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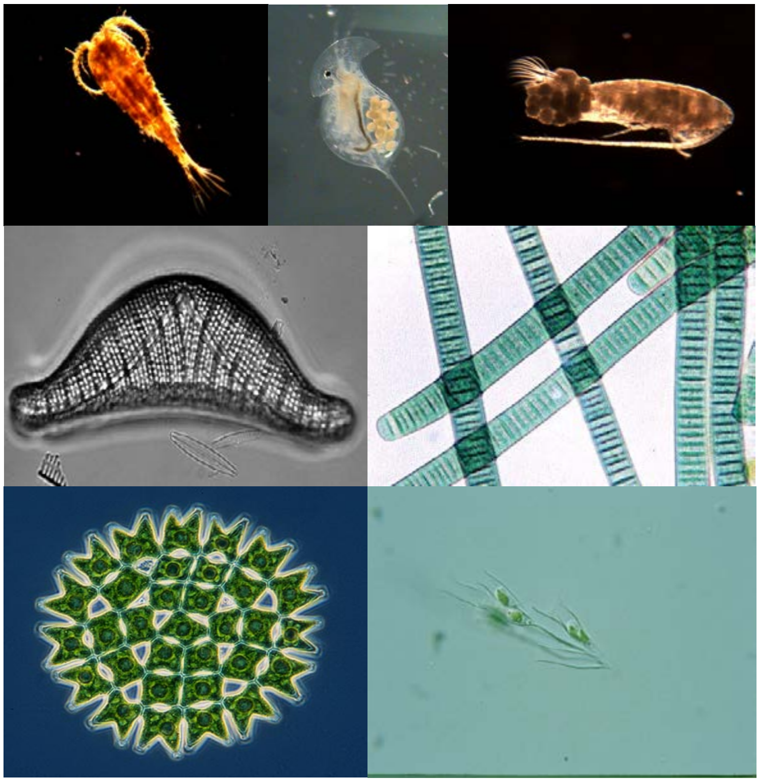
Patterns in Phytoplankton and Zooplankton in Minnesota Lakes



Minnesota Pollution Control Agency

MNDNR

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Executive Summary

The purpose of this report was to examine patterns in phytoplankton and zooplankton based on a subset of the Sentinel Lakes and to serve as a baseline for future monitoring and analysis. While zooplankton sampling has been a routine part of Sentinel Lake sample collection and was addressed in individual lake reports, phytoplankton has been sampled sporadically. This analysis provides basic descriptions of phytoplankton and zooplankton composition, seasonal cycling, and interactions in 13 Sentinel Lakes. Observations included herein can be used in future assessments as a basis for comparison and evaluating change over time. Though this analysis was limited to 13 lakes, their geographic, morphometric, and trophic ranges allow for some generalizations that may be applicable to Minnesota lakes in general. A summary of some important findings follows.

Numerous factors influence the cycling of algal forms in Minnesota lakes. Examples of these factors include: climatic drivers - sunlight, temperature, and wind; nutrients - phosphorus and nitrogen; minerals - carbonate and silica; and biological - zooplankton. These factors vary in their significance in various lakes and interactions among variables may be complex. While the literature offers numerous examples of seasonal cycling of algal forms, this analysis allows for descriptions based on Minnesota lake data. Analyzing the Sentinel Lakes across a trophic gradient provided a reasonable approach for characterizing phytoplankton and zooplankton composition and seasonal succession for Minnesota lakes. Moving from oligotrophic to hypereutrophic we observed the following:

- In oligotrophic and mesotrophic lakes, diatoms and chrysophytes are the dominant algal forms. While diatoms are prominent across the entire trophic gradient, chrysophytes are uncommon in the eutrophic lakes. This is likely the result of competition from algal forms that prosper in more nutrient-enriched water and the warmer temperatures of the lakes of central and southern Minnesota. Algal biomass is often highest at spring turnover in the oligotrophic and mesotrophic lakes and usually declines thereafter, until fall turnover. Blue-greens, while present, are never dominant and biomass, based on Chl-*a*, is far below nuisance bloom levels. Nutrient limitation, silica depletion, zooplankton grazing, and water temperature are important drivers in the observed seasonal succession.
- In eutrophic and hypereutrophic lakes, spring turnover is marked by blooms of diatoms, cryptophytes, and green algae. By June, these forms decline in prominence and are replaced by blue-greens, which remain prominent until October when the water cools and Cryptophytes become prominent again. In general, there is a steady increase in algal biomass from May through September/October and much of that is in the form of blue-greens. Since nutrients are abundant in these lakes, warm temperatures and zooplankton grazing of other algal forms (reduce competition) are among the two most important drivers allowing for blue-green dominance.

This study also provided an opportunity to identify some phytoplankton and zooplankton indicators that merit tracking in future monitoring efforts.

a. Phytoplankton indicators are summarized below:
   - *Cylindrospermopsis* is a known toxin producer and was relatively uncommon in the 2013 and 2014 collections in this study, with the exception of Madison and South Center lakes. It was previously believed to be tropical, preferring warm temperatures. Its presence and relative abundance in other Sentinel Lakes should be tracked in future collections. A significant expansion in its presence and abundance could be an indication of significant environmental changes in the affected lakes. Northward expansion would be of particular concern.
   - Blue-green algae were present in all Sentinel Lakes and are in all Minnesota lakes. Blue-green forms, shift in dominant genera, and potential increases in toxin-producers could be useful indicators of change. In the oligotrophic and mesotrophic lakes a variety of blue-green genera are found; whereas in the more eutrophic lakes potential toxin-producing *Anabaena*, *Microcystis*, and *Aphanizomenon* were dominant.

- The blue-green alga *Gloeotrichia* may be worth watching over time in these lakes. It is not considered an indicator of poor water quality and is more common in lakes of high clarity. However, literature reports suggest it draws most of its nutrients from the sediment of the lake and that it is not a good food source for zooplankton. Its increase in the future could be indicative of changes in a lake system.
- Increased water temperature favors blue-green algae over other forms. In particular, as summer temperatures increase above 20 °C and remain at 25 °C or more for extended periods, blue-greens prosper. As lakes warm, chrysophytes may be among the first forms to decrease, given their preference for cool temperatures. Chrysophytes are important in mesotrophic lakes and a good food source; should they be reduced via increased temperature or nutrient enrichment, blue-greens may fill the niche they occupy.

b. Zooplankton indicators

- *Daphnia longiremis*- This deep-water daphnid may be an indicator species, as it is found in the hypolimnion of deep, well-oxygenated lakes. This is reinforced by the findings from zooplankton analysis of 150 random lakes in the 2012 National Lakes Assessment (Hirsch 2014) where this species was found only in the more north central MN lakes.
- *Leptodiaptomus minutus*- a cool-water Diaptomidae which is restricted to deep lakes at the southern end of its range. In Minnesota, it is only found in oligotrophic and mesotrophic lakes, and its loss could be an indication of eutrophication and/or climate-induced warming.
- *Leptodiaptomus siciloides* and *Aglaodiaptomus clavipes*- both these calanoid species tend to favor or adapt better to more eutrophic conditions.

This study also provided some initial insights on the impact of invasive species on phytoplankton, zooplankton, and lake water quality.

- The impact of zebra mussels in Lake Carlos is already apparent based on trends in trophic status; whereby Secchi depth is increasing, and algal biomass appears to be decreasing. There are not adequate data to determine if there are any significant shifts in algal composition. Based on 2013 and 2014 data there was not a significant shift to blue-green forms, which sometimes occurs with increased zebra mussel infestation. However, the low TP in Lake Carlos may minimize the likelihood of this occurring.

- Zebra mussels appear to be impacting the zooplankton community in Lake Carlos, as densities of grazers have declined in post-zebra mussel infestation years, suggesting competition effects, although more post-infestation data are necessary to test this statistically.

- Spiny waterfleas in Trout Lake appear to be impacting small cladocerans by direct predation and possibly cyclopoid copepods by indirect food competition interactions, although more data are necessary to confirm this as well.

Introduction

The Minnesota Pollution Control Agency (MPCA) is working in partnership with the Minnesota Department of Natural Resources (MN DNR) on the Sustaining Lakes in a Changing Environment (SLICE) Sentinel Lakes Program. The focus of this interdisciplinary effort is to improve understanding of how major drivers of change such as development, agriculture, climate change, and invasive species can affect lake habitats and fish populations and to develop a long-term strategy to collect the necessary information to detect undesirable changes in Minnesota lakes (webpage: dnr.state.mn.us/fisheries/slice/description). To increase our ability to predict the consequences of land cover and climate change on lake habitats, SLICE utilizes intensive lake monitoring strategies on a wide range of representative Minnesota lakes. This includes analyzing land cover and land use, identifying climate stressors, and monitoring the effects on lake habitat and biological communities.

The Sentinel Lakes Program initially selected 24 lakes for long-term intensive lake monitoring (Figure 1). Lakes were selected based on three stratification criteria: major ecoregion (four levels, also referred to as "landtype"), lake mixing status (two levels: lakes that stratify, "deep" lakes; and those that remain mixed, "shallow" lakes), and nutrient status (three levels: low, medium, and high levels of TP, adjusted to the ranges observed with each ecoregion). Characterizing the selected lakes further, the "deep" lakes typically stratify during the summer months only, while "shallow" lakes mix continuously throughout the summer. "Cold water" lakes are a subset of the deep lakes and are defined as lakes that either harbor cisco, lake whitefish, or lake trout or are the focus of research funded by the Environment and Natural Resource Trust Fund (ENRTF). In 2013, one additional cold water lake, Greenwood Lake in Cook County, was added to provide a broader representation of cold water lakes and to better understand the impact of spiny water-flea on cold water lake ecology. Three lakes that support cold water fish populations, Trout, Elk, and Carlos, were identified for special targeted research and are referred to as "Super Sentinel" lakes. Research on these lakes is also funded by the ENRTF. Financial constraints later led to designation of "Tier 1" and "Tier 2" lakes. Tier 1 lakes included the three Super Sentinel Lakes, which were the subject of intensive monitoring and model development. The remainder of the Tier 1 lakes included Bear Head, Ten Mile, Pearl, Madison, and Shaokotan. These lakes also received additional monitoring and modeling effort.

The purpose of this report is to examine patterns in phytoplankton and zooplankton communities across a range of the Sentinel Lakes and serve as a baseline for future monitoring and analysis of plankton in the Sentinel Lakes. While zooplankton sampling has been a routine part of Sentinel lake sample collection and was addressed in all individual lake reports, phytoplankton has been sampled sporadically. The need for phytoplankton information in the Super Sentinel and Tier 1 lakes provided an opportunity to generate comprehensive phytoplankton data for 13 lakes (Table 1). Since zooplankton was sampled in these lakes as well, data were analyzed for these two significant compartments of the food web in a range of Sentinel Lakes.

These data allowed for a series of questions to be addressed:

1. What are the seasonal patterns in phytoplankton and zooplankton composition at division (group) and genus level?
2. What patterns exist among planktonic groups between deep and shallow lakes, among ecoregions, and by trophic state?
3. How does seasonal succession in Sentinel Lakes vary from that described in the literature?
4. How do algal metrics and seasonal patterns compare across a range of lakes?
5. How do algal metrics vary relative to total phosphorus (TP), chlorophyll-*a* (Chl-*a*), maximum mean depth, silica (Si), calcium (Ca), or alkalinity?
6. Are there distinct patterns in abundance and composition of cyanobacteria (blue-green algae) among different types of lakes?
7. What effects do aquatic invasive species have on lake ecology, especially spiny water-flea (*Bythotrephes longimanus*) and zebra mussels (*Dreissena polymorpha*)?
8. Are there "sentinel" algal groups (e.g., genera or species) or algal metrics that more closely relative to climate change, eutrophication, or other anthropogenic factors, enabling us to use them as a proxy for these impacts?

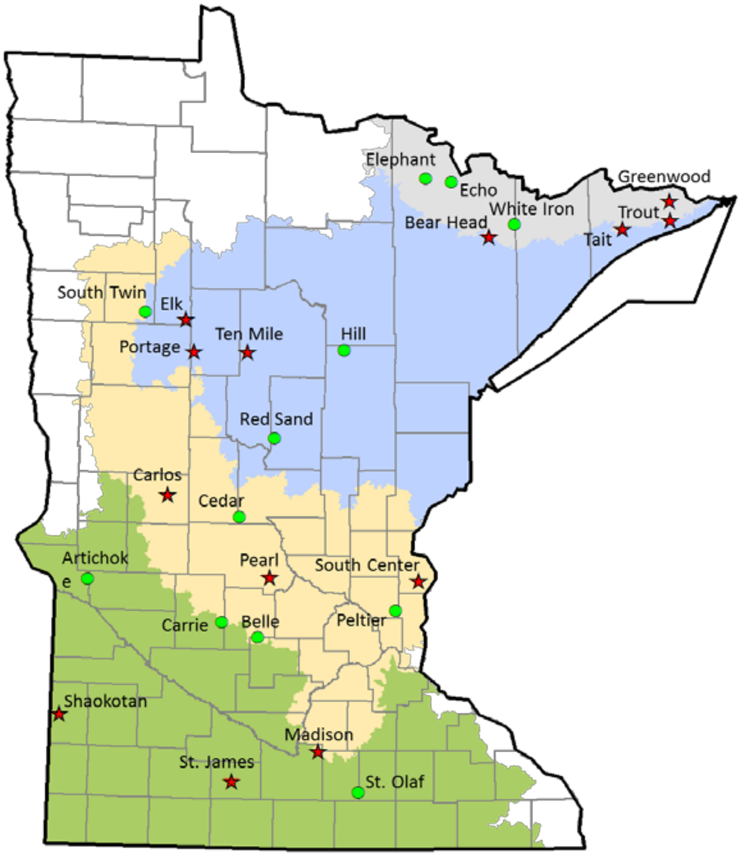


Figure 1. Map of Sentinel Lakes. Lakes included in this study noted with red star. Ecoregions are designated as follow: grey, “Canadian Shield”; blue, “Northern Forests”; tan, “Central Hardwoods” (transition forest); green, “Prairie and Corn Belt”.

Table 1. List of Sentinel Lakes and years that data were collected and included in this report. Land type refers to classification in Figure 1. Lakes sorted from northeast to southwest.

Lake ID #	Name	County	Eco-region[1]	Land-type	Lake type	Phyto 2013	Phyto 2014	Zoo 2013	Zoo 2014
16-004900	Trout	Cook	NLF	Shield	coldwater	x	x	x	x
16-007700	Greenwood	Cook	NLF	Shield	coldwater	x	x	x	x
16-008900	Tait	Cook	NLF	Shield	shallow	x		x	
69-025400	Bear Head	St. Louis	NLF	Forest	deep	x	x	x	x
11-041300	Ten Mile	Cass	NLF	Forest	coldwater	x		x	x
15-001000	Elk	Clearwater	NLF	Forest	coldwater	x	x	x	x
29-025000	Portage	Hubbard	NLF	Forest	shallow	x		x	
21-005700	Carlos	Douglas	CHF	Trans.	coldwater	x	x	x	x
73-003700	Pearl	Stearns	CHF	Trans.	shallow	x	x	x	x
13-002700	South Center	Chisago	CHF	Trans.	deep	x		x	
83-004300	St. James	Watonwan	WCP	Prairie	shallow	x		x	
07-004000	Madison	Blue Earth	WCP	Prairie	deep	x	x	x	x
41-008900	Shaokotan	Lincoln	NGP	Prairie	shallow	x	x	x	x

1 Ecoregions abbreviated as follows: NLF Northern Lakes and Forests, CHF North Central Hardwoods Forests, WCP Western Corn Belt Plains, & NGP Northern Glaciated Plains.

Methods

Field collections and lab procedures

Phytoplankton and zooplankton collections were made at the primary (pelagic) site on each lake, which was typically the site of maximum depth. Phytoplankton samples were collected with a 2-m polyvinyl chloride (PVC) integrated tube that sampled the 0-2 m strata, as were all water samples. Samples were kept in the dark and on ice until processing later the same day. Plankton samples were subsamples from the same bottle that chlorophyll-*a* sample was taken from. Samples were decanted into a dark plastic bottle and preserved with Lugol's Solution.

Phytoplankton identification was conducted at PhycoTech (St. Joseph, Michigan webpage: phycotech.com) using the Modified Minnesota Rapid Assessment Method (Swain and Dindorf, 1989; Lindon and Heiskary, 2007). The Minnesota Pollution Control Agency (MPCA) first adopted a "Rapid Assessment Method" for phytoplankton in the late 1980s, which included methods for identification and estimates of relative biovolume contributions of major algal taxa. When collected over time these data enable a description of seasonal changes in phytoplankton composition and relative biomass within a lake. Coupled with Chl-*a* concentrations, the relative biomass (measured as Chl-*a*) of major taxonomic algal groups can be estimated. Assessments of groups of lakes (e.g., the Sentinel Lakes) can provide information to compare and/or contrast lakes of different trophic status on a given date or to characterize seasonal patterns in algal succession. If sampling for multiple years, this method allows for describing changes in algal composition over time. The basic technique, with modifications, is described below (Phycotech 2014 webpage: phycotech.com/technical; adapted from Crumpton 1987). The modifications were the recommended approach for the samples in this project.

1. Check membrane filters (25-mm diameter Pall, Metricel, GN-6, 0.45-µm pore size) for leaks/holes by placing the filters onto the base of the filter tower and wetting with distilled water. Draw excess water through filter. If filter has any opaque areas (very white when wet), replace with another filter.
2. Assemble filter towers.
3. Homogenize sample by gently shaking 100 times.
4. Remove 5.0 mL of sample with a calibrated Eppendorf macropipet (Note - consistent volume allows for a comparison among systems for relative algal biomass.)
5. Add sample to the tower and open the valve to turn on vacuum. Filter the sample until water disappears from inner edge of the tower. Close the valve and remove the filtration tower.
6. Place filter, FACE DOWN, on a cover slip (# 1.5 thickness, 0.17-mm thickness; 25-mm x 25-mm). Be careful to avoid allowing bubbles under the filter.
7. For samples preserved in glutaraldehyde or Lugol's Solution.
   a. No permanent slide needed - make one slide for rapid assay.
   b. For permanently archived sample - make three permanent slides.
   Make all slides by adding 1-2 drops of HPMA (2-hydroxypropyl methacrylate) resin to the back of the filter and rotate the cover slip until the resin covers the back of the filter.
8. Put coverslips with filter into drying oven at 60 °C for ~ 1 hour. Remove from oven and place filter side down on clean microscope slide. If finishing permanent slides, leave in oven for 24 hours, and then use additional HPMA resin on the filter and place on microscope slide. Return slides to drying oven for an additional 1-3 days.
9. Scanning:
   a. Using a compound microscope scan the slide at 500x to estimate percent abundance by biovolume, for each taxon identified, also go up to 150x to scan the entire slide for larger taxa.
   b. Identify and record each taxon encountered (to species where possible) of algae present in sample. Modification - scan for all algae present in the sample that contribute 0.5-1% of the biomass.
   c. Modification - adjust for biovolume as taxa are tallied, generally scan well over 1000 Natural Units including scanning from 125x down to 500x
   d. The filtration and slide preparation method, described above, can be adapted on a compound microscope equipped with epi fluorescence to aid in species-level identification.
10. Estimate % biovolume.
    a. Considering the size and density, estimate the relative biovolume of each algal type or taxon. Record if sample is exceptionally sparse or dense.
11. Record estimated percent abundance weighted for biovolume for each taxon.

Zooplankton samples were collected monthly from May to October. One vertical tow was taken during each sampling event, using a 30-cm mouth, 80-µm mesh simple zooplankton net. The net was lowered to within 0.5 m of the bottom and withdrawn at a rate of approximately 0.5 m per second. Contents were rinsed into sample bottles and preserved with 100% reagent alcohol. Analysis was conducted by MN DNR personnel.

Each zooplankton sample was adjusted to a known volume by filtering through 80-µm mesh netting and rinsing specimens into a graduated beaker. Water was added to the beaker to a volume that provided at least 150 organisms per 5-mL aliquot. A 5-mL aliquot was withdrawn from each sample using a bulb pipette and transferred to a counting wheel. Specimens from each aliquot were counted, identified to the lowest taxonomic level possible (most to species level), and measured to within 0.01 mL using a dissecting microscope and an image analysis system. Biomass estimates were calculated with length/weight regression coefficients for individual taxa, based on dry weight, obtained from Culver et al. (1985) and Dumont et al. (1975). Densities (#/L), biomass (µg/L), percent composition by number and weight, mean length (mm), mean weight (µg), and total counts for each taxonomic group identified were calculated for each sample.

Statistical analysis

Spearman Rank Order Correlations were performed using SigmaPlot 12.5 (Systat Software, Inc., San Jose, CA) to examine interrelationships among phytoplankton, zooplankton, and chemical and physical lake characteristics. These non-parametric tests measure strength of association between pairs of variables that are not required to be linearly related nor have normal distributions. Spearman's correlation coefficient (ρ) varies between -1 and +1, with values close to +1 indicating strong positive relationships while values close to -1 indicating strong negative (inverse) relationships. Scatter matrices based on these correlations were generated for phytoplankton metrics and physicochemical parameters, as well as zooplankton metrics and physicochemical parameters.

Multivariate statistical analyses were performed using various techniques with PRIMER software version 6 (PRIMER-E Ltd, Plymouth, UK), to compare similarities and dis-similarities of communities among lakes, as well as examining inter-annual variability, environmental influences, and invasive species impacts. Zooplankton data were log (x+1) transformed, and phytoplankton data square root transformed, to reduce the influence of dominant taxa. Bray-Curtis similarity matrices were generated using zooplankton densities and phytoplankton relative abundances.

Non-metric multidimensional scaling (MDS) (Clarke 1993) analysis was used to examine similarities and dis-similarities among lakes based on both phytoplankton and zooplankton community structure. MDS is a non-parametric ordination technique that graphically represents community relationships. Lakes that are ordinated close together exhibit similar community assemblages, and those farther apart have less similarity between communities. A measure of how accurately the relationship is illustrated in the graph is indicated with a stress value. Stress values below 0.2 are considered to be an acceptable level of accuracy (Clarke 1993).

The BIOENV procedure (Clarke and Gorley 2006) was used to test which (if any) of the physicochemical parameters, best explain the pattern of lakes in the ordination, based on zooplankton community structure. BIOENV is a rank correlation (ρ) method comparing biotic and environmental similarity matrices (Clarke and Ainsworth 1993). Values of ρ can range from -1 to 1, with near zero values indicating the lack of correlation between the matrices. Bubble plots representing the relative importance of environmental variables chosen from BIOENV procedure were superimposed on MDS graphs for graphical illustration.

MDS ordinations were generated for each year individually (2013 and 2014) on lakes that were sampled both consecutive years, to examine inter-annual variability based on both zooplankton and phytoplankton community structure.

Analysis of similarity (ANOSIM) tests were performed on the zooplankton data to determine which (if any) lakes showed significant differences in zooplankton community structure between the two years. ANOSIM is a non-parametric permutation procedure that produces an *R* statistic, which is a comparative measure of the degree of separation between sites (Clarke and Warwick 2001). *R* will typically fall between 0 and 1, with values near zero indicating assemblages are similar and representing the null hypothesis of no differences between years. *R*-values closer to 1 indicate a greater degree of assemblage differences.

The similarity percentage routine (SIMPER) was used to further test which zooplankton species were contributing to the changes between years in the lakes that showed significant differences from the ANOSIM test. The SIMPER routine uses average Bray-Curtis dissimilarities between all pairs of sites to produce a percent contribution from each species, identifying the species most responsible for the dissimilarity between years (Clarke and Warwick 2001).

Finally, MDS ordinations were used to illustrate small cladoceran distribution among the lakes, in relation to spiny waterflea presence.

Results and Discussion

Lake physical and chemical characteristics

The lakes in this study represent a cross-section of the Sentinel Lakes and are representative of lakes across Minnesota (Table 2). The study lakes range in size from 221 acres (St. James) to 4,669 acres (Ten Mile) (Table 2). Maximum depths range from 10 feet (Shaokotan) to > 200 feet (Ten Mile). Of the 13 lakes, four are well mixed and eight are stratified throughout the summer (Table 2). Pearl Lake stratifies temporarily during calm periods but will readily mix under windy conditions.

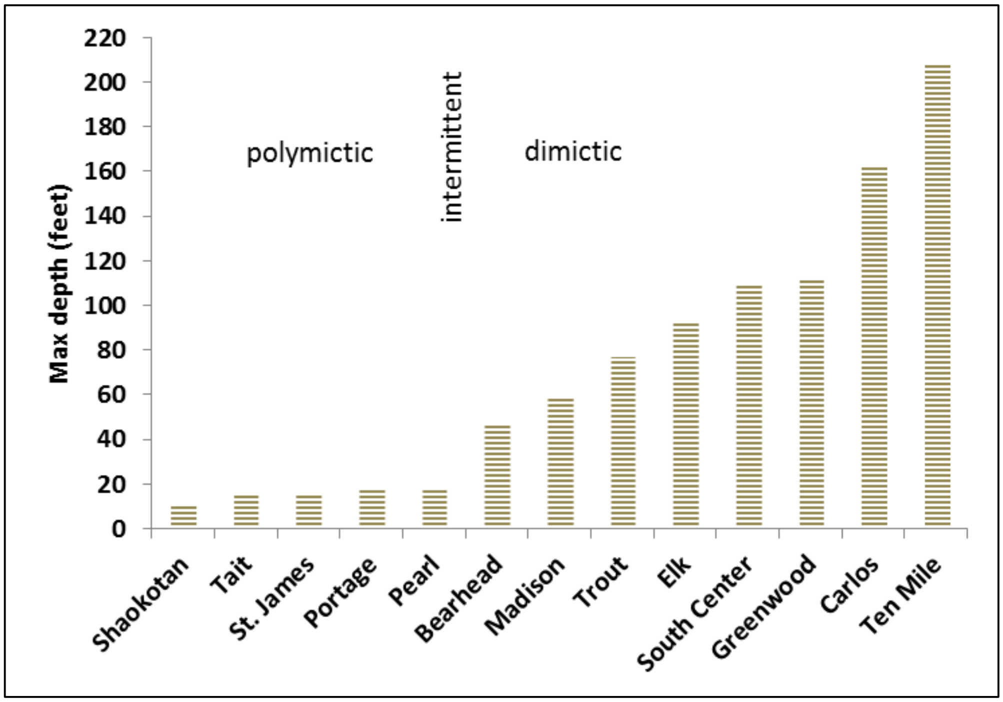
The trophic state of the lakes range from oligotrophic (Greenwood and Trout) to highly eutrophic (Shaokotan, Madison, and South Center). Water hardness (Ca, mg/L) ranges from some of the softest water lakes in Minnesota (Greenwood, Trout, Tait, and Bear Head) to some of the hardest water lakes in the state (Portage and Shaokotan). These various physical and chemical characteristics can be important in the types and amounts of phytoplankton and zooplankton found in the lakes, as well as influencing the overall ecology of the lakes. These various physicochemical variables will be used in analyses of the phytoplankton and zooplankton communities and may explain some of the observed patterns in the data.

Table 2. Summary of lake morphometry and mean summer water chemistry attributes based on Sentinel collections from 2008-2012. Lakes are sorted by ecoregion (NLF=Northern Lakes and Forests, CHF=Central Hardwoods Forests, WCP=Western Corn Belt Plains, and NGP=Northern Glaciated Plains.)

Eco-region	Lake	mix	Z max (ft)	Area (acre)	% littoral	TP (µg/L)	TN (mg/L)	TN: TP	Chl-a (µg/L)	SD (m)	Ca (mg/L)	Si (mg/L)
NLF	Trout	strat.	77	257	23	8	0.40	50	1.4	5.7	4.2	6.0
NLF	Greenwood	strat.	112	2021	26	6	0.40	67	2.0	5.0	2.6	1.2
NLF	Tait	poly.	15	338	100	15	0.40	27	2.7	2.3	4.9	5.2
NLF	Bear Head	strat.	46	674	56	14	0.46	33	7.0	2.7	5.2	1.2
NLF	Ten Mile	strat.	208	4,669	26	10	0.40	40	2.0	4.9	24.0	7.0
NLF	Elk	strat.	93	305	24	19	0.60	32	6.0	2.6	32.0	8.6
NLF	Portage	poly.	17	412	97	60	1.10	18	21.0	0.9	80.0	15.0
CHF	Carlos	strat.	163	2,598	35	18	0.73	41	3.5	3.6	27.0	4.9
CHF	Pearl	poly.	17	746	68	38	0.90	24	13.0	2.0	38.0	16.0
CHF	S. Center	strat.	109	898	67	55	1.20	22	49.0	1.1	15.0	0.5
WCP	Madison	strat.	59	1,439	50	80	1.50	19	35.0	0.9	30.0	8.7
WCP	St. James	poly.	16	221	100	55	1.20	22	20.0	1.3	40.0	9.3
NGP	Shaokotan	poly.	10	994	100	157	2.38	15	81.0	0.9	68.0	16.0

Note - parameters in the table are abbreviated as follows: mix=mixing: strat=stratified, poly=well mixed; Z max, maximum depth; TP, total phosphorus; TN, total nitrogen; Chl-a, Chlorophyll-a; SD, Secchi depth; Ca, Calcium; Si, Silica.

Figure 2. Ranking of study lakes based on maximum depth, total phosphorus (TP), chlorophyll-*a* (Chl-*a*), and calcium (Ca).



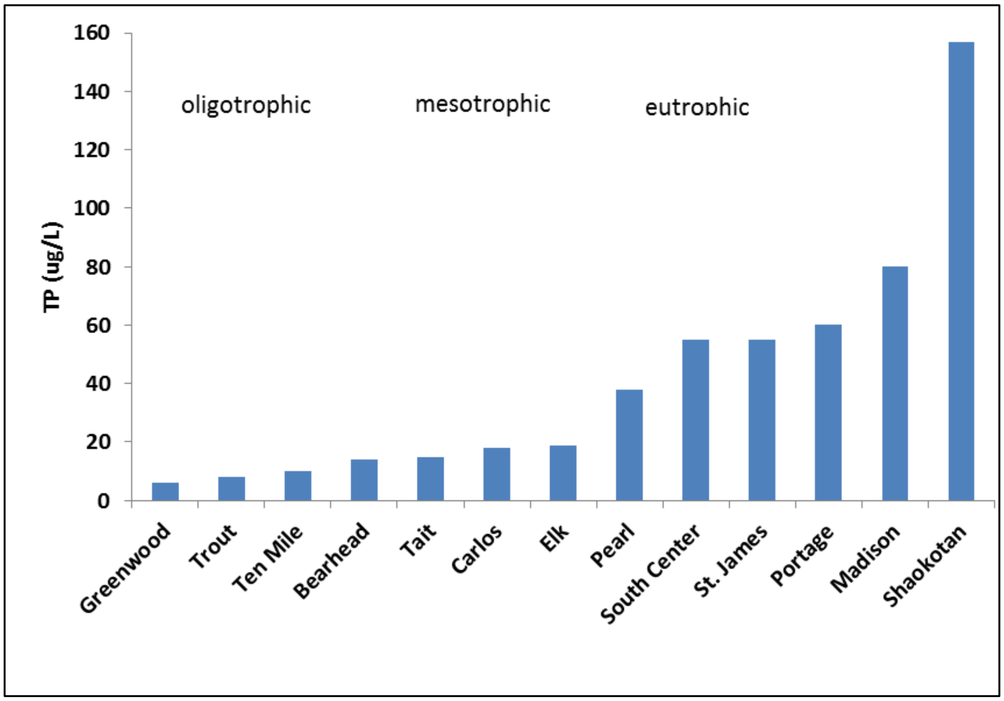
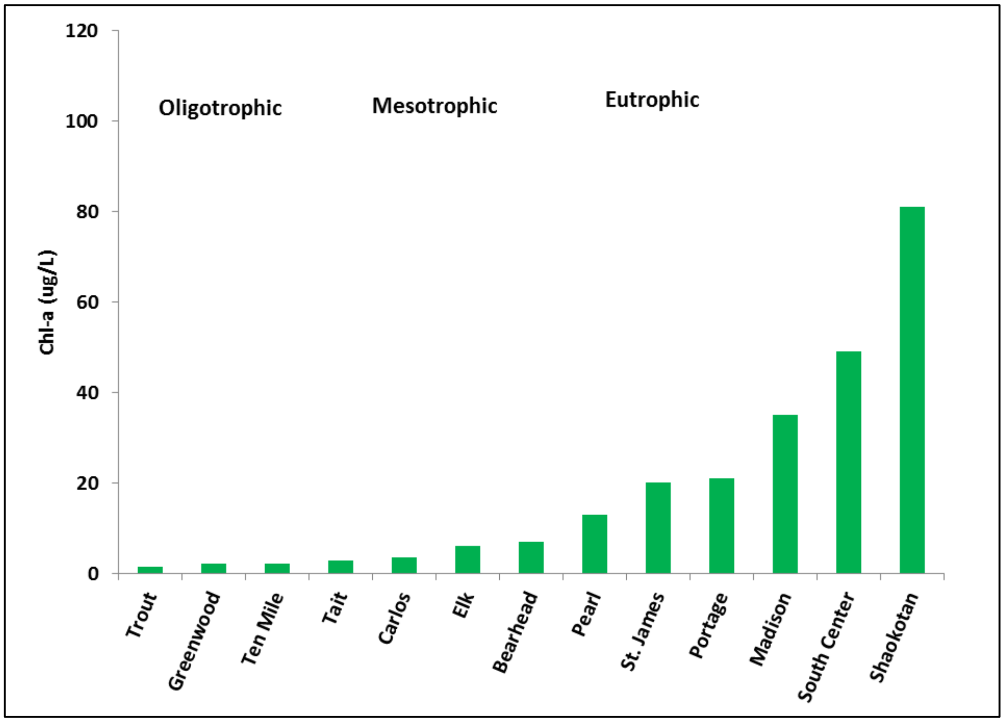
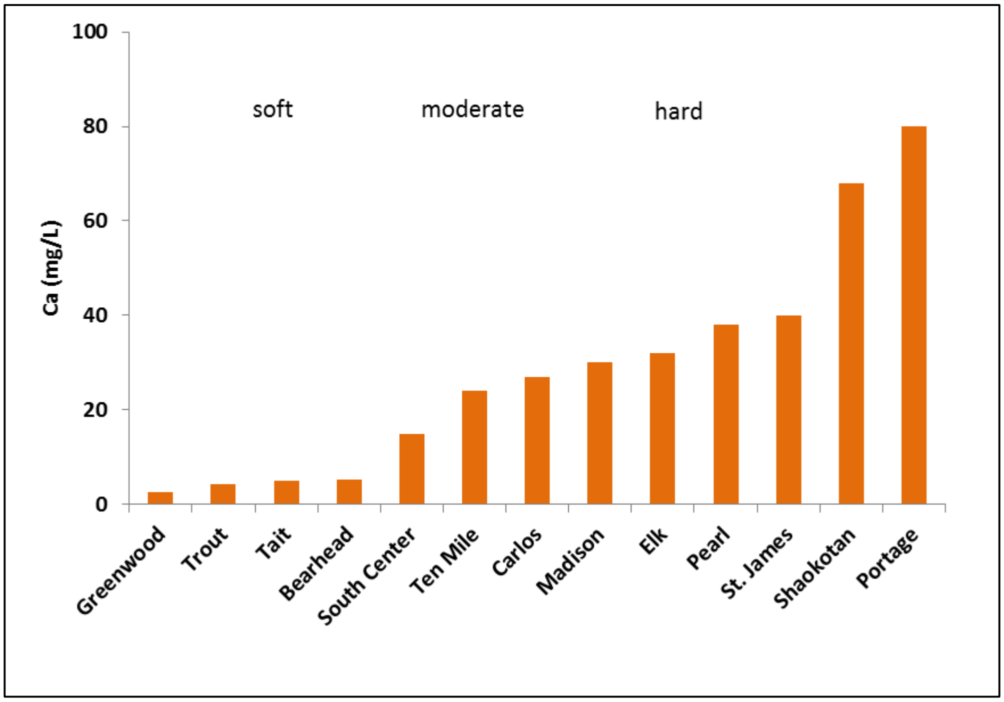


Figure 2. Continued.





Regional climate characteristics

Climate impacts lake productivity and various processes within lakes. Minnesota is characterized by distinct differences in climate across the state, with great variations in precipitation, evaporation, and runoff from the northeastern to southwestern regions of the state. Table 3 provides a general depiction as derived from Heiskary and Wilson (1994). On average lakes of northeastern Minnesota (e.g., Greenwood and Trout) receive higher precipitation and lower evaporation than lakes in central (e.g., Pearl) and southwest Minnesota (e.g., Shaokotan) where evaporation exceeds precipitation on average.

