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# Crustacean zooplankton dynamics in a natural riverine lake, Upper Mississippi River

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## ABSTRACT

Zooplankton communities in riverine systems are typically thought to be driven by abiotic forces. However, recent studies have shown that biological controls are capable of structuring these communities in large rivers and may become more influential as a river system becomes more lentic during low discharge. This study uses a long-term data set to examine several environmental variables as potential drivers of zooplankton community structure in a natural riverine lake. We hypothesized that water residence time would be the most important variable influencing zooplankton community structure. To test this, we used non-metric multidimensional scaling and correlation analysis to examine spatial and temporal patterns in zooplankton community structure. Analysis revealed that water residence time was the single most important environmental variable driving zooplankton abundance and community structure. The relationship between water residence time and taxa groups varied indicating that other taxa specific drivers had some influence on zooplankton community structure as well. Continued insight into the mechanisms driving zooplankton community structure will provide a basis for understanding zooplankton dynamics in large river ecosystems.

## ARTICLE HISTORY

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## KEYWORDS

Mississippi River; riverine lake; zooplankton; NMDS; water residence time

## Introduction

Zooplankton dynamics in lakes are generally considered to be predictable and driven biologically (Sommer et al. 1986), whereas zooplankton dynamics in rivers are largely assumed to be driven by physical processes dictated by hydrological variables (Lair 2006). While abiotic factors have historically been considered drivers of lotic zooplankton (Hynes 1970), more recent research in large river systems has shown that biological controls are capable of controlling population growth and structuring crustacean zooplankton communities. These studies demonstrated that both top-down and bottom-up trophic interactions are capable of influencing zooplankton community dynamics in river systems through fish predation (Jack & Thorp 2002; Thorp & Casper 2003) and limited algal food resources (Gueda et al. 2005). While trophic cascades are likely to be less important in rivers than in lakes, trophic interactions are likely to fluctuate in a riverine lake, where conditions vary between lotic and lentic depending on discharge in the river it is associated with. As a system becomes more lentic the potential for increased trophic interactions and biological controls should increase. Baranyi et al. (2002) found that as water residence time increased on the Danube River system, biological interactions became more important in structuring the zooplankton community

rather than physical factors. Sluss and Jack (2013) also suggested that zooplankton communities may have changed downriver in navigation pools on the Ohio River during lower discharge due to greater biotic interactions.

The dynamics of zooplankton community structure are likely going to be more complex in lotic systems as both physical and biological drivers may be at work. Known drivers of zooplankton dynamics analyzed in our study include water residence time (Pace et al. 1992; Basu & Pick 1996; Baranyi et al. 2002); water temperature (Gillooly & Dodson 2000); suspended material (Kirk & Gilbert 1990; Dejen et al. 2004) and phytoplankton abundance (Gueda et al. 2005), indicated by chlorophyll *a* concentrations. Other drivers capable of structuring the zooplankton community include fish predation (Jack & Thorp 2002) and interspecific competition (DeMott & Kerfoot 1982; Vanni 1986; Brandl 2005). Further complicating our understanding of zooplankton dynamics in river systems is the introduction of invasive species and their impact on trophic interactions. Since many invasive carps *Hypophthalmichthys* spp. are planktivorous, these fish may have immense impacts on plankton communities where they are present (Spataru & Gophen 1985; Xie & Yang 2000; Lu et al. 2002). In addition, climate change will undoubtedly affect discharge regimes in rivers (Miller & Russell 1992; Jha et al. 2004) altering hydrological conditions with unknown ecological consequences.

This study uses a long-term data (1995–2012) set to examine spatial and temporal dynamics of crustacean zooplankton and environmental variables that may regulate them in a natural riverine lake (Lake Pepin) on the Upper Mississippi River (UMR) (USA). A suite of simultaneously collected limnological variables and calculated water residence time were used to examine potential environmental factors driving zooplankton dynamics in Lake Pepin. We hypothesized that water residence time would be most influential among those variables considered, in controlling zooplankton communities and that taxon groups would be affected differentially by this variable. We suspected that cladocerans would be more affected by water residence time relative to the stronger swimming copepods (Richardson 1992). We also anticipated a community shift in zooplankton longitudinally down the lake coinciding with increasing water residence time and improved water quality (i.e. less inorganic material). The ability to assess the effect of environmental variables on the zooplankton community structure will provide a basis for understanding this important trophic level in large river ecosystems.

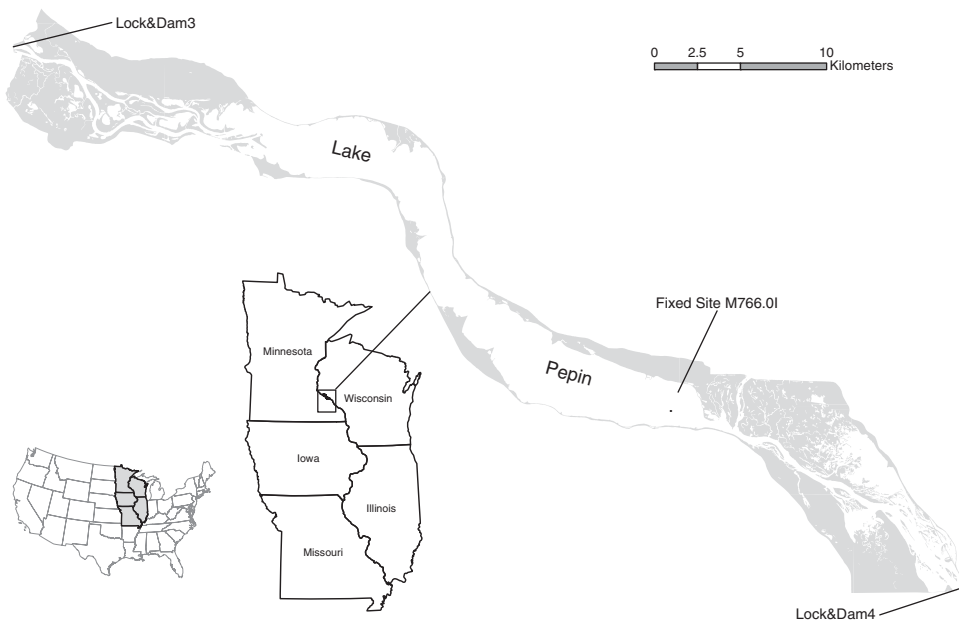
## Methods

### Study area

Lake Pepin is a 35 km long natural riverine lake located on the UMR that encompasses the entire floodplain (Figure 1). The increase in channel depth and width in the lake creates a unique semi-lentic environment with water residence times directly related to water discharge in the river. Mean depth is 5.4 m with the downriver end of the lake deeper on average than the upper. The width of the lake ranges from approximately 1.3 to 4.0 km. The lake is located in the middle of Pool 4, one of 27 navigation pools on the UMR created by a low-head lock and dam system built for navigation. Lake Pepin was created by a tributary delta constricting the flow of the UMR and existed prior to the navigation structures. The lake is an efficient sink for sediments, retaining approximately 78% of the total suspended solids load, resulting in a twofold increase in water clarity longitudinally down the lake (Popp et al. 2014). Considered a eutrophic, polymictic lake, some thermal and oxygen stratification occurs during calm, lower discharge conditions.

### Sample design

Zooplankton samples were collected in conjunction with routine water quality sampling in Lake Pepin by the Long Term Resource Monitoring element of the Upper Mississippi River Restoration Program. Samples were collected at sites that are selected quarterly as part of a stratified random



**Figure 1.** Map of Upper Mississippi River Navigation Pool 4, including Lake Pepin and fixed site M766.01.

sampling design (Soballe & Fischer 2004). Zooplankton is collected from only the ‘Lake’ stratum (Lake Pepin), and therefore the sampling design was treated as simple random sampling (SRS). Zooplankton included in this analysis were collected at 30 sites during summer (late-July to early-August) and fall (mid-October) sampling episodes during 1995–2012 with the exception of summer 2003 and fall 2001–2003. In addition, one fixed site in the lower part of the lake (Figure 1) that was sampled biweekly or monthly from May through October (1996–2012) was analyzed separately to better represent seasonal changes in the lake. This resulted in total, the analysis of over 1100 zooplankton samples spanning an 18-year period.

