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RIVER FLOODPLAIN RESTORATION

Diversity and succession of pelagic microorganism communities in a newly restored Illinois River floodplain lake

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Abstract While the success of restoration efforts frequently depends on reconstructing ecological communities, time series observations of community structure over the course of restoration are rare. Here, frequent sampling of bacterioplankton, phytoplankton, planktonic protozoa (ciliates and testaceans), and zooplankton was done along with measurements of select physical and chemical parameters during the first year of ecological restoration of Thompson Lake (TL), an Illinois River floodplain lake not connected to the river. The primary objective was to describe the microbial composition, diversity, and seasonal dynamics in TL and compare these results to similar measurements made in a nearby reference lake, river flood-pulsed Lake Chautauqua (LC). Strong seasonal patterns in bacterioplankton diversity were observed for both lakes. While TL phytoplankton diversity was lower and blooms more erratic than in LC, ciliate richness and abundance patterns were similar in both lakes. Rotifers and microcrustaceans were about 5× more abundant in TL than LC, with copepods and cladocerans exhibiting a fall abundance peak only in TL. When compared to temporal patterns of planktonic microorganisms in the reference lake (LC), the microbial dynamics in a lake recovering from decades of agriculture and drainage (TL) reflect the instability associated with early stages of ecological restoration.

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Introduction

Lands that are managed for either agriculture or quality lotic and lentic aquatic habitats are highly valued commodities, and yet, use by one often precludes existence of the other. As such, human use has degraded more than half of river systems worldwide to a status of moderately to highly threatened (Vörösmarty et al., 2010). Restorations of large river floodplains present unique and significant challenges due to the scale and assessment capacities associated with such projects. Because much of our present-day understanding of applied restoration ecology relies on projects that encompass small, defined systems, the question remains as to how applicable aspects of these projects are to larger-scale restoration efforts. Existing theories of what drives large flood-pulsed river systems (e.g., Junk et al., 1989; Tockner et al., 2000; Humphries et al., 2014) serve only as a theoretical framework for restoration (Sparks et al., 1990, 2016; Bayley, 1995; Sparks, 2010) and datasets substantiating these theories are sparse. Subsequently, there remains a critical need for datasets that can increase our understanding of floodplain river ecology and inform management of large river restoration efforts.

Microorganisms can be used as sensitive indicators of environmental changes that provide insight into the progression of large-scale aquatic habitat restoration. Composition of lake microbial communities is in continuous flux at temperate latitudes, and each year these communities exhibit seasonal succession driven by environmental conditions and species interactions (Kent et al., 2007; Sommer et al., 2012). Pelagic bacterial communities from several different systems have been shown to respond to and recover from water column disturbances rapidly (Jones et al., 2008; Shade et al., 2012). Lake microorganisms are generally categorized into trophically interconnected groups. At the base of the microbial loop, bacterioplankton reincorporate dissolved organic matter into the microbial food web and contribute to biogeochemical cycling (Azam et al., 1983; Sherr & Sherr, 1988; Fenchel, 2008). Phytoplankton are primary producers that provide labile dissolved organic carbon (DOC) to bacteria through exudates (Descy et al., 2002). Testate amoeba and ciliates are largely heterotrophic microconsumers of bacteria and algae, and are also preyed upon by zooplankton. Zooplankton serve as a direct link to the grazer food web as prey to planktivorous fish (Riemann & Christoffersen, 1993) and have the potential to impose a top-down cascade of predation pressure by (1) feeding on phytoplankton that subsequently increases the release of labile DOC resources for bacteria (Jumars et al., 1989) and (2) direct predation on protists (e.g., Arndt, 1993; Jürgens, 1994). Whereas nearly all zooplankton impose predation pressure on heterotrophic nanoflagellates (e.g., Sanders et al., 1992), cyclopoid and calanoid copepods can also consume planktonic ciliates (Burns & Gilbert, 1993).

The goal of this study was to compare microbial communities in two shallow, polymictic lakes located on the large river floodplain of the Illinois River, Illinois. Specifically, our objectives were to compare microbial composition, diversity, and seasonal dynamics in a newly restored system, Thompson Lake (TL), to those in well-established flood-pulsed system, Lake Chautauqua (LC). TL, located within The Nature Conservancy's (TNC) Emiquon Preserve, began its transition from crop field to restored lake as rain waters began to fill the basin in 2007; however, an earthen levee maintained its separation from the river and prevented inoculation of river water to the lake. The time frame of this study represents the first full year following the initiation of ecological restoration at TL after being drained and under agriculture for 80 years. LC was drained about the same time as TL; however, it was reconnected to the river about 70 years ago and currently receives seasonal flood pulses from the river. Thus, LC serves as a reference for how microbial communities change seasonally in

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lake systems that are periodically connected to the Illinois River. With the recession of floodwater after each flood disturbance, the connection between lake and river becomes less dynamic resulting in lakes that not only differed in character from the river, but also from one another in water quality, bacterial abundance, and zooplankton community composition based on observations of similar systems (Amoros & Bornette, 2002; Luef et al., 2007; De Paggi & Paggi, 2008).

Two central questions emerged as part of this study: (1) Were microbial community diversity and seasonal patterns similar between this newly restored lake and an established floodplain lake? (2) Can aquatic microorganisms be used to help document the dramatic and likely rapid changes that occurred in a newly restored lake pelagic zone? We expected that a period of ecological instability would accompany recovery and that changes in physical conditions, nutrients, and biotic interactions would affect the bacteria, phytoplankton, and consumers in the microbial food web.

Materials and methods

Study sites

TL and LC were leveed from the Illinois River and drained for agriculture in the late 1920s (Havera et al., 2003). TNC purchased the Emiquon Preserve, which includes the TL basin (about 809 ha; centroid 40°20′46.14″N, 90°01′29.56″W, Fig. 1), in 2000. Water began to fill the basin primarily from precipitation and overland runoff in late 2007, signaling the beginning of ecological restoration. The last time these lakes shared a similar role and function as intact, river flood-pulsed lakes was about 1928, though their part of the Illinois River system was described as early as 1673 (Jenkins et al., 1950). With the recession of floodwater after each flood disturbance, the connection between lake and river became less dynamic resulting in lakes that not only differed in character from the river, but also from one another in water quality, bacterial abundance, and zooplankton community composition based on observations of similar systems (Amoros & Bornette, 2002; Luef et al., 2007; De Paggi & Paggi, 2008). In the late 1920s, the lakes featured in this study were drained and the surrounding lands were farmed for agriculture as part of separate drainage and levee districts. Alterations to the Illinois River system during this period included channel dredging, levee construction, and connection of the river to Lake Michigan that raised baseline water levels by 1.5 m and introduced non-native and invasive flora and fauna (Bellrose et al., 1983; Mills et al., 1966).

The area that includes reference lake LC lies across the river and to the east of TL and was part of the United States Fish and Wildlife Service (USFWS) refuge. Water from the Illinois River frequently, yet not predictably, enters the southern basin of LC when the river height overtops the levee at 134.4 m above mean sea level. LC was drained for agriculture after organization of the Chautauqua Drainage and Levee District in 1916 (United States Army Corps of Engineers, USACE, 1991). The Chautauqua levee district was unable to maintain the levee due to financial reasons and the Illinois River was allowed to reclaim the bottomlands and shallow lakes. In 1936, the US Fish and Wildlife acquired the former drainage district designating it as part of the National Wildlife Refuge System and is managed as such today. A cross dike constructed in 1969 separated LC into north and south cells, and it is the south cell (about 1410 ha; centroid 40°21′14.92″N, 90°02′3.16″W, Fig. 1) that receives water from the Illinois River at the southern end when river height reaches 134.4 m above sea level (USACE, 2005). In this study, LC was connected to the river for three periods (Fig. 2). The LC south cell was chosen as a comparison site to TL because it contains several similarities to the projected, fully restored TL, which include having nearly similar physical locations on river and therefore either receive (LC) or may receive (TL) a flood pulse at the same time and that LC and TL have similar surrounding land-use practices. It should be noted that the use of "reference" here does not refer to a historically, unaltered, pristine site but rather is a lake that has undergone many of the changes and resource degradations inflicted upon the Illinois River, including invasive plant and animal species, an altered hydrology that imparts greater and more frequent flooding than existed in the historical hydrograph (Sparks et al., 1998), and an increased nutrient load from non-point sources throughout the catchment.