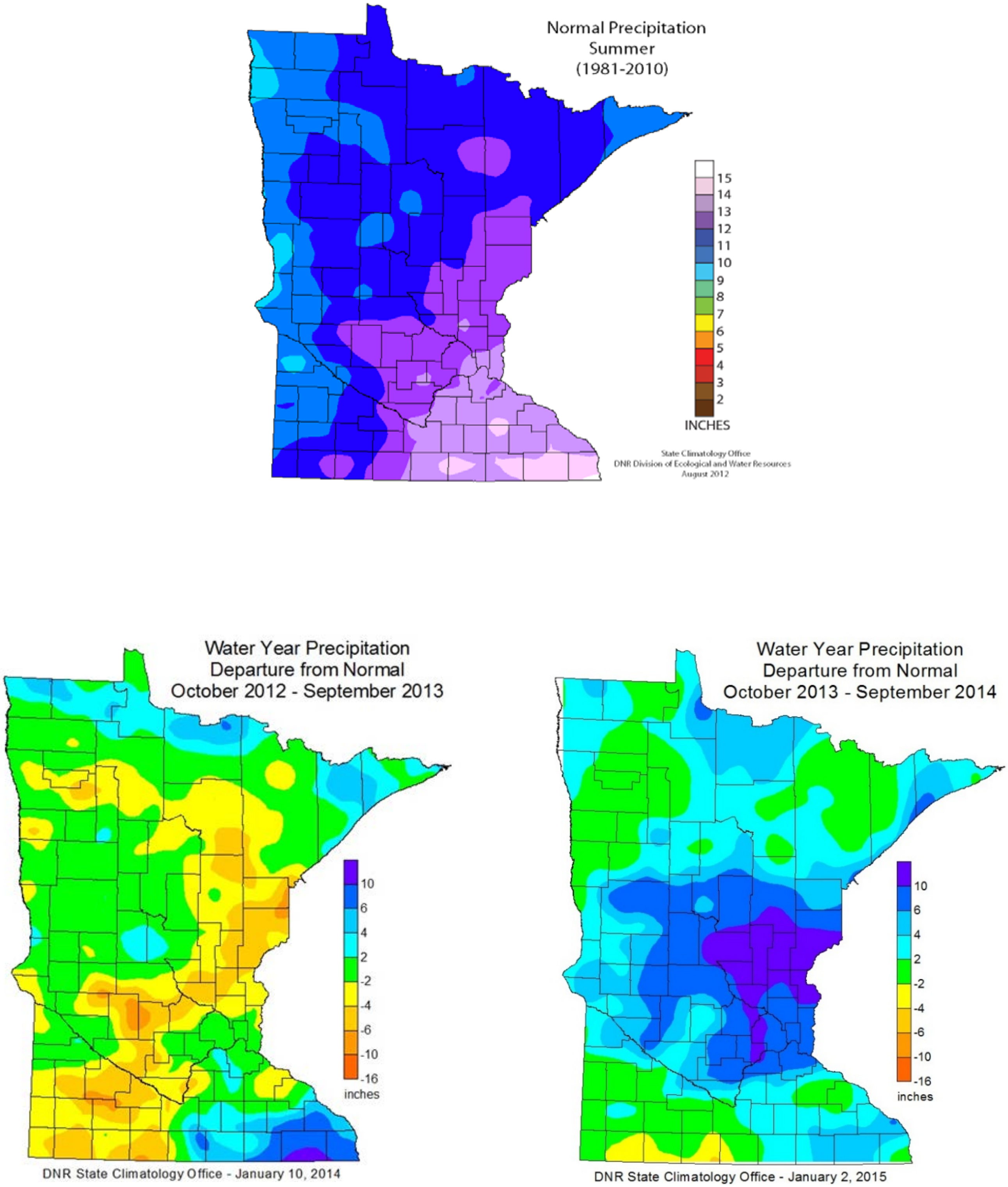
The two summers used in this study exhibited different climatic conditions. Water year 2013 exhibited dry or even drought-like conditions over much of north central, central, south, and southwest Minnesota (Figure 3); whereas precipitation in the northeast was near normal or slightly above normal. This is in contrast to 2014 when most of the state had normal to above normal precipitation (Figure 3). A review of city (region)-specific temperature and precipitation for the two years suggest minimal among-year differences for Greenwood, Trout, Tait, and Bear Head lakes (NE, Table 4) and most likely marked differences for Shaokotan, St. James, Madison, and Pearl lakes (C & SW, Table 4). Maxima and average temperature in 2013 were near normal but warmer than 2014.

Table 3. Annual precipitation, evaporation and runoff for Minnesota. Derived from Heiskary and Wilson (1994) based on summary data from c1980s.

Region	Precipitation	Evaporation	Runoff
Northeast	0.71 m (28 in)	0.66 m (26 in)	0.28 m (10.9 in)
North Central	0.66 m (26 in)	0.81 m (32 in)	0.17 m (6.6 in)
Central	0.66 m (26 in)	0.91 m (35 in)	0.14 m (5.5 in)
Southwest	0.61 m (24 in)	1.00 m (39 in)	0.08 m (3.1 in)

Table 4. Climate summary for select Minnesota stations for summer (June-August) 2013 and 2014. MN DNR climatology records from NWS sites.

Region - City	Year	Temp - high (F)	Temp - avg. (F)	Temp (avg.) - departure (F)	Precip - total (inch)	Precip - departure
NE - Grand Marais	2013	88	58.3	-1.3	12.10	2.66
	2014	83	56.0	-3.8	12.94	3.50
NC - Brainerd	2013	90	67.0	0.0	11.44	0.13
	2014	88	66.7	-0.3	13.03	1.72
C - St. Cloud	2013	95	68.6	0.7	8.04	-3.23
	2014	94	69.9	2.0	13.02	1.75
SW - Lamberton	2013	93	70.0	0.3	7.48	-4.09
	2014	89	69.0	-0.7	12.28	0.71



Normal Precipitation
Summer
(1981-2010)

State Climatology Office
DNR Division of Ecological and Water Resources
August 2012

Water Year Precipitation
Departure from Normal
October 2012 - September 2013

DNR State Climatology Office - January 10, 2014

Water Year Precipitation
Departure from Normal
October 2013 - September 2014

DNR State Climatology Office - January 2, 2015

Figure 3. Normal precipitation for summer (June-August, top panel) and departure from normal for 2014 and 2013 (bottom left and right, respectively) water years. (Minnesota DNR Climatology Office webpage: dnr.state.mn.us/climate/historical/water_year_maps)

Patterns in phytoplankton and zooplankton

We elected to sort the lakes by total phosphorus (TP) concentration, which produces groupings of **northern** - generally deep, low TP lakes; **central deep** - generally deep, moderate TP lakes; **central shallow**- generally shallow, moderately high TP lakes; and **south** - generally shallow, high TP lakes. While these groupings are somewhat intuitive they may not necessarily be the best *a priori* groupings for statistically defining similarities and differences among these lakes. Later analysis will look at the range of multiple physicochemical variables, as they relate to phytoplankton and zooplankton community composition and productivity and try to discern variable that may be the most important in explaining observed patterns.

Analysis approach

Phytoplankton

The phytoplankton analysis considers multiple taxa levels. First, the percent composition is considered; with aggregations at the division level (Figure 4). Brief descriptions of each follows as drawn from Wetzel (2001) and Horne and Goldman (1994) [summarized in Water on the Web, webpage: waterontheweb.org].

- **Bacillariophyta** - Commonly referred to as diatoms. Most are unicellular or organized in simple colonies and have siliceous shells that are often well preserved in the sediments of lakes. They are non-motile and require water turbulence to remain suspended. The environmental characteristics and requirements of numerous diatom species are well-known and can be used to characterize current or historical water quality. They are commonly divided into two groups based on morphology: centric and pennate. Common centric forms in Minnesota lakes include *Aulacoseira*, *Stephanodiscus*, and *Cyclotella*. Common pennate forms in Minnesota lakes include *Asterionella*, *Diatoma*, *Fragilaria*, *Synedra*, *Acnanthes*, *Cocconeis*, *Amphora*, *Cymbella*, *Gomphonema*, *Navicula*, *Nitzschia*, *Pinnularia*, and *Surirella*. (Note - use of term diatom in this report refers specifically to members of Bacillariophyta.)
- **Chlorophyta** - Commonly referred to as green algae and may be unicellular, multicellular, colonial or filamentous. Most planktonic forms belong to the orders Volvocales (e.g., *Chlamydomonas*, *Sphaerocystis*, *Eudorina*, and *Volvox*) and Chlorococcales (e.g., *Scenedesmus*, *Ankistrodesmus*, *Selanastrum*, and *Pediastrum*) (Wetzel 2001).
- **Chrysophyta** - Commonly referred to as golden-brown algae or "chrysophytes." The diatoms are sometimes considered as members of this group in the older literature, but here the diatoms are treated separately. The chrysophytes are often unicellular, but there are some filamentous and colonial forms. Some forms may have silica scales and flagella. Some common forms include the unicellular species with a single flagellum, e.g., *Chromulina*, *Chrysococcus*, and *Mallomonas*, which are very small and included in the nanoplankton. Colonial forms include *Dinobryon*, *Synura*, *Uroglenopsis*, and *Chrysosphaerella*. Many forms are well adapted to low temperatures and low light (Wetzel 2001).
- **Cryptophyta** - Most often unicellular with two flagella. They are included among the nanoplankton as they are rather small. They contain pigments enable them to photosynthesize under very low light conditions. Most of the planktonic members belong to the Cryptomonadinae, e.g., *Cryptomonas*, *Rhodomonas*, and *Chroomonas* (Wetzel 2001). They occur in almost all lakes and over a range in trophic status (Wetzel 2001).
- **Cyanobacteria** - Commonly referred to as blue-green algae and include unicellular and colonial species. Some forms fix nitrogen when the supply of N (e.g., nitrate-N and ammonium-N) is limiting to growth, and some forms can regulate their buoyancy. Some forms can produce toxins and their "blooms" can be referred to as harmful algal blooms. Most planktonic Cyanobacteria consist of members of the coccoid family (e.g., *Microcystis*, *Gomphosphaeria*, and *Coccochloris*) and filamentous families (e.g., *Planktothrix*, *Limnothrix*, and *Tychonema* - all formerly classified in the genus *Oscillatoria*), Nostocaceae (e.g., *Anabaena*, *Aphanizomenon*, *Nodularia*), and Rivulariaceae (e.g., *Gloeotrichia*) (Wetzel 2001). In this report, the terms Cyanobacteria and blue-greens will be used interchangeably.
- **Haptophyta** - Originally classified with golden algae (Chrysophyta). More common in the marine environment and referred to as "haptophytes." Some forms have exoskeletons with calcareous plates and like cryptophytes are very small and have flagella. They are relatively uncommon in Minnesota lakes. One genus found in Minnesota is *Chrysochromulina*.

- **Pyrrhophyta -** Commonly referred to as “dinoflagellates.” They are generally unicellular. They are more common in marine environments where they form bloom conditions known as “red tides.” Some of the freshwater genera include *Gymnodium*, *Glenodinium*, *Ceratium*, and *Peridinium*. The relatively large size of some of these forms makes them relatively inedible (Wetzel 2001).
- **Other -** This includes forms that were not routinely found in the Sentinel Lakes including Euglenophyta (the "euglenoids," e.g., *Euglena*, *Phacus*) and Xanthophyta (the "yellow-green algae," e.g., *Tribonema*). These forms were noted when found.

Algal composition at the division level (Figure 4) was used in combination with chlorophyll-*a* (Chl-*a*) for the sample date to estimate the relative contribution of each division to the Chl-*a* (a proxy for biomass). Seasonal patterns were described based on Figure 4 and Figure 5. In addition, the dominant genera (and species where appropriate) are noted for each sample date. In general, the focus will be on those taxa that account for ~10% or more of the algal composition in the sample. In the tables and discussion they are referred to as “prominent.” Certain rare or uncommon species were noted as well. Reference to “blooms” follows descriptions offered in Heiskary and Wilson (2008) whereby Chl-*a* > µg/L 10 “mild bloom,” >20 µg/L “nuisance bloom,” and >30 µg/L “severe nuisance blooms.”

There are numerous algal metrics that might be used to describe the phytoplankton population and make comparisons among lakes. Two of the most basic are the total taxonomic (taxa) richness (number of different taxa identified) and total diatom taxa richness (Table 5).

Table 5. Summary of total taxa richness, diatom richness and diatom richness as percentage of total taxa. Lakes ordered on TP gradient (see Figure 2) and generally from northeast to central to southwest.

Lake-year	Total taxa richness	Diatom richness mean	Diatom richness max	% diatoms of total
Greenwood 2013	25.4	4.2	6	17%
Greenwood 2014	24.0	4.0	6	17%
Trout 2013	20.0	1.8	6	9%
Trout 2014	18.5	2.6	4	14%
Ten Mile 2013	17.2	2.2	6	13%
Bear Head 2013	25.8	3.2	4	12%
Bear Head 2014	15.0	2.7	4	18%
Tait 2013	20.8	3.2	5	15%
Carlos 2013	15.8	2.2	5	14%
Carlos 2014	13.0	2.6	3	20%
Elk 2013	15.5	2.7	5	17%
Elk 2014	19.0	3.5	5	18%
Pearl 2013	19.0	1.8	3	10%
Pearl 2014	21.2	2.8	5	13%
South Center	17.7	3.8	6	21%
St. James 2013	14.7	2.5	5	17%
Portage 2013	18.7	2.8	5	15%
Madison 2013	16.2	2.7	5	16%
Madison 2014	20.3	3.0	7	15%
Shaokotan 2013	7.6	1.0	2	13%
Shaokotan 2014	10.2	2.8	7	28%
Mean	**17.9**	**2.8**	**5**	**16%**

Zooplankton

Similar to the phytoplankton, zooplankton taxa were categorized into major divisions, based on the following functional groups:

- **Calanoid copepods -** As a group, calanoids are common among Minnesota lakes. Of those found in the Sentinel Lakes, all but one (*Epischura lacustris*) belong to the family Diaptomidae, which are very efficient phytoplankton grazers. Some species of Diaptomidae are more ubiquitous than others, due in part to the size range of phytoplankton they can graze on, as some are specialists and others generalists in their grazing abilities (Torke 2001; Van Egeren et al. 2011).
- **Cyclopoid copepods -** Cyclopoids are very common among Minnesota lakes. They are generally considered omnivorous predators, known to prey on rotifers, cladocerans, calanoids, and copepod nauplii (Williamson 1980; Stemberger 1985), although there is evidence that some adult cyclopoids, especially smaller species will graze on phytoplankton, mainly diatoms (Adrian and Frost 1993). Nevertheless, this functional group is not known to be as efficient in grazing phytoplankton as other groups (i.e., large daphnids and calanoid copepods). Recent studies (Kerfoot et al. *unpublished*) have suggested that this group of zooplankters may decrease in lakes where the invasive spiny waterflea (*Bythotrephes longimanus*) is present, due to either direct predation or competition for food resources.
- **Large daphnids -** *Daphnia pulicaria* and *Daphnia galeata mendotae* are the two large-bodied daphnids present in the Sentinel Lakes. Both of these species are efficient phytoplankton grazers and in general, are considered more passive in their phytoplankton grazing selection than calanoid copepods (Richman and Dodson 1983). Although *Daphnia* spp. are capable of grazing on poor quality food such as Cyanobacteria (blue-green algae) when higher quality food is unavailable, their growth and reproduction can be severely hindered (Haney 1987). In many lakes, large daphnids are abundant early in the season, then tend to decline due to lack of edible food and/or fish predation. In general, the Cryptophyta, Bacillariophyta, and Chlorophyta are the groups of phytoplankton that are considered high quality food for large grazers (Brett et al. 2000; Sommer et al. 1986).
- **Small cladocerans -** This group includes members of the families Bosminidae, Chydoridae, Sididae, and the smaller daphnid species. These zooplankters are common and oftentimes very abundant in Minnesota lakes. They are generally considered grazers of phytoplankton, but because of their small size they are not as efficient as the larger daphnids. This group as a whole can be outcompeted for quality food by larger daphnids, especially early in the season, but they tend to thrive later in the season. Studies have shown that this functional group of zooplankters tend to decline or even disappear in lakes where the invasive spiny waterfleas are present, due to direct predation upon them (Yan and Pawson 1997; Barbiero and Rockwell 2008; Kerfoot et al. unpublished).
- ***Holopedium* -** The species (*Holopedium gibberum*) is confined to soft water lakes generally in the northern part of Minnesota. *Holopedium gibberum* tend to graze on smaller forms of algae which are more common in less productive, oligotrophic lakes. They are also very efficient at grazing at low densities of phytoplankton (McNaught 1978). This species has a gelatinous sheath that helps protect against predation, and some studies have shown an increase in *Holopedium gibberum* abundance in spiny waterflea infested lakes (Yan and Pawson 1997).

Zooplankton seasonal patterns were examined and compared using both densities (number individuals/L) and biomass (µg/L). Similar to the phytoplankton, prominent taxa (10% or more of composition) are noted for each sampling event.

Table 6. Zooplankton taxa richness, average seasonal densities (#/L) and average seasonal biomass (µg/L). (Excludes nauplii and copepodites)

Lake-year	Total taxa richness	Average seasonal densities	Average seasonal biomass
Greenwood 2013	10	5.0	21.3
Greenwood 2014	10	3.2	12.6
Trout 2013	10	9.9	50.3
Trout 2014	10	3.8	27.7
Ten Mile 2013	13	7.1	20.1
Ten Mile 2014	13	8.2	22.8
Bear Head 2013	11	6.0	44.4
Bear Head 2014	10	5.2	39.5
Tait 2013	11	18.2	77.6
Carlos 2013	15	10.8	40.1
Carlos 2014	14	7.4	29.5
Elk 2013	11	9.9	40.3
Elk 2014	12	15.7	49.1
Pearl 2013	10	55.0	192.8
Pearl 2014	11	63.3	206.9
South Center 2013	16	19.4	106.4
St. James 2013	10	61.8	149.2
Portage 2013	12	48.7	129.5
Madison 2013	14	38.5	227.1
Madison 2014	14	53.8	304.1
Shaokotan 2013	8	89.9	1099.5
Shaokotan 2014	10	97.0	383.6
Mean	**11.9**	**29.0**	**148.8**

Lake-specific phytoplankton and zooplankton descriptions

Greenwood Lake

Greenwood Lake, one of the two Sentinel lake trout lakes, is very deep and has low TP and Chl-*a* (Table 2). Algal biomass was low in both years typically ranging from 2-5 µg/L, with peaks in spring and fall (Figure 5). Diatoms were common or present on all sample dates with *Tabellaria*, *Cyclotella*, *Synedra*, and *Asterionella* present in both years (Figure 4, Table 7). These are generally considered "clean water forms" (APHA et al. 1998). These diatoms prefer low nutrient, low pH, and high DO waters and tolerate low concentrations of organic N (Appendix 1, Table 2). Chrysophytes were present at low levels with exception of *Uroglena* in May 2014, which comprised 23% of the sample and *Dinobryon* in June 2014, accounting for 51% of total abundance. Blue-greens were found in all months and most notable from July through October with *Aphanocapsa*, *Anabaena*, and *Lyngbya* among the most common. The maximum percent blue-greens, on all sampling dates was 62% in August 2013 (Figure 4); however, Chl-*a* was 2.4 µg/L on that date (Figure 5), and this would not represent a bloom. Total taxa richness averaged 25 across the two summers and peaked at 36 taxa in 2013 (Figure 6). Diatom taxa richness averaged 4 taxa and the maximum was 6 taxa (Table 5). The general progression was diatoms and chrysophytes in May and June with an increasing presence of blue-greens from July through October. However, there were numerous forms and taxa represented on all dates and seldom any distinct dominant species.

Table 7. Prominent algal species present in Greenwood. Those species with ~10% or greater occurrence in samples.

Greenwood	2013	2014
May		*Synedra filiformis, Uroglena*
June	*Tabellaria flocculosa, Cyclotella bodanica*	*Synedra filiformis, Dinobryon bavaricum, Cryptomonas erosa*
July	*Tabellaria flocculosa Cyclotella bodanica, Aphanothece nidulans, Rhabdoderma lineare*	*Tabellaria flocculosa, Cyclotella bodanica, Asterionella formosa, Aphanothece nidulans, Aphanocapsa elachista*
August	*Asterionella formosa, Aphanizomenon gracile, Aphanizomenon flos-aquae*	*Cyclotella bodanica, Rhodomonas minuta, Lyngbya limnetica, Aphanocapsa elachista, Aphanothece nidulans*
September	*Tabellaria flocculosa, Dinobryon bavaricum, Dinobryon divergens, Aphanizomenon flos-aquae, Anabaena planctonica*	*Asterionella formosa, Rhodomonas minuta, Anabaena planctonica*
October	*Cyclotella bodanica, Aphanocapsa elachista*	*Asterionella formosa, Cryptomonas erosa, Anabaena planctonica, Aphanocapsa elachista*

Zooplankton densities and biomass in Greenwood Lake were among the lowest of all the Sentinel Lakes (Table 6). Both densities and biomass peaked mid-summer, and were relatively low, with maximum densities < 10 individuals/L and maximum biomass < 35 µg/L (Figure 7). Cyclopoid copepods were the dominant group throughout the season, contributing to > 50% of the density and biomass community composition during all sampling events (Figure 7). Calanoid copepods were relatively rare; with the very small *Leptodiaptomus minutus* being the only Diaptomidae present (Table 8). The larger grazer, *Daphnia galeata mendotae* became abundant during mid-summer, contributing to the increase in total biomass during this time and, more notably, maintained presence throughout the latter part of the season (Figure 7). *Holopedium gibberum* was also present in Greenwood Lake, with its highest densities in June and July (Figure 7). Taxa richness was below average among the Sentinel Lakes, with only 10 taxa identified (Table 6). Spiny waterfleas have been present in Greenwood Lake for at least the past decade. Similar to other spiny waterflea infested lakes, very few, if any, small cladocerans were present due to direct predation, further contributing to lower taxa richness.

The low zooplankton density and biomass are correlated to low nutrients (Figure 2) and low algal productivity (Figure 5).Seasonal patterns in phytoplankton and zooplankton were inversely related (Figure 5, Figure 7). Peak zooplankton density and biomass reduced algal biomass. This likely accounts for the higher Chl-*a* in 2014 relative to 2013 (Figure 5). The diaptomid *L. minutus* is a small species that feeds on small algae (nanoplankton) and is usually present in oligotrophic lakes, as is the case in Greenwood Lake.

Table 8. Prominent zooplankton taxa present in Greenwood Lake. Taxa with ~10% or greater occurrence in samples noted.

Greenwood	2013	2014
May	No data	cyclopoids, *Leptodiaptomus minutus*
June	cyclopoids, *Leptodiaptomus minutus*	cyclopoids, *Holopedium gibberum*
July	cyclopoids, *Leptodiaptomus minutus, Holopedium gibberum*	cyclopoids
August	cyclopoids, *Daphnia galeata mendotae*	cyclopoids, *Leptodiaptomus minutus, Daphnia galeata mendotae*
September	cyclopoids, *Daphnia galeata mendotae*	cyclopoids, *Leptodiaptomus minutus, Holopedium gibberum, Daphnia galeata mendotae*
October	cyclopoids, *Leptodiaptomus minutus, Daphnia galeata mendotae, Holopedium gibberum*	cyclopoids, *Daphnia galeata mendotae, Leptodiaptomus minutus*

Trout Lake

Trout Lake, the other Sentinel lake with lake trout, is shallower than Greenwood but likewise has very low TP and Chl-*a* (Table 2). Algal biomass was very low ranging from 1-2 µg/L on most dates (Figure 5). Diatoms were not prominent on most dates, with the exception of the June 2013 and May 2014 samples with *Cyclotella*, *Synedra*, and *Asterionella* among the more prominent forms (Table 9). These forms prefer low nutrient conditions. Chrysophytes were present on all dates, with *Dinobryon* and *Uroglena* as the most common forms. Blue-greens were found in all months and comprised 20% or more of the algal community with the exception of June 2013 (Figure 4); however as was the case with Greenwood Lake, blue-greens were far below bloom levels (Figure 5). The most common blue-green genera were *Aphanocapsa*, *Aphanothece*, and *Planktolyngbya*. Total taxa richness averaged 22 across the two summers, which was above average for all lakes (Table 5). Diatom taxa richness averaged 2.2 and their contribution to total taxa richness was 12%, both of which were below average among the Sentinel Lakes (Table 5). Diatoms were only prominent in May and June and were replaced by chrysophytes and blue-greens for the remainder of the months. The other forms were at very low levels and often represented by a few individuals.

Table 9. Prominent algal species present in Trout Lake. Species with ~10% or greater occurrence in samples noted.

Trout	2013	2014
May		Cyclotella sp.1, Cyclotella stelligera, Pseudanabaena
June	*Synedra filiformis, Asterionella formosa, Cyclotella ocellata, Chromulina, Chrysochromulina parva*	*Uroglena, Planktolyngbya, Rhodomonas minuta*
July	*Aphanothece nidulans, Pseudanabaena, Dinobryon sociale*	*Planktolyngbya*
August	*Dinobryon sociale, Aphanocapsa elachista, Pseudanabaena*	*Planktolyngbya, Aphanocapsa elachista*
September	*Aphanothece nidulans, Aphanocapsa elachista, Pseudanabaena, Dinobryon bavaricum*	*Dinobryon bavaricum, Rhodomonas minuta, Aphanocapsa elachista, Aphanothece nidulans*
October	*Aphanothece nidulans, Pseudanabaena, Aphanocapsa elachista, Dinobryon bavaricum*	*Dinobryon sociale, Dinobryon sertularia, Aphanocapsa elachista, and Aphanothece nidulans*

Total zooplankton densities in Trout Lake were relatively low among the Sentinel Lakes, although total biomass was higher than total densities (Table 6) due to the presence of larger calanoids in Trout Lake. Both densities and biomass were lower in 2014 than during 2013. In July 2013, densities peaked at a maximum of 17 individuals/L, but in 2014, maximum densities were < 6 individuals/L (Figure 7). Calanoid copepods were the dominant zooplankton group in Trout Lake both years, contributing to over 50% of the total density (Figure 7). Three species of Diaptomidae were present (*Onychodiaptomus sanguineus, Leptodiaptomus minutus,* and *Leptodiaptomus sicilis*), which are all grazers of algae of different size ranges. The dominant species, *O. sanguineus*, is unique to Trout Lake, as this species has not been documented from any other lake in Minnesota. Cyclopoid copepods were abundant early in the season during 2013, but were relatively scarce throughout the remainder of 2013 and the 2014 season. *Daphnia galeata mendotae* was present in Trout Lake throughout the season, but at low densities. *Holopedium gibberum* was present in low densities, but no small cladocerans were found in Trout Lake. Taxa richness was below average among the Sentinel Lakes, with only 10 taxa identified (Table 10). Spiny waterfleas were first detected in Trout Lake in the fall of 2011, therefore the lake is in an early infestation stage, and differences in densities and biomass between 2013 and 2014 could be due to changes from impacts of spiny waterfleas.

Zooplankton densities and biomass were higher in 2013 relative to 2014 (Figure 7) and algal biomass was lower in 2013 as compared to 2014 (Figure 5). *D. galeata mendotae* were present during the entire season likely because high quality food sources, such as diatoms and chrysophytes, were present on most dates (Table 9).

Table 10. Prominent zooplankton taxa present in Trout Lake. Taxa with ~10% or greater occurrence in samples noted.

Trout	2013	2014
May	No data	*Onychodiaptomus sanguineus, Leptodiaptomus minutus,* cyclopoids
June	Cyclopoids, *Onychodiaptomus sanguineus, Leptodiaptomus minutus*	*Onychodiaptomus sanguineus*, cyclopoids, *Holopedium gibberum*
July	*Onychodiaptomus sanguineus*, cyclopoids	*Onychodiaptomus sanguineus*, cyclopoids, *Daphnia galeata mendotae*
August	*Onychodiaptomus sanguineus*, cyclopoids	*Onychodiaptomus sanguineus, Daphnia galeata mendotae*
September	*Onychodiaptomus sanguineus*, cyclopoids, *Daphnia galeata mendotae*	*Onychodiaptomus sanguineus*
October	*Onychodiaptomus sanguineus*	*Onychodiaptomus sanguineus*, cyclopoids

Ten Mile Lake

Ten Mile Lake is the deepest of the Sentinel lakes and has very low TP and Chl-*a* (Table 2). In 2013, algal biomass was quite low and ranged from 4 µg/L in spring to about 1.5 µg/L in mid-summer (Figure 5). Diatoms were not prominent on any dates (Figure 4, Table 11). Cryptophytes were present on all dates with *Cryptomonas* being the most common genus. Chrysophytes were present on 5 of 6 dates with *Dinobryon* the most common genus. Blue-green algae were found in all months and comprised 20% or more of the algal community with the exception of June 2013 (Figure 4); however Chl-*a* was very low and though common, blue-green algae were not at bloom levels (Figure 5). The most common blue-green genera were *Pseudanabaena* and *Aphanizomenon*. Green algae comprised 10% or more of the population in July, August, and September with *Crucigenia* and *Oocystis* being the most abundant. Total taxa richness averaged 17.2 in 2013, which was below average for all lakes (Table 5). Diatom taxa richness averaged 2.2 and contributed 13% of total taxa richness; both were below average of all Sentinel Lakes (Table 5). Taxa richness was highest in September and lowest in June (Figure 6). Given this was a single year patterns in seasonal variability between years cannot be discerned. In summary, algal biomass was highest in May during spring turnover, blue-green algae were common on all dates, and diatoms were uncommon.

Table 11. Prominent algal species present in Ten Mile Lake. Species with ~10% or greater occurrence in samples noted.

Ten Mile	2013	2014
May	*Cryptomonas erosa, Pseudanabaena*	
June	*Dinobryon sociale*, *Cryptomonas erosa, Pseudanabaena limnetica*	
July	*Crucigenia tetrapedia, Cryptomonas erosa, Anabaena lemmermannii, Lyngbya limnetica*	
August	*Oocystis parva, Cryptomonas erosa Rhodomonas minuta, Aphanizomenon flos-aquae, Peridinium umbonatum*	
September	*Oocystis parva*, *Quadrigula lacustris, Dinobryon bavaricum*	
October	*Dinobryon bavaricum, Dinobryon sociale, Cryptomonas erosa, Rhodomonas minuta, Chrysochromulina parva*	

Zooplankton densities and biomass in Ten Mile Lake were very low, and seasonal averages were similar between 2013 and 2014 (Table 6). Densities and biomass peaked in mid-summer, but maximum densities were < 15 individuals/L, and maximum biomass < 50 µg/L. In Ten Mile Lake, calanoids, cyclopoids, and small cladocerans all contributed evenly to the community composition during most sampling events (Figure 7). Large daphnids were rare and contributed < 10% to the community composition during all sampling events. The dominant small cladocerans included *Bosmina longirostris* and *Daphnia longiremis* (Table 12); the latter is a small-bodied daphnid generally found below the thermocline in deep, oligotrophic lakes (Balcer et al. 1984). Two species of Diaptomidae (calanoid copepods) were present; *Skistodiaptomus oregonensis* and *Leptodiaptomus minutus*. Taxa richness was 13, which was higher than average among the Sentinel Lakes (Table 6).

Zooplankton densities increased from May through August (Figure 7), and phytoplankton biomass declined over the same period (Figure 5). Small cladocerans were numerous throughout year (Table 12), in contrast to Trout and Greenwood lakes, where they are a primary food source for spiny waterfleas. There were edible (i.e., small) algal forms available throughout the season (e.g., cryptophytes); however large daphnids were lacking possibly due to fish predation. The deep water daphnid, *D. longiremis* was present; however this form avoids predation by living below the thermocline most of the time.

Table 12. Prominent zooplankton taxa present in Ten Mile Lake. Taxa with ~10% or greater occurrence in samples noted.

Ten Mile	2013	2014
May	cyclopoids, *Daphnia longiremis*	cyclopoids
June	cyclopoids, *Leptodiaptomus minutus, Skistodiaptomus oregonensis*	cyclopoids, *Leptodiaptomus minutus, Skistodiaptomus oregonensis*
July	cyclopoids, *Leptodiaptomus minutus, Skistodiaptomus oregonensis, Bosmina longirostris*	cyclopoids, *Leptodiaptomus minutus, Skistodiaptomus oregonensis, Bosmina longirostris*
August	cyclopoids, *Leptodiaptomus minutus, Skistodiaptomus oregonensis, Bosmina longirostris, Daphnia retrocurva*	*Leptodiaptomus minutus, Skistodiaptomus oregonensis,* cyclopoids
September	cyclopoids, *Leptodiaptomus minutus, Skistodiaptomus oregonensis, Daphnia retrocurva*	*Leptodiaptomus minutus, Skistodiaptomus oregonensis,* cyclopoids, *Daphnia longiremis*
October	cyclopoids, *Bosmina longirostris, Skistodiaptomus oregonensis*	cyclopoids, *Bosmina longirostris, Skistodiaptomus oregonensis, Daphnia longiremis, Chydorus sphaericus*

Bear Head Lake

Bear Head Lake has moderate depth and relatively low TP and Chl-*a* (Table 2). Algal biomass was highest in May 2014, while summer values were 4-6 µg/L in both years (Figure 5). Diatoms were not prominent (Figure 4), with the exception of July 2014 when *Asterionella* and the green alga *Oocystis* were the only two taxa noted (Table 13). *Asterionella formosa* prefers low nutrients, pH>7.0, and can tolerate elevated levels of organically-bound N (Appendix 1, Table 2). Chrysophytes were present on 10 of 11 dates with *Dinobryon* one of the more common genera, accounting for 87% of the algal abundance in June 2014. Cryptophytes were present on most dates, with *Rhodomonas* and *Cryptomonas* common genera. Blue-greens were found in most months but comprised 30% or less of the algal abundance, with the exception of July and August 2013 when *Aphanothece* comprised 40-50% of the algal biomass (Figure 5). Given the low Chl-*a* concentrations, blue-greens were not at bloom levels on any date. Green algae comprised 10% or more of the population in July, August, and September 2013 with no single prominent taxon. Dinoflagellates, which are typically rare, comprised 30% of the sample in May 2014, with the genus *Gymnodium* being most prominent. Total taxa richness averaged 25.8 in 2013 and 15.0 in 2014, above average in 2013 but below in 2014 (Table 5) relative to all Sentinel Lakes. Diatom taxa richness averaged 3.2 and 2.7 and as a percent of total taxa was 12% and 18%, which were lower than the Sentinel Lakes average (Table 5). There was no consistent pattern in taxa richness during the two years and the higher richness in 2013, was associated with the presence of numerous rare species (Figure 6). In summary, algal biomass was highest in May 2014 at spring turnover. Chrysophytes, blue-greens, and cryptophytes (in that order) were the most common forms on all dates and diatoms were rather uncommon.

Table 13. Prominent algal species present in Bear Head Lake. Species with ~10% or greater occurrence in samples noted.

Bear Head	2013	2014
May		*Dinobryon sociale, Cryptomonas erosa, Rhodomonas minuta Gymnodinium*
June	*Dinobryon divergens, Dinobryon sertularia, Stichogloea olivacea, Cryptomonas erosa, Aphanothece nidulans*	*Uroglena*
July	*Dinobryon divergens, Aphanothece nidulans*	*Asterionella formosa, Oocystis parva*
August	*Synura, Cryptomonas erosa, Aphanothece nidulans*	*Dinobryon divergens, Rhodomonas minuta, Aphanocapsa elachista*
September	*Synura, Woronichinia naegeliana*	*Chrysosphaerella longispina, Aphanizomenon flos-aquae*
October	*Synura, Uroglena, Woronichinia naegeliana*	*Chrysosphaerella longispina, Aphanizomenon flos-aquae,*

Zooplankton densities in Bear Head Lake were low, but biomass was relatively higher, in this case due to the presence of large-bodied daphnids throughout the season (Table 6, Figure 7). Zooplankton densities peaked in October both years, but maximum densities were only ~10 individuals/L, while biomass peaked in July of both years, at ~90 µg/L (Figure 7). All five functional groups were present in Bear Head Lake, but cyclopoids and large daphnids (*Daphnia galeata* and *Daphnia pulicaria*) contributed the highest percentages to the community composition, in densities and biomass, during most sampling events (Figure 7). Only one species of Diaptomidae (*Skistodiaptomus oregonensis*) was present in Bear Head Lake (Table 14). Taxa richness was average among the Sentinel Lakes, with 11 and 10 taxa identified in 2013 and 2014, respectively (Table 6).

Phytoplankton and zooplankton did not exhibit consistent patterns between years or correspond to each other (Figure 5, Figure 7); however, the maximum algal biomass in May 2014 occurred when zooplankton were at their minimum densities and biomass. There were abundant edible algae throughout the year (e.g., cryptophytes), which may have allowed large daphnids to persist throughout the season, despite fish predation.

Table 14. Prominent zooplankton taxa present in Bear Head Lake. Taxa with ~10% or greater occurrence in samples noted.

Bear Head	2013	2014
May	No data	*Daphnia pulicaria*, *Skistodiaptomus oregonensis*, cyclopoids
June	*Daphnia pulicaria*, cyclopoids	cyclopoids, *Daphnia pulicaria*, *Skistodiaptomus oregonensis*, *Holopedium gibberum*
July	*Daphnia pulicaria*, cyclopoids, *Daphnia galeata mendotae*	*Daphnia pulicaria*, *Daphnia galeata mendotae*
August	cyclopoids, *Skistodiaptomus oregonensis, Daphnia pulicaria*	*Daphnia pulicaria*, cyclopoids
September	cyclopoids, *Skistodiaptomus oregonensis, Daphnia galeata mendotae*	cyclopoids, *Skistodiaptomus oregonensis, Daphnia pulicaria, Daphnia galeata mendotae*
October	cyclopoids, *Daphnia galeata mendotae, Daphnia pulicaria*	cyclopoids, *Daphnia galeata mendotae, Skistodiaptomus oregonensis, Daphnia pulicaria*

Tait Lake

Tait Lake is quite shallow and has 100% littoral habitat; however, it has very low TP (Table 2). Algal biomass was low with Chl-*a* in the 4-5 µg/L range (Figure 5). Diatoms were present on all dates (Figure 4) but seldom in large abundance (Table 15). *Fragilaria crotonensis* was the sole prominent form, which prefers low nutrients, pH>7.0, and moderately high DO (Appendix 1, Table 2). Cryptophytes were present on all dates, with *Cryptomonas* and *Rhodomonas* the most common genera. Chrysophytes were present on all dates and *Uroglena* comprised 76% of the sample in June 2013 and *Synura* was prominent in July. Blue-greens were found in all months and increased in abundance from June to October, with *Woronichinia* and *Gomphosphaeria* being the prominent forms (Figure 4). Green algae were not common and there were no prominent forms. Total taxa richness averaged 20.8 in 2013, which was above average for all lakes (Table 5). Diatom taxa richness averaged 3.2 and as a percent of total taxa was 15% (Table 5). Taxa richness peaked in August and declined thereafter (Figure 6). Given that we only collected a single year of data, seasonal patterns cannot be discerned. In summary, algal biomass was low and stable across the summer (Figure 5). Chrysophytes were prominent early and gave way to the blue-greens as the season progressed (Figure 4).

