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Spatial and temporal trends of Minnesota River phytoplankton and zooplankton

Anthony R. Sindt¹ Michael C. Wolf²

¹Fish and Wildlife Division, Minnesota Department of Natural Resources, Hutchinson, Minnesota

²Fish and Wildlife Division, Minnesota Department of Natural Resources, Baudette, Minnesota

Correspondence

Anthony R. Sindt, Minnesota Department of Natural Resources, Fish and Wildlife Division, 20596 Hwy 7, Hutchinson, MN 55350. Email: anthony.sindt@state.mn.us

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Abstract

Plankton communities have important roles in aquatic ecosystems, but studies of plankton in lotic systems are infrequent. We collected over 100 water, phytoplankton, and zooplankton samples during 2016-2018 to explore spatiotemporal trends in Minnesota River plankton communities and evaluate relationships with physicochemical factors. Phytoplankton and zooplankton community structure exhibited temporal patterns but only the zooplankton community differed spatially. Cyanobacteria (M \pm SE; 11.27 \pm 1.43 mm³/L) and diatoms (8.12 \pm 1.08 mm³/L) dominated phytoplankton biovolume with seasonal peaks in Cyanobacteria occurring during July-September and peaks in diatoms occurring during May, August, and September. All phytoplankton taxa except Cryptophyta exhibited a negative relationship with relative discharge. Crustacean zooplankton biomass was greatest at two upstream sites $(146.7 \pm 32.6 \mu g/L)$ where cladocerans and copepods were likely exported from upstream of dams where water residence time is greater. Within the lower freeflowing reach rotifers dominated the zooplankton community (207.9 ± 40.9 individuals/L and $6.5 \pm 1.0 \mu g/L$). Thus, spatial differences in zooplankton community structure were primarily attributed to the influence of dams. Seasonal patterns in zooplankton community structure included peaks in Chydoridae, cyclopoid, immature copepod, and rotifer biomass during May and Bosminidae biomass during October. Excluding the influence of dams on zooplankton, the cumulative effects of month and relative discharge were the most important for explaining variability in plankton community structure. Baseline understanding of plankton community dynamics provides the ability to quantify responses to future perturbations such as climate change and establishment of invasive planktivores.

KEYWORDS lotic, lower trophic, Minnesota River, plankton

INTRODUCTION 1

Lower trophic organisms, including phytoplankton and zooplankton, are important components of aquatic ecosystems that link upper trophic levels with basal resources. Phytoplankton is an important source of primary production in the autochthonous lotic food web and zooplankton are primary and secondary consumers that serve as important food for higher trophic levels, including most fish species (Nunn, Tewson, & Cowx, 2012; Thorp & Delong, 2002). Phytoplankton and zooplankton are extensively studied in lentic systems, but understanding of plankton community dynamics in lotic systems is less complete (Lair, 2006; Reynolds, 2000). Yet, a growing number of studies have focused on evaluating factors that influence plankton communities in medium to large rivers (e.g., Burdis & Hoxmeier, 2011; ² WILEY-

Descy et al., 2016; Rossetti, Viaroli, & Ferrari, 2009; Salmaso & Braioni, 2008; Thorp & Mantovani, 2005). Influential factors identified include nutrient availability (Basu & Pick, 1996), temperature (Rossetti et al., 2009; Tavernini, Pierobon, & Viaroli, 2011), turbidity (Salmaso & Braioni, 2008; Sluss, Cobbs, & Thorp, 2008; Thorp & Mantovani, 2005), and numerous hydrologic variables (Burdis & Hirsch, 2017; Tavernini et al., 2011; Thorp & Mantovani, 2005). For instance, temporal variability of lotic phytoplankton and zooplankton communities is often associated with seasonal patterns in flow regime, temperature, photoperiod, and nutrient fluxes (Pace, Findlay, & Lints, 1992; Salmaso & Braioni, 2008; Tavernini et al., 2011). An increasing number of studies also demonstrate the importance of biological interactions on lower trophic communities (e.g., bottom-up or top-down trophic interactions; DeBoer, Anderson, & Casper, 2018; Guelda, Kock, Jack, & Bukaveckas, 2005; Thorp & Casper, 2003). Hydrological factors (such as discharge, turbulence, and water residence time), however, have a generally dominant role in structuring lotic plankton communities with phytoplankton and zooplankton biomass increasing with water residence time (Basu & Pick, 1996; Lair, 2006; Pace et al., 1992; Reynolds, 2000; Salmaso & Braioni, 2008; Søballe & Kimmel, 1987).

Lotic ecosystems are complex and ecologists often attempt to describe important riverine features and processes, including longitudinal gradients (Vannote. Minshall. Cummins. Sedell æ Cushing, 1980), the influence of dams (Ward & Stanford, 1983), occurrences of flood-pulses (Bayley, 1995; Junk, Bayley, & Sparks, 1989), hydraulic retention (Schiemer, Keckeis, Reckendorfer, & Winkler, 2001), and trophic cascades (Power, 1990). More recently, the Riverine Ecosystem Synthesis blended many of the existing theories: describing the structure and function of lotic ecosystems with consideration of both the riverscape and floodscape, and suggests that rivers are divided into unique functional zones based on hydrological and geomorphological differences (Thorp, Thoms, & Delong, 2006). Intertwined features and processes of lotic systems influence plankton community dynamics across varying spatial and temporal scales, and consequently spatiotemporal patterns of plankton communities differ among and within systems (e.g., Hardenbicker, Weitere, Ritz, Schöll, & Fischer, 2016). For instance, Varol and Sen (2018) reported a longitudinal trend of increasing phytoplankton biomass from upstream to downstream in the Tigris River, Turkey, whereas Phlips et al. (2000) reported the opposite spatial trend in the St. Johns River, Florida. Rather than longitudinal trends, Abonyi et al. (2014) and Zhao et al. (2017) reported spatial patchiness in plankton communities among river zones with unique environmental conditions. Dams and impoundments can also disrupt spatial patterns and have significant influences on plankton community structure (Havel et al., 2009; Pourriot, Rougier, & Miquelis, 1997; Prygiel & Leitao, 1994). Temporal variability in plankton communities is often influenced by environmental characteristics that exhibit predictable seasonal patterns (e.g., temperature, photoperiod), but these patterns can be disrupted by flood-pulses (Górski, Collier, Duggan, Taylor, & Hamilton, 2013), extreme hydrologic conditions (e.g., droughts; Beaver et al., 2013), or anthropogenic disturbances (Kleinteich, Hilt,

Hoppe, & Zarfl, 2020). Most of these influences on spatiotemporal dynamics are attributed to abiotic factors, but biotic interactions can also structure lotic plankton communities, and introduced populations of non-native planktivores have significant impacts on large river plankton communities with cascading impacts on higher trophic levels (Caraco et al., 1997; DeBoer et al., 2018; Pace, Findlay, & Fischer, 1998).

The Minnesota River is an important and complex ecosystem that spans 500 river kilometers (rkm), has a large complex floodplain, and experiences frequent flood-pulses. Similar to other floodplain rivers around the world, the Minnesota River has been altered by the construction of dams and is impacted by agricultural and urban development. In addition, land-use changes, climate change, and invasive species continually affect the Minnesota River ecosystem. For instance, heavy rainfall events are increasingly common and discharge of the Minnesota River has significantly increased over time (Novotny & Stefan, 2007). The threat of invasive bighead carp (Hypophthalmichthys nobilis) and silver carp (Hypophthalmichthys molitrix) expansion into the Minnesota River is also of particular concern because they may have predatory impacts on plankton communities (Pongruktham, Ochs, & Hoover, 2010) and competitive interactions with native organisms such as paddlefish (Polyodon spathula) and freshwater mussels (e.g., Pendleton, Schwinghamer, Solomon, & Casper, 2017). Unfortunately, plankton communities are poorly studied in the Minnesota River, hindering understanding of how lower trophic communities and the Minnesota River ecosystem will respond to ongoing and future changes.