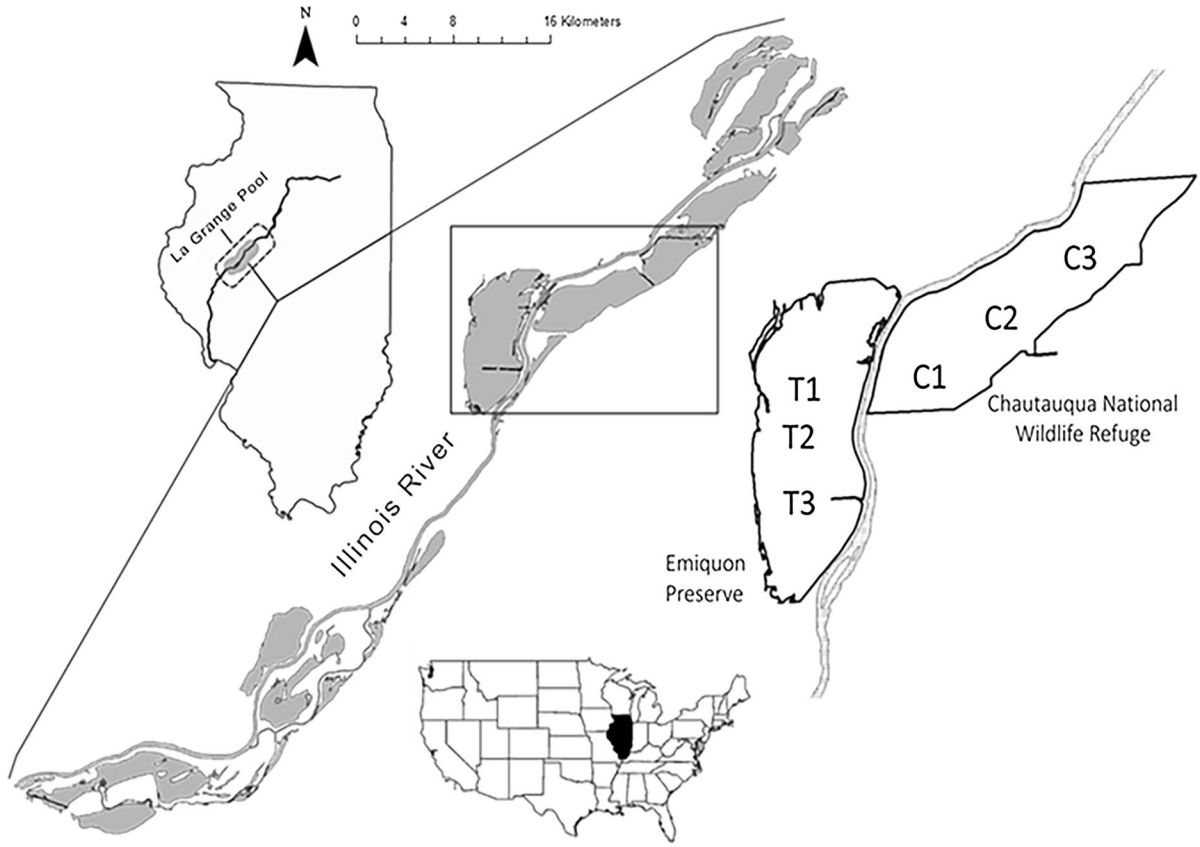

Fig. 1 Location of pelagic sampling sites *T1–T3* on Thompson Lake on the Emiquon Preserve (The Nature Conservancy) and sampling sites *C1–C3* on the south cell of Lake Chautauqua (USFWS Chautauqua National Wildlife Refuge). The Illinois River separates the two sites

Sample collection

Lake water was sampled from both lakes weekly from March 29 to November 17, 2008 and collection dates falling within March 21–June 20, June 21–September 22, and September 23–December 21 were classified as spring, summer, and fall, respectively. Flooding periods at LC occurred March 30–April 14, June 17–July 1, and September 26–October 1. Water depth (calibrated depth pole), Secchi depth, pH, conductivity, dissolved oxygen, water temperature (YSI Proplus, Yellow Springs, OH), and turbidity (Hach turbidimeter 2100P, Loveland, CO) were measured at time of sampling. Bacterioplankton at these pelagic sites were collected by taking a water sample ($n = 3$) with 500-ml sterile Whirl-Pak bags (Nasco, Fort Atkinson, WI) 10 cm beneath the surface of each lake. Bacteria were filtered from up to 150 ml of the water sample using 47-mm, 0.22-µm isopore polycarbonate, hydrophilic membrane filter (GTTP04700; EMD Millipore Corp., Darmstadt, Germany) folded in half, and stored in a UV-exposed aluminum foil at −20°C until processed for DNA extraction. Additional whole water surface samples were collected biweekly at the same depth for chlorophyll *a* (Chl *a*) estimates, water chemistry analysis, and plankton abundance (phytoplankton and ciliated protozoans; 2.38% final concentration glutaraldehyde; stored at 4°C in the dark; Wetzel & Likens, 2000). Zooplankton were concentrated from 30-l Schindler–Patalas plankton trap tows ($n = 3$/site) (61 µm filter, 90 l total; Wildco, Yulee, FL) and stored in 250-ml Nalgene bottles with Alka-Seltzer® (1/4 tablet; Bayer, Whippany, NJ) and formaldehyde (final concentration 4% v:v). Zooplankton samples were subsequently filtered through a 53-µm sieve and 70% ethanol with Rose Bengal added roughly 2 months after collection, and stored at 4°C until analysis.

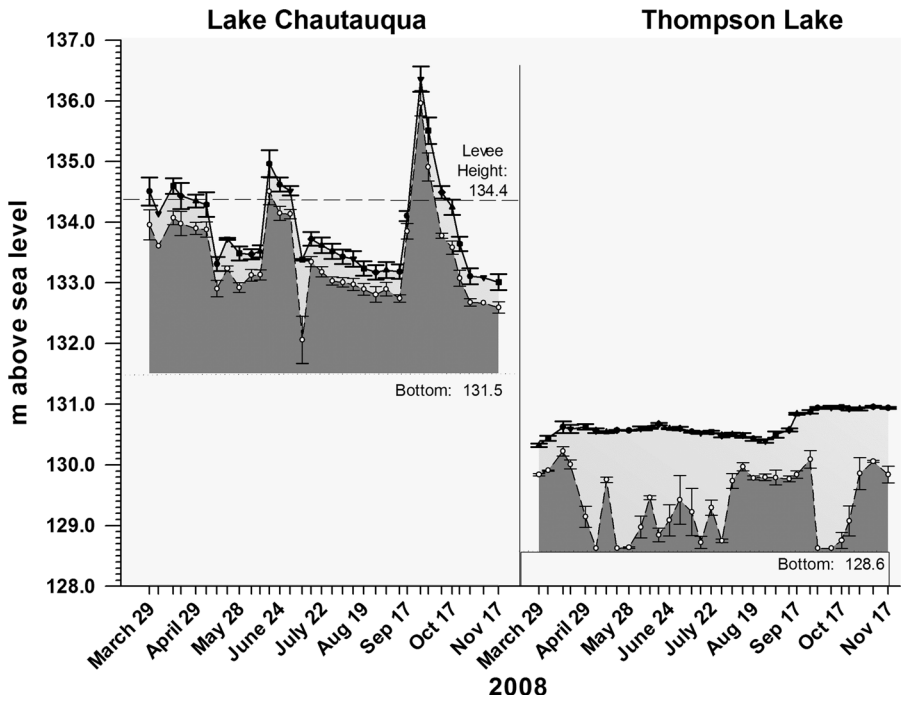

Fig. 2 Lake water (*black circle*) and Secchi (*white circle*, *light gray zone*) depths normalized by meters elevation above sea level in Lake Chautauqua and Thompson Lake

Water analysis

Chl *a* analysis was completed by filtering water under vacuum (34 kPa) through a Whatman GF/F glass fiber filter (GE Healthcare Bio-Sciences, Pittsburgh, PA) on the day of sampling, stored at −20°C, extracted with acetone overnight in the dark at 20°C, and read on a Cary 100 Bio UV–visible spectrophotometer (Agilent, Santa Clara, CA) following the method of Wetzel and Likens (2000). Total suspended solids (TSSs) were determined by filtering a measured water volume through pre-ashed GF/F filters under vacuum followed by drying (105°C) and carbon incineration (550°C) as described in American Public Health Association, APHA: Method 2540E (1998). Water chemistry analyses included nitrate and soluble reactive phosphorus (SRP; Dionex IC25 ion chromatograph with EG40, AS-17 column, AS50 autosampler; Sunnyvale, CA), total and dissolved ammonia (APHA, 1998: Method 4500-NH_3-F), total phosphorus (TP), and total nitrogen (TN; persulfate digestion followed by APHA: Method 4500-P-D (1998) and second derivative spectroscopy (Crumpton et al., 1992) on a Cary 100 Bio UV–visible spectrophotometer, respectively), and DOC (measured using a Dohrmann-Xertex DC-80 TOC analyzer with a minimum detection limit of 0.5 mg DOC/l APHA, 1998: Method 5310; McDaniel et al., 2009). Carlson trophic state index (TSI) was primarily based on Chl *a* concentration (9.81ln[Chl *a*] + 30.6), yet other indicators were used as well (60 − 14.41ln[Secchi depth]) and 14.42ln[TP] + 14.15 for comparison (Osgood, 1982). As an index for light penetration into the lakes, the ratio of euphotic zone to lake depth (Z_{eu}:Z_{max}) was calculated with $Z_{eu} = 2.66 \times$ Secchi depth (Giblin et al., 2010).

Bacterioplankton number and composition

Bacteria were enumerated from lake water collected at time of sampling and preserved with glutaraldehyde (2.4% final concentration; stored at 4°C) (after Porter & Feig, 1980; Wetzel & Likens, 2000). Briefly, the preserved subsamples (100 µl) were stained with 15.0 µg/ml 4,6-diamidino-2-phenylindole dihydrochloride hydrate (Sigma-Aldrich, St. Louis, MO) and were filtered with 0.22-µm-pore size, black polycarbonate filters (EMD Millipore Corp., Darmstadt, Germany) by vacuum (15 kPa), rinsed with MilliQ filtered water, and counted using epifluorescence microscopy (Olympus BX51; 100 W mercury

lamp, excitation 358 nm, emission 461 nm; Olympus Corp., Center Valley, PA).

DNA was extracted from two of the bacterioplankton filters using MP Biomedicals FastDNA kits (MP Biomedicals, Solon, OH) and stored at −20°C. Automated ribosomal intergenic spacer analysis (ARISA) was used to characterize bacterial community composition (Kent et al., 2007). DNA concentrations were determined using a NanoDrop 1000 Spectrophotometer (Thermo Scientific, Waltham, MA). The 23S–16S rRNA intergenic spacer region was PCR amplified from 10 ng of each DNA sample with 6-FAM-labeled, universal 16S rRNA primer 1406F (5′-TGYACACACCGCCCGT-3′) and 23S-R (5′-GGGTTBCCCCATTCRG-3′) targeting the bacterial 23S rRNA gene. The polymerase chain reaction contained 1 mM deoxynucleoside triphosphates (Promega, Madison, WI, USA), 0.4 μM of each primer, PCR buffer with 2.5 mM $MgCl_2$ (Idaho Technology, Inc., Salt Lake City, Utah, USA), and 0.05 U/μl GoTaq (Promega). PCR cycles consisted of an initial denaturation at 94°C for 2 min, followed by 30 cycles of 94°C for 35 s, 55°C for 45 s, and 72°C for 2 min, followed by a final extension at 72°C for 2 min, and were carried out in an Eppendorf MasterCycler gradient (Eppendorf AG, Hamburg, Germany). Fluorescently labeled ARISA PCR products were combined with a custom 100–1250 bp rhodamine X-labeled size standard (BioVentures, Murfreesboro, TN). PCR products were separated by length using denaturing capillary electrophoresis (ABI 3730xl DNA analyzer, Applied Biosystems, Foster City, CA) at the Keck Center for Functional Genomics at the University of Illinois at Champaign-Urbana. GeneMarker (SoftGenetics version 1.75) was used for size-calling, profile alignment, and grouping peaks into bins of operational taxonomic units (OTUs). To include the maximum number of peaks while excluding background fluorescence, a threshold of 1,000 fluorescence units was used. The signal strength of each peak was normalized to account for run-to-run variations in signal detection by dividing the area of individual peaks by the total fluorescence (area) detected in each profile.

