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Reduced Phytoplankton and Zooplankton Diversity Associated with Increased Cyanobacteria in Lake Champlain, USA

*Katelyn A. Bockwoldt[1,5], Emily R. Nodine[2,6], Timothy B. Mihuc[3], Angela D. Shambaugh[4], and Jason D. Stockwell[2]

[1]*Department of Environmental Studies, Roanoke College, Salem, VA, USA*
[2]*Rubenstein Ecosystem Science Laboratory, University of Vermont, Burlington, VT, USA*
[3]*Lake Champlain Research Institute, SUNY Plattsburgh, NY, USA*
[4]*Lakes and Ponds Program, Vermont Department of Environmental Conservation, Montpelier, VT, USA*
[5]*Currently at School of Freshwater Sciences, University of Wisconsin Milwaukee, Milwaukee, WI, USA*
[6]*Currently at Department of Environmental Studies, Rollins College, Winter Park, FL, USA*
**Corresponding Author*

Abstract: Anthropogenic inputs of nutrients threaten water quality around the world, causing eutrophication and altering phytoplankton communities. In freshwater systems, certain physiochemical conditions, including high TP, low TN:TP, and warm temperatures, can lead to problematic cyanobacteria blooms. Cyanobacteria can decrease phytoplankton diversity and phytoplankton diversity has been positively linked to zooplankton diversity, suggesting that cyanobacteria may have indirect negative effects on zooplankton diversity. Using monitoring data from Lake Champlain, we tested three hypotheses: (1) cyanobacteria density and phytoplankton diversity are inversely related; (2) phytoplankton diversity and zooplankton diversity are positively related; and by extension (3) cyanobacteria density and zooplankton diversity are inversely related. Relationships were investigated separately at shallow (4-15 m) and deep (25-100 m) sites using several diversity metrics. At deep sites, cyanobacteria density was only related (positively) to zooplankton Shannon diversity. At shallow sites, all three hypotheses were supported by three of four diversity metrics; low phytoplankton richness appears to be the link between high cyanobacteria density and low zooplankton diversity. Our results suggest that cyanobacteria may indirectly reduce zooplankton diversity by decreasing resource heterogeneity, although our results based on observational data were also consistent with well-known direct pathways. Because low biodiversity can alter ecosystem processes and impair functioning, our results suggest that shallow systems may be more responsive to global change than deeper systems.

Keywords: *eutrophication, climate change, biodiversity, ecosystem functioning*

Climate change and anthropogenic inputs of nutrients pose threats to water quality around the world (Smith et al. 1999; Michalak 2016). Nitrogen and phosphorus are typically the limiting nutrients in aquatic systems; changes in their concentrations and nutrient ratios result in changes in system productivity and phytoplankton community composition (Rhee and Gotham 1980; Smith 1983; Hecky and Kilham 1988). In freshwater systems, increased phosphorus inputs, warm temperatures, and water column stability can lead to problematic cyanobacteria blooms (Schindler 1977; Brookes and Carey 2011). While nutrient and temperature conditions are the most commonly recognized drivers of cyanobacteria growth, several other physiochemical conditions (e.g., low CO_2 supply, light limitation, etc.) have also been proposed as significant contributors to development of cyanobacteria blooms in freshwater lakes (Havens et al. 2003; Poste et al. 2013). While much debate currently exists on the primary causes of cyanobacteria blooms, the negative consequences of their presence are difficult to dispute. Intense

blooms often release harmful toxins, cause fish kills, and decrease recreational value (Paerl et al. 2001; Dodds et al. 2009). Cyanobacteria blooms are expected to intensify in the future with warmer temperatures from climate change and increased nutrient runoff resulting from intensified land use associated with population growth (Paerl and Huisman 2008; O'Neil et al. 2012). As a result, the need to fully understand the causes and effects of cyanobacteria blooms in freshwater systems has never been greater (Michalak 2016).

In recent decades, the relationship between biodiversity and ecosystem functioning has received significant attention due to the reduction of local and global biodiversity caused by anthropogenic activities (Loreau et al. 2001). Observational and experimental studies have revealed the importance of species richness and evenness in controlling ecosystem processes (i.e., productivity, nutrient cycling) and ecosystem functioning (i.e., invasibility, resilience to environmental fluctuations; Loreau et al. 2001; Hillebrand et al. 2008). In eutrophic systems, however, the community response of the lower food web to global change is not entirely clear due to a limited number of studies investigating biodiversity relationships both within (Ptacnik et al. 2008) and across trophic levels (Filstrup et al. 2014). To better develop this body of knowledge, particular emphasis must be placed on further understanding the effects of cyanobacteria on phytoplankton and zooplankton community diversity. Such efforts may provide insight into how ecosystem processes, functioning, and services may change in the future with increased cyanobacteria blooms (Cardinale et al. 2012).

Cyanobacteria dominance under high nutrient concentrations is associated with lower biomass of phytoplankton taxa and lower community diversity (Watson et al. 1997; Bouvy et al. 2001). Altered phytoplankton community composition has the potential to affect higher trophic levels by changing the quantity, quality, and diversity of food resources available for consumers (Carpenter et al. 1985; Tilman and Kareiva 1997; Brett et al. 2006). For example, the resource heterogeneity hypothesis states that species should have a positive response to variation in their resources (Connell 1978; Cardinale et al. 2012). Therefore, zooplankton abundance and diversity should be highest at high levels of phytoplankton diversity because resource variation provides opportunities for niche partitioning and reduces resource limitation (Connell 1978; Tilman and Kareiva 1997). Zooplankton and phytoplankton diversity have been shown to be positively correlated by some metrics (i.e., phytoplankton richness, Shannon diversity), adding further support for this hypothesis in freshwater systems (Soininen and Luoto 2012; Striebel et al. 2012). Conversely, low phytoplankton diversity should result in low zooplankton diversity due to resource limitation and decreased niche partitioning (Connell 1978; Tilman and Kareiva 1997).