For this study, we explore spatiotemporal patterns of Minnesota River phytoplankton and zooplankton communities, and evaluate the influence of physico-chemical factors on plankton community structure. We hypothesize that both phytoplankton and zooplankton communities will exhibit spatial and temporal patterns in response to differences in abiotic conditions (e.g., turbidity, temperature) among sample sites and months, and that variability in discharge is among the most important drivers of plankton community structure. We also hypothesize that the presence of dams amplifies spatial variability and that variability in discharge and timing of connectivity with floodplain habitats disrupts seasonal patterns and increases temporal variability of plankton community structure. Developing a baseline understanding of Minnesota River plankton community dynamics is important for predicting and understanding ecosystem responses to future perturbations such as climate change and establishment of invasive species.

2 | METHODS

2.1 | Study location

The Minnesota River watershed drains 44,030 km² and the Minnesota River flows approximately 520 rkm from Big Stone Lake on the Minnesota–South Dakota border to its confluence with the Mississippi River at St. Paul, MN (Figure 1). The upstream 125-rkm reach of the Minnesota River contains five dams, including the Lac qui Parle Dam at



FIGURE 1 Seven Minnesota River sample sites labeled with their corresponding river kilometer (rkm) and the location of nearby river gages. The sample site at rkm 424 is 24-rkm downstream of Lac qui Parle Dam and sample site rkm 385 is 10-rkm downstream of Granite Falls Dam

rkm 448 that controls water levels in a 2,323-ha natural impoundment (Lac qui Parle Reservoir) and the downstream-most dam at rkm 395, which is a 6.4-m tall run-of-the-river hydropower dam in Granite Falls, MN. With the exception of <1 km immediately above Granite Falls Dam, the entire 53-km reach upstream to the next dam at Lac qui Parle is lotic environment. Downstream of the Granite Falls Dam, the Minnesota River is a seventh- through eighth-order (Strahler stream order) floodplain river flowing through the agriculturally dominated prairie region of southern Minnesota. The Minnesota River is a low gradient, productive, and turbid warm water river. For instance, mean discharge, total phosphorus, and total suspended solids were 178.9 m³/s, 0.25 mg/L, and 127.0 mg/L, respectively, at St. Peter, MN (rkm 142; Minnesota Pollution Control Agency, n.d.) and periodic channel velocity measurements ranged from 0.17 to 2.3 m/s at Mankato, MN (rkm 164; US Geological Survey, n.d.) during 2007–2015.

We evaluated Minnesota River plankton communities by collecting phytoplankton, zooplankton, and water chemistry samples, and measuring physical factors at seven main-channel sample sites distributed along the river at monthly intervals during August–October of 2016, May–October of 2017, and May–October of 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 (hereafter referred to as "upstream sites"). The remaining five sites are distributed throughout the lower free-flowing reach of the river (hereafter referred to as "downstream sites"). 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 (US Geological Survey, n.d.).

2.2 | Water chemistry samples

During each sample event, we collected two water samples from an anchored boat near the mid-channel of each sample site for water chemistry analyses. We filled a 2-L transparent bottle and a 2-L 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 and on ice and then delivered to the Minnesota Department of Agriculture (MDA; St. Paul, MN) Laboratory Services for analyses within 48 hrs.

At the MDA laboratory, staff determined chlorophyll-*a* (Chl-*a*; μ g/L) concentrations using Environmental Protection Agency (EPA) Method 445.0 (Arar & Collins, 1997) and total Kjeldahl nitrogen (TKN; mg/L) concentrations using EPA method 351.2 (O'Dell, 1993a). Colorimetry methods determined total phosphorus (TP; mg/L) and dissolved ortho-phosphorus (Ortho-P; mg/L) concentrations (EPA method 365.1; O'Dell, 1993b). Laboratory staff determined nitrate/ nitrite (N + N; mg/L) with method SM 4500-NO3F (Eaton, Clesceri, Greenberg, & Franson, 1998). Total suspended solids (TSS; mg/L) and total dissolved solids (TDS; mg/L) were analyzed using SM 2540, parts D and C, respectively (Rice, Baird, Eaton, & Clesceri, 2012). Inductively coupled plasma mass spectrometry determined silica concentrations (Si; mg/L; EPA method 200.8; Creed, Brockhoff, & Martin, 1994).

We also recorded surface water temperature (°C) and measured water transparency (cm) with a 60-cm Secchi tube (S-tube) for each sample site during each sample event. When water temperature or S-tube readings 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 we estimated all water temperatures as 20.0°C. We also obtained hydrograph data associated with each sample event from river gages (US Geological Survey, n.d.) located near (within 0–28 rkm) each sample site.

2.3 | Phytoplankton samples

We collected one integrated water sample from each sample site during each sample event for phytoplankton analyses. First, we rinsed a large container (e.g., 19-L bucket) with river water. Next, we used a 2.5-m long by 7.6-cm diameter clear polyvinyl chloride pipe with a one-way valve (approximate capacity of 12.5 L 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 for sample preservation and refrigerated.

We shipped phytoplankton samples to BSA Environmental Services, Inc. (BSA; Beachwood, OH) where staff analyzed samples by preparing slides following a standard membrane filtration technique (McNabb, 1960). Phytoplankton enumeration occurred under compound microscopes equipped with epifluorescence with a majority of counting completed at 630× magnification. When possible, BSA enumerated and identified at least 300 units to the lowest practical taxonomic level and estimated abundance of common taxa by random field counts. Staff estimated biovolumes using formulas for solid geometric shapes that most closely match the cell shapes. For each sample, BSA reported estimated densities (cells/L) and biovolumes ($\mu m^3/L$) for each identified phytoplankton taxon.

2.4 | Zooplankton samples

We collected zooplankton samples at each sample site during each sample event with similar field methods as Burdis and Hoxmeier (2011). During 2016, we used a 2.5-m long by 7.6-cm diameter clear polyvinyl chloride pipe with a one-way valve (approximate capacity of 12.5 L) to collect two (but only one during August) 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 L and filtered the water sample through a 20- μ m plankton net. We rinsed contents of the plankton net into a 500-ml 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 to reduce the amount of sediment in samples. We acknowledge that this larger mesh size is less effective for capturing small rotifers (Chick, Levchuk, Medley, & Havel, 2010).

Crustacean zooplankton (i.e., cladocerans and copepods) were enumerated by first adjusting the sample to a known volume, and then transferring 5-ml aliquots into a counting wheel. All zooplankters were identified to the lowest practical taxon (Balcer, Korda, & Dodson, 1984; Haney et al., 2013; Pennak, 1989), counted, and measured under a $25 \times$ magnification dissecting microscope with the aid of a computerized image analysis system. Immature copepods were identified as copepodites or nauplii. The entire sample was enumerated if fewer than 30 zooplankters were counted in one 5-ml aliquot. Crustacean zooplankton biomass was estimated using taxa-specific length to weight regression coefficients (Culver, Boucherle, Bean, & Fletcher, 1985; Dumont, Van de Velde, & Dumont, 1975). For rotifer enumeration, samples were adjusted to a known volume and identification was aided by adding a few drops of Biebrich Scarlet/Erosin B stain. A 1-ml aliquot was obtained with a Hensen-Stempel pipette and placed onto a Sedgewick-Rafter cell. Rotifer counts and identification to the lowest practical taxon (Haney et al., 2013; Stemberger, 1979) occurred under a compound microscope at $200 \times$ magnification.