Based on ARISA results, representative samples were selected from spring (6 May) and fall (10 October) for further characterization using 454 pyrosequencing of the 16S rRNA gene V4–V5 region. Primer sequences were designed to produce one-way reads using the emPCR Lib-L chemistry (Roche Applied Science, Basel, Switzerland). Each 25 μl PCR reaction contained 0.02 Units/μl Phusion High-Fidelity DNA Polymerase (Thermo Scientific, Waltham, MA, USA), 1 nM Phusion HF buffer, 0.2 mM of each dNTP (New England Biolabs, Ipswich, MA, USA), and 0.2 μM of each primer. The V4–V5 region was amplified using primer A with template-specific primer 519F (5′-CAGCMGCCGCGGTAATWC-3′) and barcoded primer B with template-specific primer 926R (5′-CCGTCAATTCMTTTRAGTT-3′). Thermocycling conditions consisted of a 2-min initial denaturation at 98°C, 25 cycles of 98°C for 10 s, 60°C for 30 s, and at 72°C for 20 s, and a final extension at 72°C for 5 min. PCR products from each of the three transects sampled from the same lake on the same date were combined and purified using Agencourt AMPure XP beads (Beckman Coulter, Brea, CA, USA) according to the manufacturer's protocol to remove excess nucleotides and salts. Concentration of DNA for each sample was determined using the Invitrogen Qubit ds DNA HS assay and Qubit 2.0 Fluorometer (Invitrogen, Carlsbad, CA, USA). Amplicons were mixed in equimolar concentrations and processed from emPCR through sequencing following the May 2011 Roche emPCR Method Manual on a Roche GS FLX+ system with 2.8, flow pattern A, and analyzed through amplicon signal processing using Roche software version 2.8 at the Keck Center for Functional Genomics at the University of Illinois. Using MacQIIME v 1.9.1 (Caporaso et al., 2010), 454-pyrosequencing sequence reads were assigned to samples based on barcode sequences and sorted into OTUs using the uclust method at a 0.97 similarity threshold (Edgar, 2010). A representative set of 16S rRNA gene sequences for each OTU was classified independently using the freshwater database (July 12, 2012) compiled by the McMahon and Bertilsson research groups (Newton et al., 2011) and the Greengenes database (September 9, 2011, DeSantis et al., 2006) as taxonomy files for the classify seqs command in mother (version 1.25.0, Schloss et al., 2009).

Plankton analysis

Phytoplankton samples were analyzed according to Utermöhl (1958) and Lund et al. (1958). The phytoplankton biovolume was estimated by multiplying the density of different taxa by their respective volumes.

The cell volume was calculated from geometric models according to the shape of the cells (Hillebrand et al., 1999; Sun & Liu, 2003). Ciliate counts were performed as described by Utermöhl (1958) with 15 ml of a mixed sample concentrated by sedimentation (Lund et al., 1958). Determination of zooplankton abundance was done by subsampling (1 ml) each sample ($n = 3$) with a minimum of 80 individuals counted in Sedgewick-Rafter chambers using a BX51 Olympus microscope (Bottrell et al., 1976). Phytoplankton and zooplankton were counted to species level, whereas fixed ciliate samples were counted to the level of order.

Data analysis

A Welch's independent-samples t test was used to confirm differences between the physical and chemical measurements for the lakes and a one-way ANOVA was used to determine significant differences in physicochemical variables among seasons (SPSS version 16.0; $\alpha = 0.05$; Tukey's post hoc test). More advanced statistical analyses were carried out in the R statistical environment version 3.2.3 (R Core Development Team, 2010). Pairwise Bray–Curtis similarities were calculated for every combination of samples from each dataset (e.g., bacterial ARISA, phytoplankton). Non-metric multidimensional scaling (MDS) was used to visualize changes in ARISA-characterized bacterial communities over time using the phyloseq package (https://github.com/joey711/phyloseq). Stacked barplots were used to visualize changes in bacteria (characterized by 454-pyrosequencing), phytoplankton, protists, and zooplankton. Permutational multivariate analysis of variance (PERMANOVA) was used to test the effects of lake and date on the structure of each microbial subgroup. PERMANOVA is a non-parametric multivariate analysis of variance that generates P values using permutations (Anderson, 2001; McArdle & Anderson, 2001). PERMANOVA tests were run using the adonis function from the vegan package (Oksanen et al., 2011). Potential relationships between community patterns and environmental variables were determined by correlating Bray–Curtis similarity matrices of each biological dataset for each lake with Euclidian distance matrices of environmental variables using bioenv and related functions from the vegan package (Oksanen et al., 2011).

Results

Limnological characteristics

Precipitation and overland runoff filled the 80-year, former TL basin to an average lake depth of 2.0 m, 0.5 m lower than the average LC depth (Table 1). The Illinois River flooded LC on three occasions in 2008, doubling its average depth during the autumn flood (Fig. 2). Temperature was similar between lakes (Table 1) and, due to the polymictic nature of both lakes, showed mixture of the water column (Z_{mix}:Z_{max} >0.9) for most of the sampling period (Supplemental Fig. 1).

The average Secchi depth was over twice as great in TL as it was in LC and showed much greater variability throughout the year (Table 1; Fig. 2). The difference in light availability was reflected in turbidity and TSS measurements; turbidity and suspended solids were 2–3× lower and suspended solids contained more organic matter in TL compared to LC (Table 1). Z_{eu}:Z_{max} for TL had greater variability with periods when the light reached the lake bottom to those when penetration was about 1.5 m (ratio avg. 1.2; range 0.5–2.5). LC Z_{eu}:Z_{max} was more consistent (avg. 0.5; range 0.2–0.7) than that of TL. Average dissolved oxygen, pH, Chl a, ammonia, TN, and TP were similar between lakes, while LC had significantly ($P < 0.01$) less SRP and higher soluble NO_3-N than TL (Table 2; Supplemental Fig. 1A–H). In TL, there were no significant seasonal differences in TP (avg. 296 µg/l), TN (avg. 1.72 mg/l), total nitrate (0.04 mg N/l), or ammonia (avg. 0.06 mg N/l). Dissolved oxygen decreased in the bottom waters of TL beginning in late June 2008 and was accompanied by a spike in SRP (248 µg P/l) in the same time period (Table 2).

For TL, the Carlson TSI based on Chl a was 60.6 [averaged across months; range 45.5 (May) to 73.4 (August)] indicating that the lake productivity shifted from mesotrophic in spring to hypereutrophic (North American Lake Management Society, NALMS, 1988) by mid-summer (TSI based on Secchi depth gave similar results (TSI[SD] = 59.6 avg.), while TSI[TP] slightly overestimated the index (85.9)), even though TL water remained comparatively low in nitrogen content throughout the sampling period. LC fell into the eutrophic–hypereutrophic state (TSI[Chl a] = 64.3 avg.; range = 50.5 October flood–72.8 in June) for the year; LC TSI based on Secchi depth (71.4

Table 1 Physical and biotic measurements of surface water column samples from Thompson Lake and Lake Chautauqua (average ± standard error of mean; range in parenthesis) measured March–November 2008

Lakes	Depth* (m)	Secchi* (m)	Temp. (°C)	Spec Cond* (μS/cm)	Turbidity* (NTU)	TSS* (mg/l)	%AFDM*	Chl *a* (mg/l)	Bacteria* (number × 10^6/ml)
Thompson	2.02 ± 0.02 (1.70–2.33)	1.24 ± 0.06 (0.40–2.32)	19.7 ± 0.7 (5.8–29.3)	481 ± 5 (398–678)	7.3 ± 0.6 (1.4–19.4)	9.3 ± 1.1 (2.0–22.3)	65.2 ± 4.4 (12.0–95.2)	0.03 ± 0.01 (0.00–0.08)	8.1 ± 0.4 (3.2–18.7)
Chautauqua	2.48 ± 0.08 (1.55–4.90)	0.45 ± 0.01 (0.25–0.72)	20.3 ± 0.7 (4.9–29.8)	589 ± 10 (393–850)	18.0 ± 0.8 (9.6–32.0)	23.4 ± 2.2 (11.8–50.4)	41.7 ± 2.7 (14.9–79.3)	0.04 ± 0.00 (0.01–0.07)	12.8 ± 0.8 (4.7–25.7)

Spec Cond specific conductivity, *TSSs* total suspended solids, *%AFDM* percentage of ash-free dry mass, *Chl a* chlorophyll *a*, *Bacteria* total number of bacteria

* Parameters are significantly different ($P < 0.01$)

Table 2 Chemical measurements of surface water column samples from Thompson Lake and Lake Chautauqua (average ± standard error of mean; range in parenthesis) measured March–November 2008

Lakes	DO (mg/l)	pH	NO_3-N* (mg/l)	NH_3 (mg N/l)	TN (mg/l)	SRP* (μg P/l)	TP (μg/l)	DOC* (mg C/l)	Cl^{-}* (mg/l)	SO_4^{2-}* (mg/l)
Thompson	8.8 ± 0.2 (4.7–14.7)	8.40 ± 0.05 (7.02–9.01)	0.04 ± 0.01 (0.00–0.18)	0.06 ± 0.01 (0.00–0.25)	1.7 ± 0.1 (1.0–2.6)	119 ± 12 (0–248)	296 ± 16 (124–464)	11.1 ± 0.2 (8.8–14.0)	27.4 ± 0.4 (21.8–30.5)	11.7 ± 1.0 (3.3–22.1)
Chautauqua	8.8 ± 0.4 (3.7–18.0)	8.40 ± 0.06 (6.60–9.34)	0.55 ± 0.12 (0.00–2.27)	0.04 ± 0.01 (0.00–0.12)	1.8 ± 0.1 (0.8–3.1)	45 ± 7 (0–113)	268 ± 17 (45–389)	5.8 ± 0.3 (0.0–7.5)	81.6 ± 4.5 (40.3–154.8)	38.3 ± 0.8 (30.5–45.8)

DO dissolved oxygen, *TN* total nitrogen, *SRP* soluble reactive phosphorus, *TP* total phosphorus, *DOC* dissolved organic carbon

* Parameters are significantly different ($P < 0.01$)

avg.) and TP (84.46) gave slightly higher but similar results.

