large Midwestern rivers.
    - 73 phytoplankton genera, 22 crustacean zooplankton genera, 24 rotifer genera.
    - Blue-green algae are the most abundant phytoplankton, including the *Aphanizomenon* and *Merismopedia* genera.
    - *Keratella spp*. are the most abundant rotifers.
- The occurrence of dams and impoundments has a significant influence on Minnesota River zooplankton communities.
    - Total zooplankton biomass is greatest at sites downstream of dams (mean biomass of 142.6 µg l^{-1} and mean density of 241.7 l^{-1} at river kilometers 424 and 385) where crustacean zooplankton are typically > 80% of the total zooplankton biomass.
    - At sites within the lower free-flowing reach of the Minnesota River (downstream of river kilometer 315), total zooplankton biomass is much lower (mean of 10.8 µg l^{-1} with mean density of 208.5 l^{-1}) and rotifers are typically > 60 % of the biomass.
    - Mean crustacean zooplankton density and biomass is 18.6 individuals l^{-1} and 135.6 µg l^{-1} at the two upstream sites and 0.9 individuals l^{-1} and 5.2 µg l^{-1} at the five downstream sites.
- Overall, spatial variability in plankton communities is strongly influenced by the occurrence of dams, but plankton communities also significantly differ among months which is likely driven by phenology and temporal variability in discharge.
    - Excluding the influence of dams, plankton communities do not significantly differ spatially within the lower free-flowing reach of the Minnesota River.
- Relationships between other abiotic factors (e.g., water temperature, total suspended solids) and plankton communities were generally weak or insignificant.
- Zooplankton communities in the lower-free flowing reach of the Minnesota River are similar to zooplankton communities described from the lower Missouri River, the lower Illinois River, and other turbid prairie rivers.
- Zooplankton communities in the upstream reaches, downstream of dams, are similar to those reported from the Mississippi River above and within Lake Pepin and from the Ohio River.

Resulting Hypotheses

- Establishment of invasive carps in the Minnesota River will likely shift zooplankton communities towards smaller species within reaches and habitats where crustacean zooplankton are abundant (i.e., rotifers).
    - A shift in zooplankton communities and competitive interactions with invasive carps may lead to declines in abundance and conditions of native planktivores (e.g., Bigmouth Buffalo).
- Increased flows resulting from changes in climate and land use will likely increase durations of reduced main channel phytoplankton biovolume.
- Increased flows are also likely to favor small bodied rotifers rather than large bodied crustacean zooplankton within the main channel of the Minnesota River.
- Natural impoundments may provide an important source of crustacean zooplankton for Minnesota River fishes.
- Plankton production within the Minnesota River floodplain is likely important to the overall dynamics of the Minnesota River ecosystem, providing important forage for higher trophic levels (e.g., fish).
- Natural flow regimes, including natural flood-pulses that connect the main channel with complex floodplain habitats, will facilitate the greatest species diversity and ecosystem health.

Abstract

Phytoplankton and zooplankton communities play important roles in aquatic ecosystems, but are poorly studied in lotic systems such as the Minnesota River. We collected > 100 water chemistry, phytoplankton, and zooplankton samples from seven locations along the Minnesota River during April–October 2016–2018 to establish a baseline understanding of phytoplankton and zooplankton communities, with emphasis on quantifying spatial and temporal trends and identifying relationships between plankton communities and environmental parameters (e.g., water chemistry, discharge). As hypothesized, phytoplankton and zooplankton communities were diverse and significantly differed among both months (i.e., temporally) and sites (i.e., spatially). Blue-green algae and diatoms dominate Minnesota River phytoplankton communities and we observed annual peaks in blue-green algae biovolume during July–October and diatom biovolume during both spring and fall. The presence of dams strongly influenced zooplankton communities with the greatest biomass of crustacean zooplankton at sites downstream of dams while rotifers dominated zooplankton assemblages at sites within the free-flowing reaches. Excluding the influence of dams, the most important factors influencing plankton communities are likely seasonal phenology and temporal variability in river discharge. Water chemistry parameters had insignificant or weak relationships with plankton community dynamics. Invasive species, climate change, and land-use alteration are hypothesized to influence the lower trophic ecology of the Minnesota River, and because of baseline datasets collected during this study, we now have the ability to quantify and understand future changes resulting from these and other perturbations.

Introduction

Riverine ecosystems support important biodiversity that provide valuable ecosystem goods and services including recreation opportunities, commercial fisheries, and sustenance. Lower trophic organisms, including phytoplankton and zooplankton, are important components of aquatic ecosystems that serve as vital links in the aquatic food web. Phytoplankton are an important source of primary production for the autochthonous lotic food web while zooplankton are primary and secondary consumers that serve as important food for higher trophic levels, including most fish species (Thorp and Delong 2002; Nunn et al. 2011). Furthermore, plankton are a vital component of carbon cycling in large river ecosystems (Thorp and Delong 2002; Winemiller 2004). Although phytoplankton and zooplankton are extensively studied in lentic systems, understanding of plankton community dynamics in lotic systems is less complete (Reynolds 2000). Generally in rivers, abiotic factors rather than biotic factors regulate plankton community dynamics because of the unidirectional force of river flow that constantly transports plankton downstream and influences light availability for primary production (Vannote 1980; Reynolds 2000; Lair 2006). River discharge (volume of water flowing through a channel per unit of time) is very dynamic, constantly changing both spatially and temporally, and consequently planktonic carrying capacity and communities are similarly variable and dynamic. Furthermore, unlike in most lentic systems, plankton community dynamics in flowing waters may be impacted by the influence of dams (and resulting impoundments; Havel et al. 2009) and floodplain connectivity (with floodplain lakes; Gorski et al. 2013). Other abiotic factors that

may influence plankton communities include current velocity, water residence time (e.g., Soballe and Kimmel 1987; Burdis and Hirsch 2017), nutrient availability (e.g., Soballe and Kimmel 1987), temperature (e.g., Gillooly and Dodson 2000), and turbulence (e.g., Sluss et al. 2008). For instance, some studies suggest nutrients (e.g., phosphorous) rather than hydrologic factors are the most important factors influencing phytoplankton in rivers (Soballe and Kimmel 1987; Basu and Pick 1996). All of the aforementioned factors can influence abundance, composition, and timing of phytoplankton and zooplankton communities which can have measurable impacts on aquatic food webs and the survival, growth, and recruitment of fishes (Cushing 1990).

The Minnesota River is an important aquatic resource with significant biological, cultural, recreational, and economic value. The Minnesota River watershed, and consequently the Minnesota River ecosystem, has been highly altered for agricultural and urban development purposes. Additionally, conservation efforts, land-use changes, climate change, artificial drainage, and invasive species continue to affect the Minnesota River ecosystem. For instance, heavy rainfall events are becoming increasingly common and discharge of the Minnesota River has significantly increased over time (Novotny and Stefan 2007). The threat of invasive carps (Bighead Carp *Hypophthalmichthys nobilis* and Silver Carp *Hypophthalmichthys molitrix*) expansion into the Minnesota River is of particular concern as they would have predatory impacts on plankton communities (e.g., Pongruktham et al. 2010) and potentially competitive interactions with native organisms such as Paddlefish *Polyodon spathula* and freshwater mussels. For example, research conducted on the Illinois River shows the zooplankton community shifted towards smaller species (i.e., rotifers) and condition and relative abundance of native planktivores (i.e., Bigmouth Buffalo *Ictiobus cyprinellus* and Gizzard Shad *Dorosoma cepedianum*) declined since the establishment of invasive carps (Sass et al. 2014; Pendleton et al. 2017). Zebra mussel *Dreissena polymorpha* infestation in the Minnesota River may also have negative impacts on the plankton communities by directly filtering out phytoplankton while competing with zooplankton for these resources (e.g., Caraco et al. 1997). Unfortunately, very little is known about how the Minnesota River ecosystem and organisms in lower trophic levels will respond to these potential changes, largely because dynamics of these taxa groups are poorly studied in the Minnesota River.

Several ecological concepts describe important features and processes that influence riverine ecosystems from longitudinal (i.e., upstream to downstream) trends in abiotic and biotic factors (Vannote et al. 1980) to the presence of dams (Ward and Stanford 1983), occurrences of flood-pulses (Junk et al. 1989; Bayley 1995), and connectivity with floodplain waterbodies. All of these features and processes have influences on plankton communities (Lair 2006) that have subsequent impacts on the aquatic food web (Power 1992). For instance, Havel et al. (2009) found proximity to upstream dams explained important variability in Missouri River zooplankton communities, highlighting the influence of dams on riverine plankton communities and the potentially important inputs of crustacean zooplankton from impoundments. Gorski et al. (2013) corroborated the hypothesis that connectivity with floodplains may govern zooplankton densities and community structure in large rivers by discovering greater abundance and varying composition of

zooplankton communities in floodplain lakes and inflow channels than in the main channel of a large temperate river. For the Mississippi River, Burdis and Hoxmeier (2011) similarly described the influence of a natural riverine impoundment on zooplankton communities along with differences in zooplankton communities between main channel and backwater habitats. These processes and characteristics presumably apply to the Minnesota River which has several dams and impoundments, a longitudinal gradient spanning over 500 river kilometers (rkm) from upstream to downstream, frequent flood-pulses, and a large complex floodplain that contains an abundance and diversity of floodplain waterbodies. These complex and intertwined physical features and processes influencing plankton dynamics increase the likelihood that changing hydrology resulting from changing land-use and climate will substantively impact Minnesota River plankton communities and the ecosystem.

The purpose of this study is to establish a baseline understanding of phytoplankton and zooplankton communities in the Minnesota River, with emphasis on quantifying spatial and temporal trends and identifying relationships between plankton communities and environmental parameters (e.g., water chemistry, discharge). Establishing a baseline understanding will aid in predicting and measuring future impacts of climate change, land alteration, conservation efforts, and invasive species while strengthening understanding of Minnesota River ecosystem processes. We hypothesize Minnesota River plankton communities will vary both spatially and temporally resulting from abiotic features and particularly hydrodynamics that similarly differs from upstream to downstream and through time. We also hypothesize the presence of dams and impoundments will amplify spatial variability in plankton communities while variable discharge and timing of connectivity with floodplain habitats may disrupt temporal trends and amplify temporal variability in plankton communities.

Methods

Study location

The Minnesota River flows approximately 515 rkm from Big Stone Lake on the Minnesota–South Dakota border to its confluence with the Mississippi River at St. Paul, Minnesota (1,358 rkm from the confluence with the Ohio River; Figure 1). The upstream 129 rkm reach of the Minnesota River contains 5 dams including the Lac qui Parle Dam at rkm 438 that impounds 2,323 ha Lac qui Parle Reservoir and the downstream most dam at rkm 386 which is a run of the river hydropower dam in Granite Falls, MN. Downstream of Granite Falls Dam the Minnesota River is an entirely free flowing seventh thru eighth-order (Strahler stream order) river flowing through the agriculturally dominated prairie region of southern Minnesota. The Minnesota River is a warm water river that is generally low gradient, productive, and turbid. For instance, at St. Peter, Minnesota (rkm 142, approximately half way between Granite Falls Dam and the mouth), mean discharge, total phosphorous, and total suspended solids were 178.9 m^3/s, 0.25 mg l^{-1}, and 127.0 mg l^{-1}, respectively, during 2007–2015 (Minnesota Pollution Control Agency; www.pca.state.us/wplmn, December 2018).

We evaluated Minnesota River plankton communities by collecting phytoplankton, zooplankton and water chemistry samples, and measuring physical parameters once per month at seven sites distributed along the longitudinal gradient of the Minnesota River during July–October

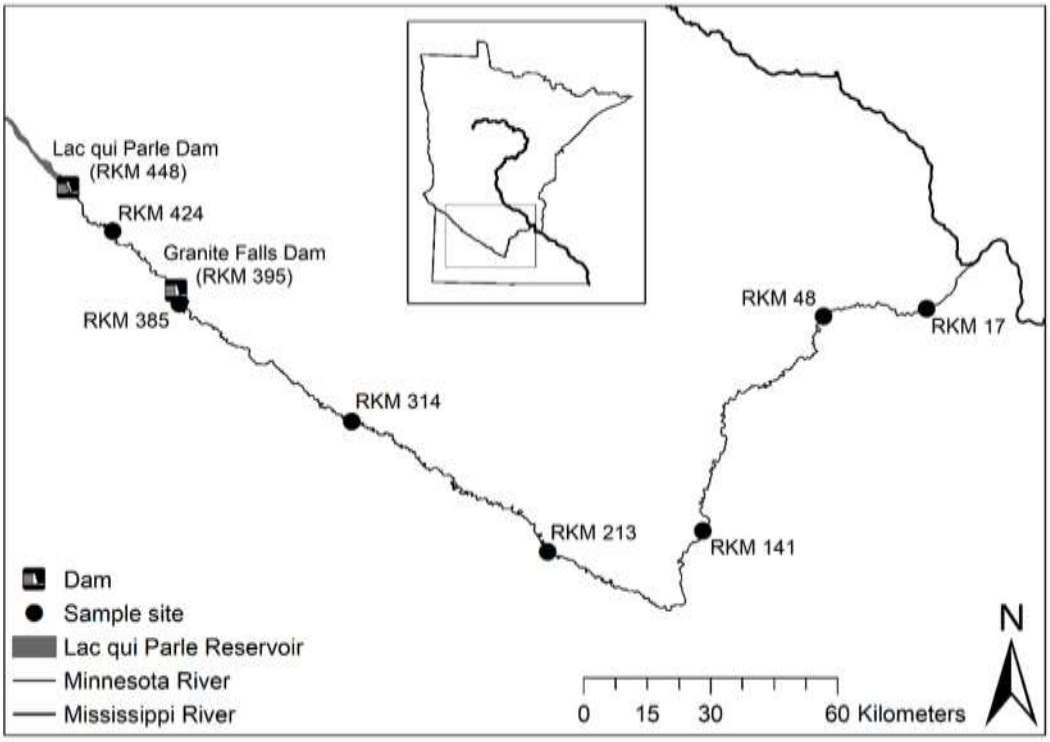

Figure 1. Location of seven Minnesota River sample sites and their corresponding river kilometer (rkm) where water chemistry, phytoplankton, and zooplankton samples were collected during July–October 2016, April–October 2017, and May–October 2018. The sample site at rkm 424 is 24 rkm downstream of Lac qui Parle Reservoir and sample site rkm 385 is 10 rkm downstream of Granite Falls Dam.

2016, April–October 2017, and May–October 2018. The upstream most site at rkm 424 is 24 rkm downstream of Lac qui Parle Dam and the second-most upstream site at rkm 385 is 10 rkm downstream of Granite Falls Dam. The remaining five sites are distributed throughout the lower free-flowing reach of river with two sites located upstream of the Blue Earth River confluence (rkm 167; largest tributary of the Minnesota River) at rkm 314 and 213 and three sites downstream at rkm 141, 48, and 17. On average, during the 10 years prior to this study (i.e., 2006–2015), mean daily discharge at the downstream most site was approximately four to five times greater than at the upstream most site (USGS Surface-Water Daily Data for the Nation; https://waterdata.usgs.gov/nwis).

Water chemistry samples

During each sampling event, we collected two water samples from an anchored boat near the mid-channel of each site for water chemistry analyses. We filled a 2.0-liter transparent bottle and a 2.0-liter opaque amber colored bottle with surface water from the upstream side of the boat after rinsing each bottle three times with river water. We immediately stored all water samples in the dark on ice and delivered to the Minnesota Department of Agriculture (MDA; St. Paul, MN) Laboratory Services within 48 hours for analyses.

Upon arrival to the MDA laboratory, samples were placed in a dark cooler until analysis. Chlorophyll a (Chl-a; µg l^{-1}) concentrations were determined using EPA Method 445.0 (Arar and Collins 1997) and total Kjeldahl nitrogen (TKN; mg l^{-1}) concentrations were determined using EPA

Table 1. Location (river kilometer) and name of USGS river gages associated with each study sites (river kilometer).

Site (rkm)	Gage name	Gage rkm
17	Fort Snelling	5
48	Jordan	64
141	Mankato	164
213	Judson	185
314	Morton	312
385	Granite Falls	394
424	Montevideo	424

method 351.2 (O'Dell 1993a). Total phosphorous (TP; mg l^{-1}) and ortho-phosphorus (Ortho-P; mg l^{-1}) concentrations were determined using colorimetry (EPA method 365.1; O'Dell 1993b). Nitrate/Nitrite (N+N; mg l^{-1}) and ammonia (Ammonia-N; mg l^{-1}) samples were analyzed using SM 4500-NO3F and SM 4500-NH3D, respectively (Eaton et al. 1998). Total suspended solids (TSS; mg l^{-1}) and total dissolved solids (TDS; mg l^{-1}) were analyzed using SM 2540, parts D and C, respectively (Rice et al. 2012). Silica (Si; mg l^{-1}) concentrations were measured using inductively coupled plasma mass spectrometry (EPA method 200.8; U.S. EPA 1992).

Prior to collecting water samples, we also recorded surface water temperature (°C) and measured Secchi depth (m) with a 60-cm turbidity tube. When water temperature or Secchi depth were not measured in the field, we calculated estimates by taking the mean of measured values from the nearest upstream site and nearest downstream site. However, during August 2018, all water temperatures were estimated to be 20.0°C. We obtained hydrograph data from the United States Geological Survey (USGS, https://waterdata.usgs.gov/nwis) for river gages near each sample site (Table 1).

Phytoplankton samples

We collected one integrated water sample from each site during each sample period for phytoplankton analyses. First, we rinsed a large container (e.g., 19 liter bucket) with river water. Next, we used a 2.5-meter long by 7.6-cm diameter clear PVC pipe with a one-way valve (approximate capacity of 12.5 liter after accounting for extra volume associated with the valve fitting) to collect an integrated water sample from the surface of the river to approximately 2.5 m depth. We emptied the sample into the large container, and then filled a 250-ml opaque amber bottle with approximately 230 ml of the integrated water sample. We then added 5–10 ml of Lugol's iodine solution (10 g potassium iodide, 5 g iodine, 10 ml acetic acid, and 100 ml distilled water) for sample preservation and refrigerated until samples were analyzed.

Once per year we shipped phytoplankton samples to BSA Environmental Services, Inc. (BSA; Beachwood, OH). BSA analyzed phytoplankton samples by preparing slides following a standard membrane filtration technique. Enumeration of phytoplankton occurred under compound microscopes equipped with epifluorescence with a majority of counting completed at 630× magnification. When possible, BSA enumerated at least 300 natural units to the lowest practical taxonomic level and estimated abundance of common taxa by random field counts. Biovolumes were estimated using formulae for solid geometric shapes that most closely match the cell shape. For each sample, BSA reported estimated densities (cells l^{-1}) and biovolumes (μm^3 l^{-1}) for each phytoplankton taxon identified.

Zooplankton samples

We collected zooplankton samples by filtering integrated water samples through a Wisconsin plankton net at each site during each sample period. During 2016, we used a

2.5-meter long by 7.6-cm diameter clear PVC pipe with a one-way valve (approximate capacity of 12.5 liters) to collect two integrated water samples from the surface of the river to approximately 2.5 m depth. We measured and recorded the volume of each integrated sample to the nearest 0.1 liter and filtered the water sample through a 20-µm plankton net. We rinsed contents of the plankton net into a 500-ml transparent bottle and diluted the sample to at least 70% reagent alcohol for preservation. During 2017 and 2018, we used similar methods except we collected three rather than two integrated water samples and filtered samples through a 53-µm rather than 20-µm plankton net in an effort to reduce the amount of sediment within each sample.

Jodie Hirsch (zooplankton specialist, Minnesota Department of Natural Resources) enumerated crustacean zooplankton by first adjusting sample volumes to a known volume, and then transferring 5-ml aliquots to a counting wheel. All zooplankters were identified to the lowest practical taxon, counted, and measured under a 25× magnification dissecting microscope with the aid of a computerized image analysis system. When an insufficient number of zooplankters were counted in one 5-ml aliquot (i.e., < 30), the entire sample was enumerated. Crustacean zooplankton biomass was estimated using taxa-specific length to weight regression coefficients obtained from Culver et al. (1985) and Dumont et al. (1975). For rotifer enumeration, samples were adjusted to a known volume and a few drops of Biebrich Scarlet/Erosin B stain was added to aid in identification. A 1-ml aliquot was obtained with a Hensen-Stempel pipette and placed onto a Sedgewick-Rafter cell. All rotifers were counted and identified to the lowest practical taxon under a compound microscope at 200× magnification.

We also collected replicate zooplankton samples from rkm 385 and rkm 17 for enumeration by BSA. We excluded these replicate samples from further analyses in this report. However, we calculated mean taxa specific rotifer biomass determined from samples processed by BSA (based on established length–width relationships) to estimate biomass of rotifers enumerated in the primary zooplankton samples (Table 2).

Statistical analyses

We initially evaluated spatial and temporal trends in water chemistry, environmental characteristics, phytoplankton biovolume, and zooplankton biomass by calculating means and standard errors among months (pooling data among sites and years) and among sites (pooling data among months and years) for all collected samples. We calculated mean phytoplankton biovolumes for each of seven divisions (Bacillariophyta, Chlorophyta, Chrysophyta, Cryptophyta, Cyanobacteria, Euglenophyta, Pyrrophyta) and mean zooplankton biomasses for five rotifer families (Brachionidae, Gastropodidae, Sychaetidae, Trichocercidae, other), seven cladoceran families (Bosminidae, Chydoridae, Daphniidae, Leptodoridae, Macrothricidae, Moinidae, Sididae), and four copepod groups (order Cyclopoida, order Calanoida, copepodites, nauplii).

Discharge is an important environmental driver of plankton dynamics and lotic ecosystems and is therefore an important variable to consider when evaluating Minnesota River plankton communities. Discharge follows an upstream to downstream gradient, making absolute discharge highly correlated with river kilometer and difficult to compare among locations in the river. For example, an absolute discharge of 200 m^3/s may be indicative of flood conditions at an upstream

Table 2. Mean biomass of rotifer taxa estimated from 20 replicate zooplankton samples processed by BSA Environmental Inc. (Beachwood, Ohio).

Rotifer taxa	Mean biomass (µg l^{-1})
Anuraeopsis genus	0.001
Ascomorpha genus	0.014
Asplanchna genus	2.426
Bdelloidea order	0.035
Brachionus genus	0.040
Cephalodella genus	0.025
Colurella genus	0.002
Encentrum genus	0.002
Euchlanis genus	0.109
Filinia genus	0.024
Gastropus genus	0.014
Kelicottia genus	0.007
Keratella genus	0.013
Keratella quadrata	0.073
Lecane genus	0.028
Lepadella genus	0.011
Mytilina genus	0.025
Notholca genus	0.018
Platyias quadricornus	0.040
Ploesoma genus	0.012
Polyarthra genus	0.029
Pompholyx genus	0.012
Synchaeta genus	0.012
Testudinella genus	0.014
Trichocerca genus	0.014
Trichotria genus	0.014
Unidentified	0.020

site, while indicative of seasonally low water conditions at a downstream site. For these reasons, we calculated relative discharge for more appropriate comparisons of discharge conditions among sites and sample events. Specifically, we calculated relative discharge as the percentile value of mean daily discharge for each day, relative to all mean daily discharges during the study period of July 1, 2016–October 16, 2018. We calculated relative discharge for each sample site based on hydrograph data obtained from the nearest river gage (USGS). Additionally, we identified the relative discharge quartile (low = 0.0–0.25, moderate low = 0.25–0.50, moderate high = 0.50–0.75, high = 0.75–1.0) associated with each sample for use as a discrete variable in multivariate analyses.

Before further evaluation of spatial and temporal trends with multivariate analyses, we identified correlated variables to prevent multicolinearity issues and identified potentially biologically relevant relationships among variables. We calculated Pearson correlation coefficients and corresponding *P*-values with R 3.4.3 (R Core Team, 2017) package PerformanceAnalytics 1.5.2 (Peterson et al. 2018) for all pairwise comparisons of abiotic variables (i.e., month, rkm, environmental variables, water chemistry parameters) and all pairwise comparisons of zooplankton taxa (with all rotifer taxa combined). We ln(x +1) transformed all variables except month, rkm, relative discharge, Secchi depth, and water temperature to increase normality of distributions. We considered Pearson correlation coefficients ≥ 0.60 with associated $P \leq 0.05$ indicative of strong relationships among variables. We then selected one variable from groups of highly correlated explanatory variables for inclusion in further analyses, unless we had important hypothesized justification for retaining multiple correlated variables. Additionally, we calculated Pearson correlation coefficients for pairwise comparisons among retained abiotic variables and retained plankton taxa variables.

We evaluated complex spatial and temporal patterns in Minnesota River plankton and relationships with environmental variables by calculating a Bray-Curtis dissimilarity matrix with ln(x +1) transformed phytoplankton taxa biovolumes (mm^3 l^{-1}) and zooplankton taxa biomasses (µg l^{-1}) associated with each sample collected during May–October of 2017 and 2018 (i.e.,

excluding data collected during August–October 2016 and April 2017). We visually interpreted Bray-Curtis dissimilarity matrices by plotting results of 2-dimensional non-metric multidimensional scaling (NMDS) analyses (Clarke 1993). For simplified visual interpretation, we performed NMDS analyses using total crustacean zooplankton biomass (sum of all crustacean zooplankton taxa biomasses excluding copepodites and nauplii), total rotifer biomass (sum of all rotifer taxa biomasses), and phytoplankton biovolume (sum of Bacillariophyta, Chlorophyta, Cryptophyta, and Cyanobacteria biovolumes) of each sample. We then used permutational multivariate analysis of variance (PERMANOVA) to examine effects of both continuous and categorical spatial (i.e., rkm), temporal (e.g., month), and environmental

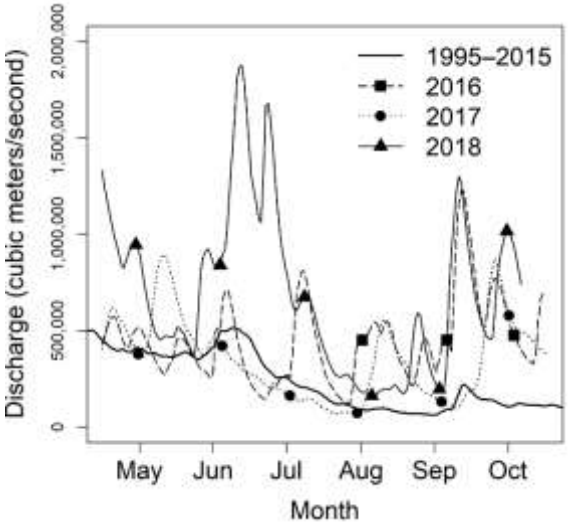

Figure 2. Mean daily discharge (m^3/s) of the Minnesota River at Mankato (river kilometer 164) during May–October of 2016–2018 along with mean historical daily discharge during 1995–2015. Symbols indicate the approximate date and discharge when water chemistry and plankton samples were collected from the Minnesota River during 2016, 2017, and 2018.

variables (e.g., relative discharge, chlorophyll a) on plankton communities (using the Bray-Curtis dissimilarity measure). Permutational multivariate analysis of variance is a geometric partitioning of multivariate variation in the space of a chosen dissimilarity measure (Anderson 2014). We plotted vectors on NMDS plots depicting the general direction of relationships associated with statistically significant ($P \leq 0.05$) continuous variables identified with PERMANOVA that had $r^2 \geq 0.10$. Finally, we further evaluated the influence of spatial, temporal, and relative discharge variables on only phytoplankton communities (taxa biovolumes), only zooplankton communities (taxa biomasses), and combined phytoplankton and zooplankton communities by conducting PERMANOVA with four datasets: 1) all samples collected during May–October of 2017 and 2018, 2) excluding samples collected from the two upstream most sites influenced by impoundments (rkm 385 and 424), 3) excluding the month of May when zooplankton biomass was greatest, and 4) excluding the two upstream most sites and the month of May. We performed multivariate analyses with the package vegan 2.5-4 (Okansen et al. 2019) in R 3.4.3 and accepted a 5% type I error rate (i.e., $\alpha = 0.05$).

Results

We successfully collected at least partial sample suites from all seven sites during July–October 2016, April–October 2017, and May–October 2018, totaling 112 sample events. During five sample events we collected samples from the bank rather than from a boat, and consequently we either failed to collect plankton samples (n = 2), collected only phytoplankton samples from the bank (n = 1), or collected both phytoplankton and zooplankton samples from the bank (n = 2). Discharge varied widely among sample periods and sample sites. For instance, at Mankato, MN (rkm 164; near sample site at rkm 141), hydrograph trends varied among years during the study period with discharge often exceeding mean discharge recorded

during 1995–2015 (Figure 2). Similarly, relative discharge at Mankato, MN, varied among sampling events, with relative discharge exceeding 0.5 during 10 of 15 sample periods (Figure 3). Relative discharge associated with each sample site during each sample period varied from 0.05 at rkm 213 during August 2017 to 0.97 at rkm 424 during October 2017 (Table 3). Mean water chemistry parameters, water temperature, and Secchi depth were similar when calculated from monthly means (pooled among sites) or site means (pooled among months) with several parameters differing spatially (e.g., TSS), temporally (e.g., chlorophyll a), or both (Tables 4 & 5; supplementary Figures S1–S24).

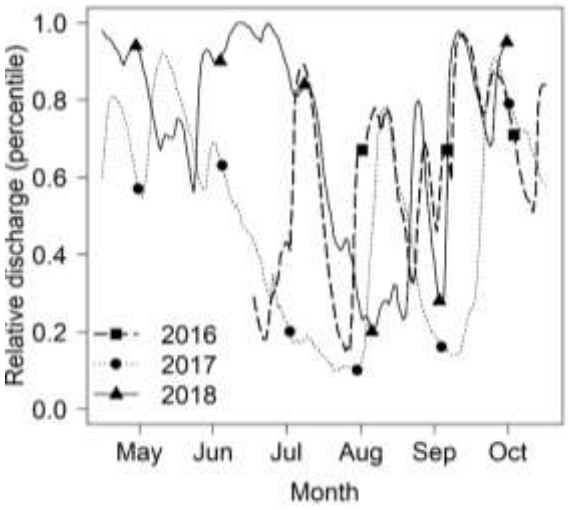

Figure 3. Relative discharge of the Minnesota River at Mankato (river kilometer 164) during May–October of 2016–2018. Symbols indicate the approximate date and relative discharge when water chemistry and plankton samples were collected from the Minnesota River during 2016, 2017, and 2018. Relative discharge is the percentile value of mean daily discharge relative to all mean daily discharge values during the study period of July 1, 2016–October 16, 2018.

During this study, Bacillariophyta (diatoms) and Cyanobacteria (blue-green algae) dominated the biovolume of Minnesota River phytoplankton, varying temporally from 6.33 ± 0.95 $mm^3 l^{-1}$ (mean ± SE) during October to 37.04 ± 5.47 $mm^3 l^{-1}$ during August and

Table 3. Relative discharge (percentile of mean daily discharge relative to the study period of 1 July 2016–16 October 2018) associated with each corresponding sample period (months May–October) and sample site (river kilometer) during the study years of 2016–2018.

River kilometer	May	Jun	Jul	Aug	Sep	Oct
			2016			
17				0.69	0.65	0.81
48				0.71	0.67	0.78
141				0.67	0.63	0.67
213				0.71	0.30	0.52
314				0.95	0.19	0.49
385				0.75	0.09	0.32
424				0.77	0.12	0.38
			2017			
17	0.62	0.50	0.21	0.06	0.14	0.88
48	0.58	0.59	0.18	0.09	0.15	0.84
141	0.55	0.60	0.17	0.10	0.15	0.78
213	0.62	0.65	0.14	0.05	0.21	0.88
314	0.63	0.72	0.17	0.16	0.26	0.89
385	0.48	0.72	0.10	0.10	0.26	0.96
424	0.56	0.81	0.13	0.13	0.36	0.97
			2017			
17	0.91	0.93	0.82	0.17	0.30	0.89
48	0.92	0.94	0.83	0.21	0.30	0.93
141	0.93	0.92	0.83	0.21	0.28	0.94
213	0.87	0.93	0.90	0.21	0.77	0.94
314	0.82	0.82	0.92	0.27	0.20	0.95
385	0.93	0.86	0.72	0.31	0.11	0.80
424	0.94	0.84	0.73	0.37	0.12	0.87

spatially from 14.45 ± 4.00 $mm^3 l^{-1}$ at rkm 213 to 30.75 ± 6.36 $mm^3 l^{-1}$ at rkm 424 (Tables 6 and 7). We sampled at least 73 genera of phytoplankton from the Minnesota River that also included genera of Chlorophyta, Chrysophyta, Cryptophyta, Euglenophyta, and Pyrrophyta (Table 8). Blue-green algae biovolume peaked during July–August and tended to be greatest at upstream sites while mean diatom biovolumes were greatest during May, August, and September (see supplementary Figures S25–S30).

Samples included diverse communities of zooplankton with at least 7 families and 14 genera of cladocerans, 2 families and 8 genera of copepods, and 14 families and 24 genera of

Table 4. Monthly means (standard error) of water chemistry and quality parameters measured from Minnesota River water samples collected during July–October 2016, April–October 2017, and May–October 2018. Samples were pooled among sites (up to seven) and years (up to three).