Table 15. Prominent algal species present in Tait Lake. Species with ~10% or greater occurrence in samples noted.

Tait	2013	2014
May		
June	*Uroglena*	
July	*Synura, Cryptomonas erosa, Rhodomonas minuta, Merismopedia tenuissima*	
August	*Fragilariacrotonensis, Dinobryon divergens, Rhodomonas minuta*	
September	*Rhodomonas minuta, Woronichinia naegeliana, Gomphosphaeria lacustris*	
October	*Rhodomonas minuta, Woronichinia naegeliana, Gomphosphaeria lacustris*	

Zooplankton densities and biomass were below average relative to all the Sentinel Lakes (Table 6). During most months densities were relatively low (< 20 individuals/L) with the exception of August when densities doubled (Figure 7). The increase in densities in August was due to the abundance of small cladocerans, mostly *Bosmina longirostris* and *Chydorus sphaericus* (Table 16). Biomass also peaked in August and was > 100 µg/L. Similar to Bear Head Lake, all five functional groups were represented during most sampling events. Overall, no particular group was dominant, except for the small cladocerans in August, which contributed 70% to the community composition in densities, but because of their small size, contributed to only 30% of the biomass (Figure 7). Large daphnids (*Daphnia galeata mendotae* and *Daphnia pulicaria*) were present throughout the entire season and contributed to over 50% of the biomass in both June and again in September and October (Table 16). Only one Diaptomidae species (*Skistodiaptomus oregonensis*) was present in Tait Lake. *Holopedium gibberum* was present and most abundant in June. Taxa richness, at 11, was average among the Sentinel Lakes (Table 6).

With only one year of data, patterns were hard to discern. There were good food sources available for large daphnids, with diatoms and cryptophytes present throughout season (Figure 5). Since Tait Lake is shallow, fish predation may be a limiting factor on large daphnids, especially *D. pulicaria*, which seem to be present only early (June) and late (October) in the year, with *D. galeata mendotae* dominant during the summer. The latter can develop helmets to protect against fish and invertebrate predation.

Table 16. Prominent zooplankton taxa present in Tait Lake. Taxa with ~10% or greater occurrence in samples noted.

Tait	2013	2014
May	No data	
June	*Holopedium gibberum, Daphnia galeata mendotae, Skistodiaptomus oregonensis, Daphnia pulicaria*	
July	cyclopoids, *Daphnia galeata mendotae, Bosmina longirostris, Diaphanosoma birgei, Skistodiaptomus oregonensis*	
August	*Chydorus sphaericus, Bosmina longirostris,* cyclopoids, *Skistodiaptomus oregonensis*	
September	*Daphnia galeata mendotae,* cyclopoids, *Skistodiaptomus oregonensis*	
October	*Daphnia pulicaria*, cyclopoids, *Skistodiaptomus oregonensis, Daphnia galeata mendotae*	

Lake Carlos

Lake Carlos is the second deepest Sentinel Lake and has low TP and very low Chl-*a* (Table 2). In 2013 and 2014 Chl-*a* ranged from 1-3 µg/L on most dates (Figure 5). Diatoms were not prominent (Figure 4) with the exception of *Fragilaria* in October 2013 and September 2014 (Table 17). Chrysophytes were prominent in May and June with *Dinobryon* being common. Cryptophytes were present on most dates with *Rhodomonas* and *Cryptomonas* commonly recorded. Blue-greens were present in most months and were most abundant in August and September, with *Aphanocapsa* and *Anabaena* the most common genera (Figure 4). Green algae comprised >20% of the community in July and August 2013 and an unidentified Chlorococcaceae was most abundant (Table 17). Total taxa richness was low relative to other lakes with 15.8 and 13.0 taxa present in 2013 and 2014, respectively (Table 5). This was above average in 2013 but below average in 2014 among Sentinel Lakes (Table 5). Diatom taxa richness averaged 2.2 and 2.6 and was below average. Total taxa richness peaked in August in both years (Figure 6). Chrysophytes are dominant in May and June, with a transition to blue-greens, cryptophytes, and some greens from July through September. Cryptophytes, diatoms, and chrysophytes were prominent in October coinciding with fall mixing.

Table 17. Prominent algal species present in Lake Carlos. Species with ~10% or greater occurrence in samples noted.

Carlos	2013	2014
May	*Dinobryon sertularia, divergens, bavaricum; Rhodomonas minuta*	*Dinobryon sociale, divergens*
June	*Dinobryon divergens, sertularia*	*Cyclotella, Chrysosphaerella longispina, Dinobryon sociale*
July	*Chlorococcaceae, Stichogloea olivacea, Cryptomonas erosa, Aphanocapsa elachista*	*Dinobryon sociale, Chrysosphaerella longispina*
August	*Chlorococcaceae, Anabaena circinalis, Aphanocapsa elachista*	*Chrysosphaerella longispina, Aphanocapsa elachista, Chrysochromulina parva*
September	*Cryptomonas erosa, Rhodomonas minuta, Aphanocapsa elachista*	*Fragilaria crotonensis, Rhodomonas minuta, Aphanocapsa elachista, Aphanocapsa delicatissima*
October	*Fragilaria crotonensis, Cryptomonas erosa, Rhodomonas minuta*	*Dinobryon bavaricum, Cryptomonas erosa, Rhodomonas minuta*

Seasonal zooplankton densities and biomass were low in Lake Carlos, especially during 2014 (Table 6). Densities peaked during June for both years, with a maximum of 17 individuals/L in 2013, but only 9 individuals/L in 2014. Biomass peaked in July of 2013, at 70 µg/L, while peak biomass in 2014 was < 50 µg/liter and occurred in October with increased biomass of *Daphnia galeata mendotae* (Figure 7, Table 18). Cyclopoids contributed over 50% to the community composition in densities and biomass during most sampling periods, with the remaining a combination of calanoids (*Skistodiaptomus oregonensis*) and small cladocerans including *Bosmina longirostris*, *Daphnia retrocurva*, and *Daphnia longiremis*. (Among the Sentinel Lakes, *D. longiremis* was only present in Carlos and Ten Mile lakes). Large daphnids (*D. galeata mendotae*) were present in low densities throughout the season, with the exception of October of 2014, where they contributed over 30% to the community composition in both densities and biomass (Figure 7). Taxa richness was above average among the Sentinel Lakes, with 15 and 14 taxa identified in 2013 and 2014, respectively (Table 6).

Increased zooplankton density and biomass in June and July 2013 (Figure 7) resulted in a decline in algal biomass (Figure 5). As zooplankton declined there were subtle increases in algal biomass. High quality food was present in Lake Carlos, with cryptophytes present on most dates, and green algae present during the summer. *D. galeata mendotae* was present in low numbers throughout season, likely because of the abundance of edible algae. Lake Carlos was the only lake in this study that had zebra mussels present. Research from other lakes with zebra mussels suggest that they may compete for food with large grazing daphnids (Dzialowski 2013; Kissman et al. 2010), which may already be the case in Lake Carlos. As zebra mussels have become more abundant in recent years, zooplankton densities have decreased (see “Invasive species impacts on phytoplankton, zooplankton, and water quality” section of this report), although more data are necessary to test for statistical significance.

Table 18. Prominent zooplankton taxa present in Lake Carlos. Taxa with ~10% or greater occurrence in samples noted.

Carlos	2013	2014
May	cyclopoids	cyclopoids
June	cyclopoids, *Bosmina longirostris, Skistodiaptomus oregonensis*	cyclopoids, *Bosmina longirostris*
July	cyclopoids, *Skistodiaptomus oregonensis, Bosmina longirostris, Daphnia retrocurva*	cyclopoids, *Skistodiaptomus oregonensis, Daphnia retrocurva, Bosmina longirostris*
August	cyclopoids, *Skistodiaptomus oregonensis, Daphnia galeata mendotae*	cyclopoids, *Skistodiaptomus oregonensis, Daphnia retrocurva, Bosmina longirostris*
September	cyclopoids, *Skistodiaptomus oregonensis, Bosmina longirostris*	cyclopoids, *Skistodiaptomus oregonensis, Daphnia longiremis*
October	cyclopoids, *Skistodiaptomus oregonensis, Bosmina longirostris, Daphnia galeata mendotae*	cyclopoids, *Daphnia galeata mendotae, Skistodiaptomus oregonensis*

Elk Lake

Elk Lake is quite deep and has moderate TP and low Chl-*a* (Table 2). Algal biomass in Elk Lake was variable with Chl-*a* ranging from 7-8 µg/L in May, then declining to ~2-4 µg/L in June through August, followed by an increase to 5-9 µg/L in September or October (Figure 5). Diatoms were prominent and present on most dates (Figure 4). *Asterionella* and *Cyclotella* were common (Table 19). *A. formosa* prefers low-moderate nutrients, pH>7.0, and can tolerate elevated concentrations of organically-bound N (Appendix 1, Table 2). Chrysophytes were prominent on several dates and were represented by *Synedra* and *Dinobryon*. Cryptophytes were present in low numbers on most dates with the exception of October 2013, when *Cryptomonas* accounted for 41% of the phytoplankton (Figure 4). Blue-greens were present in most months and abundant in July, August, and September with *Aphanizomenon*, *Aphanocapsa*, and *Anabaena* the most common genera (Figure 4). Green algae were present in many of the samples but there were no prominent genera noted (Table 19). The dinoflagellate, *Ceratium*, was prominent (Table 19) on two dates (Figure 4). Total taxa richness was low in 2013 and increased in 2014 (Figure 6), and no consistent pattern was evident. Diatom taxa richness averaged 2.7 and 3.5 taxa, accounting for 17% and 18% of total taxa, which was average for the Sentinel Lakes. Chrysophytes and diatoms were dominant in May and June, with a transition to blue-greens, cryptophytes, and some greens from July through September. Diatoms and chrysophytes are prominent in October with the onset of fall mixing.

Table 19. Prominent algal species present in Elk Lake. Species with ~10% or greater occurrence in samples noted.

Elk	2013	2014
May	*Asterionella formosa, Dinobryon sertularia, Cryptomonas erosa, Aphanizomenon flos-aquae*	*Diatoma tenuis, Cyclotella ocellata, Dinobryon sociale*
June	*Cyclotella hakanssoniae, Synedra ulna, Dinobryon sociale*	*Stephanodiscus medius, Gloeocystis, Dinobryon bavaricum, Ceratium hirundinella*
July	*Chlorococcaceae, Anabaena lemmermannii, Ceratium hirundinella*	*Oocystis parva, Dinobryon sociale, Anabaena lemmermannii, augstumalis, circinalis*
August	*Cyclotella hakanssoniae, Anabaena lemmermannii,*	*Synedra tenera, Aphanocapsa elachista, delicatissima; Aphanothece nidulans*
September	*Synura, Cryptomonas erosa, Aphanocapsa elachista*	*Dinobryon divergens, Aphanizomenon gracile, Woronichinia naegeliana, Anabaena macrospora*
October	*Cryptomonas erosa, Rhodomonas minuta*	*Dinobryon divergens, sociale; Aphanizomenon gracile*

Seasonal zooplankton densities in Elk Lake were variable, with higher densities in 2014 than in 2013 (Table 6). However, seasonal patterns were similar between the two years, with peak densities occurring in June, followed by very low densities (10 or fewer individuals/L) for the remainder of the season (Figure 7). Average biomass between the two years was less variable and was low relative to all the Sentinel Lakes (Table 6). Biomass peaked during June of both years, with a maximum of > 120 µg/L in 2014. Cyclopoids contributed the most to community composition, followed by calanoids (*Skistodiaptomus oregonensis*) and small cladocerans (*Bosmina longirostris* and *Daphnia retrocurva*) (Table 20). Large daphnids (*Daphnia galeata mendotae*) were relatively rare, and only in October 2013 did they contribute to at least 10% of the community composition in densities (Figure 7). Taxa richness was average among the Sentinel Lakes, with 11 and 12 taxa collected in 2013 and 2014, respectively (Table 6).

In general, as zooplankton increased, phytoplankton decreased in Elk Lake (Figure 7, Figure 5). Edible algae, including diatoms, cryptophytes and greens, were available throughout the season, although in relatively low numbers. In October 2013, cryptophytes were the dominant form (Figure 4) and this was the only sampling event with large daphnids prominent (*D. galeata mendotae*) (Table 20). Elk Lake stratifies by June and dissolved oxygen (DO) falls to 0 mg/L below the thermocline (O'Hara et al. 2011). This may limit migration of zooplankton below the thermocline and allow for fish predation of daphnids and other large zooplankton.

Table 20. Prominent zooplankton taxa present in Elk Lake. Taxa with ~10% or greater occurrence in samples noted.

Elk	2013	2014
May	cyclopoids, *Skistodiaptomus oregonensis*	cyclopoids
June	cyclopoids, *Skistodiaptomus oregonensis, Bosmina longirostris*	cyclopoids, *Daphnia retrocurva, Bosmina longirostris*
July	*Skistodiaptomus oregonensis,* cyclopoids, *Daphnia retrocurva, Bosmina longirostris*	cyclopoids, *Daphnia retrocurva, Bosmina longirostris, Skistodiaptomus oregonensis*
August	cyclopoids, *Skistodiaptomus oregonensis, Daphnia retrocurva*	cyclopoids, *Daphnia retrocurva, Skistodiaptomus oregonensis*
September	cyclopoids, *Daphnia retrocurva, Skistodiaptomus oregonensis*	cyclopoids, *Skistodiaptomus oregonensis, Daphnia retrocurva*
October	cyclopoids, *Daphnia retrocurva, Skistodiaptomus oregonensis, Daphnia galeata mendotae*	cyclopoids, *Bosmina longirostris*

Pearl Lake

Pearl Lake is shallow relative to other lakes in this study, has moderate nutrient concentrations (Figure 2), and has extensive macrophyte growth. Algal biomass in Pearl Lake was low in May (<5 µg/L) but increased quickly thereafter (Figure 5). Nuisance blooms (Chl-*a*>20 µg/L) occurred on 3 of 6 dates in 2013 but only one date in 2014 and blue-greens were the most common form on all dates with blooms (Figure 5). Diatoms were prominent in May, with *Asterionella* and *Fragilaria* common and indicative of mildly eutrophic conditions (Table 21), but diatoms were relatively absent during other months (Figure 4). The chrysophyte, *Dinobryon*, was prominent in June of 2013 and again in October of 2014, but uncommon in other months (Table 21). Green algae were present on several dates with *Oocystis* the most abundant. The haptophyte, *Chrysochromulina*, was prominent in September and October 2014 (Figure 5). The pyrrhophyte, *Ceratium*, was present on several dates and was prominent (Table 21) on two dates. Blue-greens were dominant from June through September in both years with *Microcystis* the most common genus, followed by *Anabaena*. Total taxa richness was lowest in May and June and increased over the summer in both years (Figure 6). Diatom taxa richness was relatively low (Table 5). The general transition in algal forms includes diatoms, cryptophytes, and green and blue-green algae in May and June; then blue-green algae dominate from July through September. Taxa richness increased during fall mixing, including some less common forms like the haptophytes.

Table 21. Prominent algal species present in Pearl Lake. Species with ~10% or greater occurrence in samples noted.

Pearl	2013	2014
May	*Asterionella formosa, Fragilaria crotonensis, Microcystis aeruginosa*	*Oocystis parva, Rhodomonas minuta*
June	*Oocystis parva, Dinobryon divergens, Microcystis aeruginosa, Ceratium hirundinella*	*Microcystis aeruginosa, Microcystis wesenbergii*
July	*Microcystis aeruginosa*	*Microcystis aeruginosa, Microcystis wesenbergii*
August	*Anabaena lemmermannii, Anabaena crassa, Anabaena planctonica; Microcystis aeruginosa, Microcystis wesenbergii*	*Microcystis aeruginosa, Microcystis wesenbergii*
September	*Anabaena crassa, Microcystis aeruginosa, Microcystis wesenbergii; Ceratium hirundinella*	*Microcystis aeruginosa, Chrysochromulina parva*
October	*Microcystis aeruginosa, Microcystis wesenbergii*	*Dinobryon divergens, Chrysochromulina parva*

Zooplankton densities and biomass in Pearl Lake were higher than average among the Sentinel Lakes (Table 6). Seasonal density patterns varied between the two years, with densities peaking at 140 individuals/L in May 2014 (Figure 7). Maximum biomass occurred during May of both years, with 400 and 900 µg/L, in 2013 and 2014, respectively (Figure 7). Large daphnids (*Daphnia galeata mendotae*) contributed up to 80% of this early peak in biomass, but were not detected by July (Figure 7). Community composition in Pearl Lake changed as the seasons progressed, with the general pattern consisting of *D. galeata mendotae* in May and June, followed by an increase in cyclopoids and small cladocerans (*Diaphanosoma birgei*, *Daphnia retrocurva*, and *Chydorus sphaericus*) during the latter part of the season (Table 22). Calanoid copepod densities varied throughout the season, but were relatively low, with only one species (*Skistodiaptomus oregonensis*) present (Figure 7, Table 22). Taxa richness was average among the Sentinel Lakes, with 10 and 11 taxa identified in 2013 and 2014, respectively (Table 6).

When zooplankton densities and biomass peaked (Figure 7), algal biomass was low (Figure 5), and when zooplankton declined over summer, algal biomass increased. Edible forms early in May and June (Cryptophytes, diatoms and greens) allowed for concurrent increases in large daphnids (*D. galeata mendotae*). When edible forms were replaced by blue-greens, (*Microcystis* and *Anabaena*), large daphnids were no longer present.

Table 22. Prominent zooplankton taxa present in Pearl Lake. Taxa with ~10% or greater occurrence in samples noted.

Pearl	2013	2014
May	*Daphnia galeata mendotae*, cyclopoids, *Bosmina longirostris*	*Daphnia galeata mendotae*, cyclopoids, *Skistodiaptomus oregonensis*
June	*Daphnia galeata mendotae*, cyclopoids	*Daphnia galeata mendotae, Chydorus sphaericus,* cyclopoids,
July	cyclopoids, *Skistodiaptomus oregonensis*	*Chydorus sphaericus, Skistodiaptomus oregonensis,* cyclopoids
August	cyclopoids, *Skistodiaptomus oregonensis, Diaphanosoma birgei*	cyclopoids, *Chydorus sphaericus, Diaphanosoma birgei*
September	cyclopoids, *Daphnia retrocurva*	cyclopoids
October	cyclopoids, *Chydorus sphaericus, Daphnia retrocurva*	cyclopoids

South Center Lake

South Center Lake is nutrient-rich (Figure 2). The lake is deep, but has a substantial littoral area (Table 2), with extensive growth of curly-leaf pondweed (*Potamageton crispus*). Algal biomass was high in May 2013 during spring turnover but decreased by June (Figure 5). Nuisance blue-green blooms were observed from July through September. The cryptophytes, *Cryptomonas* and *Rhodomonas*, along with the haptophyte, *Chrysochromulina*, were prominent in May (Figure 5). The dinoflagellate, *Ceratium*, was the dominant form in June (Table 23). Blue-greens were dominant from July through September, and this included some genera that are not common in the other Sentinel Lakes, such *as Cylindrospermopsis*. Total taxa richness was lowest in May and highest in July through September (Figure 6). Diatom taxa richness was high relative to total richness (Table 5), but represented a very small part of the overall biomass. The general transition in algal forms included a diverse community in May and June, including diatoms, cryptophytes, haptophytes, and pyrrhophytes. Blue-greens dominated from July through September. A shift in dominance (Figure 4) occurred during fall mixing, with cryptomonads dominant, along with blue-greens.

Table 23. Prominent algal species present in South Center Lake. Species with ~10% or greater occurrence in samples noted.

South Center	2013	2014
May	*Rhodomonas minuta, Cryptomonas erosa, Chrysochromulina parva*	
June	*Ceratium hirundinella, Anabaena lemmermannii*	
July	*Cuspidothrix issatschenkoi, Woronichinia naegeliana, Microcystis aeruginosa, Anabaena planctonica, Anabaena crassa*	
August	*Cylindrospermopsis raciborskii, Anabaena planctonica, Anabaena macrospora, Anabaena aphanizomenoides*	
September	*Aphanizomenon flos-aquae, Cuspidothrix issatschenkoi, Cylindrospermopsis raciborskii*	
October	*Cryptomonas erosa, Aphanizomenon flos-aquae*	

South Center Lake was only sampled during 2013. Zooplankton densities and biomass were comparable to the Sentinel Lakes means (Table 6). Densities peaked in May, with 30 individuals/L while biomass peaked in June with 190 µg/L (Figure 7). Similar to Pearl Lake, zooplankton community composition changed as the season progressed. Cyclopoids were dominant in May (Figure 7, Table 24), then large daphnids (*Daphnia pulicaria*) appeared in June, but disappeared by July, when the community was composed of a mix of cyclopoids, small cladocerans (*Diaphanosoma birgei*, *Daphnia retrocurva*, *and Eubosmina coregoni*) and calanoid copepods (*Leptodiaptomus siciloides*) for the remainder of the season (Figure 7, Table 24). Although *Leptodiaptomus siciloides* was the only prominent calanoid species (10% or greater occurrence), there were three other Diaptomidae present in South Center Lake (*Skistodiaptomus oregonensis*, *Leptodiaptomus sicilis*, and *Aglaodiaptomus clavipes*). *A. clavipes* is a large species, generally found co-existing with the smaller *L. siciloides* in eutrophic lakes. *Skistodiaptomus oregonensis* is a ubiquitous species, while *L. sicilis* is generally found in deeper, less productive lakes (Torke 2001, Hirsch 2014). The presence of *L. sicilis* in South Center Lake is somewhat surprising, as although this lake is very deep, it also is very productive. Taxa richness, at 16, was the highest of all the Sentinel Lakes (Table 6).

Zooplankton density and biomass peaked in May and June when numerous edible algal forms were present (e.g., cryptophytes and diatoms). Large *Daphnia pulicaria* were prominent in June, but when edible algae were replaced by blue-greens, large daphnids were not found (Figure 7). The large daphnids were replaced by small cladocerans, especially small *Daphnia retrocurva* and *Eubosmina coregoni*. As blue-green blooms senesced in October, edible algal forms increased (Figure 5) and zooplankton densities and biomass increased (Figure 7).

Table 24. Prominent zooplankton taxa present in South Center Lake. Taxa with ~10% or greater occurrence in samples noted.

South Center	2013	2014
May	cyclopoids, *Bosmina longirostris*	
June	cyclopoids, *Daphnia pulicaria, Leptodiaptomus siciloides*	
July	*Diaphanosoma birgei, Leptodiaptomus siciloides*	
August	*Daphnia retrocurva, Leptodiaptomus siciloides,* cyclopoids, *Diaphanosoma birgei*	
September	*Daphnia retrocurva,* cyclopoids, *Eubosmina coregoni, Leptodiaptomus siciloides*	
October	cyclopoids, *Eubosmina coregoni, Leptodiaptomus siciloides, Daphnia retrocurva*	

St. James Lake

St. James Lake is shallow and nutrient-rich (Figure 2). It has extensive coverage of curly-leaf pondweed. Algal biomass was moderate in May 2013 during spring turnover and declined in June (Figure 5). There were nuisance bloom levels of blue-green algae from July through September. The diatom *Fragilaria* and green algal *Scenedesmus* were dominant and all other forms were represented by few individuals in May. In June, *Asterionella* was most dominant and *Cryptomonas* and *Anabaena* were prominent (Table 25). Blue-greens were the dominant form and *Microcystis* was the dominant genus from July through September. Cryptomonads were dominant in October with *Cryptomonas* and *Rhodomonas* the most common genera. Total taxa richness was lowest in May and increased through the summer (Figure 6). Diatom taxa richness was average relative to all Sentinel Lakes, comprising 17% of the total taxa (Table 5). The general transition in algal forms included a variety of taxa in May and June, including diatoms and cryptophytes. In July through September blue-greens dominated. A shift to cryptophytes again being dominant occurred during fall mixing (Figure 4).

Table 25. Prominent algal species present in St. James Lake. Species with ~10% or greater occurrence in samples noted.

St. James	2013	2014
May	*Fragilaria crotonensis, Scenedesmus bijuga*	
June	*Asterionella formosa, Cryptomonas erosa, Anabaena lemmermannii*	
July	*Microcystis aeruginosa, Microcystis wesenbergii*	
August	*Microcystis aeruginosa*	
September	*Microcystis aeruginosa, Tetraedron muticum*	
October	*Cryptomonas erosa, Rhodomonas minuta, Anabaena lemmermannii*	

Although average seasonal zooplankton densities were high in St. James Lake compared to the other Sentinel Lakes, biomass was closer to average (Table 6). The lower biomass was due to the abundance of small cladocerans during most of the season. The seasonal averages for St. James Lake may be misleading, as both zooplankton densities and biomass decreased substantially after May, resulting in high seasonal variability. St. James Lake had high densities (180 individuals/L) and biomass (600 µg/L) during May, but lower densities and biomass for the remainder of the season (Figure 7). In May, about half of the community density was composed of cyclopoid copepods and the other half small cladocerans (*Chydorus sphaericus*). In June, the dominant species was the large daphnid (*Daphnia galeata mendotae*). During the remainder of the season, a mix of small cladocerans contributed to the majority of the community density and biomass composition (Figure 7), including *Bosmina longirostris*, *Chydorus sphaericus*, *Ceriodaphnia sp*., and *Diaphanosoma birgei* (Table 26). Interestingly, St. James Lake was the only Sentinel Lake where calanoid copepods were not detected during any sampling event. Taxa richness was below the Sentinel Lakes average, with only 10 taxa identified throughout the study (Table 6).

Edible algae were present in May and June (e.g., cryptophytes and diatoms) and large *D. galeata mendotae* were prominent in June (Table 26). From July - September blue-greens (Microcystis) were dominant and mostly small cladocerans were present. As Microcystis blooms senesced in October, edible forms were again present (Table 25); however, large daphnids did not reappear in this lake as they sometimes do in other lakes. This may be a result of the shallow lake depth and lack of refugia for large daphnids.

Table 26. Prominent zooplankton taxa present in St. James Lake. Taxa with ~10% or greater occurrence in samples noted.

St. James	2013	2014
May	cyclopoids, *Chydorus sphaericus*	
June	*Daphnia galeata mendotae*, cyclopoids, *Bosmina longirostris*	
July	*Bosmina longirostris, Ceriodaphnia sp.*	
August	*Diaphanosoma birgei, Chydorus sphaericus, Ceriodaphnia sp., Bosmina longirostris*	
September	*Bosmina longirostris, Ceriodaphnia sp.*	
October	*Bosmina longirostris, Chydorus sphaericus*	

Portage Lake

Portage Lake is shallow, has abundant macrophytes, and is seasonally-dominated by curly-leaf pondweed. Relative to other NLF ecoregion lakes it is more nutrient enriched (Table 2). Algal biomass in Portage Lake was moderate in May (7 µg/L), declined in June and ranged from 15-38 µg/L in July through September. Algal biomass declined again in October (Figure 5). There were nuisance blooms (Chl-*a*>20 µg/L) on 2 of 6 dates in 2013 (Figure 4). The chrysophyte, *Dinobryon* and the cryptophyte, *Cryptomonas* were the dominant genera in May, with the haptophyte, *Chrysochromulina* also prominent (Table 27). In June the chlorophyte, *Schroederia* and an unidentified Chlorococcaceae were prominent and blue-greens were present with *Anabaena* the most abundant form. July was characterized by high diversity with the chrysophytes, *Chromulina* and *Dinobryon* prominent. Other prominent genera included the dinoflagellate, *Ceratium*; the haptophyte, *Chrysochromulina*; and an uncommon blue-green genus, *Cyanogranis*. Diversity remained high in August with six divisions represented (Figure 4). Blue-greens increased in significance, with *Aphanizomenon* and *Pseudoanabaena* the most prominent. Fall mixing and cooling of the lake was marked by an increase in the cryptophytes and haptophytes (Table 27). Total taxa richness increased from May through September and declined in October (Figure 6). Total taxa and diatom taxa richness were average relative to the Sentinel Lakes (Table 5). The general transition in algal forms included a variety of taxa in May with cryptophytes and haptophytes being prominent, while greens and blue-greens dominated in June. From July through September, a variety of forms were noted with blue-greens and cryptophytes the most prominent. In October, cryptophytes and haptophytes returned to prominence. While diatoms were present on all dates they were seldom prominent.

Table 27. Prominent algal species present in Portage Lake. Species with ~10% or greater occurrence in samples noted.

Portage	2013	2014
May	*Cryptomonas erosa, Dinobryon sociale, Chrysochromulina parva*	
June	*Schroederia judayi, Chlorococcaceae, Anabaena circinalis*	
July	*Chromulina, Dinobryon sociale, Cyanogranis ferruginea, Chrysochromulina parva, Ceratium hirundinella*	
August	*Synedra filiformis, Cryptomonas erosa, Pseudanabaena limnetica, Aphanizomenon gracile*	
September	*Aphanizomenon gracile, Cryptomonas erosa*	
October	*Cryptomonas erosa, Rhodomonas minuta, Chrysochromulina parva*	

Seasonal zooplankton densities were high relative to the other Sentinel Lakes, but biomass was closer to average (Table 6). The high densities were due to the abundance of small cladocerans, peaking in October (140 individuals/L), while maximum biomass occurred in June (500 µg/L) due to the abundance of large daphnids and calanoid copepods (Figure 7). Similar to other more productive Sentinel Lakes, zooplankton densities, biomass, and community composition changed substantially as the season progressed (Table 28). During May, cyclopoid copepods contributed to over 90% of the relative zooplankton abundance, but densities and biomass were relatively low. In June, densities and biomass increased due to the presence of large daphnids (*Daphnia galeata mendotae*) and calanoids (*Skistodiaptomus oregonensis*) but decreased substantially in July through September. In October, densities peaked due to the abundance of small cladocerans (*Bosmina longirostris*), although total biomass remained relatively low. Taxa richness was average among the Sentinel Lakes, with 12 taxa identified (Table 6).

Edible algal forms were available throughout the season (Table 27). Large daphnids were only present during June (Figure 7, Table 28) and algae were reduced accordingly (Figure 5). Cryptophytes appeared again in July-September but large daphnids did not. Again, there is an absence of refugia in this shallow lake absent the abundant curly-leaf pondweed.

Table 28. Prominent zooplankton taxa present in Portage Lake. Taxa with ~10% or greater occurrence in samples noted.

Portage	2013	2014
May	cyclopoids	
June	*Daphnia galeata mendotae, Skistodiaptomus oregonensis*, cyclopoids	
July	*Skistodiaptomus oregonensis, Bosmina longirostris,* cyclopoids	
August	cyclopoids, *Skistodiaptomus oregonensis, Bosmina longirostris*	
September	*Bosmina longirostris,* cyclopoids	
October	*Bosmina longirostris*	

Madison Lake

Madison Lake is one of the deepest lakes in the WCP ecoregion (Table 2) and is nutrient rich (Figure 2). It has 50% littoral areal coverage and extensive macrophytes, with curly-leaf pondweed among the dominant forms. Algal biomass in May varied between the two years (5 µg/L in 2013 and 35 µg/L in 2014), but diatoms were dominant in May of both years (Table 29). Diatom nutrient preference ranged from oligotrophic (*Asterionella formosa* and *Aulacoseira granulata*) to hypereutrophic (*Synedra filiformis* and *Stephanodiscus parvus*). Diatom pH preference is >7.0 for all taxa, with *S. parvis* obligate to pH>7.0. June had moderate Chl-*a* concentrations in both years (10-16 µg/L), with diatoms dominant in 2013 but blue-greens dominate in 2014. June through September of both years had nuisance-level blooms with July 2013 having concentrations of 100 µg/L. The blooms were dominated by the blue-greens *Aphanizomenon* and *Anabaena*. *Microcystis*, *Cylindrospermopsis*, *Lyngbya*, and *Cuspidothrix* were noted as well (Table 29). Nuisance blooms *of Planktothrix*, *Aphanizomenon*, and *Pseudoanabaena* continued into October during 2013. In October 2014 algal biomass was very low and the cryptophytes were dominant (Figure 4). Total taxa richness was low in May and peaked in August or September (Figure 6). The reduced taxa richness in July was a result of the complete dominance of the blue-green forms. Diatom taxa richness was near average relative to the Sentinel Lakes as a whole and comprised 15-16% of the total taxa (Table 5). The general transition in algal forms began with diatoms in May, varied taxa in June (diatoms were dominant in 2013 and blue-greens in 2014). July through September was marked by blue-green dominance with several genera represented. Taxa identities in October varied, with high Chl-*a* associated with a blue-green dominated system in 2013 and low Chl-*a* related to cryptophyte dominance in 2014 (Figure 4).

Table 29. Prominent algal species present in Madison Lake. Species with ~10% or greater occurrence in samples noted.

Madison	2013	2014
May	*Asterionella formosa, Chrysochromulina parva*	*Nitzschia acicularis, Stephanodiscus parvus, Synedra filiformis*
June	*Fragilaria crotonensis, Stephanodiscus niagarae*	*Anabaena lemmermannii, circinalis, Aphanizomenon flos-aquae*
July	*Aphanizomenon flos-aquae, Anabaena lemmermannii, Microcystis aeruginosa*	*Aulacoseira granulate, Stephanodiscus parvus, Woronichinia naegeliana*
August	*Aphanizomenon flos-aquae, Anabaena lemmermannii, Cylindrospermopsis raciborski Microcystis aeruginosa*	*Anabaena lemmermannii, circinalis, Cylindrospermopsis raciborskii, Cuspidothrix issatschenkoi, Lyngbya limnetica, lagerheimia, Cylindrospermopsis raciborskii*
September	*Planktothrix agardhii, Cylindrospermopsis raciborskii, Aphanizomenon flos-aquae, Microcystis aeruginosa*	*Aulacoseira granulate, Cryptomonas erosa, Planktothrix agardhii, Anabaenacircinalis, Cylindrospermopsis raciborskii*
October	*Planktothrix agardhii, Anabaena lemmermannii, Aulacoseira granulata*	*Cryptomonas erosa*

Zooplankton densities and biomass in Madison Lake were higher than average for the Sentinel Lakes (Table 6). Densities peaked both years during October at ~100 individuals/L in 2013 and ~120 individuals/L in 2014 (Figure 7). Biomass was more variable than densities between the two years, peaking in October 2014 at 600 µg/L (Figure 7). Although seasonal density patterns were similar between the two years at the functional group level, species composition was different. Cyclopoids and large daphnids were the dominant groups during May and June of both years, but in 2013 *Daphnia pulicaria* was the prominent large daphnid, while in 2014 it was replaced by *Daphnia galeata mendotae* (Table 30). Calanoids were more abundant during 2013 than in 2014, and both *Leptodiaptomus siciloides* and the larger *Aglaodiaptomus clavipes* were prominent in 2013. In 2014, among calanoids, only *Leptodiaptomus siciloides* was present but not prominent (Table 30). Small cladocerans were present during September and October of both years. During 2013, *Diaphanosoma birgei*, *Eubosmina coregoni*, and *Chydorus sphaericus* were prominent species, whereas in 2014, *Daphnia retrocurva* and *Eubosmina coregoni* were prominent species. Taxa richness was 14 and above average for the Sentinel Lakes (Table 6).

Edible algal forms were present in May of both years and into June during 2013 (Figure 5). Zooplankton densities and biomass were relatively low until October in both years. The difference in daphnid species from 2013-2014 could be due to higher abundances of the blue-green algae, *Aphanizomenon flos-aquae* in 2013, which co-exists with large *D. pulicaria* (Lynch 1980; Lynch and Shapiro 1981). More edible forms (greens, cryptophytes and diatoms) were present in 2014 compared to 2013. This may have allowed the persistence of *D. galeata mendotae* later in the year in 2014.

Table 30. Prominent zooplankton taxa present in Madison Lake. Taxa with ~10% or greater occurrence in samples noted.

Madison	2013	2014
May	cyclopoids, *Daphnia pulicaria*	cyclopoids, *Daphnia galeata mendotae*
June	*Daphnia pulicaria*	*Daphnia galeata mendotae*, cyclopoids
July	*Daphnia pulicaria, Daphnia galeata mendotae*, cyclopoids	cyclopoids
August	cyclopoids, *Leptodiaptomus siciloides, Aglaodiaptomus clavipes*	cyclopoids
September	cyclopoids, *Leptodiaptomus siciloides, Diaphanosoma birgei*	cyclopoids, *Daphnia retrocurva*
October	cyclopoids, *Eubosmina coregoni*, *Chydorus sphaericus*	cyclopoids, *Eubosmina coregoni*, *Daphnia galeata mendotae*

Lake Shaokotan

Lake Shaokotan is the shallowest of the Sentinel Lakes (Figure 2) and is nutrient rich. It is 100% littoral but typically is depauperate of macrophytes, because of high algal concentrations and low transparency. However, anecdotal reports in 2014 and preliminary plant survey results (Donna Perleberg, MN DNR personal communication 2015) indicated a robust community of macrophytes across the lake. Algal biomass was highly variable between the two years (Figure 5). May Chl-*a* concentrations were low in both years with cryptophytes, *Rhodomonas* and *Cryptomonas* among the dominant forms in 2013 and relatively equal dominance by a diatom, a cryptophyte, and a blue-green in 2014 (Table 31). In June through September in both years, blue-greens were dominant; however there was higher algal biomass in 2013, with 4 of 6 months having nuisance blooms, compared to none in 2014 (Figure 5). While several blue-green genera were found, *Aphanizomenon* was consistently the dominant genus, which has long been the case for Shaokotan (Engel et al. 2009). With the low algal biomass in 2014, some cryptophytes and diatoms were among the prominent forms in 2014 (Table 31). *Aulacoseira granulata* prefers eutrophic conditions, pH>7.0, moderate DO, and can tolerate elevated organically-bound N (Appendix 1, Table 2). Total taxa richness in Lake Shaokotan was the lowest of the Sentinel Lakes, as was diatom richness (Table 5). In 2013, taxa richness declined from May to September, whereas in 2014 it increased over this same period (Figure 6). Diatoms were more abundant in 2014, and they comprised 28% of the total taxa. Based on long-term observations (various unpublished MPCA reports), the 2013 transition from cryptophytes and diatoms in May to complete blue-green dominance throughout the summer was typical. In contrast, a mix of cryptophytes, diatoms and blue-greens were present on all dates in 2014, but blue-greens dominated in July through September, but were at non-bloom levels.