We also collected replicate zooplankton samples from sample sites at rkm 385 and rkm 17 for enumeration by BSA. We excluded these replicate samples from further analyses in this manuscript. However, we calculated mean taxon-specific rotifer biomass determined from samples processed by BSA (based on established length-biomass or width-biomass relationships) to estimate biomass of rotifers enumerated in the primary zooplankton samples (Appendix A).

2.5 | Statistical analyses

We performed all statistical analyses with R (R Core Team, 2020) and accepted a 5% probability of false positives ($\alpha = .05$) when testing null hypotheses. We first characterized Minnesota River water chemistry, the phytoplankton community, and the zooplankton community by calculating summary statistics (e.g., M, SE, quartiles) for all samples pooled. We specifically characterized the phytoplankton community with biovolume (mm³/L) of the four dominant taxa (Bacillariophyta, Chlorophyta, Cryptophyta, and Cyanobacteria) and the zooplankton community with biomass (µg/L) of five dominant cladoceran families (Bosminidae, Chydoridae, Daphniidae, Leptodoridae, and Sididae), two copepod orders (Cyclopoida and Calanoida), copepodites, copepod nauplii, and rotifers (all taxa combined). We identified correlated physicochemical variables by calculating Pearson correlation coefficients (using chart. Correlation function from the "PerformanceAnalytics" package version 1.5.2; Peterson et al., 2018) to prevent multicollinearity issues in multivariate analyses. We increased normality and homoscedasticity of distributions by ln(x + 1) transforming all physico-chemical variables except S-tube reading and water temperature. We considered statistically significant Pearson correlation coefficients ≥0.60 indicative of strong relationships between variables. We then selected the variable

hypothesized to have the most direct influence on plankton communities (e.g., selection of TSS rather than S-tube reading) from groups of strongly correlated explanatory variables for inclusion in multivariate analyses.

Discharge is an important environmental driver of plankton dynamics in lotic ecosystems, and is, therefore, an important variable for consideration when evaluating Minnesota River plankton communities. Discharge follows an upstream to downstream gradient, making absolute discharge strongly correlated with river kilometer and comparisons among locations in the river difficult. For example, discharge of 200 m³/s may cause flood conditions at an upstream site but seasonally low water conditions at a downstream site. For these reasons, we calculated a relativized measure of discharge as a surrogate for hydrologic conditions that allowed for more appropriate comparisons among samples. 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 (US Geological Survey, n.d.).

We tested the null hypotheses that physico-chemical variables, phytoplankton taxa biovolumes, and zooplankton taxa biomasses do not differ among months (temporally) or exhibit linear relationships with rkm (spatially) by first plotting un-transformed or ln(x + 1) transformed data as a function of the categorical variable of month (boxplots) and the continuous variable of sample site rkm (scatter-plots). We statistically evaluated the spatial and temporal null hypotheses by conducting one-way Analysis of Variances (ANOVA) and linear regression analyses, respectively, with ln(x + 1) transformed response variables (except for temperature) to increase normality and homoscedasticity of distributions. We then fit a linear regression line for significant (i.e., $p \le .05$) linear relationships with an adjusted $r^2 \ge .13$. We interpreted adjusted $r^2 < .13$ as small and non-meaningful effects, from 0.13 to 0.26 as medium and moderately meaningful effects, and >0.26 as large and meaningful effects (Cohen, 1988). Following ANOVA tests that indicated significant differences among months, we performed pairwise t tests, but did not report all results for brevity. We also tested the null hypothesis of no linear relationship between plankton biovolume or biomass and relative discharge by plotting ln(x + 1) transformed taxa biovolume or taxa biomass as a function of relative discharge and performing linear regression analyses.

We further evaluated trends in Minnesota River phytoplankton and zooplankton community structure (also referred to as community composition) among months and sample sites by calculating Bray– Curtis dissimilarity matrices with ln(x + 1) transformed phytoplankton biovolume or zooplankton biomass data. We then conducted permutational multivariate analysis of variance (PERMANOVA; with 999 permutations) on the dissimilarity matrices (using the *adonis* function from the "vegan" package; Okansen et al., 2019) to examine individual effects of the categorical temporal variable, month; the categorical spatial variables, reach (i.e., upstream or downstream) and sample site; the continuous spatial variable, rkm; and continuous physico-chemical variables (e.g., relative discharge, water chemistry variables) on phytoplankton and zooplankton community structure. Permutational multivariate analysis of variance is a geometric partitioning of multivariate variation in the space of a chosen dissimilarity measure (Anderson, 2017). The adonis function calculates a pseudo-F statistic, a p value, and an R^2 for each independent variable included in a PERMANOVA. The R^2 is the sum-of-squares for the independent variable divided by the total sum-of-squares and provides a measure of "variability explained". We visually interpreted Bray-Curtis dissimilarity matrices by plotting two-dimensional non-metric multidimensional scaling (NMDS; Clarke, 1993) ordinations (using the metaMDS function from the "vegan" package) and fit vectors (using the envfit function from the "vegan" package) depicting the general direction of relationships for significant ($p \le .13$) and meaningful ($R^2 \ge .13$) continuous variables identified with PERMANOVA. On separate NMDS plots, we plotted the 95% confidence interval ellipses (using the ordiellipse function from the "vegan" package) around the average weighted centroids of statistically significant categorical variables with $R^2 \ge .13$. Additionally, we evaluated patterns in phytoplankton and zooplankton community structure while excluding the influence of dams by conducting the same PERMANOVA analyses with data only collected from the five downstream sample sites. Omitting the two upstream sample sites from these additional analyses allowed for evaluation of spatial trends without the confounding influence of dams that are located upstream of the two upstream sites. Finally, we also used PERMANOVA to evaluate the combined effect of month, relative discharge, and their interaction on phytoplankton and zooplankton community structure.

3 | RESULTS

We collected complete or partial samples from all seven sample sites during August–October of 2016, May–October of 2017, and May– October of 2018; totaling 105 samples. We collected samples from the bank rather than from a boat for five samples that occurred during flood conditions, 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 generally decreased with river kilometer (Pearson correlation coefficient: r = -.63, $p \le .001$) and relative discharge varied widely among sample events (Figure 2). For example, relative discharge varied 0.05–0.94 among sample events at rkm 213 (river gage at rkm 185), exceeding 0.5 for 10 of 15 samples.

We identified several strongly correlated physico-chemical variables and selected Chl-*a*, TP, silica, TDS, temperature, and TSS for inclusion in multivariate analyses (Table 1). The most variable Minnesota River physico-chemical variables included Chl-*a* and TSS with medians (interquartile range, IQR) of 51.2 (70.6) μ g/L and 65 (40) mg/L, respectively (Table 2). All retained physico-chemical variables significantly differed among months except TSS (Figure 3). Chlorophyll-*a* and temperature exhibited negative relationships with relative discharge and TDS was the only physico-chemical variable

that exhibited a significant and meaningful (positive) relationship with rkm (Figure 4).