### **Environmental variables**

A suite of limnological variables was collected simultaneously with all zooplankton samples (Soballe & Fischer 2004). Variables included in the analysis with zooplankton were water temperature, chlorophyll *a* (an indicator of phytoplankton abundance), total suspended solids, volatile suspended solids and percent organic matter. In addition, specific water residence times were assigned to each sample using a steady state segmented model developed with the software BATHTUB (BATHTUB, U.S. Army Corps of Engineers, Vicksburg, MS, USA). Water residence times were calculated for 3.2 km (2.0 mi) reaches of Lake Pepin using volume and discharge relationships. Discharge data from Lock and Dam 3 was obtained from the U.S. Army Corps of Engineers and converted to a 10-day mean discharge for use in the model. Twelve reaches were established and identified by the lower river mile in each reach, starting with 786 at the upper part of the lake to 764 at the lower end. Zooplankton samples were associated with the water residence time corresponding to the reach and hydraulic conditions in which they were collected.

### **Zooplankton sampling and enumeration**

Zooplankton collections were made with an 80  $\mu\text{m}$  mesh Wisconsin net, hauled vertically from 1 m above the lake bottom to the surface. The number of hauls per site was depth dependent with

multiple tows collected at shallow sites and a single tow at deeper sites. Multiple shallow site hauls were composited into one sample to increase the volume of water sampled. All samples were preserved in reagent alcohol.

Sample volumes were adjusted, and a 5 ml aliquot was transferred to a counting wheel and individual zooplankters were identified, counted and measured under an Olympus SZ60 dissecting microscope at 25 $\times$  magnification, with the aid of a computerized image analysis system and the ZCOUNT software program (Charpentier & Jamnick 1994). Biomass estimates were calculated with length/weight regression coefficients for individual taxa obtained from Culver et al. (1985) and Dumont et al. (1975). Adult copepods were identified to suborder and immature copepods were counted as nauplii or copepodites. A subset of 50 randomly chosen samples from the fixed site was further examined to identify adult copepods to species for a taxa list. Cladocerans were identified to either the genus or species level with the exception of Macrothricidae, which were identified to family.

### Statistical analysis

Multivariate analyses were performed using various routines with PRIMER software version 6 (PRIMER-E Ltd, Plymouth, UK). Rare taxa that occurred in less than 5% of the samples were excluded from multivariate analysis, as were copepodites and nauplii. Zooplankton data were square root transformed to reduce the influence of dominant taxa and a Bray–Curtis similarity matrix was generated using biomass. Non-metric multidimensional scaling (NMDS) (Clarke 1993) analysis was used to examine spatial and temporal patterns in zooplankton communities, using summer and fall SRS data. Abundance was averaged over sites by year or reach for presentation in the NMDS graphs, otherwise multivariate statistical tests were performed using abundance from individual sites.

Two-way analysis of similarity (ANOSIM) was performed to determine if there were significant differences in zooplankton community structure between years and between river reaches. ANOSIM is a non-parametric permutation procedure that produces an  $R$  statistic, which is a comparative measure of the degree of separation between samples (Clarke & Warwick 2001).  $R$  will typically fall between 0 and 1, with values near zero indicating that assemblages are similar and support the null hypothesis of no differences between samples.  $R$  values closer to 1 indicate greater assemblage differences.

The similarity percentages routine (SIMPER) in PRIMER software was used to determine the contribution of individual species toward the separation among samples. The SIMPER routine uses average Bray–Curtis dissimilarities between all pairs of samples to produce a percent contribution from each species, which identifies the species most responsible for the dissimilarity among samples (Clarke & Warwick 2001).

The BIOENV procedure (Clarke & Gorley 2006) was used to identify which environmental variables best explained zooplankton community structure. BIOENV is a rank correlation ( $\rho$ ) method between biotic and environmental (dis)similarity matrices (Clarke & Ainsworth 1993). Values of  $\rho$  can range from  $-1$  to  $1$  with near zero values indicating the lack of correlation between the matrices. Prior to analysis, inter-correlated environmental variables were reduced to eliminate autocorrelation. Environmental data were  $\log(x + 1)$  transformed when needed to approximate a normal distribution and standardized prior to generation of a Euclidean distance matrix.

Finally, Spearman's rank correlations were performed to examine the relationship of cladoceran and copepod biomass with water residence time and chlorophyll  $a$  concentrations with water residence time. Correlation analyses were performed using SAS software version 9.4 (SAS Institute Inc. Cary, NC, USA). Significance for all statistical tests was set at  $\alpha = 0.05$ .

## Results

### Zooplankton composition and seasonality

Twenty-one cladoceran taxa were identified from Lake Pepin, including six *Daphnia* species (Tables 1 and 2). *Daphnia* were a large component of cladoceran density and biomass during most

**Table 1.** Percent occurrence (percentage of samples where taxa occurred) of crustacean zooplankton collected in Lake Pepin. Fixed site data were collected at site M766.01 from 1996 through 2012. Stratified random sampling (SRS) data were collected during summer (late-July to early-August) and fall (mid-October) SRS episodes from 1995 through 2012.

	Percent occurrence							
	Fixed site						SRS episodes	
	May	Jun	Jul	Aug	Sep	Oct	Summer	Fall
<b>Cladocera</b>								
<i>Alona</i> sp.	2.9	5.3	0	0	0	0	0.2	0.7
<i>Bosmina longirostris</i>	85.3	76.3	32.4	65.6	80.0	100	48.4	91.4
<i>Ceriodaphnia</i> sp.	20.6	23.7	2.9	15.6	0	11.8	16.5	16.2
<i>Chydorus sphaericus</i>	88.2	60.5	29.4	25.0	28.0	35.3	14.8	41.8
<i>Diaphanosoma birgei</i>	0	18.4	61.8	93.4	96.0	35.3	87.4	28.9
<i>Daphnia ambigua</i>	5.9	0	2.9	0	0	0	0	0
<i>Daphnia galeata mendotae</i>	64.7	84.2	79.4	68.8	72.0	76.5	56.3	59.4
<i>Daphnia lumholtzi</i> <sup>a</sup>	0	0	0	18.5	33.3	16.7	0.2	27.6
<i>Daphnia parvula</i>	32.4	29.0	5.9	9.4	20.0	35.3	6.3	23.7
<i>Daphnia pulicaria</i>	58.8	50.0	11.8	21.9	8.0	11.8	12.6	15.3
<i>Daphnia retrocurva</i>	32.4	97.4	97.0	96.9	96.0	70.6	86.2	78.8
<i>Eubosmina coregoni</i>	5.9	13.2	5.9	12.5	8.0	11.8	5.3	12.0
<i>Eurycerus lamellatus</i>	0	7.9	0	0	0	0	0.2	0.7
<i>Latona setifera</i>	0	0	0	0	0	0	0.2	0.2
<i>Leptodora kindtii</i>	5.9	34.2	32.4	31.2	32.0	0	28.2	8.1
Macrothricidae	8.8	10.5	2.9	0	0	0	4.5	1.8
<i>Moina</i> sp.	0	2.6	0	12.5	4.0	5.9	18.3	5.6
<i>Pleuroxus</i> sp.	0	0	0	0	0	0	0	0.2
<i>Scapholeberis</i> sp.	0	0	0	0	0	0	0.6	0
<i>Sida crystallina</i>	0	2.6	0	3.1	0	0	1.8	0.2
<i>Simocephalus</i> sp.	0	5.3	0	0	0	5.9	0	0.4
<b>Copepoda</b>								
Calanoid	41.2	28.9	47.0	68.8	80.0	94.1	38.4	84.4
Copepodite	97.0	92.1	100	100	100	100	97.8	96.4
Cyclopoid	100	97.4	100	100	100	100	99.2	99.1
Harpacticoid	0	0	0	0	0	0	0	0.2
Nauplii	97.0	94.7	100	96.9	100	100	99.0	99.1

<sup>a</sup> *Daphnia lumholtzi* was first recorded in 1999. Frequency calculated from 1999 through 2012.

sampling periods. *Daphnia retrocurva* was the most abundant cladoceran and was also one of the most ubiquitous cladocerans, occurring in over 95% of June through September fixed site samples, and in 86% and 78% of the summer and fall SRS episodes, respectively (Table 1). *Bosmina longirostris* was the second most abundant cladoceran and was most common in the spring and fall samples. Other abundant and ubiquitous cladocerans included *Daphnia galeata mendotae*, *Diaphanosoma birgei* and *Chydorus sphaericus*.