Table 31. Prominent algal species present in Lake Shaokotan. Species with ~10% or greater occurrence in samples noted.

Shaokotan	2013	2014
May	*Rhodomonas minuta, Cryptomonas erosa*	*Surirella, Rhodomonas minuta, Chlorococcaceae, Synechococcus*
June	*Anabaena circinalis, lemmermannii, Gloeotrichia echinulata*	*Aulacoseira granulatae, Aphanizomenon flos-aquae, Anabaena lemmermannii*
July	*Aphanizomenon flos-aquae,*	*Anabaena circinalis, Microcystis aeruginosa, Aphanizomenon flos-aquae*
August	*Aphanizomenon flos-aquae*	*Aulacoseira granulate, Mallomonas, Aphanizomenon flos-aquae, Anabaena circinalis*
September	*Aphanizomenon flos-aquae, Microcystis aeruginosa, Pseudanabaena limnetica*	*Aphanizomenon flos-aquae, Anabaena circinalis, Cryptomonas rostratiformis*
October		*Cyclotella, Cocconeis placentula, Cryptomonas erosa*

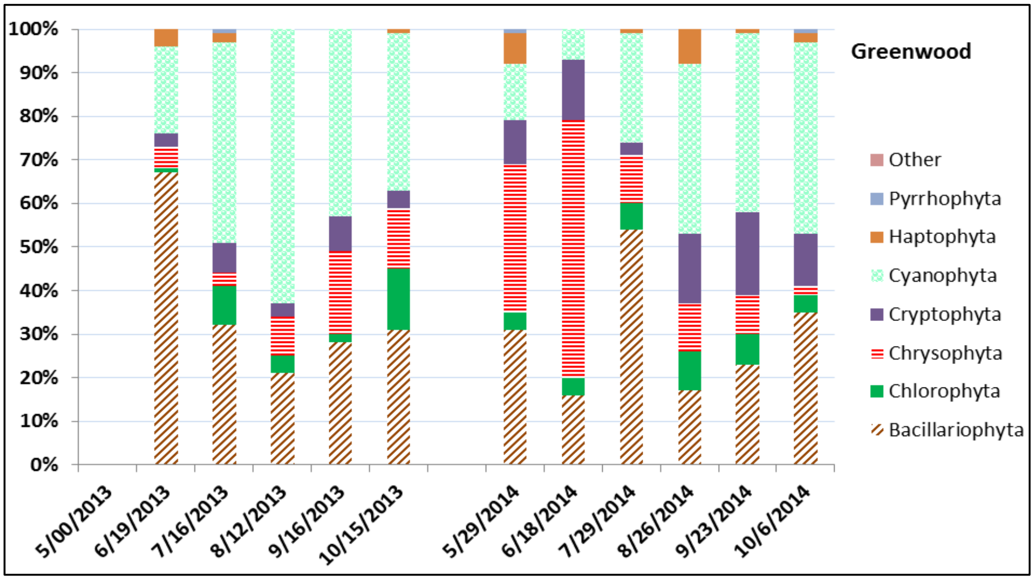
Lake Shaokotan had the highest average zooplankton densities and biomass of all the Sentinel Lakes (Table 6). Although densities were similar between years, biomass and community composition differed. Maximum biomass during 2013 was >3000 µg/L, while in 2014 biomass peaked at 500 µg/L (Figure 7). Average seasonal biomass decreased from 1099 µg/L in 2013 to 384 µg/L in 2014 (Table 6). This enormous loss of biomass was due to the decrease of large daphnids (*Daphnia pulicaria*) in 2014. During August and September of 2013, *D. pulicaria* contributed >95% of the biomass, whereas in 2014 they contributed < 5% during these same months (Figure 7). The seasonal pattern during 2013 consisted of low densities of cyclopoids and calanoids in May, followed by continued increasing densities of calanoids (*Aglaodiaptomus clavipes*), large daphnids (*Daphnia pulicaria*), and small cladocerans (*Chydorus sphaericus* and *Ceriodaphnia sp.*) through September (Figure 7, Table 32). Densities decreased in October to levels similar to the previous spring (Figure 7). Seasonal patterns were different during 2014, with a more even distribution of functional groups throughout the season (Figure 7). Calanoid copepods contributed a higher percentage to the community composition in densities and biomass during 2014, and the prominent species was *Leptodiaptomus siciloides* rather than *A. clavipes*, which was prominent in 2013 (Table 32). Taxa richness was the lowest of all the Sentinel Lakes during 2013, with only 8 taxa present, but increased to 10 in 2014 (Table 6).

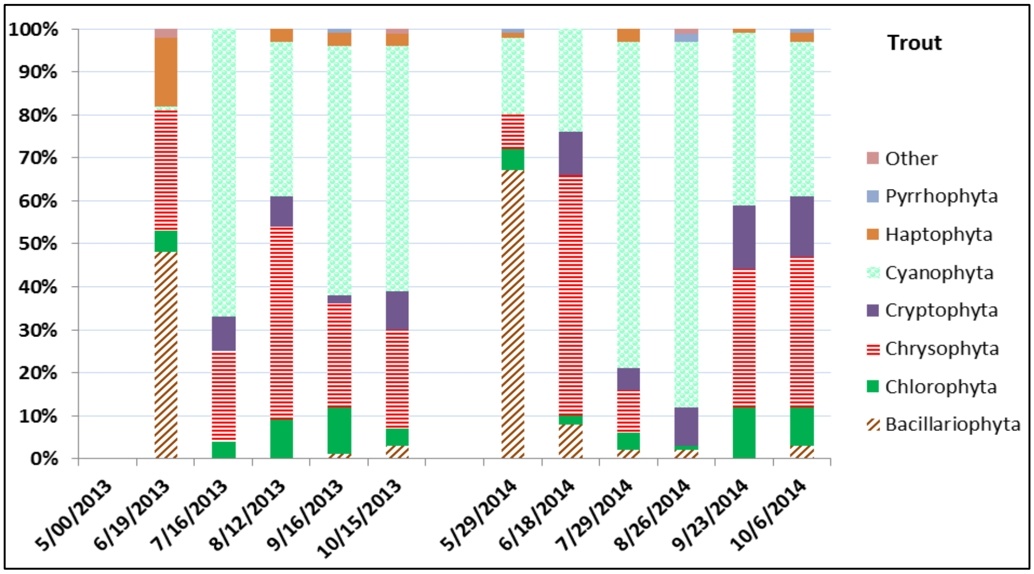
Edible algal forms were present in May of both years, although they had low biomass (Figure 5, Table 31). *Daphnia pulicaria* were present in June of both years, with high densities and biomass through the season in 2013, when *Aphanizomenon flos-aquae* was the dominant blue-green algae (similar to Madison Lake). In 2014, algal biomass was low and *Aphanizomenon* was not the sole dominant blue-green. Low algal biomass and lack of *Aphanizomenon* contributed to lower zooplankton biomass and a general lack of large daphnids (Figure 7, Table 32). The presence of rooted plants in 2014 apparently did not provide adequate refugia for the large daphnids in this instance, or alternately, there was insufficient food to support them.

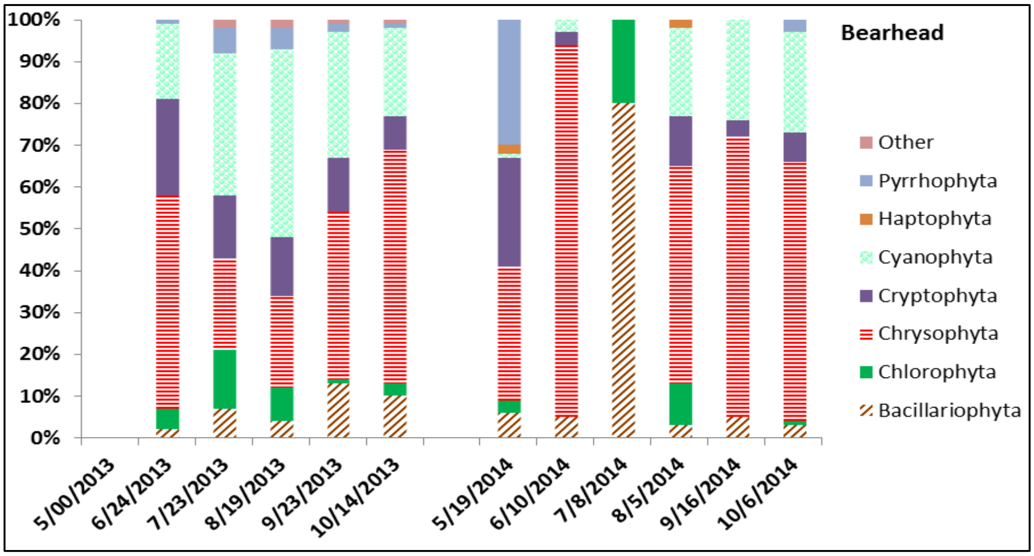
Table 32. Prominent zooplankton taxa present in Lake Shaokotan. Taxa with ~10% or greater occurrence in samples noted.

Shaokotan	2013	2014
May	cyclopoids, *Aglaodiaptomus clavipes*, *Daphnia pulicaria*	*Leptodiaptomus siciloides*, cyclopoids
June	*Aglaodiaptomus clavipes*, *Daphnia pulicaria*	*Leptodiaptomus siciloides*, *Daphnia pulicaria*
July	*Aglaodiaptomus clavipes*, *Daphnia pulicaria*, cyclopoids, *Chydorus sphaericus*	*Leptodiaptomus siciloides*, *Diaphanosoma birgei*, *Ceriodaphnia sp.*, cyclopoids
August	*Daphnia pulicaria*, *Ceriodaphnia sp.*, *Chydorus sphaericus*	*Leptodiaptomus siciloides*, *Ceriodaphnia sp.*, cyclopoids
September	*Daphnia pulicaria*, *Chydorus sphaericus*	*Ceriodaphnia sp.*, *Leptodiaptomus siciloides*, cyclopoids
October	*Daphnia pulicaria*, *Aglaodiaptomus clavipes*, *Leptodiaptomus siciloides*, cyclopoids	*Leptodiaptomus siciloides*, cyclopoids

Figure 4. Phytoplankton percent composition at division level for 2013 & 2014. Lakes sorted by TP.







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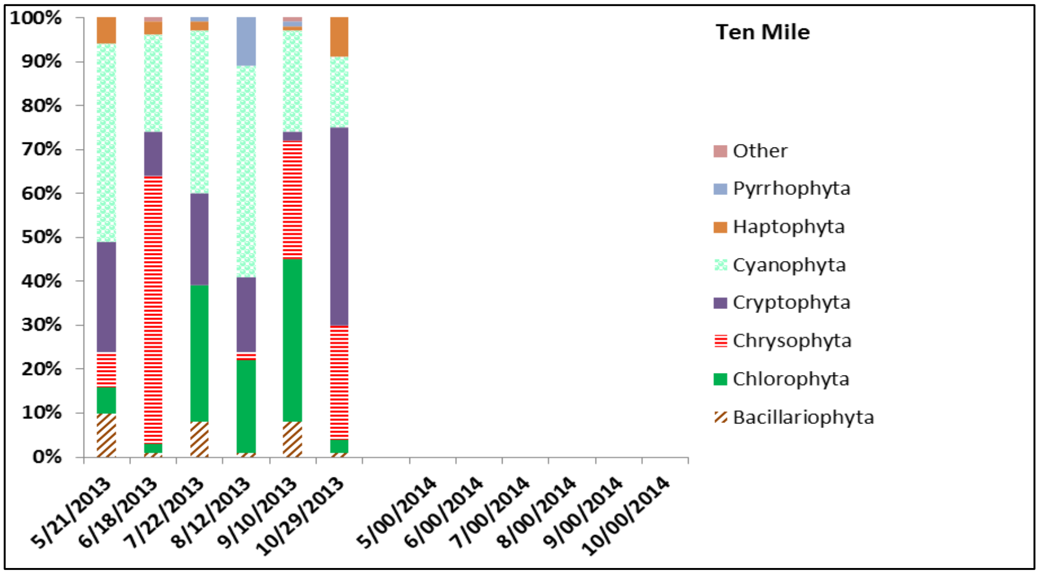

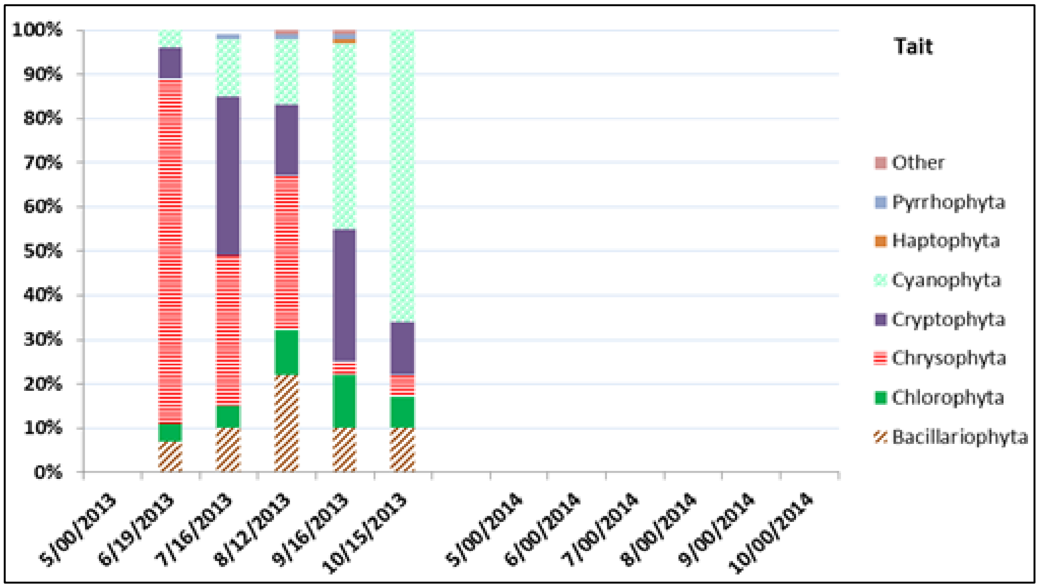

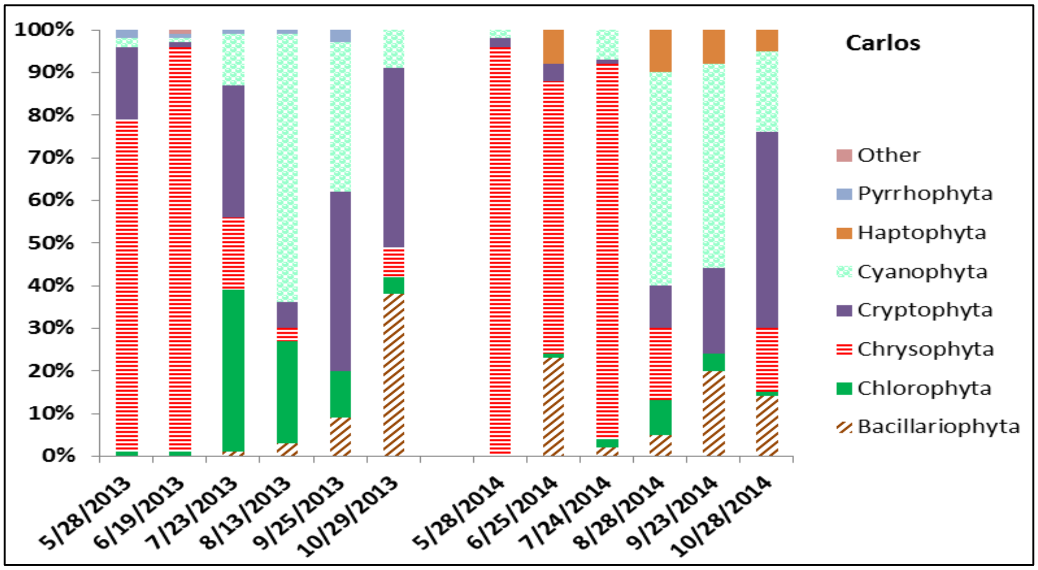

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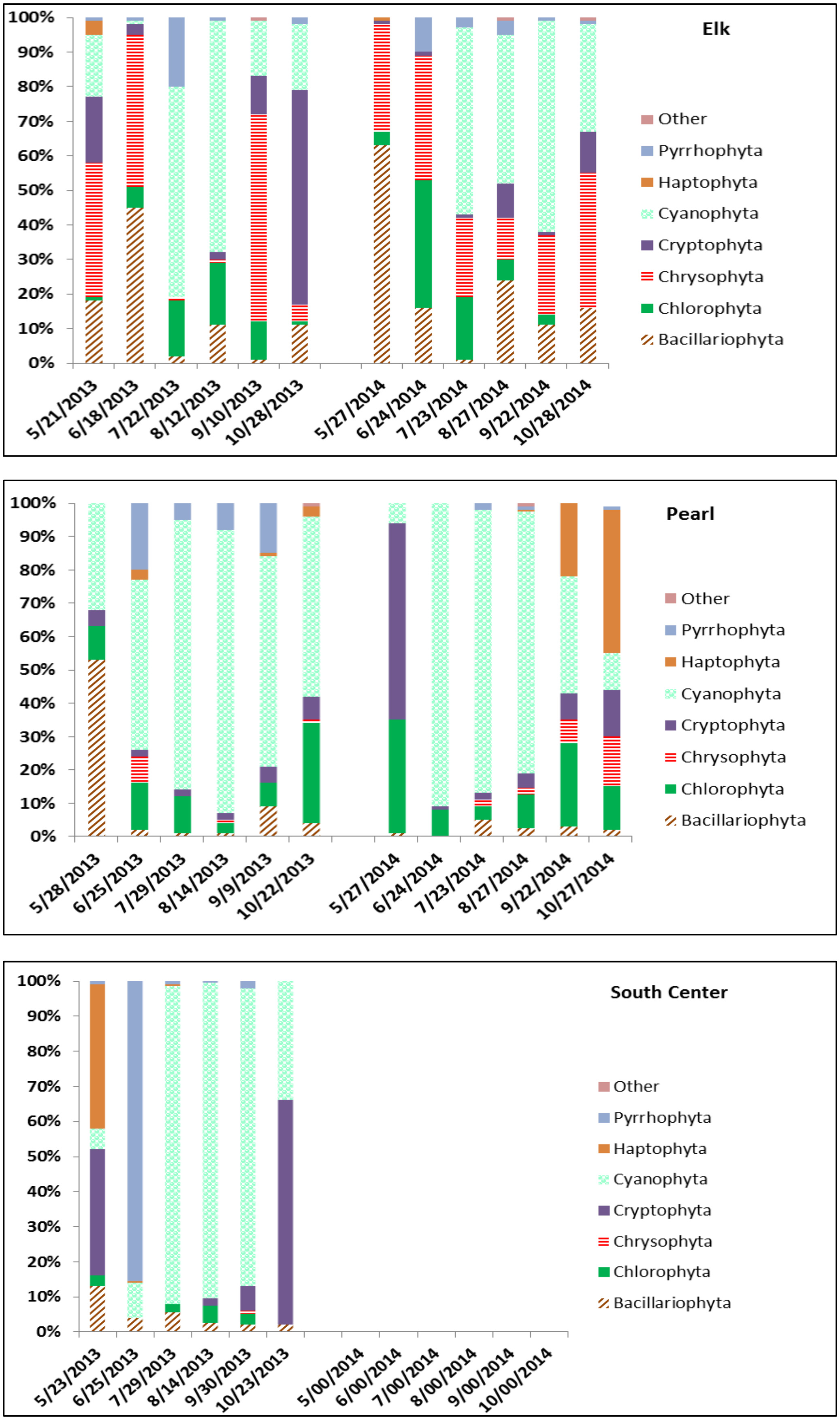

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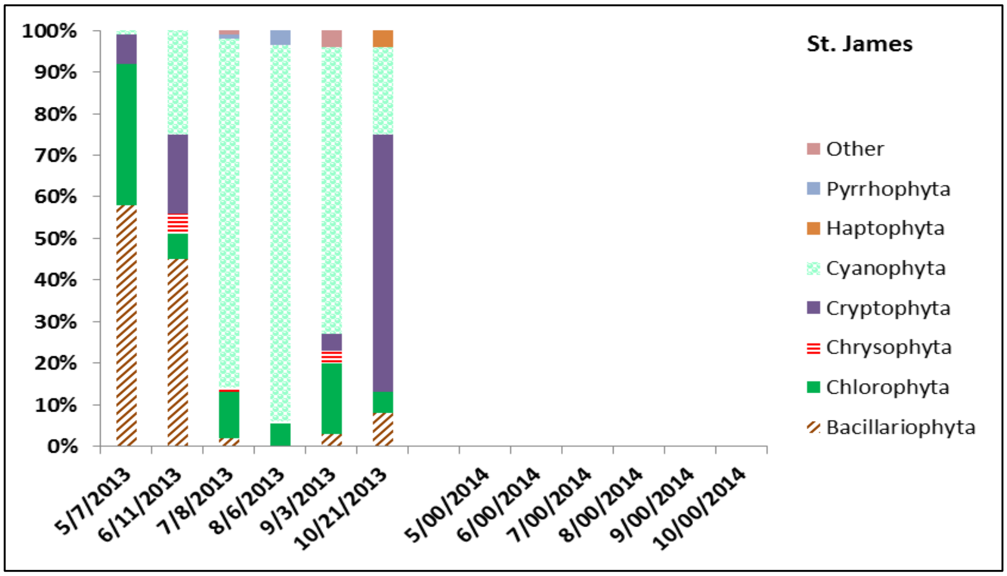

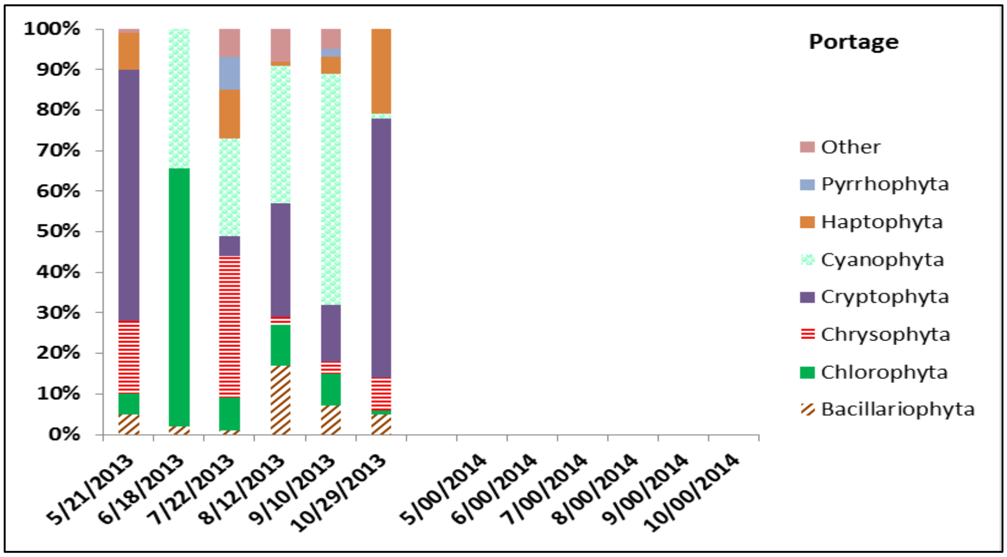

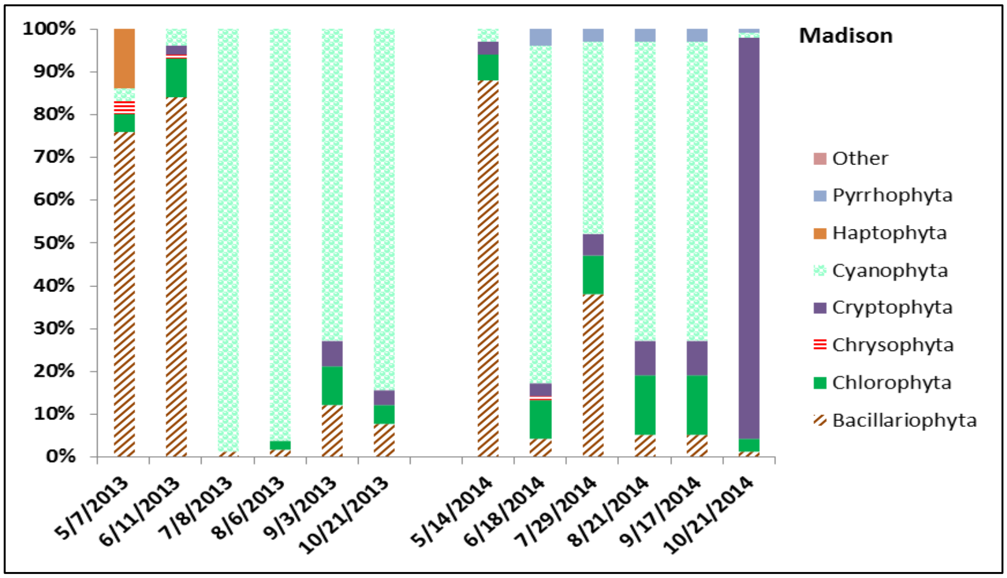

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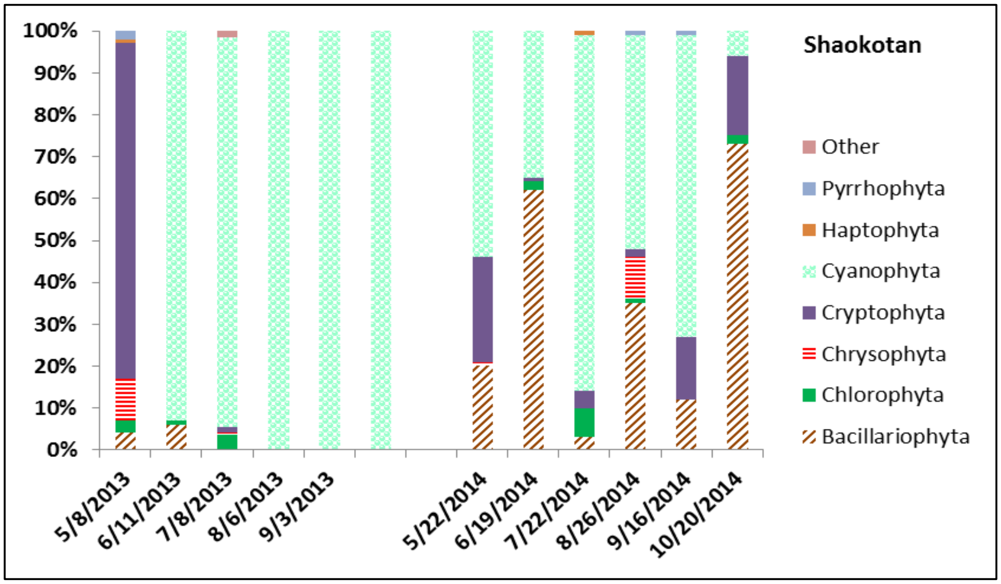
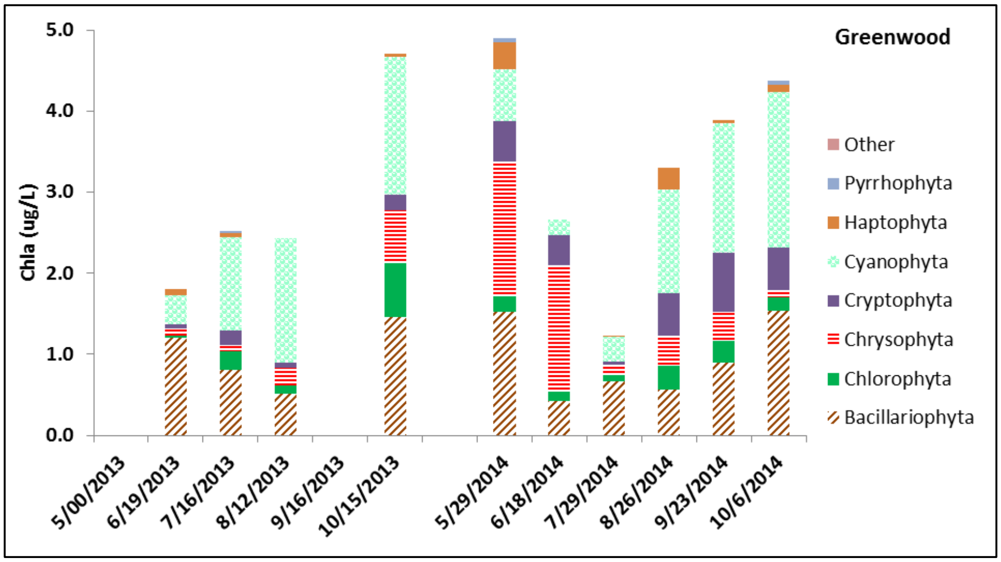


Figure 5. Relative percent composition of chlorophyll-a by algal division (type). Lakes sorted by TP.



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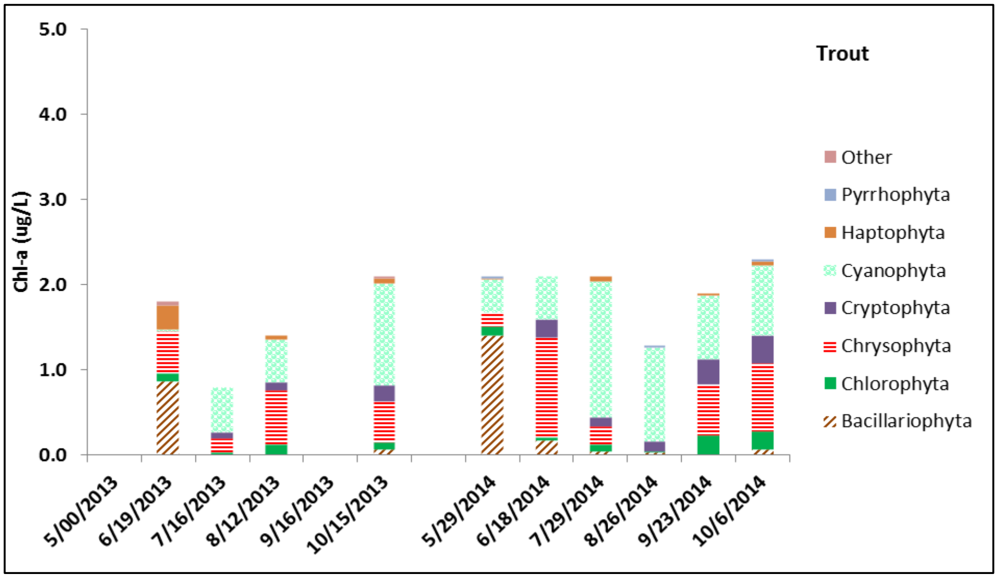

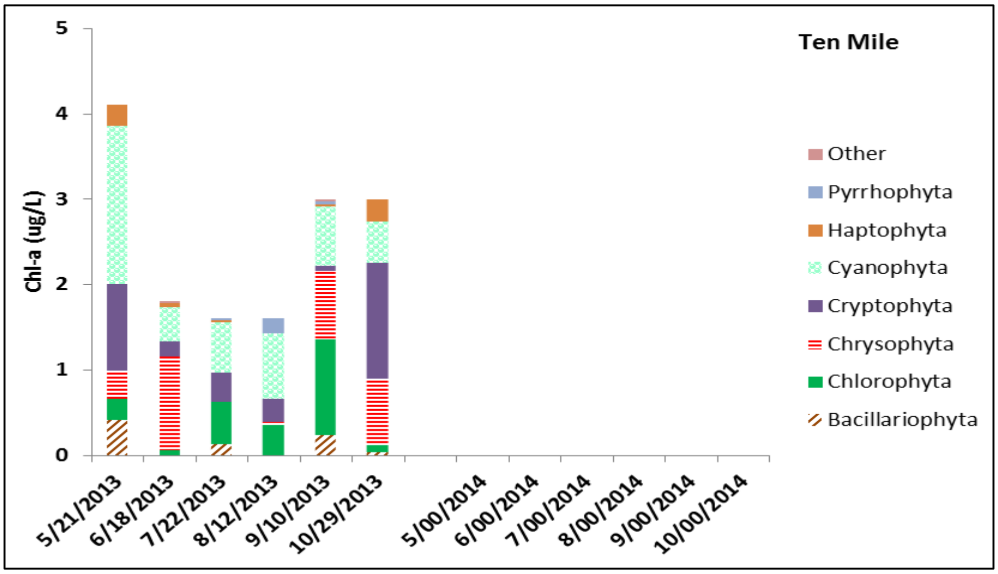

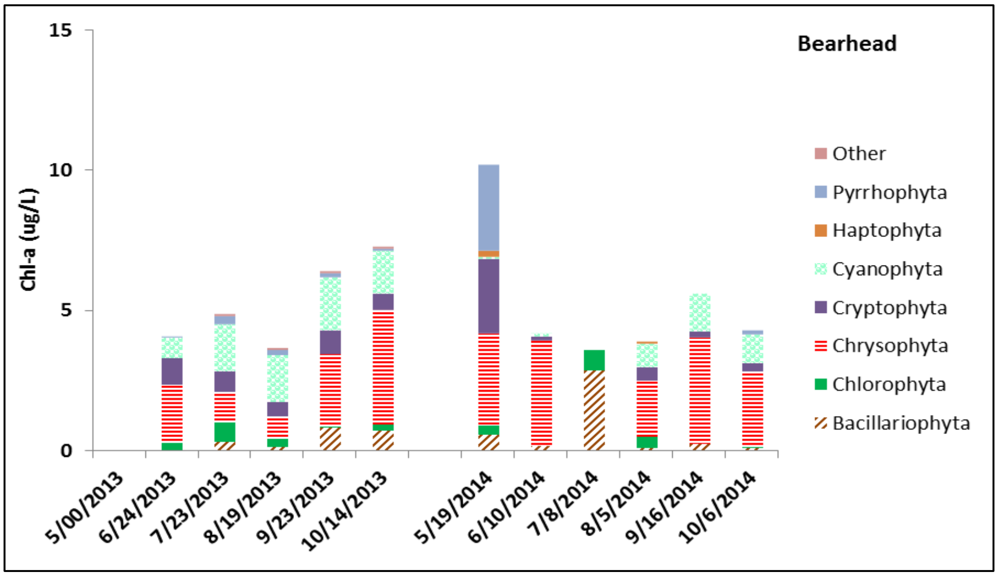

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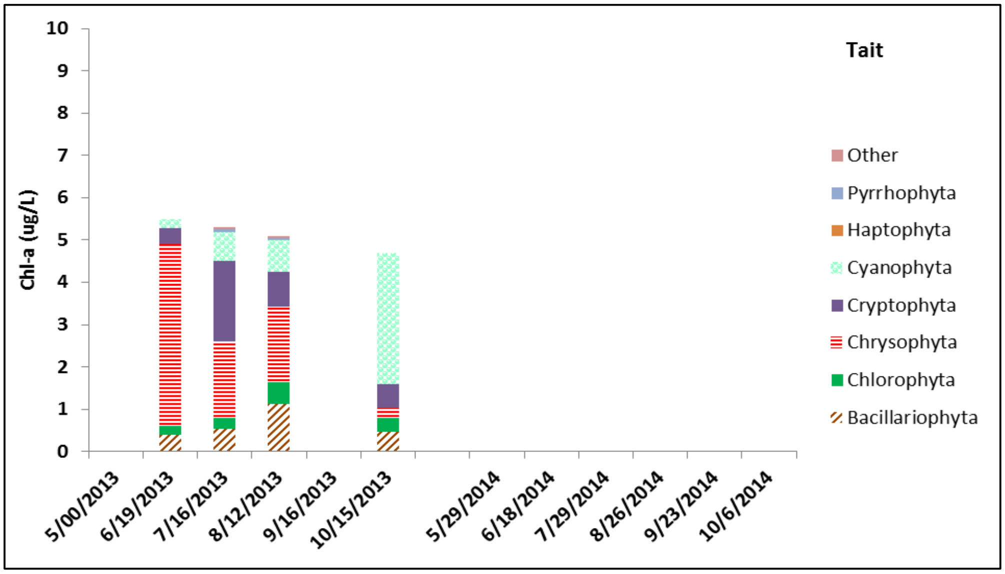