Bacterial composition

There was a significantly greater number of bacteria enumerated in LC than were in TL (Table 1), and the difference between the two lakes was most pronounced in summer when the abundance of LC bacteria peaked (Supplemental Fig. 2B). Bacterial composition differed between lakes and through time (PERMANOVA: lake $R^2 = 0.07$, $P < 0.001$, date $R^2 = 0.37$, $P < 0.001$, lake * date $R^2 = 0.24$, $P < 0.001$; Supplemental Table 1; Fig. 3). Within each lake, the sampling date explained over 60% of the variation in bacterial community composition (LC: PERMANOVA, $R^2 = 0.66$, $P < 0.001$; TL: PERMANOVA, $R^2 = 0.65$, $P < 0.001$; Fig. 3A, B; Supplemental Fig. 2A). Between-lake differences were apparent within seasons (Fig. 3C–E). Bacteria from water samples fell primarily into seven phyla/proteobacterial classes, with Actinobacteria, Bacteroidetes, Betaproteobacteria, and Cyanobacteria being the most abundant in both lakes (Table 3; Fig. 4). Bacterial composition between lakes was more similar in May than in October when more than 75% of

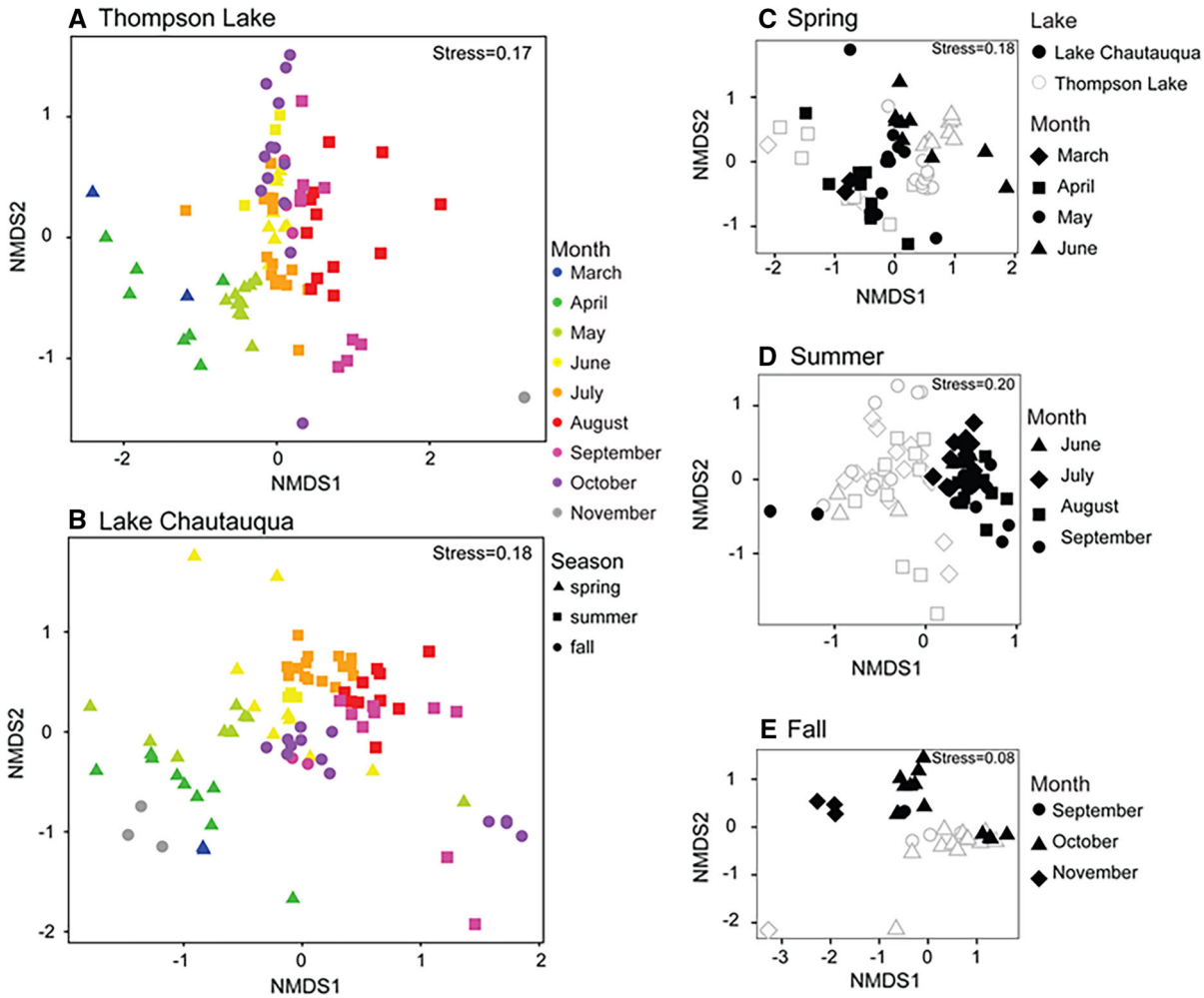

Fig. 3 Non-metric multidimensional scaling ordinations of bacterial assemblages emphasizing seasonal changes within Thompson Lake (**A**) and Lake Chautauqua (**B**) and highlighting between-lake differences for samples collected during spring (**C**), summer (**D**), and fall (**E**)

Table 3 Relative abundance of the most abundant operational taxonomic units (OTUs) identified in May and October from each lake using 16S rRNA gene tag pyrosequencing

OTU IDs	Classification	Thompson Lake		Lake Chautauqua	
		May	October	May	October
Actinobacteria					
3374	acI-A	0.028	0.001	0.002	
7682	acI-A			0.004	0.070
19240	acI-A	0.012		0.002	0.005
9072	acI-B	0.004	0.001	0.001	0.045
9342	acI-C				0.018
5423	acI (98)				0.014
25912	Actinobacteria (83)		0.010		
25130	Actinomycetales	0.021	0.002		
4658	Luna1-A	0.055	0.016	0.007	0.002
24627	Luna1-A	0.012	0.002	0.001	
Betaproteobacteria					
18007	betI-A			0.047	0.005
23608	betI-A	0.051	0.002	0.002	0.001
5649	betIV-A				0.014
10265	Pnec (98)	0.010		0.016	
Cyanobacteria					
1477	*Dolichospermum*		0.045		
3399	*Dolichospermum*		0.066		
6614	*Dolichospermum*		0.462		0.002
20113	*Dolichospermum*		0.068		
Bacteroidetes					
13313	bacV	0.023		0.001	
17156	bacV	0.004		0.002	0.016
24452	bacI			0.015	
30	bacIII-A	0.202	0.006		0.022

Numbers in parentheses indicate the confidence values of taxonomic assignments if less than 100 as determined by mothur

sequences in TL were identified as Cyanobacteria, primarily from the genus *Dolichospermum* (Table 3; Fig. 4).

Phytoplankton

In general, the phytoplankton biovolume showed two compositionally different blooms in TL. The first was composed of primarily Bacillariophyceae and Cryptophyceae during 14 April–13 May. The second, more sustaining assemblage from about June 11 to October 8 was predominately Cyanobacteria with Bacillariophyceae and Cryptophyceae (Fig. 5). The biovolume in LC was primarily Bacillariophyceae, Cyanobacteria, and Chlorophyceae, with Bacillariophyceae being dominant in spring and fall, Cyanobacteria more abundant in late spring and early summer, and Chlorophyceae growing in abundance in late summer–early fall. Cyanobacteria in TL included *Aphanizomenon* with greatest numbers on July 8 and a second cyanobacteria peak in fall composed primarily of *Planktolyngbya*, *Snowella*, and *Geitlerinema* (Fig. 6A). LC cyanobacteria had the greatest numbers following subsidence of the first two flooding periods with *Aphanocapsa*, *Planktolyngbya*, and *Merismopedia* in greatest numbers.

While 26% of the 143 taxa were found in both lakes, over 50% of all taxa identified were unique to TL, 18% to LC, and the balance (30%) were common to both lakes (Table 4). Thirty-five genera of

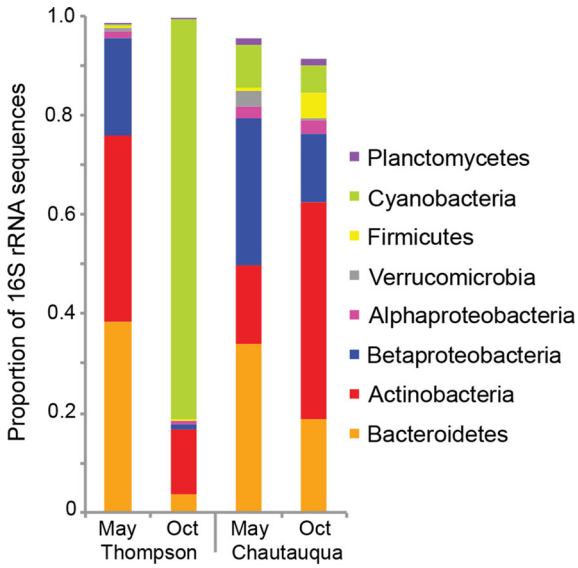

Fig. 4 Relative abundance of the most abundant bacterial phyla and proteobacterial classes in samples collected in May and October from each lake as determined by 454 sequencing

Chlorophyceae were identified with 62 species from both lakes. TL had about one-half as many individuals per volume than LC and those in TL occurred primarily in late summer–early fall (Fig. 6B). Of the 34 Bacillariophyceae taxa identified, 65% were only found in TL (Table 4). This algal group did not show as great diversity as seen with the green algae, but did show a spring and late fall peak in LC composed primarily of *Achnanthes*, *Discostella, and Orthoseira* (Fig. 6C). TL had about twice as many diatoms as did LC; however, the early peak was almost exclusively *Cyclotella* and the autumn *Aulacoseira*.

The remaining algal groups were more minor components (<25/l) of the phytoplankton community. Both lakes had genera *Chroomonas* and *Cryptomonas* of the Cryptophyceae throughout the ice-off sampled months; however, TL had about four times as many *Cryptomonas* in autumn than did LC (Supplemental Fig. 3A). In class Euglenophyceae, genera *Euglena*, *Trachelomonas*, and *Phacus* were evident in both lakes with an especially notable *Euglena* peak in autumn in LC (Supplemental Fig. 3B). There was little contribution of Chrysophyceae in LC (Supplemental Fig. 4A); however, *Dinobryon* was evident in the pelagic TL waters in spring and fall. The predominate genus in class Xanthophyceae was *Goniochloris* clearly present in LC and barely evident in TL (Supplemental Fig. 4B). Members of the class Zygnemaphyceae were, for the most part, different in each lake with *Spyrogyra*, *Closterium* evident in TL and *Cosmarium* and *Staurastrum* in LC (Supplemental Fig. 5A). The main presence of the Dinophyceae was *Ceratium* occurring in autumn in TL (Supplemental Fig. 5B).