Taken together, theory and observations suggest that because cyanobacteria can alter phytoplankton communities and decrease taxonomic diversity (Watson et al. 1997; Bouvy et al. 2001), cyanobacteria may have indirect effects on zooplankton diversity. However, studies examining the relationships between cyanobacteria and zooplankton have typically focused on the direct effects of cyanobacteria nutrition, toxicity, or morphology on zooplankton individuals and species (Ger et al. 2016). Cyanobacteria generally are a nutritionally poor, toxic, or difficult to graze food source for zooplankton, and have been found to decrease zooplankton growth, reproduction, and abundance when dominant (Lampert 1987; Brett et al. 2000; Ger et al. 2016). Less attention has been paid to the effects of cyanobacteria density on zooplankton taxonomic diversity. Bouvy et al. (2001) found an increase in zooplankton diversity (Shannon index) during and after a single cyanobacteria bloom, while Leonard and Pearl (2005) found low zooplankton diversity during periods of high cyanobacteria density. Given these contradicting results and the expected increase of cyanobacteria blooms with climate change and intensified land use, a more complete understanding of the impacts of cyanobacteria on zooplankton diversity is needed to elucidate how cyanobacteria could potentially affect intermediate trophic levels and biodiversity (Loreau et al. 2001).

In this study, we tested three linked hypotheses: (1) cyanobacteria density and phytoplankton diversity are inversely related; (2) phytoplankton diversity and zooplankton diversity are positively

related; and by extension (3) cyanobacteria density and zooplankton diversity are inversely related. The hypotheses were tested using monitoring data from Lake Champlain, a highly heterogeneous, large-lake system with habitats ranging from shallow eutrophic bays to deep oligotrophic/mesotrophic basins (Facey et al. 2012). The frequency and intensity of cyanobacteria blooms in Lake Champlain have been increasing (Smeltzer et al. 2012), providing an excellent system in which to test our hypotheses. Our goal is to expand the understanding of biodiversity in eutrophic and mesotrophic systems by testing a conceptual model that indirectly connects cyanobacteria density to zooplankton diversity (Figure 1).

Methods

Lake Champlain is a large, temperate lake with a surface area of 1,127 km^2, mean and maximum depths of 20 and 122 m, and a drainage basin of 21,326 km^2 (Facey et al. 2012). The lake is divided into five major basins: South Lake, Main Lake, Northeast Arm, Malletts Bay, and Missisquoi Bay. South Lake and Missisquoi Bay are shallow, warm, and eutrophic and the Main Lake, Malletts Bay, and Northeast Arm are mesotrophic to oligotrophic (Table 1; Figure 2; Facey et al. 2012). Existing phytoplankton and zooplankton data from the Lake Champlain Long-Term Monitoring Program (LTMP; http://dec.vermont.gov/watershed/lakes-ponds/monitor/lake-champlain) were used to test hypotheses. The LTMP monitors 15 sites distributed across all five basins, encompassing the physical, chemical, and biological heterogeneity of Lake Champlain (Figure 2; Table 1). Phytoplankton data were available from 2006 to 2014, and zooplankton data were available from 2006 to 2010. In 2006, zooplankton data were only available from five sites during July.

Phytoplankton and zooplankton sampling protocols are outlined elsewhere (Vermont DEC and New York State DEC 2015). Briefly, sites were sampled approximately twice per month from May to October each year. Phytoplankton samples were collected during the day using a 13-cm diameter, 63-µm mesh net towed vertically from twice the Secchi depth to surface. Samples were preserved in 1% Lugol's solution and species counts were completed by the Vermont Department of Environmental Conservation (Montpelier, VT) using settling chambers or Sedgewick Rafter cells and an Olympus CKX41 inverted microscope. Phytoplankton densities were calculated as the number of cells/L. Zooplankton were sampled during the day with a 30-cm diameter, 153-µm mesh net towed vertically from just above the sediment to surface. Samples were narcotized with carbonated water and preserved in formalin. Species counts were completed by the Lake Champlain Research Institute (Plattsburgh, NY) using Sedgewick Rafter cells and a Leica DM IL inverted microscope. Zooplankton densities were calculated as the number of individuals/m^3.

For phytoplankton and zooplankton, individuals were delineated to the species level whenever

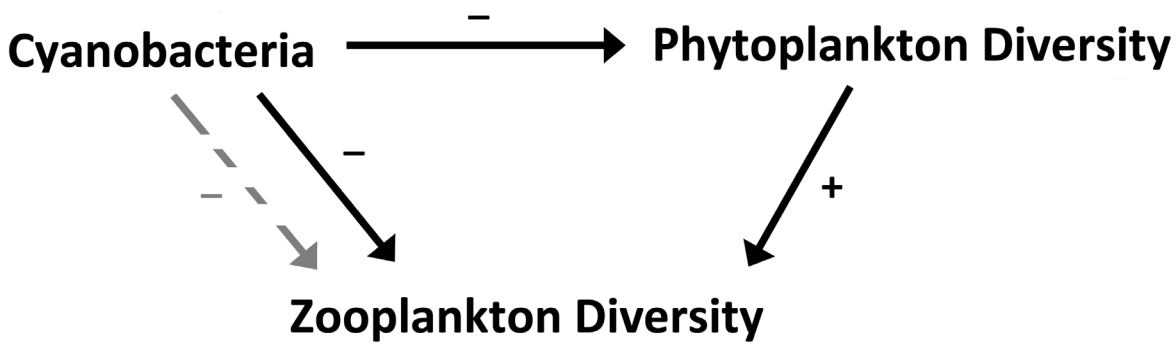

Figure 1. Established and hypothesized relationships among cyanobacteria, phytoplankton diversity, and zooplankton diversity. Solid lines represent observed direct relationships and dashed line represents hypothesized indirect relationships.

Table 1. Characteristics of 15 Lake Champlain sampling sites used in the long-term monitoring program (LTMP). Sites numbers are LTMP station numbers. Total phosphorus (TP) values are averages for each site from 2006 to 2010.

Site #	Site Name	Basin	TP (µg/L)[1]	Trophic Status[1]	Depth (m)	Latitude	Longitude
50	Missisquoi Bay	Missisquoi Bay	49.18	Eutrophic	4	45.013	-73.174
51	Missisquoi Bay Central	Missisquoi Bay	52.18	Eutrophic	5	45.042	-73.130
2	South Lake B	South Lake	49.15	Eutrophic	5	43.715	-73.383
46	Isle LaMotte (Rouses Point)	Main Lake	16.54	Mesotrophic	7	44.948	-73.340
40	St. Albans Bay	Northeast Arm	27.89	Eutrophic	7	44.785	-73.162
4	South Lake A	South Lake	34.27	Eutrophic	10	43.952	-73.408
33	Cumberland Bay	Main Lake	13.83	Mesotrophic	11	44.701	-73.418
21	Burlington Bay	Main Lake	13.62	Mesotrophic	15	44.475	-73.232
16	Shelburne Bay	Main Lake	13.14	Mesotrophic	25	44.426	-73.232
25	Malletts Bay	Mallets Bay	11.85	Oligotrophic	32	44.582	-73.281
7	Port Henry Segment	Main Lake	16.44	Mesotrophic	50	44.126	-73.413
34	Northeast Arm	Northeast Arm	20.89	Mesotrophic	50	44.708	-73.227
36	Isle LaMotte (Grand Isle)	Main Lake	12.62	Mesotrophic	50	44.756	-73.355
9	Otter Creek Segment	Main Lake	17.23	Mesotrophic	97	44.242	-73.329
19	Main Lake	Main Lake	13.32	Mesotrophic	100	44.471	-73.299