Phytoplankton identified in samples represented diverse assemblages that included 73 genera from six phytoplankton divisions and Cyanobacteria (Appendix B), but Bacillariophyta (diatoms) and Cyanobacteria (blue-green algae) dominated the biovolume with medians (IQR) of 3.60 (9.8) $\rm mm^3/L$ and 5.69 (14.4) $\rm mm^3/L$, respectively



FIGURE 2 Discharge (m³/s) of the Minnesota River at gaging stations located near three sample sites (rkm 48, rkm 213, rkm 424) during the study period of July, 2016–October, 2018. Symbols indicate the relative discharge (percentile) during each sample events

(Table 2). Cyanobacterial biovolume peaked during July-September while diatom biovolume was generally greatest during May, August, and September (although not significantly different for all pairwise comparisons; Figures 5 and 6). Biovolume of all four phytoplankton taxa had statistically significant negative linear relationships with relative discharge (Figure 6); however, the relationship was not meaningful (r^2 = .03) for Cryptophyta. Multivariate analyses indicated the variables month, relative discharge, Chl-a, and silica had significant relationships ($p \le .05$ and $R^2 \ge .13$) with phytoplankton community structure (when all sites were included in analyses; Table 3 and Figure 7). None of the phytoplankton taxa exhibited a significant linear relationship with RKM, and phytoplankton community structure did not significantly differ among sample sites. Non-metric multidimensional scaling plots revealed various relationships including that, phytoplankton communities with greater relative biomass of Chlorophyta and Cyanobacteria were positively associated with Chl-a concentration and negatively associated with relative discharge, and that silica concentration was negatively associated with diatoms and Cryptophyta. Analyses (PERMANOVA) indicated the variables that independently had the strongest relationships with phytoplankton community structure included month ($R^2 = .34 - .36$), Chl-a concentration ($R^2 = .33-.38$), and relative discharge ($R^2 = .24-.33$); regardless of inclusion or exclusion of data from upstream sites influenced by dams. The combination of month, relative discharge, and their interaction explains 57% of the variability in phytoplankton community structure.

Zooplankton identified in samples also represented diverse assemblages that included 7 families and 14 genera of cladocerans, 2 families and 8 genera of copepods, and 14 families and 24 genera of rotifers (Appendixes C and D). Overall, we found median rotifer biomass (3.48 μ g/L) exceeded median crustacean zooplankton biomass

TABLE 1 Statistically significant ($p \le .05$) Pearson correlation coefficients for pairwise comparisons of physico-chemical variables measured at seven Minnesota River sites and correlations with river kilometer and relative discharge

	Pearson o	Pearson correlation coefficient								
Variable	Chl-a	N/N	Ortho-P	TDS	Temp.	TKN	TP	TSS	S-tube	Silica
Chl-a										
N/N	-0.75									
Ortho-P	-0.40	0.26								
TDS			-0.35							
Temp.	0.48	-0.29		-0.26						
TKN	0.65	-0.72			0.43					
ТР			0.64	-0.50	0.25					
TSS	-0.26	0.39	0.33	-0.27			0.64			
S-tube		-0.19	-0.33	0.32	-0.24		-0.61	-0.69		
Silica			0.42				0.46		-0.27	
River kilometer	0.20	-0.47		0.43		0.41		-0.29	0.31	
Relative discharge	-0.74	0.57	0.43		-0.43	-0.54		0.21		

Note: All variables were ln(x + 1) transformed except temperature, S-tube depth, river kilometer, and relative discharge.

Abbreviations: Chl-a, chlorophyll-a; N/N, nitrate/nitrite; Ortho-P, dissolved ortho-phosphorus; S-tube, Secchi tube depth; TDS, total dissolved solids; Temp, water temperature; TKN, total Kjeldahl nitrogen; TP, total phosphorus; TSS, total suspended solids.

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Variable or taxa	n	Mean	SE	Min	Q ₁	Median	Q ₃	Max
Water chemistry								
S-tube (cm)	105	21.1	0.7	3.6	16.6	20.0	25.0	49.0
Temp (°C)	105	19.0	0.5	5.0	16.0	20.0	22.5	27.1
Ammonia-N (mg/L)	98	0.03	0.00	0.01	0.01	0.01	0.03	0.12
Chl- <i>a</i> (µg/L)	105	66.6	4.4	7.8	28.0	51.2	98.6	206.0
N/N (mg/L)	105	4.6	0.3	0.0	1.3	3.9	7.5	13.0
Ortho-P (mg/L)	105	0.060	0.004	0.012	0.029	0.052	0.083	0.157
Silica (mg/L)	105	11.6	0.3	4.2	10.9	12.3	13.6	16.2
TDS (mg/L)	105	659	13	376	560	644	748	992
TKN (mg/L)	105	1.4	0.0	0.2	1.2	1.3	1.6	2.5
TP (mg/L)	105	0.207	0.006	0.105	0.161	0.195	0.234	0.396
TSS (mg/L)	105	82	8	26	50	65	90	758
Phytoplankton biovolum	e (mm³/	/L)						
Bacillariophyta	103	8.12	1.08	0.19	1.53	3.60	11.28	66.44
Chlorophyta	103	0.45	0.06	0.00	0.05	0.20	0.58	3.76
Cryptophyta	103	1.15	0.13	0.02	0.35	0.81	1.43	8.60
Cyanobacteria	103	11.27	1.43	0.00	0.69	5.69	15.05	57.14
Cladoceran biomass (µg/	L)							
Family Bosminidae	102	0.10	0.02	0.00	0.00	0.01	0.12	0.70
Family Chydoridae	102	0.08	0.04	0.00	0.00	0.00	0.01	3.43
Family Daphniidae	102	27.33	7.95	0.00	0.00	0.09	4.18	485.81
Family Leptodoridae	102	0.30	0.22	0.00	0.00	0.00	0.00	21.41
Family Sididae	102	0.34	0.12	0.00	0.00	0.00	0.05	8.21
Copepod biomass (µg/L)								
Order Calanoida	102	5.76	1.47	0.00	0.00	0.00	2.51	90.50
Order Cyclopoida	102	11.31	3.11	0.00	0.17	0.77	4.92	191.60
Copepodites	102	1.45	0.34	0.00	0.05	0.25	0.88	24.89
Nauplii	102	0.25	0.06	0.00	0.01	0.05	0.18	3.94
Rotifer biomass (µg/L)								
Rotifers	102	7.07	0.91	1.07	1.96	3.48	6.97	56.10

Abbreviations: Chl-*a*, Chlorophyll-*a*; N/N, nitrate/nitrite; Ortho-P, dissolved ortho-phosphorus; TDS, total dissolved solids; Temp, water temperature; TKN, total Kjeldahl nitrogen; TP, total phosphorus; TSS, total suspended solids; S-tube, Secchi tube depth.

(ranging from 0.00 for several taxa to 0.77 for cyclopoid copepods). However, $M \pm SE$ crustacean zooplankton biomass was greater than mean rotifer biomass with mean crustacean zooplankton biomass ranging from 0.08 ± 0.04 Chydoridae µg/L to 27.33 ± 7.95 Dapniidae µg/L and mean rotifer biomass of 7.07 ± 0.91 µg/L (Table 2). Additional analyses revealed that mean crustacean zooplankton biomass (146.7 ± 32.6 µg/L) was greater than mean rotifer biomass (8.3 ± 2.0 µg/L) at upstream sites (one tailed *t* test: *t* = 4.23, *df* = 29.2, *p* < .001) but not at downstream sites (one tailed *t* test: *t* = -0.54, *df* = 104.78, *p* = .29; Table 4). In terms of density rather than biomass, rotifers were more abundant than crustacean zooplankton at both upstream and downstream sites (Table 4).

Zooplankton community structure differed among months with a significant peak in Bosminidae biomass occurring during October (but not greater than during June) and peaks in Chydoridae, cyclopoid copepods, copepodite, nauplii, and rotifer biomass occurring during May (Figure 8). We did not find significant and meaningful linear relationship between rkm and biomass of Bosminidae, Chydoridae, Leptodoridae, nauplii, and rotifers, but identified positive linear relationships for the other taxa groups (particularly for daphnids and adult copepods; Figures 9 and 10). We typically observed the greatest biomass of these taxa at the two upstream sites that are influenced by dams. We also failed to find significant and meaningful linear relationship between relative discharge and biomass for most zooplankton taxa groups (Figures 9 and 10), but identified positive relationships with Bosminidae ($r^2 = .19$) and nauplii ($r^2 = .15$) biomass.