Protists and zooplankton

Testate amoeba genera *Centropyxis*, *Cucurbitella*, and *Difflugia* were present in both lakes with the greatest abundance of *Difflugia* occurring in spring in LC and *Centropyxis* in late autumn in TL (Fig. 7A). Twelve taxonomic groups of ciliates existed in the lakes in 2008 (Table 4) and showed a summer peak with numbers reaching about 60,000 organisms/l in both lakes with class Oligotrichia being the most evident and Hymenostomatia, Protomatea, Scuticociliatia, and Haptorida emerging late summer–early autumn (Fig. 7B). While high overall rotifer diversity existed in both lakes (34 taxa, Table 4), the largest abundance of rotifers occurred at LC in late October and consisted of *Synchaeta*, *Polyarthra*, *Keratella*, and Flosculariidae (Fig. 8A). In contrast, TL had *Keratella* throughout 2008 and *Polyarthra* evident in spring and late summer. Both lakes had spring peaks of cladocerans (*Bosmina*, *Daphnia*, and *Diaphanosoma* with *Chydorus* occurring in TL, Fig. 8B). Copepods (adult + early stages, Fig. 8C) and cladocerans had peak abundances in the spring though more evident for cladocerans and copepods in TL. Interestingly, a second peak of microcrustaceans emerged in TL in autumn.

Discussion

The microbial composition, diversity, and seasonal dynamics in a lake in its first year of restoration (TL) were compared to the same attributes measured in a nearby, river flood-pulsed lake, which served as a reference site (LC). Large and often rapid changes in environmental factors contributed to system variability, and thus ecological instability, in the first full year of lake recovery in TL, and included nutrient fluxes, phytoplankton blooms, aquatic macrophyte encroachment, the stocking of over one and one-half million fish comprising 32 species (Retzer et al., 2009), and increased lake volume (about 20 times the 2007

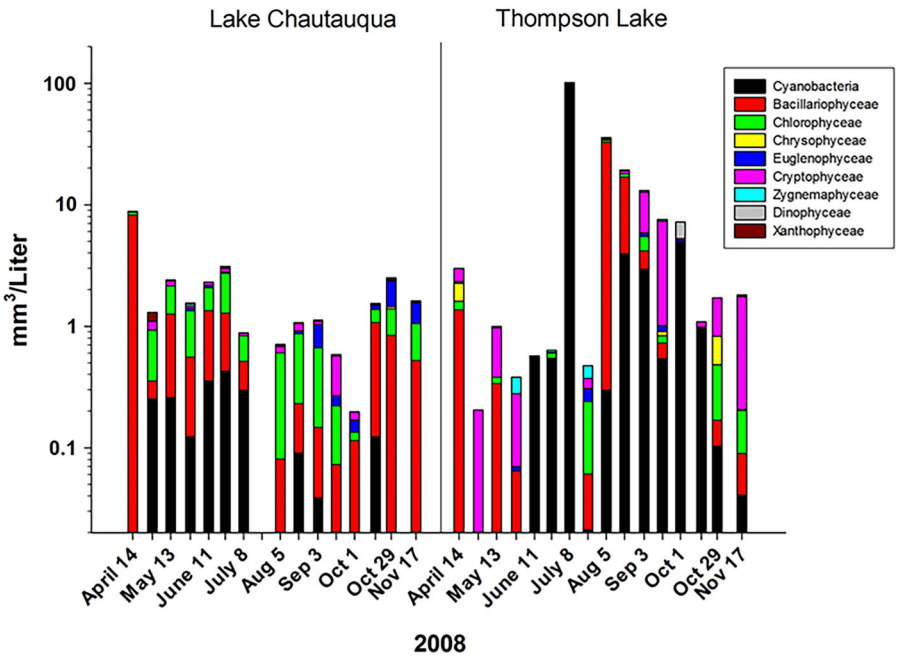

Fig. 5 Phytoplankton biovolume by class in biweekly samples collected from Lake Chautauqua and Thompson Lake

volume; TNC unpublished data). While the structural aspects of the newly restored lake developed, competition and population re-adjustment among many microbial species were observed.

Unlike LC, TL had clear water periods where light reached the lake bottom punctuated with water conditions with reduced Secchi depth and cyanobacterial blooms. About one-half of the TSSs were inorganic content likely due to bottom particle resuspension from mixing caused by a long wind fetch (1.6–7.7 km) across the shallow lake. A surge of phosphorus (464 µg/l) in June appeared to trigger a change in primary productivity to the point that the Carlson TSI shifted nearly 30 points creating a condition that likely favored cyanobacteria.

The bacterioplankton assemblage exhibited a temporal change in both study lakes. Seasonal change in bacterial community composition has been observed in pelagic bacterioplankton in Lake Mendota and humic lakes in Wisconsin (e.g., Kent et al., 2004, 2007; Shade et al., 2007), as well as in large rivers within a region (Crump et al., 2009). The 16S rRNA gene sequences showed the predominant bacterial groups to be Betaproteobacteria, Actinobacteria, and Bacteroidetes in May and October in LC and in May in TL. All of these groups are common to the upper waters of lakes and are abundant as either free-living or particle-associated bacteria (Newton et al., 2011). A notable difference in October sequence results is that cyanobacteria dominated TL during October, likely due to abundance of SRP (Supplemental Fig. 1B). Cyanobacterial blooms in Lake Champlain were attributed to SRP release and low NO_3^- concentrations (Isles et al., 2015).

In LC, phytoplankton succession generally followed the well-documented plankton ecology group model for temperate lakes in which early spring species are *r*-selected, food web-edible species (e.g., flagellate greens small diatoms, cryptomonads) followed by the less edible *k*-selected species (e.g., large diatoms, large greens, cyanobacteria, and dinoflagellates). In this model, changes in abundance over time were driven by grazing and nutrient fluxes (Sommer et al., 1986, 2012; Reynolds, 1988; Sterner, 1989). In LC, a spring bloom of green algae and diatoms gave way to a modest increase in cyanobacteria followed by a second green algae increase and then an increase in diatoms. The spring bloom of diatoms had greater species richness in river-connected LC than in isolated TL. It is likely that the presence of these organisms in LC was associated with the floods that inoculated the lake with river water, since diatom growth and

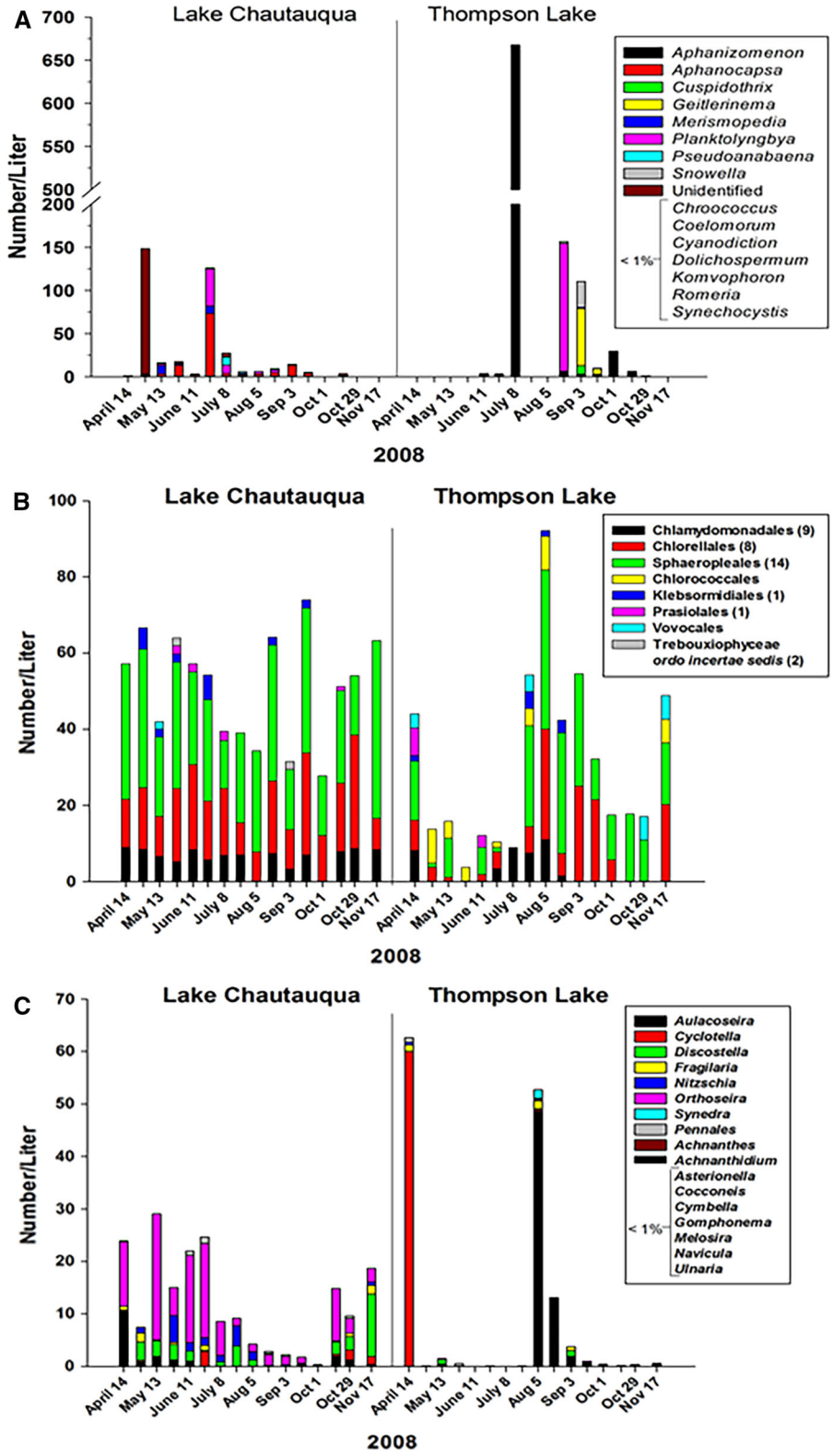

Fig. 6 Phytoplankton abundance found in Lake Chautauqua and Thompson Lake for the **A** cyanobacteria (average abundance stacked by genus; <1% abundance in either lake are not shown), **B** Chlorophyceae (stacked by level of order), and **C** Bacillariophyceae (genera making up 1% of the total abundance in either lake were not included in the stacked bars)