Three species of calanoids, all belonging to the Diaptomidae family, were identified from the subset of samples examined for a copepod taxa list (Table 3). *Skistodiaptomus oregonensis* was the most common calanoid, whereas *Skistodiaptomus pallidus* and *Leptodiaptomus siciloides* were much less common. Seven species of cyclopoids were identified with *Acanthocyclops vernalis* and *Mesocyclops edax* being the most common. *Diacyclops bicuspidatus thomasi* was relatively uncommon and present only in samples collected during May. Other less common cyclopoids included *Tropocyclops prasinus mexicanus*, *Macrocyclus albidus*, *Eucyclops prionophorus* and *Ectocyclops phaleratus*.

Total cladoceran density and biomass at the fixed site peaked in June and declined as the season progressed (Figure 2). In contrast, copepod density and biomass remained relatively consistent throughout the sampling season (Figure 2). Immature copepods (copepodites and nauplii) contributed over 50% of the total copepod densities, while their relative contribution to biomass was small (Table 2). Cyclopoids, copepodites and nauplii were very common, present in over 90% of both fixed and random site samples. Calanoids were far less common, especially during early summer months (Table 1; Figure 2).

**Table 2.** Mean density, biomass and maximum abundance of crustacean zooplankton collected in Lake Pepin. Fixed site data were collected at site M766.0l from 1996 through 2012. Stratified random sampling (SRS) data were collected during summer (late-July to early-August) and fall (mid-October) SRS episodes from 1995 through 2012. Numbers in parentheses show standard error of the mean.

Zooplankton	Density (individual l <sup>-1</sup> )				Biomass (µg l <sup>-1</sup> )			
	Fixed	Summer	Fall	Max.	Fixed	Sum	Fall	Max.
<b>Cladocera</b>								
<i>Alona</i> sp.	<0.1(<0.1)	<0.1(<0.1)	<0.1(<0.1)	0.6 <sup>d</sup>	<0.1(<0.1)	<0.1(<0.1)	<0.1(<0.1)	0.2 <sup>d</sup>
<i>Bosmina longirostris</i>	2.0 (0.4)	0.2(<0.1)	1.7 (0.2)	82.1 <sup>d</sup>	3.7 (0.8)	0.3(<0.1)	2.6 (0.3)	98.3 <sup>d</sup>
<i>Ceriodaphnia</i> sp.	<0.1(<0.1)	<0.1(<0.1)	<0.1	1.3 <sup>b</sup>	0.1(<0.1)	<0.1(<0.1)	<0.1(<0.1)	1.4 <sup>b</sup>
<i>Chydorus sphaericus</i>	0.4 (0.1)	0.1(<0.1)	0.1(<0.1)	15.8 <sup>c</sup>	0.5 (0.1)	0.1(<0.1)	0.1(<0.1)	16.2 <sup>b</sup>
<i>Diaphanosoma birgei</i>	1.1 (0.2)	1.4 (0.1)	0.1(<0.1)	23.5 <sup>c</sup>	3.5 (0.5)	4.1 (0.3)	0.5 (0.1)	55.9 <sup>c</sup>
<i>Daphnia ambigua</i>	<0.1(<0.1)	0	0	0.6 <sup>b</sup>	<0.1(<0.1)	0	0	1.3 <sup>b</sup>
<i>Daphnia galeata mendotae</i>	2.1 (0.3)	0.4(<0.1)	0.7 (0.1)	36.2 <sup>c</sup>	22.4 (4.3)	5.4 (1.0)	5.1 (0.7)	439.5 <sup>b</sup>
<i>Daphnia lumholtzi</i> <sup>a</sup>	<0.1(<0.1)	<0.1(<0.1)	<0.1(<0.1)	3.9 <sup>b</sup>	0.4 (0.2)	<0.1(<0.1)	0.5 (0.1)	25.4 <sup>d</sup>
<i>Daphnia parvula</i>	0.1(<0.1)	<0.1(<0.1)	<0.1(<0.1)	5.0 <sup>b</sup>	0.9 (0.4)	0.1(<0.1)	0.2(<0.1)	74.5 <sup>b</sup>
<i>Daphnia pulicaria</i>	0.3(<0.1)	<0.1(<0.1)	<0.1(<0.1)	6.3 <sup>b</sup>	2.9 (0.7)	0.2(<0.1)	0.2(<0.1)	86.7 <sup>b</sup>
<i>Daphnia retrocurva</i>	6.2 (0.8)	6.0 (1.0)	0.9(<0.1)	430.9 <sup>c</sup>	23.7 (3.6)	23.7 (3.4)	2.6 (0.2)	1080.8 <sup>c</sup>
<i>Eubosmina coregoni</i>	0.1(<0.1)	<0.1(<0.1)	0.1(<0.1)	5.4 <sup>d</sup>	0.3 (0.1)	0.1 (0.0)	0.3 (0.1)	16.4 <sup>d</sup>
<i>Eurycyerus lamellatus</i>	<0.1(<0.1)	<0.1(<0.1)	<0.1(<0.1)	2.2 <sup>c</sup>	<0.1(<0.1)	<0.1(<0.1)	<0.1(<0.1)	4.2 <sup>c</sup>
<i>Latona setifera</i>	0	<0.1(<0.1)	<0.1(<0.1)	<0.1 <sup>d</sup>	0	<0.1(<0.1)	<0.1(<0.1)	0.4 <sup>d</sup>
<i>Leptodora kindtii</i>	<0.1(<0.1)	0.1(<0.1)	<0.1(<0.1)	9.8 <sup>c</sup>	0.9 (0.2)	0.7 (0.1)	0.1(<0.1)	45.2 <sup>c</sup>
Macrothricidae	<0.1(<0.1)	<0.1(<0.1)	<0.1(<0.1)	1.5 <sup>c</sup>	<0.1(<0.1)	<0.1(<0.1)	<0.1(<0.1)	2.1 <sup>c</sup>
<i>Moina</i> sp.	<0.1(<0.1)	<0.1(<0.1)	<0.1(<0.1)	3.9 <sup>c</sup>	<0.1(<0.1)	0.1(<0.1)	<0.1(<0.1)	5.3 <sup>c</sup>
<i>Pleuroxus</i> sp.	0	0	<0.1(<0.1)	<0.1 <sup>d</sup>	0	0	<0.1(<0.1)	<0.1 <sup>d</sup>
<i>Scapholeberis</i> sp.	0	<0.1(<0.1)	0	0.1 <sup>c</sup>	0	<0.1(<0.1)	0	<0.1 <sup>c</sup>
<i>Sida crystallina</i>	<0.1(<0.1)	<0.1(<0.1)	<0.1(<0.1)	3.6 <sup>c</sup>	<0.1(<0.1)	<0.1(<0.1)	<0.1(<0.1)	18.0 <sup>c</sup>
<i>Simocephalus</i> sp.	<0.1(<0.1)	0	<0.1(<0.1)	0.5 <sup>b</sup>	<0.1(<0.1)	0	<0.1(<0.1)	4.8 <sup>b</sup>
<b>Copepoda</b>								
Calanoid	0.6 (0.1)	0.2(<0.1)	0.9(<0.1)	19.9 <sup>d</sup>	4.8 (0.2)	1.4 (0.2)	8.8 (1.0)	225.0 <sup>d</sup>
Copepodite	3.3 (0.3)	3.2 (0.2)	1.3(<0.1)	42.4 <sup>c</sup>	4.0 (0.4)	3.9 (0.2)	1.6 (0.1)	46.3 <sup>c</sup>
Cyclopoid	8.3 (0.6)	6.6 (0.4)	4.0 (0.3)	59.0 <sup>b</sup>	39.4 (3.2)	27.7 (1.6)	16.1 (1.2)	281.7 <sup>b</sup>
Harpacticoid	0	0	<0.1(<0.1)	0.2 <sup>d</sup>	0	0	<0.1(<0.1)	1.3 <sup>d</sup>
Nauplii	9.6 (0.8)	9.5 (0.6)	4.0 (0.3)	164.5 <sup>c</sup>	1.7 (0.1)	1.6 (0.1)	0.7(<0.1)	27.2 <sup>c</sup>
<b>Total</b>	<b>34.4</b>	<b>28.0</b>	<b>13.9</b>		<b>109.2</b>	<b>69.5</b>	<b>39.5</b>	