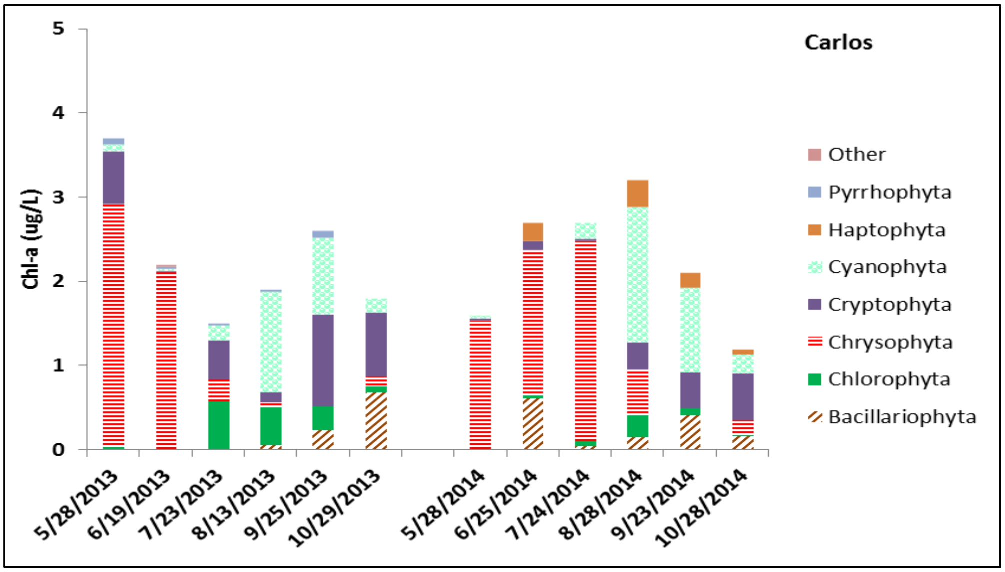

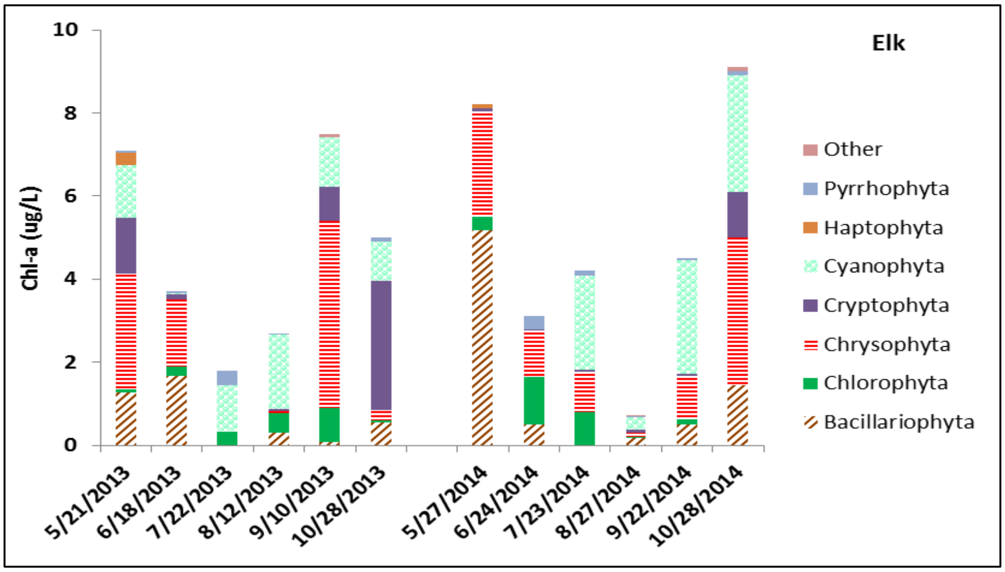

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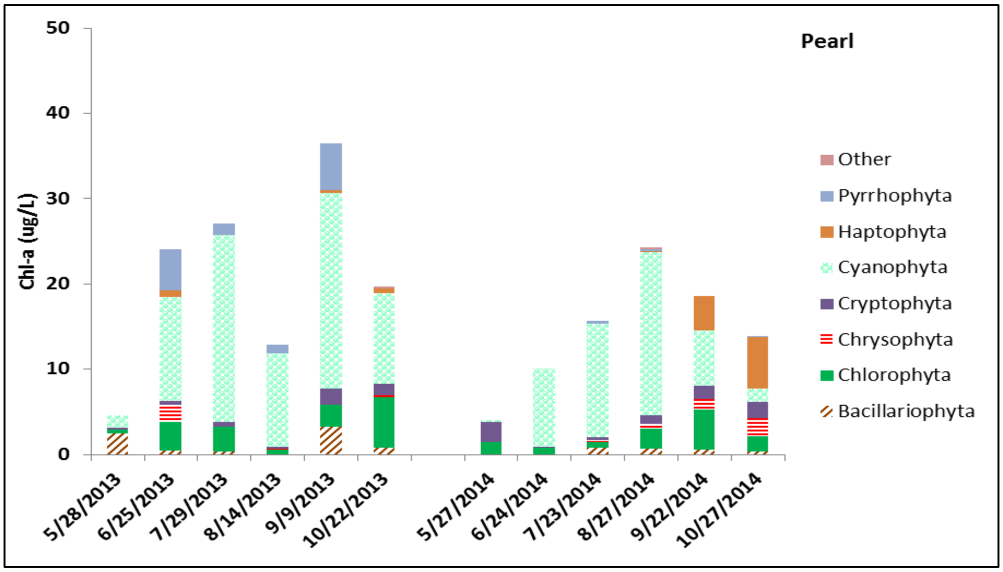

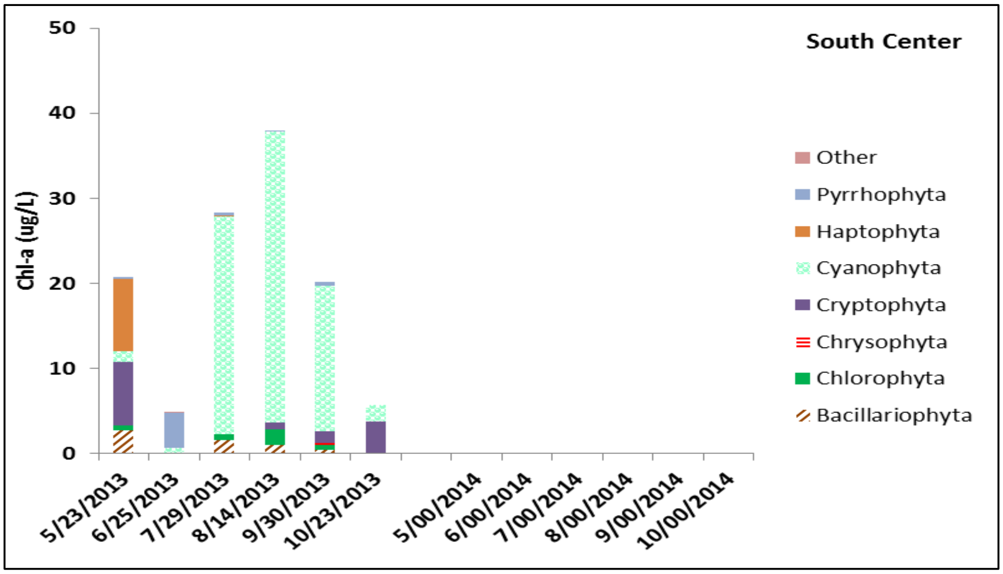

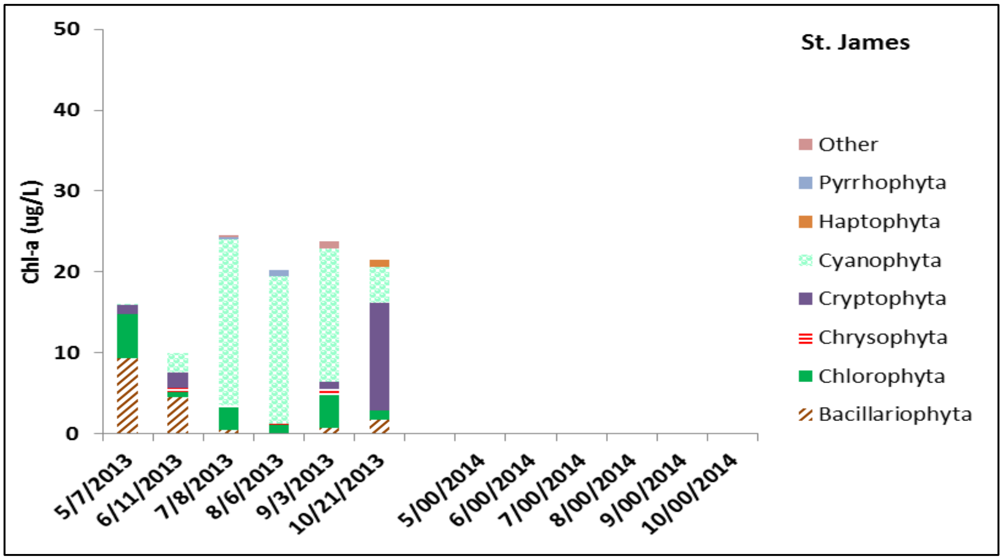

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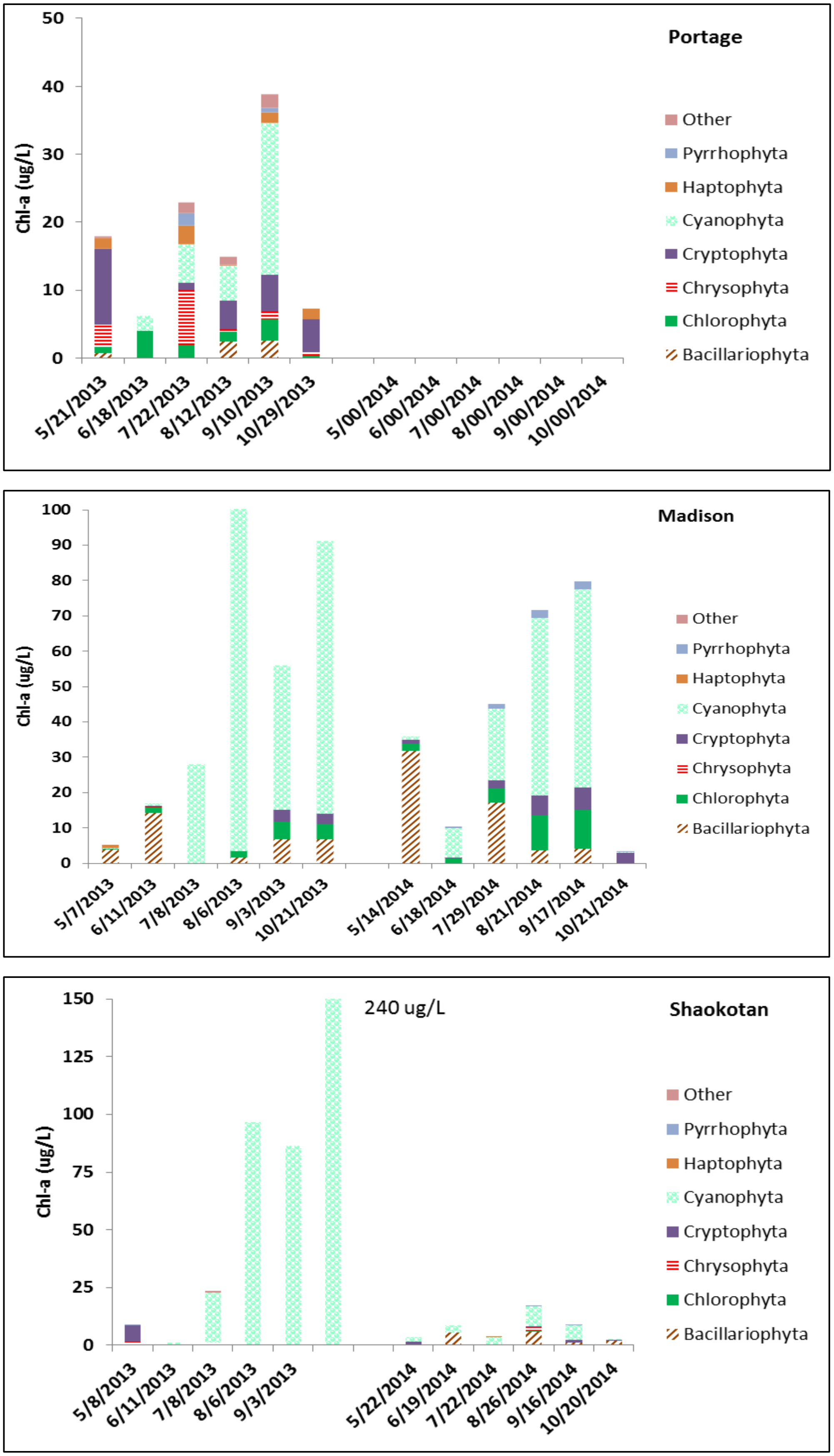
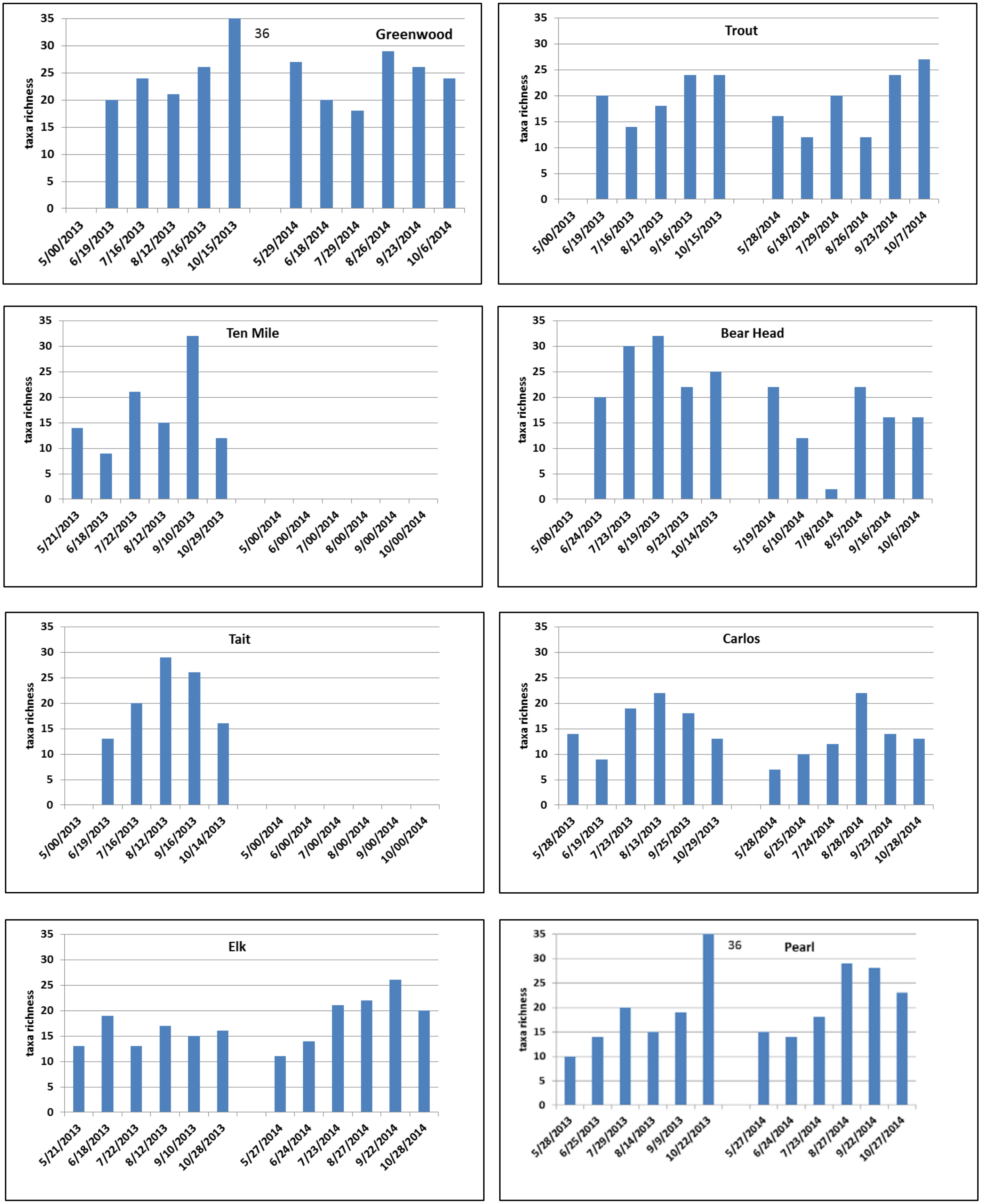


Figure 6. Number of algal taxa (total taxa richness). Lakes sorted from northeast to southwest.



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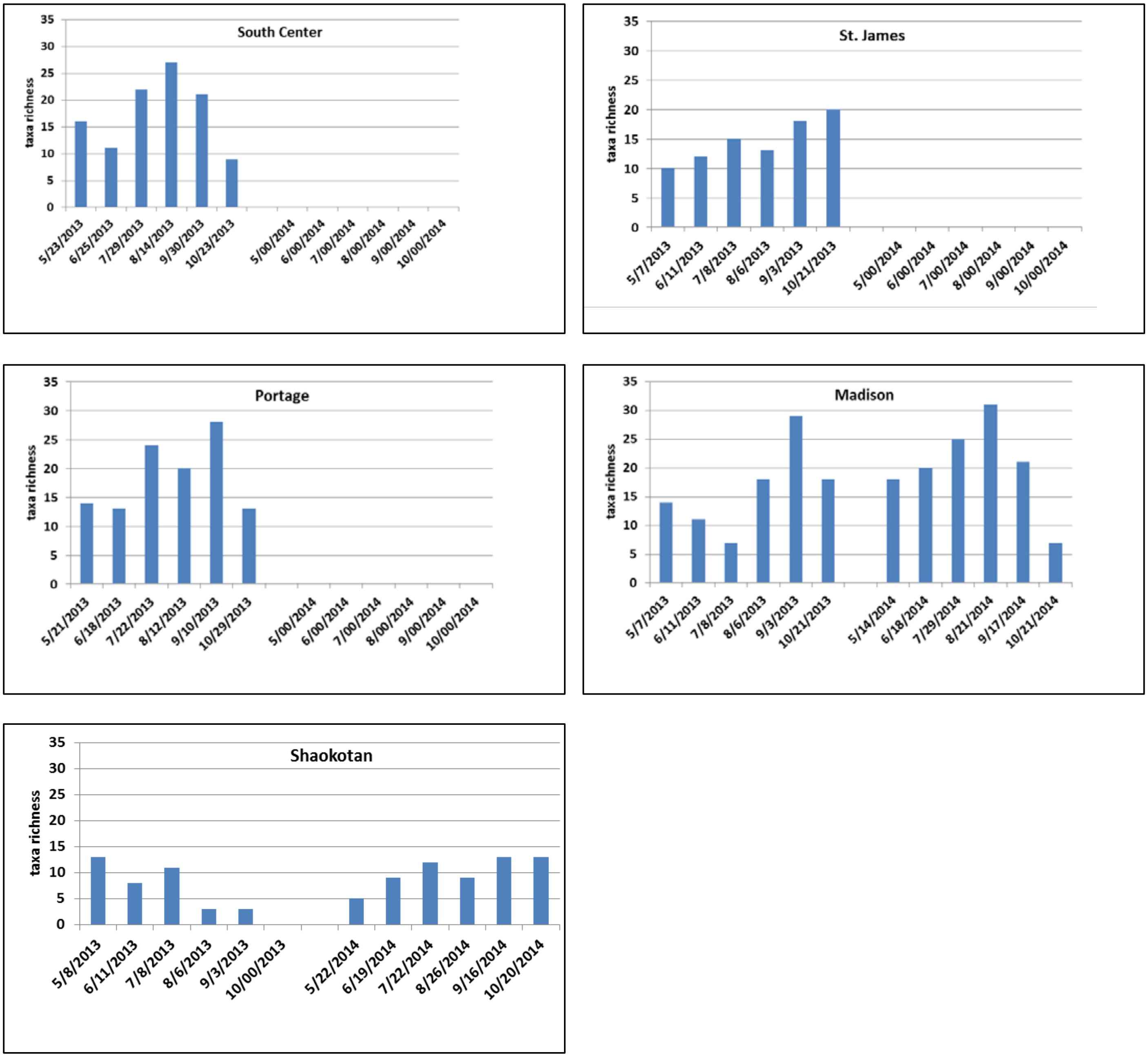
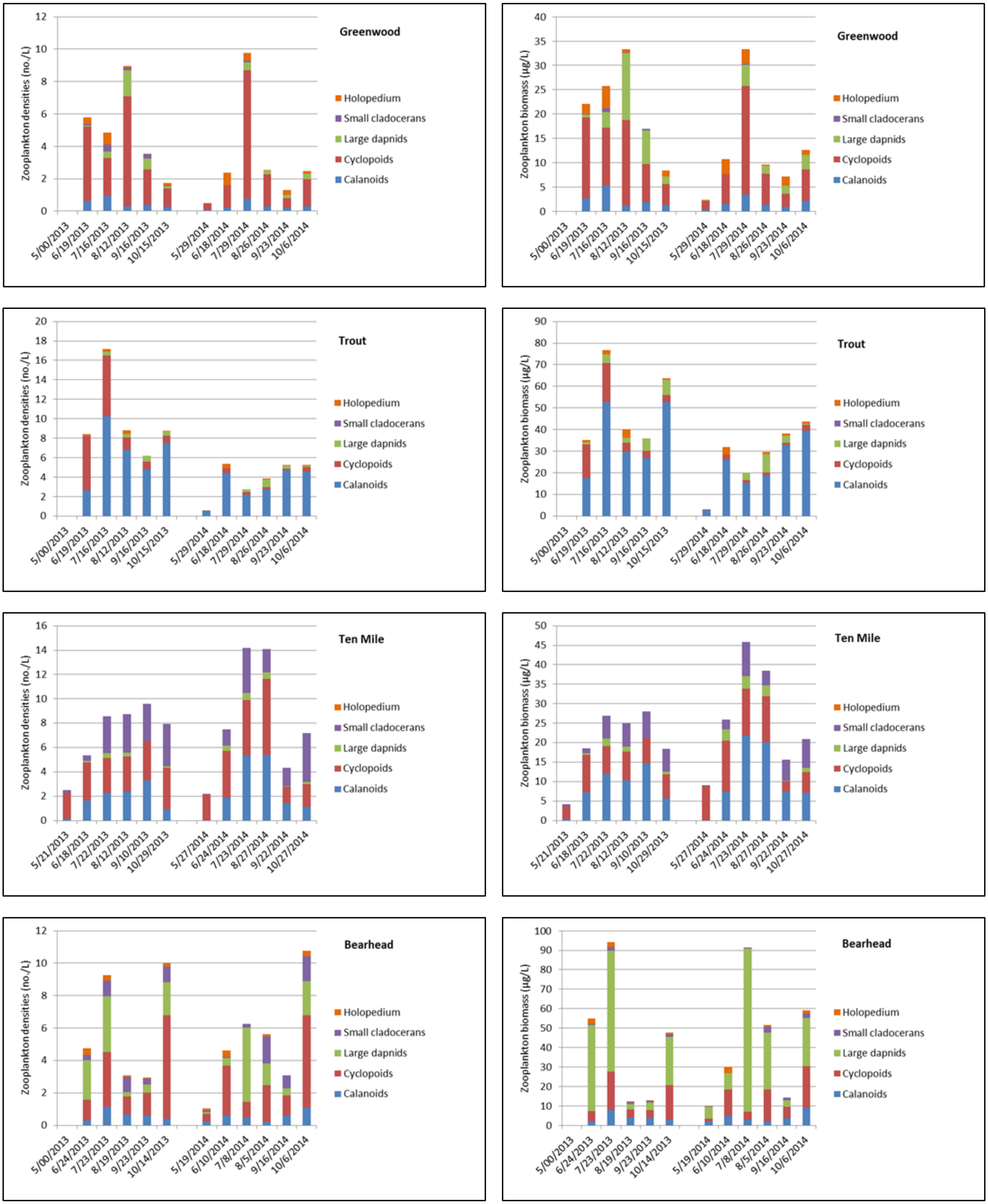


Figure 7. Zooplankton functional group densities (number/liter) and biomass (µg/liter), 2013-2014.



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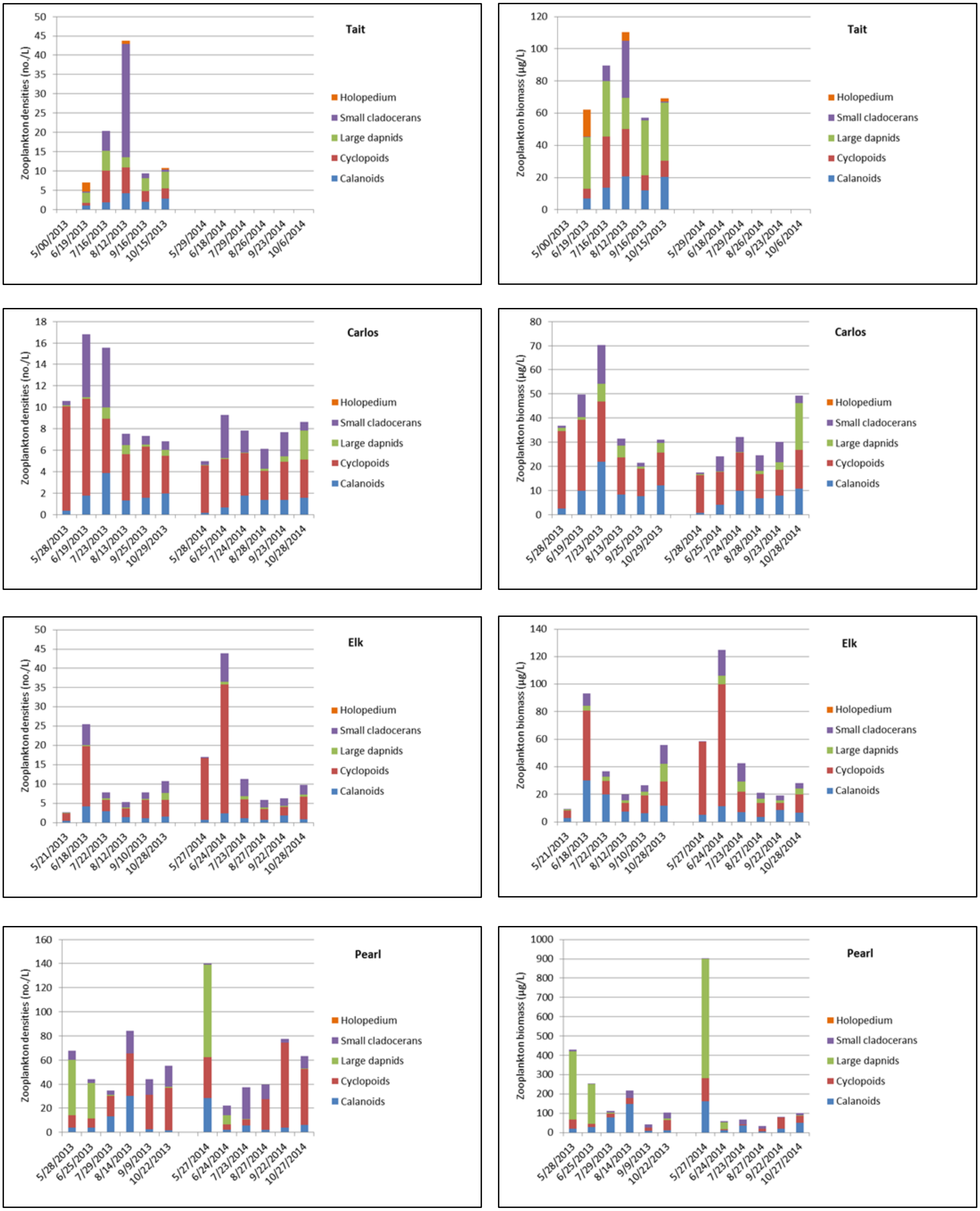

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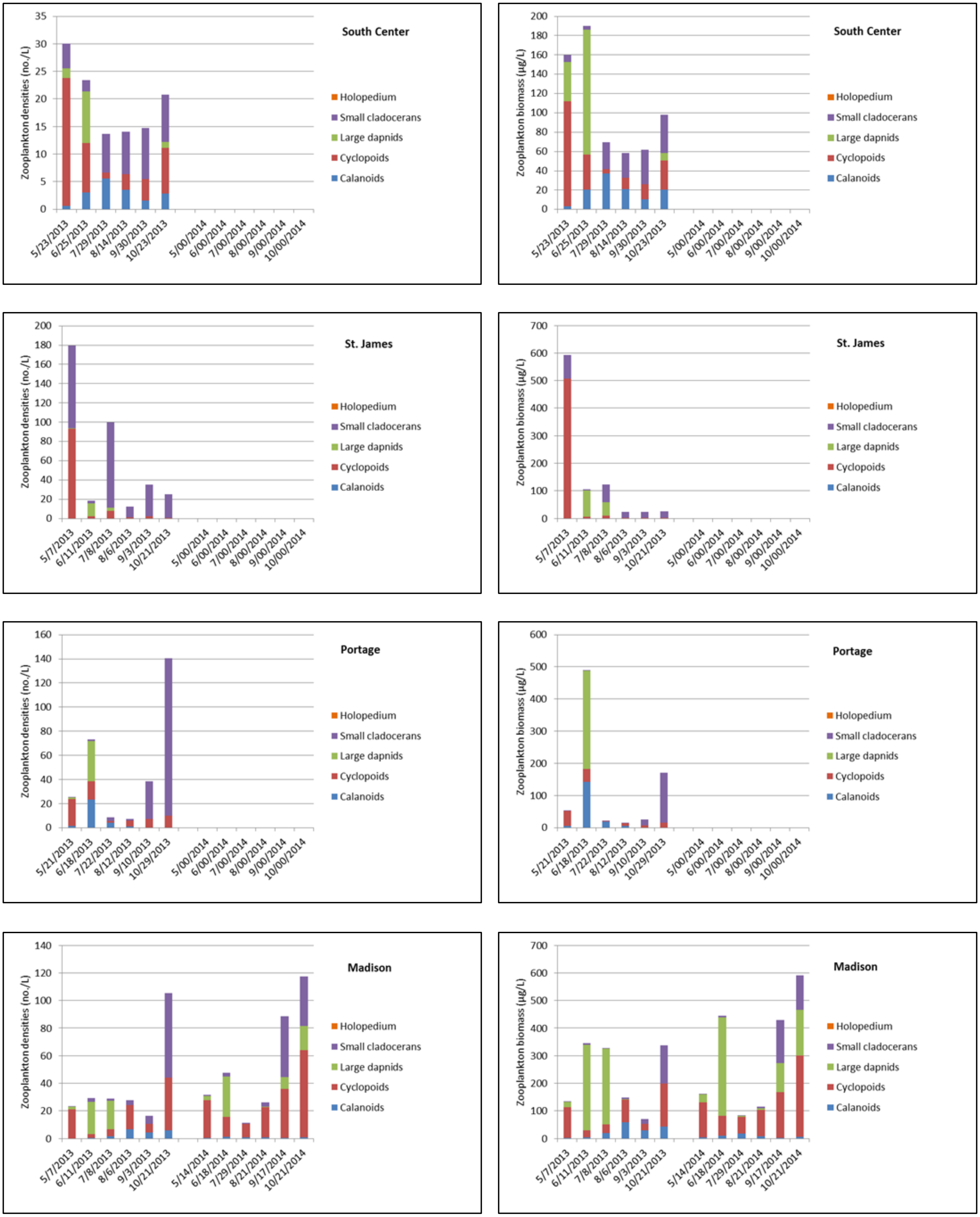

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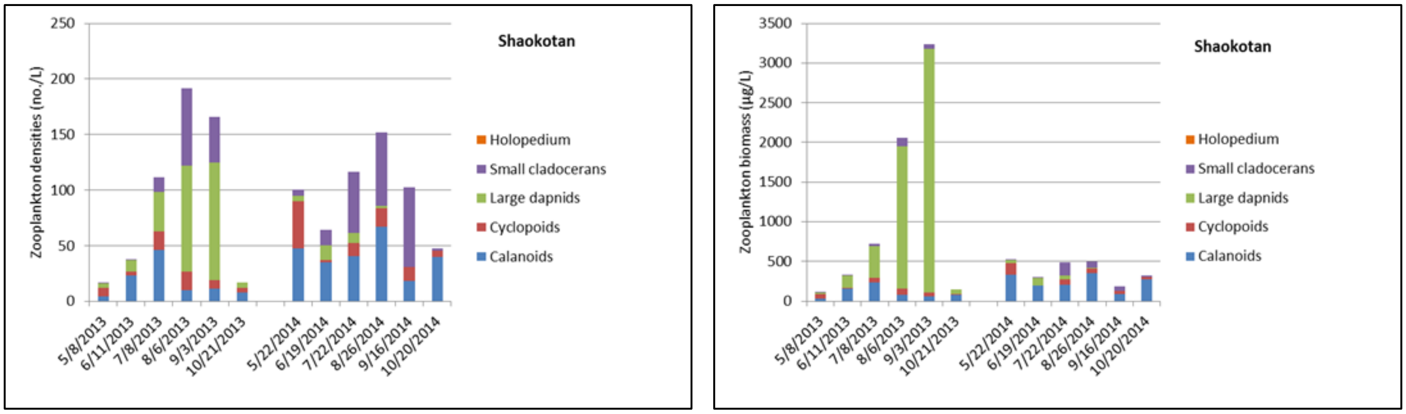


Seasonal transition in algal forms

The seasonal succession in phytoplankton populations for northern temperate lakes is often represented as in Figure 8. As a generalized depiction, Figure 8 may be adequate; however, actual transitions in Minnesota lakes are quite variable. Reynolds (1990) described phytoplankton succession as a function of lake trophic status based on observations from a range of lakes. In oligotrophic lakes diatoms were dominant from spring through autumn, with some dinoflagellates and blue-green algae present. Mesotrophic lakes transitioned from diatoms, to chrysophytes, to dinoflagellates, Cyanobacteria, greens and back to diatoms. Eutrophic lakes transitioned from diatoms, to greens/cryptophytes to blue-greens, to dinoflagellates/blue-greens and back to diatoms in the fall. Hypereutrophic lakes transitioned from small diatoms, to greens (midsummer and autumn), and blue-greens in the fall.

The Sentinel Lakes afford the opportunity to describe patterns of algal succession for Minnesota lakes. We elected to represent this by lake trophic state following the TP & Chl-*a* patterns in Figure 2 and based it on the 2013 data, when all study lakes were sampled. Lakes were grouped as follows: oligotrophic - Greenwood, Trout, and Ten Mile lakes; mesotrophic - Tait, Bear Head Carlos, and Elk lakes; eutrophic - Pearl, St. James, and Portage lakes; and hypereutrophic - South Center, Madison, and Shaokotan lakes. Percent composition was averaged by month across each of the lakes in the groups and summed to 100% for each month (Figure 9). Chl-*a* was averaged by month in a similar fashion to provide a relative comparison in algal biomass for lakes in each trophic class (Figure 10).

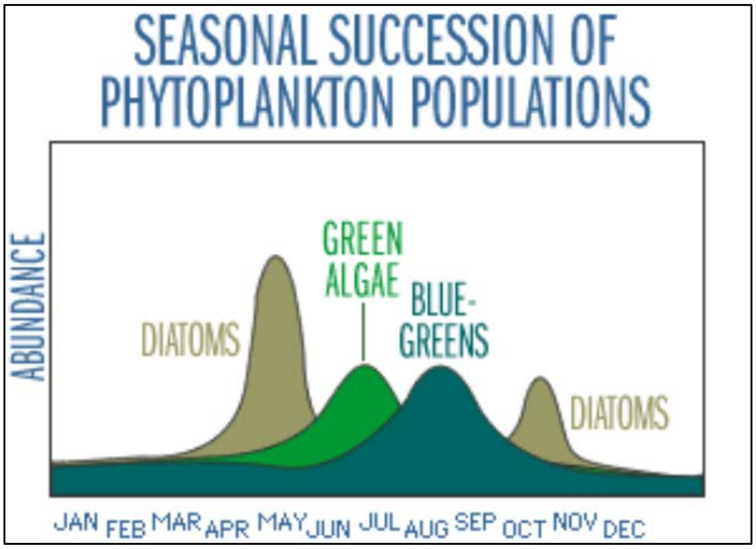


Figure 8. Typical algal succession as drawn from Water on the Web (webpage: waterontheweb.org, based on Horne and Goldman, 1994).

Water temperature and sunlight are important factors that influence algal productivity (which we estimated using biomass) and composition and account, in part, for seasonal succession (Figure 8). Wetzel (2001) noted the importance of increasing sunlight as a driver in the spring, since water temperature is quite low. Temperature data from 2013 were summarized for the study lakes to demonstrate seasonal transition across a range of lakes (Figure 11). There is a distinct lag in warming of the northeastern lakes (Trout and Bear Head lakes) compared to the southern lakes (Madison and Shaokotan lakes). The central and southern lakes can exceed 20 °C in June, whereas the northern lakes may not reach this temperature until July and remain above 20 °C only through August. Warm temperatures may extend into September in the central and southern lakes.

In the oligotrophic Sentinel Lakes, diatoms (e.g., *Cyclotella* and *Tabellaria*; typical oligotrophic taxa, [Rawson 1956]) and chrysophytes (typically *Dinobryon*, *Synura*, and *Uroglena*) are dominant in May and June and decline slightly thereafter (Figure 9). Wetzel (2001) and others note that chrysophytes often proliferate in nutrient-poor lakes because they are able to take up P effectively at very low concentrations and are adapted to cool temperatures. Smol and Cumming (2000) suggest that because chrysophytes are highly seasonal, their occurrence may prove to be good indicators of lake water temperatures. Blue-greens were present in all months and were dominant in July-September; however, mean total algal biomass was very low on all dates (Figure 10) and nuisance blooms were not observed in these lakes. Cryptophytes and greens were present at low relative abundances throughout the summer. Total algal biomass was low and declined somewhat from spring through summer and increased in fall (Figure 10).