[1]Lake Champlain Basin Program data

possible (Tables S1 and S2). In cases when species could not be resolved, identification was to genus level. Genera level taxa were counted as a single taxon in diversity calculations. Diversity indices based on both species and genera level data are not ideal for diversity studies. Certain genera have species that are hard to resolve, such that the diversity of these taxa will be underrepresented compared to genera with species easier to resolve. Using genera taxa in our study, however, is consistent with the methods of other large-lake studies because many phytoplankton and zooplankton genera are difficult to delineate to species (Filstrup et al. 2014; Reavie et al. 2014; Burgess et al. 2015).

Four common measures of diversity were

used because no single metric can perfectly characterize community diversity (Hillebrand et al. 2008; Morris et al. 2014). Diversity metrics were calculated using the 'vegan' package in R (Oksanen et al. 2013):

(1) Species richness: S

(2) Shannon index: $H' = -\sum_{i=1}^{S} p_i \log_{10} p_i$

(3) Simpson index: $D' = 1-\sum_{i=1}^{S} p_i^2$

(4) Evenness: $H'/log(S)$

where S is the total number of species (or genera) and p_i is the proportion of species i based on cell and individual densities for phytoplankton and zooplankton, respectively. Briefly, D' measures the probability that two random individuals will be from different species; H' is an abstract index measuring the uncertainty of unknown individual's identity in systems of varying diversity; and evenness is a measure of the relative abundance of all species present (Morris et al. 2014).

Cyanobacteria density and phytoplankton diversity metrics were averaged for each site-year from 2006 to 2014. Cyanobacteria were included in all measures of phytoplankton diversity. Zooplankton diversity was averaged for each site and year from 2006 to 2010. Only data from July, August, and September were included in the analyses because these months encompassed the period of highest cyanobacteria density in Lake Champlain. Generalized linear models were used to test the relationships among $\log_{10}$-transformed cyanobacteria densities, phytoplankton diversity, and zooplankton diversity metrics. Each site-year was used as an observation and grouped by depth (shallow or deep with 25 m as the threshold; Table 1) for statistical tests. Sites were grouped in this manner due to expected differences resulting from the influence of basin characteristics on nutrient distributions (Smeltzer et al. 2012). Shallow sites had an average total phosphorus concentration of 32.08 µg/L during the study period, while deep sites had an average concentration of 15.07 µg/L (Table 1). Site classification in this manner allowed for the comparison of plankton diversity in generally eutrophic versus mesotrophic sites. All statistical analyses ($\alpha = 0.05$) were performed using R version 3.2.0 (R Core Development Team 2014).

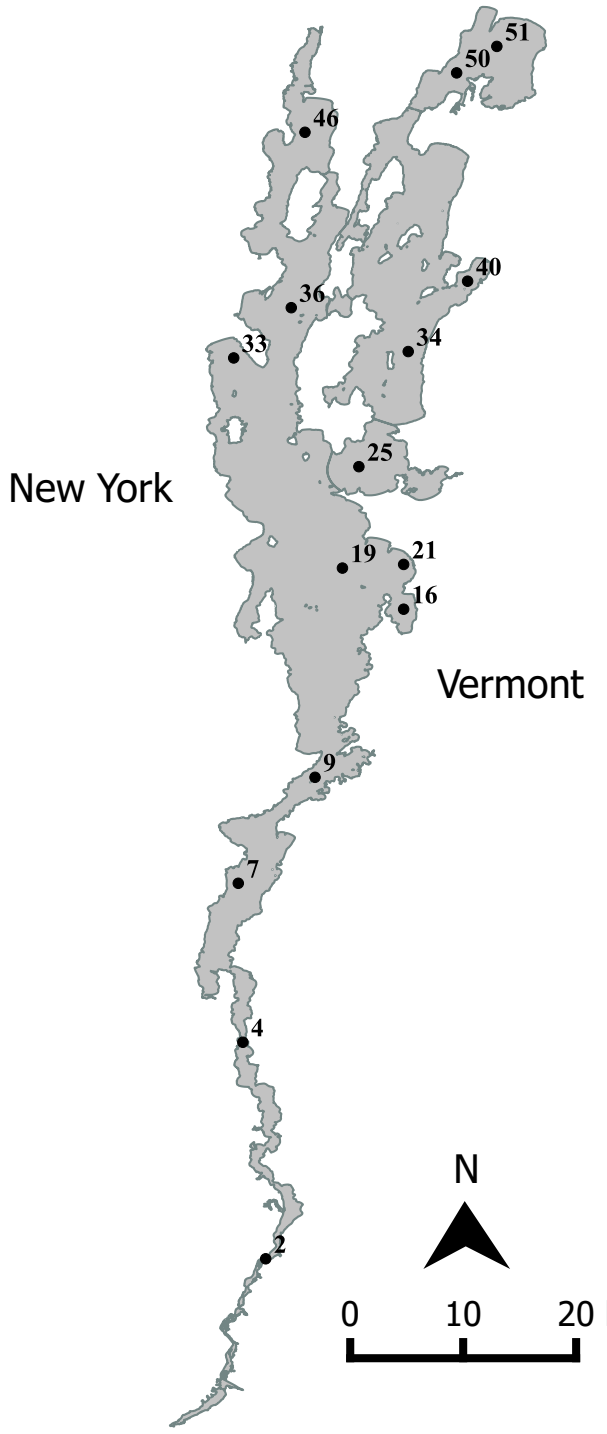

Figure 2. Locations of the 15 sampling sites used in the Lake Champlain Long-Term Monitoring Program. See Table 1 for specific site information.