Table 4 Composition of pelagic plankton in Lake Chautauqua (LC) and Thompson Lake (TL) in 2008

Phytoplankton	LC	TL	Phytoplankton	LC	TL	Zooplankton	LC	TL
BACILLARIOPHYCEAE			**CHLOROPHYCEAE**			**Testate amoebae**		
Achnanthes sp.	×	×	*Actinastrum aciculare* Playf. var. *aciculare*		×	*Arcella discoides*		×
Achnanthidium minutissimum (Kütz.) Czarn.	×		*Ankistrodesmus fusiformis* Cor.		×	*Arcella hemisphaerica*		×
Amphipleura lindheimeri Grun.		×	*Actinastrum hantzschii* Lagerh.	×	×	*Centropyxis aculeata*	×	×
Asterionella sp.	×		*Ankyra judayi* (G.W. Smith) Fott		×	*Cucurbitella* sp.	×	×
Aulacoseira ambigua (Grun.) Sim. var. *ambigua*	×	×	*Chlamydomonas* sp.		×	*Curcubitella dentata*		×
Aulacoseira ambigua (Grun.) Sim. var. *ambigua*. fa. *spiralis*		×	*Closteriopsis* sp.		×	*Difflugia corona*	×	×
Aulacoseira distans (Ehr.) Sim.	×		*Coelastrum microporum* Näg.		×	*Difflugia* cf *gramen*	×	×
Aulacoseira granulata (Ehr.) Sim. var. *granulata*		×	*Coelastrum pseudomicroporum* Kors.	×		*Difflugia* cf. *pseudogramen*	×	
Cocconeis sp.		×	*Coenochloris planconvexa*		×	*Difflugia* sp.	×	×
Cyclotella meneghiniana Kütz.	×	×	*Crucigenia fenestrata* (Schm.) Schm.	×	×	*Plagiopyxis* sp.		×
Cyclotella sp.		×	*Crucigenia tetrapedia* (Kirch.) W & G.S. West	×	×	*Protocucurbitella* sp.	×	×
Cymbella affinis Kütz.		×	*Crucigeniella pulchra* (W. & G. S. West) Kom.	×				
Cymbella sp.		×	*Crucigeniella rectangularis* (Näg.) Kom.	×		**Rotifers**		
Discostella stelligera (Cleve & Grun.) Holk & Klee	×	×	*Desmodesmus abundans* (Kirch.) E. Hegew.	×		*Anueropsis* sp.	×	×
Eunotia sp.		×	*Desmodesmus armatus* (Chod.) Hegew.	×		*Asplanchna* sp.	×	×
Fragilaria capuccina Desm.		×	*Desmodesmus armatus* var. *bicaudatus* (Gugl.) Hegew.		×	*Brachionus calyciflorus*	×	
Fragilaria sp.	×	×	*Desmodesmus communis* (Hegew.)	×	×	*Brachionus* cf. *angularis*	×	×
Fragilaria sp. 1		×	*Desmodesmus intermedius* var. *acutispinus* (Roll) E. Hegew.	×	×	*Brachionus* cf. *caudatus*	×	×
Gomphonema angustatum (Kütz.) Rab.		×	*Desmodesmus maximus* (W. West & G. S. West) E. Hegew.	×	×	*Brachionus bidentatus*	×	
Gomphonema olivaceum (Horn.) Ehr.		×	*Desmodesmus opoliensis* (P. Rich.) E. Hegew.	×	×	*Brachionus havanensis*		×
Gomphonema parvulum (Kütz.) Kütz.	×	×	*Desmodesmus spinosus* (Chod.) Hegew.		×	*Brachionus* sp.	×	×
Gomphonema sp.		×	*Desmodesmus* sp.		×	Bdelloidea	×	×
Gyrosigma sp.		×	*Desmodesmus* sp. 1		×	*Colurella* sp.	×	
Navicula cryptocephala Kütz.		×	*Dictyosphaerium elegans* Bachm.	×		*Conochilus* sp.	×	×
Navicula schroeterii Meist.		×	*Dictyosphaerium ehrenbergianum* Näg.		×	*Filinia longiseta*		×
Navicula sp.		×	*Dictyosphaerium pulchellum* Wood		×	*Filinia* cf *terminalis*	×	×
Nitzschia palea (Kütz.) Wm. Sm.	×		*Dictyosphaerium tetrachotomum* Printz	×		Floscularidae	×	×
Orthoseira sp.	×		*Elakatothrix* sp.		×	*Hexarthra* sp.	×	×
Surirella sp.		×	*Golenkinia radiata* Chod		×	*Keratella americana*	×	×

Table 4 continued

Phytoplankton	LC	TL	Phytoplankton	LC	TL	Zooplankton	LC	TL
Synedra goulardii Bréb.		×	*Koliella* cf. *spiculiformis* (Visch.) Hind.		×	*Keratella cochlearis*	×	×
Synedra sp.	×	×	*Micractinium pusillum* Fres.	×	×	*Keratella lenzi*	×	×
Ulnaria ulna (Nitzs.) Comp.		×	*Monactinus simplex* (Meyen) Corda *Monoraphidium arcuatum* (Kors.) Hind.	×	×	*Keratella quadrata*	×	×
Urosolenia sp.		×	*Monoraphidium contortum* (Thur.) Kom. – Legn.	×	×	*Keratella tropica*	×	
Pennales não identificada 1		×	*Monoraphidium convolutum* (Corda) Kom.-Legn.		×	*Lecane bulla*		×
Pennales não identificada 2		×	*Monoraphidium griffithii* (Berk.) Kom.-Legn.	×	×	*Lecane cornuta*		×
CYANOBACTERIA			*Monoraphidium irregulare* (G. M. Sm.) Kom.-Legn.	×	×	*Lecane curvicanis*	×	×
Anabaena circinalis Rab.		×	*Monoraphidium komarkovae* Nyg.		×	*Lecane dorissa*	×	
Anabaena spiroides Kleb.		×	*Monoraphidium minutum* (Näg.) Kom.-Legn.		×	*Lecane leontina*		×
Aphanizomenon gracile (Lemn.) Lemm.	×	×	*Monoraphidium tortile* (W. & G.S. West) Kom.-Legn.	×	×	*Lepadella* sp.	×	×
Aphanizomenon tropicale Hor. Et Kom.		×	*Oocystis borgei* Snow.		×	*Lecane* sp.	×	×
Aphanocapsa delicatissima w. et G.S. West	×	×	*Oocystis* sp.		×	*Notholca* cf. *labis*	×	×
Aphanocapsa elachista W. & West	×	×	*Pandorina morum* (F. Muller) Bory	×	×	*Polyarthra* sp.	×	×
Aphanocapsa holsatica (Lemm.) Cronb. & Kom.		×	*Pediastrum boryanum* (Turpin) Meneg.	×		*Synchaeta* sp.	×	×
Aphanocapsa koordersii Strom		×	*Pediastrum duplex* Mey.	×		*Testudinella patina*		×
*Chroococcus dispersu*s (Keissl.) Lemmerm.		×	*Scenedesmus acuminatus* (Lag.) Chod.	×		*Trichocerca* cf *similis*		×
Chroococcus minimus (Keis.) Lemm		×	*Scenedesmus alternans* Reins.	×		*Trichocerca capucina*	×	×
Cyanodictyon imperfectum Cromb. Et Weib.	×		*Scenedesmus ecornis* (Ehr.) Chod.		×	*Trichocerca* sp.	×	×
Geitlerinema cf. *amphibium* (Agardh ex Gom.) Anag.	×		*Scenedesmus linearis* Kom.	×		Rotifer not identified		×
Geitlerinema sp.	×	×	*Scenedesmus* sp.	×				
Lemmermaniella parva Hind.	×		*Schroederia antillarum* Kom.		×	**Cladocerans (Family)**		
Merismopedia tenuissima Lemm.	×	×	*Schroederia setigera* (Schröd.) Lemm.		×	*Bosmina* sp.	×	×
Pseudanabaena limnetica (Lemm.) Kom.	×	×	*Spermatozopsis exsultans* Kors.		×	*Ceriodaphnia* sp.		×
Snowella atomus Kom. & Hind	×	×	*Sphaerocystis planctonica* (Kors.) Bourr.		×	*Chydorus* sp.	×	×
Synechocystis aquatilis Sauv.		×	*Sphaerellopsis* sp.	×	×	*Daphnia* sp.	×	×
EUGLENOPHYCEAE			*Stauridium tetras* (Ehr.) E. Hegew., *Tetraedron caudatum* (Corda) Hans.		×	*Diaphanosoma* sp.	×	×
Euglena fusca (Klebs) Lemm.	×		*Tetraedron minimum* (A. Braun) Hansg.		×			
Euglena sp.	×	×	*Tetranephris brasiliensis* Leite & Bic.	×		**Copepods (Family)**		