The mesotrophic lakes were dominated by chrysophytes (typically *Rhodomonas*, *Dinobryon*, *Cryptomonas*, *Uroglena*, and *Synura*) in May and June, with a distinct decline in July (Figure 9) as water temperature increased (Figure 11). Abundance of blue-greens increased in July through September. Relative abundance of diatoms was low, but stable from spring through fall. Cryptophytes were present in all months and were most prominent in October with fall mixing. Greens had low abundance in most months, increasing slightly in July. Algal biomass was notably higher in this group than in the oligotrophic lakes, and maximum concentrations of Chl-*a* were observed in spring and fall (Figure 10). The decline in Chl-*a* from spring through late summer was presumably due to nutrient limitation (primarily P limitation). Wetzel (2001; after Hutchinson 1967) suggests that dinoflagellates may be dominant in some mesotrophic lakes, but that was not the case in the Sentinel Lakes (Figure 9) with the exception of, *Gymnodium* (a dinoflagellate), which was dominant in Bear Head Lake in May 2013.

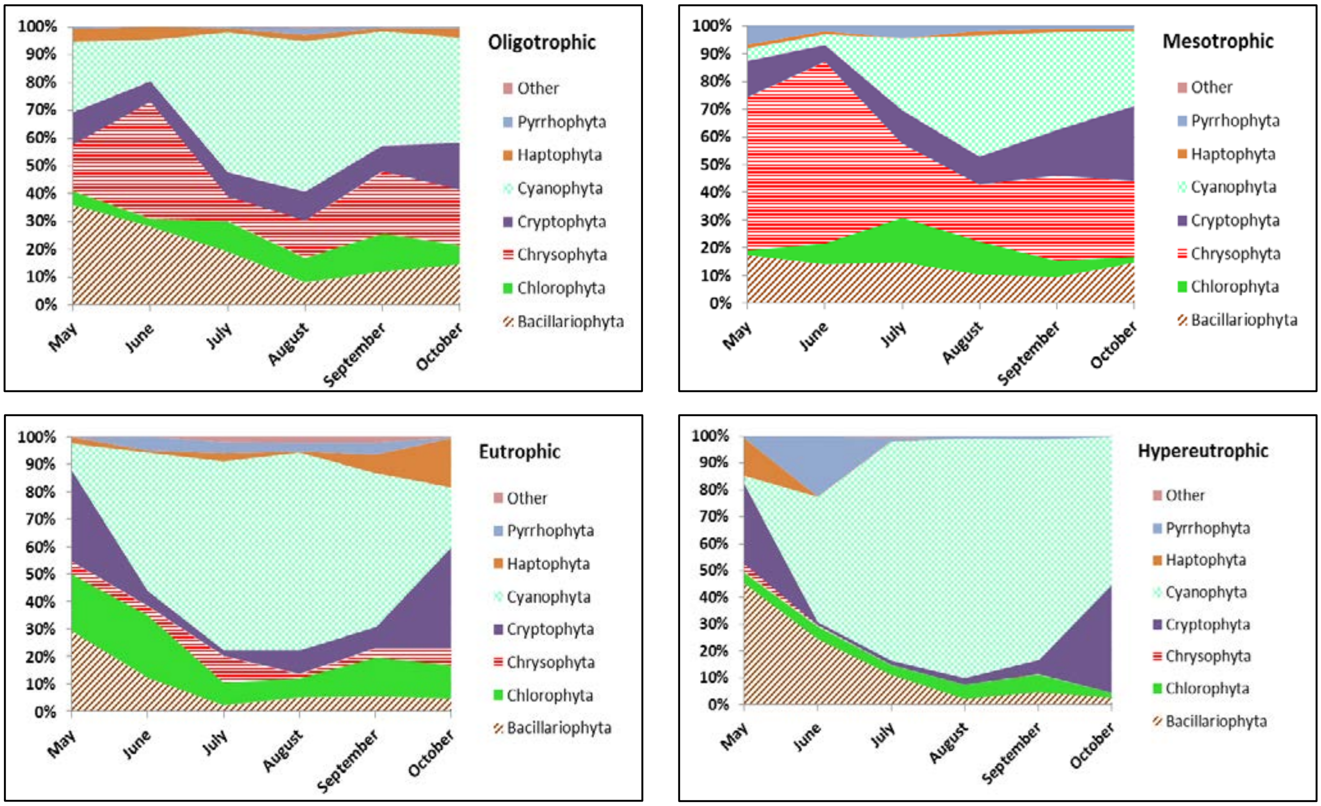


Figure 9. Mean relative seasonal algal abundance by lake trophic status. Sentinel Lakes were grouped as follows: oligotrophic - Greenwood, Trout, & Ten Mile lakes; mesotrophic - Tait, Bear Head, Carlos, & Elk lakes; eutrophic - Pearl, St. James, & Portage lakes; & hypereutrophic - South Center, Madison, & Lake Shaokotan (all based on 2013 data).

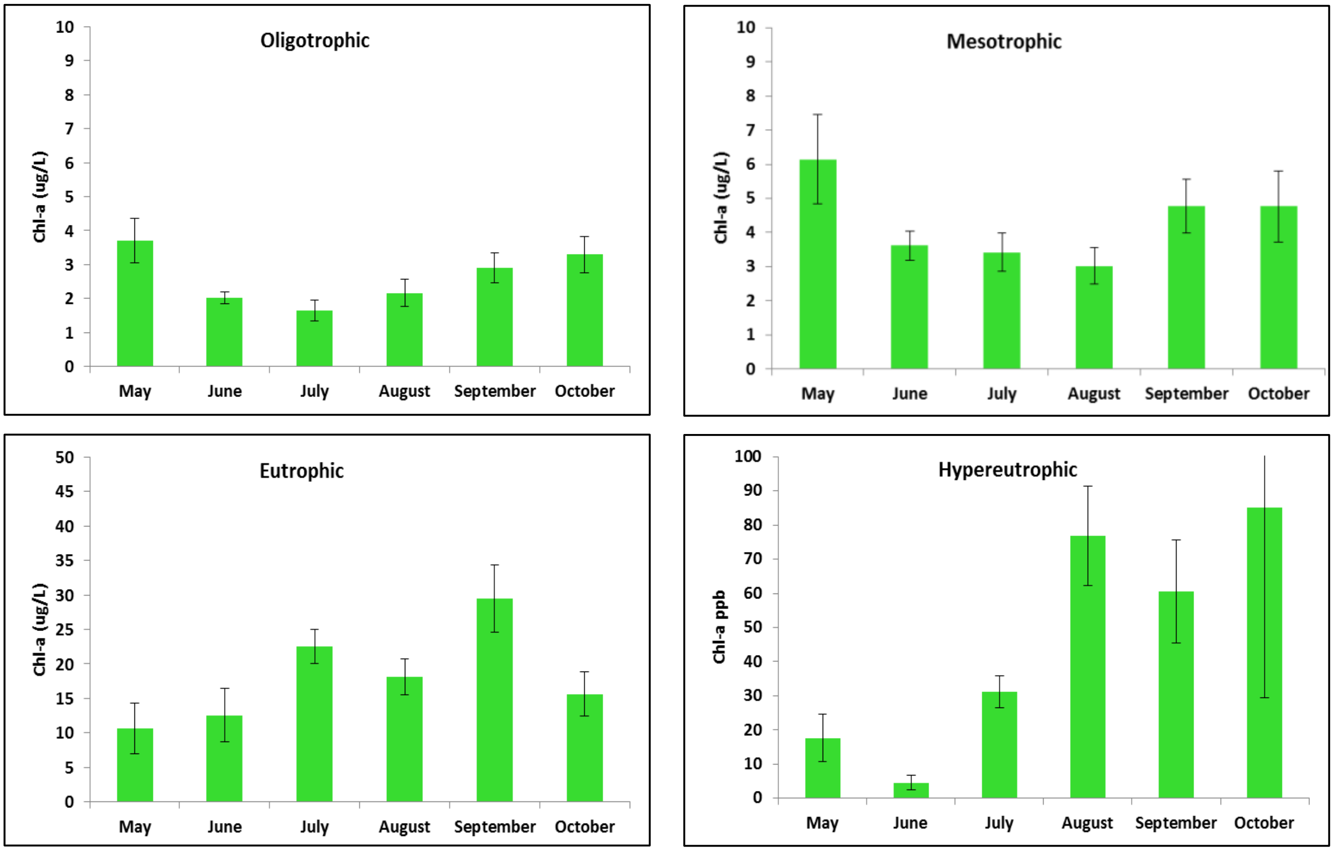


Figure 10. Seasonal patterns in Chl-*a* concentration by lake trophic state. This figure is based on 2013 Chl-*a* data for the lakes in Figure 9. Note variation in y-axis scales. Standard error bars included.

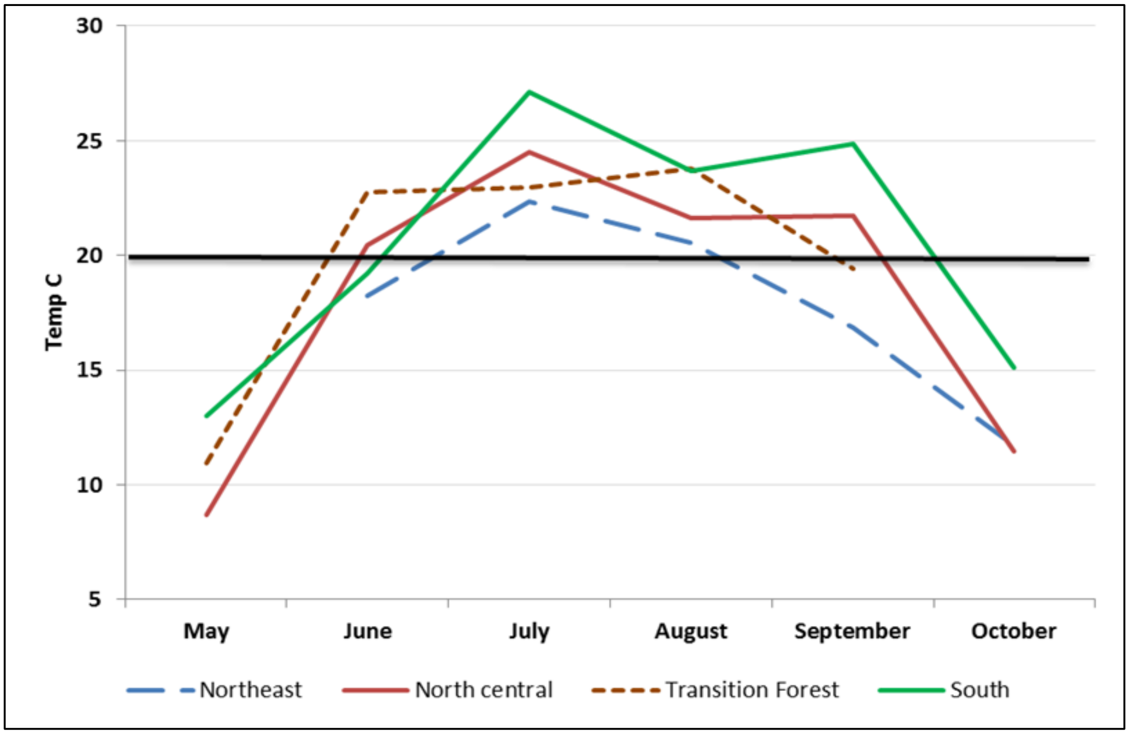


Figure 11. Mean monthly surface water temperatures for Sentinel Lakes based on 2013 data. Study lake data summarized by location in state (Table 1) as follows: Northeast- Greenwood, Trout, Tait and Bear Head; North Central Elk, Ten Mile, and Portage; Transition - Carlos, Pearl, and South Center; South - Madison, St. James, and Shaokatan. The black line indicates minimum optimal temperature for blue-green growth.

The eutrophic lakes exhibited high taxa diversity in May with no clear dominant group (Figure 9). Diatoms were most abundant in spring, with *Asterionella* and *Fragilaria* being common (these taxa are noted dominants in eutrophic lakes; Rawson 1956). As other forms decline in relative abundance, blue-greens increase and are the dominant form from June-September (Figure 9). Cryptophytes increased after fall mixing. The haptophytes, which were relatively rare, were most abundant after fall mixing. Greens were ubiquitous, and, on a relative basis, were more common in eutrophic lakes relative to the oligo-, meso-, or hypereutrophic lakes. The dinoflagellate, *Ceratium*, was prominent in Pearl and South Center lakes on two dates. Total algal biomass was lowest in the spring and increased through the summer, peaking in September (Figure 10). This pattern was distinctly different compared to the oligo- and mesotrophic lakes and is presumably a result of increased nutrient availability as the lake mixed, enhancing internal recycling, and the displacement of blue-green algae from the lake bottom to the surface waters.

In the hypereutrophic lakes all algal forms were present, and "eutrophic" diatoms (*Asterionella, Nitzschia,* and *Stephanodiscus*) were dominant in May (Figure 9). Most forms declined in June, while blue-greens increased. The pyrrhophytes, which were relatively rare in the Sentinel Lakes, were common in this group in June. Blue-greens dominated from July through September and most other forms were represented by a few individuals. Cryptophytes increased during fall mixing, but blue-greens remained dominant. Increases in cryptophytes during the fall was common across all trophic states (Figure 9), and Wetzel (2001) notes this increase often follows the "demise" of previously dominant bloom algal populations. In May and June Chl-*a* was relatively low (for values within this group) and increased during July through October (Figure 10).

Seasonal Transition in Zooplankton Communities

The seasonal succession of zooplankton communities in temperate lakes is driven by both biotic and abiotic factors, including water temperature, edible phytoplankton, and predation by both invertebrates and planktivorous fish (Reynolds 1984; Lampert et al. 1986). Sommers et al. (1986) described the seasonal succession of zooplankton and phytoplankton communities in an idealized "standard" lake, known as the PEG (Plankton Ecology Group)-model. This model consists of 24 sequential statements that describe the step by step events that drive temporal changes of both the zooplankton and phytoplankton communities in lakes. In the PEG-model, the generalized zooplankton community succession is described as small, herbivorous species with short generation times hatching first, followed by the larger species with longer generation times, grazing on edible algal forms. As the season progresses into summer, edible algae are often replaced by inedible forms and while fish predation increases, the larger zooplankton species are replaced with smaller species. Smaller zooplankton species are less vulnerable to fish predation and are less affected by adverse consequences from grazing on non-edible algal forms. During autumn, the abundance of larger species increases as edible forms of algae increase (Sommers et al. 1986).

Similar to the phytoplankton, the Sentinel Lakes provided the opportunity to describe zooplankton community succession for Minnesota lakes. Figure 12 illustrates the relative seasonal zooplankton community composition by lake trophic status, based on percent composition of functional group densities. In general, as the trophic status of lakes progress from oligotrophic to eutrophic, the relative abundance of copepods decreases and the relative abundance of cladocerans increases (Figure 12).

In the oligotrophic lakes, copepods were dominant, approximately evenly split between calanoids and cyclopoids, and as a whole, contributed to 80-90% of the zooplankton community abundance throughout the season (Figure 12). Cladocerans comprised less than 20% of the abundance of the community during all sampling events. Small cladocerans and large daphnids were rare in May and June, but they became more abundant during the summer and fall months as water temperatures increased, while *Holopedium* was most abundant during June. *Holopedium spp*. are very efficient at grazing at low densities of phytoplankton (Mc Naught 1978), which was the case early in the season in the oligotrophic lakes. The small percentage of cladocerans in these lakes could also be the result of predation by spiny waterfleas, since two of these three lakes are infested with spiny waterfleas.

The mesotrophic lakes were also dominated by copepods, contributing 60-90% to the community but with higher percentages of cyclopoids than calanoids (Figure 12). Similar to the oligotrophic lakes, cladocerans were rare in May, but contributed higher percentages (up to 40%) to the community composition during the summer and fall. Large daphnids and small cladocerans were abundant during the summer and fall, while *Holopedium* was most abundant in June, a similar pattern as we observed in the oligotrophic lakes.

In the eutrophic lakes, copepods contributed only 30-60% of total abundance throughout the season, with cladocerans consistently contributing a higher percentage (Figure 12). Large daphnids were abundant early in the season, contributing up to 50% of the total abundance during June, but disappeared by July, most likely due to edible algal forms (cryptophytes and diatoms) being replaced with inedible blue-green forms (Figure 9). Fish predation may be a more important factor in the reduction of the large daphnids in the shallow lakes, due to the lack of refugia below the thermocline to migrate into during the day and avoid fish predation; although aquatic macrophytes have been found to provide refugia for zooplankton in some shallow lakes (Schriver et al. 1995; Meerhoff et al. 2007). Small cladocerans replaced large daphnids by July, contributing up to 60% of the total abundance during the remainder of the season. Small cladocerans are less vulnerable to predation (Sommers et al. 1986) and can tolerate adverse effects of grazing on inedible algae better than large daphnids (Haney 1987).

The hypereutrophic lakes displayed similar seasonal successional patterns as the eutrophic lakes, with the exception of large daphnids, which were a major component of the community throughout the season (Figure 12). The hypereutrophic Sentinel Lakes included Shaokotan and Madison lakes which had high relative abundances of the blue-green algae, *Aphanizomenon flos-aquae*, during at least one of the two sampling years. Large daphnids and *A. flos-aquae* have been found to co-exist in shallow, hypereutrophic lakes, most likely because large daphnids do not graze on *A. flos-aquae* but preferentially graze on other forms of algae (Lynch 1980; Lynch and Shapiro 1981). Furthermore, due to the physical nature of *A. flos-aquae*, producing large grass-like clippings, it may provide refugia for large daphnids in these shallow lakes.

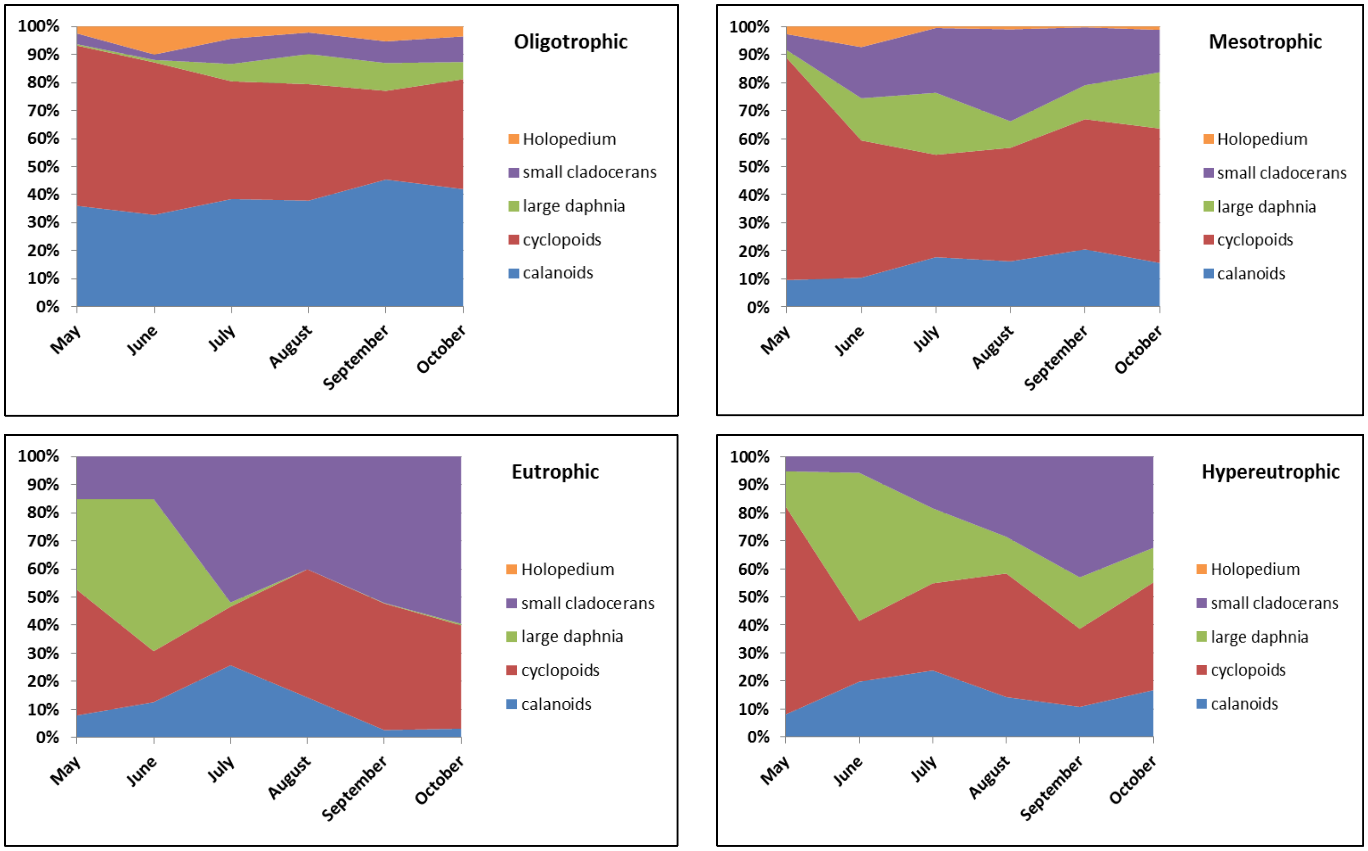


Figure 12. Relative seasonal zooplankton community composition by lake trophic status based on functional group densities in the Sentinel Lakes.

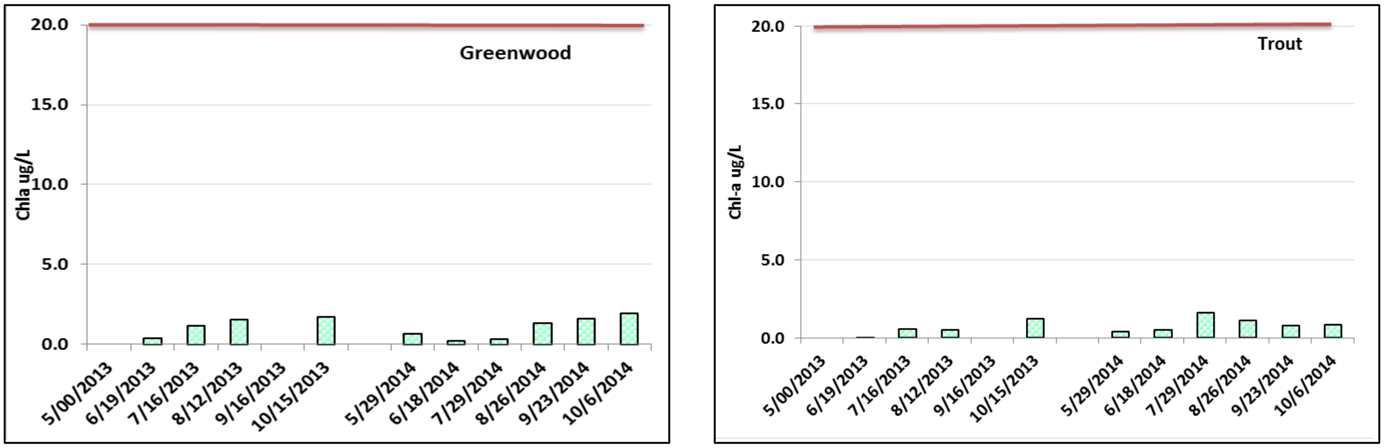
Cyanobacteria abundance, nuisance blooms, and toxin producers

In general, as lakes become more nutrient-enriched Cyanobacteria (blue-green algae) become the dominant algal form. This concept was reinforced by the data collected in the Sentinel Lakes (e.g., Figure 4). Examining only the blue-green forms, seasonal patterns, abundance, and biomass of blue-greens is more clear (Figure 13). Blue-green forms were present in all lakes and on most sample dates. In the oligotrophic and mesotrophic lakes, blue-green biomass was very low and there were no strong seasonal patterns. As lakes transition into eutrophic conditions, nuisance blue-green blooms (Chl-*a* >20 µg/L) were apparent (e.g., Pearl, South Center, and St. James lakes) and peaked in mid to late summer (Figure 13). As TP increased further (80-100 µg/L or more, as in Madison and Lake Shaokotan), nuisance blue-green blooms occurred throughout the summer. The effect of reduced TP was also evident in Lake Shaokotan where summer-mean TP decreased from >75 µg/L in 2013 to 33 µg/L in 2014 and blue-green nuisance blooms did not reoccur (Figure 13).

While nutrient supply is important, water temperature can be an important driver of blue-green growth and blooms as well. Knopka and Brock (1978) noted that in spring when temperatures were < 20 °C, blue-green abundance was insignificant. They noted optimal temperature for blue-green growth was in the range of 20-30 °C, with optima of 25 °C. Based on this study, northern MN lakes do not achieve 20 °C until late June to July; central and southern lakes may achieve 20 °C by early June (Figure 11). The northern lakes may remain in the "optimal" range of 20-30 °C for a shorter duration, compared to central and southern lakes, and may not reach 25 °C in some years.

In addition to difference in the magnitude of blue-green algal biomass, there are differences in the dominant blue-green forms (genera). For example, in Trout Lake, *Aphanocapsa*, *Aphanothece*, and *Planktolyngbya* were among the most common forms (Table 9). *Aphanothece* was also a common form in Bear Head Lake (Table 13). In Tait Lake, *Woronichinia* and *Gomphosphaeria* were prominent forms (Table 15). As lakes became more eutrophic, *Anabaena*, *Microcystis*, and *Aphanizomenon* were more common (e.g., Pearl Lake, Table 21; South Center Lake, Table 23). In hypereutrophic Lake Shaokotan, several blue-green genera were found; however, *Aphanizomenon* accounted for over 80% of the total algal abundance from July through September 2013. This is contrast to 2014 when TP and Chl-*a* declined drastically (Figure 5) and a mix of blue-green genera were found (Table 31).

Figure 13. Blue-green algae biomass estimated as proportion of total Chl-*a* attributable to blue-green algae. Lakes sorted by trophic state based on TP & Chl-*a* concentrations: Greenwood, Trout, & Ten Mile (oligo, TP <10 µg/L), Bear Head, Tait, Carlos & Elk (mesotrophic, TP 14-19 µg/L), Pearl, Portage, & St. James (mildly eutrophic, TP ~40-60 µg/L), South Center, Madison, and Shaokotan (highly to hypereutrophic, TP ≥ 70-100 µg/L). Red line represents nuisance bloom level (20 µg/L; Heiskary and Wilson 2008). Note changes in y axes.



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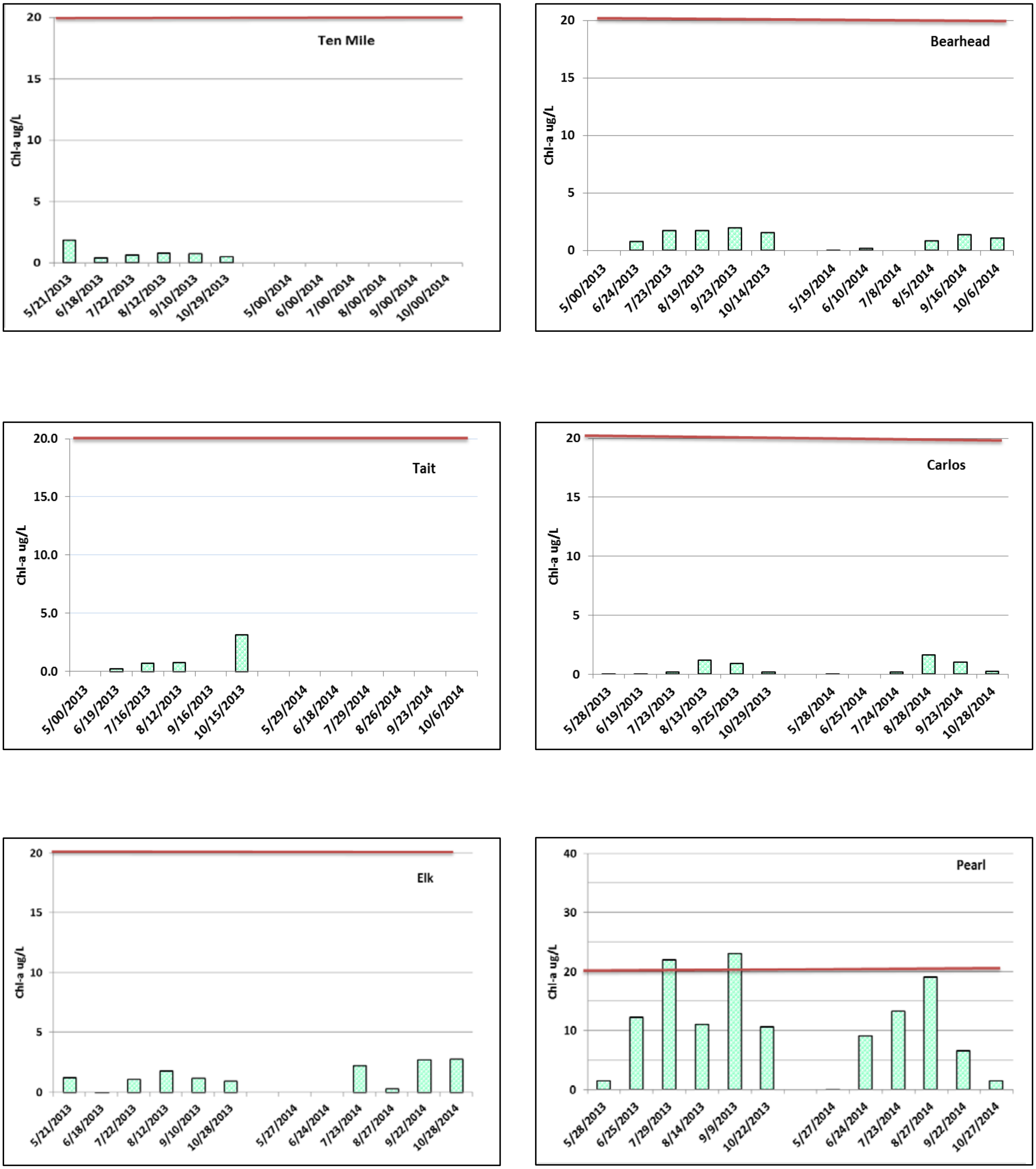

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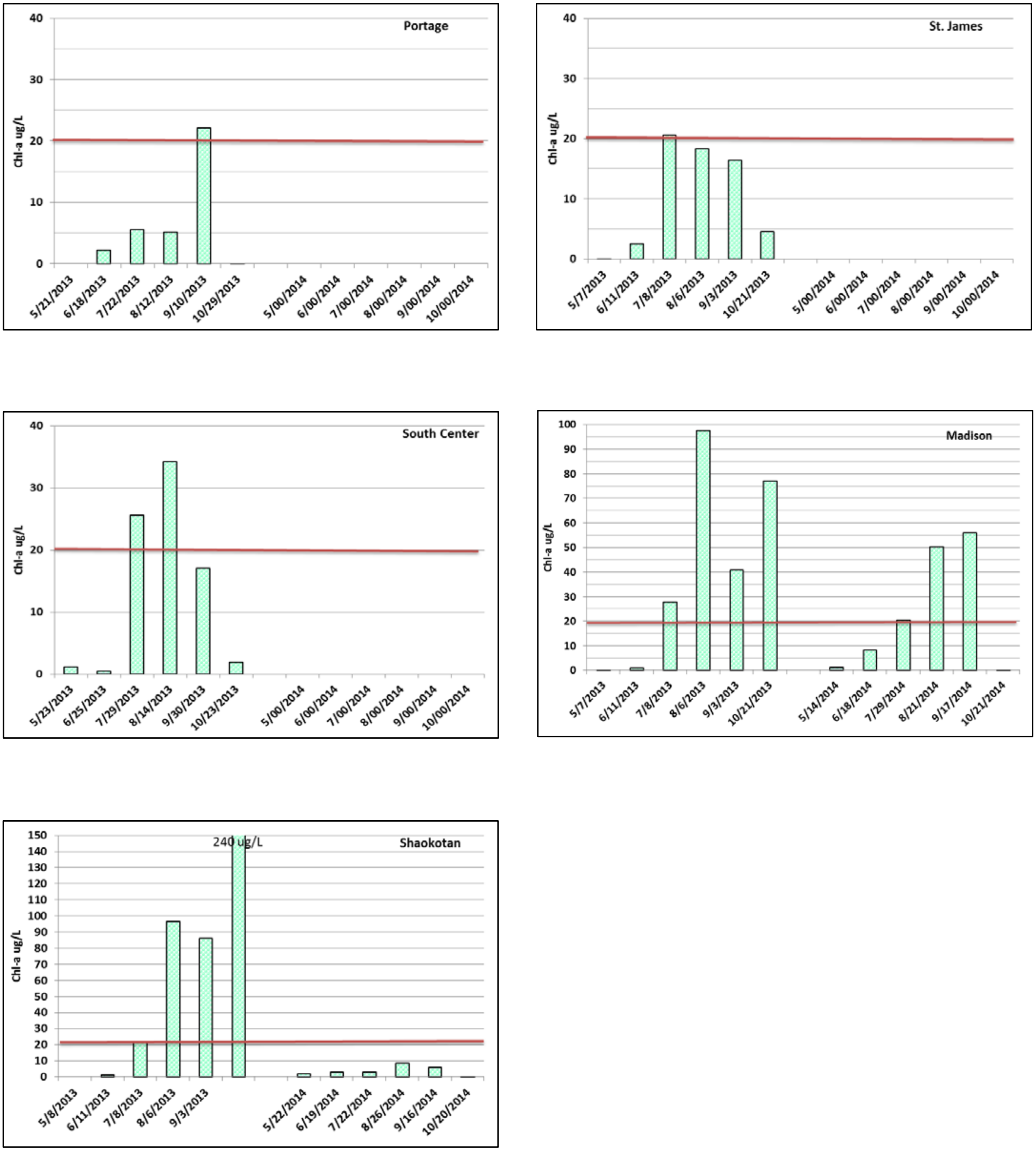

Total nitrogen:total phosphorus ratios (TN:TP) have been used a basis for predicting which nutrient limits phytoplankton growth and as a basis for predicting when blue-greens become dominant in lakes. TN:TP≥17:1 has often been used to indicate "P limitation," whereas TN:TP≤10:1 indicates "N limitation" (Smith 1983). Figure 14 ranks the Sentinel Lakes based on TN:TP and indicates the majority are considered P-limited, with Shaokotan intermediate between N and P limitation. Smith (1983) noted further, that blue-green dominance was associated with TN:TP<29:1. This suggests that the Sentinel Lakes from Elk through Shaokotan may be blue-green dominated (Figure 14). Though our sample size is small (13 lakes), phytoplankton composition (Figure 4), relative percent composition (Figure 5), and blue-green biomass (Figure 13) suggest the transition to blue-green dominance occurs across a range from 27:1 (Elk) to 24:1 (Pearl). Based on our limited data, it appears there is a shift from a mix of toxin (e.g., *Anabaena*) and non-toxin producing (e.g., *Aphanocapsa* and *Aphanothece*, Table 19) blue-green forms in Elk Lake to predominately toxin-producing forms (*Microcystis* and *Anabaena*, Table 21) in Pearl Lake. Future phytoplankton collections across the entire range of the Sentinel Lake may provide further insight into this.

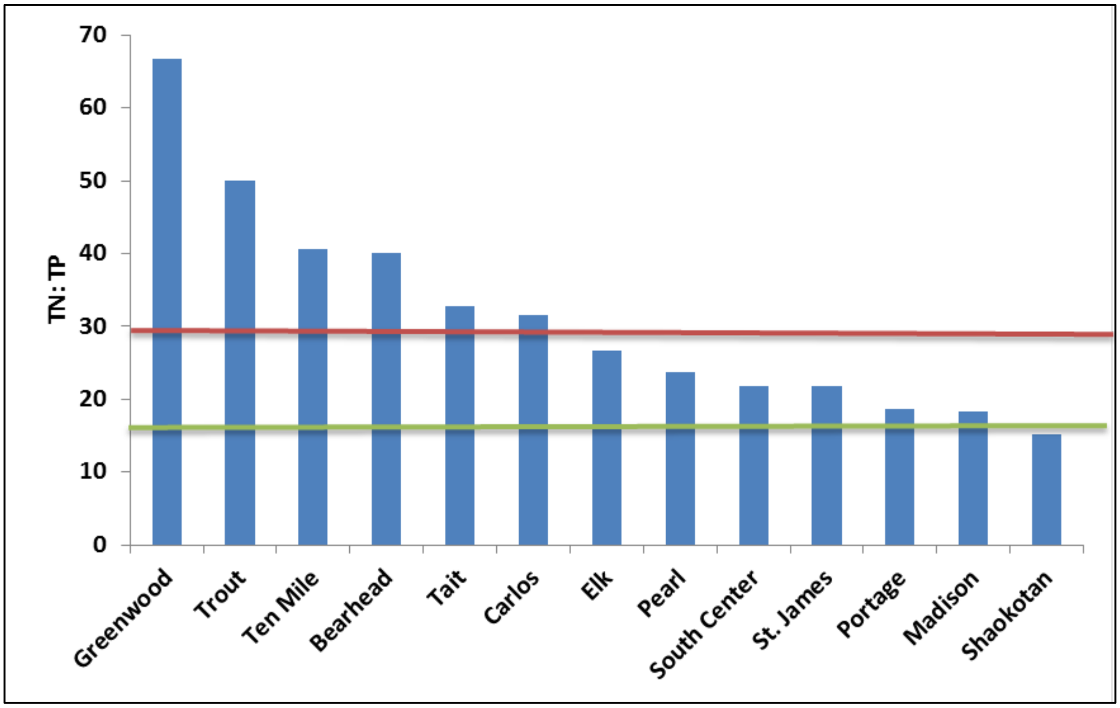

Figure 14. Sentinel Lakes ranked by TN: TP ratios. Ratios >17:1 (P limitation) indicated by green line and potential for blue-green dominance (<29:1) indicated by red line.