Multivariate analyses indicated that continuous (rkm) and categorical (sample site, reach) variables associated with sample sites ($R^2 = .24$ -.36) and the categorical variable of month ($R^2 = .18$) had significant relationships with zooplankton community structure

TABLE 2Summary statistics forphysico-chemical variables,phytoplankton taxa biovolume, andzooplankton taxa biomass across allsample sites and years

FIGURE 3 Measured Minnesota River physico-chemical variables (Chl-a, Chlorophyll-a; TP, total phosphorus; TDS, total dissolved solids; Temperature; TSS, total suspended solids; Silica) among months (M, May; Jn, June; Jl, July; A, August; S, September; O, October). Analysis of variance was used to test the null hypothesis of no difference among months using ln(x + 1)transformed response variables (except for Temperature). Lines within the boxes indicate medians; ends of boxes indicate the 25th and 75th percentiles; ends of the whiskers indicate values up to $1.5 \times$ the interguartile ranges; black circles indicate outliers. One extreme outlier (>700 mg/L) for TSS falls outside the bounds of the figure



0.6

0.5

0.4

0.3

0.2

0.1

400

300

200

mg L ⁻¹

TP

F = 17.7, P < 0.001



Chl-a

F = 29.4, P < 0.001

8

. Dn 300

100

100 0 0.6 TP = 0.196 0.4 0.2 0.0 2000 TDS = 0.667 1500 1000 500 0 60 Temperature 45 = 0.18, P < 0.001 30 15 0 450 300 0 150 2 0 30 ilica 20 10 0 0.2 0.4 0.6 0.8 0.0 1.0 Relative discharge (percentile)

Chl-a

< 0.001

0.54 P

FIGURE 4 Relationships between Minnesota River physico-chemical variables (Chl-*a*, Chlorophyll-*a*; TP, total phosphorus; TDS, total dissolved solids; Temperature; TSS, total suspended solids; Silica) and river kilometer and relative discharge. Linear regression analyses were used to test the null hypothesis of no linear relationship with river kilometer or relative discharge using ln(x + 1)transformed response variables. Regression lines are provided for statistically significant ($p \le .05$) and meaningful linear relationships with $r^2 \ge .13$. One extreme outlier (>700 mg/ L) for TSS falls outside the bounds of the figure

FIGURE 5 Minnesota River Phytoplankton taxa ln(x + 1) transformed biovolume (mm³/L) among months (M, May; Jn, June; Jl, July; A, August; S, September; O, October). Analysis of variance was used to test the null hypothesis of no difference among months using ln(x + 1) transformed response variables. Lines within the boxes indicate medians; ends of boxes indicate the 25th and 75th percentiles; ends of the whiskers indicate values up to $1.5 \times$ the interquartile ranges; black circles indicate outliers



FIGURE 6 Relationships between Minnesota River phytoplankton taxa ln(x + 1) transformed biovolume (mm³/L) and river kilometer and relative discharge. Linear regression analyses were used to test the null hypothesis of no linear relationship with river kilometer or relative discharge using ln(x + 1)transformed response variables. Regression lines are provided for statistically significant ($p \le .05$) and meaningful linear relationships with $r^2 \ge .13$

	All samples			Excluding upstream si)	
Variable	F	R ²	р	F	R ²	р
Continuous variables						
River kilometer	5.3	.05	.004	0.7	.01	.572
Relative discharge	31.2	.24	<.001	33.9	.33	<.001
Chl-a	48.4	.33	<.001	43.5	.38	<.001
ТР	5.4	.05	<.001	7.7	.10	<.001
Silica	15.1	.13	<.001	7.6	.10	<.001
TDS	2.1	.02	.117	0.6	.01	.656
Temperature	7.3	.07	<.001	6.1	.08	.003
TSS	11.3	.10	<.001	9.4	.12	<.001
Categorical variables						
Sample site	1.4	.08	.135	0.7	.04	.714
Month	10.7	.36	<.001	6.9	.34	<.001
Upstream vs. downstream	5.06	.05	.005			
Combined model						
Month +	14.9	.36	<.001	11.1	.34	<.001
Relative discharge $+$	27.2	.13	<.001	33.3	.21	<.001
$\text{Month} \times \text{relative discharge}$	3.3	.08	<.001	2.6	.08	.002

TABLE 3 Results (pseudo-*F*, *R*², and *p* values) from permutational multivariate analysis of variance using distance matrices (Bray–Curtis) of Minnesota River phytoplankton community samples and fitting individual linear models for spatial, temporal, and physico-chemical variables

Note: Analyses were performed with data from all sample sites and with data excluding the two upstream most sites that are influenced by dams. All biovolume and water chemistry data were ln(x + 1) transformed.

Abbreviations: Chl-*a*, Chlorophyll-*a*; TP, total phosphorus; TDS, total dissolved solids; TSS, total suspended solids. All biovolume and water chemistry data were ln(x + 1) transformed.

(Table 5 and Figure 11). Similar to results from linear regression analyses, rkm was positively associated with zooplankton communities that have greater relative biomass of larger-bodied cladocerans and adult copepods and the zooplankton community structure in the upstream reach differed from the downstream reach (PERMANOVA: $R^2 = .28$; p < .001). When we excluded data from upstream sites, the strength of relationships with relative discharge and silica become meaningful, the relationship with month is stronger, and the strength of the relationship with $R^2 = .05$) and sample site ($R^2 = .08$) is weaker and not meaningful. The combination of month, relative discharge, and their interaction only explain 29% of the variability in zooplankton community structure among all seven sample sites, but 49% of variability among the five samples sites within the downstream reach.

4 | DISCUSSION

This study unveiled diverse plankton assemblages within the main channel of the Minnesota River and contributed to an expanding knowledge about spatiotemporal dynamics of lotic plankton communities. Diatoms and Cyanobacteria dominate the Minnesota River phytoplankton community, while rotifers numerically dominate the zooplankton community and typically outnumber crustacean zooplankton by one to three orders of magnitude. Plankton communities in the Minnesota River generally resemble those found in other medium to large rivers (Basu & Pick, 1996; Havel et al., 2009; Thorp & Mantovani, 2005), including downstream in the Mississippi River (Baker & Baker, 1981; Burdis & Hoxmeier, 2011). Results of this study support our hypothesis, revealing that both phytoplankton and zoo-plankton communities exhibit temporal patterns among years. Differing from expectations, the phytoplankton community did not exhibit longitudinal trends (Basu & Pick, 1997; Hardenbicker et al., 2016; Vannote et al., 1980) or spatial patchiness (Abonyi et al., 2014), but zooplankton communities at the two upstream sites had significantly greater biomass of larger-bodied cladocerans and adult copepods than at downstream sites.

Relatively abundant cladocerans and copepods at the two upstream sites are likely exports from upstream of Granite Falls Dam and Lac Qui Parle Dam where water residence time is greater and zooplankton species with longer generation times are favored (Baranyi, Hein, Holarek, Keckeis, & Schiemer, 2002; Burdis & Hirsch, 2017; Pourriot et al., 1997). Within the lower 300-km freeflowing reach of the Minnesota River, we failed to identify meaningful differences in the zooplankton communities among five sample sites. Thus, we attribute spatial differences in zooplankton communities to the influence of dams rather than longitudinal processes or spatial heterogeneity in other abiotic or biotic conditions. Several other studies document similar influences of dams and reservoirs on downstream lotic zooplankton communities (Akopian, Garnier, & Pourriot, 1999; Burdis & Hoxmeier, 2011; Havel et al., 2009; Pourriot et al., 1997). For instance, Burdis and Hoxmeier (2011) similarly found

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greater biomass of daphnids and copepods in the Mississippi River downstream of Lake Pepin compared with upstream. Havel et al. (2009) also observed high densities of crustacean zooplankton immediately downstream of Missouri River dams and densities exponentially declined with distance downstream. These findings support our claim that impounded reaches upstream of dams likely serve as a source of crustacean zooplankton for downstream reaches and strongly influence the spatial patterns we observed. In contrast with zooplankton, phytoplankton communities did not exhibit meaningful differences between the upstream and downstream reaches.