Results

Relationships among cyanobacteria density, phytoplankton diversity, and zooplankton diversity metrics were generally stronger at shallow sites and rarely significant at deep sites. Cyanobacteria density was inversely related to phytoplankton diversity at shallow sites, but variable across the four diversity metrics (Figure 3). Phytoplankton richness, *H′*, and *D′* each showed a negative relationship with cyanobacteria density at shallow sites (all $p < 0.01$; Figures 3a, 3c, 3d); phytoplankton evenness was not significantly correlated with cyanobacteria density (Figure 3b). At deep sites, no significant relationships were observed between cyanobacteria density and any measure of phytoplankton diversity (Figures 3a-d).

Phytoplankton richness was the only phytoplankton diversity metric that showed significant relationships with zooplankton diversity metrics (Figure 4); phytoplankton evenness, *H′*, and *D′* were not significantly correlated with zooplankton diversity metrics ($p \geq 0.18$ for each; data not shown). The relationship between phytoplankton richness and zooplankton diversity was significant at shallow sites, but insignificant at deep sites ($p \geq 0.34$ for each). At shallow sites, zooplankton evenness, H′, and D′ were positively related to phytoplankton richness ($p < 0.05$; Figures 4b-d).

Relationships between cyanobacteria density and zooplankton diversity metrics were also strongest at shallow sites by most metrics, but revealed one significant relationship at deep sites (Figure 5). Zooplankton evenness, *H′*, and *D′* were negatively

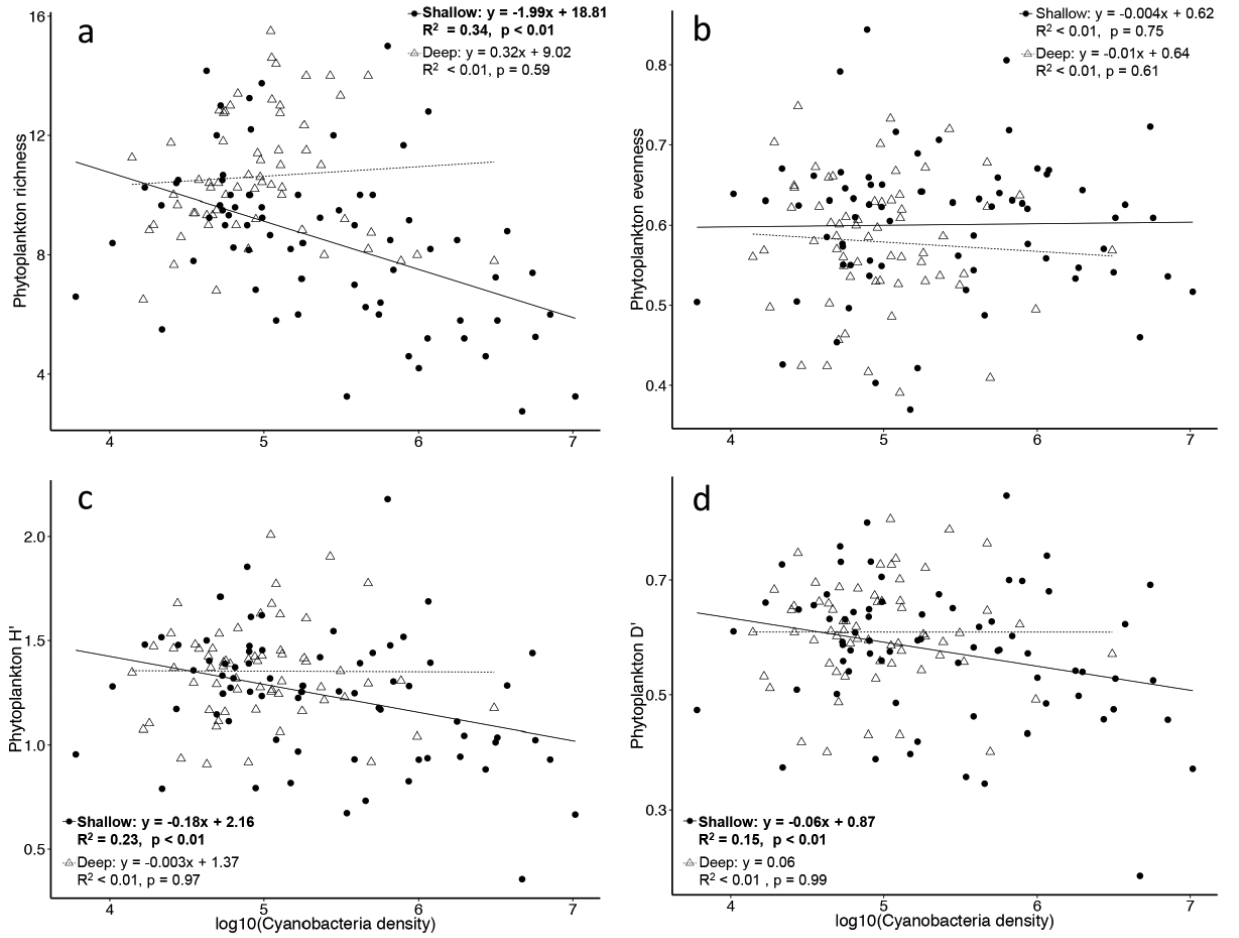

Figure 3. Relationships between $\log_{10}$-transformed cyanobacteria density and (a) phytoplankton richness, (b) phytoplankton evenness, (c) Shannon diversity, and (d) Simpson diversity for deep and shallow sites in Lake Champlain 2006-2014. Significant relationships bolded.