Parameter	Apr	May	Jun	Jul	Aug	Sep	Oct	Mean
Chlorophyl a (µg l^{-1})	50.2 (2.9)	62.3 (4.7)	23.1 (3.1)	86.6 (10.7)	98.7 (10.2)	94.4 (9.3)	25.0 (2.6)	62.9 (12.0)
Ammonia-N (mg l^{-1})	0.01 (0.00)	0.01 (0.00)	0.04 (0.01)	0.03 (0.01)	0.02 (0.00)	0.02 (0.00)	0.01 (0.00)	0.02 (0.01)
Nitrate + Nitrite (mg l^{-1})	6.3 (1.1)	4.5 (0.7)	6.4 (0.8)	3.6 (0.6)	2.3 (0.6)	4.0 (1.0)	7.0 (0.6)	4.9 (0.7)
Total Kjeldahl Nitrogen (mg l^{-1})	1.3 (0.1)	1.2 (0.0)	1.3 (0.1)	1.5 (0.1)	1.7 (0.1)	1.6 (0.1)	1.2 (0.1)	1.4 (0.1)
Ortho Phophorous (mg l^{-1})	0.01 (0.00)	0.03 (0.00)	0.08 (0.01)	0.07 (0.01)	0.08 (0.01)	0.04 (0.00)	0.06 (0.00)	0.05 (0.01)
Total Phosphorous (mg l^{-1})	0.14 (0.01)	0.13 (0.01)	0.23 (0.02)	0.21 (0.01)	0.27 (0.02)	0.20 (0.01)	0.19 (0.01)	0.20 (0.02)
Silicon (mg l^{-1})	6.4 (0.03)	5.5 (0.3)	10.6 (0.4)	12.2 (0.4)	12.7 (0.4)	12.7 (0.2)	13.8 (0.2)	10.6 (1.2)
Total dissolved solids (mg l^{-1})	673 (30)	622 (34)	698 (39)	666 (20)	528 (19)	670 (19)	771 (31)	661 (28)
Total suspended solids (mg l^{-1})	77.1 (11.1)	65.2 (5.7)	134.0 (49.2)	71.0 (5.9)	90.9 (13.8)	75.4 (9.8)	61.9 (4.9)	82.2 (9.3)
Temperature (°C)	13.1 (0.2)	17.2 (0.6)	22.0 (0.2)	25.3 (0.4)	21.8 (0.3)	19.9 (0.4)	10.4 (0.7)	18.5 (2.0)
Secchi (m)	0.26 (0.02)	0.27 (0.02)	0.18 (0.01)	0.18 (0.01)	0.18 (0.01)	0.22 (0.02)	0.24 (0.02)	0.22 (0.01)

Table 5. Mean (standard error) water chemistry and quality parameters for water samples collected from seven Minnesota River sites (river kilometers 17, 48, 141, 213, 314, 385, and 434) during July–October 2016, April–October 2017, and May–October 2018. Samples were pooled among months and years.

Parameter	17	48	141	213	314	385	424	Mean
Chlorophyl a (µg l^{-1})	52.9 (8.5)	61.2 (11.7)	59.4 (11.0)	70.0 (15.2)	71.8 (12.3)	78.2 (10.5)	65.2 (7.6)	65.5 (3.2)
Ammonia-N (mg l^{-1})	0.03 (0.01)	0.02 (0.01)	0.01 (0.00)	0.01 (0.00)	0.01 (0.00)	0.03 (0.01)	0.03 (0.01)	0.02 (0.00)
Nitrate + Nitrite (mg l^{-1})	6.3 (0.1)	6.3 (0.9)	6.3 (0.9)	5.9 (1.0)	4.1 (0.7)	2.1 (0.4)	1.8 (0.3)	4.7 (0.8)
Total Kjeldahl Nitrogen (mg l^{-1})	1.3 (0.1)	1.3 (0.1)	1.3 (0.1)	1.3 (0.1)	1.4 (0.1)	1.7 (0.1)	1.6 (0.1)	1.4 (0.1)
Ortho Phophorous (mg l^{-1})	0.06 (0.01)	0.06 (0.01)	0.06 (0.01)	0.05 (0.01)	0.05 (0.01)	0.05 (0.01)	0.06 (0.01)	0.06 (0.00)
Total Phosphorous (mg l^{-1})	0.20 (0.02)	0.22 (0.02)	0.21 (0.02)	0.20 (0.01)	0.20 (0.02)	0.19 (0.02)	0.19 (0.02)	0.20 (0.00)
Silicon (mg l^{-1})	11.3 (0.7)	11.5 (0.6)	11.3 (0.6)	11.1 (0.7)	11.2 (0.8)	11.4 (1.0)	11.2 (1.0)	11.3 (0.0)
Total dissolved solids (mg l^{-1})	569 (22)	585 (25)	596 (26)	711 (31)	732 (34)	725 (33)	699 (34)	659 (27)
Total suspended solids (mg l^{-1})	81.9 (12.8)	96.7 (15.0)	127.3 (43.1)	78.6 (4.5)	74.0 (9.4)	53.7 (5.6)	57.6 (7.0)	81.4 (9.4)
Temperature (°C)	19.0 (1.3)	19.1 (1.3)	18.6 (1.3)	18.4 (1.3)	18.8 (1.3)	18.5 (1.4)	18.3 (1.4)	18.7 (0.1)
Secchi (m)	0.21 (0.01)	0.19 (0.01)	0.18 (0.01)	0.19 (0.01)	0.21 (0.01)	0.24 (0.01)	0.27 (0.01)	0.21 (0.01)

Table 6. Monthly mean (standard error) total and taxon specific biovolume ($mm^3 l^{-1}$) of phytoplankton in water samples collected from the Minnesota River during July–October 2016, April–October 2017, and May–October 2018. Samples were pooled among sites (up to seven) and years (up to three).

Taxa	Apr	May	Jun	Jul	Aug	Sep	Oct	Mean
Bacillariophyta	7.99 (1.35)	10.22 (1.41)	7.13 (2.93)	5.38 (1.86)	10.97 (2.82)	12.82 (3.30)	1.13 (0.22)	7.95 (1.48)
Chlorophyta	0.16 (0.05)	0.34 (0.10)	0.21 (0.06)	0.66 (0.28)	0.72 (0.14)	0.68 (0.17)	0.05 (0.01)	0.40 (0.11)
Chrysophyta	0.04 (0.04)	0.45 (0.19)	0.01 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.02 (0.01)	0.08 (0.06)
Cryptophyta	0.59 (0.15)	1.58 (0.34)	0.95 (0.21)	1.07 (0.19)	1.39 (0.36)	1.35 (0.44)	0.55 (0.11)	1.07 (0.15)
Cyanobacteria	0.40 (0.12)	3.18 (1.08)	0.24 (0.05)	17.92 (5.11)	20.99 (3.88)	16.33 (3.12)	4.58 (0.85)	9.09 (3.38)
Euglenophyta	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.01 (0.00)	0.00 (0.00)	0.00 (0.00)
Pyrrophyta	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.01 (0.00)	0.36 (0.21)	0.06 (0.06)	0.00 (0.00)	0.06 (0.05)
Total	9.18 (1.28)	15.77 (2.18)	8.54 (3.14)	25.04 (5.57)	34.43 (4.78)	31.24 (5.04)	6.33 (0.95)	18.65 (4.36)

Table 7. Mean (standard error) total and taxon specific biovolume ($mm^3 l^{-1}$) of phytoplankton in water samples collected from seven Minnesota River sites (river kilometers 17, 48, 141, 213, 314, 385, and 434) during July–October 2016, April–October 2017, and May–October 2018. Samples were pooled among months and years.

Taxa	17	48	141	213	314	385	424	Mean
Bacillariophyta	8.77 (2.18)	10.42 (3.65)	7.92 (2.22)	6.51 (1.77)	5.96 (1.26)	5.24 (1.13)	11.44 (4.55)	8.03 (0.88)
Chlorophyta	0.39 (0.12)	0.59 (0.22)	0.80 (0.27)	0.29 (0.10)	0.38 (0.14)	0.24 (0.06)	0.34 (0.09)	0.43 (0.07)
Chrysophyta	0.06 (0.06)	0.02 (0.02)	0.07 (0.06)	0.07 (0.07)	0.04 (0.04)	0.18 0.15)	0.02 (0.02)	0.07 (0.02)
Cryptophyta	1.60 (0.63)	1.05 (0.28)	1.09 (0.25)	0.68 (0.16)	0.88 (0.20)	1.04 (0.30)	1.38 (0.27)	1.10 (0.11)
Cyanobacteria	3.79 (1.12)	5.75 (2.25)	9.18 (3.23)	6.90 (3.16)	11.84 (3.57)	18.54 (4.76)	17.30 (4.42)	10.47 (2.15)
Euglenophyta	0.01 (0.00)	0.00 (0.00)	0.00 (0.00)	0.01 (0.01)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Pyrrophyta	0.00 (0.00)	0.04 (0.04)	0.10 (0.09)	0.00 (0.00)	0.07 (0.05)	0.09 (0.08	0.27 (0.27)	0.08 (0.03)
Total	14.62 (3.79)	17.87 (5.60)	19.16 (4.75)	14.45 (4.00)	19.17 (4.32)	25.33 (4.74)	30.75 (6.36)	20.19 (2.23)

Table 8. List of 7 phytoplankton divisions and 73 genera identified in water samples collected from seven sites along the Minnesota River during July–October 2016, April–October 2017, and May–October 2018.

Phytoplankton taxa		
Bacillariophyta	Chlorophyta	Cyanobacteria
Genus *Achnanthidium*	Genus *Ankistrodesmus*	Genus *Anabaena*
Genus *Amphora*	Genus *Characium*	Genus *Aphanizomenon*
Genus *Asterionella*	Genus *Chlamydomonas*	Genus *Aphanocapsa*
Genus *Aulacoseira*	Genus *Chlorella*	Genus *Aphanothece*
Genus *Cocconeis*	Genus *Closteriopsis*	Genus *Chroococcus*
Genus *Craticula*	Genus *Closterium*	Genus *Cylindrospermopsis*
Genus *Cyclotella*	Genus *Coelastrum*	Genus *Dolichospermum*
Genus *Cymatopleura*	Genus *Cosmarium*	Genus *Limnothrix*
Genus *Cymbella*	Genus *Crucigenia*	Genus *Merismopedia*
Genus *Diatoma*	Genus *Dictyosphaerium*	Genus *Microcystis*
Genus *Encyonema*	Genus *Kirchneriella*	Genus *Phormidium*
Genus *Fragilaria*	Genus *Monoraphidium*	Genus *Planktolyngbya*
Genus *Gomphoneis*	Genus *Oocystis*	Genus *Pseudanabaena*
Genus *Gomphonema*	Genus *Pediastrum*	Genus *Raphidiopsis*
Genus *Gyrosigma*	Genus *Scenedesmus*	Genus *Woronichinia*
Genus *Hannaea*	Genus *Selenastrum*	Pyrrophyta
Genus *Mastogloia*	Genus *Sphaerocystis*	Genus *Ceratium*
Genus *Melosira*	Genus *Staurastrum*	Genus *Glenodinium*
Genus *Meridion*	Genus *Tetraedron*	
Genus *Navicula*	Chrysophyta	
Genus *Nitzschia*	Genus *Dinobryon*	
Genus *Planothidium*	Genus *Mallomonas*	
Genus *Rhoicosphenia*	Genus *Synura*	
Genus *Rhopalodia*	Cryptophyta	
Genus *Staurosira*	Genus *Cryptomonas*	
Genus *Staurosirella*	Genus *Rhodomonas*	
Genus *Stephanodiscus*	Euglenophyta	
Genus *Surirella*	Genus *Euglena*	
Genus *Synedra*	Genus *Phacus*	

rotifers (Tables 9 and 10). Among months, we found crustacean zooplankton (cladocerans and copepods) rather than rotifers dominated the biomass of Minnesota River zooplankton community with mean ± SE rotifer biomass of 11.62 ± 3.11 µg l^{-1}, cladoceran biomass of 22.48 ± 9.25 µg l^{-1}, and copepod biomass of 19.57 ± 5.03 µg l^{-1} (Tables 11 and 12). However, zooplankton communities significantly differed between downstream and upstream sites with rotifers comprising most of the zooplankton biomass at the four downstream most sites and crustacean zooplankton comprising most of the zooplankton biomass at the two upstream most sites (supplementary Figures S31–S44). At the upstream most site (rkm 424) mean ± SE rotifer biomass was 15.16 ± 3.56 µg l^{-1}, mean ± SE cladoceran biomass was 131.17 ± 41.59 µg l^{-1}, and mean ± SE copepod biomass was 81.72 ± 15.67 µg l^{-1}. Family Brachionidae was the dominant rotifer taxon by biomass in

Table 9. List including 3 orders, 14 families, and 24 genera of rotifers identified in samples collected from the Minnesota River during July–October 2016, April–October 2017, and May–October 2018.

Rotifers taxa
Order Bdelloidea
Order Floscullariaceae
Family Testudinellidae
Genus *Pompholyx*
Genus *Testudinella*
Family Trochosphaeridae
Genus *Filinia*
Order Ploima
Family Asplanchnidae
Genus *Asplanchna*
Family Brachionidae
Genus *Anuraeopsis*
Genus *Brachionus*
Genus *Kelicottia*
Genus *Keratella*
Genus *Notholca*
Genus *Platyias*
Family Dicranophoridae
Genus *Encentrum*
Family Euchlanidae
Genus *Euchlanis*
Family Gastropodidae
Genus *Ascomorpha*
Genus *Gastropus*
Family Lecanidae
Genus *Lecane*
Family Lepadellidae
Genus *Colurella*
Genus *Lepadella*
Family Mytiliidae
Genus *Mytilina*
Family Synchaetidae
Genus *Ploesoma*
Genus *Polyarthra*
Genus *Synchaeta*
Family Trichocercidae
Genus *Trichocerca*
Family Trichotriidae
Genus *Tricotria*

the Minnesota River, family Daphniidae was the dominate cladoceran taxon, and order Cyclopoida was the dominant copepod group. Although crustacean zooplankton biomass exceeded rotifer biomass in some samples, rotifer densities (individuals l^{-1}) were generally much greater (Table 13), and exceeded crustacean zooplankton density in all samples except at rkm 424 during October 2016.

Among continuous abiotic variables, Pearson correlation coefficients indicated strong ($r^2 \geq 0.60$) positive correlations among month and Si; Chl-a and TKN; Ortho-P and TP; and TP and TSS (Table 14). Similarly, we identified strong negative correlations between Secchi and TP; Secchi and TSS; relative discharge and Chl-a; Chl-a and N+N; and N+N and TKN. We identified several strong correlations among biomass estimates of large bodied cladocerans (i.e., Daphniidae, Sididae) and copepod groups (e.g., Calanoida, copepodies; Table 15). After considering issues of multicolinearity, we selected the explanatory continuous variables rkm, temperature, relative discharge, Chl-a, Ortho-P, TDS, TSS, and Si for inclusion in multivariate analyses. We also included the discrete (categorical) explanatory variables month, site (i.e., rkm as discrete sites), year, year × month (i.e. sample period), and relative discharge quartile. We summarized plankton communities with four variables representing phytoplankton biovolumes (Bacillariophyta, Chlorophyta, Cryptophyta, Cyanobacteria) and seven variables representing zooplankton biomasses (Calanoida, Cyclopoida, Daphniidae, Sididae, Leptodoridae, small cladocerans, and rotifers). Small cladocerans is the sum of Bosminidae, Chydoridae, Macrothricidae, and Moinidae biomass. We excluded copepodite and nauplii biomass from multivariate analyses. Among selected variables, we found strong correlations ($r^2 \geq 0.60$) between rkm and Calanoida and Daphniidae biomass; relative discharge and

Table 10. List of cladoceran (7 families and 14 genera) and copepod (2 families and 8 genera) zooplankton taxa identified in samples collected from the Minnesota River during July–October 2016, April–October 2017, and May–October 2018.

Cladocerans (Class Branchiopoda)	Copepods (Class Maxillopoda)
Order Cladocera	Order Calanoida
Family Bosminidae	Family Diaptomidae
Genus *Bosmina*	Genus *Aglaodiaptomus*
Family Chydoridae	Genus *Leptodiaptomus*
Genus *Alona*	Genus *Skistodiaptomus*
Genus *Chydorus*	Order Cyclopoida
Genus *Eurycercus*	Family Cyclopidae
Genus *Oxyurella*	Genus *Acanthocyclops*
Genus *Pleuroxus*	Genus *Diacyclops*
Family Daphniidae	Genus *Eucyclops*
Genus *Daphnia*	Genus *Mesocyclops*
Daphnia ambigua	Genus *Tropocyclops*
Daphnia galeata mendotae	
Daphnia parvula	
Daphnia pulicaria	
Daphnia retrocurva	
Genus *Scapholeberis*	
Genus *Simocephalus*	
Family Leptodoridae	
Genus *Leptodora*	
Family Macrothricidae	
Family Moinidae	
Genus *Moina*	
Family Sididae	
Genus *Diaphanosoma*	
Genus *Sida*	

Cyanobacteria biovolume; Chl-a and phytoplankton taxa biovolumes; and between rotifer biomass and Si concentration (Table 16). For NMDS analyses, we condensed the dependent variables into three variables representing phytoplankton biomass, total rotifer biomass, and total crustacean zooplankton biomass.

Ordination plots (NMDS) visually reveal a positive relationship (confirmed with PERMANOVA) between phytoplankton biovolume and Chl-a concentrations, a negative relationship between phytoplankton biovolume and relative discharge, and a positive relationship between crustacean zooplankton biomass and rkm for all samples collected during May–October 2017 and 2018 (n = 82; Figure 4). However, when excluding the two upstream most sites from analyses, the spatial relationship with rkm is no longer significant and significant relationships with Ortho-P, Si, and temperature are identified (Figures 5 and 7). Excluding the month of May from analyses does not change relationships between plankton communities with Chl-a, rkm, or relative discharge, but relationships

Table 11. Monthly mean (standard error) taxon specific zooplankton biomass (µg l^{-1}) in water samples collected from seven Minnesota River sites (river kilometers 17, 48, 141, 213, 314, 385, and 434) during July–October 2016, April–October 2017, and May–October 2018. Samples were pooled among sites (up to seven) and years (up to three).

Taxa	Apr	May	Jun	Jul	Aug	Sep	Oct	Mean
Rotifers	**10.94 (0.79)**	**30.02 (3.32)**	**9.49 (1.24)**	**7.28 (0.67)**	**8.59 (0.48)**	**7.3 (0.47)**	**7.67 (0.63)**	**11.62 (3.11)**
Family Brachionidae	4.28 (0.32)	12.39 (1.26)	2.97 (0.67)	2.13 (0.29)	2.56 (0.19)	2.31 (0.39)	2.49 (0.51)	4.16 (1.40)
Family Gastropodidae	1.32 (0.13)	2.23 (0.46)	1.05 (0.01)	1.03 (0.03)	1.10 (0.04)	1.06 (0.01)	1.15 (0.04)	1.28 (0.16)
Family Sychaetidae	2.05 (0.26)	2.15 (0.20)	1.74 (0.16)	1.09 (0.03)	1.23 (0.07)	1.22 (0.05)	1.18 (0.04)	1.52 (0.17)
Family Trichocercidae	1.01 (0.00)	1.01 (0.00)	1.02 (0.01)	1.22 (0.17)	1.38 (0.10	1.10 (0.02)	1.00 (0.00)	1.11 (0.05)
Other	2.29 (0.67)	12.24 (3.05)	2.71 (0.68)	1.81 (0.40)	2.31 (0.38)	1.66 (0.24)	1.85 (0.43)	3.55 (1.45)
Cladocerans	**0.50 (0.22)**	**27.76 (19.53)**	**18.85 (11.26)**	**2.61 (1.75)**	**28.18 (24.54)**	**7.77 (5.57)**	**71.69 (26.29)**	**22.48 (9.25)**
Family Bosminidae	0.03 (0.02)	0.09 (0.03)	0.14 (0.04)	0.01 (0.01)	0.10 (0.04)	0.01 (0.01)	0.21 (0.05)	0.08 (0.03)
Family Chydoridae	0.14 (0.06)	0.44 (0.25)	0.10 (0.05)	0.02 (0.02)	0.00 (0.00)	0.00 (0.00)	0.02 (0.01)	0.10 (0.06)
Family Daphniidae	0.31 (0.20)	27.23 (19.44)	18.11 (10.88)	2.17 (1.64)	26.52 (23.16)	7.56 (5.45)	70.59 (26.6)	27.78 (9.12)
Family Leptodoridae	0.00 (0.00)	0.00 (0.00)	0.42 (0.42)	0.05 (0.05)	1.02 (1.02)	0.15 (0.13)	0.00 (0.00)	0.23 (0.14)
Family Macrothricidae	0.02 (0.01)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Family Moinidae	0.00 (0.00)	0.00 (0.00)	0.01 (0.01)	0.04 (0.04)	0.01 (0.01)	0.00 (0.00)	0.00 (0.00)	0.01 (0.01)
Family Sididae	0.00 (0.00)	0.00 (0.00)	0.06 0.02)	0.32 (0.22)	0.53 (0.36)	0.05 (0.04)	0.88 (0.46)	0.26 (0.13)
Copepods	**19.77 (5.57)**	**48.65 (22.93)**	**15.14 (9.58)**	**9.16 (5.28)**	**15.08 (9.52)**	**11.66 (6.73)**	**17.51 (6.34)**	**19.57 (5.03)**
Order Cyclopoida	17.09 (5.03)	38.39 (17.97)	5.46 (2.85)	5.27 (3.39)	7.05 (4.72)	8.16 (5.54)	7.87 (2.97)	12.75 (4.53)
Order Calanoida	0.32 (0.12)	4.72 (3.19)	8.00 (6.41)	3.23 (2.03)	6.90 (4.12)	2.71 (1.34)	8.46 (3.22)	4.91 (1.14)
Copepodites	2.12 (0.50)	4.56 (1.86)	1.40 (0.66)	0.61 (0.32)	1.00 (0.65)	0.72 (0.38)	1.02 (0.37)	1.63 (0.52)
Nauplii	0.24 (0.08)	0.99 (0.31)	0.29 (0.13)	0.05 (0.02)	0.12 (0.06)	0.07 (0.04)	0.17 (0.07)	0.27 (0.12)
Total	**31.21 (5.92)**	**106.43 (40.35)**	**43.49 (19.31)**	**19.06 (6.96)**	**51.85 (33.76)**	**26.77 (12.40)**	**96.88 (32.06)**	**53.67 (13.08)**

Table 12. Mean (standard error) taxon specific zooplankton biomass (µg l^{-1}) in water samples collected from the Minnesota River during July–October 2016, April–October 2017, and May–October 2018. Samples were pooled among months and years.

Taxa	17	48	141	213	314	385	424	Mean
Rotifers	**12.28 (2.12)**	**10.67 (2.24)**	**9.29 (1.61)**	**10.14 (2.01)**	**10.27 (2.20)**	**9.35 (1.10)**	**15.16 (3.56)**	**11.02 (0.79)**
Family Brachionidae	3.60 (1.14)	3.63 (1.30)	3.37 (1.13)	3.27 (0.89)	3.73 (0.86)	4.03 (0.82)	5.44 (1.07)	3.87 (0.28)
Family Gastropodidae	1.34 (0.16)	1.39 (0.20)	1.41 (0.21)	1.41 (0.36)	1.05 (0.01)	1.07 (0.03)	1.09 (0.03)	1.25 (0.06)
Family Sychaetidae	1.41 (0.10)	1.30 (0.06)	1.39 (0.14)	1.39 (0.13)	1.43 (0.16)	1.42 (0.17)	1.74 (0.19)	1.44 (0.05)
Family Trichocercidae	1.31 (0.14)	1.16 (0.07)	1.18 (0.11)	1.10 (0.06)	1.03 (0.01)	1.02 (0.01)	1.05 (0.02)	1.12 (0.04)
Other	4.62 (0.96)	3.19 (0.87)	1.94 (0.34)	2.97 (0.90)	3.03 (1.58)	1.81 (0.37)	5.84 (2.76)	3.34 (0.54)
Cladocerans	**0.28 (0.06)**	**0.37 (0.10)**	**0.61 (0.40)**	**1.36 (0.58)**	**10.33 (6.47)**	**35.74 (14.22)**	**131.17 (41.59)**	**25.69 (18.24)**
Family Bosminidae	0.14 (0.04)	0.12 (0.03)	0.03 (0.02)	0.05 (0.02)	0.08 (0.04)	0.09 (0.05)	0.12 (0.05)	0.09 (0.02)
Family Chydoridae	0.06 (0.02)	0.02 (0.01)	0.01 (0.01)	0.04 (0.02)	0.01 (0.01)	0.09 (0.06)	0.35 (0.22)	0.08 (0.05)
Family Daphniidae	0.02 (0.01)	0.19 (0.08)	0.56 (0.42)	1.24 (0.58)	10.20 (6.44)	35.10 (14.14)	127.17 (40.27)	24.93 (17.70)
Family Leptodoridae	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.07 ()0.05)	1.87 (1.36)	0.28 (0.27)
Family Macrothricidae	0.00 (0.00)	0.01 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.01 (0.01)	0.00 (0.00)
Family Moinidae	0.00 (0.00)	0.01 (0.01)	0.00 (0.00)	0.01 (0.01)	0.00 (0.00)	0.00 (0.00)	0.03 (0.03)	0.01 (0.00)
Family Sididae	0.06 (0.02)	0.02 (0.02)	0.00 (0.00)	0.01 (0.01)	0.04 (0.03)	0.40 (0.21)	1.61 (0.67)	0.31 (0.22)
Copepods	**2.56 (0.82)**	**1.96 (0.72)**	**1.81 (0.72)**	**2.97 (1.69)**	**6.19 (2.62)**	**31.45 (15.78)**	**81.72 (15.67)**	**18.38 (11.30)**
Order Cyclopoida	1.62 (0.58)	1.25 (0.51)	1.21 (0.64)	2.13 (1.23)	4.22 (2.17)	20.20 (11.64)	49.19 (12.19)	11.40 (6.81)
Order Calanoida	0.22 (0.15)	0.11 (0.06)	0.31 (0.23)	0.05 (0.04)	1.34 (0.84)	8.43 (2.84)	26.47 (6.80)	5.28 (3.71)
Copepodites	0.58 (0.19)	0.04 (0.19)	0.21 (0.08)	0.54 (0.30)	0.53 (0.20)	2.47 (1.52)	5.42 (1.00)	1.46 (0.72)
Nauplii	0.14 (0.04)	0.16 (0.08)	0.08 (0.03)	0.25 (0.18)	0.10 (0.04)	0.36 (0.24)	0.65 (0.16)	0.25 (0.08)
Total	**15.13 (2.60)**	**13.00 (2.52)**	**11.70 (2.25**	**14.47 (3.87)**	**26.79 (9.27)**	**76.56 (21.47)**	**228.04 (53.78)**	**55.10 (30.11)**

Table 13. Summary of zooplankton densities (individuals l^{-1}) in 109 samples collected from seven sites along the Minnesota River during July–October 2016, April–October 2017, and May–October 2018. Copepod densities exclude nauplii and copepodites.

Zooplanton taxa	Mean	SE	Min	25th percentile	Median	75th percentile	Max
Cladocerans	3.3	1.0	0.0	0.3	0.2	0.6	92.0
Copepods	2.9	0.6	0.0	0.7	0.3	1.7	36.2
Rotifers	215.7	30.0	3.5	54.0	117.8	246.3	1,685.3

with Ortho-P and TDS are also identified as significant (Figures 6 and 7).

Performing PERMANOVA analyses on various subsets of plankton and abiotic data reveal that combined plankton communities (i.e., both phytoplankton and zooplankton data) significantly differ both spatially and temporally, and the strongest influential factors are likely proximity to upstream impoundments, time of year (e.g., month), and relative discharge. We found phytoplankton communities significantly differ temporally (e.g., among months and years) but failed to reject the null hypothesis that phytoplankton communities are similar among sites. Relative discharge variables explained significant amounts of phytoplankton community variability among samples (Table 17). Zooplankton communities only differ spatially (among sites) when the two upstream most sites are included in analyses but differed temporally among months (except when only the month of May was excluded from analyses; Table 18). Analyses also indicate zooplankton communities significantly differ among relative discharges, but associated r^2 values are low (0.09–20). When we combined phytoplankton and zooplankton community data for PERMANOVA analyses, results again indicate that plankton communities differ spatially because of the influence of the two upstream most sites. However, plankton communities consistently differ temporally with the greatest r^2 values associated with month and relative discharge variables (Table 19).

Discussion

Our findings support the hypothesis that phytoplankton and zooplankton communities vary both spatially and temporally in the Minnesota River. Although the river continuum concept (Vannote et al. 1980) and other studies (e.g., Zimmermann-Timm et al. 2007; Viroux 2002) suggest phytoplankton and zooplankton increase from upstream to downstream in lotic systems, we found total zooplankton biomass greater at upstream sites than downstream sites in the study reach of the Minnesota River. Our study reach spanned 407 rkm, but stream order only varied 7–8 compared to the longitudinal gradient discussed by Vannote et al. (1980) that spanned first order streams thru twelfth order rivers. The greater zooplankton biomass found at upstream sites is likely a consequence of dams and impoundments located within the upper reaches of the Minnesota River (i.e., Lac qui Parle Dam, Granite Falls Dam) which disrupt longitudinal river processes (Ward and Sanford 1983) affecting zooplankton communities (Akopian et al. 1991; Havel et al. 2009; Sluss and Jack 2013). Similar to most turbid rivers, rotifers dominated the zooplankton community within the lower free-flowing reach of the Minnesota River (e.g., Thorp and Mantovani 2005; Burdis and Hoxmeier 2011; Sluss and Jack 2013; Sass et al. 2014), but larger-bodied crustacean

Table 14. Statistically significant ($P \leq 0.05$) Pearson correlation coefficients ≥ 0.5 for pairwise comparisons among water chemistry parameters, field measurements, and spatial (river kilometer) and temporal variables (month) measured at seven Minnesota River sites during July–October 2016, April–October 2017, and May–October 2018. All water chemistry concentrations were ln(x + 1).

	Month	River km	Secchi	Temp.	Relative discharge	Chl. a	Ortho P	Total P	Nitrate + Nitrite	TKN	TDS	TSS	Silicon
Month													0.80
River km													
Secchi								-0.63				-0.67	
Temp.													
Relative discharge						-0.73			0.55	-0.53			
Chl. a									-0.74	0.65			
Ortho P								0.67					0.50
Total P												0.61	0.51
Nitrate + Nitrite										-0.71			
TKN													
TDS													
TSS													
Silicon													

Table 15. Statistically significant ($P \leq 0.05$) Pearson correlation coefficients ≥ 0.5 for pairwise comparisons among zooplankton taxa biomass (µg l^{-1}) in samples collected from seven Minnesota River sites during July–October 2016, April–October 2017, and May–October 2018. All biomass densities were ln(x + 1) transformed.

	Rotifers	Bosminidae	Chydoridae	Daphniidae	Leptodoridae	Macrothricidae	Moinidae	Sididae	Calanoida	Cyclopoida	Copepodites	Nauplii
Rotifers											0.52	0.57
Bosminidae												
Chydoridae											0.52	0.51
Daphniidae								0.59	0.81		0.70	0.50
Leptodoridae												
Macrothricidae												
Moinidae												
Sididae									0.64			
Calanoida										0.75	0.72	
Cyclopoida												
Copepodites												0.81
Nauplii												

Table 16. Statistically significant ($P \leq 0.05$) Pearson correlation coefficients ≥ 0.5 for pairwise comparisons between abiotic variables and phytoplankton taxa biovolume ($mm^3\ l^{-1}$) and zooplankton taxa biomass ($\mu g\ l^{-1}$) in samples collected from seven Minnesota River sites during July–October 2016, April–October 2017, and May–October 2018. All variables were ln(x + 1) transformed except month, river kilometer (divided by 100), relative discharge, and water temperature.

	Bacillariophyta	Chlorophyta	Cryptophyta	Cyanobacteria	Calanoida	Cyclopoida	Daphniidae	Sididae	Leptodoridae	Small cladocerans	Rotifers
Month											-0.55
River km					0.63	0.58	0.61				
Temp.											
Relative discharge		-0.57		-0.67							
Chl. a	0.65	0.54		0.69							
Ortho P											
TDS											
TSS											
Silicon											-0.75

zooplankton dominated biomass at upstream sites where they were likely exported from reaches with greater water residence time upstream of dams. Several other studies have documented similar influences of dams and reservoirs on large river zooplankton communities (e.g., Akopian et al. 1991; Havel et al. 2009; Burdis and Hirsch 2017). For instance, Havel et al. (2009) found distance from the nearest upstream dam as the most important predictor of crustacean zooplankton communities in the Missouri River with the greatest densities observed immediately downstream of impoundments. We ultimately found that zooplankton communities did not significantly differ spatially within the Minnesota River after removing sites influenced by dams from analyses. Spatial variables did not explain variation in Minnesota River phytoplankton communities, but similar to crustacean zooplankton, mean phytoplankton biovolume was greatest at sites downstream of dams. Abundant blue-green algae at these sites strongly influenced this trend, but when excluding those sites, spatial trends were not significant. We also failed to identify significant differences in mean Chl-a concentrations among sites, a common surrogate measure of phytoplankton abundance and biomass. These results indicate that abiotic factors influencing plankton communities in the Minnesota River may not exhibit the typical longitudinal trends hypothesized by the river continuum concept (Vannote et al. 1980). Rather, we suspect plankton communities are more influenced by the occurrence of dams as described by the serial discontinuity concept (Ward and Sanford 1983; Sanford and Ward 2001) and temporal variability in discharge and floodplain connectivity as described by the flood-pulse concept (Junk et al. 1989).