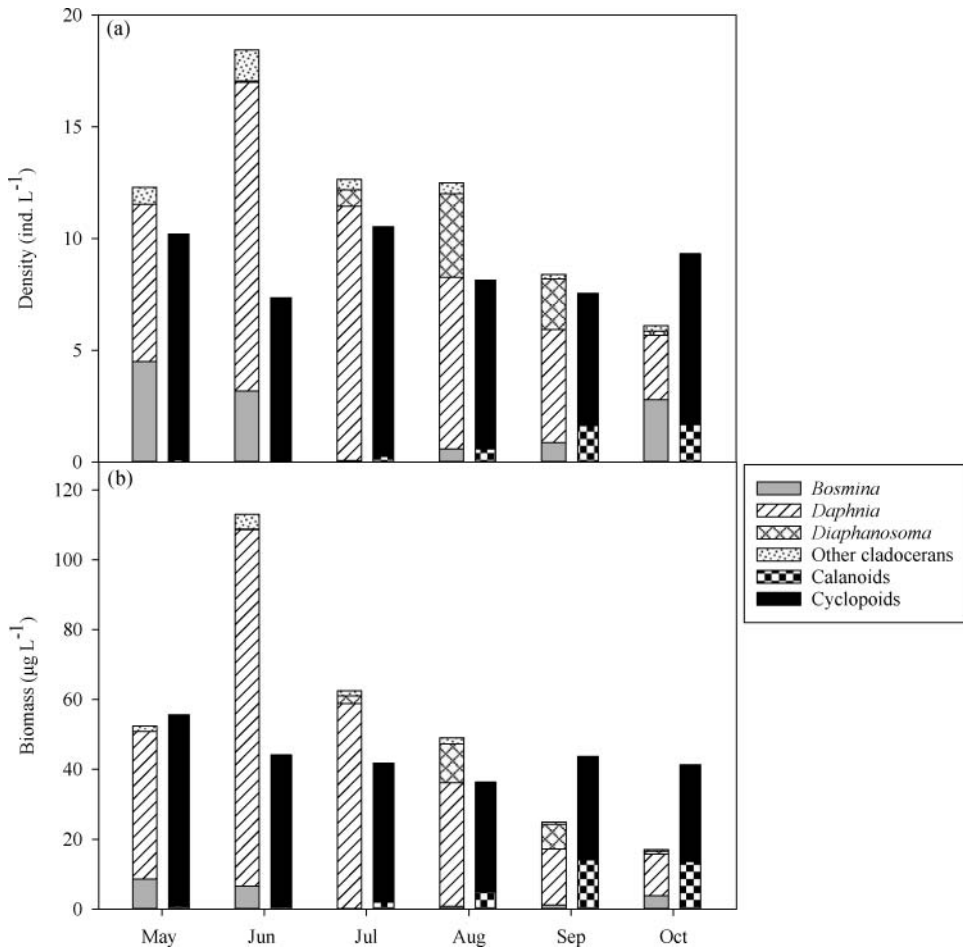
<sup>a</sup>Abundance for *Daphnia lumholtzi* was calculated from 1999 through 2012 as it was first discovered in 1999. <sup>b</sup>Maximum abundance occurred at the fixed site, <sup>c</sup>during summer SRS or <sup>d</sup>fall SRS.

**Table 3.** Percent occurrence (percentage of samples where taxa occurred) of copepod zooplankton collected at site M766.0l in Lake Pepin (50 randomly chosen samples were analyzed from 1996 through 2012).

	Percent occurrence
<b>Calanoids</b>	
<i>Skistodiaptomus oregonensis</i>	46.0
<i>Leptodiaptomus siciloides</i>	12.0
<i>Skistodiaptomus pallidus</i>	4.0
<b>Cyclopoids</b>	
<i>Acanthocyclops vernalis</i>	90.0
<i>Mesocyclops edax</i>	42.0
<i>Diacyclops bicuspidatus thomasi</i>	20.0
<i>Tropocyclops prasinus mexicanus</i>	10.0
<i>Eucyclops prionophorus</i>	4.0
<i>Macrocyclus albidus</i>	2.0
<i>Ectocyclops phaleratus</i>	4.0

### Spatial and temporal community structure

Crustacean zooplankton communities showed structural differences both annually and longitudinally through the lake (Figures 3 and 4). A two-way crossed ANOSIM revealed significant differences among years during summer ( $R = 0.56$ ,  $P < 0.001$ ) and fall ( $R = 0.73$ ,  $P < 0.001$ ), and also among reaches during summer ( $R = 0.37$ ,  $P < 0.001$ ) and fall ( $R = 0.31$ ,  $P < 0.001$ ). SIMPER analysis revealed that in almost all pair-wise comparisons, three of five taxa (*D. retrocurva*, *D. galeata*



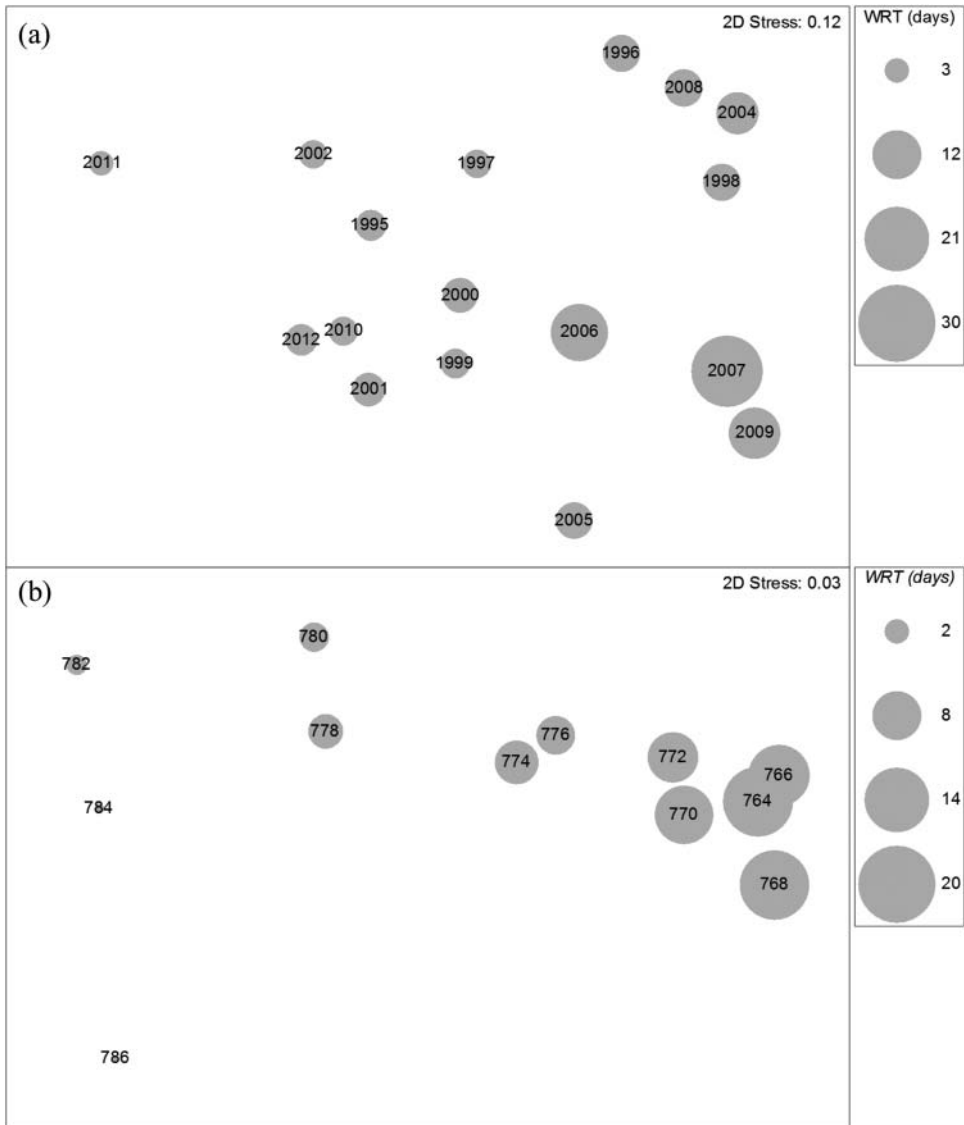
**Figure 2.** Mean monthly abundance of cladocerans and copepods in Lake Pepin from 1996 through 2012 at fixed site M766.01. Nauplii and copepodites are not included.