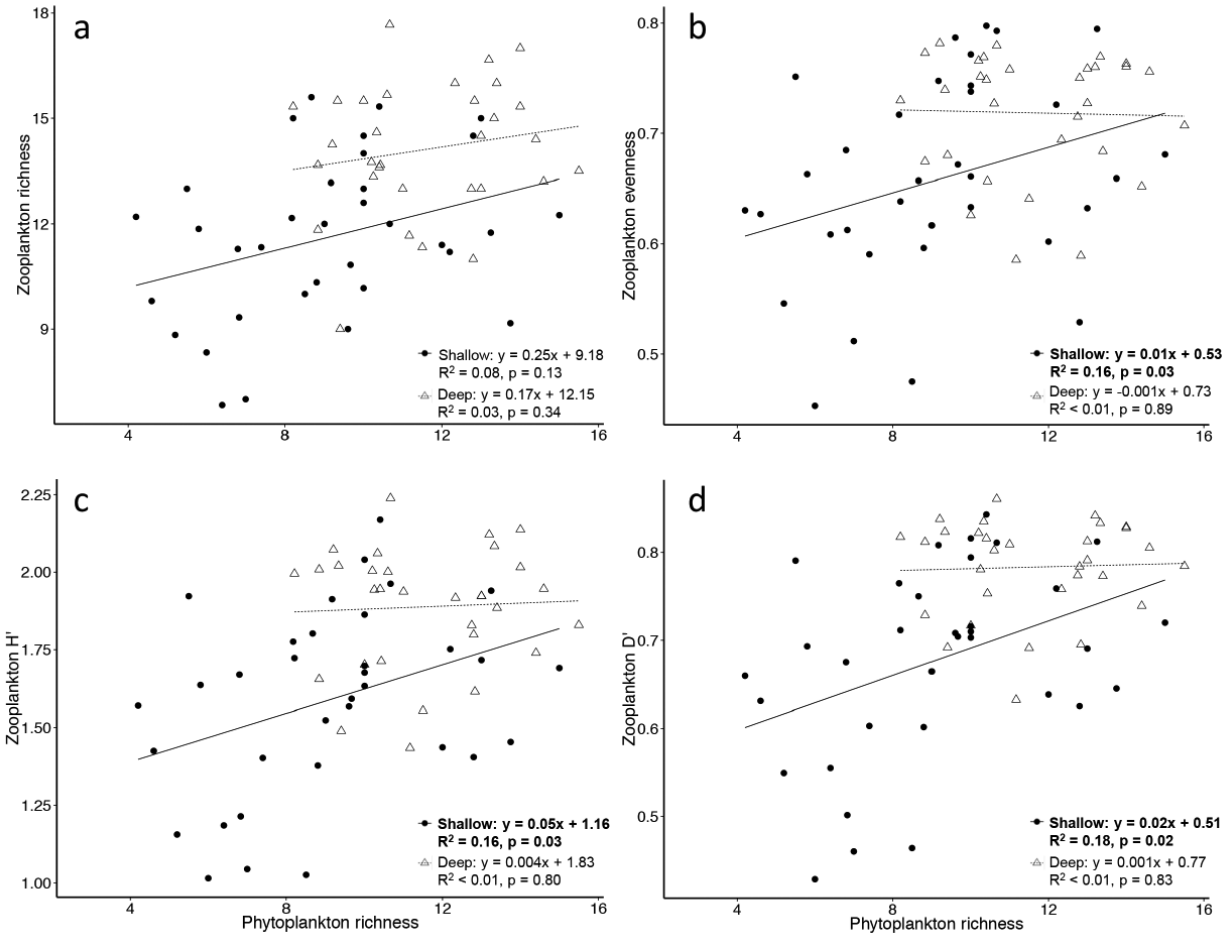

Figure 4. Relationships between phytoplankton richness and (a) zooplankton richness, (b) zooplankton evenness, (c) Shannon index, and (d) Simpson index for deep and shallow sites in Lake Champlain 2006-2010. Significant relationships bolded.

related to cyanobacteria density at shallow sites (all $p < 0.01$; Figures 5b-d); zooplankton richness was not significantly correlated with cyanobacteria density (Figure 5a). Interestingly, while the relationships with all metrics at shallow sites were negative as predicted, zooplankton *H′* was positively related to cyanobacteria density at deep sites ($p < 0.05$; Figure 5c). No other significant relationships between zooplankton diversity and cyanobacteria density were found at deep sites, although generally positive relationships were observed with each metric (Figures 5a, b, and d).

Discussion

Research on the relationships between cyanobacteria density and zooplankton has typically focused on the direct effects of cyanobacteria on zooplankton grazing and growth (e.g., Lampert 1987; Brett et al. 2000; Paerl et al. 2001). To our knowledge, our study is the first to investigate potential indirect relationships between cyanobacteria density and zooplankton diversity through phytoplankton diversity. Across shallow sites in Lake Champlain, we found negative relationships between cyanobacteria density and both phytoplankton and zooplankton diversity metrics, and positive relationships between phytoplankton and zooplankton diversity metrics, providing support for our conceptual model of indirect effects of cyanobacteria on zooplankton diversity (Figure 1). In contrast, our model was not supported at deep sites, as no relationships were observed among most of the comparisons.