Blue-green algal toxins are particularly potent and their occurrence and magnitude has been the subject of several studies in Minnesota (e.g., Lindon and Heiskary, 2009; Heiskary et al., 2014). While microcystin is the most commonly studied toxin, others such as anatoxin, saxitoxin, cylindrospermopsin, and beta-Methylamino-L-alanine (BMAA) are of concern as well. Many of the blue-greens found in the Sentinel Lakes are known toxin producers including: *Anabaena, Aphanizomenon, Microcystis, Planktothrix*, and *Cylindrospermopsis* (some less common blue-green genera known to produce toxins include *Nodularia*, *Nostoc*, *Lyngbya*, *Hapalosiphon*, and *Umezakia*). *Aphanizomenon* and *Anabaena* were found in many of the lakes including oligotrophic lakes, like Greenwood and Ten Mile, but at very low levels. *Microcystis* was present in the more eutrophic lakes like Pearl, Madison, St. James, and Shaokotan, and was often a prominent form in the highly eutrophic lakes. *Planktothrix* (previously *Oscillatoria*) was found in lakes ranging from Elk and Ten Mile to Madison and Shaokotan; however, it was found in very low numbers in all lakes, with the exception of Madison in September 2014 when it was among the prominent forms. In general, the toxin-producing blue-greens were the most dominant blue-green form in Pearl, Portage, St. James, South Center, Madison and Shaokotan lakes. On each of these lakes, nuisance blooms were recorded on one or more sample dates (Figure 13). In contrast, Greenwood, Trout, Ten Mile, Bear Head, Tait, and Carlos lakes exhibited a mix of blue-green forms (including non-toxin producers) and never approached nuisance blooms levels (Figure 13).

Gloeotrichia, which has also been noted to produce toxins, was uncommon in the Sentinel Lakes; however, in 2013 it was found in Shaokotan (Table 31) and was present in very low numbers in Carlos and Madison. It apparently was not present in the 2014 collections. This blue-green grows on the sediment and rises to the surface of the lake in "ball-like" colonies (Roelofs and Oglesby 1970) where it is disbursed by the wind and can accumulate on downwind shorelines. Because of the large size of the colonies it has a negligible effect on transparency and has been noted to be more common in lakes of high clarity. Roelofs and Oglesby (1970) also note that it is likely a nitrogen fixer and is subjected to limited consumption by most copepods and cladocerans because of the size of the colonies.

Cylindrospermopsis is uncommon in Minnesota lakes (based on this study and limited historical records), but was found in Madison (prominent August 2013, September 2014) and South Center (September 2013) lakes. Jones and Sauter (2005) provide an informative description of the distribution of *C. raciborskii* in Indiana lakes and reservoirs, which is relevant to Minnesota. The following is paraphrased from their work.

> "C. raciborskii is unique to cyanobacteria for two reasons. First, it typically does not form surface blooms. Maximum densities of *C. raciborskii* cells occur at 2-3 m below the surface (Saker and Griffiths 2001). Therefore, *C. raciborskii* blooms are hard to detect. *C. raciborskii* has often been considered a tropical species due to its affinity for warm water temperatures (25-30 °C), but its tolerance to a wide variety of temperatures may have facilitated its immigration to more temperate regions (such as Indiana). The major factor influencing *C. raciborskii* populations seems to be temperature. While it can survive perennially in tropical areas (e.g., Briand et al. 2004); it seems to be limited to warm summer months in temperate regions (e.g., Briand et al. 2002; Saker et al. 2003). *C. raciborskii* tends to favor surface water temperatures over 25 °C (Saker et al. 1999) and seasonal warming of hypolimnetic waters (>23 °C) (e.g., Padisák 1997)."

While its temperature optimum seems to be 30 °C, its 'sub-optimum,' from 25-35 °C is within the range of temperatures observed in the Sentinel Lakes (Figure 11). Based on these reported temperature preferences, St. James and Shaokatan (in addition to Madison and South Center) lakes have temperatures in the preferred range (Figure 11); whereas, most of the northern lakes do not, suggesting that *C. raciborskii* could be present in any lake in the southern third of Minnesota. While *C. raciborskii* may be present in more Minnesota lakes, it is heartening to note that the forms found in the U.S. do not often produce toxins (Yilmaz et al. 2008; Yilmaz and Philips 2011).

Interrelationships among phytoplankton, zooplankton, and chemical and physical lake characteristics

A wide variety of data have been collected on the Sentinel Lakes, and we sought to determine correlations between physicochemical variables and various phytoplankton and zooplankton metrics. If strong associations (correlations) are found, specific variables might be useful for predicting change in the biotic metrics (e.g., TP or TN on phytoplankton or zooplankton biomass).

A scatter matrix was compiled using three phytoplankton metrics: taxa richness, Shannon diversity, and evenness (based on Shannon diversity) relative to a suite of physicochemical variables (Figure 15). The three algal metrics were highly correlated to each other ($\rho>0.59$). Percent littoral area (% of lake <15 feet; relative measure that reflects overall shallowness of the lake) was weakly correlated with algal community metrics (ρ ranged from -0.24 to -0.50), but in general, as % littoral declined the algal metrics increased. All three algal metrics were inversely related to TP, TN, and Chl-*a*; however, there was high variability at low concentrations of TP, TN, and Chl-*a*.

A similar approach made use of Spearman Rank Order Correlation (Table 33). Similar patterns between algal metric and chemical variables were evident in this analysis – as nutrient concentrations increased, the values of the algal metrics declined. The comparatively stronger relationship of the algal metrics with TN, as compared to TP, became evident in this analysis. Ca was negatively correlated with all three algal metrics ($p<0.05$). However, TP, TN, and Ca are all highly correlated as well ($\rho >0.83$, $p<0.001$ for all comparisons).

Silica (Si) is essential for diatom and some chrysophyte growth. Extensive diatom or chrysophyte growth can reduce available Si, and when reduced to limiting levels (<0.5 mg/L) the lack of Si contributes to the decline in diatoms (Wetzel 2001). The Sentinel Lakes exhibited a wide range in Si (0.5-16.0 mg/L, Table 2). While most lakes had abundant Si, Greenwood, Bear Head, and South Center lakes had low concentrations of Si (<2-3 mg/L; Wetzel 2001). Seasonal Si measures are presented for a range of lakes (Figure 16; Note - Si data may not correspond directly to phytoplankton collection dates; however, seasonal Si patterns are quite consistent from year-to-year based on personal review of Sentinel Lakes data). Si depletion from May to July was evident in all five lakes; however, 5 of the 6 lakes did not fall to "limiting" levels (Figure 16). Diatoms and chrysophytes were common in Greenwood, Bear Head, Elk, Ten Mile, and Lake Carlos in May and June, but were uncommon in South Center Lake (Figure 4). By July, diatoms and chrysophytes were present but at very reduced levels in Greenwood, Elk, Ten Mile, and Lake Carlos, as compared to May and June (Figure 5). Chrysophytes were prominent in Bear Head Lake on all sample dates.

A scatter matrix based on Spearman Rank Order Correlation was also plotted using total zooplankton densities and biomasses and the same suite of physicochemical variables as was done with the algal metrics (Figure 17). As would be expected, zooplankton densities and biomasses were highly correlated to each other ($\rho>0.93$ for all). Both zooplankton densities and biomass were significantly correlated with all six lake variables ($p< 0.01$ in all cases). Zooplankton densities and biomasses were positively correlated with % littoral area ($\rho>0.68$, $p<0.01$), TP ($\rho>0.85$, $p<0.01$), TN ($\rho>0.84$, $p<0.01$), Chl-*a* ($\rho>0.77$, $p<0.01$) and Ca ($\rho>0.72$, $p<0.01$), while negatively correlated with Secchi depth ($\rho<-0.77$, $p<0.01$; Table 34).

The non-metric multidimensional scaling (MDS) ordination, comparing zooplankton community structure similarities, among all 13 lakes during 2013 is illustrated in Figure 20. The closer symbols are on the ordination, the more similar the lakes they represent are, based on zooplankton community densities. Based on this analysis, Trout and Lake Shaokotan lakes are the most dis-similar to one another, and they do not cluster with any of the other Sentinel Lakes. Lakes that cluster together at the 60% similarity level include Greenwood and Bear Head; Elk, Carlos, and Ten Mile; Madison, Pearl, South Center, and Tait; and St. James and Portage lakes (Figure 18).

Cluster analysis was also used to compare similarities among lakes, based on relative phytoplankton community structure data (Figure 19). Although lakes based on the phytoplankton community clustered at lower similarity levels, these clusters generally grouped lakes with similar trophic status. All oligotrophic and mesotrophic lakes clustered together, two of the three eutrophic lakes clustered together, and all three hypereutrophic lakes clustered together. The only lake that did not cluster with any of the other lakes in this analysis was Portage (Figure 19).

The BIOENV procedure (Clarke and Gorley 2006) was used to test which (if any) of the lake physical or chemical parameters best explain similarities and dis-similarities among lakes, based on zooplankton community structure. In the Sentinel Lakes, of all the environmental variables measured (Zmax, lake area, % littoral area, TP, TN, Chl-*a*, Secchi depth, Ca, spring Si, mean Si, mean alkalinity, ratio of Si to TP, and TN:TP) the suite of parameters that best explained differences in the zooplankton species community structure (among lakes) was a combination of % littoral area, TN, and Secchi depth (0.63).

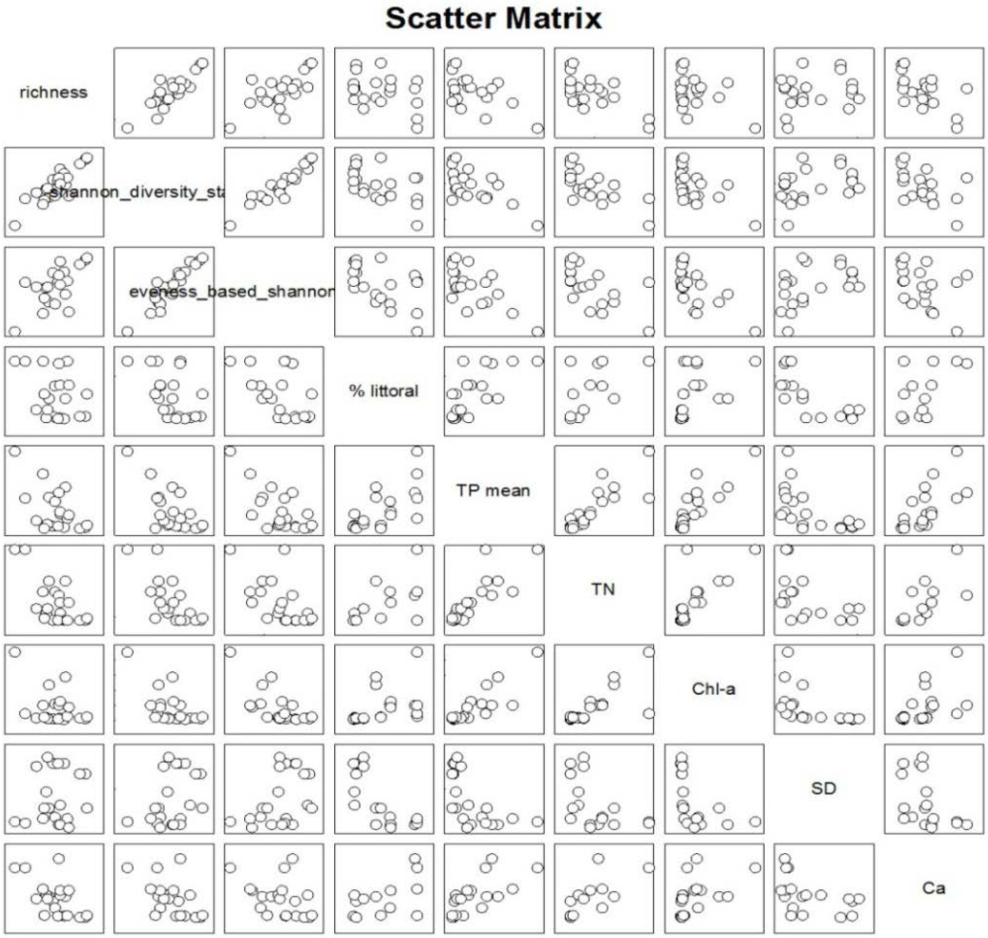

Figure 15. Scatter matrix for phytoplankton metrics, water chemistry (mean measures), and lake morphometry. Abbreviations are as follow: phytoplankton taxa richness, phytoplankton diversity, % littoral=percent of the lake surface area < 15 feet in depth, m, TP = total phosphorus, TN=total nitrogen, Chl-*a* =chlorophyll-a, SD=Secchi disk, and Ca=calcium.

Table 33. Spearman Rank Order correlations (and p-values) for algal metrics, water quality attributes and % littoral. Only significant correlations (p<0.05) are noted. Evenness was based on Shannon diversity.

Metric	% littoral	TP	TN	Chl-*a*	SD	Ca
Taxa richness			-0.508 (0.018)			-0.503 (0.019)
Shannon diversity	-0.499 (0.02)	-0.508 (0.018)	-.0706 (<0.01)	-0.527 (0.01)		-0.564 (<0.01)
Evenness	-0.469 (0.031)	-0.553 (<0.01)	-0.683 (<0.01)	-0.62 (<0.01)	0.412 (0.06)	-0.496 (0.02)

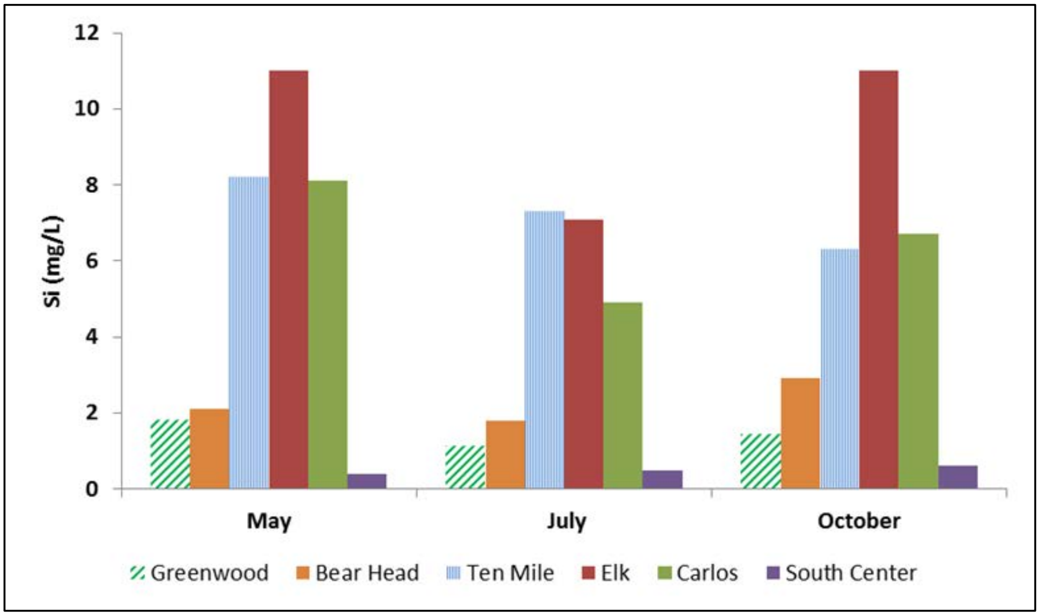

Figure 16. Silica concentrations (mg/L) from selected of Sentinel Lakes. Lakes ordered north to south.

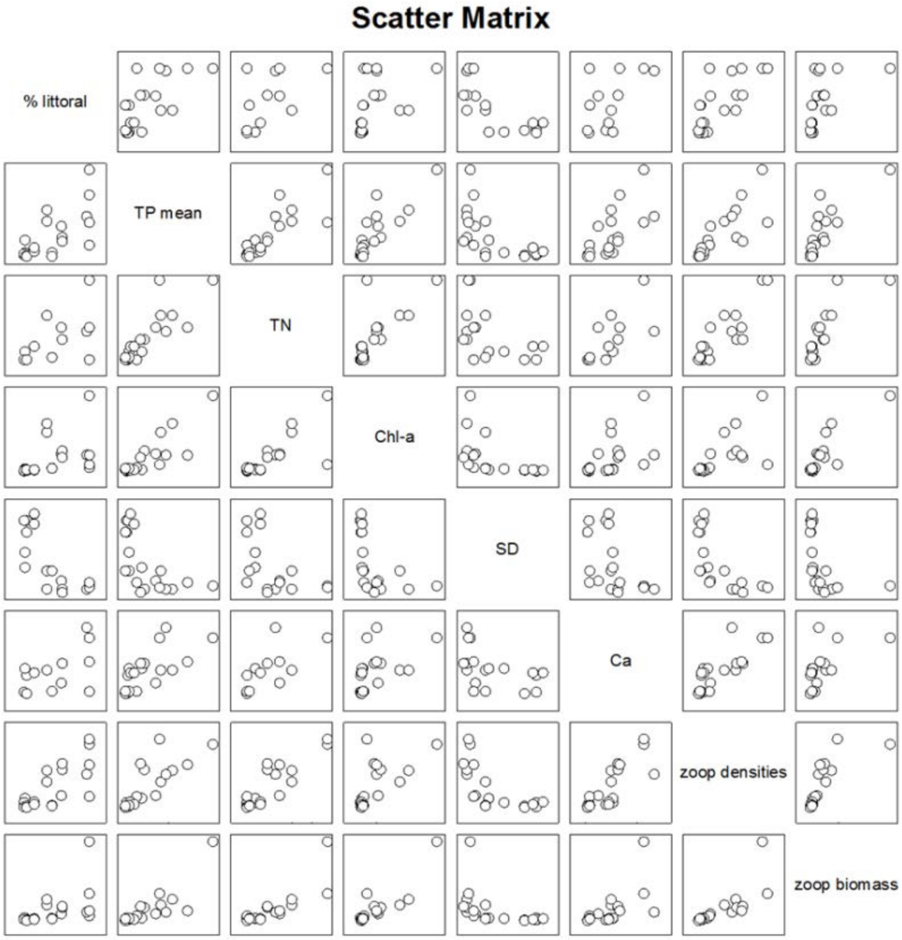

Figure 17. Scatter matrix for zooplankton metrics, water chemistry (mean), and lake morphometry. Abbreviations as follow: zooplankton taxa richness, zooplankton diversity, % littoral=percent of the lake surface area < 15 feet in depth, m, TP = total phosphorus, TN=total nitrogen, Chl-*a* =chlorophyll-a, SD=Secchi disk, and Ca=calcium.

Table 34. Spearman Rank Order correlations (ρ) for zooplankton metrics and water quality and % littoral. (p-value in parenthesis). (% littoral = area < 15 feet, TP= total phosphorus (μg/L), TN=total nitrogen (mg/L), Chl-*a*= Chlorophyll *a* (μg/L), SD=Secchi depth (m), Ca=calcium (mg/L), zooplankton densities (no./L), zooplankton biomass (μg/L)).

Metric	% littoral	TP	TN	Chl-a	SD	Ca
Zooplankton densities	0.725 (<0.01)	0.879 (<0.01)	0.842 (<0.01)	0.767 (<0.01)	-0.772 (<0.01)	0.843 (<0.01)
Zooplankton biomass	0.675 (<0.01)	0.854 (<0.01)	0.841 (<0.01)	0.836 (<0.01)	-0.795 (<0.01)	0.722 (<0.01)

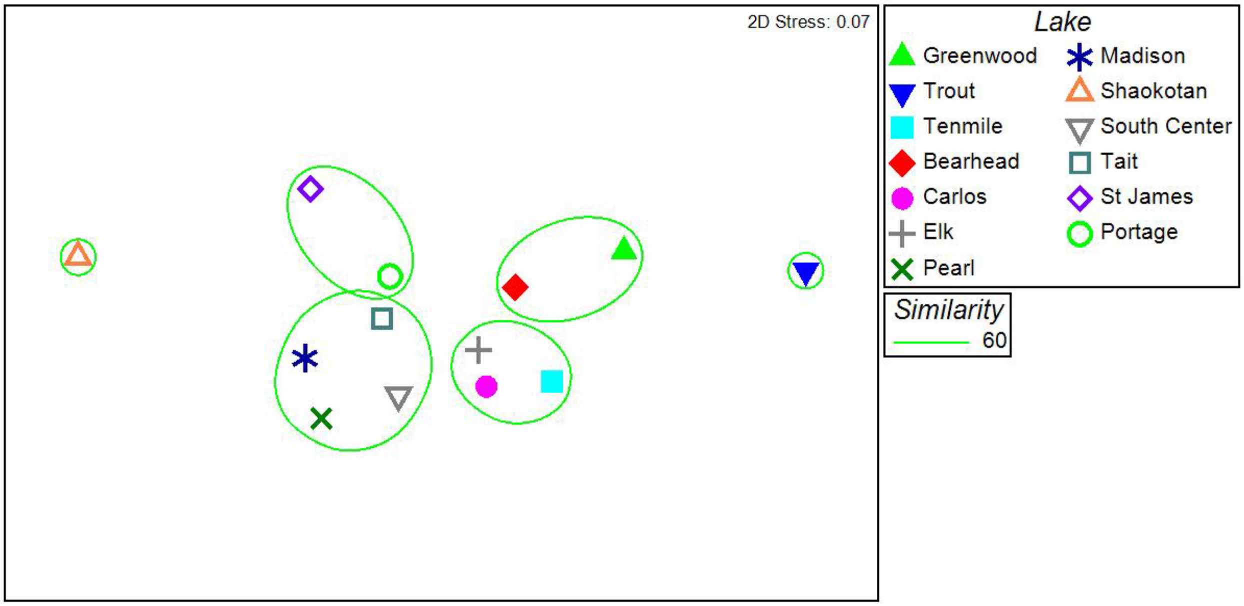

Figure 18. Non-metric multidimensional scaling (MDS) ordination of mean zooplankton densities based on the Bray-Curtis similarity matrix, in 13 Sentinel Lakes during 2013. Groups of lakes contained in green borders represent lakes that have at least 60% similarity. Data were log (x+1) transformed to reduce influence of dominant taxa.

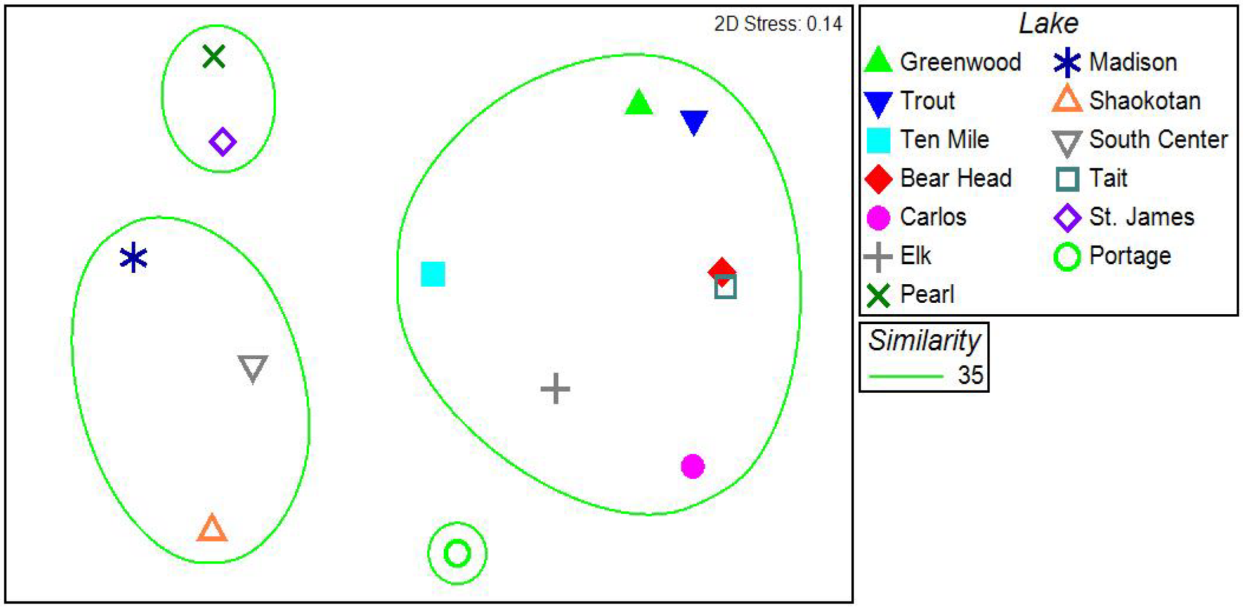

Figure 19. Non-metric multidimensional scaling (MDS) ordination of mean phytoplankton relative abundance based on the Bray-Curtis similarity matrix, in 13 Sentinel Lakes during 2013. Groups of lakes contained in green borders represent lakes that have at least 35% similarity. Data were square root transformed to reduce influence of dominant taxa.

Bubble plots representing the suite of lake parameters (% littoral area, TN, and Secchi depth) that were selected in the BIOENV analysis, were superimposed individually on MDS ordinations (Figure 20). In general, most lakes that clustered together, based on zooplankton community composition (Figure 18) had similar sized bubbles for these three lake parameters, with the exception of Tait Lake. Tait Lake clustered with Madison, Pearl, and South Center lakes, but % littoral area and Secchi depth were relatively greater, while total nitrogen was lower in Tait than in the other lakes that clustered with this lake, based on zooplankton community composition. Although Tait Lake has low productivity, it is also relatively shallow with a large percentage of littoral area and has a zooplankton community that may be similar to some of the more productive eutrophic lakes, with similar littoral zooplankton species.

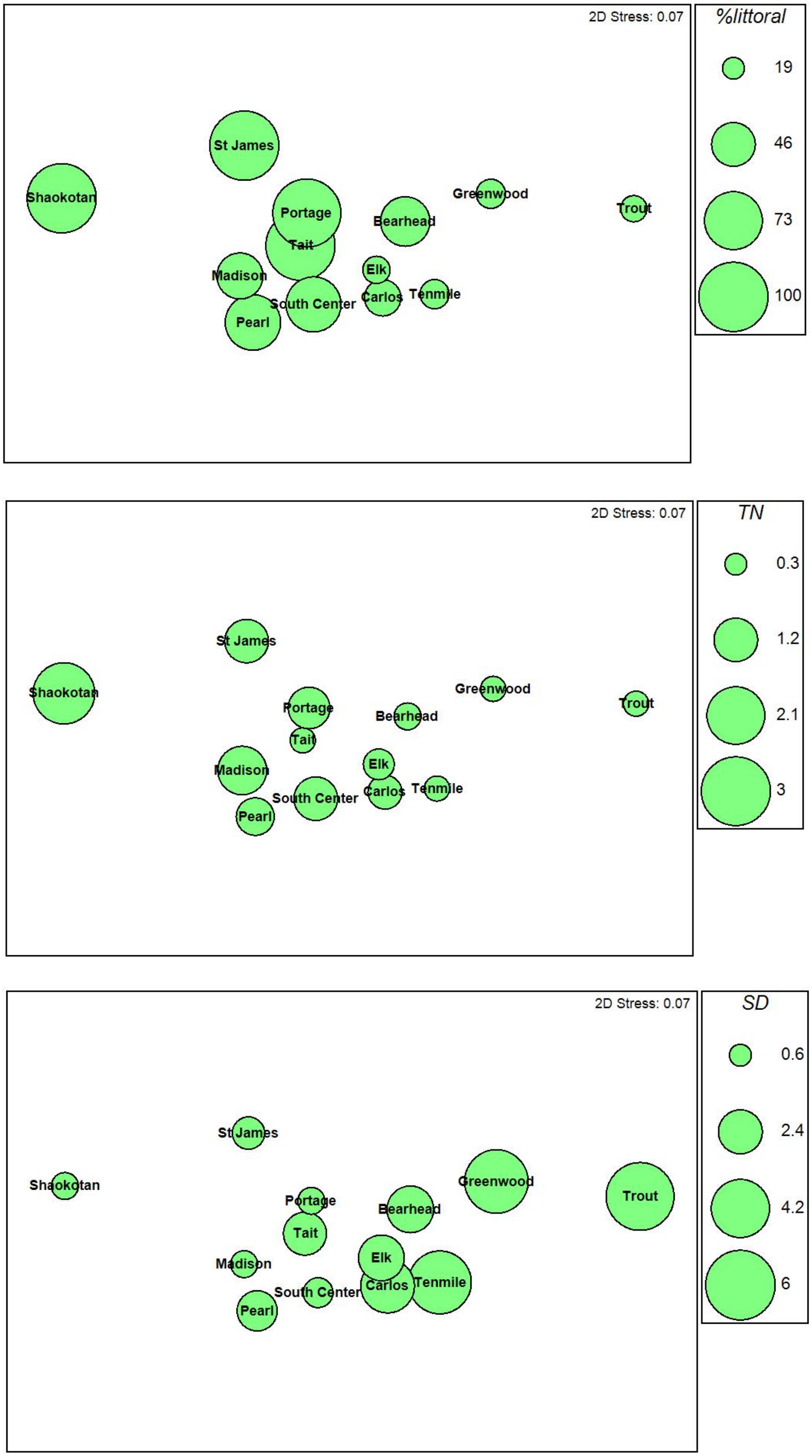

Figure 20. Non-metric multidimensional scaling (MDS) ordination of average seasonal zooplankton densities in 13 Sentinel Lakes during 2013 with bubble size representing lake parameters (percent littoral area, TN (mg/L), and Secchi depth (m)) that were selected as best explaining patterns in zooplankton community structure in the BIOENV analysis.

Zooplankton/phytoplankton inter-annual variability

Zooplankton data were collected from nine of the 13 lakes during 2013 and 2014, while phytoplankton data were collected from eight lakes both years. To examine inter-annual variability in these lakes, MDS ordination graphs based on zooplankton densities (Figure 21) and phytoplankton relative abundance (Figure 22) were generated. Generally, zooplankton community structure in most lakes appeared to be more similar between years than did the phytoplankton community structure.

Results from the analysis of similarity (ANOSIM) tests showed significant differences in zooplankton community structure between years, in only three of the nine lakes (Greenwood, Trout and Shaokotan), with p-values < 0.05 (Table 35). The remaining six lakes showed inter-annual variability to be very low (Table 35, Figure 21). Similar low inter-annual variability in the zooplankton communities from all 24 Sentinel Lakes was found during the first phase of the Sentinel Lakes Study as well (Hirsch 2013). Differences in the zooplankton structure between 2013 and 2014 in Trout Lake could be a result of the recent infestation of spiny waterfleas in this lake, although Greenwood Lake also showed significant differences between years, where spiny waterfleas are already well established. The significant difference detected between years in Lake Shaokotan is most likely due to recent changes in nutrient loading and expansion of macrophytes in this lake.

To further test which zooplankton species were contributing to the changes between the years in the three lakes, the similarity percentage routine (SIMPER) was used. In both Greenwood and Trout lakes, cyclopoids contributed over 30% of the change between the two years, which decreased in densities from 2013 to 2014. In Shaokotan Lake, the large daphnid (*Daphnia pulicaria*) was responsible for 20% of the change, having much lower densities in 2014.

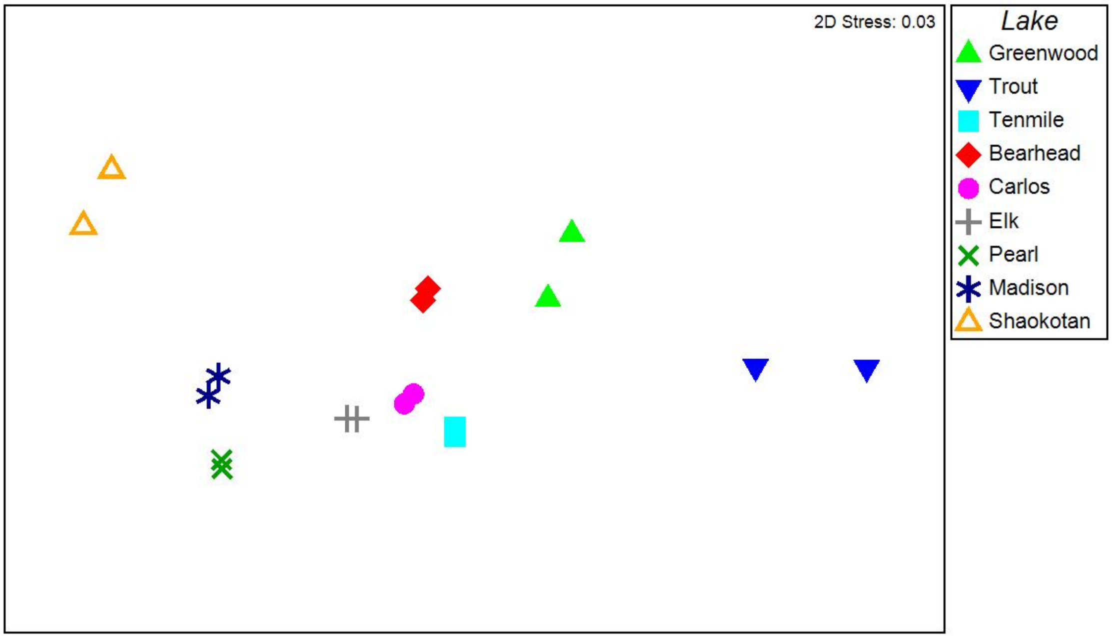

Figure 21. Non-metric multidimensional scaling (MDS) ordination of average seasonal zooplankton densities in 2013 and 2014, showing inter-annual variability in the Sentinel Lakes that were sampled both consecutive years.

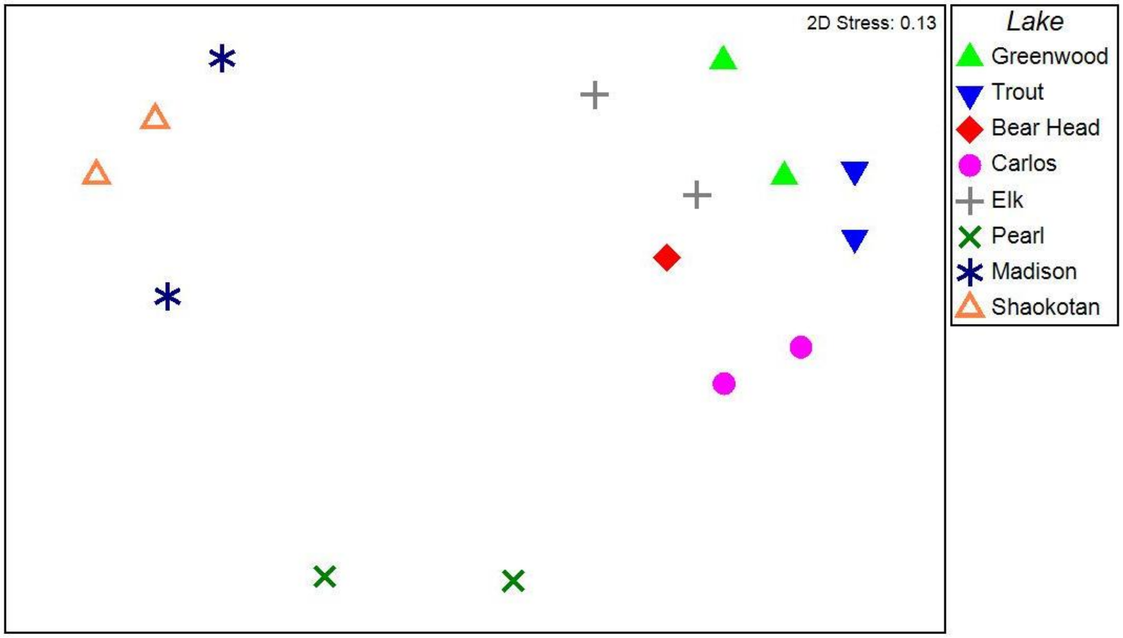

Figure 22. Non-metric multidimensional scaling (MDS) ordination of average seasonal phytoplankton densities in Sentinel Lakes that were sampled in both 2013 and 2014.

Table 35. Results from Analysis of Similarity (ANOSIM) comparing zooplankton community structure variability between 2013 and 2014. Lakes with significant *R*-statistic (which shows significant differences between years) at p<0.05 level are in bold.

Lake	*R*-statistic	p-value
Greenwood	**0.27**	**0.03**
Trout	**0.24**	**0.02**
Ten Mile	-0.05	0.68
Bear Head	-0.30	1.00
Carlos	-0.03	0.58
Elk	-0.08	0.79
Pearl	-0.11	0.82
Madison	0.06	0.29
Shaokotan	**0.39**	**0.01**

Invasive species impacts on phytoplankton, zooplankton, and water quality

The relationships among TP, Chl-*a*, and Secchi is well established through Carlson's Trophic State Index (TSI) (Carlson 1977). In general, as TP concentrations in lakes increase so does algal biomass (Chl-*a*), while transparency (Secchi depth) declines. Carlson TSI values based on summer-mean measures often show close correspondence for these three variables (typically within ±5 TSI units). Likewise, interactions among phytoplankton and zooplankton groups are well understood, and these top-down effects are reinforced in this report. Invasive species such as zebra mussels, spiny water fleas, carp (*Cyprinus carpio)*, and curly-leaf pondweed can have direct and/or indirect impacts on the food web or nutrient supply of a lake, causing changes in water quality or biological characteristics. Curly-leaf pondweed impacts were the subject of an earlier Sentinel Lakes study (Heiskary and Valley, 2012). The current study allows for the consideration of zebra mussels (Lake Carlos) and spiny waterfleas (Greenwood and Trout lakes).

Zebra mussels (*Dreissena polymorpha*)

To date, Lake Carlos is the only Sentinel Lake that has zebra mussels. Although they were first detected in 2009, adult populations were not well established in Lake Carlos until 2013. Zebra mussels generally filter food particles up to 400 µm in size, which includes phytoplankton, rotifers, and some microzooplankton (MacIsaac et al., 1991). Therefore, zebra mussels have the potential to impact zooplankton populations both indirectly by competition for food with phytoplankton grazers, and directly by filtering out copepod nauplii and other small zooplankters. Pace et al. (2010) found that zooplankton biomass declined about 50% in the Hudson River after zebra mussel establishment, but has recently recovered due to increased mortality of zebra mussels. Zebra mussels can impact phytoplankton communities in lakes by direct filtering of algae (decreasing Chl-*a*) (Dzialowski 2013) but have also been found to change the algal community structure, favoring cyanobacteria (Knoll et al. 2008). Increases in water clarity often follow the establishment of zebra mussels (Idrisi et al. 2001).