Table 4 continued

Phytoplankton	LC	TL	Phytoplankton	LC	TL	Zooplankton	LC	TL
Lepocinclis ovum (Ehr.) Lemm.		×	*Tetrastrum komarekii* Hind.	×	×	Cyclopoida-adult	×	×
Phacus longicauda (Ehr.) Duj. var. *tortus* Lemm.		×	*Tetrastrum staurogeniaeforme* (Schröd.) Lemm.		×	Cyclopoida-adult sp2	×	×
Strombomonas ovalis (Play.) Defl.		×	*Ulothrix* sp.		×	Cyclopoida-adult sp3		×
Trachelomonas cervicula Stokes		×	*Volvox aureus*	×		Cyclopoida-naupli	×	×
Trachelomonas hispida (Perty) Stein.		×	Tetrasporales não identificada	×		Cyclopoida-copepodids	×	×
Trachelomonas oblonga Lemm.		×			×	Calanoida - adults	×	×
Trachelomonas rotunda (Playf.) Playf.		×			×	Calanoida - copepodids	×	×
Trachelomonas volvocinopsis Swir.		×				Calanoida - naupli	×	×
Trachelomonas sp.		×						
CRYPTOPHYCEAE			**CHRYSOPHYCEAE**					
Chroomonas acuta Uterm.	×	×	*Dinobryon divergens* Imhof		×	**Ciliates (Order)**		
Cryptomonas marssonii Skuja Bic	×	×	*Kephyrion littorale* JWG Lund	×		Colpodida		×
Cryptomonas sp.	×	×	*Mallomonas* sp.		×	Cyrtophorida	×	×
Cryptomonas sp1	×	×				Haptorida	×	×
Cryptomonas sp2		×				Heterotrichida		×
						Hymenostomatida	×	×
ZYGNEMAPHYCEAE			**XANTHOPHYCEAE**			Hypotrichida	×	×
Closterium lineatum Ehr.		×	*Goniochloris mutica* (A. Braun) Fott	×		Oligotrichida	×	×
Closterium sp.		×	*Isthmochloron gracile* (Reins.) Skuja		×	Peritrichida	×	×
Cosmarium regnesi Reins.		×	*Tetraplektron torsum* (Skuj.) Dedus.Sceg.		×	Pleurostomatida	×	×
Spyrogyra sp.		×	*Tetraplektron* sp.	×		Prostomatida	×	×
			Pseudostaurastrum enorme (Ralfs) Chod.		×	Scuticociliatida	×	×
DINOPHYCEAE						Suctorida		×
Ceratium cf. *furcoides* (Lev.) Langh.	×	×						

abundance is favored by the physical mixing of rivers and low light conditions (Reynolds & Descy, 1996; Reynolds et al., 2002; Padisák et al., 2009).

Even though seasonal change was evident in the phytoplankton on the level of taxonomic class, no clear temporal change of the number of species was evident (overall richness = 61). Because holomixis typically ends the shift in algal group dominance in temperate lakes, frequent holomixis in polymictic LC may have slightly obscured the otherwise recognizable trends (Roelke et al., 2004). The phytoplankton in polymictic TL appeared to be driven by nutrient fluxes that induced several post-June cyanobacterial blooms. Before this time, cryptophytes and diatoms dominated TL and green algae produced a minor spring bloom with high species richness, not unlike that observed at LC. In another lake recovering from intermittent drought, chlorophytes were the richest group, then cyanobacteria and diatoms (Michaloudi et al., 2012).

Protozoans are an important component of the microbial food web and increase nutrient cycling among the microbial community (Finlay & Esteban, 1998). This study emphasized testate amoeba and ciliates. Testate amoeba are associated with lake substrate, yet planktonic forms become more abundant

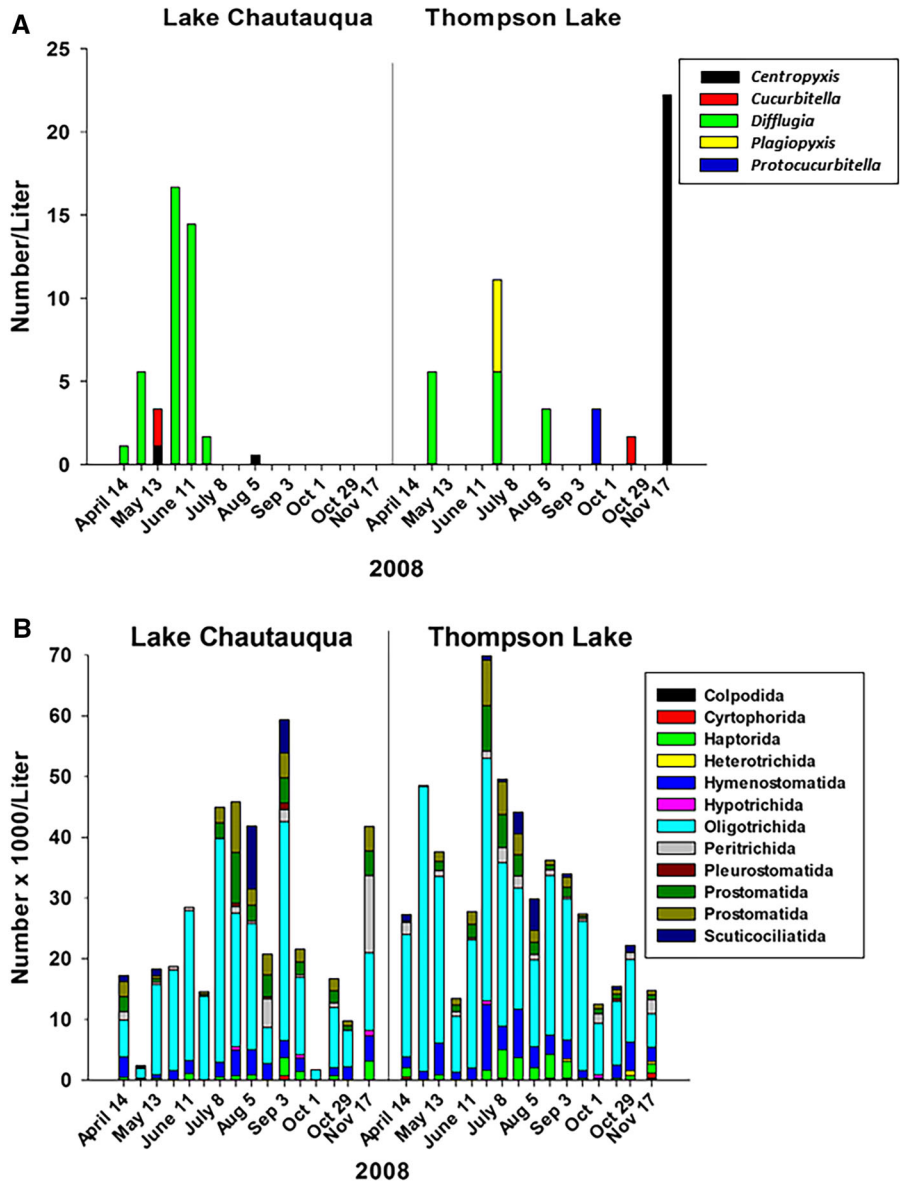

Fig. 7 Protist abundance in Lake Chautauqua and Lake Thompson in 2008 featuring the **A** testate amoeba listed by class and **B** ciliates listed by class

in shallow lakes after rain events and during flooding (Velho et al., 1999, 2004; Alves et al., 2010). LC had a great abundance of testate amoeba in the genera *Centropyxis*, *Cucurbitella*, and *Difflugia* early in the year, while at this time in TL there were *Difflugia* and *Plagiopyxis.* Later in the year in TL, *Centropyxis* (greatest abundance) and *Protocucurbitella* and *Cucurbitella* were evident. Members of the families Difflugidae, Arcellidae, and Centropyxidae can dominate lakes in general (e.g., Hunt & Chein, 1983) and members of the Arcellidae have appeared in high abundance in floodplain aquatic habitats. These observations are consistent with higher numbers in flood-affected LC as opposed to TL.

The ciliate community can be affected by the physical, chemical, and geomorphological characteristics of large rivers (Madonni & Baghiroli, 2007) including the effect of river flood pulse (Pauleto et al., 2009). Yet, of all the groups studied, the ciliates were the most similar between the two lakes. Ciliophora had the greatest standing crop abundance in summer in both lakes, although both lakes appeared to have a

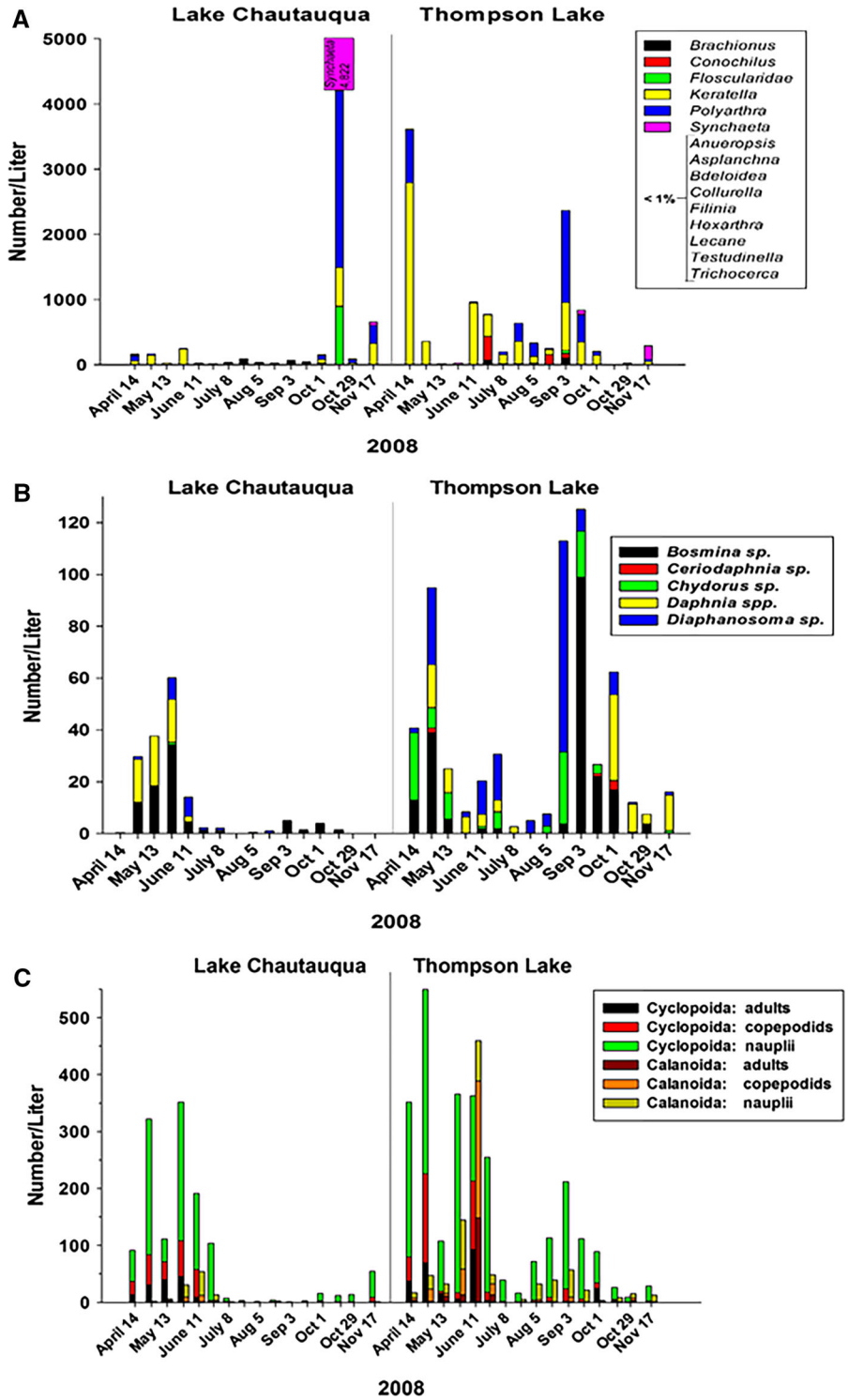

Fig. 8 Zooplankton in Lake Chautauqua and Lake Thompson in 2008 featuring **A** rotifer abundance stacked by genus (genera <1% in either lake are not shown), **B** cladoceran abundance listed by genus, and **C** copepod abundance listed by order and featuring life stages

spring increase in number that is likely a response first to diatom and then to green algae abundances. Of particular note is that ciliate abundance followed the same pattern as bacterial numbers in both lakes, even though bacterial numbers were overall lower in TL than in LC.