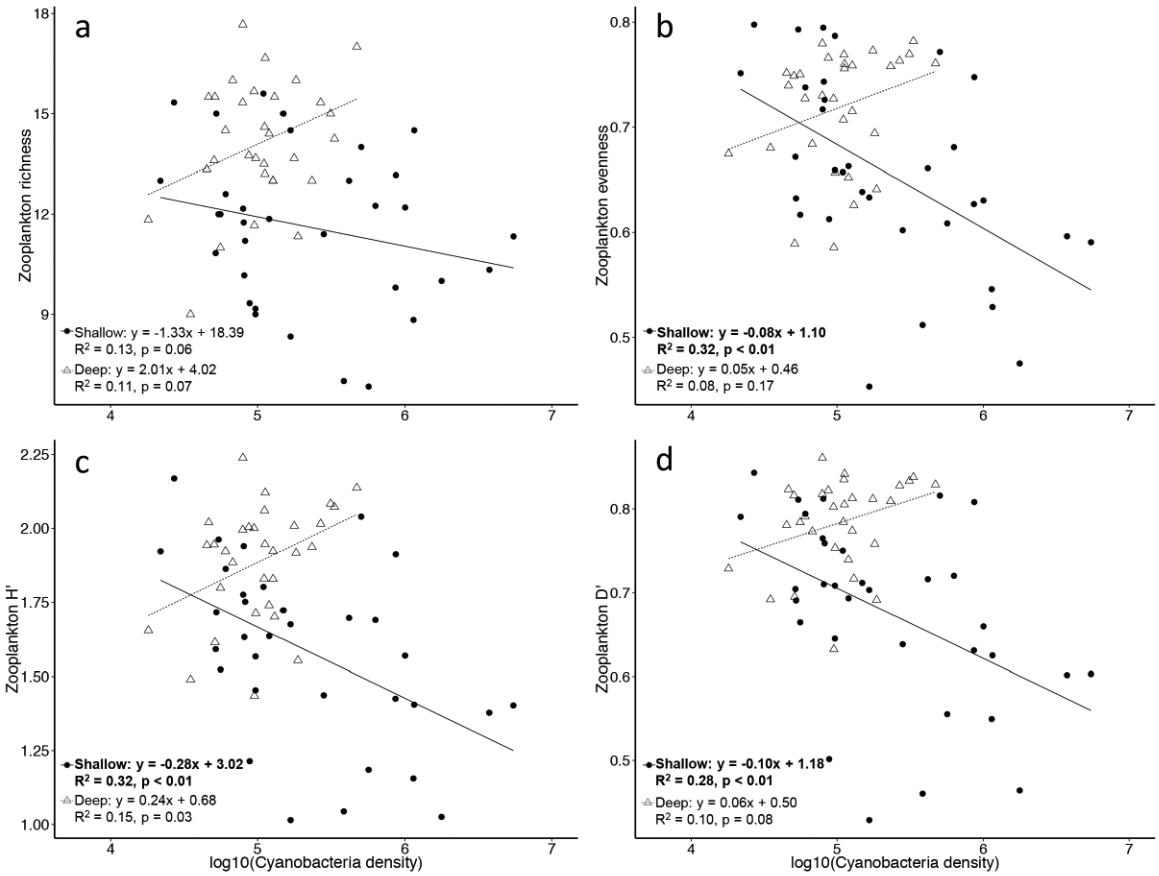

Figure 5. Relationships between cyanobacteria density and (a) zooplankton richness, (b) zooplankton evenness, (c) Shannon index, and (d) Simpson index for deep and shallow sites in Lake Champlain 2006-2010. Significant relationships bolded.

The positive relationships between phytoplankton richness and zooplankton diversity metrics at shallow sites are consistent with the resource heterogeneity hypothesis (Figure 1; Connell 1978; Tilman and Kareiva 1997). Striebel et al. (2012) also found an increase in zooplankton *H′* with phytoplankton richness, and inferred that phytoplankton richness corresponded to an increase in phytoplankton cell shapes, sizes, structures, and nutritional value that benefited the zooplankton community. The reduced phytoplankton richness we observed with increased cyanobacteria density at shallow sites suggests cyanobacteria may indirectly reduce zooplankton diversity by reducing resource heterogeneity (i.e., phytoplankton richness). While we did not assess specific taxonomic relationships in light of the resource heterogeneity hypothesis, high phytoplankton richness has a greater probability of representing higher phenotypic diversity in the phytoplankton community (Loreau et al. 2001). Thus, phytoplankton richness may be an important connection between cyanobacteria and zooplankton diversity.

Unexpectedly, phytoplankton evenness was not related to cyanobacteria density in Lake Champlain (Figure 3b). Phytoplankton evenness is expected to decrease under eutrophic conditions when the relative abundance of cyanobacteria increases with increasing phosphorus concentrations (Watson et al. 1997; Downing et al. 2001). The absence of such a relationship in our data may be a result of (1) reliance on samples from a 63-µm mesh net which selects against smaller phytoplankton taxa, or (2) the limited scope of our data set.

Filstrup et al. (2014) found lower phytoplankton evenness with high cyanobacteria densities using a 9-year, 131-lake data set. Our phytoplankton analyses were limited to a single temperate lake sampled over nine years. The analysis of a single lake or filtered samples could have limited the spatial or taxonomic ranges under which relationships between phytoplankton evenness and cyanobacteria density could be detected.

Our conceptual model (Figure 1) was not supported at deep sites, where few relationships were observed among the comparisons. The overall lack of relationships between cyanobacteria and phytoplankton and zooplankton diversity metrics at deep sites is perhaps not surprising. The deeper regions of Lake Champlain may be less suitable for cyanobacteria dominance than the shallow, protected sites (e.g., lower P concentrations, Table 1). Cyanobacteria densities were lower at deep sites compared to shallow sites (Figures 3, 5), consistent with general theory and observations that deeper lakes are less susceptible to cyanobacteria blooms due to less favorable nutrient and physical conditions for cyanobacteria (Finnendegg 1966; Ghadouani et al. 2003; Nixdorf et al. 2003). The one significant relationship at deep sites between cyanobacteria density and zooplankton H', and the general (but insignificant) patterns of positive relationships between cyanobacteria and the other zooplankton metrics, were contrary to expectations and our observations at shallow sites (Figure 5). Zooplankton growth can be enhanced by mixed diets of cyanobacteria and high-quality phytoplankton (e.g., chrysophytes, chlorophytes) compared to unmixed diets (Lundstedt and Brett 1991; DeMott 1998; Alva-Martinez et al. 2007). Thus, regions of lakes where cyanobacteria are present but do not reach dominance may enhance zooplankton diversity by contributing to resource heterogeneity, although further investigations are needed. Overall, the differences in the relationships we observed between deep and shallow sites suggest a tighter coupling of cyanobacteria dynamics to primary consumers in shallow systems (Ghadouani et al. 2003).

Arguably, attribution of cyanobacteria impacts on zooplankton diversity as indirect or direct is a tenuous proposition when based on observational data alone. Our inference of indirect effects is also complicated by the complexity of cyanobacteria-zooplankton relationships. Cyanobacteria can negatively affect zooplankton in many direct ways, including low nutritional quality (i.e., lack of essential fatty acids and sterols), harmful metabolites (i.e., cyanotoxins), and defensive morphology (Ger et al. 2016). Such direct effects of cyanobacteria on zooplankton could plausibly lead to the patterns we observed. Experiments are needed to draw conclusions about pathways. Nonetheless, the results of our observational study provide suggestive evidence of an additional channel through which cyanobacteria may affect zooplankton diversity (i.e., reduced resource heterogeneity).

Our analyses relied on phytoplankton and cyanobacteria samples collected from a long-term monitoring program using a 63-µm mesh net. Thus, we cannot fully account for phytoplankton and cyanobacteria community changes and their relationships because the net selects against picoplankton, nanoplankton, and some microplankton. If phytoplankton community responses to cyanobacteria blooms include shifts to smaller species, then our diversity metrics would be biased. Despite such limitations, the data were standardized across all sampling events and thus represent valid comparisons of the representative taxa sampled by the net. That we did observe changes in diversity relationships with changes in cyanobacteria density points to important food web changes as a result of increasing cyanobacteria density, albeit within limited size ranges of the communities sampled. Any retrospective analyses of long-term monitoring data, for which the data were not originally intended, can suffer from similar limitations as our study, but do not necessarily preclude the usefulness of such analyses.