NMDS axis 1

FIGURE 7 Results of NMDS (stress = 0.13, non-metric fit R^2 = .98) showing phytoplankton community structure differed with (a) relative discharge (RD), Chlorophyll-*a* concentration (Chl-*a*), and silica concentration and (b) among months (M, May; Jn, June; Jl, July; A, August; S, September; O, October). Significant relationships ($p \le .05$; $R^2 \ge .13$) between phytoplankton community structure and continuous physico-chemical variables determined with permutational multivariate analysis of variance (PERMANOVA) are displayed as vectors depicting the general direction of the relationship. Significant differences (PERMANOVA; $p \le .05$; $R^2 \ge .13$) in phytoplankton community structure among months are displayed with 95% confidence interval ellipses around average weighted centroids

However, impounded reaches upstream of dams likely provide inoculum that influence downstream phytoplankton communities (Grabowska & Mazur-Marzec, 2011; Prygiel & Leitao, 1994), and those influences may be relatively consistent throughout the entire study reach. Alternatively, phytoplankton exports from upstream of dams may include taxa that are unable to survive the riverine environment long enough to reach our sample sites that are 10 km and further downstream. Future studies should address these questions and advance understanding of the influence of dams and impoundments on lotic plankton communities by sampling plankton from various distances upstream and downstream of dams and within impounded reaches during varying hydrologic conditions.

Excluding the influence of dams, relatively spatially homogenous plankton communities observed in the Minnesota River differ from numerous studies that document spatial patterns or patchiness in lotic plankton communities attributed to longitudinal processes or differences in environmental conditions among river reaches (e.g., Abonyi et al., 2014: Basu & Pick, 1997: Hardenbicker et al., 2016: Massicotte, Frenette, Proulx, Pinel-Alloul, & Bertolo, 2014; Varol & Sen, 2018). Many abiotic and biotic attributes (e.g., in-stream habitat complexity, lateral connectivity, fish communities) differ spatially within the Minnesota River at varying scales, but only one of the physico-chemical factors (TDS) evaluated during this study exhibited a meaningful spatial pattern. Similarities in TP (e.g., nutrients), TSS (e.g., turbidity), relative discharge, and water temperature among sample sites likely contributes to the spatial similarities in Minnesota River plankton communities. Zhao et al. (2017) similarly demonstrated spatial homogenization of zooplankton communities in the Ying River system of China associated with homogenization of environmental conditions during high flow events compared with greater heterogeneity among habitats during the dry season. Under certain environmental conditions (e.g., drought) or over a larger spatial scale (e.g., including tributaries) where abiotic factors exhibit greater spatial variability, we would also expect greater spatial variability in plankton communities.

In contrast with spatially homogenous abiotic factors, we found significant temporal variability in Minnesota River physico-chemical attributes that likely influenced temporal patterns in plankton community structure. Both phytoplankton and zooplankton communities exhibited seasonal patterns with differences between spring (May and June), summer (July–September), and fall (October) months. Besides the presumed influence of dams on zooplankton, the variable "month" explained the greatest amount of variability in plankton community

TABLE 4	Minnesota River crustacean zooplankton (cladocerans and copepods, excluding nauplii and copepodites) and rotifer biomass and
density in sa	mples collected from five downstream sites and from two upstream sites (influenced by dams) across all study years

		Downstre	Downstream				Upstream	ı		
Biomass or density	n	Mean	SE	Min	Max	n	Mean	SE	Min	Max
Crustacean biomass (µg/L)	72	4.8	1.9	0	118.8	30	142.3	31.9	0.0	695.6
Rotifer biomass (µg/L)	72	6.5	1.0	1.1	36.5	30	8.3	2.0	1.3	56.1
Crustacean density (ind./L)	72	0.8	0.2	0.0	13.3	30	19.4	4.6	0.0	121.3
Rotifer density (ind./L)	72	207.9	40.9	3.5	1,685.3	30	230.8	47.9	13.3	1,197.8



FIGURE 8 Minnesota River zooplankton taxa ln(x + 1) transformed biomass (µg/L) among months (M, May; Jn, June; Jl, July; A, August; S, September; O, October). Analysis of variance was used to test the null hypothesis of no difference among months using ln(x + 1) transformed response variables. Lines within the boxes indicate medians; ends of boxes indicate the 25th and 75th percentiles; ends of the whiskers indicate values up to $1.5 \times$ the interquartile ranges; black circles indicate outliers

structure. For phytoplankton, we observed seasonal trends similar to those reported downstream in the Mississippi River (Baker & Baker, 1981) with diatoms being dominant during spring. Cvanobacteria dominant during summer, and that other taxa (e.g., green algae, cryptophytes) are present but rarely dominant. Similar seasonal succession of phytoplankton community structure has also been reported for eutrophic Minnesota lakes (Heiskary, Hirsch, & Rantala, 2016), and numerous other studies have documented seasonal succession of phytoplankton communities in lotic systems (e.g., Kleinteich et al., 2020; Peterson & Stevenson, 1989; Salmaso & Braioni, 2008; Tavernini et al., 2011). For zooplankton, community structure differed during May and October compared with other months, and several taxa groups, including rotifers, cyclopoids, copepodites, and nauplii were notably most abundant during May. Other studies have also documented consistent spring or summer peaks in certain zooplankton taxa, especially for rotifers, which are often the most abundant taxa in lotic systems (Lair, 2006). Similar to our findings, Wahl, Goodrich, Nannini, Dettmers, and Soluk (2008) found that rotifer abundance peaked during May in the Illinois River. Pace et al. (1992) and Thorp, Black, Haag, and Wehr (1994) also documented seasonal trends in lotic zooplankton communities, including peaks in rotifer abundance occurring between late spring (June) and mid-summer (July-August). Temperature is often one of the most influential drivers of seasonal patterns, and peaks in rotifers are often associated with seasonal increases in water temperature (Arora & Mehra, 2003; Burdis & Hoxmeier, 2011). Gillooly and Dodson (2000) found that water temperature also influences Daphniidae abundance, with peaks occurring between 15 and 20°C. Accordingly, we typically observed the lowest biomass of Daphniidae in the Minnesota River during summer months when water temperatures exceeded 20°C. Our results did not reveal meaningful relationships between water temperature and plankton community structure, but similarities in temporal patterns among years and among systems indicate that plankton communities exhibit seasonal succession that is influenced by phenological patterns and factors that vary predictably with season (e.g., temperature, photoperiod, nutrient fluxes). However, extreme hydrological and meteorological events (e.g., floods, droughts; Beaver et al., 2013) and anthropogenic disturbances (e.g., draw downs, impoundments) are likely capable of disrupting these seasonal patterns.