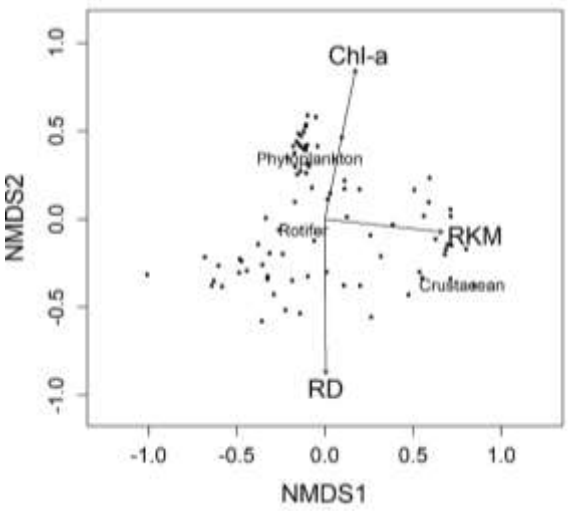

Figure 4. Non-metric multidimensional scaling (NMDS) ordination of phytoplankton biovolume (mm3/l), rotifer biomass (µg/l), and crustacean zooplankton biomass (µg/l) in samples collected from seven sites along the Minnesota River during May–October 2017 and 2018 (stress = 0.08, non-metric fit r2 = 0.99). The dissimilarity matrix was calculated using the Bray-Curtis method and all biomass, biovolume, and water chemistry variables were ln(x + 1) transformed. Each point represents a sample event (i.e., site, month, and year combination). Significant relationships (P ≤ 0.05; r2 ≥ 0.10) between plankton assemblages and abiotic variables determined with permutational multivariate analysis of variance (ADONIS function within Vegan Package for R) are displayed as vectors depicting the general direction of the relationship. In general, phytoplankton biovolume is positively correlated with Chlorophyll a concentrations (ChlA) and negatively correlated with relative discharge (RD) while crustacean zooplankton biomass is positively correlated with river kilometer (RKM).

As hypothesized, phytoplankton and zooplankton communities differed among months, exhibiting seasonal patterns. The variable representing month explained the greatest amount of variability in phytoplankton communities with blue-green algae strongly influencing temporal trends in phytoplankton biovolume; peaks of both (and Chl-a) occurring during July, August, and September. Diatoms are also abundant in the Minnesota River, annually exhibiting peaks in biovolume during spring (around May) and fall (around August and September). Other taxa (e.g., green algae, cryptophytes) are often present but represent a small portion of the total biovolume. Similar seasonal succession of phytoplankton communities occurs in

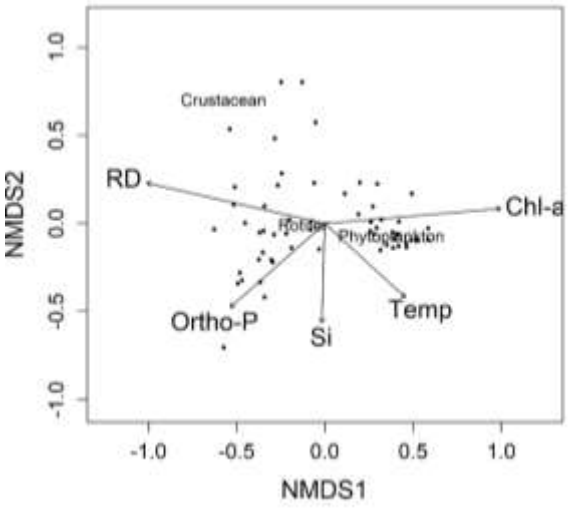

Figure 5. Non-metric multidimensional scaling (NMDS) ordination of phytoplankton biovolume (mm^3/l), rotifer biomass (µg/l), and crustacean zooplankton biomass (µg/l) in samples collected from five downstream sites (excluding two upstream most sites influenced by proximity to impoundments) along the Minnesota River during May–October 2017 and 2018 (stress = 0.07, non-metric fit r^2 = 0.99). The dissimilarity matrix was calculated using the Bray-Curtis method and all biomass, biovolume, and water chemistry variables were ln(x + 1) transformed. Each point represents a sample event (i.e., site, month, and year combination). Significant relationships ($P \leq 0.05$; $r^2 \geq 0.10$) between plankton assemblages and abiotic variables determined with permutational multivariate analysis of variance (ADONIS function within Vegan Package for R) are displayed as vectors depicting the general direction of the relationship.

eutrophic Minnesota lakes and the upper Mississippi River (Heiskary et al. 2016; Baker and Baker 1981) indicating that these trends may be primarily driven by abiotic factors and phenology that vary predictably with season (e.g., temperature, length of day, nutrient fluxes). In the Mississippi River (<100 km)

downstream from the Minnesota River confluence) Baker and Baker (1981) also found diatoms dominant during spring and fall, blue-green algae dominant during summer, and that other taxa (e.g., green algae, cryptophytes) were present but rarely dominant. *Aphanizomenon flos-aquae*, a dominant species of blue-green algae in most eutrophic Minnesota lakes (Heiskary et al. 2016), was the most abundant species in the Minnesota River during summer and was similarly reported by Baker and Baker (1981) as the dominant species of blue-green algae in the Mississippi River.

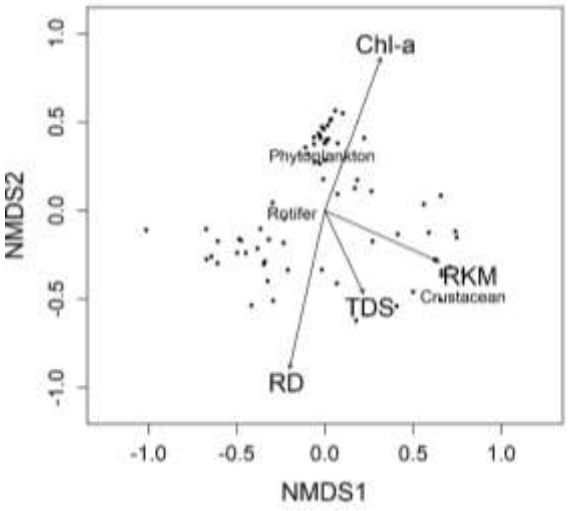

Figure 6. Non-metric multidimensional scaling (NMDS) ordination of phytoplankton biovolume (mm^3/l), rotifer biomass (µg/l), and crustacean zooplankton biomass (µg/l) in samples collected from seven sites along the Minnesota River during June–October 2017 and 2018 (excluding the month of May, stress = 0.06, non-metric fit r^2 = 0.99). The dissimilarity matrix was calculated using the Bray-Curtis method and all biomass, biovolume, and water chemistry variables were ln(x + 1) transformed. Each point represents a sample event (i.e., site, month, and year combination). Significant relationships ($P \leq 0.05$; $r^2 \geq 0.10$) between plankton assemblages and abiotic variables determined with permutational multivariate analysis of variance (ADONIS function within Vegan Package for R) are displayed as vectors depicting the general direction of the relationship.

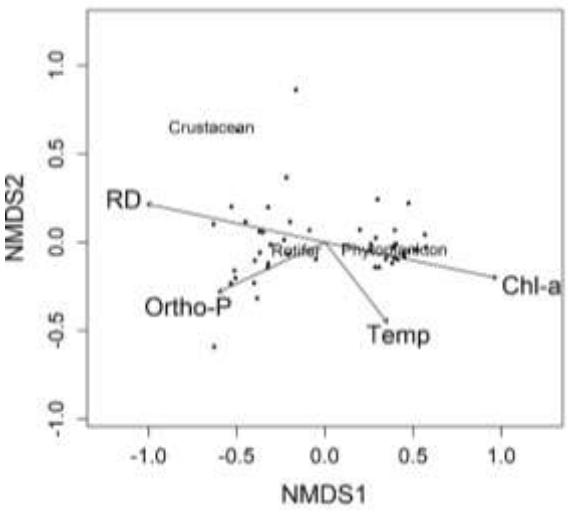

Figure 7. Non-metric multidimensional scaling (NMDS) ordination of phytoplankton biovolume (mm^3/l), rotifer biomass (µg/l), and crustacean zooplankton biomass (µg/l) in samples collected from five downstream sites (excluding two upstream most sites influenced by proximity to impoundments) along the Minnesota River during June–October 2017 and 2018 (excluding the month of May, stress = 0.06, non-metric fit r^2 = 0.99). The dissimilarity matrix was calculated using the Bray-Curtis method and all biomass, biovolume, and water chemistry variables were ln(x + 1) transformed. Each point represents a sample event (i.e., site, month, and year combination). Significant relationships ($P \leq 0.05$; $r^2 \geq 0.10$) between plankton assemblages and abiotic variables determined with permutational multivariate analysis of variance (ADONIS function within Vegan Package for R) are displayed as vectors depicting the general direction of the relationship.

Zooplankton communities also differed among months, which appears driven by seasonal peaks in rotifer and copepod biomass. With data pooled among years and sites, we found the greatest mean daphnid biomass during October, and greatest mean rotifer and copepod biomass during May. Individual sampling events and sites downstream of dams strongly influenced some of these trends. For instance, daphnid biomass was always relatively high (mean 214.3 µg l^{-1}) during October at the two upstream sites. Cyclopoid copepod biomass was also high (mean 189.6 µg l^{-1}) during May

Table 17. *F*-statistic, r^2, and *P*-values from permutational multivariate analysis of variance (ADONIS function within Vegan Package for R) using distance matrices (Bray-Curtis) of phytoplankton taxa (Bacillariophyta, Chlorophyta, Cryptophyta, Cyanobacteria) biovolume ($mm^3\ l^{-1}$) in samples from seven Minnesota River sites (during July–October 2016, April–October 2017, and May–October 2018) and fitting linear models for continuous and categorical spatial, temporal, and relative discharge variables. Analyses were performed with data from all samples and excluding the two upstream most sites (rkm 385 and rkm 424). All biovolume data were ln(x + 1) transformed.

	All May–October 2017 and 2018 samples			Excluding upstream sites (RKM 385 and 424)		
	F	r^2	*P*	*F*	r^2	*P*
Continuous variables						
River kilometer	2.18	0.03	0.09	0.32	0.01	0.80
Relative discharge	36.86	**0.32**	< 0.01	38.94	**0.41**	< 0.01
Categorical variables						
Month	14.42	**0.49**	< 0.01	11.06	**0.52**	< 0.01
Site	0.77	0.06	0.69	0.50	0.04	0.90
Year	6.71	0.08	< 0.01	6.03	0.10	< 0.01
Year * Month	11.86	**0.65**	< 0.01	12.00	**0.74**	< 0.01
Relative discharge quartile	12.96	**0.33**	< 0.01	13.69	**0.43**	< 0.01

of 2018 at the two upstream sites, whereas rotifer biomass was always relatively high in May samples. Wahl et al. (2008) observed similar annual spring peaks in rotifer density within the main channel of the Illinois River along with variable peaks in cyclopoid densities in backwater habitats. Burdis and Hirsch (2017), however, found somewhat different seasonal zooplankton trends in a riverine lake of the Mississippi River. They found mean cladoceran and daphnid biomass was greatest during June and lowest during October, and that mean cyclopoid biomass was also greater during spring and early summer than during fall. Significant temporal variability of plankton communities within the free-flowing reach of the Minnesota River further indicates that important abiotic factors influencing plankton communities also vary temporally, and potentially predictably. These abiotic factors may include temperature (Gillooly and Dodson 2000), light availability, turbidity (Sluss and Jack 2013), turbulence (Sluss et al. 2008), water residence time (Burdis and Hirsch 2017), and nutrients (Soballe and Kimmel 1987); all of which are likely influenced by discharge. Although discharge and relative discharge can also vary spatially, relative discharge only significantly varied temporally during this study, and we believe our analyses support the theory that discharge is the most influential driver of variability in Minnesota River phytoplankton communities and temporal variability in zooplankton communities.

Similar to other large floodplain rivers, we unveiled abundant and diverse communities of phytoplankton and zooplankton within the main channel of the Minnesota River. We captured at least 22 crustacean zooplankton genera (> 31 species), 24 rotifer genera, and 73 phytoplankton genera with mean zooplankton biomass (excluding nauplii and copepodites) of 49.5 µg l^{-1}, phytoplankton biovolume of 20.4 $mm^3\ l^{-1}$, and Chl-a concentration of 65.5 µg l^{-1} (indicative of a hypereutrophic system) for all samples collected during this study. Ten percent of samples had > 160.0 µg l^{-1} zooplankton, > 48.0 $mm^3\ l^{-1}$ phytoplankton, and or > 127.0 µg l^{-1} Chl-a. Despite dominating zooplankton biomass at the two upstream

Table 18. *F*-statistic, r^2, and *P*-values from permutational multivariate analysis of variance (ADONIS function within Vegan Package for R) using distance matrices (Bray-Curtis) of zooplankton taxa (Rotifers, Daphniidae, Calanoida, Cyclopoida, Leptodoridae, Sididae, and small cladocerans [Bosminidae, Chydoridae, Macrothricidae, and Moinidae]) biomass (µg l^{-1}) and in samples from seven Minnesota River sites (during July–October 2016, April–October 2017, and May–October 2018) and fitting linear models for continuous and categorical spatial, temporal, and relative discharge variables. Analyses were performed with data from all samples, excluding samples from the two upstream most sites (rkm 385 and rkm 424), excluding samples from the month of May, and excluding samples from the two upstream most sites and the month of May. All biomass data were ln(x + 1) transformed.

	All May–October 2017 and 2018 samples			Excluding upstream sites (RKM 385 and 424)			Excluding month of May			Excluding upstream sites and month of May		
	F	*r2*	*P*	*F*	*r2*	*P*	*F*	*r2*	*P*	*F*	*r2*	*P*
Continuous variables												
River kilometer	40.82	**0.34**	< 0.01	3.96	0.07	0.02	43.00	**0.40**	< 0.01	4.25	0.09	0.02
Relative discharge	8.22	0.09	< 0.01	9.38	0.15	< 0.01	5.27	0.08	< 0.01	6.99	0.13	< 0.01
Categorical variables												
Month	3.88	**0.21**	< 0.01	7.36	**0.42**	< 0.01	2.05	0.12	0.07	3.04	**0.22**	< 0.01
Site	11.31	**0.48**	< 0.01	1.47	0.10	0.17	13.35	**0.57**	< 0.01	1.85	0.15	0.06
Year	1.32	0.02	0.24	1.18	0.02	0.27	1.43	0.02	0.21	2.66	0.06	0.05
Year * Month	2.31	0.27	< 0.01	4.59	0.54	< 0.01	1.21	0.16	0.28	2.01	0.33	0.01
Relative discharge quartile	3.63	0.12	< 0.01	4.45	**0.20**	< 0.01	2.60	0.11	0.03	3.13	0.18	0.01

Table 19. *F*-statistic, r^2, and *P*-values from permutational multivariate analysis of variance (ADONIS function within Vegan Package for R) using distance matrices (Bray-Curtis) of zooplankton taxa (Rotifers, Daphniidae, Calanoida, Cyclopoida, Leptodoridae, Sididae, and small cladocerans [Bosminidae, Chydoridae, Macrothricidae, and Moinidae]) biomass (µg l^{-1}) and phytoplankton taxa (Bacillariophyta, Chlorophyta, Cryptophyta, Cyanobacteria) biovolume (mm^3 l^{-1})in samples from seven Minnesota River sites (during July–October 2016, April–October 2017, and May–October 2018) and fitting linear models for continuous and categorical spatial, temporal, and relative discharge variables. Analyses were performed with data from all samples, excluding samples from the two upstream most sites (rkm 385 and rkm 424), excluding samples from the month of May, and excluding samples from the two upstream most sites and the month of May. All biomass and biovolume data were ln(x + 1) transformed.

	All May–October 2017 and 2018 samples			Excluding upstream sites (RKM 385 and 424)			Excluding month of May			Excluding upstream sites and month of May		
	F	*r2*	*P*	*F*	*r2*	*P*	*F*	*r2*	*P*	*F*	*r2*	*P*
Continuous variables												
River kilometer	22.86	0.22	< 0.01	2.23	0.04	0.07	21.12	0.24	< 0.01	2.03	0.04	0.1
Relative discharge	23.29	0.23	< 0.01	29.86	0.35	< 0.01	21.55	0.25	< 0.01	34.69	0.43	< 0.01
Categorical variables												
Month	7.54	**0.33**	< 0.01	9.91	**0.49**	< 0.01	6.93	**0.31**	< 0.01	9.39	**0.47**	< 0.01
Site	5.69	**0.31**	< 0.01	1.00	0.07	0.42	5.56	**0.35**	< 0.01	1.00	0.09	0.43
Year	3.66	0.04	0.02	4.39	0.07	< 0.01	3.08	0.04	0.03	3.95	0.08	0.02
Year * Month	5.08	0.44	< 0.01	8.90	**0.68**	< 0.01	4.27	0.40	< 0.01	7.84	0.65	< 0.01
Relative discharge quartile	8.26	**0.24**	< 0.01	10.81	**0.38**	< 0.01	8.48	**0.28**	< 0.01	14.25	**0.49**	< 0.01

most sites with a mean density of 18.6 individuals l^{-1} and biomass of 135.6 µg l^{-1}, mean crustacean zooplankton density is lower in the lower free-flowing reach (0.9 individuals l^{-1}) and correspondingly mean total zooplankton biomass at downstream sites (10.8 µg l^{-1}) is also tenfold lower than at upstream sites (142.6 µg l^{-1}). Rotifer densities are more similar among reaches, with mean density of 223.0 l^{-1} at the two upstream sites and 207.6 l^{-1} at the five downstream sites. Zooplankton densities in the lower free-flowing Minnesota River are similar to those found in the lower reaches of the Missouri River (Havel et al. 2009), the lower Illinois River (Sass et al. 2014), and other turbid prairie rivers (Thorp and Mantovani 2005). Whereas, crustacean zooplankton densities downstream of Minnesota River impoundments are more similar to those found in the Mississippi River above and within Lake Pepin (Burdis and Hoxmeier 2011; Burdis and Hirsch 2017) and the Ohio River (Thorp and Mantovani 2005; Sluss and Jack 2013). In the Illinois River, Sass et al. (2014) reported mean zooplankton biomass (collected with 55 µm filter) of 14.6 µg l^{-1} in the lower reaches (108.0 rotifers l^{-1} and 4.4 custacean zooplankton l^{-1}) where invasive carps are most abundant and 7.8 µg l^{-1} in the upper reaches (29.4 rotifers l^{-1} and 8.3 crustacean zooplankton l^{-1}) where invasive carps are less abundant. Burdis and Hoxmeier (2017) compared the maximum rotifer density of 2,385 l^{-1} observed in the main channel of the Mississippi River with maximum rotifer densities reported in literature and found that maximum rotifer densities varied widely, with maximum main channel densities of > 18,000 l^{-1} reported in the Great Ouse River, England (see Bass et al. 1997). In the Minnesota River, we observed maximum rotifer densities at all sites during May of 2017, varying 765–1,684 individuals l^{-1}, which corresponded with typical discharge (mean relative discharge = 0.58) compared to relatively high discharge during May of 2018 (mean relative discharge = 0.90). Havel et al. (2009) reported relatively similar maximum rotifer densities of 1,800-2,200 l^{-1} in the main channel of the lower Missouri River, but these occurred during summer low flows. Crustacean zooplankton diversity in the Minnesota River is similar to downstream in the Mississippi River (Burdis and Hoxmeier 2017; Burdis and Hirsch 2017); Burdis and Hirsch (2017) noting that diversity was significantly greater than in typical Minnesota lakes, likely due to the inherent complexity of floodplain river systems. Within the Missouri River, including reaches downstream of impoundments, Dickerson et al. (2011) also reported diverse zooplankton communities (34 rotifer genera, 49 cladocera species, and 22 copepod species) with similar common and abundant taxa including the crustacean zooplankton species *Diacyclops thomasi*, *Daphnia retrocurva*, *Leptodiaptomus siciloides*, and *Mesocyclops edax* and the rotifer genera *Keratella*, *Polyarthra*, *Brachionus*, *Trichocerca*, and *Synchaeta*. Hirsch (2014) reported species richness of crustacean zooplankton only varying 1–15 among 149 Minnesota Lakes which emphasizes the diversity of zooplankton in the Minnesota River, and other lotic systems, compared to lentic systems.

Factors associated with discharge that influence planktonic organisms, and particularly zooplankton, are well established (Soballe and Kimmel 1987; Reynolds 2000; Viroux 2002; Lair 2006). The constant downstream transport in lotic systems is a dominant force influencing plankton community dynamics and many studies have demonstrated that water residence time has a significant positive relationship with abundance and density of phytoplankton and zooplankton, and influences species

composition (e.g., Soballe and Kimmel 1987; Basu & Pick 1996; Reckendorfer et al. 1999; Burdis and Hirsch 2017). Impoundments, floodplain lakes, and inshore retention zones have greater water residence time than mid-channel habitats, providing important sources of plankton that is vital for lotic ecosystem function and health. Unlike other studies (Pace et al. 1992; Thorp et al. 1994), but similar to Burdis and Hoxmeier (2014), we found that discharge had little influence on total zooplankton biomass, and that some taxa were most abundant (e.g., *Bosmina spp.*, cyclopoids) during periods of high relative discharge. However, corroborating general theories, we found a negative relationship between phytoplankton biovolume and relative discharge. Although man-made dams can have negative impacts on riverine ecosystems by fragmenting populations (e.g., fish, freshwater mussels) and altering habitats, riverine lakes like Lac qui Parle Lake, naturally provide increased plankton biomass and important forage and habitats for fishes and other biota. Most unaltered rivers with natural flow regimes also have important connectivity with floodplain habitats (Poff et al. 1997). These connections allow fish and other biota to utilize the floodplain habitat during flood pulses and nutrients and plankton to flush into the main channel as water levels recede. Gorski et al. (2013) postulate that heterogeneity and connectivity of floodplain habitats is important for diverse zooplankton assemblages that are important for higher trophic organisms and ecosystem health. Although we did not directly evaluate plankton communities in floodplain habitats, Nickel (2014) corroborated this hypothesis and showed that Minnesota River backwaters generally had greater diversity and densities of crustacean zooplankton than nearby main channel habitats. Similarly in the Missouri River, Dzialowski et al. (2013) showed that zooplankton were more abundant and diverse, phytoplankton were more diverse, and certain phytoplankton taxa were more abundant in created backwater habitats than in chute (i.e., side channel) or main channel habitats. Undoubtedly, water retention zones (habitat complexities, floodplain lakes, side channels, impoundments) within the Minnesota River are important for abundant and diverse phytoplankton and zooplankton communities.

Positive relationships between nutrients (i.e., phosphorous, nitrogen), turbidity, phytoplankton biomass (frequently represented by Chl-a concentration), and zooplankton biomass often exist when compared among systems (e.g., Soballe and Kimmel 1987; Basu and Pick 1996; Heiskary and Markus 2001; Heiskary et al. 2016). However, oftentimes these relationships are not as strong or differ when evaluating temporal or spatial variability within an individual system (Thorp and Mantovani 2005; Bukaveckas et al. 2011). For example, when comparing zooplankton densities among seven rivers, Thorp and Mantovani (2005) found positive relationships between rotifer density and turbidity and negative relationships between crustacean zooplankton density and turbidity. However, Thorp and Mantovani (2005) found opposite relationships when evaluating zooplankton communities within one of these rivers (i.e., Kansas River). During this study, the only strong correlations we identified between water chemistry and plankton biomass variables was a positive correlation between Chl-a and phytoplankton biomass (i.e., diatoms, blue-green algae, and green algae biomass) and a negative correlation between rotifer biomass and Si concentration. We also identified strong correlations between TP and turbidity (i.e., positive relationship with TSS and negative relationship with Secchi depth)

and TP and nitrogen (i.e., positive relationship with TKN and a negative relationship with N+N). Interestingly, we did not find a strong relationship between Chl-a and phosphorous concentrations. Multivariate analyses (i.e., NMDS, PERMANOVA) also revealed that Ortho-P, Si, and TDS explained some variability ($r^2 \leq 0.20$) in plankton communities when we excluded upstream sites and the month of May from analyses, but these relationships are difficult to interpret. We may not have identified many strong relationships between plankton communities and water chemistry parameters because water chemistry was relatively similar among sites in the Minnesota River compared to the variability often observed among systems. Basu and Pick (1996) demonstrated a strong relationship between TP and Chl-a concentration (representing phytoplankton) and a weak relationship between Chl-a and zooplankton biomass across 31 Ontario and Quebec, Canada, rivers sampled during July 1994. For their study, TP varied from as little as 7 µg l^{-1} up to 212 µg l^{-1} across the 31 rivers while during our study TP varied 105–396 µg l^{-1}, and was unlikely a limiting factor. We also found much higher Chl-a concentration in the Minnesota River (varying 14.4–156.0 µg l^{-1}) during June and July compared to Basu and Pick (1996) that found Chl-a varying 1.9–27.6 µg l^{-1} among rivers. The Minnesota River is a very productive system that we suspect is rarely nutrient limited, and thus physical forces (e.g., discharge) that vary spatially and temporally likely have a greater influence on plankton communities than water chemistry and nutrient availability.

Most studies in lotic systems identify abiotic rather than biotic factors primarily regulating plankton community dynamics (Reynolds 2000; Lair 2006). However, several studies provide evidence that under certain abiotic conditions, biotic factors may become increasingly important for influencing lotic plankton communities (e.g., Pace et al. 1998; Akopian et al. 1999; Thorp and Casper 2003; Guelda et al. 2005; Burdis and Hirsch 2017). For instance, Pace et al. (1998) attributed significant declines in phytoplankton and zooplankton with the invasion of zebra mussels while Guelda et al. (2005) demonstrated that zooplankton can be biologically limited from the bottom-up by phytoplankton production. Additionally, Thorp and Mantovani (2005) suggest that positive relationships between turbidity and rotifer density may be an indirect consequence of reduced competition and predation from other zooplankton and predators (e.g., fish) that are more susceptible to suspended sediments. During our study, we did not evaluate biological factors that may influence plankton communities in the Minnesota River, but it is difficult to ignore the possibility. Although we do not suspect the Minnesota River is often nutrient limited, we do hypothesize that abundant populations of planktivorous fishes such as Bigmouth Buffalo, Gizzard Shad, and Emerald Shiner may influence zooplankton communities, at least at smaller spatial and temporal scales (e.g., within backwater habitats, downstream of dams, during periods of low flow). For instance, similar to what was observed by Akopian et al. (1999) in the Marne River, France, high densities of crustacean zooplankton below dams may quickly diminish downstream due to fish predation.

Climate change projections suggest Minnesota will likely receive increasingly more frequent and greater magnitude heavy rain-fall events (Moss et al. 2017). These changes, coupled with extensive artificial drainage within the Minnesota River watershed, will likely result in an increased frequency, duration, and magnitude of flood events. Consequently, changing hydrology will affect

the Minnesota River ecosystem, from phytoplankton to fishes. Based on results from this study and review of relevant literature, we anticipate decreased phytoplankton biomass in the Minnesota River associated with high flow events along with shifts towards smaller zooplankton (i.e., rotifer rather than crustacean zooplankton) which tend to be more tolerant of turbid and turbulent conditions (Kirk and Gilbert 1990). Yet, greater connectivity with floodplain habitats may provide increased inputs of plankton and nutrients from floodplain lakes, and it is difficult to predict how these processes interact.

Invasive species also threaten the Minnesota River ecosystem with difficult to predict consequences. Radke and Kahl (2002), Cooke et al. (2009), and Sass et al. (2014), among others, show that invasive carps can affect plankton communities, and subsequently may affect native fishes (Pendleton et al. 2017). In Mississippi River and Illinois River backwaters where rotifers typically dominate zooplankton communities numerically, Sampson et al. (2009) showed that invasive carps primarily consumed rotifers (*Keratella* spp. and *Brachionus* spp.) which are among the most abundant zooplankton in the Minnesota River. Sampson et al. (2009) found that invasive carps consumed similar diets as native Gizzard Shad, but encouragingly invasive carps consumed more dissimilar diets than Paddlefish, a state threatened species in Minnesota. Yet, backwater habitats with high relative abundances of invasive carps generally had low densities of crustacean zooplankton which are preferred prey of Paddlefish, Bigmouth Buffalo, and other fishes (Sampson et al. 2009). Also in the Illinois River and in one of the few studies evaluating invasive carp impacts on lotic plankton communities, Sass et al. (2014) found correlated declines in crustacean zooplankton and increases in rotifer zooplankton with establishment of invasive carps. Prior to invasive carp establishment in the La Grange reach of the Illinois River, Sass et al. (2014) reported mean crustacean zooplankton density (90.8 individuals l^{-1}) greater than mean densities we found in the upstream reaches of the Minnesota River (18.6 individuals l^{-1}), but after invasive carp establishment mean density significantly declined to 4.7 individuals l^{-1}. Establishment of invasive carps could have similar impacts in the Minnesota River, significantly reducing crustacean zooplankton in reaches where they currently dominate biomass of the zooplankton community. Zebra mussels are another aquatic invasive species that can influence plankton communities in lotic ecosystems (e.g., Caraco et al. 1997; Pace et al. 1998; Thorp and Casper 2003). In some instances, zebra mussel invasion is associated with greater than 70% declines in phytoplankton and zooplankton biomass (Caraco et al. 1997; Pace et al. 1998). Zebra mussels have been recently discovered (i.e., during 2016) in the Minnesota River (including veligers in samples collected for this study), and while main channel habitats may provide generally unsuitable conditions for them, they may have significant ecological impacts on small microhabitats where they may become abundant (e.g., backwaters, upstream of dams). Similarly, we hypothesize that if invasive carps establish in the Minnesota River, they will have the most significant ecological impact on plankton communities and other biota within smaller confined habitats such as backwaters (Pongruktham et al. 2010).

This study provides the first spatially and temporally comprehensive evaluation of phytoplankton and zooplankton communities in the Minnesota River, providing a rare baseline understanding of lower trophic

ecology in a lotic system prior to the potential proliferation of invasive planktivores (i.e., invasive carps and zebra mussels). Large floodplain rivers are extremely dynamic; influenced by countless natural and anthropogenic climate, landscape, and local scale processes and features (Thorp et al. 2006). Our findings, corroborated by other research on lotic systems around the world, indicates that lower trophic communities in lotic systems, like the Minnesota River, are primarily controlled by abiotic factors such as discharge (or more appropriately hydrodynamics). Consequently, lotic ecosystems and food webs are sensitive to changes in hydrology resulting from land use alteration, artificial drainage practices, and a changing climate. Unique to lotic systems, flood-pulses are a naturally important process that not only connects important sources of nutrients, phytoplankton, and zooplankton to the main channel, but also provides access to important habitat and forage for higher trophic organisms (Junk et al. 1989; Poff et al. 1997). Interestingly, we found that the greatest influence on zooplankton communities in the Minnesota River is the presence of dams and impoundments (e.g., Lac qui Parle Reservoir) which export crustacean zooplankton downstream resulting in much greater densities than are naturally produced within the main channel habitats (similar to Havel et al. 2009 and Akopian et al. 1999). Despite the strong abiotic regulation of lotic plankton communities, biotic controls may have influences, and establishment of invasive planktivores could have similar impacts on the Minnesota River ecosystem as documented in other similar rivers (e.g., Sass et al. 2014; Pace et al. 1998). With the exception of large-scale efforts to restore the natural landscape and increase water storage, maintaining natural riverine processes (e.g., natural flow regime; Poff et al. 1997), such as flood plain connectivity and natural floodplain habitats, is the greatest priority for maintaining a healthy Minnesota River ecosystem with diverse biota (Gorski et al. 2013). This study provided an invaluable baseline understanding of Minnesota River phytoplankton and zooplankton communities, providing the capability for predicting and identifying changes in the future associated with a changing environment, landscape, species assemblage, and climate.

Supplemental Material

Table S1. Water chemistry parameters measured from water samples collected from seven sites along the Minnesota River during July–October 2016, April–October 2017, and May–October 2018. Water chemistry parameters include chlorophyll a (Chl-a; µg l^{-1}), total Kjeldahl nitrogen (TKN; mg l^{-1}), total phosphorous (TP; mg l^{-1}), nitrate + nitrite (N+N; mg l^{-1}), ammonia (Ammonia-N; mg l^{-1}), total suspended solids (TSS; mg l^{-1}), total dissolved solids (TDS; mg l^{-1}), ortho-phosphorous (Ortho-P; mg l^{-1}), and silica (Si; mg l^{-1}). Attached file.

Table S2. Site specific data (date, discharge, relative discharge, Secchi depth, water temperature, etc.) associated with sampling events at seven sites along the Minnesota River during July–October 2016, April–October 2017, and May–October 2018. Attached file.

Table S3. Phytoplankton taxa densities (cells l^{-1}) and biovolumes (µm^3 l^{-1}) measured from water samples collected from seven sites along the Minnesota River during July–October 2016, April–October 2017, and May–October 2018. Attached file.

Table S4. Rotifer taxa densities (individuals l^{-1}) and biomasses (µg l^{-1}) measured from water samples collected from seven sites along the Minnesota River during July–October 2016, April–October 2017, and May–October 2018. Attached file.

Table S5. Crustacean zooplankton taxa densities (individuals l^{-1}) and biomass ($\mu g\ l^{-1}$) measured from water samples collected from seven sites along the Minnesota River during July–October 2016, April–October 2017, and May–October 2018. Attached file.

Figures S1–S44. Bar graphs depicting spatial (among sites as river kilometers) or temporal (among months April–October) trends in means (and standard error bars) of water chemistry, site measurement, phytoplankton taxa biovolume ($mm^3\ l^{-1}$), and zooplankton taxa biomass ($\mu g\ l^{-1}$) variables. We calculated site means by pooling data among months and years and monthly means by pooling data among sites and years. We used analysis of variance (ANOVA) and ln(x + 1) transformed data (except for temperature, Secchi depth, and relative discharge) to test for differences among months and sites ($\alpha = 0.05$).

References

Akopian, M, Garnier J, Pourriot R. 1999. A large reservoir as a source of zooplankton for the river: structure of the population and influence of fish predation. Journal of Plankton Research 21:285–297.