Many studies have illustrated the negative effects of decreased biodiversity on ecosystem functioning, health, and services (Loreau et al. 2001; Hillebrand et al. 2008; Cardinale et al. 2012). The combined decreases in phytoplankton and zooplankton diversity associated with cyanobacteria blooms observed in our study suggest potential for declines in shallow, freshwater ecosystem functioning, given the

expected increase in cyanobacteria blooms with climate change (Paerl and Huisman 2008). Shallow, nearshore ecosystems will likely experience greater changes in biodiversity and ecosystem functioning than deep, pelagic communities because they will be more strongly affected by global change (e.g., higher direct nutrient inputs resulting from increased land use from population growth, faster warming water temperatures due to climate change; Mooij et al. 2007). As biodiversity and ecosystem health are valued intrinsically and economically, collaboration between scientists and policy makers to develop ways to reduce the impacts of anthropogenic activities on freshwater systems is needed.

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Author Bio and Contact Information

Katelyn A. Bockwoldt received a Bachelor of Science in Environmental Studies and Biology from Roanoke College in December 2016. As an undergraduate, she served as a research assistant in the Biology Department, and also participated in the 2015 REU program at UVM's Rubenstein Ecosystem Science Laboratory. Katelyn is currently pursuing a MS in Freshwater Sciences at the University of Wisconsin-Milwaukee. Her current research is quantifying lower food web production and trophic efficiency in post-dreissenid Lake Michigan. She may be reached at bockwol2@uwm.edu or School of Freshwater Sciences, 600 E Greenfield Ave., University of Wisconsin Milwaukee, Milwaukee, WI 53204.

Emily R. Nodine served as a mentor for the 2015 REU program as a post-doctoral associate at UVM's Rubenstein Ecosystem Science Laboratory. She is now an assistant professor in the Environmental Studies department at Rollins College, and may be contacted at enodine@rollins.edu or Department of Environmental Studies, 1000 Holt Avenue, Rollins College, Winter Park, FL 32789.

Timothy B. Mihuc may be reached at mihuctb@plattsburgh.edu or Lake Champlain Research Institute, 101 Broad Street, SUNY Plattsburgh, Plattsburgh, NY 12901 USA.

Angela D. Shambaugh may be reached at angela.shambaugh@vermont.gov or Lakes and Ponds Program, Vermont Department of Environmental Conservation, 1 National Life Drive, Main 2, Montpelier, VT 05620.

Jason D. Stockwell may be reached at jason.stockwell@uvm.edu or Rubenstein Ecosystem Science Laboratory, 3 College Street, University of Vermont, Burlington, VT 05401.

Supplemental Tables (S1-S2)

Table S1. Phytoplankton taxonomic data for the 15 Lake Champlain sampling sites. X indicates presence of taxon on at least one occasion from 2006 to 2014.

Taxon	Shallow Sites								Deep Sites						
	50	51	2	46	40	4	33	21	16	25	7	34	36	9	19
Asterionella formosa	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Asterionella spp.	X	X	X			X			X	X	X		X		X
Attheya spp.			X	X		X					X			X	
Aulocoseira granulata	X	X	X	X	X	X	X	X	X		X	X	X		X
Aulocoseira spp.	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Centrales spp.	X	X	X	X	X	X	X				X	X	X		
Cymatopleura spp.			X			X				X		X			
Cymbellaceae			X												
Diatoma spp.	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Fragilaria crotonensis	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Fragilaria spp.	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Gyrosigma spp.			X	X											
Pennales spp.	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Rhizosolenia spp.		X	X	X	X	X	X	X	X	X	X	X	X	X	X
Stephanodiscus spp.	X	X		X	X	X	X	X	X	X	X	X	X	X	X
Surirella spp.						X				X					
Synedra spp.	X								X	X					
Synedra ulna	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Tabellaria flocculosa	X	X	X	X						X			X		
Tabellaria spp.	X	X	X	X		X	X	X	X	X	X		X	X	X
Total Bacillariophyta	**14**	**14**	**17**	**15**	**11**	**16**	**12**	**11**	**13**	**15**	**14**	**12**	**14**	**11**	**12**

Table S1 (continued).

Taxon	Shallow Sites								Deep Sites							
	50	51	2	46	40	4	33	21	16	25	7	34	36	9	19	
Ankyra spp.													X			
Arthrodesmus spp.					X		X			X		X				
Botryococcus spp.					X	X	X	X								
Bulbochaete spp.					X		X	X	X		X	X	X	X	X	
Chaetophorales				X	X		X	X	X		X	X	X	X	X	
Closteriopsis spp.				X	X		X	X	X		X	X	X	X	X	
Closterium spp.	X															
Coelastrum microporum		X														
Cosmarium spp.															X	
Dictyosphaerium spp.	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	
Elakatothrix viridis										X						
Eudorina spp.	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	
Gloeocystis gigas							X									
Gloeocystis spp.	X	X		X	X		X			X		X				
Gonium spp.	X	X		X												
Kirchneriella spp.	X												X		X	
Micractinium pusillum			X		X				X		X			X	X	
Mougeotia spp.	X	X	X	X	X	X	X	X	X	X	X	X	X		X	
Nephrocytium spp.	X															

Table S1 (continued).

Taxon	Shallow Sites								Deep Sites						
	50	51	2	46	40	4	33	21	16	25	7	34	36	9	19
Oedogonium spp.				X	X		X	X	X	X	X	X	X	X	X
Oocystis spp.		X									X	X			
Pandorina morum	X		X			X	X			X	X				
Pediastrum boryanum					X			X						X	
Pediastrum duplex	X	X	X	X	X			X				X			X
Pediastrum simplex	X	X	X		X	X		X	X		X	X	X		X
Quadrigula spp.							X			X					
Scenedesmus quadricauda			X			X									
Schizochlamys spp.					X										
Schroederia spp.		X													
Sphaerocystis spp.	X				X			X	X	X	X				
Spirogyra spp.	X		X	X	X	X									
Spondylosium spp.												X			
Staurastrum spp.	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Staurodesmus spp.					X							X			
Stigeoclonium spp.							X								
Tetraspora lamellosa				X	X										X
Tetraspora spp.	X			X	X	X	X	X	X	X	X	X	X	X	X
Ulothrix spp.			X			X	X	X			X			X	
Volvox spp.			X	X		X	X		X						X
Total green algae	**15**	**11**	**12**	**14**	**21**	**12**	**18**	**15**	**13**	**12**	**15**	**16**	**12**	**11**	**16**

Table S1 (continued).