*mendotae*, cycloids, calanoids and *D. birgei*) in various combinations were the greatest contributors to dissimilarity of community structure. Given these taxa generally constitute the greatest biomass; it is understandable that they would tend to have the largest impact on community structure. There was an obvious longitudinal pattern down the lake as biomass increased during both fall and summer (Figure 5). The contribution of *Daphnia* to the community structure increased longitudinally during summer whereas calanoids and *B. longirostris* made a larger contribution to community structure in fall (Figure 5). Inter-annual patterns revealed that not only did community structure vary but that biomass varied substantially among years as well (Figure 6). Community structure or abundance did not appear to be related between summer and fall episodes. Summer and fall zooplankton abundance were independent of each other as summer abundance had no bearing on fall abundance. Abundance patterns varied by year (Figure 6) where fall abundance would either be similar, lower or higher to those observed in summer.

### **Environmental variables and community structure**

Water residence time was the single best environmental variable that explained the patterns observed in the crustacean zooplankton community as indicated by the BIOENV procedure

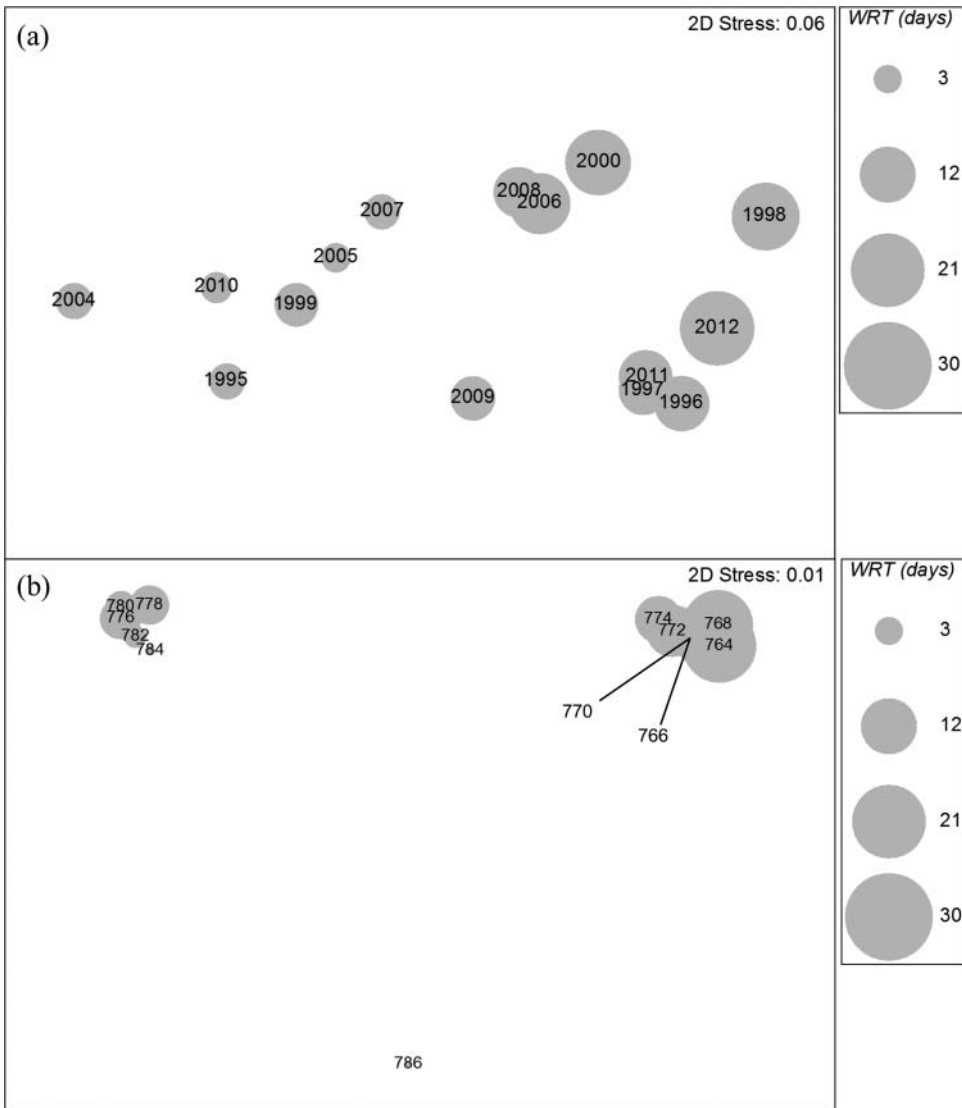




**Figure 3.** Non-metric multidimensional scaling (NMDS) ordination of Lake Pepin crustacean zooplankton sampled during summer stratified random sampling (SRS) episodes from 1995 through 2012. For graphical presentation, abundance was averaged over sites by (a) year and (b) 3.2 km reach (numbers are river miles) and overlaid with average water residence time.

(Table 4). This was the case for both summer ( $\rho = 0.317$ ) and fall ( $\rho = 0.299$ ). No other combination of environmental variables improved the correlation between zooplankton and environmental patterns. When bubble plots of water residence time were superimposed on the NMDS graphs, easily perceived patterns emerged as similar community assemblages tended to group together based on water residence times (Figures 3 and 4). During this study period, mean water residence time for the entire lake ranged from 3.0 to 25.7 days during summer SRS and from 3.3 to 21.7 days during fall SRS. Maximum water residence time during the study period ranged from less than 1 day in the upper reach to over 46 days in the lower reach.

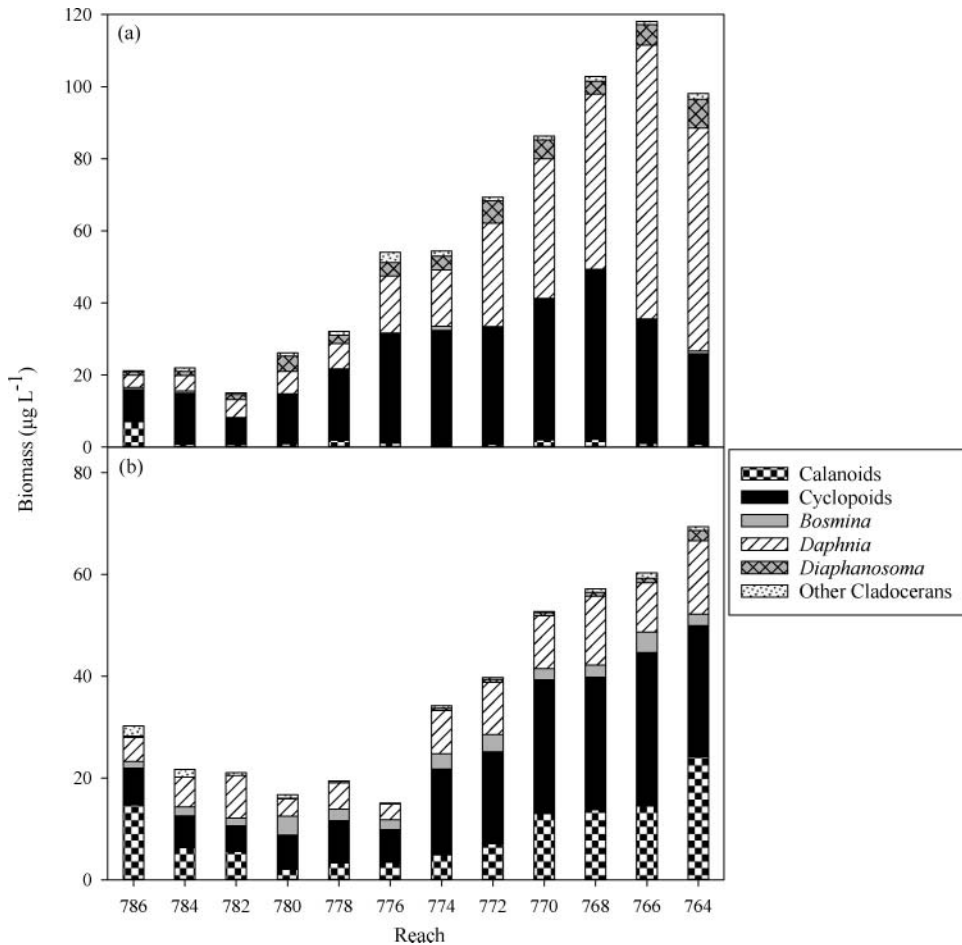
The link between zooplankton abundance and water residence time was further investigated by using Spearman's rank-order correlation statistic to examine the relationship between total cladoceran and copepod biomass and water residence time. Analysis revealed significant positive



**Figure 4.** NMDS ordination of Lake Pepin crustacean zooplankton sampled during fall SRS episodes from 1995 through 2012. For graphical presentation, abundance was averaged over sites by (a) year and (b) reach and overlaid with average water residence time.

correlations during both summer and fall (Figure 7). Copepods had a strong correlation with residence time during both summer ( $r = 0.88$ ) and fall ( $r = 0.87$ ). Cladocerans also displayed significant correlations with residence time (summer  $r = 0.59$ , fall  $r = 0.75$ ). Cladocerans in fact had relatively low biomass during the three summers of longest residence time (Figure 7(a)) in contrast to copepods where biomass may have peaked (Figure 7(c)).