Anderson MJ. 2017. Permutational Multivariate Analysis of Variance (PERMANOVA). In N Balakrishnan, Colton T, Everitt B, Piegorsch W, Ruggeri F, Teugels JL, editors. Wiley StatsRef: Statistics Reference Online.

Arar EJ, Collins GB. 1997. Method 445.0 In vitro determination of chlorophyll a and pheophytin in marine and freshwater algae by fluorescence. U.S. Environmental Protection Agency, Washington, DC.

Baker KK, Baker AL. 1981. Seasonal succcesson of the phytoplankton in the upper Mississippi River. Hydrobiologia 83:295–301.

Bass JAB, Pinder LCV, Leach DV. 1997. Temporal and spatial variation in zooplankton populations in the River Great Ouse: an ephemeral food resource for larval and juvenile fish. Regulated Rivers: Research and Management 13:245–258.

Basu BK, Pick FR. 1996. Factors regulating phytoplankton and zooplankton biomass in temperate rivers. Limnology and Oceanography 41:1572–1577.

Bayley PB. 1995. Understanding large river: floodplain ecosystems. BioScience 45:153–158.

Burdis RM, Hirsch JK. 2017. Crustacean zooplankton dynamics in a natural riverine lake, Upper Mississippi River. J Freshwater Ecol 32:247–265.

Burdis RM, Hoxmeier RJH. 2011. Seasonal zooplankton dynamics in main channel and backwater habitats of the Upper Mississippi River. Hydrobiologia. 667:69–87.

Bukaveckas PA, MacDonald A, Aufdenkampe A, Chick JH, Havel JE, Schultz R, Angradi TR, Bolgrien DW, Jicha TM, Taylor D. 2011. Phytoplankton abundance and contributions to suspended particulate matter in the Ohio, Upper Mississippi and Missouri Rivers. Aquatic Sciences 73:419–436.

Caraco NF, Cole JJ, Raymond PA, Strayer DL, Pace ML, Findlay SEG, Fischer DT. 1997. Zebra Mussel invasion in a large, turbid river: phytoplankton response to increased grazing. Ecology 78:588–602.

Clarke KR. 1993. Non-parametric multivariate analysis of changes in community structure. Aust J Ecol. 18:117–143.

Cooke SL, Hill WR, Meyer KP. 2009. Feeding at different plankton densities alters invasive bighead carp (*Hypophthalmichthys nobilis*) growth and zooplankton species composition. Hydrobiologia 625:185–193.

Core Team R. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Culver DA, Boucherle MM, Bean DJ, Fletcher JW. 1985. Biomass of freshwater crustacean zooplankton form length-weight regressions. Can J Fish Aquat Sci. 42:1380–1390.

Cushing DH. 1990. Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. Advances in Marine Biology 26:249–293.

Dickerson KD, Medley KA, Havel JE. 2010. Spatial variation in zooplankton community structure is related to hydrologic flow units in the Missouri River, USA. River Research and Applications 26:605–618.

Dumont HJ, Van de Velde I, Dumont S. 1975. The dry weight estimate of biomass in a selection of Cladocera, Copepoda, and Rotifera from the plankton, periphyton and benthos of continental waters. Oecologia. 19:75–97.
Dzialowksi AR, Bonneau JL, Gemeinhardt TR. 2013. Comparisons of zooplankton and phytoplankton in created shallow water habitats of the lower Missouri River: implications for native fish. Aquatic Ecology 14:13–24.
Eaton AD, Clesceri LS, Greenberg AE, Franson MAH. 1998. Standard methods for the examination of water and wastewater, 20th edition. American Public Health Association, Washington, DC.
Gillooly JF, Dodson SI. 2000. Latitudinal patterns in the size distribution and seasonal dynamics of new word, freshwater cladocerans. Limnology and Oceanography 45:22–30.
Gorski K, Collier KJ, Duggan IC, Taylor CM, Hamilton DP. 2013. Connectivity and complexity of floodplain habitats govern zooplankton dynamics in a large temperate river system. Freshwater Biology 58:1458–1470.
Guelda DL, Kock RW, Jack JD, Bukaveckas PA. 2005. Experiemental evidence for density-dependent effects and the importance of algal production in determining population growth rates of riverine zooplankton. River Research and Application 21:595–608.
Havel JE, Medley KA, Dickerson KD, Angradi TR, Bolgrien DW, Bukaveckas PA, Jicha TM. 2009. Effect of main-stem dams on zooplankton communities of the Missouri River (USA). Hydrobiologia 628:121–135.
Heiskary S, Hirsch J, Rantala H. 2016. Patterns in phytoplankton and zooplankton in Minnesota Lakes. Minnesota Department of Natural Resources, Special Publication 178.
Heiskary S, Markus H. 20011111. Establishing relationships among nutrient concentrations, phytoplankton abundance, and biochemical oxygen demand in Minnesota, USA, rivers. Journal of Lake and Reservoir Management 17:251–262.
Hirsch J. 2014. National Lakes Assessment 2012: Zooplankton communities in Minnesota Lakes. USEPA National Lake Assessment Grant (#100E00998).
Junk WJ, Bayley PB, Sparks RE. 1989. The flood pulse concept in river-flooplain systems. Pages 110–127 in Dodge PD, editor. Proceedings of the International Large River Symposium. Canadian Special Publication of Fisheries and Aquatic Sciences 106.
Kirk KL, Gilbert JJ. 1990. Suspended clay and the population dynamics of planktonic rotifers and cladocerans. Ecology 71:1741–1755.
Lair N. 2006. A review of regulation mechanisms of metazoan plankton in riverine ecosystems: aquatic habitat versus biota. River Research and Application 22:567–593.
Moss P. 2017. Adopting to climate change in Minnesota 2017 report of the interagency climate adaptation team. Minnesota Pollution Control Agency.
Nickel AD. 2014. An investigation of connectivity relationships with abiotic conditions and community dynamics in Minnesota River backwater lakes. Master's thesis. Mankato, Minnesota: Minnesota State University, Mankato.
Novotny EV, Stefan HG. 2007. Stream flow in Minnesota: Indicator of climate change. Journal of Hydrology 334:319–333.
Nunn AD, Tewson LH, Cowx IG. 2012. The foraging ecology of larval and juvenile fishes. Reviews in Fish Biology and Fisheries 22:377–408.
O'Dell JW. 1993a. Determination of total Kjeldahl Nitrogen by semi-automated colorimetry.

U.S. Environmental Protection Agency, Cincinnati, Ohio.
O'Dell JW. 1993b. Determination of phosphorous by semi-automated colorimetry. U.S. Environmental Protection Agency, Cincinnati, Ohio.
Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens HH, Szoecs E, Wagner H. 2019. Community Ecology Package. R package version 2.5-4. https://CRAN.R-project.org/package=vegan
Pace ML, Findaly SEG, Fischer D. 1998. Effects of an invasive bivalve on the zooplankton community of the Hudson River. Freshwater Biology 39:103–116.
Pace ML, Findlay SEG, Lints D. 1992. Zooplankton in advective environments: the Hudson River community and a comparative analysis. Canadian Journal of Fisheries and Aquatic Sciences 49:1060–1069.
Pendleton RM, Schwinghamer C, Solomon LE, Casper AF. 2017. Competition among river planktivores: are native planktivores still fewer and skinnier in response to the Silver Carp invasion? Environmental Biology of Fishes 100:1213–1222.
Peterson BG, Carl P, Boudt K, Bennett R, Ulrich J, Zivot E, Cornilly D, Hung E, Lestel M, Balkissoon K, Wuertz D. 2018. PerfomanceAnalytics: Econometric Tools for Performance and Risk Analysis. R package version 1.5.2. https://CRAN.R-project.org/package=PerformanceAnalytics.
Poff NL, Allan JD, Bain MB, Karr JR, Prestegaard KL, Richeter BD, Sparks RE, Stromberg JC. 1997. The natural flow regime a paradigm for river conservation and restoration. BioScience 47:769–784.
Pongruktham O, Ochs C, Hoover JJ. 2010. Observations of Silver Carp (*Hypophthalmichthys molitrix*) planktivory in a floodplain lake of the lower Mississippi River basin. Journal of Freshwater Ecology 25:85–93.
Power ME. 1992 Top-down and bottom-up forces in food webs: do plants have primacy. Ecology 73:733–746.
Radke RJ, Kahl U. 2002. Effects of a filter-feeding fish [silver carp, *Hypophthalmichthys moitrix* (Val.)] on phyto- and zooplankton in a mesotrophic reservoir: results from an enclosure experiment. Freshwater Biology 47:2337–2344.
Reckendorfer W, Keckeis H, Winkler G, Schiemer F. 1999. Zooplankton abundance in the River Danube, Austria: the significance of inshore retention. Freshwater Biology 41:583–591.
Reynolds CS. 2000. Hydroecology of river plankton: the role of variability in channel flow. Hydrological processes. 14:3119–3132.
Rice EW, Baird RB, Eaton AD, Clesceri LS. 2012. Standard methods for the examination of water and wastewater, 22nd edition. American Public Health Association, Washington, DC.
Sampson SJ, Chick JH, Pegg MA. 2009. Diet overlap among two Asian carp and three native fishes in backwater lakes on the Illinois and Mississippi rivers. Biological Invasions 11:483–496.
Sanford JA, Ward JV. 2001. Revisiting the serial discontinuity concept. River Research and Applications 17:303–310.
Sass G, Hinz C, Erickson AC, McClelland NN, McClelland MA, Epifanio JM. 2014. Invasive bighead and slver carp effects on zooplankton communities in the Illinois River, Illinois, USA. Journal of Great Lakes Research 40:911–921.

Sluss TD, Cobbs GA, Thorp JH. 2008. Impact of turbulence on riverine zooplankton: a mesocosm experiment. Freshwater Biology 53:1999–2010.

Sluss T, Jack JD. 2013. Ohio River zooplankton growth rates and community assemblages and their relationship to abiotic and biotic factors in navigational dam pools. River Systems 21:55–70.

Soballe DM, Kimmel BL. 1987. A large-scale comparison of factors influencing phytoplankton abundance in rivers, lakes, and impoundments. Ecology 68:1943–1954.

Thorp JH, Black AR, Haag KH. 1994. Zooplankton assemblages in the Ohio River: seasonal, tributary, and navigation dam effects. Canadian Journal of Fisheries and Aquatic Sciences 51:1634–1643.

Thorp JH, Casper AF. 2003. Importance of biotic interactions in large rivers: an experiment with planktivorous fish, dreissenid mussels and zooplankton in the St. Lawrence River. River Research and Applications 19:265–279.

Thorp JH, Delong MD. 2002. Dominance of autochthonous autotrophic carbon in food webs of heterotrophic rivers. Oikos 96:543–550.

Thorp JH, Mantovani S. 2005. Zooplankton of turbid and hydrologically dynamic prairie rivers. Freshwater Biology 50:1474–1491.

Thorp JH, Thoms MC, Delong MD. 2006. The riverine ecosystem synthesis: biocomplexity in river networks across space and time. River Research and Applications 22:123–147.

U.S. EPA. 1994. Method 200.8: determination of trace elements in waters and wastes by inductively coupled plasma-mass spectrometry, revision 5.4. U.S. Environmental Protection Agency, Cincinnati, Ohio.

Vannote RL, Minshall GW, Cummins KW, Sedell JR, Cushing CE. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences. 37:130–137.

Viroux L. 2002. Seasonal and longitudinal aspects of microcrustacean (cladocera, copepod) dynamics in a lowland river. Journal of Plankton Research 24:281–292.

Wahl DH, Goodrich J, Nannini MA, Dettmers JM, Soluk DA. 2008. Exploring riverine zooplankton in three habitats of the Illinois River ecosystem: Where do they come from? Limnology and Oceanography 23:2538–2593.

Ward JV, Sanford JA. 1983. The serial discontinuity concept of lotic ecosystems. Pages 29–42 in Fontaine TD, Bartell SM, editors. Dynamics of Lotic Ecosystems. Ann Arbor Science, Ann Arbor, MI.

Winemiller KO. 2004. Floodplain river food webs: generalizations and implications for fisheries management. Pages 285–309 in Welcomme RL, Petr T, editors. Proceedings of the Second International Symposium on the Management of Large Rivers for Fisheries, Volume 2. Food and Agricultural Organization of the United Nations and the Mekong River Commission, 2004, Bangkok Thailand.

Zimmerman-Timm H, Holst H, Kausch H. 2007. Spatial dynamics of rotifers in a large lowland river, the Elbe, Germany: How important are retentive shoreline habitats for the plankton community. Hydrobiologia 593:49–58.

Supplemental Figures

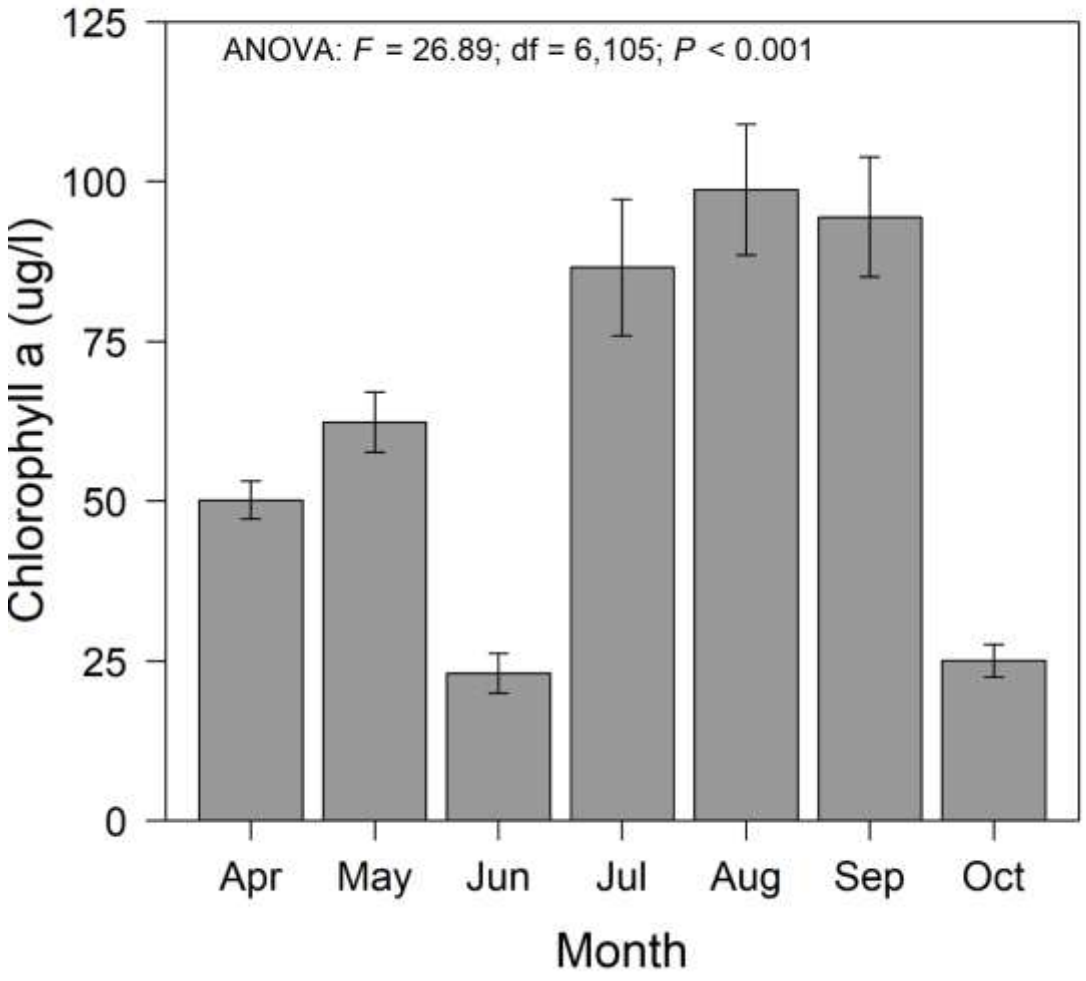

FIgure S 1. Mean (and standard error bars) Minnesota River Chlorophyll a concentration (µg/l) among months based on samples collected from seven sites during July–October 2016, April–October 2017, and May–October 2018.

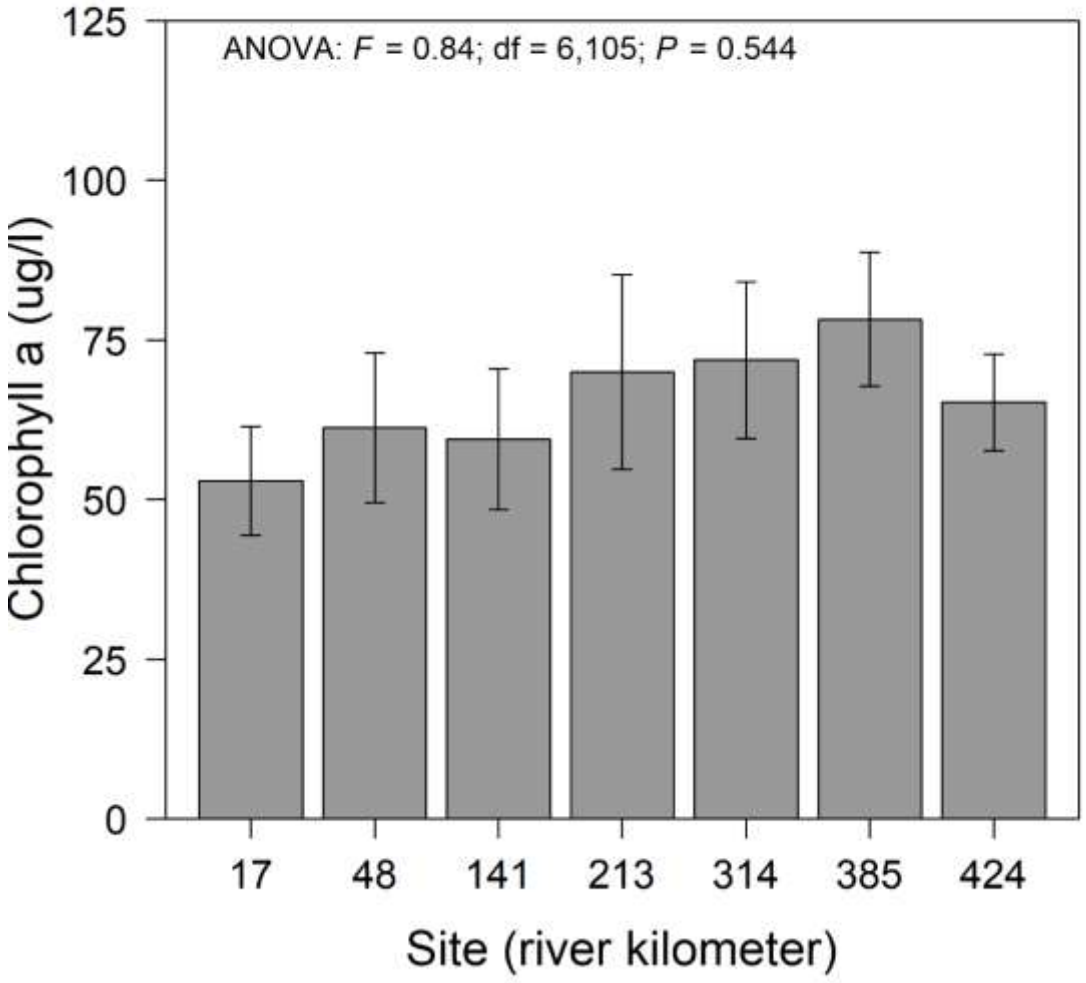

FIgure S 2. Mean (and standard error bars) Minnesota River Chlorophyll a concentration (µg/l) among sites (river kilometers) based on samples collected from all seven sites during July–October 2016, April–October 2017, and May–October 2018.

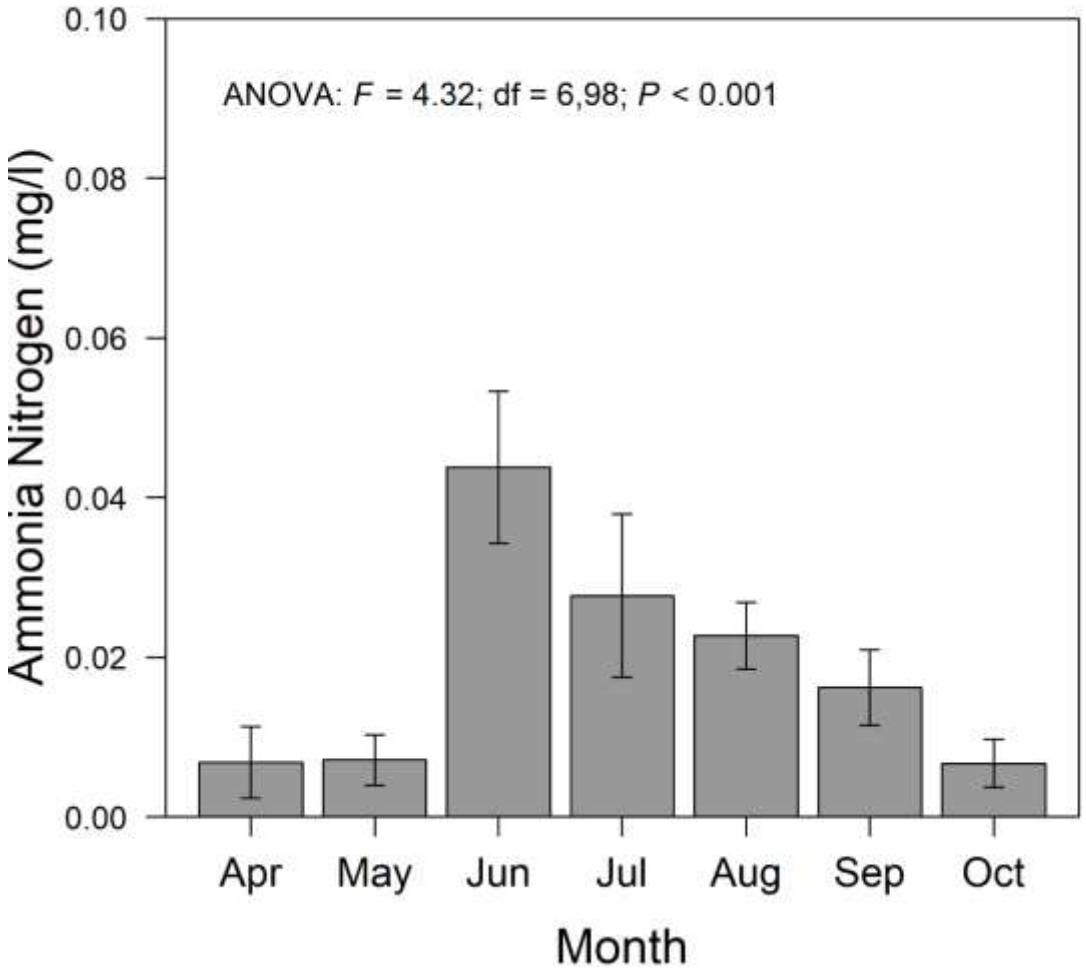

FIgure S 3. Mean (and standard error bars) Minnesota River Ammonia concentration (mg/l) among months based on samples collected from seven sites during July–October 2016, April–October 2017, and May–October 2018.

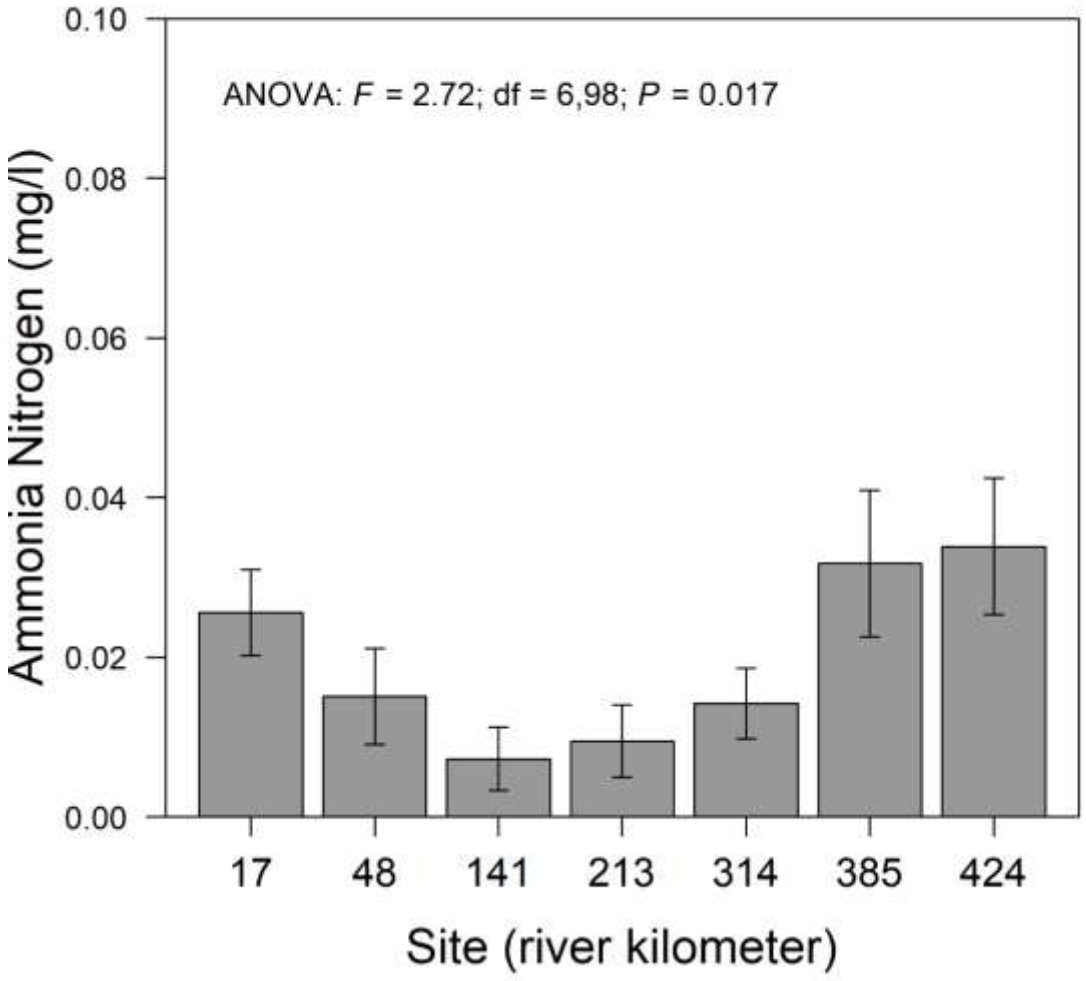

FIgure S 4. Mean (and standard error bars) Minnesota River Ammonia concentration (mg/l) among sites (river kilometers) based on samples collected from all seven sites during July–October 2016, April–October 2017, and May–October 2018.

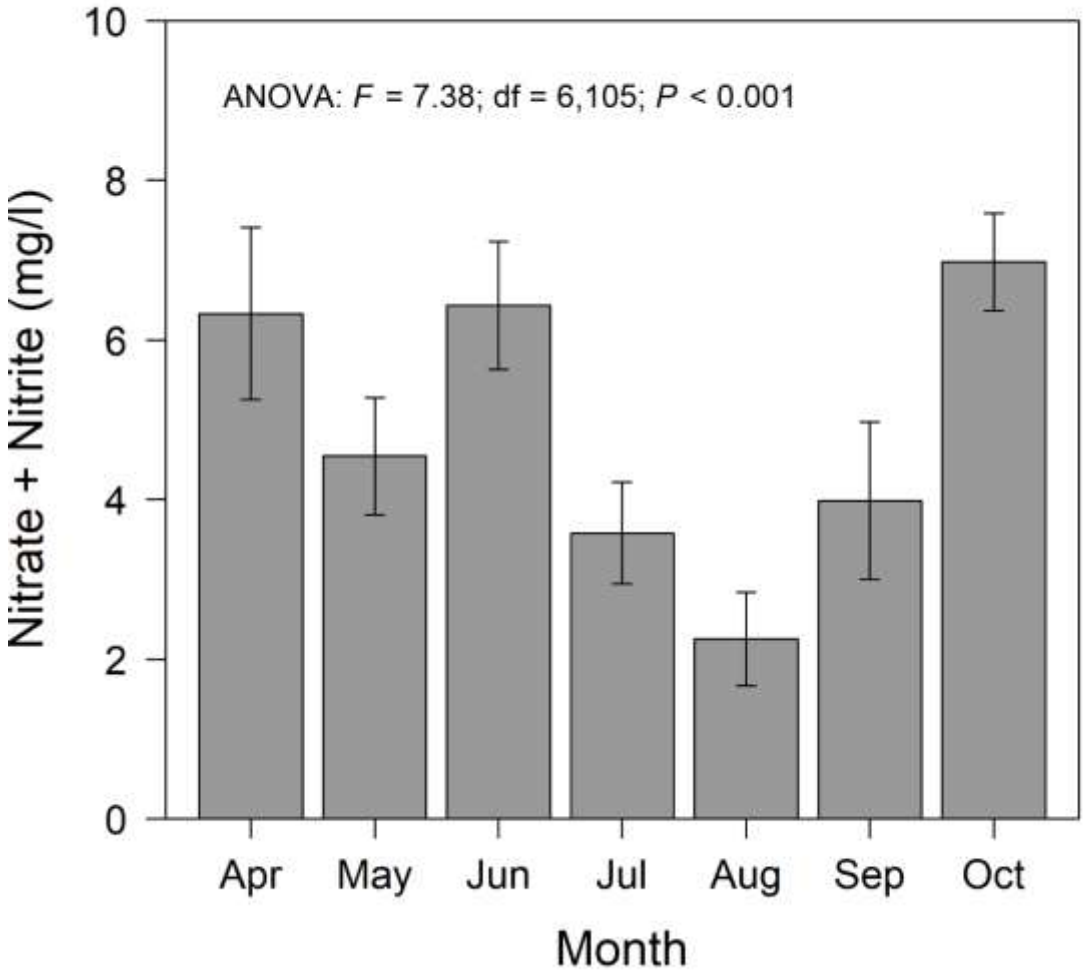

FIgure S 5. Mean (and standard error bars) Minnesota River Nitrate + Nitrite concentration (mg/l) among months based on samples collected from seven sites during July–October 2016, April–October 2017, and May–October 2018.

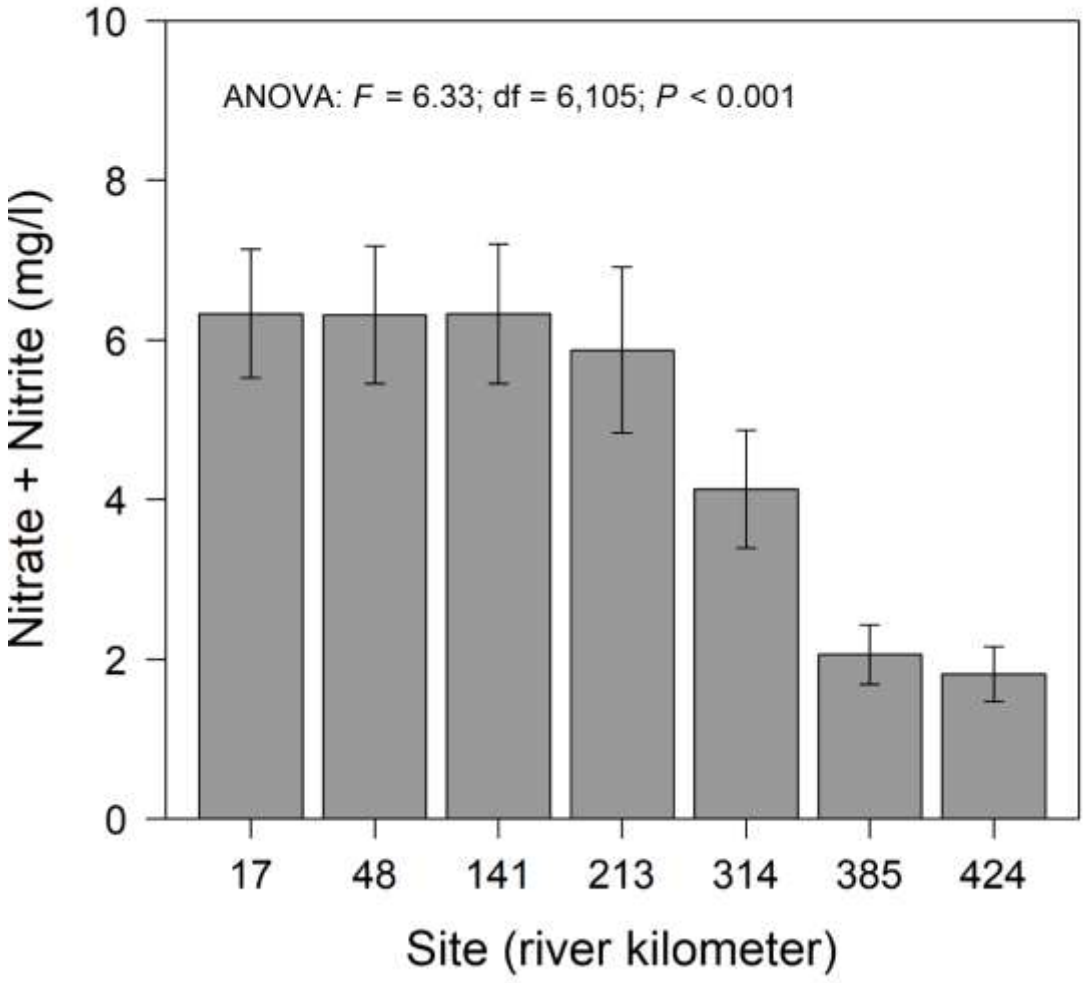

FIgure S 6. Mean (and standard error bars) Minnesota River Nitrate + Nitrite concentration (mg/l) among sites (river kilometers) based on samples collected from all seven sites during July–October 2016, April–October 2017, and May–October 2018.