Taxon	Shallow Sites								Deep Sites						
	50	51	2	46	40	4	33	21	16	25	7	34	36	9	19
Dinobryon bavaricum	X	X	X	X		X	X			X	X			X	
Dinobryon cylindricum			X	X	X	X		X		X	X	X	X	X	
Dinobryon divergens	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Dinobryon sertularia	X		X	X		X			X	X	X			X	
Dinobryon sociale	X	X	X			X	X						X		
Dinobryon spp.	X	X	X	X		X		X	X	X	X		X	X	X
Mallomonas spp.	X		X				X	X	X	X			X		X
Synura spp.	X	X	X	X	X	X	X	X	X	X	X		X	X	X
Uroglenopsis spp.						X			X		X				X
Total Chrysophyta	**7**	**5**	**8**	**6**	**3**	**8**	**5**	**5**	**6**	**7**	**7**	**2**	**6**	**6**	**5**
Anabaena circinalis	X	X		X	X	X			X		X	X			
Anabaena flos-aquae	X	X		X	X	X	X	X	X	X	X	X		X	X
Anabaena planctonica			X	X	X	X	X	X	X		X		X	X	X
Anabaena spp.	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Aphanizomenon flos-aquae	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Aphanizomenon gracile	X											X	X		
Aphanizomenon spp.		X			X		X	X	X	X			X	X	X
Aphanocapsa spp.	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Aphanothece spp.	X	X	X	X	X	X	X	X	X	X	X	X	X		X
Chroococcales	X	X			X			X	X				X		
Chroococcus prescotti							X		X	X	X			X	X
Chroococcus spp.		X					X			X	X	X			X
Coelosphaerium spp.				X			X	X		X	X			X	X

Table S1 (continued).

Taxon	Shallow Sites								Deep Sites						
	50	51	2	46	40	4	33	21	16	25	7	34	36	9	19
Dactylococcopsis spp.															X
Gloeotrichia spp.					X		X						X		
Gomphosphaeria lacustris									X			X			
Hormonogonales spp.			X	X		X				X	X	X			
Lyngbya spp.				X											
Microcystis spp.	X	X	X	X	X		X	X	X	X	X	X	X	X	X
Microcystis wesenbergii	X	X			X	X	X	X				X	X		
Oscillatoria spp.				X	X										
Oscillatoriaceae		X		X		X	X			X		X		X	
Pannus spp.			X												
Phormidium mucicola	X	X		X			X		X		X	X		X	X
Phormidium spp.	X										X	X	X		
Radiocystis spp.								X	X	X					X
Romeria spp.				X											
Snowella spp.	X	X	X				X		X	X		X	X	X	X
Woronichinia spp.	X			X	X	X	X	X	X	X	X	X	X	X	X
Total Cyanobacteria	**14**	**14**	**10**	**16**	**14**	**11**	**17**	**13**	**16**	**15**	**15**	**17**	**14**	**13**	**16**
Ceratium hirundinella	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Ceratium spp.	X	X	X		X							X			
Glenodinium spp.		X			X	X									
Peridinium spp.			X	X	X	X	X			X	X	X		X	
Total Pyrrophyta	**2**	**3**	**3**	**2**	**4**	**3**	**2**	**1**	**1**	**2**	**2**	**3**	**1**	**2**	**1**

Table S2. Zooplankton taxonomic data for the 15 Lake Champlain sampling sites. X indicates presence of taxon on at least one occasion from 2006 to 2010.

Taxon	Shallow Sites								Deep Sites						
	50	51	2	46	40	4	33	21	16	25	7	34	36	9	19
Alona bicolor						X									
Alonella spp.										X		X		X	
Bosmina longirostris	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Bosmina spp.	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Ceriodaphnia spp.	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Chydorus spp.	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Daphnia spp.	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Diaphanosoma birgei	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Diaphanosoma spp.	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Epischura spp.		X	X	X		X		X	X	X		X	X	X	X
Eubosmina spp.	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Eurycercus spp.						X									
Holopedium gibberum	X	X		X	X	X	X	X	X	X	X	X	X	X	X
Leptodora kindti	X	X	X	X	X	X		X	X	X	X	X	X		X
Pleuroxus spp.						X									
Polyphemus pediculus		X		X	X	X	X	X	X	X	X		X	X	X
Sida crystallina	X	X		X		X		X	X				X		X
Total Cladocera	**11**	**13**	**10**	**13**	**11**	**16**	**10**	**13**	**12**	**13**	**11**	**12**	**13**	**12**	**13**
Acanthocyclops spp.	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Cyclops scutifer					X			X							
Diacyclops thomasi	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Eucyclops serrulatus	X	X		X	X	X	X	X	X	X	X	X	X	X	X
Mesocyclops edax	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Mesocyclops spp.	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Thermocyclops crassus	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Tropocyclops spp.				X	X	X	X	X	X			X	X		X
Total Cyclopoida	**6**	**6**	**5**	**7**	**8**	**7**	**7**	**8**	**7**	**6**	**6**	**7**	**7**	**6**	**7**

Table S2 (continued).

Taxon	Shallow Sites								Deep Sites						
	50	51	2	46	40	4	33	21	16	25	7	34	36	9	19
Leptodiaptomus spp.	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Limnocalanus spp.		X	X	X	X	X	X	X	X	X	X	X	X	X	X
Senecella calanoides	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Total Calanoida	**2**	**3**	**3**	**3**	**3**	**3**	**3**	**3**	**3**	**3**	**3**	**3**	**3**	**3**	**3**
Ascomorpha/Gastropus spp.	X		X			X		X	X		X	X	X	X	X
Asplanchna spp.	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Brachionus calyciflorus		X								X					
Collotheca spp.	X	X			X	X	X		X	X			X		
Conochilus spp.	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Euchlanis spp.	X	X	X	X	X	X	X			X		X	X		X
Filinia spp.	X	X		X	X	X	X	X	X			X	X	X	X
Kellicottia spp.	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Keratella cochlearis	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Keratella quadrata	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Keratella spp.	X			X						X					
Lecane spp.			X	X		X	X								
Monostyla spp.					X	X									
Nothalca laurentiae		X		X	X	X	X	X	X	X			X	X	X
Nothalca squamula		X	X	X		X	X		X			X	X	X	X
Ploesoma spp.			X	X		X	X	X	X		X	X	X	X	X
Polyarthra spp.	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Synchaeta spp.	X					X									
Trichocerca spp.	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Total Rotifera	**13**	**13**	**12**	**14**	**12**	**17**	**14**	**11**	**13**	**12**	**9**	**12**	**14**	**12**	**13**
Harpaticoid spp.			X			X			X		X				
Ergasilus spp.			X	X		X						X			

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