Chlorophyll *a* had a strong correlation with residence time during the summer episodes (Figure 7(e)); however, chlorophyll *a* when used in NMDS analysis did not help explain patterns in zooplankton community structure in either summer or fall. Likewise, total suspended solids and percent organic matter showed distinct longitudinal patterns down the lake (Figure 8) due in large part to the settling of inorganic material, but also did not improve the explanation of community patterns.

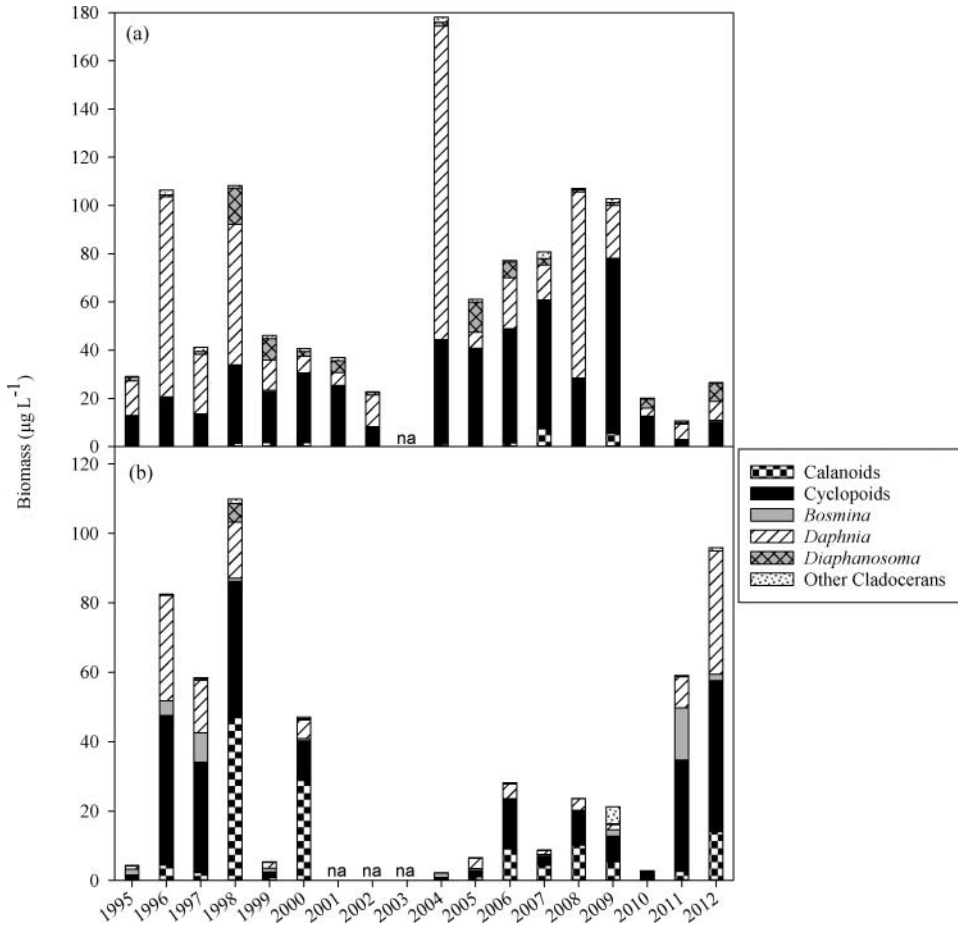


**Figure 5.** Mean biomass of crustacean zooplankton in Lake Pepin from 1995 through 2012 by 3.2 km reach during (a) summer and (b) fall SRS episodes.

## Discussion

### Zooplankton community patterns

Our results demonstrated that water residence time was an important environmental driver of crustacean zooplankton community structure, thus confirming our initial hypothesis. Longer water residence times were associated with a community shift toward larger-bodied crustacean zooplankton and higher overall zooplankton biomass driven primarily by *Daphnia* and copepods. Water residence time was not only associated with year-to-year differences but spatial differences as well. As we had hypothesized, zooplankton biomass increased from upriver to downriver in Lake Pepin and community structure shifted to one more typical of lakes. While others have shown that residence time was the primary driver controlling zooplankton biomass in river systems (Pace et al. 1992; Basu & Pick 1996; Baranyi et al. 2002), our results show dissimilar relationships with residence time between crustacean taxon groups. Copepods exhibited a very strong positive correlation, whereas cladocerans demonstrated a weaker correlation where biomass did not always increase with residence time. During the three summers with the longest residence times, cladoceran biomass was actually lower compared to biomass at intermediate levels of residence time. This was in contrast to copepod biomass that appeared to continue to increase with residence time. Examination of the



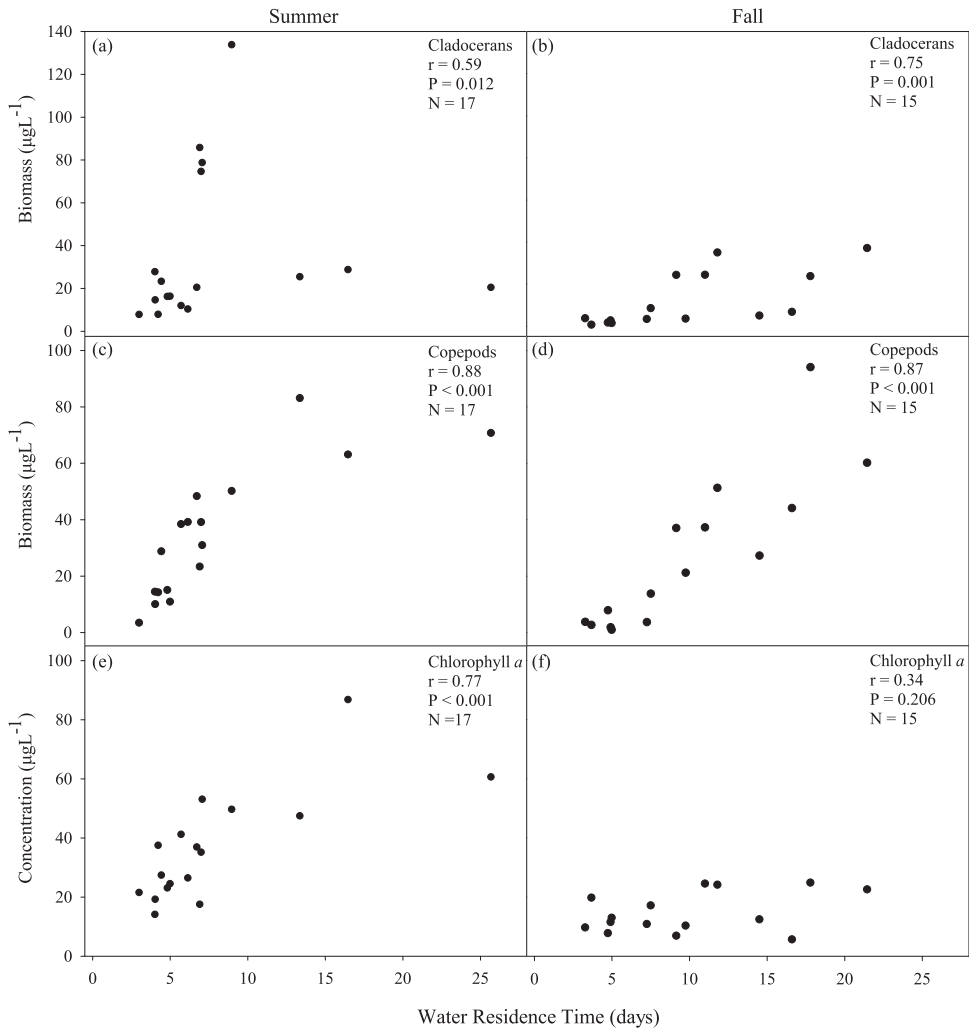
**Figure 6.** Mean biomass of crustacean zooplankton in Lake Pepin from 1995 through 2012 during (a) summer and (b) fall SRS episodes.