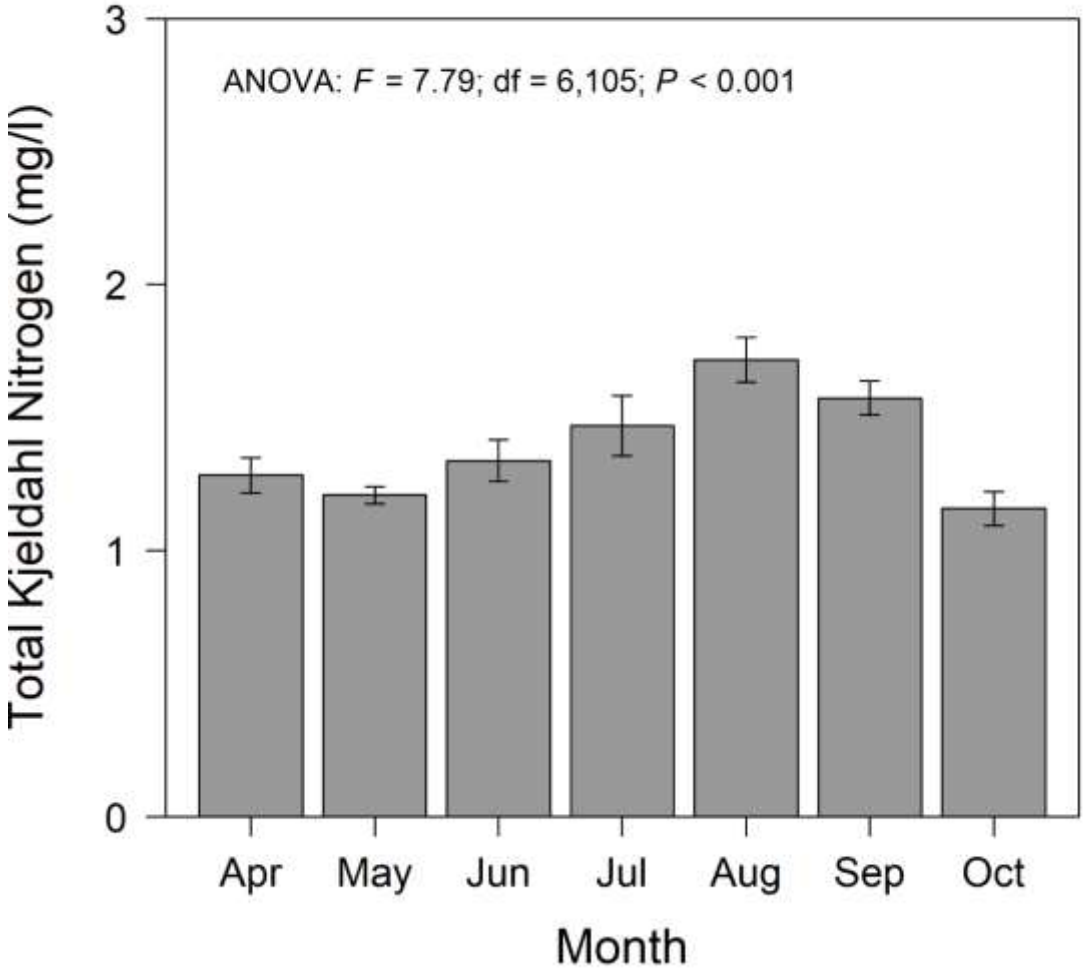

FIgure S 7. Mean (and standard error bars) Minnesota River Total Kjeldahl Nitrogen concentration (mg/l) among months based on samples collected from seven sites during July–October 2016, April–October 2017, and May–October 2018.

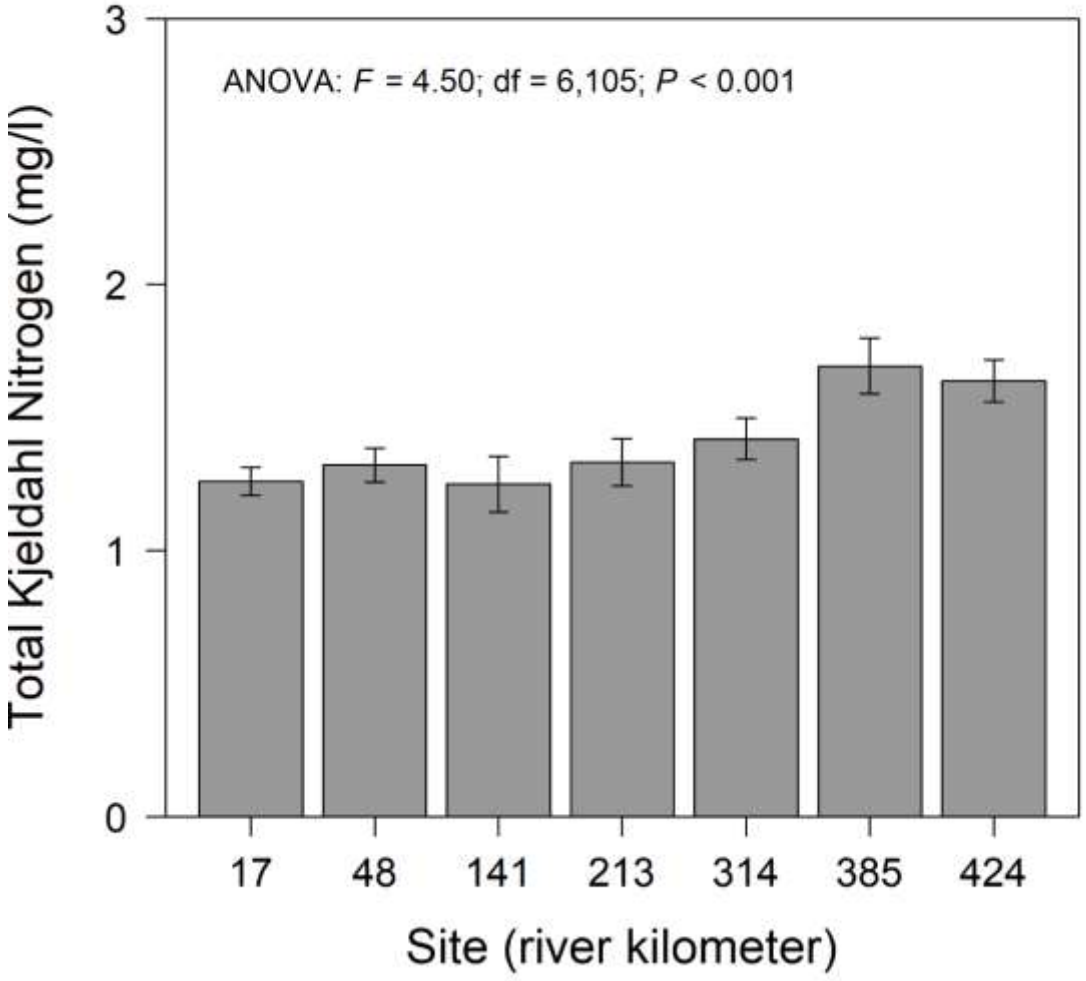

FIgure S 8. Mean (and standard error bars) Minnesota River Total Kjeldahl Nitrogen concentration (mg/l) among sites (river kilometers) based on samples collected from all seven sites during July–October 2016, April–October 2017, and May–October 2018.

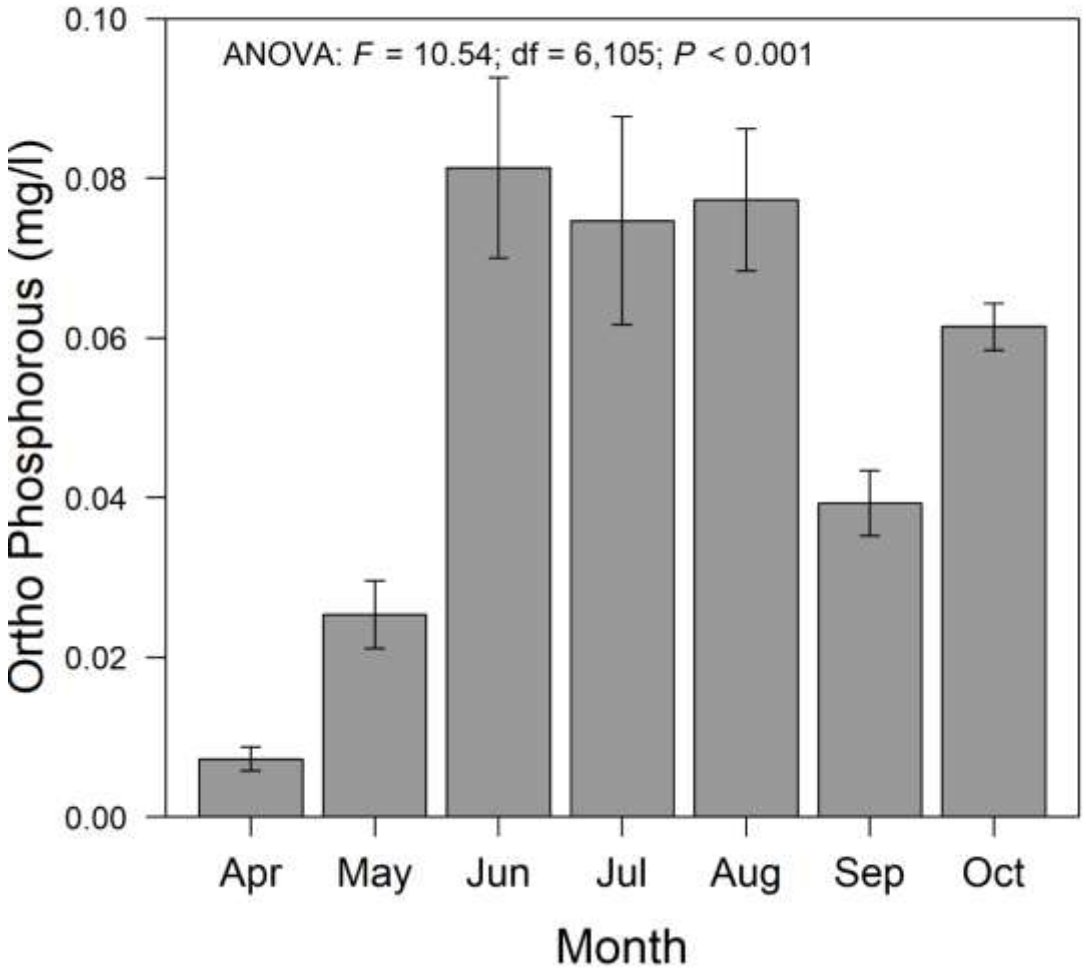

FIgure S 9. Mean (and standard error bars) Minnesota River Ortho Phosphorous concentration (mg/l) among months based on samples collected from seven sites during July–October 2016, April–October 2017, and May–October 2018.

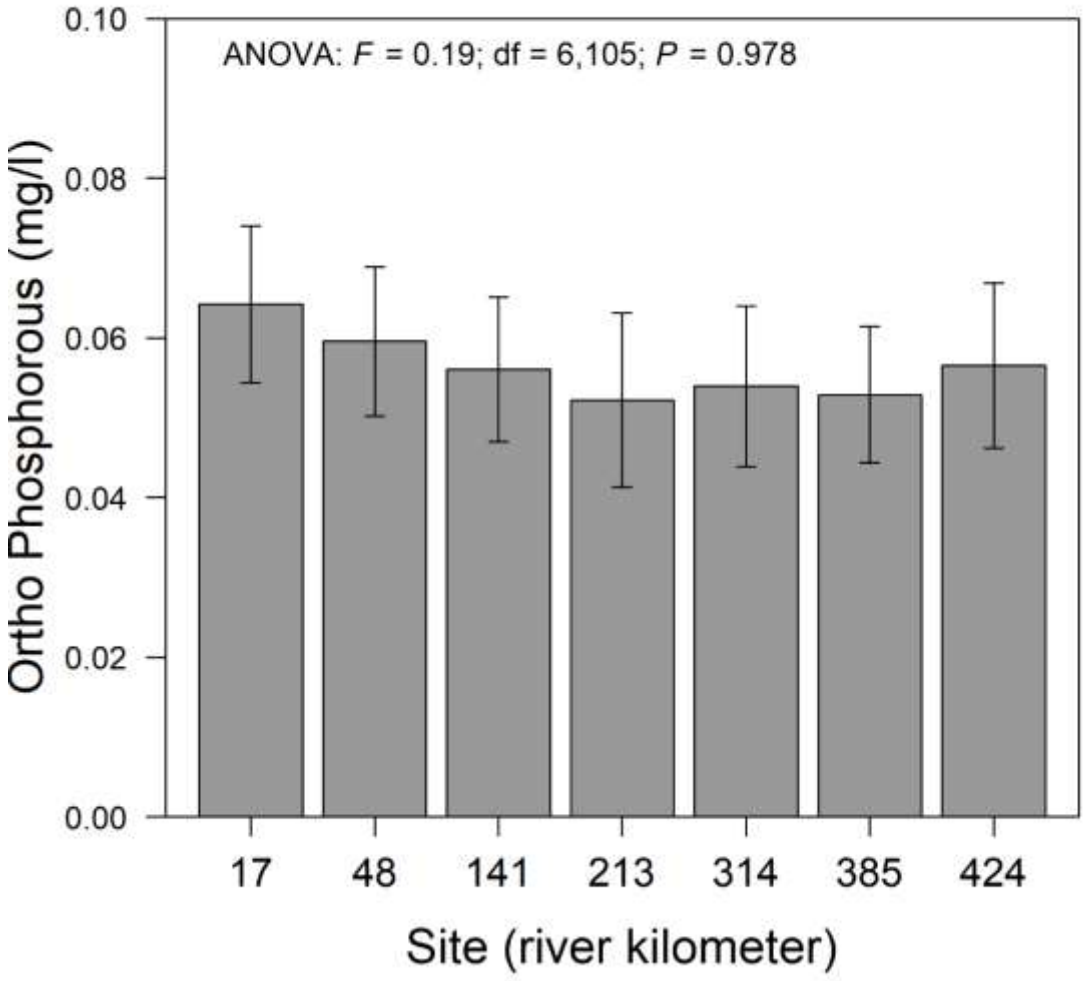

FIgure S 10. Mean (and standard error bars) Minnesota River Ortho Phosphorous concentration (mg/l) among sites (river kilometers) based on samples collected from all seven sites during July–October 2016, April–October 2017, and May–October 2018.

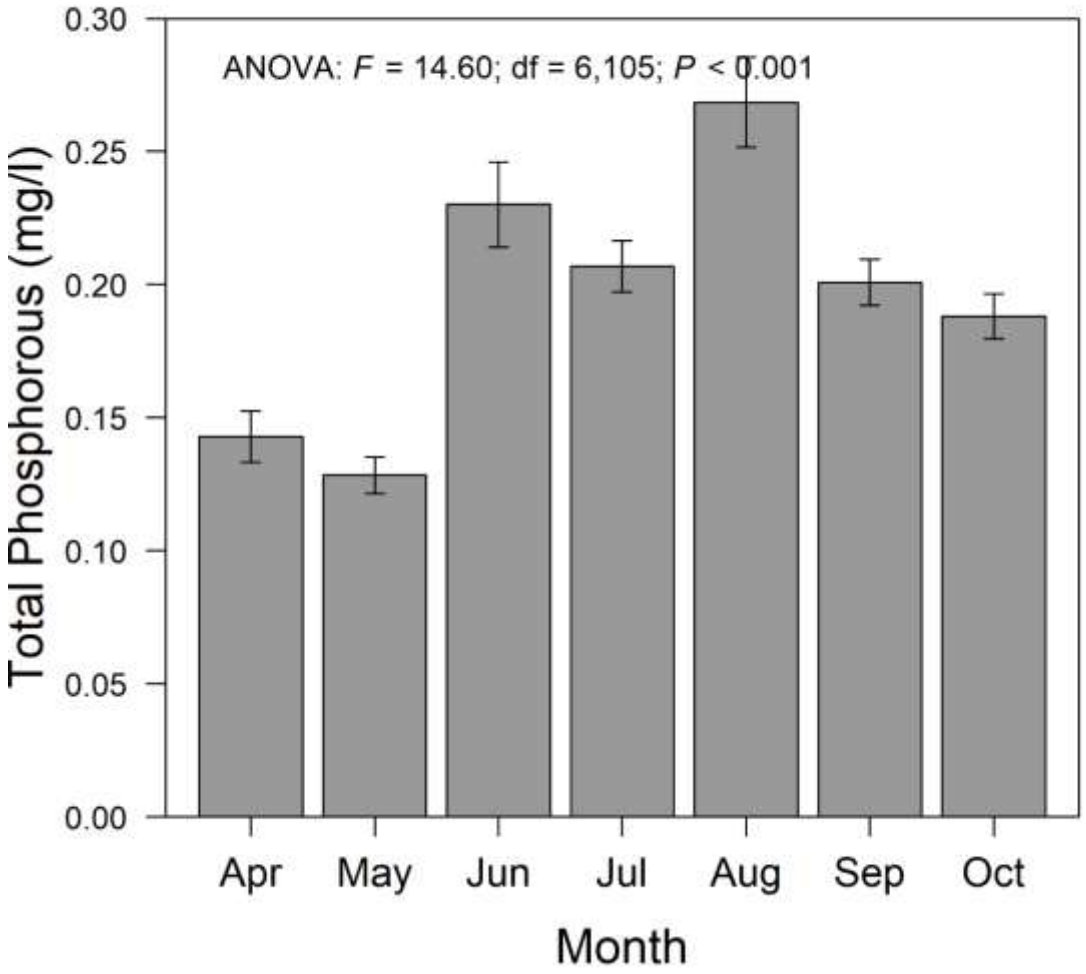

FIgure S 11. Mean (and standard error bars) Minnesota River Total Phosphorous concentration (mg/l) among months based on samples collected from seven sites during July–October 2016, April–October 2017, and May–October 2018.

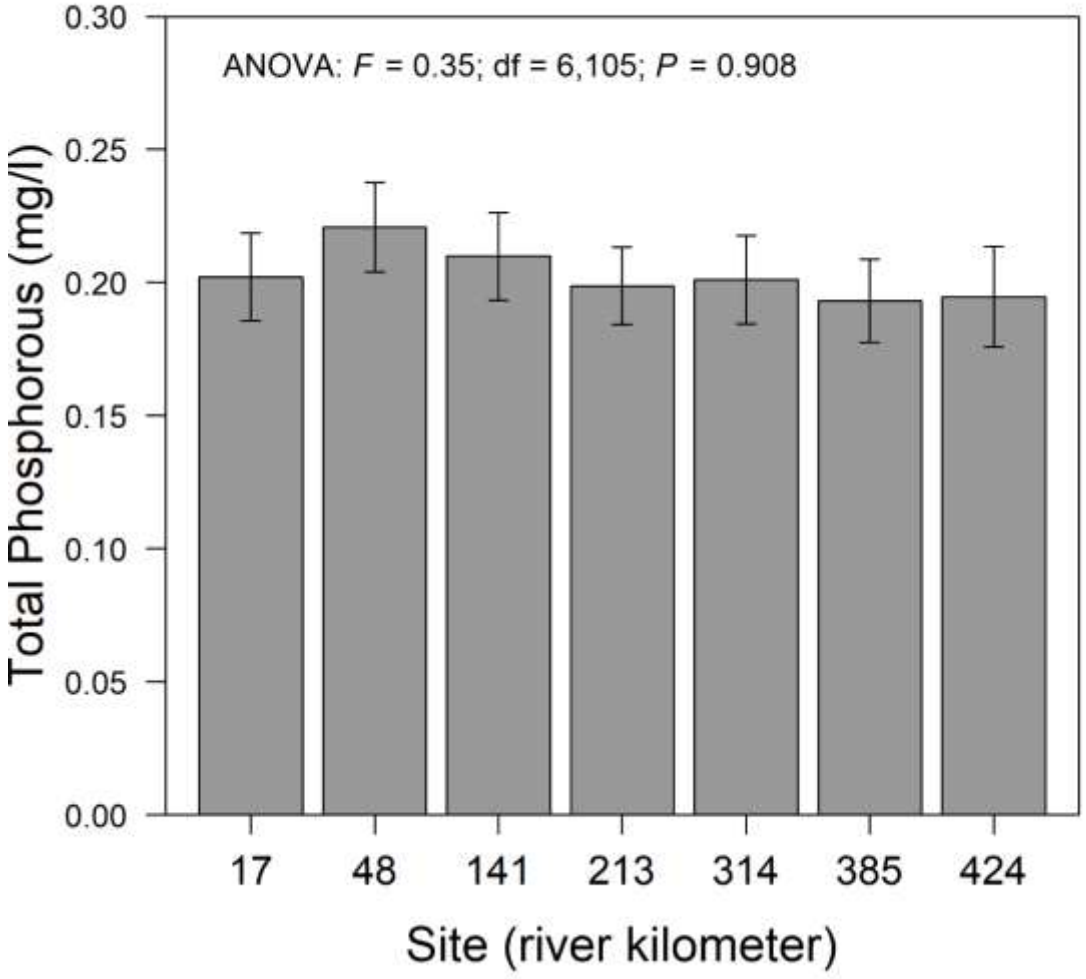

FIgure S 12. Mean (and standard error bars) Minnesota River Total Phosphorous concentration (mg/l) among sites (river kilometers) based on samples collected from all seven sites during July–October 2016, April–October 2017, and May–October 2018.

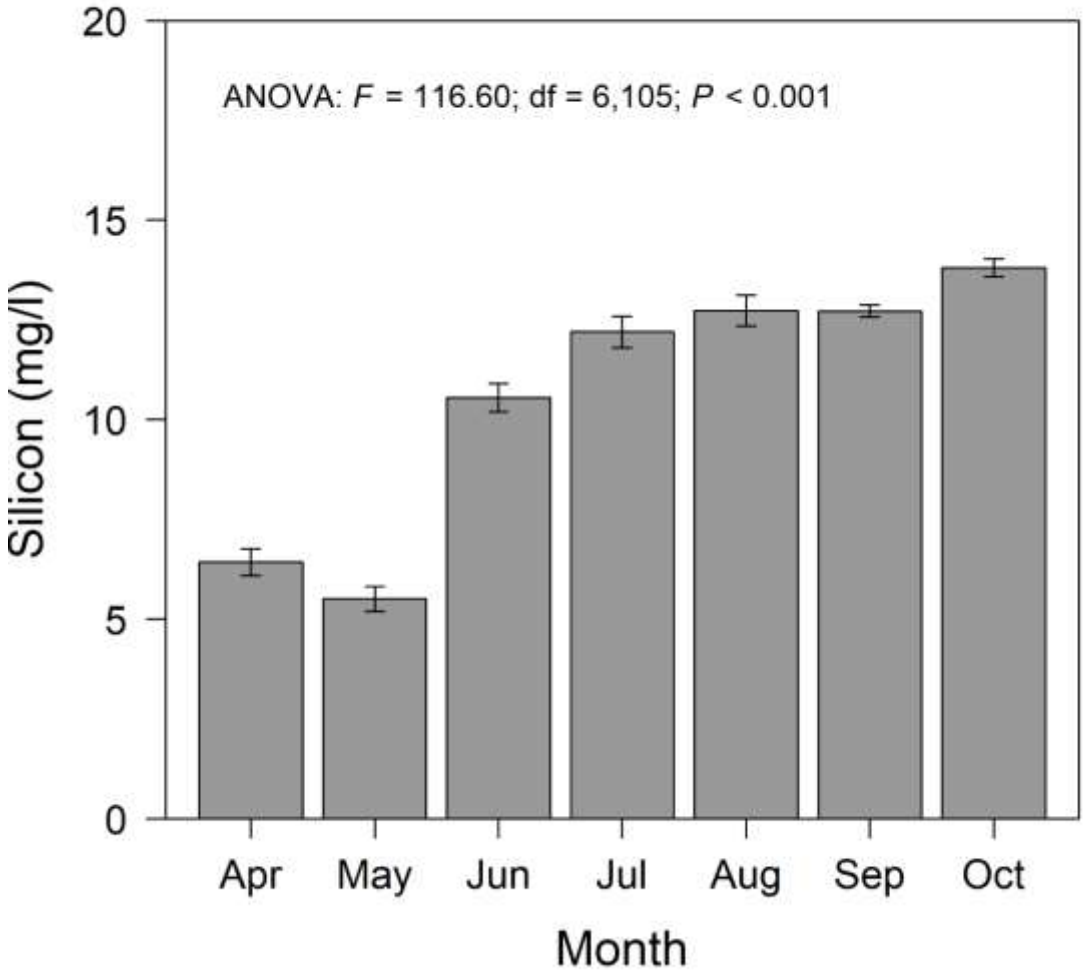

FIgure S 13. Mean (and standard error bars) Minnesota River Silicon concentration (mg/l) among months based on samples collected from seven sites during July–October 2016, April–October 2017, and May–October 2018.

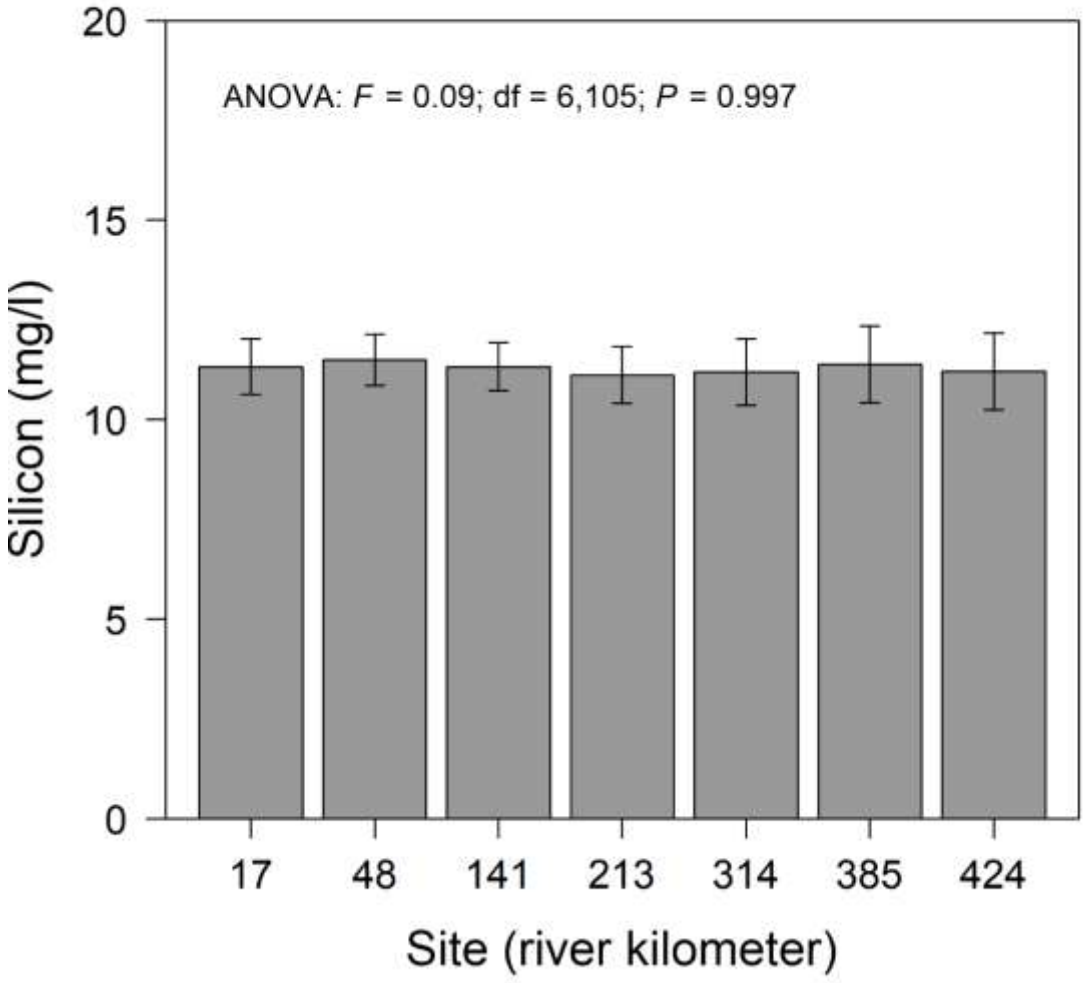

FIgure S 14. Mean (and standard error bars) Minnesota River Silicon concentration (mg/l) among sites (river kilometers) based on samples collected from all seven sites during July–October 2016, April–October 2017, and May–October 2018.

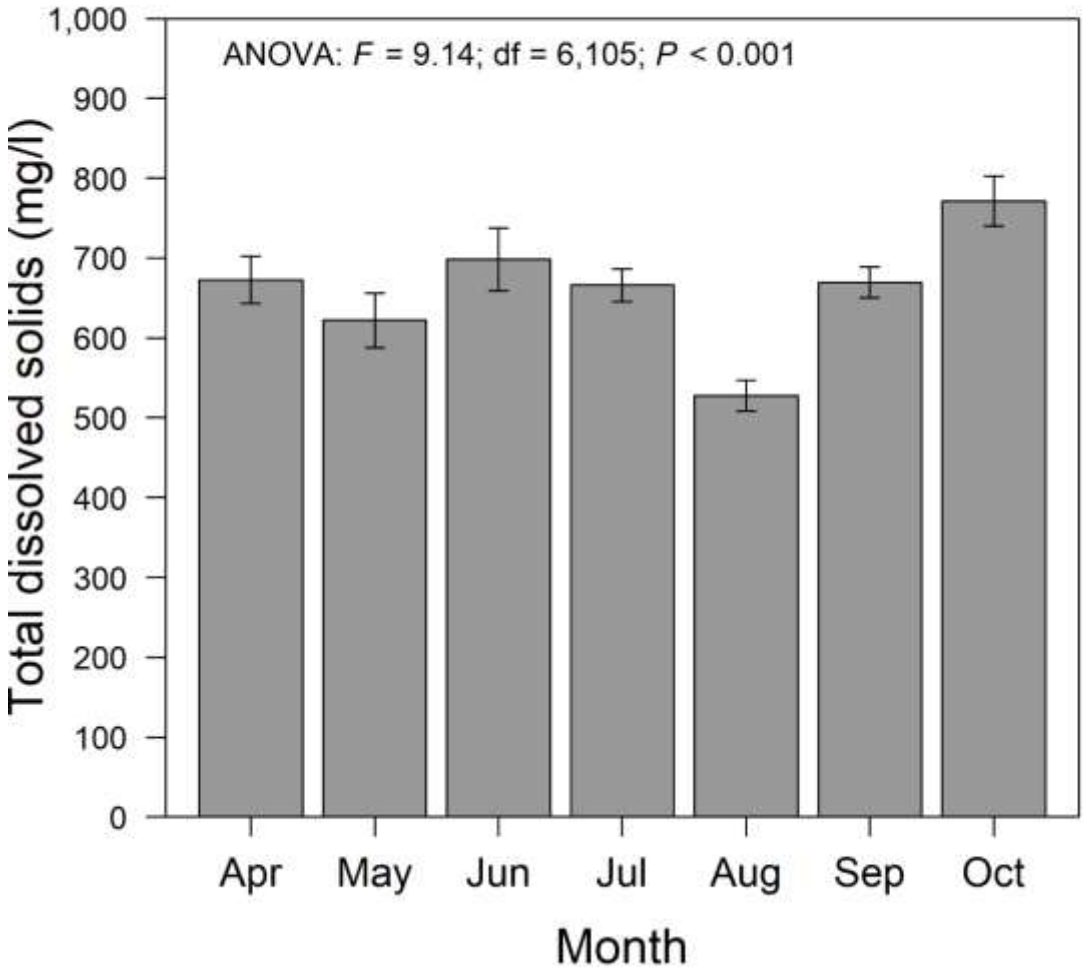

FIgure S 15. Mean (and standard error bars) Minnesota River Total Dissolved Solids concentration (mg/l) among months based on samples collected from seven sites during July–October 2016, April–October 2017, and May–October 2018.