The constant downstream transport in lotic systems is a dominant force influencing plankton community dynamics and many studies demonstrate that water residence time has a significant positive relationship with abundance and density of phytoplankton and zooplankton, and can influence species composition (Basu & Pick, 1996; Burdis & Hirsch, 2017; Reckendorfer, Keckeis, Winkler, & Schiemer, 1999; Salmaso & Braioni, 2008; Søballe & Kimmel, 1987). Consistent with that notion, our results revealed strong negative relationships between phytoplankton biovolume and relative discharge, and relative discharge independently explained 24% of variability in phytoplankton community structure. During this study, relative discharge was generally high during May, June, and October, relatively **FIGURE 9** Relationships between Minnesota River cladoceran zooplankton taxa ln(x + 1) transformed biomass (µg/L) and river kilometer and relative discharge. Linear regression analyses were used to test the null hypothesis of no linear relationship with river kilometer or relative discharge using ln(x + 1)transformed response variables. Regression lines are provided for statistically significant ($p \le .05$) and meaningful linear relationships with $r^2 \ge .13$



low during September, and more variable during July and August among years. Accordingly, phytoplankton biovolume was typically lowest during months with consistently high relative discharge (May, June, and October), especially for green algae and Cyanobacteria. Phytoplankton biovolume presumably decreased with discharge because of increased advective losses and dilution, and because of decreased light availability caused by greater turbulence and river depths (Descy et al., 2016; Reynolds, 2000). Hydrologic factors, such as water residence time, are thought to have an even greater influence on zooplankton communities because of their longer generation times and lesser ability to compensate for advective loss (Basu & Pick, 1996; Pace et al., 1992). Yet, in contrast with other studies (Basu & Pick, 1996; Pace et al., 1992; Rossetti et al., 2009; Sluss & Jack, 2013), we found that relative discharge alone explained a minimal amount of variability in zooplankton community structure and that Bosminidae and nauplii biomass tended to increase with relative discharge. Basu and Pick (1997) similarly found that river discharge was a poor predictor of zooplankton biomass in the Rideau River, Canada, and Burdis and Hoxmeier (2011) found that peaks in zooplankton abundance and biomass in the Mississippi River often occurred during May and June when discharge was greatest. Seasonal in zooplankton biomass are likely influenced peaks bv seasonal changes, such as increasing water temperature, and outcomes from this study and others indicate that temporal patterns can have a stronger influence on lotic zooplankton communities than

variability in discharge among years. Lotic systems with short water residence times generally favor smaller zooplankton with shorter generation times and taxa that are more tolerant of turbid and turbulent conditions (e.g., rotifers, Bosminidae; Baranyi et al., 2002; Lair, 2006; Pace et al., 1992). The Minnesota River was generally turbid (never exceeding 0.5 m S-tube depth) regardless of relative discharge conditions, which is demonstrated by weak or insignificant relationships between relative discharge and TSS and S-tube depth. Thus, variability within the range of discharge conditions typical of the Minnesota River may have minimal influence on the main channel zooplankton community that is dominated by rotifers and other taxa adapted to turbid riverine environments. Even during periods of low relative discharge sampled during this study, water residence times may not have exceeded thresholds that allow larger-bodied cladocerans to outcompete rotifers and influence significant shifts in zooplankton community structure (Baranyi et al., 2002; Gilbert, 1988).

Although relative discharge independently had a small effect on zooplankton community structure, our analyses revealed that the cumulative effects of month, relative discharge, and their interaction explained 49% of the variability in zooplankton community structure within the downstream reach and 57% of the variability in phytoplankton community structure. These results corroborate the findings of others by demonstrating that seasonal succession and hydrological factors can be interconnected and are both important for regulating lotic plankton communities (Pace et al., 1992; Rossetti et al., 2009;



FIGURE 10 Relationships between Minnesota River copepod and rotifer zooplankton $\ln(x + 1)$ transformed biomass (µg/L) and river kilometer and relative discharge. Linear regression analyses were used to test the null hypothesis of no linear relationship with river kilometer or relative discharge using $\ln(x + 1)$ transformed response variables. Regression lines are provided for statistically significant ($p \le .05$) and meaningful linear relationships with $r^2 \ge .13$

Salmaso & Braioni, 2008; Tavernini et al., 2011; Thorp et al., 1994). Relative discharge exhibited seasonal patterns among years in the Minnesota River, making it difficult to decouple the influence of hydrologic conditions and seasonal succession. For instance, seasonal succession is likely a primary factor contributing to differences in phytoplankton and zooplankton community structure between the months of May and October, but it is difficult to evaluate the potential influence of relative discharge during these months because mean relative discharge was relatively high (>0.50) among years. Time of year (month) explained the greatest amount of variability in Minnesota River plankton communities during this study, but hydrologic condition likely influences the temporal trend and may also explain deviations from typical seasonal patterns among years (Burdis & Hirsch, 2017).

With the exception of relative discharge, relationships between physico-chemical variables and plankton community structure were generally weak or indirect. Other studies demonstrate significant relationships between nutrients (i.e., phosphorus, nitrogen), turbidity (e.g., Secchi depth), phytoplankton (frequently represented by Chl-a concentration), and zooplankton among systems (e.g., Basu & Pick, 1996; Heiskary & Markus, 2001; Søballe & Kimmel, 1987; Thorp & Mantovani, 2005). However, these relationships are often different or less evident within individual systems (Bukaveckas et al., 2011; Thorp & Mantovani, 2005). For example, when comparing zooplankton densities among seven rivers. Thorp and

Mantovani (2005) found that turbidity had a positive relationship with rotifer density and a negative relationship with crustacean zooplankton density. However, Thorp and Mantovani (2005) found opposite relationships when evaluating the zooplankton community within just one of the rivers (Kansas River). Although most physico-chemical variables differed among months in the Minnesota River, the ranges of values observed are smaller than or outside of ranges typically observed among a diversity of systems, and did not explain substantial variability in Minnesota River plankton communities. Silica and Chl-a concentrations are the exceptions, but relationships with these parameters are likely a consequence of the phytoplankton community rather than a mechanisms that directly influences plankton communities. Chlorophyll-a is a component of phytoplankton that is often measured as a surrogate for phytoplankton biomass (e.g., Basu & Pick, 1996), and we accordingly observed increases in Chl-a associated with increases in phytoplankton biovolume, particularly for Chlorophyta and Cyanobacteria. Similarly, silica concentration declines because of uptake by diatoms, and typically increases following diatom blooms (Kleinteich et al., 2020; Tavernini et al., 2011). The Minnesota River is a fertile hypereutrophic system (Dodds, Jones, & Welch, 1998), and similar to many medium to large rivers, we suspect is rarely nutrient-limited (Salmaso & Braioni, 2008; Wehr & Descy, 1998). Basu and Pick (1996) found that among rivers, TP was the most important predictor ($r^2 = .76$) of phytoplankton biomass (measured as Chl-a), but mean TP concentrations were below

	All samples		Excluding upstream sites (RKM 385 and 424)			
	F	R ²	p	F	R ²	р
Continuous variables						
River kilometer	30.8	.24	<.001	3.9	.05	.013
Relative discharge	8.3	.08	<.001	9.9	.12	<.001
Chl-a	2.7	.03	.054	5.0	.07	.002
ТР	4.4	.04	.009	3.1	.04	.038
Silica	10.3	.09	<.001	15.6	.18	<.001
TDS	3.7	.04	.014	2.2	.03	.068
Temperature	5.4	.05	.008	5.8	.08	.003
TSS	4.6	.04	.010	0.3	.00	.868
Categorical variables						
Sample site	8.8	.36	<.001	1.48	.08	.121
Month	4.3	.18	<.001	6.7	.34	<.001
Upstream vs. downstream	39.4	.28	<.001			
Combined model						
Month +	4.6	.18	.001	7.9	.34	.001
Relative discharge $+$	2.3	.02	.092	5.0	.04	.004

TABLE 5 Results (pseudo-*F*, *R*², and *p* values) from permutational multivariate analysis of variance using distance matrices (Bray–Curtis) of Minnesota River zooplankton community samples and fitting individual linear models for spatial, temporal, and physico-chemical variables

Note: Analyses were performed with data from all sample sites and with data excluding the two upstream most sites that are influenced by dams. All biomass and water chemistry data were ln(x + 1) transformed.