**Table 4.** Rank correlation coefficients ( $\rho$ ) between zooplankton among-sample patterns of assemblage and associated environmental variables. Data collected during summer and fall SRS episodes (1995–2012).

Season	$\rho$	No.	Variables
Summer	0.317	1	WRT
	0.298	2	WRT, SS
	0.279	2	WRT, PCTOM
	0.279	3	WRT, SS, PCTOM
	0.272	4	WRT, SS, PCTOM, TEMP
	0.271	3	WRT, SS, TEMP
Fall	0.299	1	WRT,
	0.257	2	WRT, VSS
	0.236	2	WRT, SS
	0.227	3	WRT, VSS, TEMP
	0.225	2	WRT, TEMP
	0.225	2	WRT, CHL

Note: Variables are defined as water residence time (WRT) suspended solids (SS), percent organic matter (PCTOM), water temperature (TEMP), volatile suspended solids (VSS) and chlorophyll *a* (CHL).

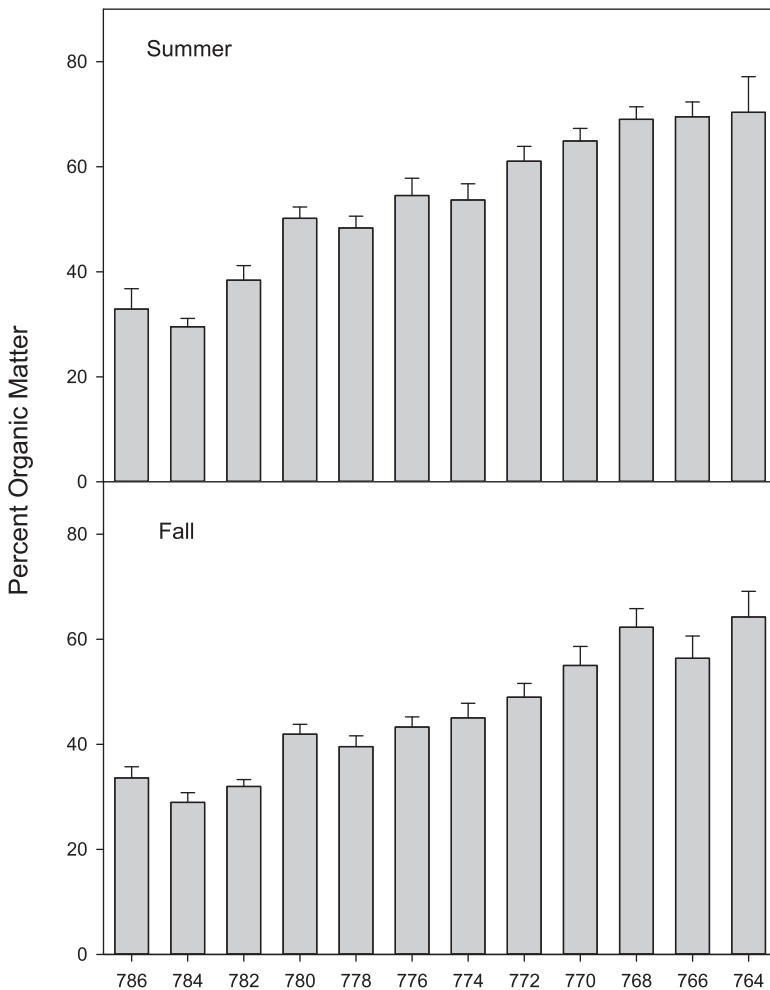
$P < 0.001$ .



**Figure 7.** Spearman's rank correlation between water residence time and cladocerans during (a) summer and (b) fall SRS episodes, copepods during (c) summer and (d) fall SRS episodes and chlorophyll *a* during (e) summer and (f) fall episodes.

fixed site data (sampled at two-week intervals) showed that *Daphnia*, the primary contributor to cladoceran biomass, was in fact abundant during these low discharge summers, but prior to the sampling in late-July, their abundance decreased. This suggests that cladocerans, particularly *Daphnia*, may have become driven by biological factors during late summer.

In north temperate lakes, planktonic herbivores such as *Daphnia* tend to be temporal, being most abundant following spring algal blooms and then decreasing over the course of the season due to food limitations and fish predation (Sommer et al. 1986; Vanni 1987). We observed similar patterns in Lake Pepin as *Daphnia* densities and biomass were greatest during June and decreased throughout the season. This mid-summer decline was likely the result of some combination of a decrease in quality food resources and predation by fish. Summer declines in *Daphnia* abundance in Lake Mendota (Luecke et al. 1990) and Lake Erie (Wu & Culver 1994) were attributed to food limitation in early summer; however, despite the return of quality food resources in late summer, *Daphnia* abundance remained low due to fish predation. The consumption of crustacean zooplankton by fishes in riverine systems has been well documented (Rosen & Hales 1981; Hoxmeier & DeVries 1997; Dettmers et al. 2001; Jack & Thorp 2002; Thorp & Casper 2003). Of the 85 species of fish collected



**Figure 8.** Mean total suspended solids during (a) summer and (b) fall SRS episodes and percent organic matter during (c) summer and (d) fall SRS episodes. Sites sampled in Lake Pepin from 1995 through 2012 and averaged by 3.2 km reach (numbers are river miles).

in Pool 4 of the Mississippi River, 22 (26%) have been reported to consume zooplankton as one of their primary diet items as adults (Simon 1999). Van Dijk and Van Zanten (1995) reported a similar food web in the Lower River Rhine where 30% of the fish community was zooplanktivorous. Additional studies in river systems have found that gizzard shad *Dorosoma cepedianum* (Dettmers & Stein 1996) and emerald shiners *Notropis atherinoides* (Jack & Thorp 2002) can reduce zooplankton abundance through predation. Gizzard shad and emerald shiners are the most abundant fishes in Lake Pepin (Meerbeek 2006) with larvae beginning exogenous feeding by July. Given the fish community in Lake Pepin, the potential for substantial predation on zooplankton and control of their abundance seems great and may explain in part the lower cladoceran biomass during late summer. This top-down trophic interaction may be more prevalent during periods of long water residence times.

Phytoplankton is generally considered the most important food source for herbaceous zooplankton and food availability can influence zooplankton growth (Sterner & Schulz 1998). Guelda et al. (2005) estimated the carbon phytoplankton biomass necessary to maintain positive population growth rates of *B. longirostris* in a river mesocosm experiment translated to approximately  $2 \mu\text{g l}^{-1}$

of chlorophyll *a*. They found that the food saturation threshold, where food resources were no longer limiting, occurred at  $9 \mu\text{g l}^{-1}$ . Similar chlorophyll *a* concentrations ( $6\text{--}15 \mu\text{g l}^{-1}$ ) required for *Daphnia* maximum growth were put forward by Sterner and Schulz (1998). These estimates suggest that food quantity during the summer was likely not limiting population growth for cladocerans in Lake Pepin. However, fall chlorophyll *a* concentrations were often below these estimated thresholds required for maximum growth and therefore food resources had the potential to be a factor in zooplankton population dynamics. An abundance of phytoplankton does not guarantee saturation of quality food or increased zooplankton growth (Sterner et al. 1993). The nutritional content of phytoplankton has been shown to influence *Daphnia* growth (Sterner & Schulz 1998; Elser et al. 2001), as has phytoplankton size that can interfere and inhibit consumption (Gliwicz 1990). In addition, toxicity from cyanobacteria has also been reported to inhibit growth (Porter & Orcutt 1980). The most common copepods in Lake Pepin do not have to rely on phytoplankton as a primary food source as they can be omnivorous or carnivorous as adults. Guelda et al. (2005) found that phytoplankton concentration did not correlate with cyclopoid growth and surmised that a shift to a carnivorous diet as adults may be responsible. Diet and food resources may play a role in seasonal abundance patterns within and among taxa groups in Lake Pepin. Spatially we would anticipate cladoceran growth to improve as inorganic suspended solids settle out and the percentage of organic matter increases longitudinally down the lake. Dejen et al. (2004) suspected that turbidity may have played a role in the distribution of zooplankton taxa in a large tropical lake. Negative impacts of turbidity and suspended solids have been recognized on cladocerans (McCabe & O'Brien 1983; Kirk & Gilbert 1990); however, the effects on copepods are less understood. Hart (1990) points out that the effects of sediment inflow on the spatial structure of zooplankton communities in reservoirs are essentially unstudied. While both cladoceran and copepod abundance increased down the lake along with decreasing turbidity and suspended solids, our analysis did not identify suspended solids as an important driver to community structure.