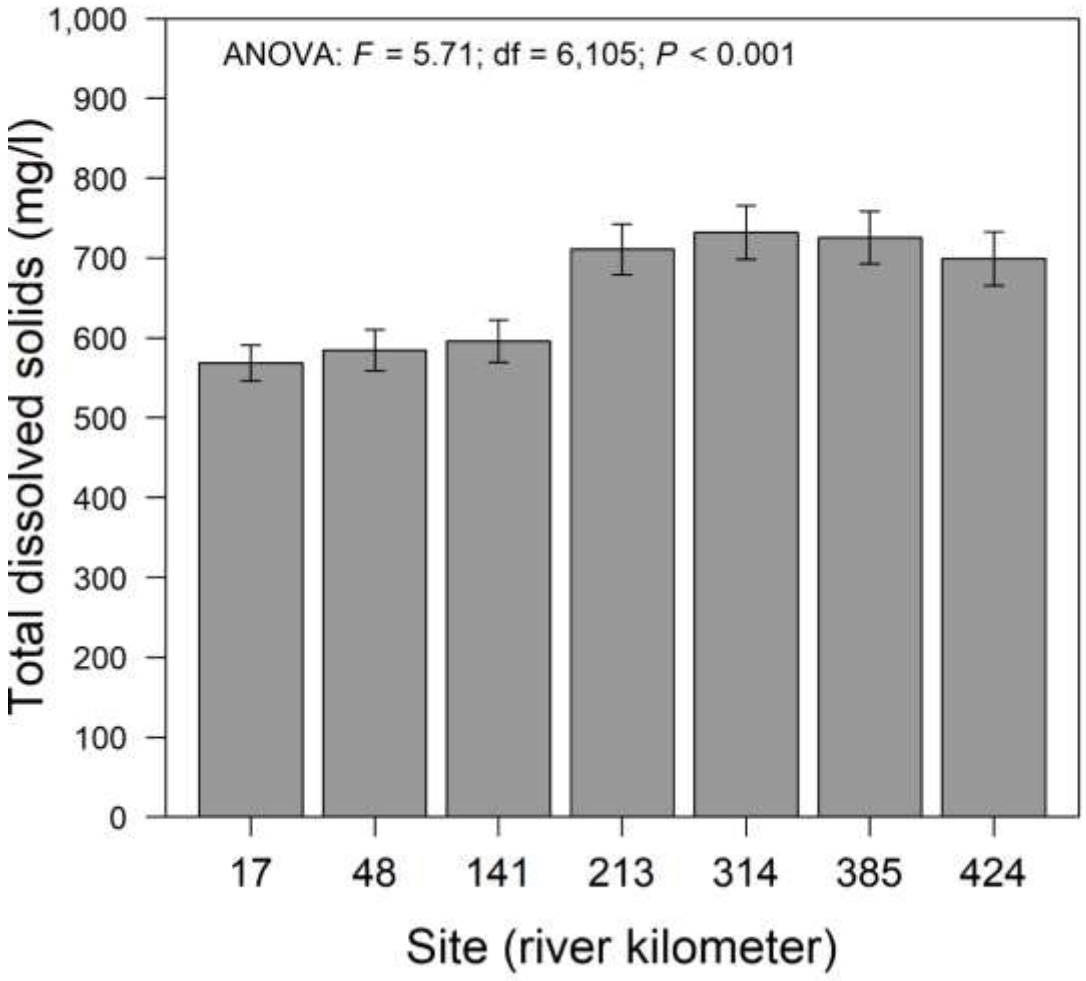

FIgure S 16. Mean (and standard error bars) Minnesota River Total Dissolved Solids concentration (mg/l) among sites (river kilometers) based on samples collected from all seven sites during July–October 2016, April–October 2017, and May–October 2018.

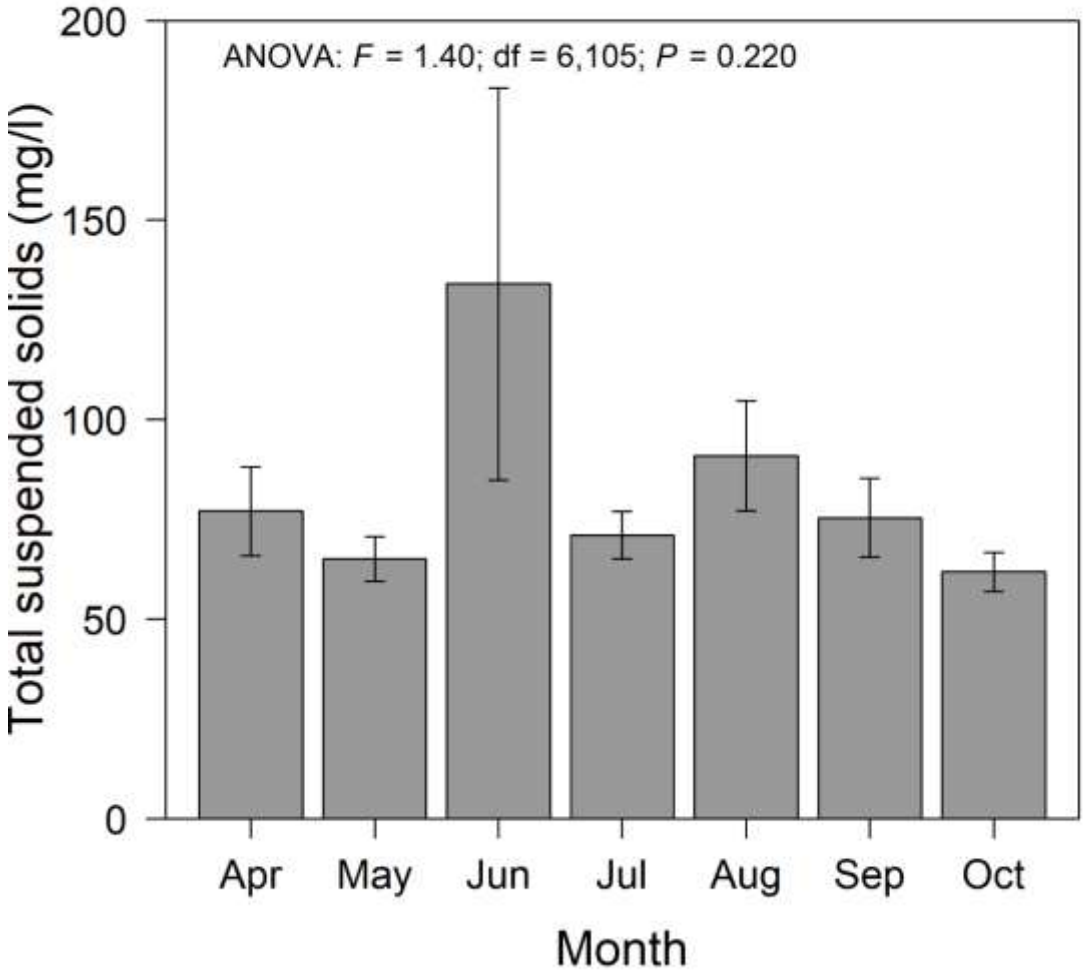

FIgure S 17. Mean (and standard error bars) Minnesota River Total Suspended Solids concentration (mg/l) among months based on samples collected from seven sites during July–October 2016, April–October 2017, and May–October 2018.

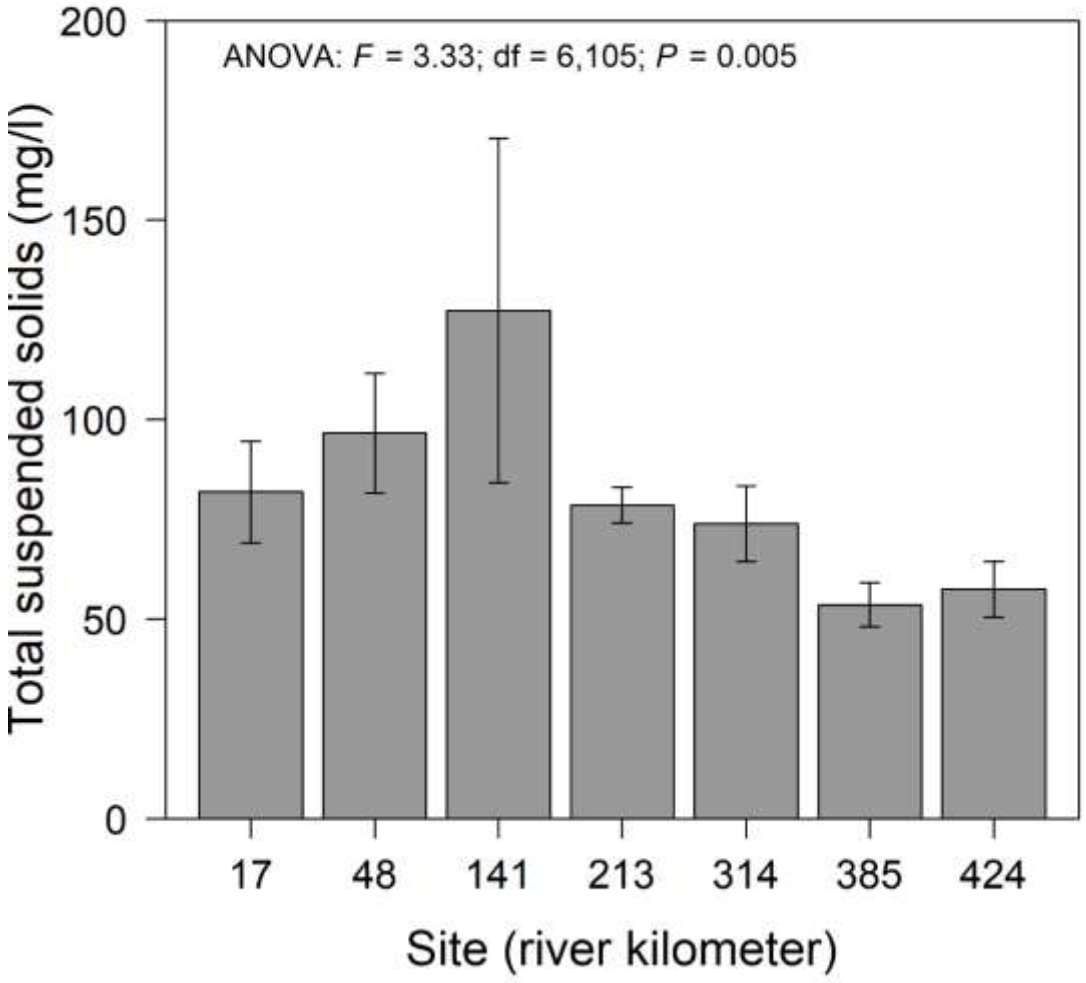

FIgure S 18. Mean (and standard error bars) Minnesota River Total Suspended Solids concentration (mg/l) among sites (river kilometers) based on samples collected from all seven sites during July–October 2016, April–October 2017, and May–October 2018.

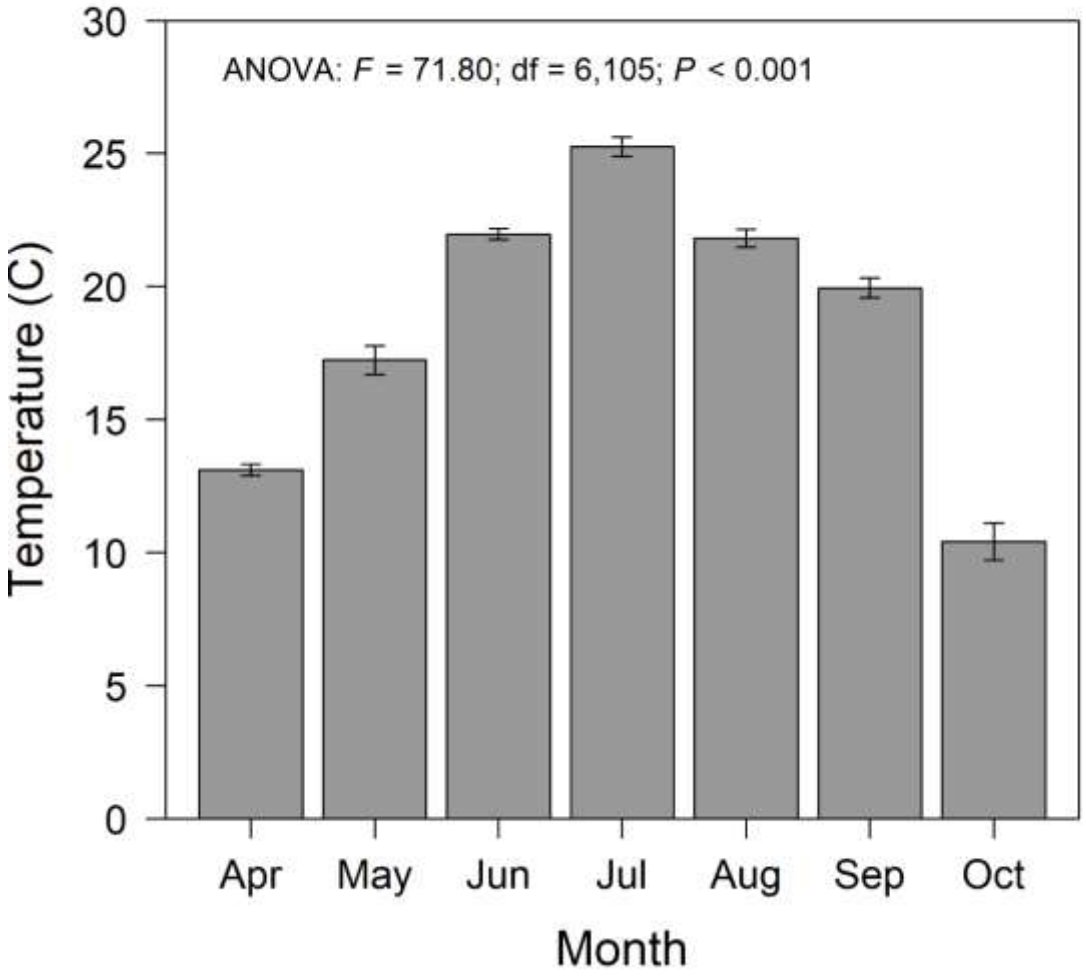

FIgure S 19. Mean (and standard error bars) Minnesota River water temperature (℃) among months based on samples collected from seven sites during July–October 2016, April–October 2017, and May–October 2018.

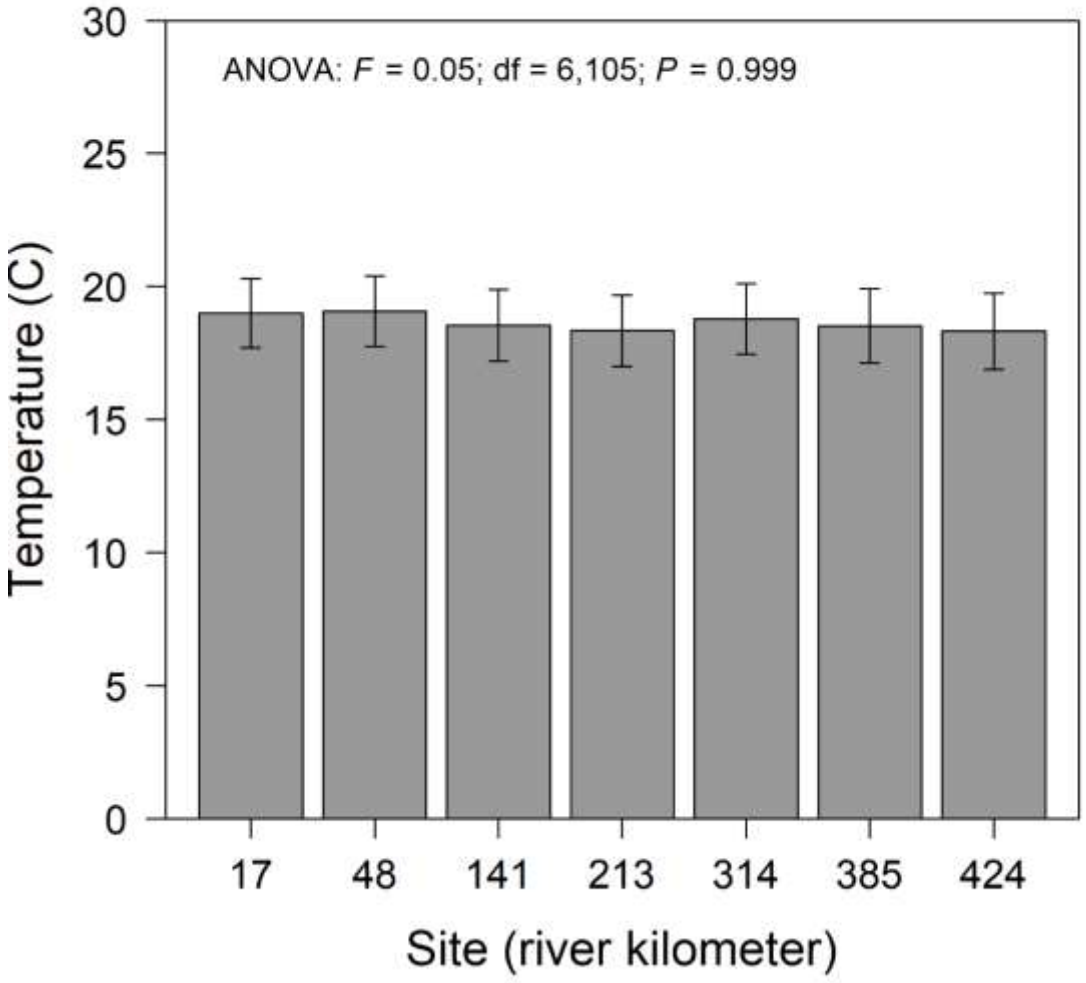

FIgure S 20. Mean (and standard error bars) Minnesota River water temperature (℃) among sites (river kilometers) based on samples collected from all seven sites during July–October 2016, April–October 2017, and May–October 2018.

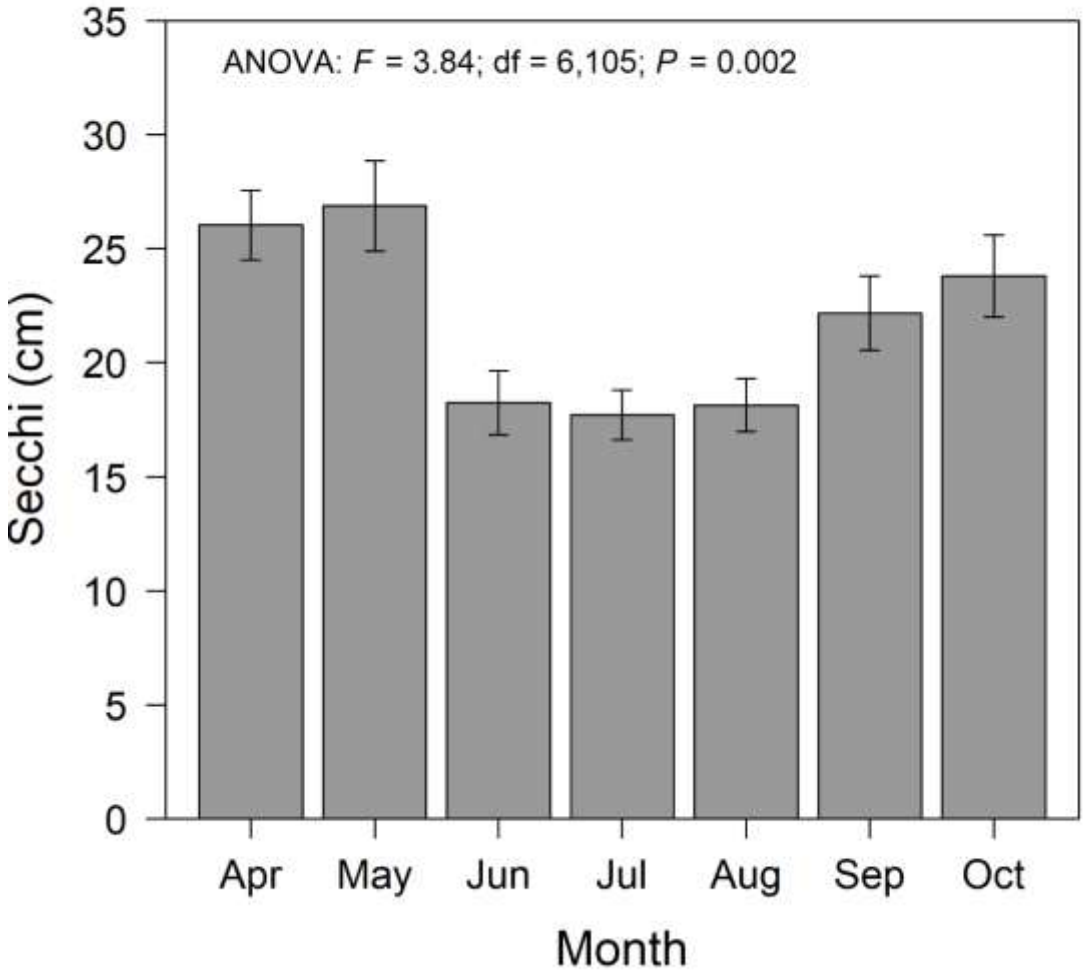

FIgure S 21. Mean (and standard error bars) Minnesota River Secchi depth (cm) among months based on samples collected from seven sites during July–October 2016, April–October 2017, and May–October 2018.

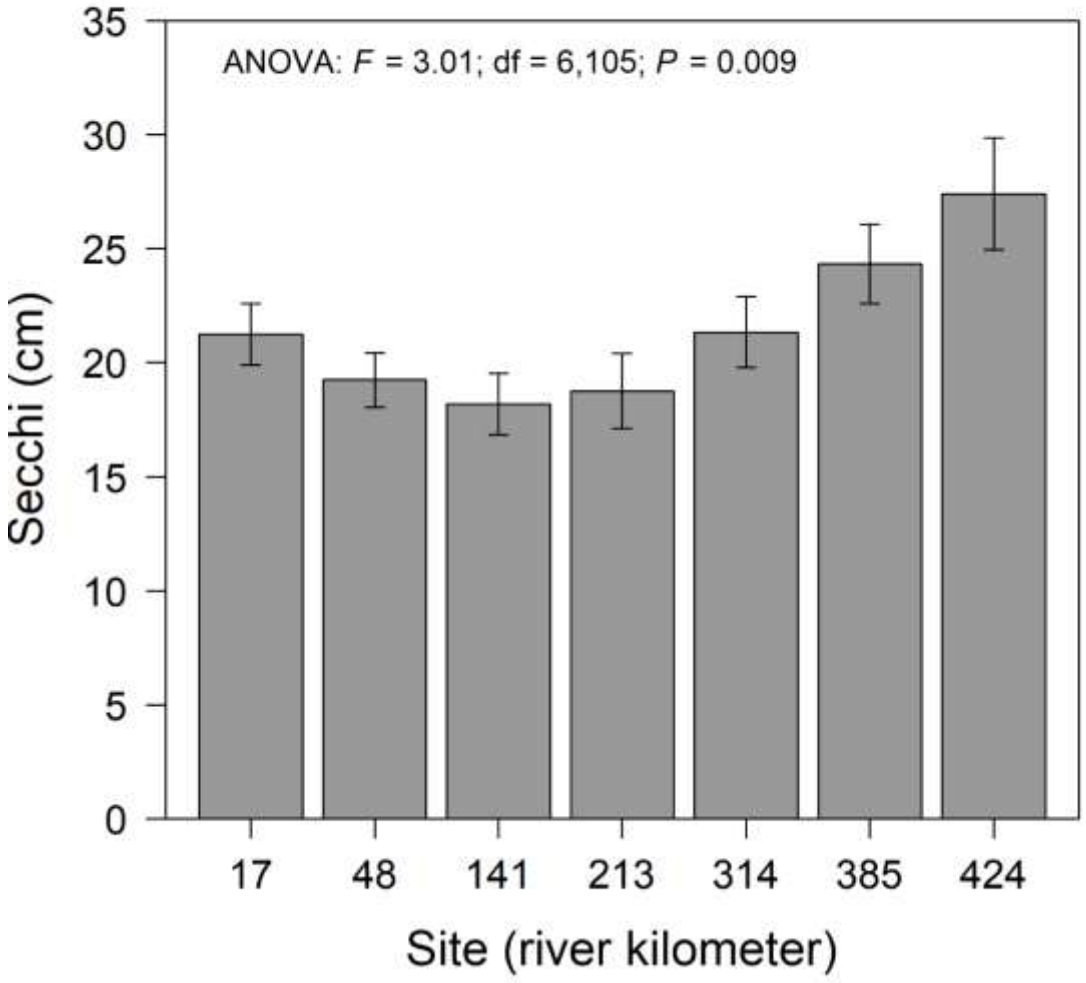

FIgure S 22. Mean (and standard error bars) Minnesota River Secchi depth (cm) among sites (river kilometers) based on samples collected from all seven sites during July–October 2016, April–October 2017, and May–October 2018.

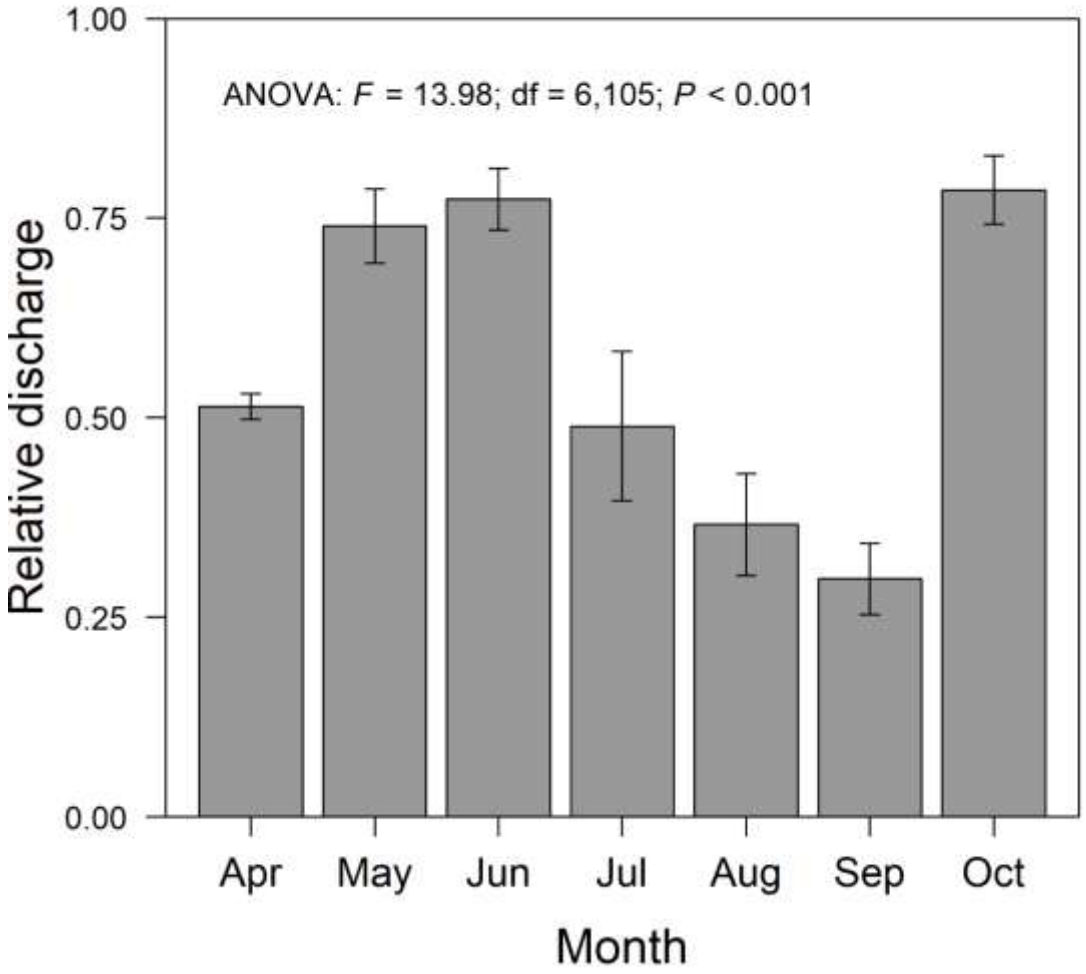

FIgure S 23. Mean (and standard error bars) monthly Minnesota River relative discharge (percentile) during sample events at seven sites during July–October 2016, April–October 2017, and May–October 2018.

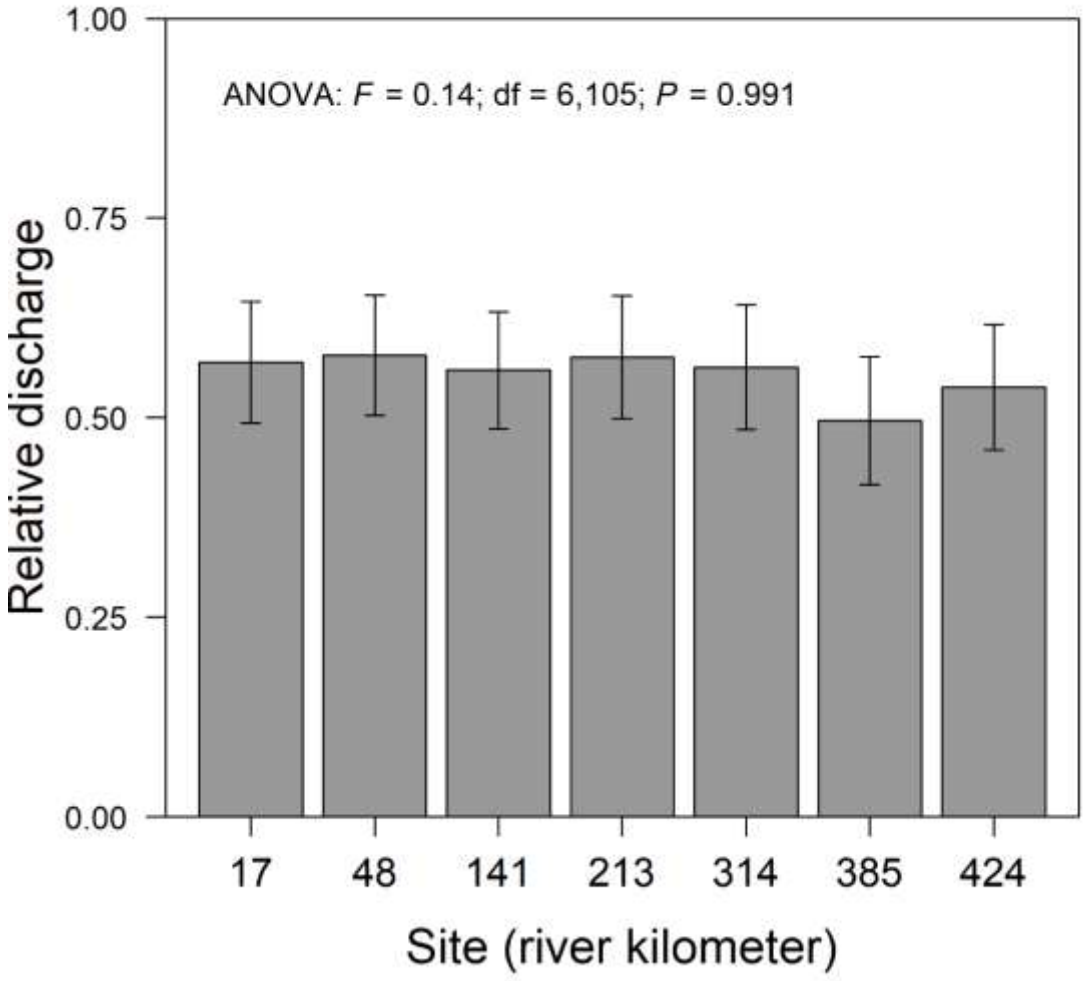

FIgure S 24. Mean (and standard error bars) Minnesota River relative discharge (percentile) during sample events for all seven sites during July–October 2016, April–October 2017, and May–October 2018.

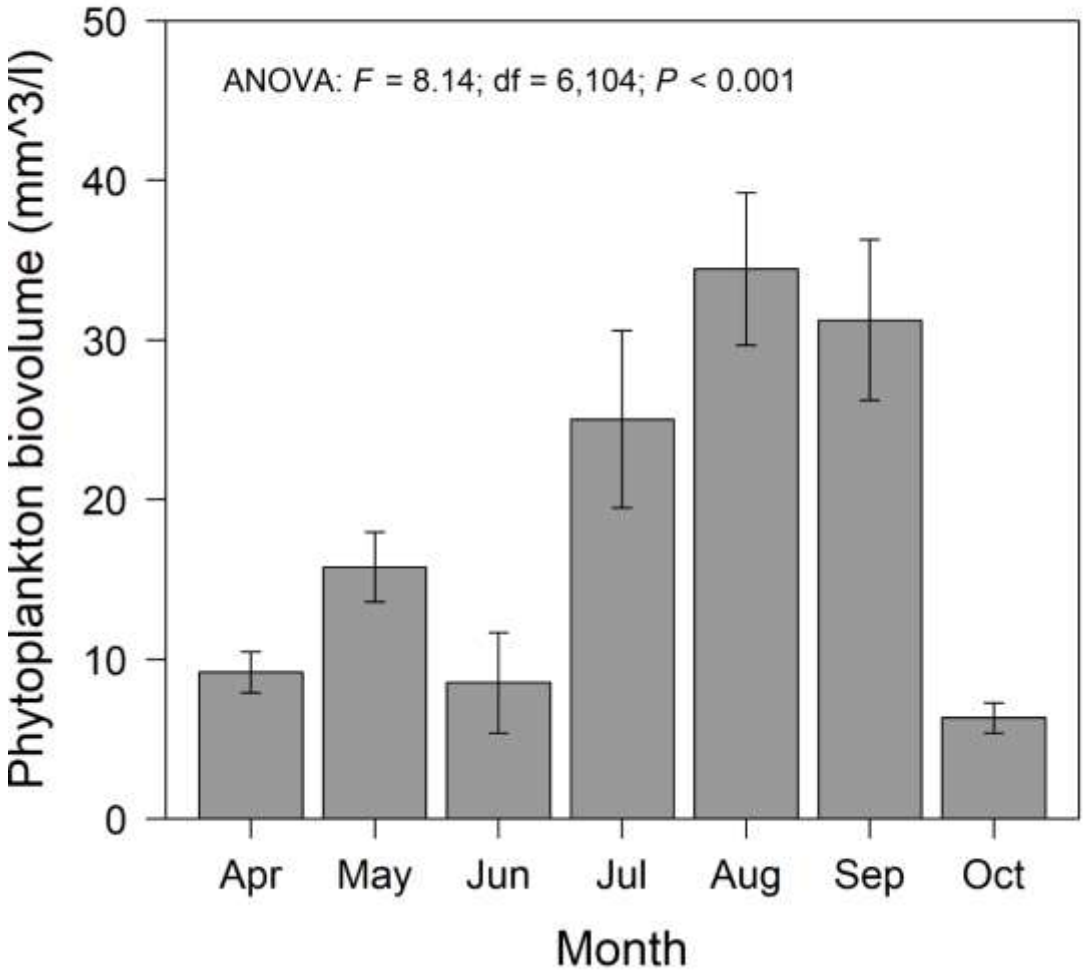

FIgure S 25. Mean (and standard error bars) Minnesota River phytoplankton biovolume (mm^3/l) among months based on samples collected from seven sites during July–October 2016, April–October 2017, and May–October 2018.