.010

2.6

Abbreviations: Chl-a, Chlorophyll-a; TP, total phosphorus; TDS, total dissolved solids; TSS, total suspended solids.

.09

2.3

100 μ g/L in all but one of the rivers. Total phosphorus concentrations in the Minnesota River varied from 105 to 396 μ g/L during this study, likely exceeding concentrations that would limit phytoplankton growth. Water chemistry and nutrient availability have demonstrable influences on plankton communities in other lotic systems (e.g., Arora & Mehra, 2003; Kleinteich et al., 2020; Rossetti et al., 2009; Varol & Şen, 2018), but their influence on Minnesota River plankton communities is minimal at the scale of our analyses (e.g., taxa groups rather than species) and less important than the significant influences associated with seasonal succession, hydrologic condition, and dams.

Month \times relative discharge

We evaluated Minnesota River plankton communities in midchannel habitats, but water retention or storage zones (e.g., habitat complexities, floodplain lakes, side channels, impoundments) within the river channel (Casper & Thorp, 2007; Reckendorfer et al., 1999; Schiemer et al., 2001) and the floodplain (Górski et al., 2013) likely support differing plankton communities that serve important roles in the floodplain river ecosystem (Casper & Thorp, 2007). Nickel (2014) corroborated this hypothesis for the Minnesota River and showed that Minnesota River backwaters generally have greater abundance and diversity of zooplankton than nearby main channel habitats. Most unaltered rivers with natural flow regimes have important connectivity with floodplain habitats (Poff et al., 1997) and these connections allow fish and other biota to utilize the floodplain habitat during flood pulses and for a flush of nutrients and plankton into the main channel as water levels recede. Górski et al. (2013) postulate that heterogeneity and connectivity of floodplain habitats are important for diverse zooplankton assemblages that are important for higher trophic organisms and ecosystem health. Future studies should explore spatial and temporal trends in plankton communities among a diversity of habitat types within the floodplain ecosystem (e.g., nearshore zones, floodplain lakes) to provide a more comprehensive understanding of lotic plankton community dynamics.

.11

This study focused on evaluating abiotic factors, but numerous studies provide evidence that under certain conditions biotic factors significantly influence plankton communities (Akopian et al., 1999; Burdis & Hirsch, 2017; Guelda et al., 2005; Pace et al., 1998; Thorp & Casper, 2003). For instance, Guelda et al. (2005) demonstrated that zooplankton can be biologically limited from the bottom-up by phytoplankton production, and 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 negatively impacted by increased suspended sediments. We did not evaluate biological factors that may influence plankton communities during this study, but we do not suggest dismissing the possibility. We hypothesize that abundant populations of planktivorous fishes such as bigmouth buffalo (Ictiobus cyprinellus), gizzard shad (Dorosoma cepedianum), paddlefish, and emerald shiner (Notropis atherinoides) may influence zooplankton community structure at smaller spatial and

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.002



FIGURE 11 Results of NMDS (stress = 0.09, non-metric fit R^2 = .99) showing zooplankton community structure differed with (a) river kilometer (Rkm), (b) among months (M, May; Jn, June; Jl, July; A, August; S, September; O, October), and (c) between sample sites. Significant relationships ($p \le .05$; $R^2 \ge .13$) between zooplankton community structure and continuous physico-chemical and spatial variables determined with permutational multivariate analysis of variance (PERMANOVA) are displayed as vectors depicting the general direction of the relationship. Significant differences (PERMANOVA; $p \le .05$; $R^2 \ge .13$) in phytoplankton community structure among months and sample sites are displayed with 95% confidence interval ellipses around average weighted centroids

temporal scales (e.g., within backwater habitats, during periods of low flow). For example, Akopian et al. (1999) found that fish predation quickly reduced densities of crustacean zooplankton downstream of dams in the Marne River, France. Establishment of non-native planktivores could also have biological influences on Minnesota River plankton communities with cascading impacts to the entire ecosystem. For example, Sass et al. (2014) found correlated declines in crustacean zooplankton and increases in rotifer zooplankton associated with establishment of invasive carps in the Illinois River, and zebra mussels (Dreissena polymorpha) are attributed with greater than 70% declines in phytoplankton and zooplankton biomass in other lotic systems (Caraco et al., 1997; Pace et al., 1998). These aforementioned studies, among numerous others, demonstrate the impact of invasive species on plankton communities, and these impacts can have consequent impacts on higher trophic levels (Pendleton et al., 2017). We recommend that future studies attempt to identify important biological factors that may regulate plankton communities in the Minnesota River (and similar river systems), and determine the impacts of invasive species on plankton communities if they become established.

This was the first spatially and temporally extensive evaluation of phytoplankton and zooplankton communities in the Minnesota River. Our results corroborate others (Burdis & Hirsch, 2017; Pace

et al., 1992; Rossetti et al., 2009; Salmaso & Braioni, 2008; Tavernini et al., 2011), demonstrating that seasonal patterns and river discharge are important drivers of phytoplankton and zooplankton community structure in lotic systems. In contrast with other lotic systems, we found that hydrologic conditions had a greater influence on phytoplankton than zooplankton community structure, and that phytoplankton communities did not exhibit significant spatial variability within the 400-km study reach of the Minnesota River. However, similar with findings in other impounded rivers, we found larger-bodied crustacean zooplankton more abundant downstream of dams where they are likely exported from impounded reaches that have greater water residence time (Akopian et al., 1999; Havel et al., 2009; Pourriot et al., 1997). For this study, we explored coarse-scale trends in plankton communities by evaluating broad taxonomic groups, and we hypothesize that trends in community structure are more nuanced and complex at a finer taxonomic resolution. This study provides a baseline understanding of lower trophic communities in a mediumsized river of the Midwestern. USA that will aid in understanding responses of lotic ecosystems associated with a changing climate, landscape, and species assemblage.

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CONFLICT OF INTEREST

The authors declare there is no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author, A. Sindt, upon reasonable request.

ORCID

Anthony R. Sindt D https://orcid.org/0000-0001-5239-3537

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APPENDIX: A

MEAN BIOMASS OF ROTIFER TAXA ESTIMATED FROM 20 MINNESOTA RIVER ZOOPLANKTON SAMPLES PROCESSED BY BSA ENVIRONMENTAL INC. (BEACHWOOD, OHIO)

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

APPENDIX: B

LIST OF CYANOBACTERIA, 6 PHYTOPLANKTON DIVISIONS, AND 73 GENERA IDENTIFIED IN WATER SAMPLES COLLECTED FROM SEVEN SITES ALONG THE MINNESOTA RIVER DURING AUGUST-OCTOBER OF 2016 AND MAY-OCTOBER OF 2017 AND 2018

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

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APPENDIX: C

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 AUGUST -OCTOBER OF 2016 AND MAY -OCTOBER OF 2017 AND 2018

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 Diacyclops Genus Pleuroxus 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

APPENDIX: D

LIST INCLUDING 3 ORDERS, 14 FAMILIES, AND 24 GENERA OF ROTIFERS IDENTIFIED IN SAMPLES COLLECTED FROM THE MINNESOTA RIVER DURING AUGUST-OCTOBER OF 2016 AND MAY-OCTOBER OF 2017 AND 2018.

Order Bdelloidea	
Order Flosculariaceae	
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	