While it is likely that ciliates were preying upon the bacteria (Stabell, 1996), the trophic position among planktonic ciliates is variable (Velho et al., 2005). Ciliate order Oligotrichida had the greatest abundance, yet species in the orders Hymenostomatida, Prostomatida, Peritrichida, Scuticociliatida, and Haptorida appeared consistently throughout the study period. The Oligotrichia mainly ingest bacteria as well as autotrophic and heterotrophic nanoplankton (2–20 μm) and are preyed upon by a wide variety of planktonic metazoans (e.g., copepods, fish larvae (Chróst et al., 2009; Agatha, 2011).

The results for ciliate abundance and taxa of these Illinois River lakes were similar to a trend seen in the Paraná River floodplain lakes in which Oligotrichida were the most abundant group followed by members in the Haptorida, Prostomatida (more species especially during limnophase or low-water phase), Hymenostomatida, and Scuticociliatida (Pauleto et al., 2009). Members of the order Prostomatida and Oligotrichida are common to pelagic habitats and were dominant also in over 50 German lakes (Pfister et al., 2002). The filter-feeding Oligotrichida frequently are the most diverse of the pelagic water ciliates (Müller et al., 1991; Song, 2000; Mieczan, 2007; Pauleto et al., 2009), while Hymenostomatida and Scuticociliatida are omnivores and detritivores (Scherwass et al., 2005; Pauleto et al., 2009) and can be important components of ciliate community in shallow lakes of floodplain systems (Pauleto et al., 2009).

The zooplankton community was similar between the lakes; however, a second, autumn abundance peak was evident in TL in addition to a spring peak common to both lakes. Of the zooplankton found in floodplain environments, rotifers typically reach the highest densities (e.g., Hardy et al., 1984; Bozelli, 1994), especially during low-water stages (Baranyi et al., 2002). *Polyarthra*, and more notably *Synchaeta*, have been associated with autumn rotifer abundance first documented in Illinois River floodplain lakes in the Emiquon area circa 1894 by Hempel (1898). *Polyarthra vulgaris* is a permanent inhabitant of all types of freshwaters reaching maximum densities in summer and preferring flagellates to algae for food (Sládeček, et al., 1958; Gilbert & Bogdan, 1981). In contrast, *Keratella* was evident in TL throughout the sampling period. The most abundant rotifers, especially in TL, were in the genus *Keratella*, and specifically, *K. cochlearis*, one of the most common planktonic species in temperate region standing and slowly running waters (Sládeček, 1983). It has been found in large densities ($3–9 \times 10^3$ ind./l) during the growing season (May–September) in Europe (Sládeček et al., 1958; Bartoš, 1959). It should be noted that for a positive identification a chitinous lorica with a living rotifer inside is required for *Keratella* as well as for the *Brachionus* and other loricates.

A microcrustacean bloom occurred in spring through early summer (April 14–June 11/July 8), likely imposing predation pressure on lower trophic levels (e.g., Šimek et al., 1995; Gilbert and Jack, 1993; Adrian & Schneider-Olt, 1999). Looking at the ratio of copepods to cladocerans, LC had copepod dominance in the spring and fall, while there is about equal abundance of both groups in the summer in both lakes. Plankton cladocerans and calanoid copepods are filter feeders, while cyclopoid copepods are, in general, omnivores that collect their food items. It is possible, as well, that autumn-blooming *Synchaeta* was preyed upon by *Daphnia* (Gilbert, 1988) in TL. In general, 2–10 times more cladocerans (genera *Chydorus*, *Diaphanosoma*, and *Bosmina*) were found per volume of pelagic TL water in the spring and fall than were found in LC. An impressive number of immature microcrustaceans (nauplii of the cyclopoida followed by copepodites of the cyclopoida) were evident in TL for both zooplankton peaks. Occurrence of a fall bloom of immature forms may be due to (1) the autumn rain events or (2) decadent macrophytes, one or both that may provide a nutrient or DOC pulse to the lake and/or a secondary "bloom" of green algae in TL.

Framing the interactions of the microorganism communities studied here within the context of the microbial loop, it appears that consistent numbers and diversity of ciliates in the reference and newly restored lakes may indicate emergent stability in the food web of TL as an early response to restoration. Ciliate numbers are likely supported from the bottom up by the algae, and to some extent by bacteria (e.g., Lischke et al., 2016), while competition with rotifers (e.g., Weisse & Frahm, 2002) and microcrustacean predation on ciliates (Kalinowska et al., 2015) may have imposed a top-down effect. For example, in this study there was a clear increase in ciliate abundance in the summer in both lakes when zooplankton abundances were lower. An explanation for the abundance of ciliates in both lakes may be a result of a middle-out effect (Li et al., 2016; Garvey & Whiles, 2017) among

the microorganism communities. DeVries and Stein (1992) explained that disturbances, such as increased organic input, can enhance the importance of microbial components of the planktonic food web and induce a middle-out effect of filter-feeding fish: in their example, gizzard shad (note, not a species stocked in 2007 or 2008), zooplankton, and algae (DeVries & Stein, 1992).

Yet, the microorganisms in this study were not studied in isolation. The influence of higher-order predators (i.e., planktivorous fish; Karus et al., 2014; Özen et al., 2014) and the effect of macrophyte growth (in TL more than LC), as well as other factors, likely influenced the microbial community interactions. Some explanations for factors influencing the zooplankton–ciliate link are more obvious than others. One of our group (Velho, unpublished data) found that when a predator (i.e., planktivorous fish) controlled the zooplankton abundance, ciliates became more abundant. At the Emiquon Preserve in TL, zooplankton abundance was most likely influenced by the presence of edible algae and planktivorous fish, and of the latter, the visual predators being influenced by shifts in water clarity. Although dependent on fish size, centrarchid fish may effectively use zooplankton as a food source (e.g., Mills & Schiavone, 1982), and thus zooplankton predation in TL was likely profound. Of the over 30 species stocked from 2007 to 2010, over a million largemouth bass (*Micropterus salmoides*) fry were stocked in spring 2007 alone (VanMiddlesworth et al., 2016). Catch per unit effort from late 2007 and in 2008 showed that bluegill (*Lepomis macrochirus*) and pumpkinseed (*L. gibbosus*) went from 19 individuals to 4,456 and 5 to 1,545, respectively, with the bluegill maintaining their number in 2009, while the pumpkinseed diminished by about 50% in 2009 (VanMiddlesworth et al., 2016).

While our report describes microorganism abundance and composition at the initial, critical time in lake restoration, it is only part of a larger story. There are many reasons why the microorganisms of TL should be different from LC. It cannot be assumed that the microbial ecology of the two lakes will ever be indistinguishable nor will ever resemble historical descriptions. The communities from the two lakes in the study, as any two lakes, probably never were identical, even pre-disturbance (draining in the 1920s). Although certain patterns may be robust and seen in both lakes, such as seasonal succession of microbial groups, it was thought that even though water returned to TL, it may take considerable time for ecological structure and function to stabilize, so a great deal of variability would be seen. Understanding the recovery of planktonic microbial communities in an aquatic system that has changed from a dry lake bed used for agriculture allows assessment of ecological resilience of floodplain lakes.

Conclusion

The objectives of this study were to describe and contrast the microbial community composition and seasonal dynamics in two contrasting floodplain lakes with very different roles in the large river system of the Illinois River. Although the initial disturbance of water drainage was similar to both lakes, TL incurred this disturbance for 50 years longer than LC, and was also isolated from the influence of river flood pulse microorganism inoculations. The disturbance imposed by floodplain drainage can create direct effects (e.g., loss of water, habitat, and river connectivity) and also be indirect (e.g., change in water quality, loss of food sources) (Lake, 2003). As a result, TL recovery may have had an initial bottleneck effect in that repopulation occurred through the vitalization of resting stages of microbial species adapted to drought, as well as reliance on dispersal mechanisms (e.g., wind, waterfowl migration). Even though LC received Illinois River water on three occasions during the study period, the lake maintained a more constant level of transparency and nutrient concentration than did TL. The transition from dry agricultural field to aquatic habitat in the first year of restoration of TL had a greater effect than seasonal flooding, due to release of phosphorus from the soil and the re-colonization of a vast volume of water that was simultaneously creating microhabitats and reconnecting trophic links.

It is clear from visualizing bacteria, phytoplankton, protists, and zooplankton community composition that differences existed in both lakes and changes occurred seasonally. With reference to agriculture and drought recovery in TL, plankton succession is likely more determined by past phytoplankton and zooplankton species residing within the system and less to new colonists (Michaloudi et al., 2012). In particular, the plankton may have come from soil/sediment or spread from extant aquatic habitat that survived the initial

drainage and persisted on the property in the form of drainage canals cut into the fields to facilitate pumping of water. A great diversity of green algae was seen in both lakes, with some shared species. It may be possible that the reduced numbers of green algae in early summer in TL represents grazing by rotifers and microcrustaceans that produced a fall bloom in those microconsumers. From a microbial perspective, newly restored TL was an unstable and rapidly changing environment in its transition from eight decades of agriculture to an aquatic ecosystem with initially simple ecological structure and function.

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