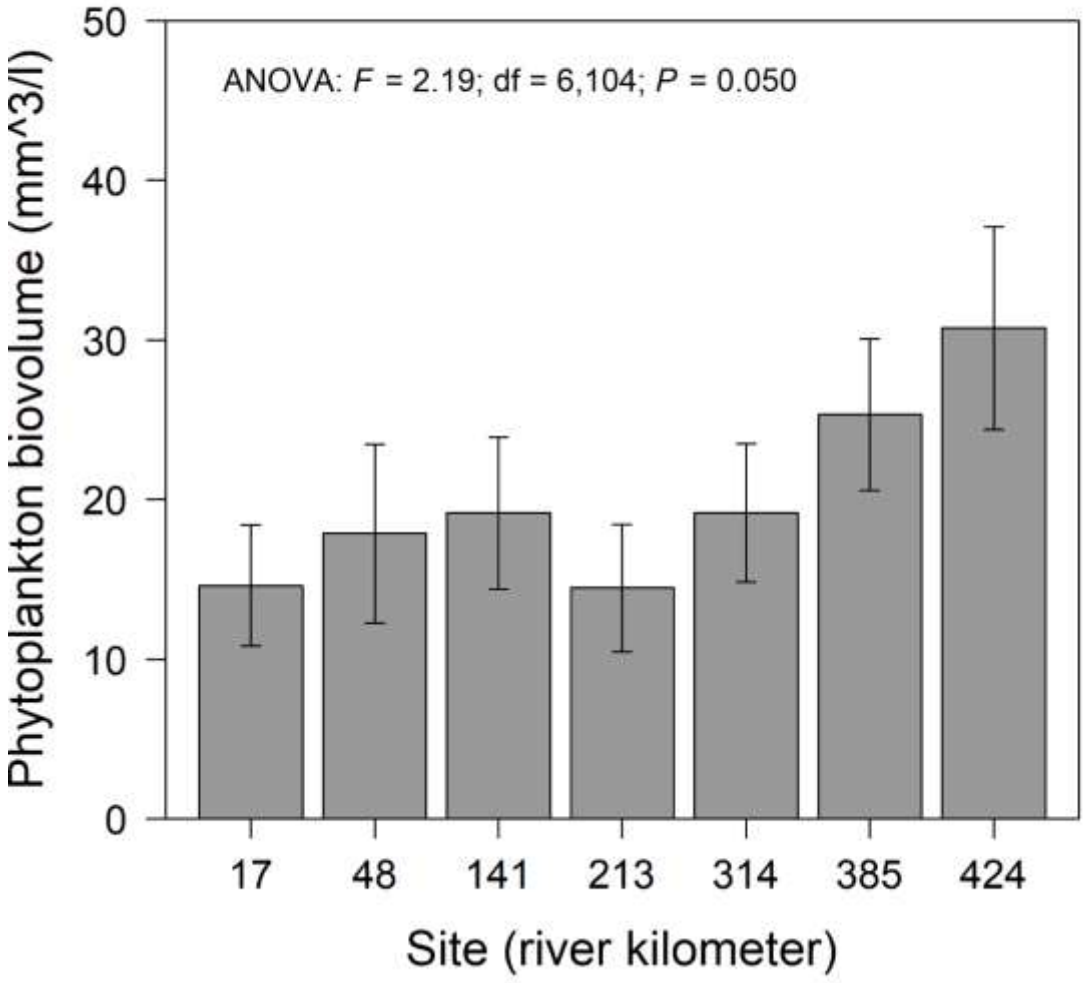

FIgure S 26. Mean (and standard error bars) phytoplankton biovolume (mm^3/l) among sites (river kilometers) based on samples collected from all seven sites during July–October 2016, April–October 2017, and May–October 2018.

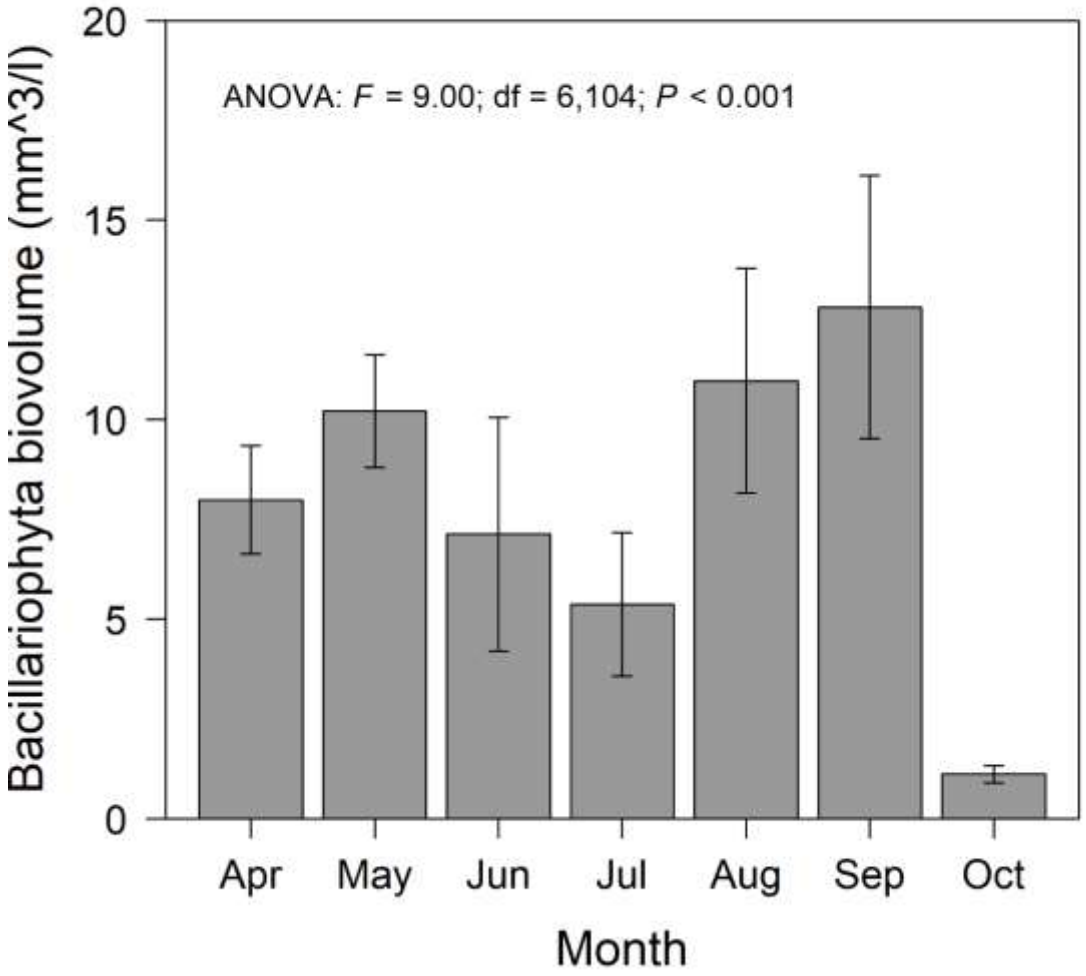

FIgure S 27. Mean (and standard error bars) Minnesota River Bacillariphyta biovolume (mm^3/l) among months based on samples collected from seven sites during July–October 2016, April–October 2017, and May–October 2018.

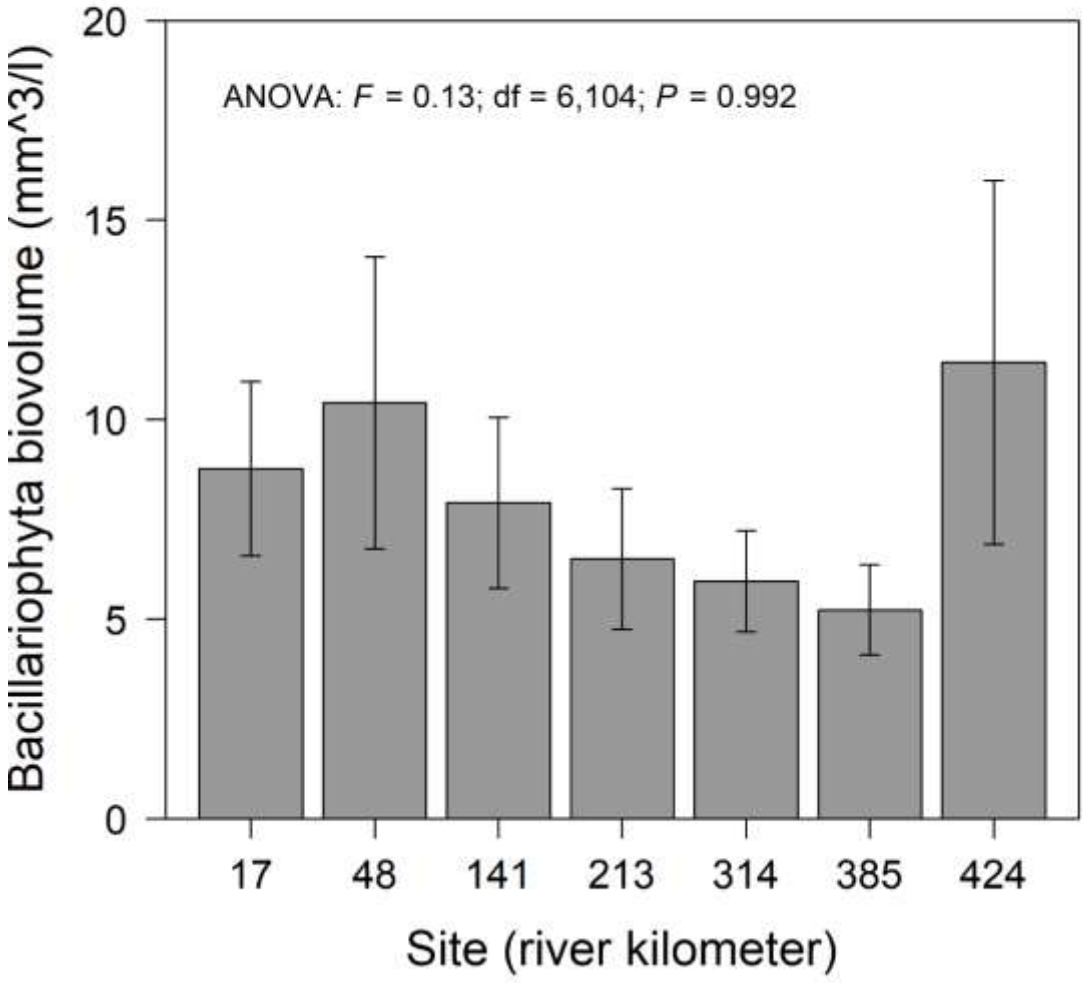

FIgure S 28. Mean (and standard error bars) Bacillariophyta biovolume (mm^3/l) among sites (river kilometers) based on samples collected from all seven sites during July–October 2016, April–October 2017, and May–October 2018.

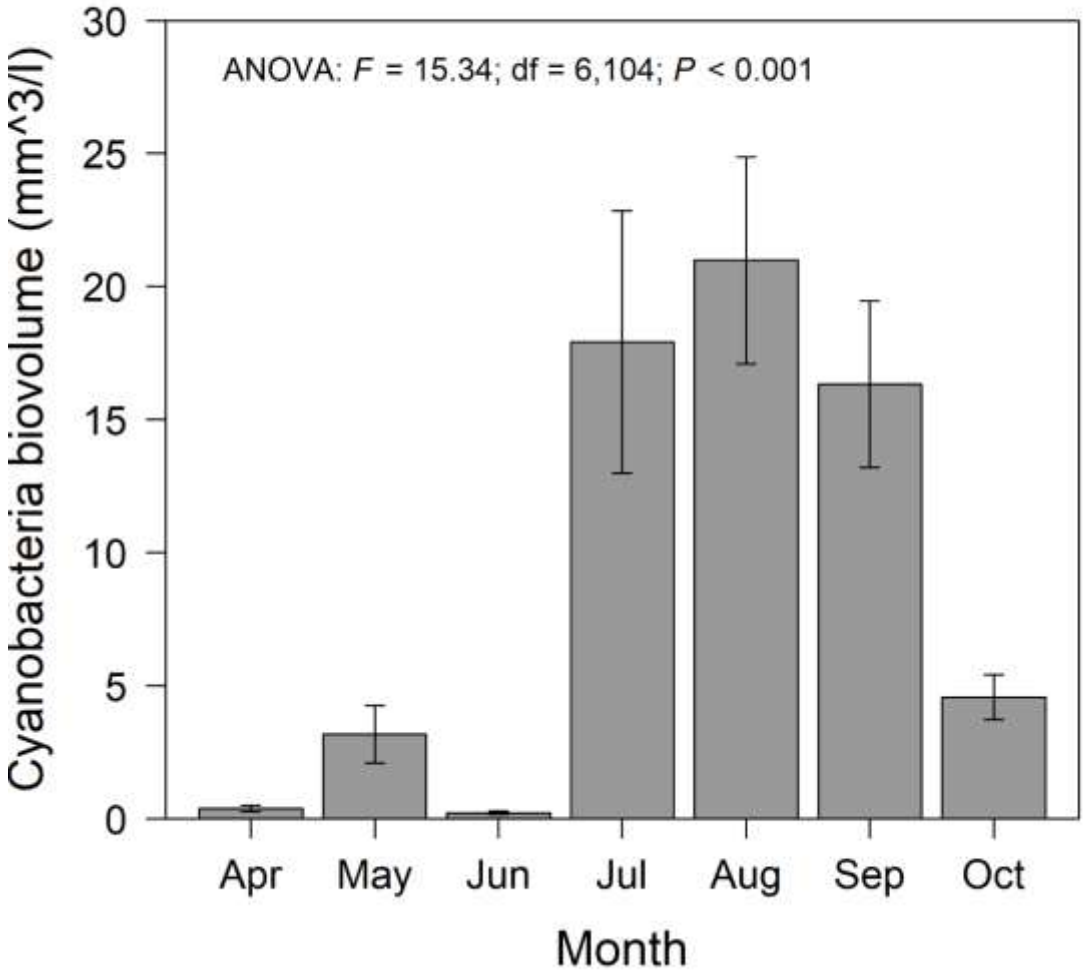

FIgure S 29. Mean (and standard error bars) Minnesota River Cyanobacteria biovolume (mm^3/l) among months based on samples collected from seven sites during July–October 2016, April–October 2017, and May–October 2018.

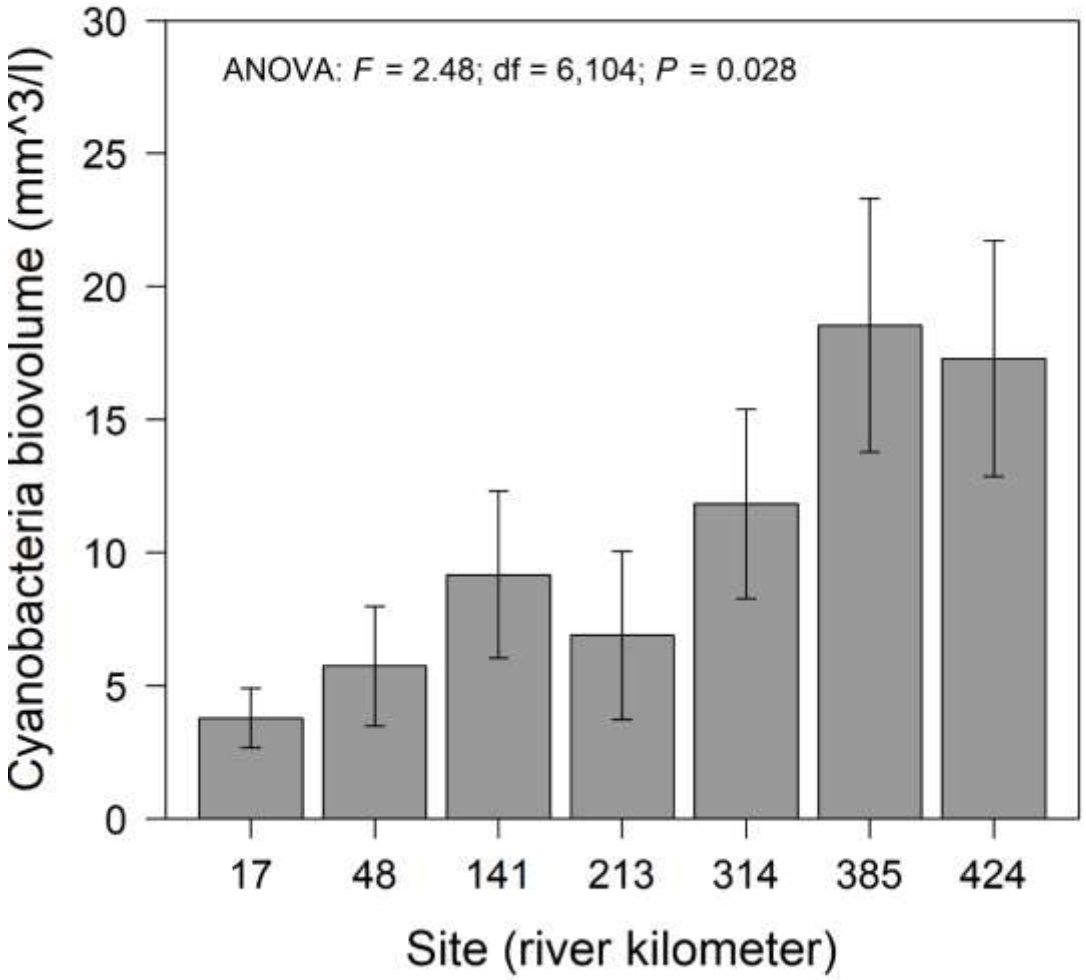

FIgure S 30. Mean (and standard error bars) Cyanobacteria biovolume (mm^3/l) among sites (river kilometers) based on samples collected from all seven sites during July–October 2016, April–October 2017, and May–October 2018.

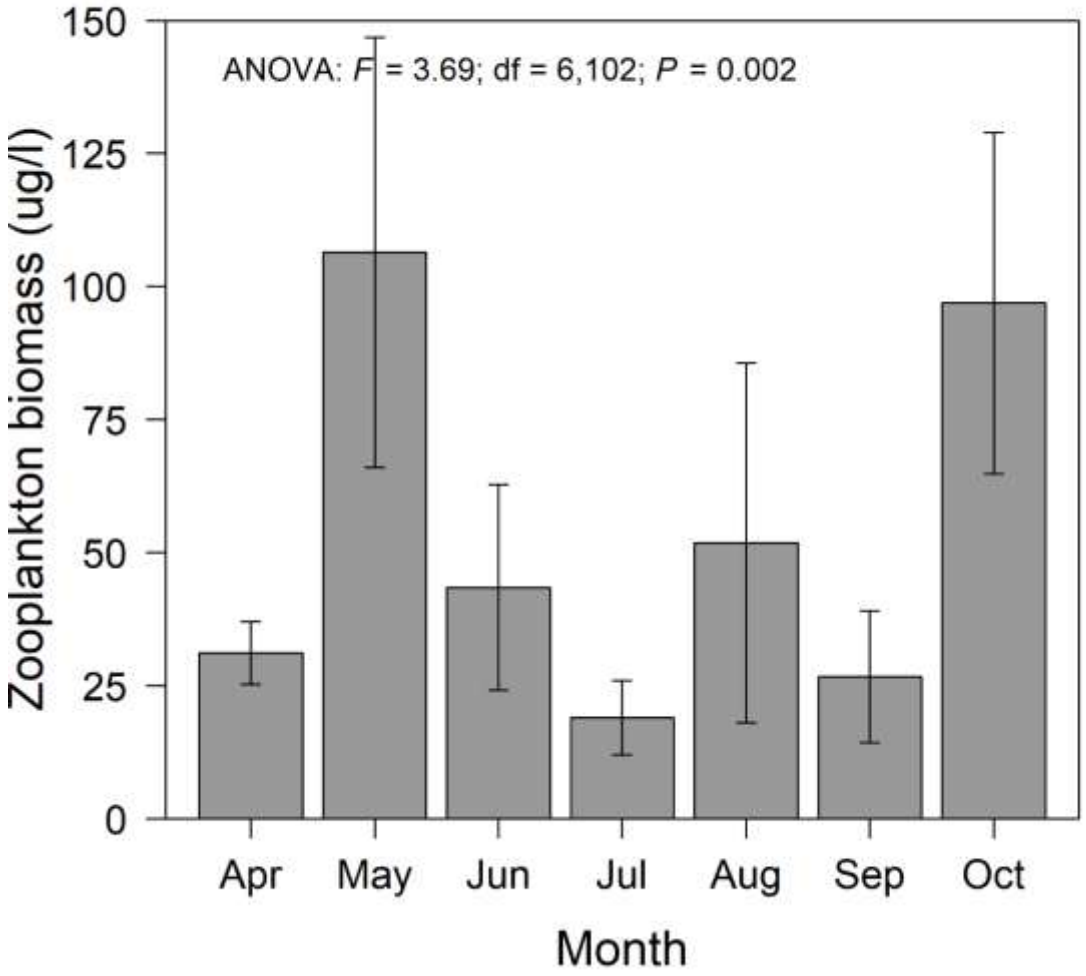

FIgure S 31. Mean (and standard error bars) Minnesota River Zooplankton biomass (µg/l) among months based on samples collected from seven sites during July–October 2016, April–October 2017, and May–October 2018.

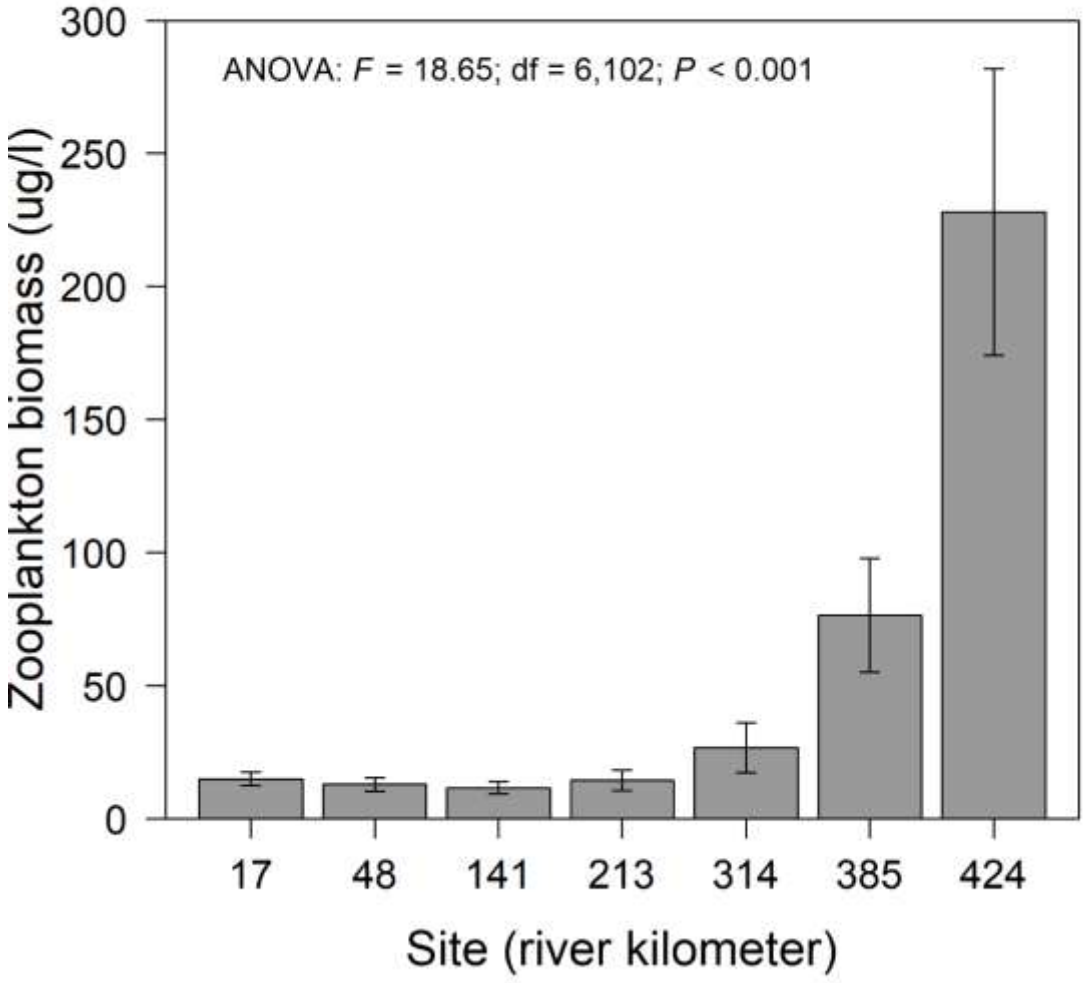

FIgure S 32. Mean (and standard error bars) zooplankton biomass (µg/l) among sites (river kilometers) based on samples collected from all seven sites during July–October 2016, April–October 2017, and May–October 2018.

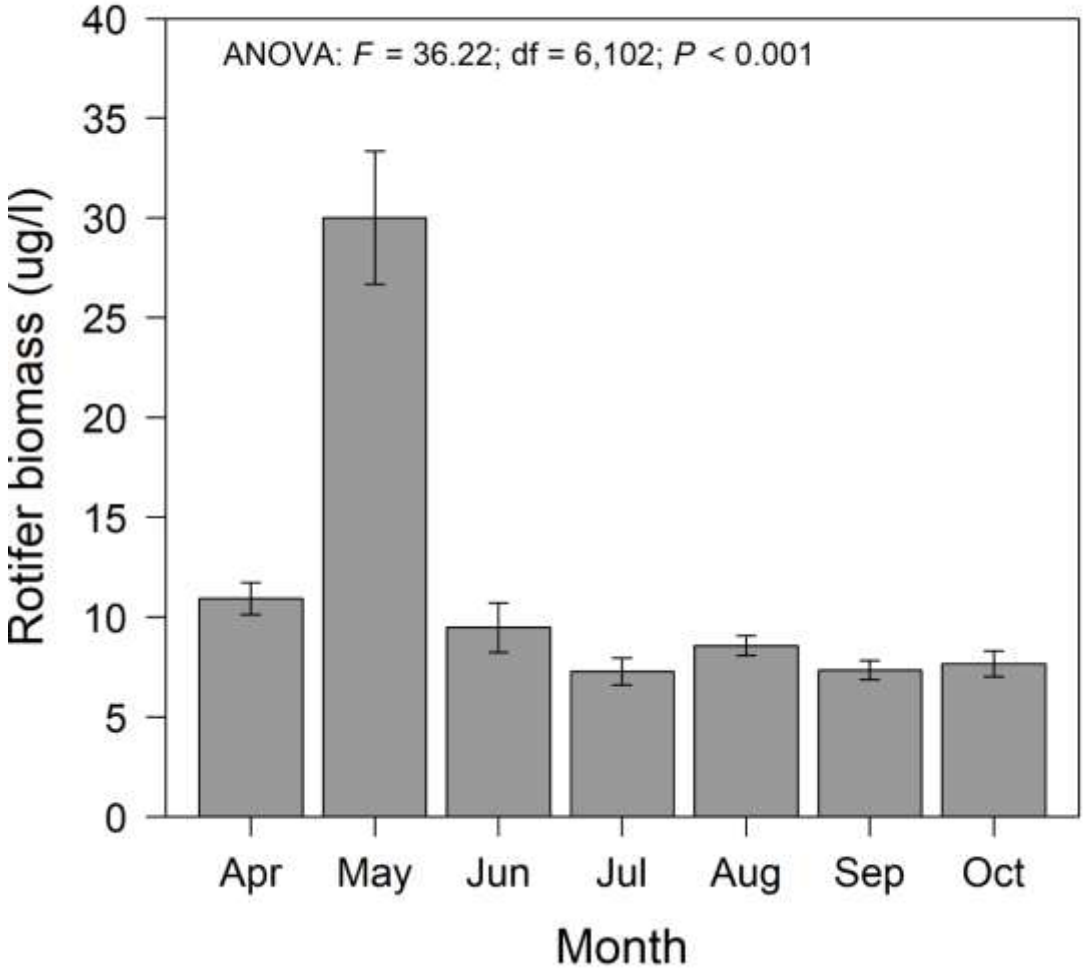

FIgure S 33. Mean (and standard error bars) Minnesota River rotifer biomass (µg/l) among months based on samples collected from seven sites during July–October 2016, April–October 2017, and May–October 2018.

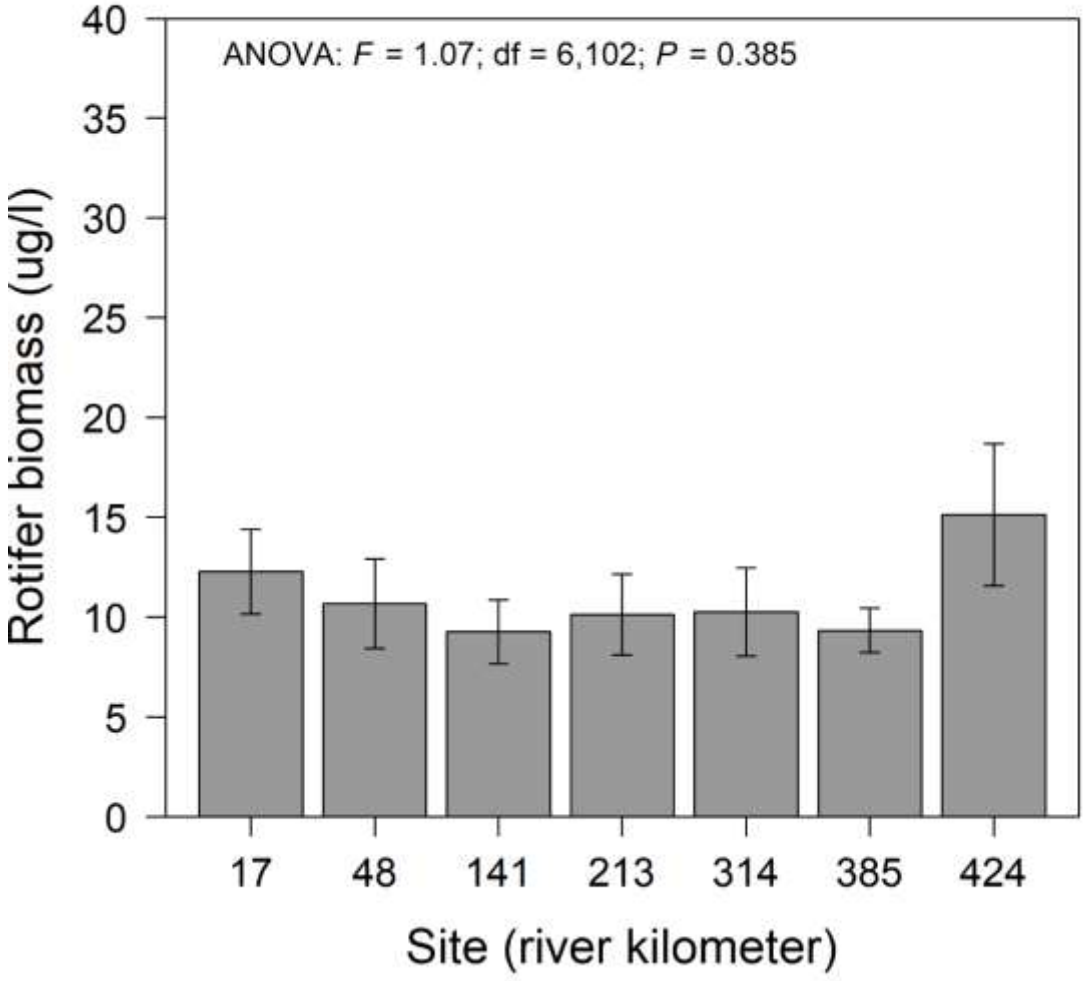

FIgure S 34. Mean (and standard error bars) rotifer biomass (µg/l) among sites (river kilometers) based on samples collected from all seven sites during July–October 2016, April–October 2017, and May–October 2018.