Another environmental variable potentially affecting community dynamics is water temperature. Gillooly and Dodson (2000) suggest that the pattern of peak *Daphnia* abundance in water bodies is driven by water temperature. Their study looked at lakes, reservoirs and ponds across various latitudes in North America and found a strong relationship between latitude and date of maximum *Daphnia* abundance. Peak abundances typically occurred between  $15$  and  $20^\circ\text{C}$ , and their reported mean temperature of  $18.5^\circ\text{C}$  at maximum abundance corresponds well to *Daphnia* peaks observed in Lake Pepin. They also found that *Daphnia* abundance declined at temperatures  $>20^\circ\text{C}$ , a threshold that is consistently exceeded during the summer months in Lake Pepin. We suspect that water temperature does control the start of the *Daphnia* peak in Lake Pepin and may contribute to the late summer decline; however, other factors such as food availability, predation and water residence time likely control their ultimate abundance. Seasonal patterns were also apparent in *B. longirostris* with greater abundance in the spring and fall and near absence in July. This may be due to competition by the larger more efficient grazer *Daphnia* (Hall et al. 1976; Vanni 1986) during mid-summer. However, water temperature may also be important in controlling seasonal patterns of *B. longirostris* as well since they have been shown to be more successful at lower temperatures (Bhajan & Hynes 1972) and may explain their greater abundance in the spring and fall. The other major cladoceran contributing to biomass was *D. birgei*, which became most abundant in mid-summer to late summer suggesting higher optimal temperatures. Davidson et al. (1998) reported *D. birgei* as a late summer species in the Atchafalaya River with abundance being positively related to water temperature.

Calanoid copepods also displayed a seasonal pattern where densities and biomass of adult calanoids were very low in spring and early summer, but increased in late summer and into fall. The most common calanoid species in Lake Pepin *S. oregonensis* was also reported to be most abundant during late summer and fall in the Great Lakes (Balcer et al. 1984). *S. oregonensis* may produce as few as one or two generations per year (Balcer et al. 1984; Torke 2001), which may in part explain the seasonal pattern observed. In addition, all of the calanoid species identified from Lake Pepin can utilize large algal cells (e.g. blue-green cyanobacteria) in their diet (Comita 1972; Torke 2001), which

may give them an advantage later in the season when blue-greens are more abundant. In contrast to the calanoids, cyclopoid copepods as a group did not exhibit much temporal variation in Lake Pepin where densities and biomass remained relatively stable throughout the season. Cyclopoids also tend to have longer life cycles and fewer generations, and are less likely to attain the high rates of population growth of cladocerans, which utilize parthenogenetic reproduction and have short multivoltine life cycles (Allan 1976). In addition, copepods have been shown to be more able to avoid fish predation than cladocerans (Drenner & McComas 1980) and may not be as important in fish diets as cladocerans (Smith 2001). However, Jack and Thorp (2002) found larval bluntnose minnows *Pimephales notatus* and emerald shiners readily fed on the cyclopoid *Diacycops thomasi* and reduced its abundance in an enclosure study on the Ohio River. While we are uncertain about which mechanisms may be contributing to seasonal patterns in the zooplankton community, it is clear that copepod abundance in Lake Pepin is more stable than that of cladocerans.

### Zooplankton composition

We found a diverse crustacean zooplankton community in Lake Pepin with 31 taxa identified over the 18-year study period. Similar diversity was reported on the Missouri River from a study that spanned nearly the entire river (Dickerson et al. 2010). Taxa richness in Lake Pepin was approximately six times higher on average than regional lakes in Minnesota (Hirsch 2014). The higher diversity of zooplankton in Lake Pepin could be due to a variety of factors, including the longer sampling time frame, extensive spatial sampling coverage, including shallow sites where littoral species are more likely to be collected and the fact that Lake Pepin receives an influx of zooplankton from various upriver areas. However, much of this zooplankton diversity may simply be due to the physical complexity inherent in floodplain river systems where species diversity is expected to be high (Junk et al. 1989).

Six species of *Daphnia* were identified from Lake Pepin, one of which was the previously reported invasive *D. lumholtzi* (Burdis & Hirsch 2004). Interestingly, these six species were also the only *Daphnia* reported in the Missouri River (Dickerson et al. 2010), *D. retrocurva* being the most common in both rivers. *Daphnia* have been reported from the other large North American rivers (e.g. Illinois and Ohio) but were less abundant (Thorp et al. 1994; Wahl et al. 2008; Sluss & Jack 2013). The difference in *Daphnia* abundance among these rivers is likely due to the availability of lentic habitat. Our study was done on a large natural riverine lake in the Mississippi River; likewise, the middle section of the Missouri River includes very large impoundments that produce genera typical of lakes and lentic conditions not generally found on the Ohio and Illinois rivers. Burdis and Hoxmeier (2011) investigated the zooplankton communities in the UMR above and below Lake Pepin and found the cladoceran community above the lake to be dominated by the smaller-bodied *B. longirostris* compared to one dominated by *Daphnia* below the lake. When water residence time was sufficient, the lentic habitat of Lake Pepin produced a longitudinal transition to larger-bodied crustaceans altering the zooplankton community structure through the lake. Similarly, the uppermost zones of reservoirs, where advective effects of river inflows are most prominent, are typically composed of riverine zooplankton communities, whereas communities in lacustrine zones of reservoirs resemble those of natural lakes (Hart 1990; Bernot et al. 2004).

Copepods were most abundant and the dominant taxa group in the fall. The two most common cyclopoids identified from Lake Pepin were *M. edax* and *A. vernalis*, both of which are omnivorous and oftentimes predacious, feeding on other zooplankters (Brandl & Fernando 1974; Kerfoot 1978; Williamson 1980). *M. edax* is common throughout North America and is a large copepod that will feed on rotifers, other copepods and cladocerans including *Daphnia* and *Bosmina* (Balcer et al. 1984; Williamson 1984). The most common calanoid species identified from Lake Pepin was *S. oregonensis*. This species is ubiquitous in the region and can utilize a wide size range of algal cells in its diet, resulting in its presence in a variety of lake types (Torke 2001; Van Egeren et al. 2011). The two less common calanoids found in Lake Pepin, *S. pallidus* and *L. siciloides*, are associated with eutrophic conditions and *L. siciloides* has the ability to utilize large cyanobacteria cells in its diet (Comita



1972). The copepod species in Lake Pepin appear to have a diverse diet that may be advantageous, particularly in the fall when phytoplankton abundance decreases.

## Conclusions

Our hypothesis that water residence time would be the most influential variable structuring the zooplankton community was confirmed. Spatial and temporal patterns in the zooplankton community were best explained by water residence time while other environmental variables such as water temperature, chlorophyll *a* and suspended solids did not help to explain the observed patterns. Copepod abundance correlated well with residence time while cladoceran abundance did not always increase with longer water residence time suggesting that biotic controls such as fish predation or food availability may have at times influenced cladoceran dynamics. Seasonal patterns in zooplankton typical of lakes were observed in Lake Pepin; however, these patterns could be disrupted during short water residence times. As Lake Pepin became more fluvial in character, total zooplankton biomass decreased and the zooplankton community became more typical of those found in rivers where large cladocerans such as *Daphnia* are scarce. Biotic interactions influencing zooplankton abundance and community structure likely became more extensive during longer water residence times and appeared most conspicuous with cladocerans. Our results illustrate the diversity and complexity of zooplankton dynamics in a large riverine lake and accentuate the importance of water residence in structuring the zooplankton community. We also demonstrated that the relationship between zooplankton abundance and water residence time varied among taxa groups.

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No potential conflict of interest was reported by the authors.

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