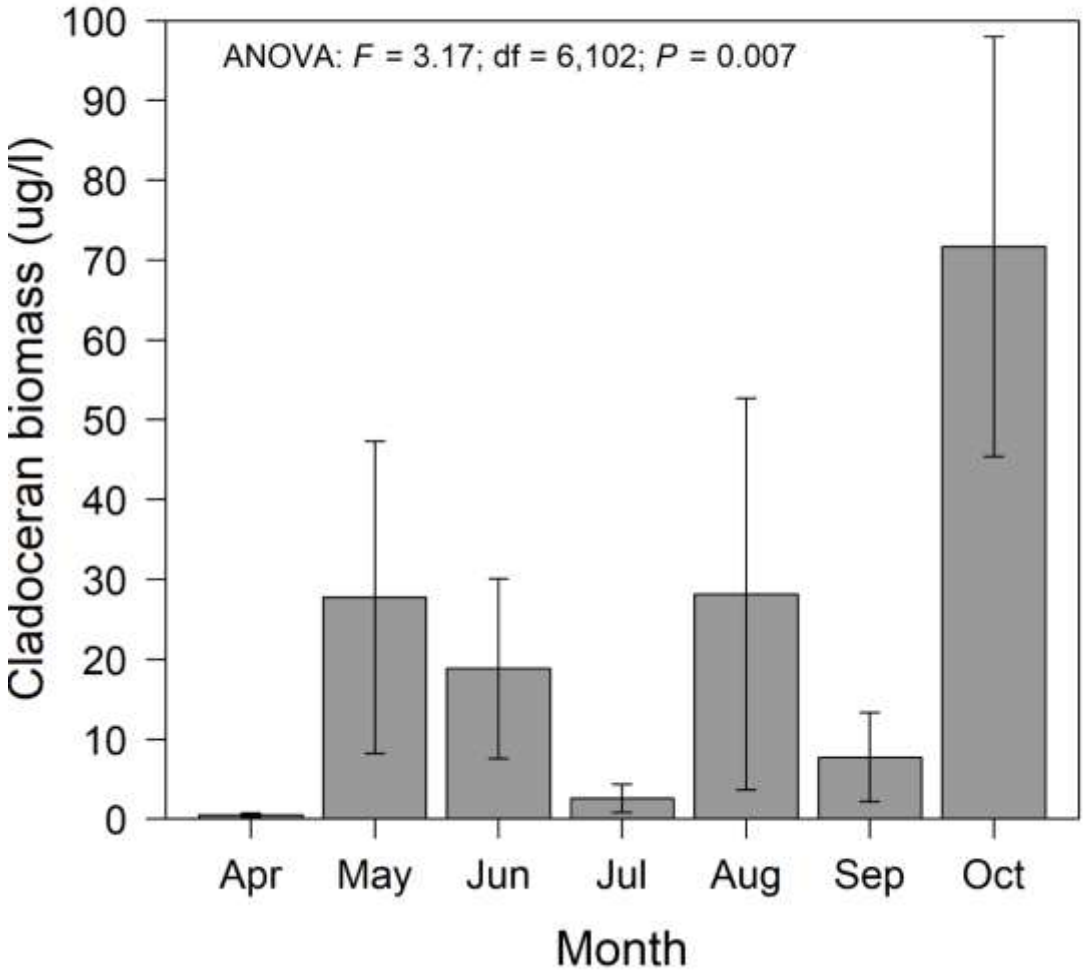

FIgure S 35. Mean (and standard error bars) Minnesota River Cladoceran biomass (µg/l) among months based on samples collected from seven sites during July–October 2016, April–October 2017, and May–October 2018.

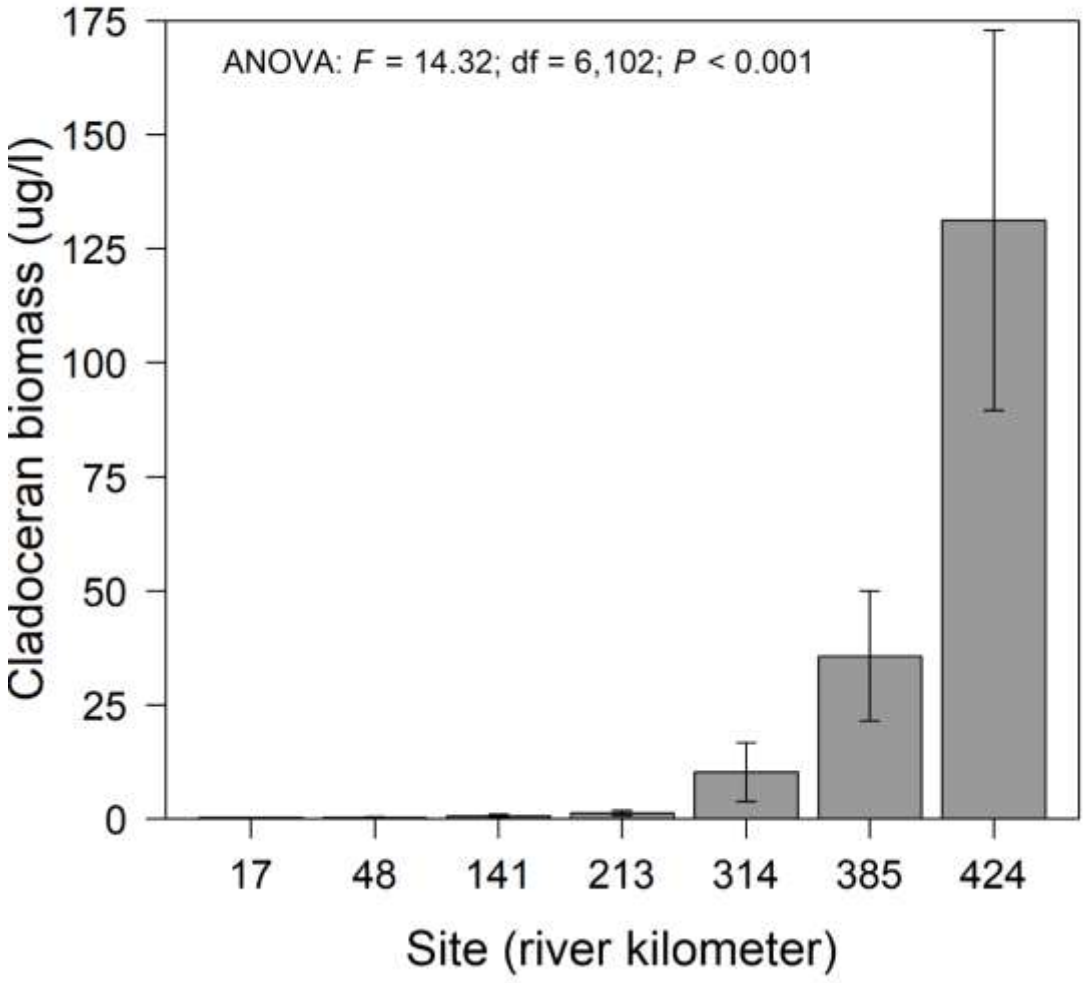

FIgure S 36. Mean (and standard error bars) Cladoceran biomass (µg/l) among sites (river kilometers) based on samples collected from all seven sites during July–October 2016, April–October 2017, and May–October 2018.

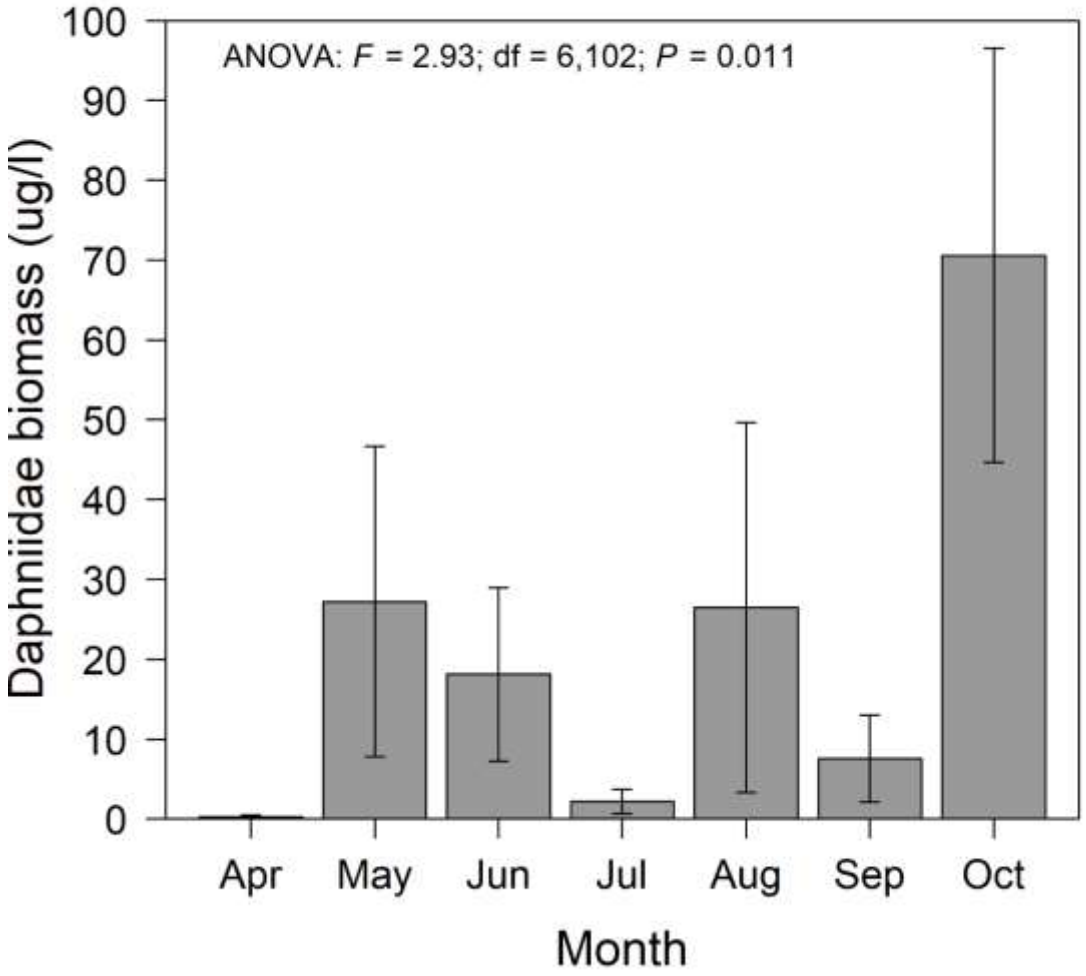

FIgure S 37. Mean (and standard error bars) Minnesota River Daphniidae biomass (µg/l) among months based on samples collected from seven sites during July–October 2016, April–October 2017, and May–October 2018.

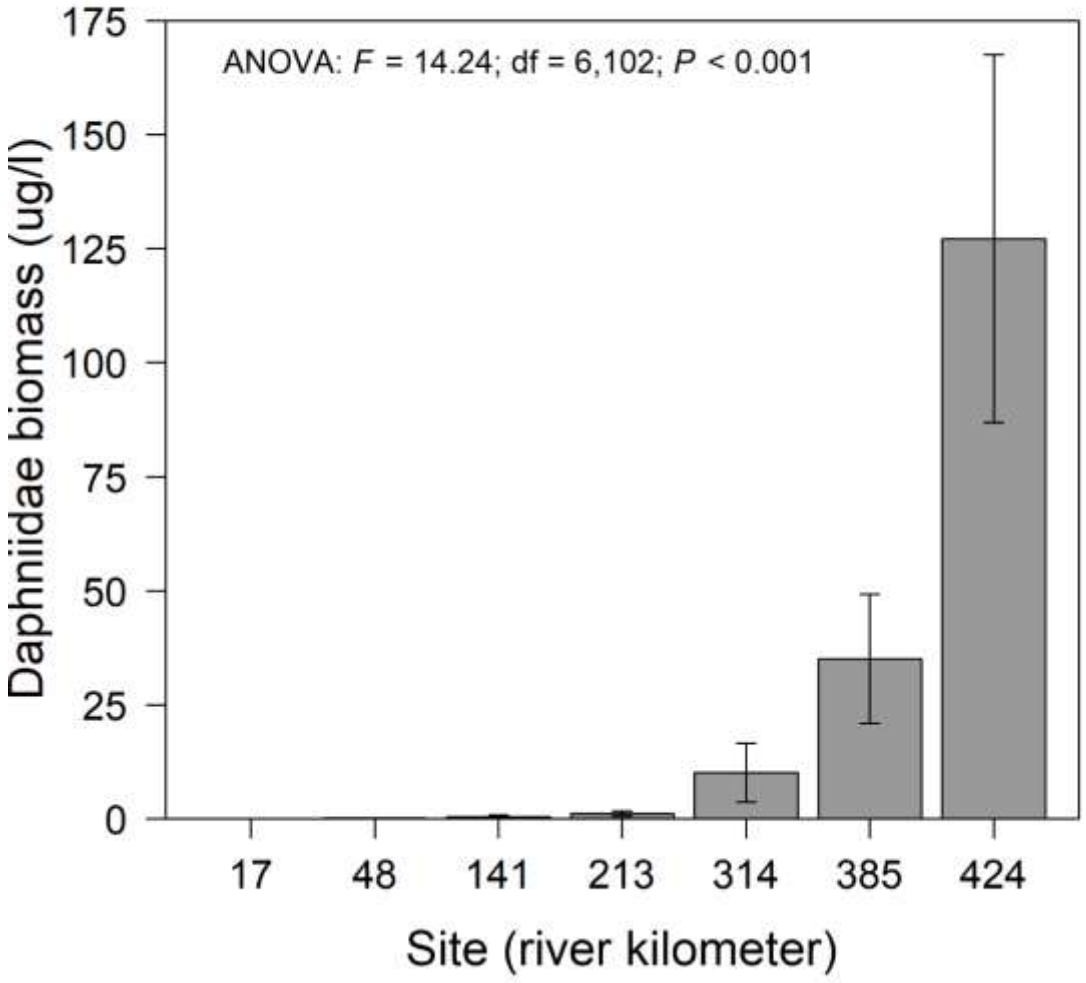

FIgure S 38. Mean (and standard error bars) Daphniidae biomass (µg/l) among sites (river kilometers) based on samples collected from all seven sites during July–October 2016, April–October 2017, and May–October 2018.

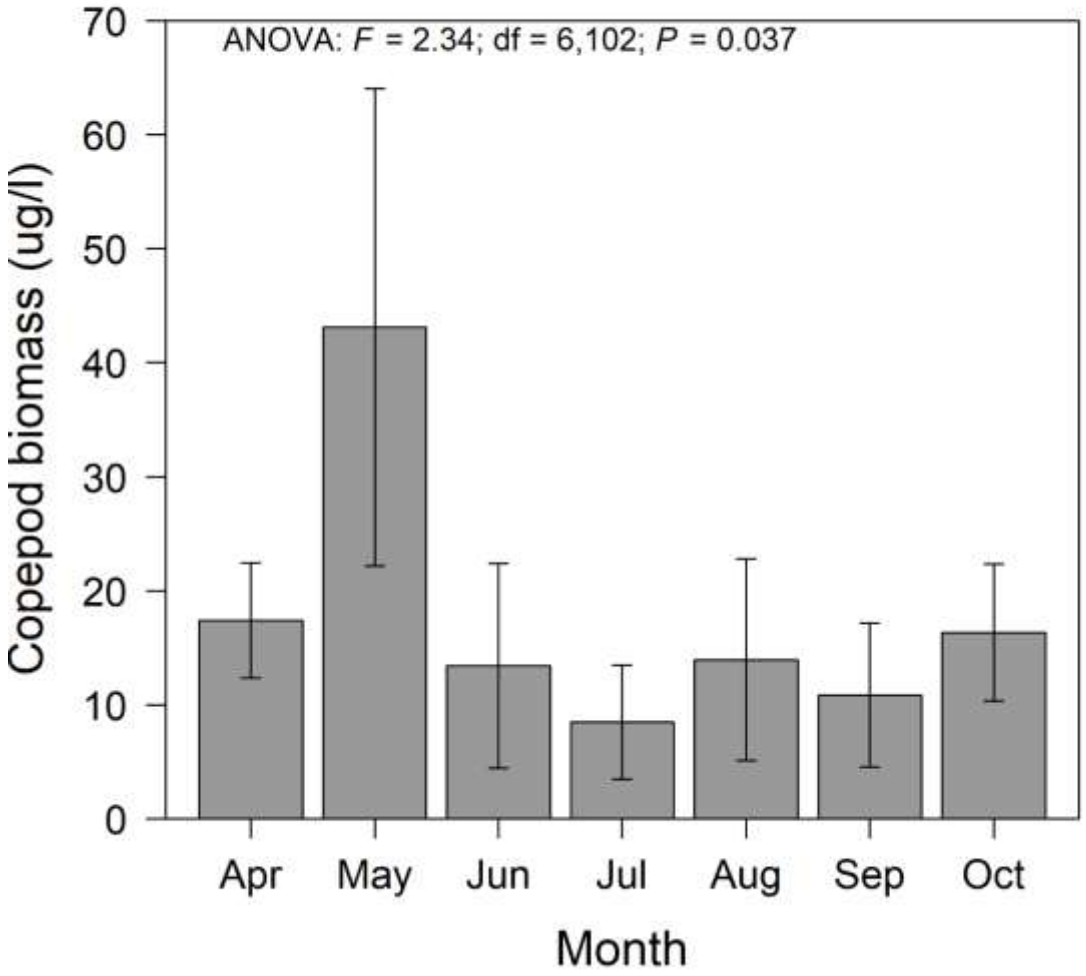

FIgure S 39. Mean (and standard error bars) Minnesota River Copepod biomass (µg/l) among months based on samples collected from seven sites during July–October 2016, April–October 2017, and May–October 2018.

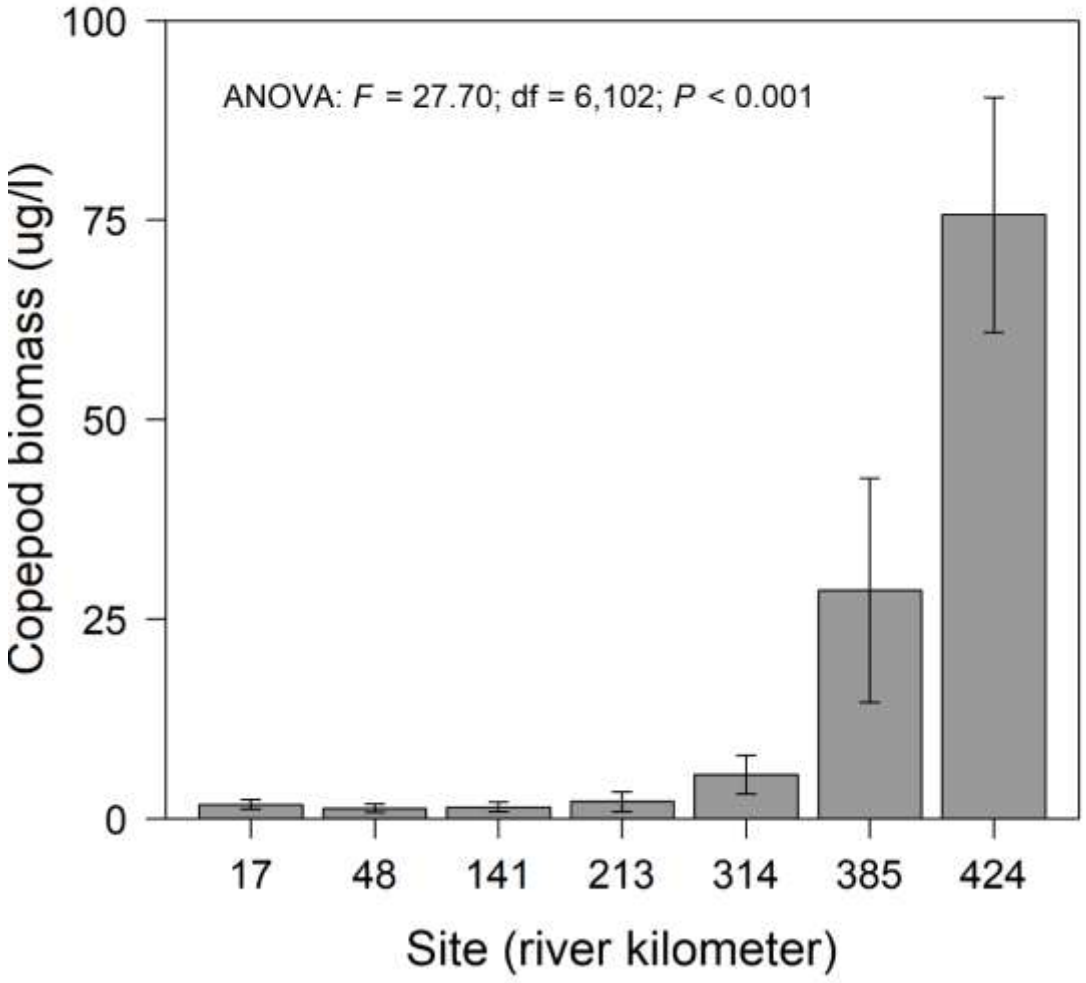

FIgure S 40. Mean (and standard error bars) Copepod biomass (µg/l) among sites (river kilometers) based on samples collected from all seven sites during July–October 2016, April–October 2017, and May–October 2018.

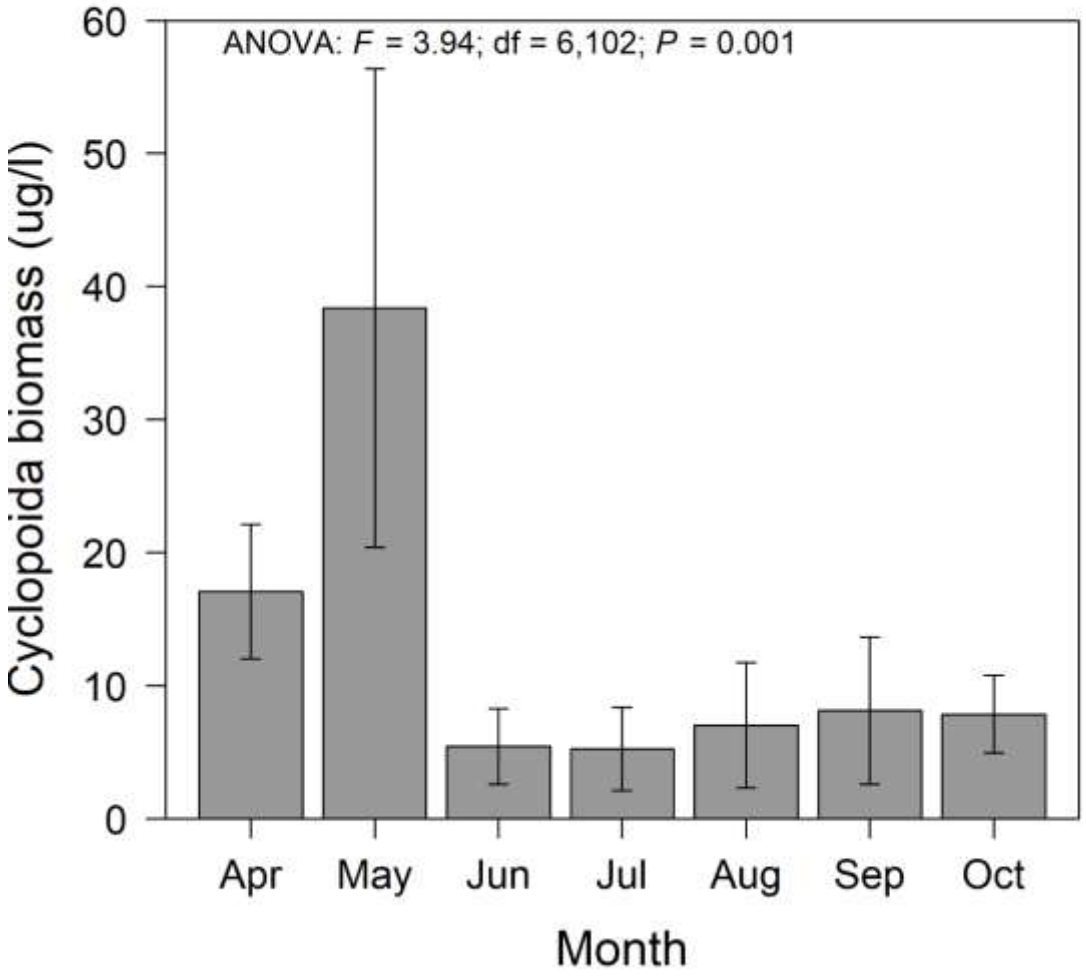

FIgure S 41. Mean (and standard error bars) Minnesota River Cyclopoida biomass (µg/l) among months based on samples collected from seven sites during July–October 2016, April–October 2017, and May–October 2018.

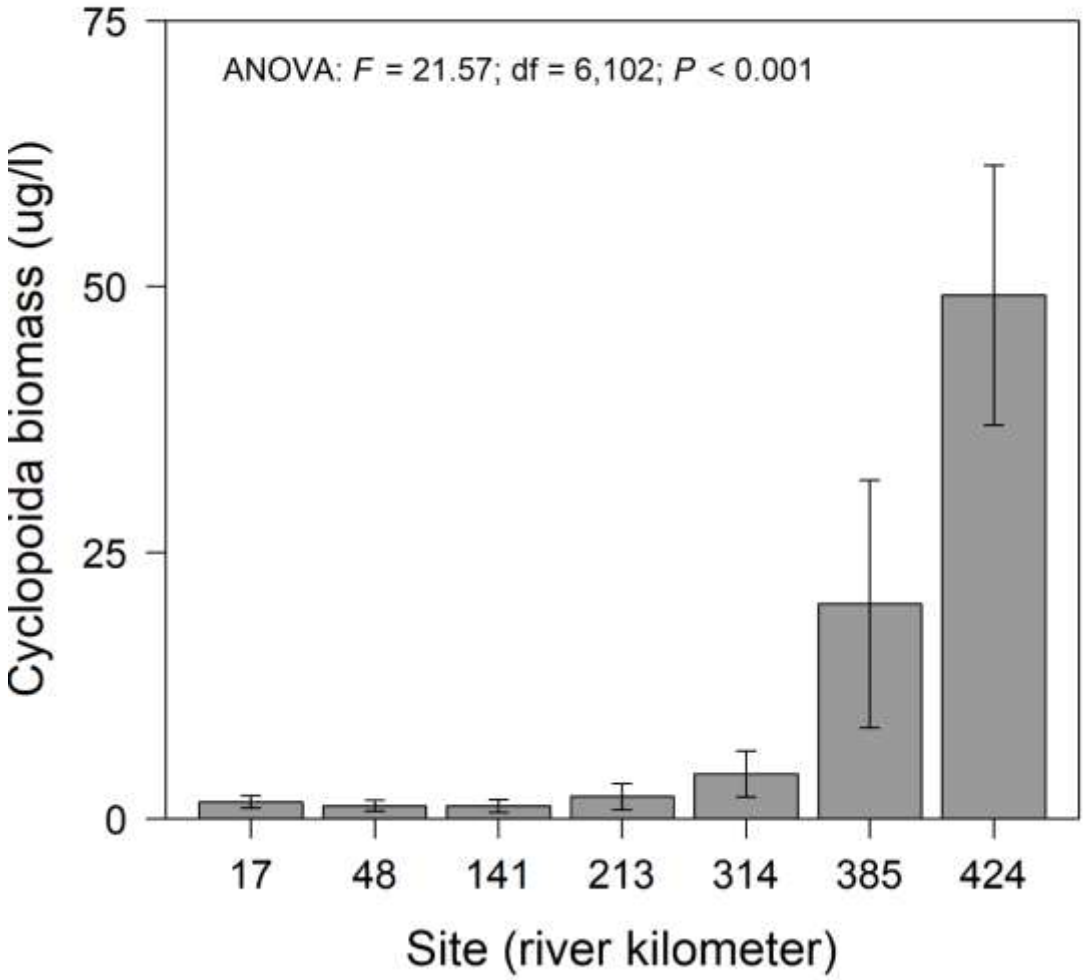

FIgure S 42. Mean (and standard error bars) Cyclopoida biomass (µg/l) among sites (river kilometers) based on samples collected from all seven sites during July–October 2016, April–October 2017, and May–October 2018.

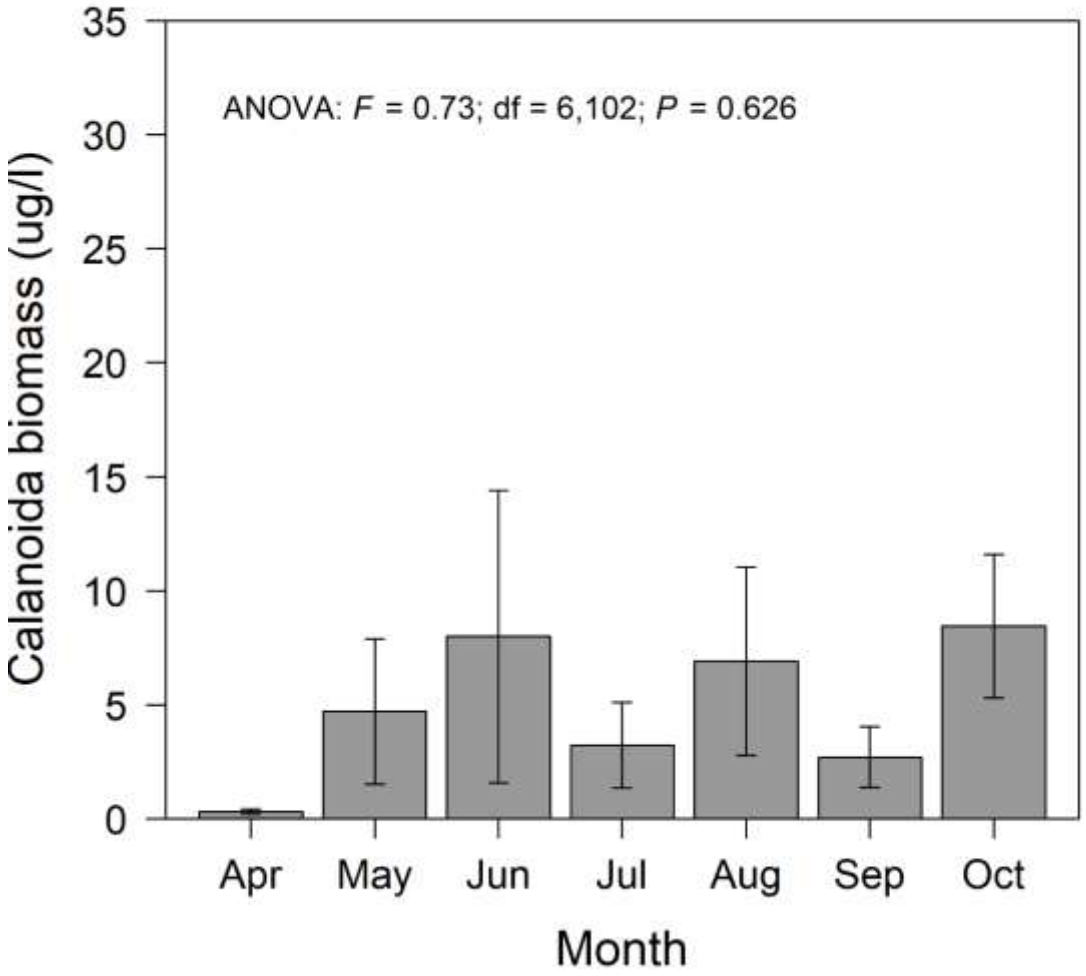

FIgure S 43. Mean (and standard error bars) Minnesota River Calanoida biomass (µg/l) among months based on samples collected from seven sites during July–October 2016, April–October 2017, and May–October 2018.

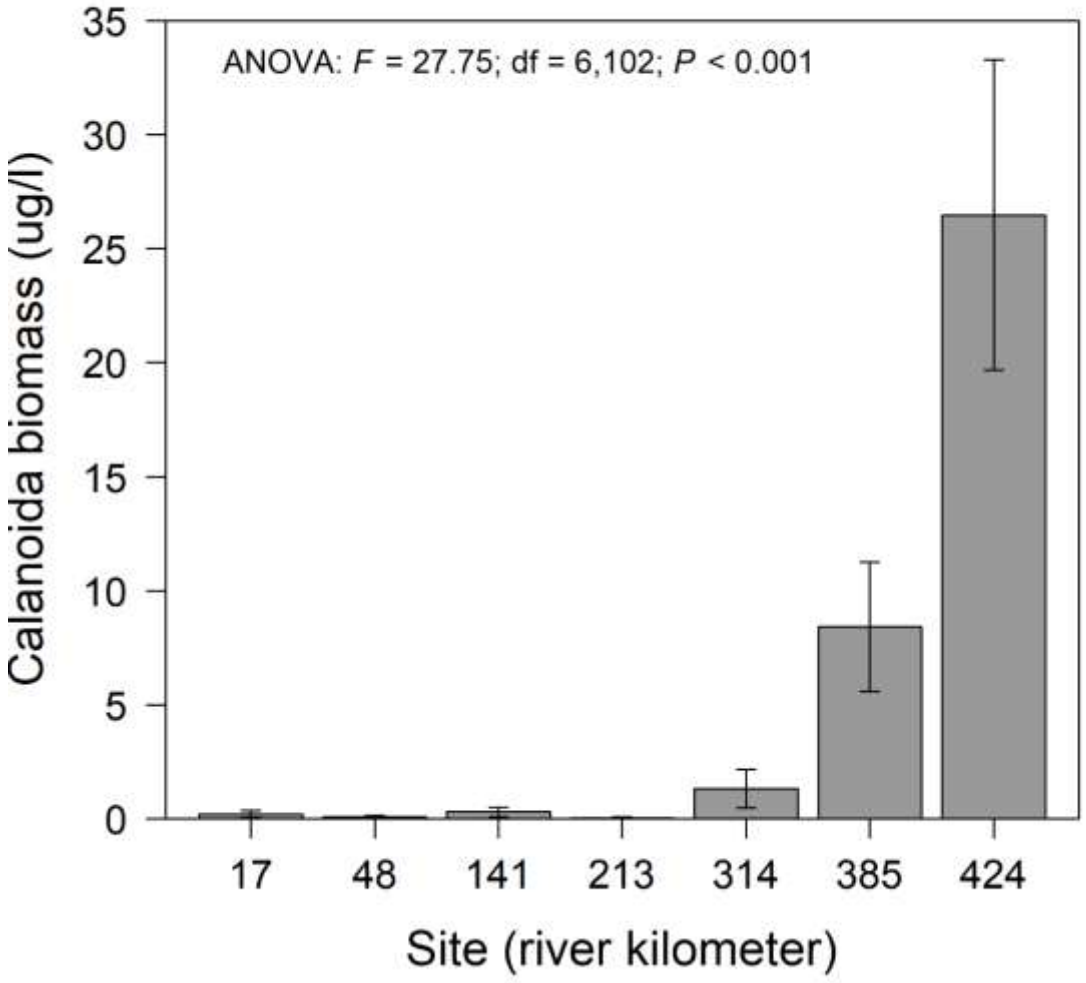

FIgure S 44. Mean (and standard error bars) Calanoida biomass (µg/l) among sites (river kilometers) based on samples collected from all seven sites during July–October 2016, April–October 2017, and May–October 2018.