Lake Carlos is part of a chain of lakes located near Alexandria, Minnesota. The head of the chain is in Alexandria, MN, and comprises Winona, Agnes, and Henry lakes which flow toward Le Homme Dieu and to Lake Carlos. The Alexandria Lake Area Sanitary District (ALASD) wastewater treatment facility (WWTF) discharges into Lake Winona. Effluent TP is discharged at a very low concentration (~300 µg/L), and downstream impacts in Lake Carlos are minimal. Lake Darling flows into Lake Carlos from the southwest. Zebra mussels were first detected in Le Homme Dieu and shortly thereafter in Lake Carlos (2009). Adults were noted extensively throughout the lake by 2013. The spread upstream to Darling Lake occurred over this time period as well.

TSI data from lakes Carlos, Le Homme Dieu, and Darling were analyzed to see what, if any, trends may be occurring for TP, Chl-*a*, and Secchi depth. Since all three have varying degrees of zebra mussel infestation, Lake Miltona, located immediately north of Lake Carlos was included as a "control," since this lake is in a very early stage of infestation compared to the other three lakes. The years from 2000-2014 were used for this comparison (Figure 23).

Since 2008, TP exhibits a similar pattern among the four lakes with Lakes Miltona and Le Homme Dieu having slightly higher TP and Lake Carlos the lowest (Figure 23). Chl-*a* is similar for the four lakes, and a slight decline is noted since 2011. Secchi transparency shows the greatest departure from historical levels with Carlos, Le Homme Dieu, and Darling Lakes exhibiting a significant increase in transparency from 2011-2014; while Lake Miltona exhibited a subtle decline (though within its typical range).

Charting Carlson's TSI values for Lakes Carlos and Miltona allow for direct comparison of TP, Chl-*a*, and Secchi when converted to TSI values (Figure 24). In Carlos, all three TSI variables declined from 2011-2014 (i.e. lower TP & Chl-*a* and increased Secchi), and the values diverged from one another. This is in contrast to 2000-2010 when Chl-*a* and Secchi depth were in close correspondence over much of the record. From 2007 forward, Secchi TSI (TSIS) is consistently lower than the Chl-*a* TSI (TSIC), implying that the lake is clearer than expected based on the algal biomass. These patterns contrast with Lake Miltona, where TSIP and TSIC are in close correspondence as is TSIS in 2013 and 2014. A qualitative comparison of Lake Carlos phytoplankton data from 2008 (Engel et al. 2010) with that from 2013 and 2014 indicated similar assemblages among all three years, and at this point there is no indication that there has been a shift in algal composition.

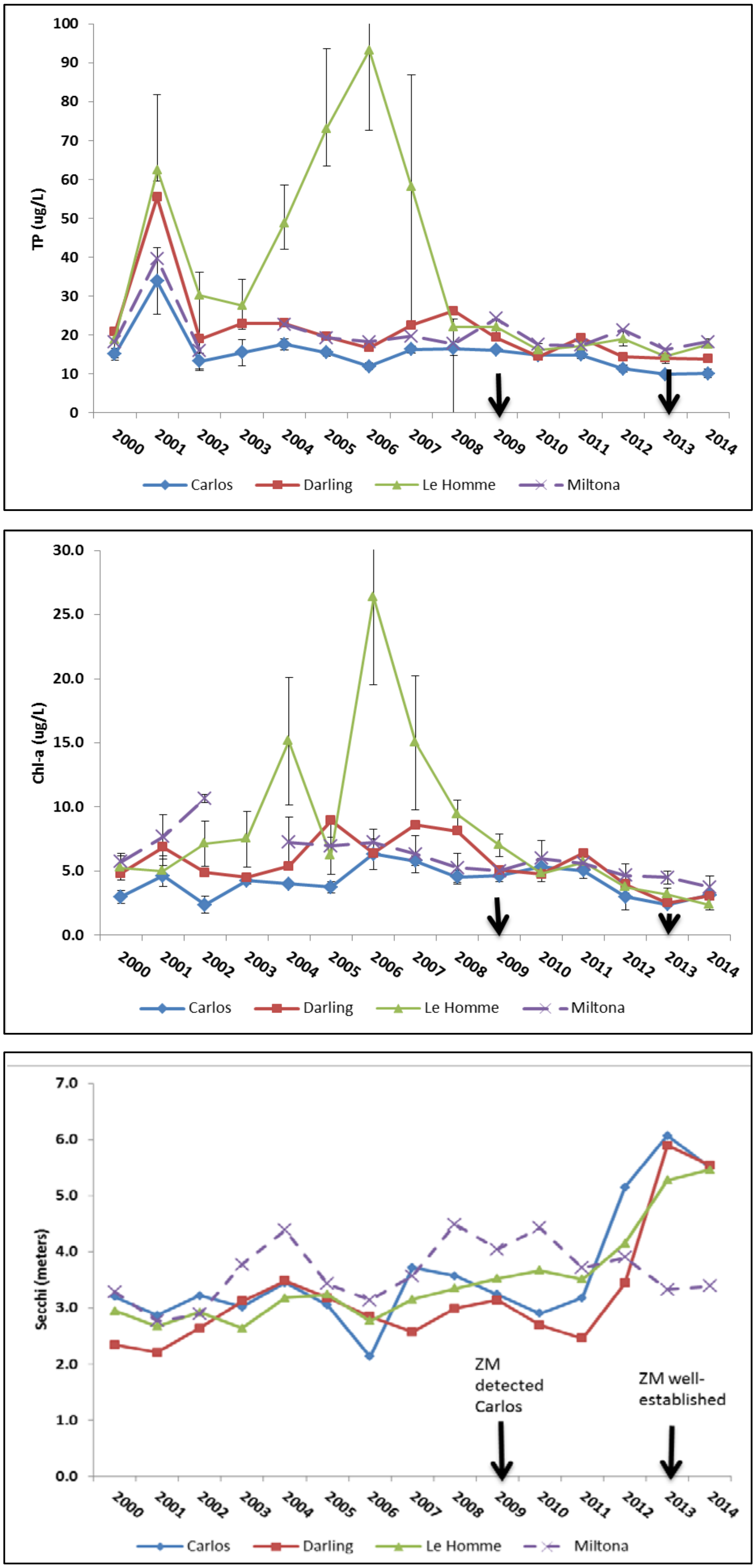

Figure 23. Summer-mean TP, Chl-*a*, and Secchi depth for Carlos, Le Homme Dieu, Darling, and Miltona Lakes. Bars represent standard error. Detection and establishment of zebra mussels in Carlos noted.

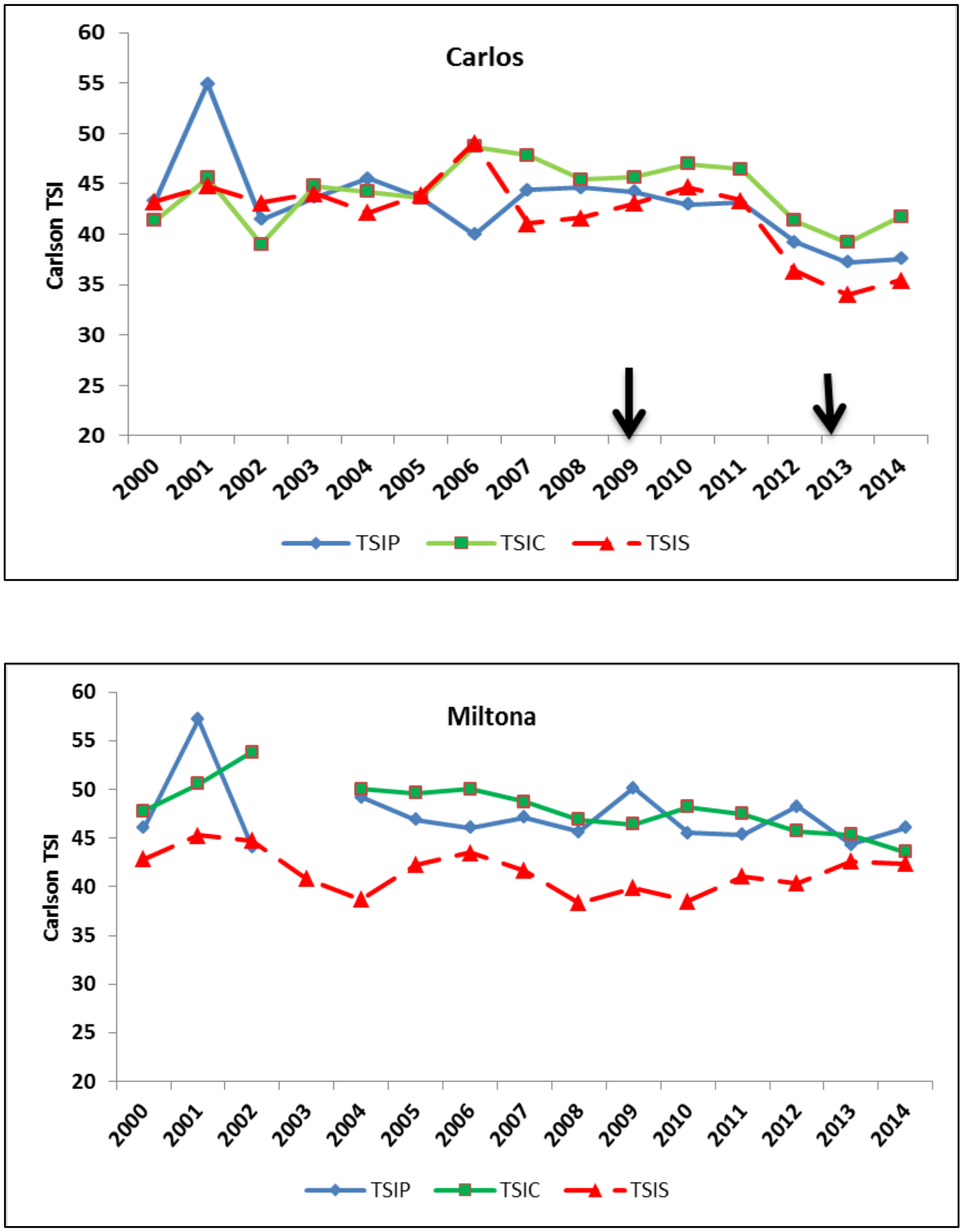

Figure 24. Lakes Carlos and Miltona Carlson TSI values based on summer-mean measures. TSIP=TP-based TSI, TSIC=Chl-a-based TSI, and TSI=Secchi-based TSI. ZM detection in Carlos (2009) and full establishment (2013) noted.

Zooplankton samples have been collected from Lake Carlos since the beginning of the Sentinel Lake Study in 2008. Therefore, Lake Carlos is one of only a few zebra mussel infested lakes in Minnesota where zooplankton data exist from pre-zebra mussel conditions. Since 2009, when zebra mussels were first found in Lake Carlos, there appears to be a trend of decreasing total zooplankton densities, especially in the last two years (2013-2014), when zebra mussel adults were well established in this lake (Figure 25). The phytoplankton grazers (calanoids, large daphnids, and small cladocerans) decreased the most. The decline in these groups of zooplankters, which coincides with the zebra mussel infestation, suggests that indirect food competition interactions, and possibly direct impacts by zebra mussel filtering, could be beginning to occur in Lake Carlos. Although a trend is apparent, a couple more years of post-infestation data is necessary to test for significant differences between pre- and post- zebra mussel infestation years.

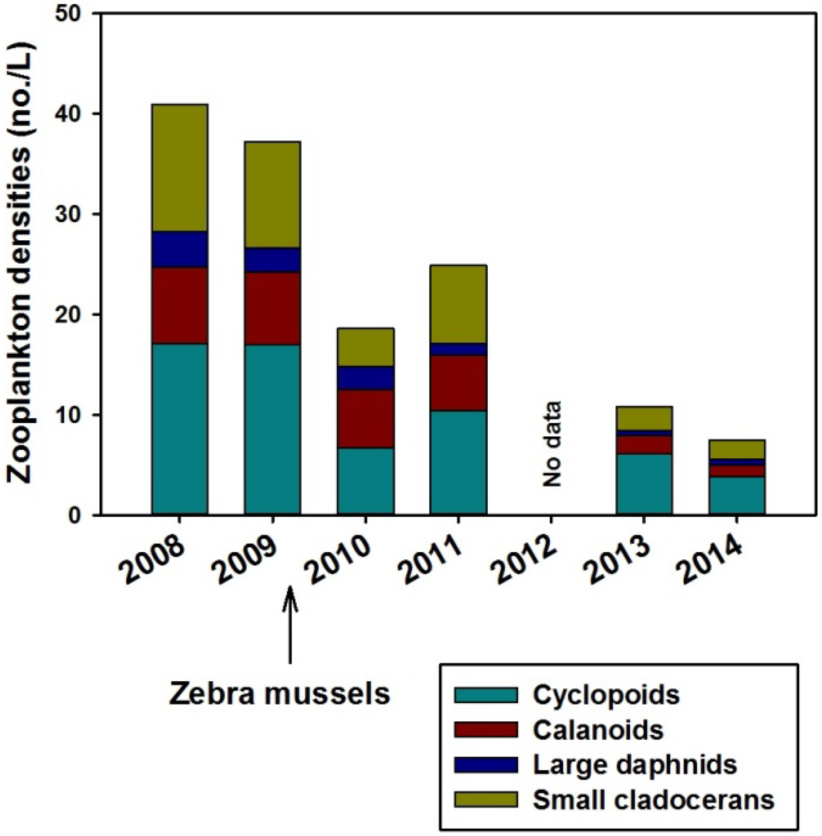

Figure 1. Lake Carlos zooplankton densities (number/L) for 2008-2014 for four major zooplankton groups. Note the arrow in 2009, when zebra mussels were first detected in the lake.

Spiny waterflea (*Bythotrephes longimanus*)

Over the past few decades, an invasive zooplankton species (*Bythotrephes longimanus)*, commonly known as the spiny waterflea, has become established across the Great Lakes Region, invading many lakes along the Minnesota and Ontario border (Kerfoot *et al*., 2011). To date, two of the Sentinel Lakes in Minnesota have spiny waterfleas. Greenwood Lake has a well-established population, first detected over a decade ago, while Trout Lake was more recently infested, first detected in 2012. Spiny waterfleas are large predacious zooplankters, which prey on smaller zooplankton species and have been associated with significant reductions in native zooplankton densities, biomass, and species richness in lakes (Yan *et al*., 2001, 2002). In Minnesota, lakes infested with spiny waterfleas have experienced significant losses in small cladocerans due to direct predation impacts (Kerfoot *et al*., in peer review).

To examine densities of small cladocerans in the spiny waterflea infested lakes (Trout and Greenwood) relative to the other Sentinel Lakes, a bubble plot representing small cladoceran densities (Figure 26) was superimposed on the original MDS ordination graph from 2013 (Figure 18). Very low densities of small cladocerans were found in both Greenwood and Trout lakes. St. James Lake, a shallow eutrophic lake, exhibited the highest density of small cladocerans.

Zooplankton samples have been collected from Trout Lake since the beginning of the Sentinel Lake study in 2008, therefore zooplankton data from pre-spiny waterflea conditions are available to compare with post-infestation data. Greenwood Lake was just recently added to the list of Sentinel Lakes in 2013, therefore no pre-spiny waterflea zooplankton data are available. Zooplankton densities from 2008 through 2014 are plotted in Figure 27. There does not appear to be any change in total zooplankton densities through the years, although small cladocerans appeared to decrease in 2013 and 2014 and cyclopoid copepods showed an apparent decrease in 2014. Trout Lake is still in the early stage of spiny waterflea infestation, therefore impacts may not have occurred yet. A few more years of post-infestation data should help elucidate additional impacts trophic level impacts from *Bythotrephes* beyond the zooplankton community are not well documented, but under conditions of significant losses of zooplankton grazers, increases in phytoplankton biomass might be expected. Strecker and Arnott (2008) found a weak trophic cascade where *Bythotrephes* introductions reduced zooplankton biomass and subsequently increased phytoplankton growth in experimental mesocosms in boreal lakes. Jeppesen et al. (2003) suggested that less productive lakes may not respond to top-down trophic changes (given nutrient limitation) as much as more productive lakes.

Greenwood and Trout lakes provide a unique opportunity for tracking the impact of spiny waterfleas on phytoplankton, and potentially water quality, since pre-infestation data are available for both lakes. A comparison of TSI values from Greenwood, Trout, and Bear Head (control) lakes was compiled to discern patterns that may be attributable to the presence of spiny water flea. These lakes do not have as much historical data as Lake Carlos, and 2008 (start of Sentinel Lake monitoring) was used as the base year (Figure 28).

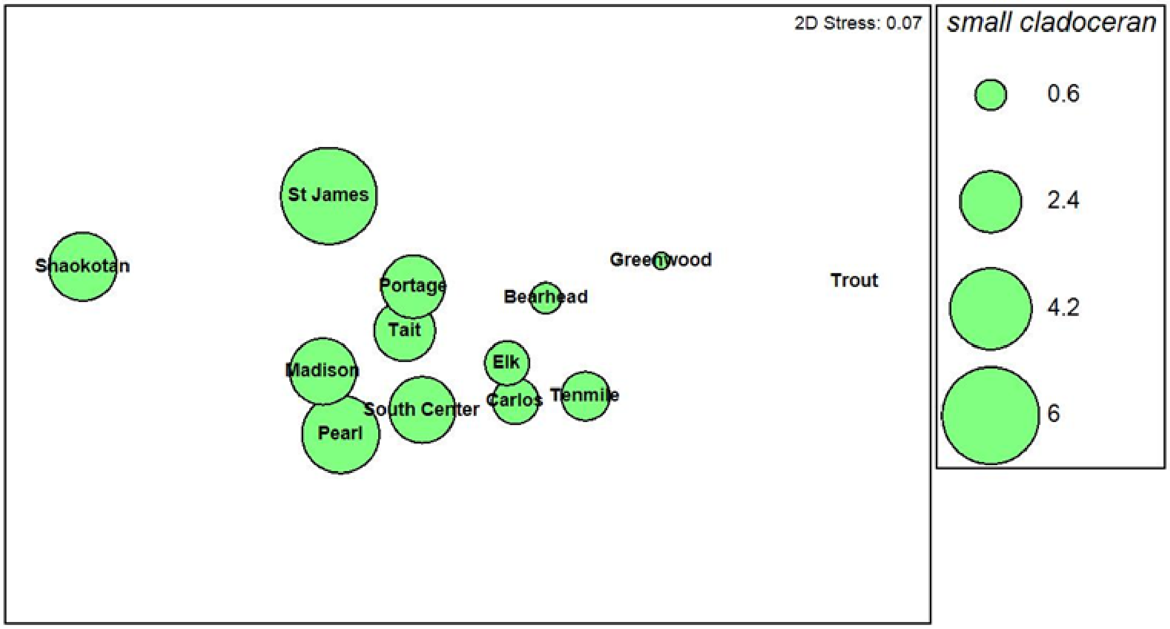

Figure 26. Non-metric multidimensional scaling (MDS) ordination of average seasonal zooplankton densities in 13 Sentinel Lakes during 2013 with bubble plots representing densities (number per liter) of small cladocerans.

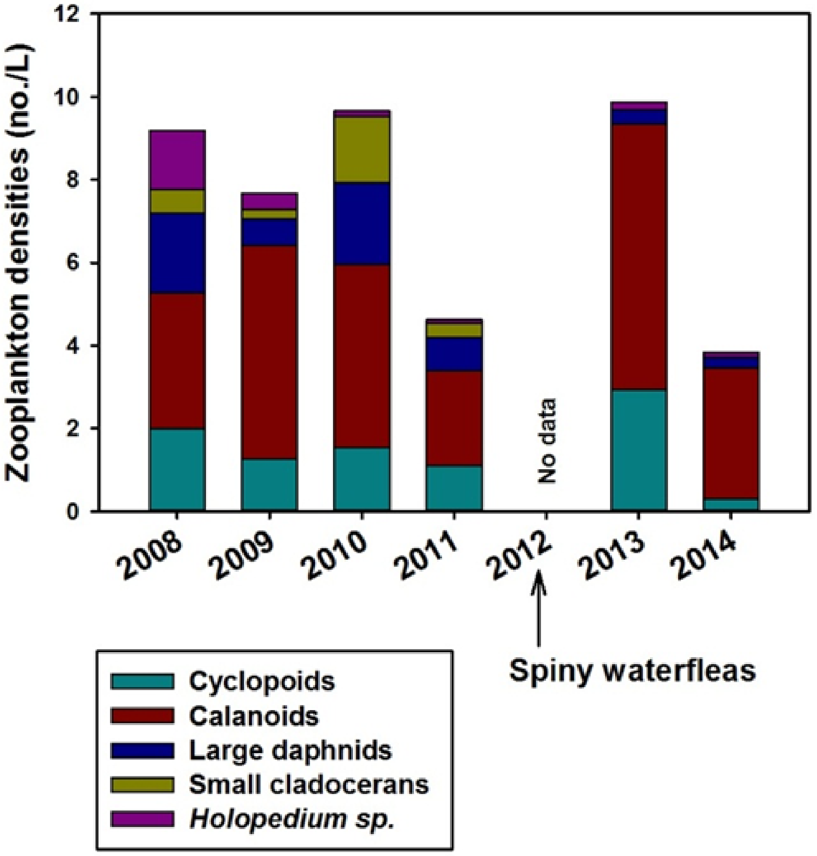

Figure 27. **Trout Lake zooplankton densities (number/L) for 2008-2014 for the five major zooplankton groups. Arrow denotes when spiny waterfleas detected.**

In general, there is good correspondence of Secchi depth and Chl-*a* for these lakes (Figure 28), and no real trend is evident. [*Note - The 2013-2014 TSIP decline in all three lakes is an artifact of a change in TP analytical method, which allowed for a lower detection limit and more precise measurement of phosphorus*.] While no distinct patterns were evident, it is worth examining in the future when more data are available and spiny waterfleas have become well established.

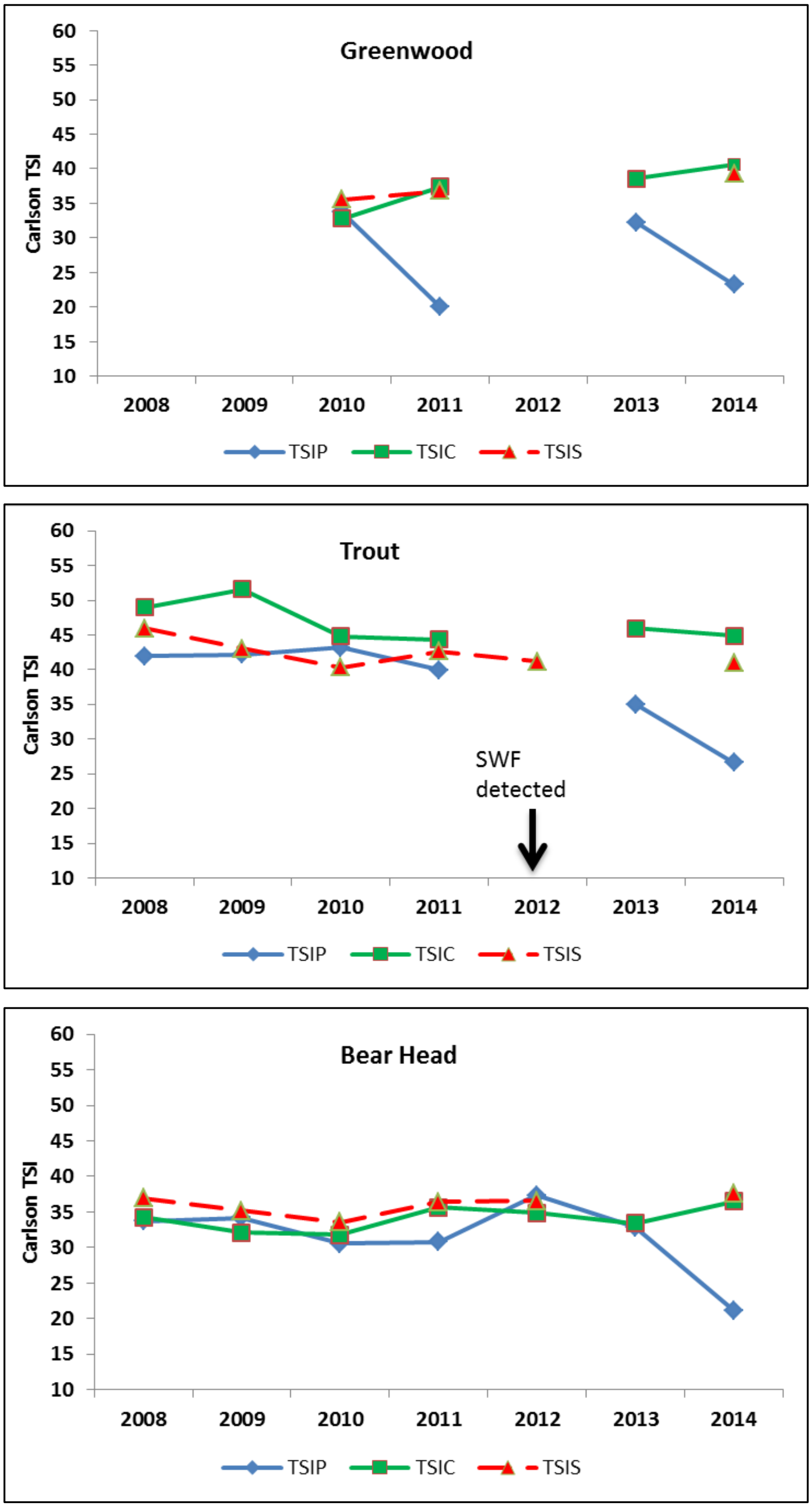

Figure 28. Carlson TSI values for Greenwood, Trout, and Bear Head Lakes.

Summary and Recommendations

The purpose of this report was to examine patterns in phytoplankton and zooplankton based on a subset of the Sentinel Lakes. While zooplankton sampling has been a routine part of Sentinel Lake sample collection and was addressed in individual lake reports, phytoplankton has been sampled sporadically. The need for phytoplankton information for the Super Sentinel and Tier 1 lakes provided an opportunity to generate comprehensive phytoplankton data for 13 lakes in 2013 and 2014. Since zooplankton were sampled in these lakes as well, this allowed for an analysis of data for these two significant parts of the food web. This analysis provides basic descriptions of phytoplankton and zooplankton composition, seasonal cycling, and interactions in 13 Sentinel Lakes. Observations included herein can be used in future assessments as a basis for comparison and evaluating change over time. Though this analysis was limited to 13 lakes, their geographic, morphometric, and trophic ranges allow for some generalizations that may be applicable to Minnesota lakes in general.

Ideally, all Sentinel Lakes would have been incorporated into this analysis; however, phytoplankton collections and identification was limited to a subset of the lakes in 2013 and 2014. Another limitation was that samples were collected only at a mid-lake site and reflect only the upper 2 m of the water column. By virtue of this, algae that reside at greater depths (e.g., metalimnion) may be absent from this assessment, as are algal forms found primarily in the littoral areas of the lakes (e.g., periphytic or benthic forms that may be associated with plants or sediments). Following is a summary of findings from this study and recommendations for future consideration.

1. All Sentinel Lakes should have phytoplankton collections coincident with future water quality and zooplankton sampling. A minimum of two years of data should be obtained from each lake in order to establish a baseline for future assessments. When data are available for all 25 lakes it would be desirable to update the analyses conducted in this report.

2. Algal succession: Numerous factors influence the cycling of algal forms in Minnesota lakes. Examples of these factors include: climatic drivers - sunlight, temperature, and wind; nutrients - phosphorus and nitrogen; minerals - carbonate and silica; and biological: zooplankton. These factors vary in their significance among lakes and interactions among variables may be complex. The literature offers numerous examples of seasonal cycling of algal forms, and this aids in our characterization of patterns in Minnesota lakes. Analyzing the Sentinel Lakes across a trophic gradient provides a reasonable approach for characterizing phytoplankton and zooplankton composition and seasonal succession for Minnesota lakes. Moving from oligotrophic to hypereutrophic we observed the following:
   - In oligotrophic and mesotrophic lakes, diatoms and chrysophytes are the dominant forms. While diatoms are prominent across the entire trophic gradient (Figure 9), chrysophytes are uncommon in the eutrophic lakes (Figure 9). This is likely the result of competition from algal forms that prosper in more nutrient-enriched water and the warmer temperatures of the lakes of central and southern Minnesota. Algal biomass is often highest at spring turnover in the oligotrophic and mesotrophic lakes and usually declines thereafter, until fall turnover (Figure 10). Blue-greens, while present, are never dominant and biomass, based on Chl-*a*, is far below nuisance bloom levels (Figure 13). Nutrient limitation, Si depletion, zooplankton grazing, and water temperature are important drivers in the observed seasonal succession.
   - In eutrophic and hypereutrophic lakes, spring turnover is marked by blooms of diatoms, cryptophytes, and green algae. By June, these forms decline in prominence and are replaced by blue-greens, which remain prominent until October when the water cools (Figure 11) and cryptophytes become prominent again (Figure 5). In general, there is a steady increase in algal biomass from May through September/October and much of that is in the form of blue-greens (Figure 13). Since nutrients are abundant in these lakes, warm temperatures and zooplankton grazing of other algal forms (reduce competition) are among the two most important drivers allowing for blue-green dominance.

3. Indicators of changing lakes:
    a. Algal indicators
        - Blue-green algae were present in all Sentinel Lakes and most likely present in all Minnesota lakes. Blue-green forms, shifts in dominant genera, and potential increases in toxin-producers could be useful indicators of change. For example, in the oligotrophic (e.g., Table 7, Table 9) and mesotrophic lakes a variety of blue-green genera are found (generally non-toxin producers), whereas in the more eutrophic lakes (e.g., Table 29) potential toxin-producing *Anabaena*, *Microcystis*, and *Aphanizomenon* were dominant (Figure 13). Increases in the occurrence of toxin-producing blue-greens in Sentinel Lakes where they are currently rare could be a cause for concern.
        - *Cylindrospermopsis* is a known blue-green algal toxin producer and was relatively uncommon in the 2013 and 2014 collections in this study, with the exception of Madison and South Center lakes. It was previously believed to be tropical, preferring warm temperatures. Its presence and relative abundance in other Sentinel Lakes should be tracked in future collections. A significant expansion in its presence and abundance could be an indication of significant environmental changes in the affected lakes. Northward expansion would be of particular concern.
        - The blue-green alga *Gloeotrichia* may be worth watching over time in these lakes. It is not considered an indicator of poor water quality and it is more common in lakes of high clarity. However, literature reports suggest it draws most of its nutrients from the sediment of the lake and that it is not a good food source for zooplankton (Roelofs and Oglesby 1970). Future increases in this algal form could be indicative of changes in a lake system.
        - Increased water temperature favors blue-green algae over other forms. In particular, as summer temperatures increase above 20 °C and remain at 25 °C or more for extended periods, blue-greens prosper. As lakes warm, chrysophytes may be among the first forms to decrease, given their preference for cool temperatures. Chrysophytes are important in mesotrophic lakes (Figure 9) and a good food source; should they be reduced via increased temperature or nutrient enrichment, blue-greens may fill the niche they occupy.
        - Blue-green algal toxins, such as microcystin, have not been a part of the Sentinel Lakes monitoring effort. It would be desirable to begin to include measurement of at least microcystin (and perhaps other toxins) in the Sentinel Lakes effort. The incorporation of blue-green toxins should occur only after a thoughtful study plan has been developed. This plan would define when and where measurements would be taken, frequency of collection, and plans for data analyses.
        - Euglenoids are known indicators of organic pollution (APHA et al. 1998). Euglenoids were uncommon in the 2013 and 2014 Sentinel Lake samples. When found, it was typically a single natural unit (cell), as was the case in Elk, Pearl, Ten Mile, South Center, Tait, Bear Head, and St. James. The exception was Portage Lake where multiple genera, represented by more than one natural unit were found. The three genera found were *Euglena*, *Trachelmonas*, and *Phacus*. A fourth genera, *Lepocinclis*, was found only in St. James Lake. Increases in the relative abundance of euglenoids could be an indicator of increased organic or nutrient pollution in a lake.
    b. Zooplankton indicators
        - *Daphnia longiremis*- This deep-water daphnid may be an indicator species, as it is found in the hypolimnion of deep, well-oxygenated lakes. This is reinforced by the findings from zooplankton analysis of 150 random lakes in the 2012 National Lakes Assessment (Hirsch 2014) where this species was found only in the north central MN lakes.
        - *Leptodiaptomus minutus*- a cool-water Diaptomidae that is restricted to deep lakes at the southern end of its range. In Minnesota, it is only found in oligotrophic and mesotrophic lakes, and its loss could be an indication of eutrophication and/or climate-induced warming.
        - *Leptodiaptomus siciloides* and *Aglaodiaptomus clavipes*- both these calanoid species tend to favor or are better adapted to more eutrophic conditions.

4. Invasive species
    - The impact of zebra mussels in Lake Carlos is already apparent based on trends in TSI; whereby Secchi depth is increasing and algal biomass appears to be decreasing. There are not adequate data to determine if there are significant shifts in algal composition. Based on 2013 and 2014 data there was not a significant shift to blue-green forms, which sometimes occurs with increased zebra mussel infestation. However, the low TP in Lake Carlos may minimize the likelihood of this occurring. Future investigators should be particularly watchful for increases in *Microcystis aeruginosa*, which has been shown to increase in lakes with significant zebra mussel infestations.
    - Zebra mussels appear to be affecting the zooplankton community in Lake Carlos, as densities of grazers have declined in post-zebra mussel infestation years, suggesting competition effects, although more post-infestation data are necessary to test this statistically.
    - Spiny waterfleas in Trout Lake appear to be affecting small cladocerans by direct predation and possibly cyclopoid copepods by indirect food competition interactions, although more data are necessary to confirm this.
    - Benthic macroinvertebrate sampling has been conducted on several of the Sentinel Lakes. Data from these lakes should be analyzed and reported on. There may be valuable insights with respect to this separate energy pathway that can have a significant contribution to the energetics of the entire lake. This may also provide a basis for quantifying zebra mussel densities. In addition, since benthic invertebrates are longer-lived than zooplankton they may integrate changes in a lake at a different time scale.

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Appendix

1. Algal indices as summarized by Phyco Tech (June 25, 2005).

Index Name-Algae	**Formula**	**Explanation of variables**
Shannon Index-standard (H', Shannon Weaver) SHST	$-\sum p_i*\ln p_i$ e.g., SHSTRCONC	p_i is the relative proportion of each taxa (taxa/total sample taxa). This is summed for all unique taxa in the sample
Shannon Index-small sample (Hss', Shannon Weaver) SHSS	$-\sum p_i*\ln p_i-((S-1)/N)+((1-\sum p_i^{-1})/12*N^2)+$ $((\sum (p_i^{-1}-p_i^{-2}))/12*N^3)$ e.g., SHSSRCONC	p_i is the relative proportion of each taxa (taxa/total sample taxa). This is summed for all unique taxa in the sample
McIntosh U	Square root($\sum (n_i^2)$)	n_i is the concentration of each taxa, (e.g., taxa/mL)
Maximum Diversity based on Shannon	$\ln S$	S is the total number of unique taxa
Evenness Based on Shannon Standard ESHST	$(-\sum p_i*\ln p_i)/(\ln S)$ e.g., SHSTRCONC /(lnS)	p_i is the relative proportion of each taxa (taxa/total sample taxa). This is summed for all unique taxa in the sample, S is the total number of unique taxa
Evenness Based on Shannon-small sample ESHSS	$(-\sum p_i*\ln p_i-((S-1)/N)+((1-\sum p_i^{-1})/12*N^2)+$ $((\sum (p_i^{-1}-p_i^{-2})/12*N^3))/(\ln S)$ e.g., SHSSRCONC /(lnS)	p_i is the relative proportion of each taxa (taxa/total sample taxa). This is summed for all unique taxa in the sample, S is the total number of unique taxa
Variation based on Shannon	$(((\sum p_i*(\ln p_i)^2)-(\sum p_i*\ln p_i)^2)/N)-((S-1)/(2*N^2))$	p_i is the relative proportion of each taxa (taxa/total sample taxa). This is summed for all unique taxa in the sample, S is the total number of unique taxa, N is the total number of individuals within each taxa summed (e.g., total sample concentration, total sample biovolume, etc.)
Richness	Species Taxa count	S is the total number of unique taxa
Berger-Parker Index	$1/(N_{max}/N)$	N_{max} is the # of Individuals in the most abundant taxa, N is the total number of individuals within each taxa summed (e.g., total sample concentration, total sample biovolume, etc.)
Margalef's Index	$(S-1)/\ln N$	S is the total number of unique taxa, N is the total number of individuals within each taxa summed (e.g., total sample concentration, total sample biovolume, etc.)
Simpson's Index	$1/(\sum (p_i^2))$	p_i is the relative proportion of each taxa (taxa/total sample taxa).
Evenness Based on Simpson	$(1/(\sum (p_i^2)))*(1/S)$	p_i is the relative proportion of each taxa (taxa/total sample taxa); S is the total number of unique taxa.
α (alpha)	$\alpha = (N*(1-x))/x$, where: $S/N=((1-x)/x)*(-\ln*(1-x))$, this is an iterative process until you determine x	S is the total number of unique taxa, N is the total number of individuals within each taxa summed (e.g., total sample concentration, total sample biovolume, etc.)

Index Name-Algae	**Formula**	**Explanation of variables**
Pollution Tolerance Index	$(\sum n_i * \text{PTClass})/N$	n_i is the concentration of each taxa, (e.g., taxa/mL), PTI is the value for the Pollution Tolerance Index, N is the total number of individuals within each taxa summed (e.g., total sample concentration, total sample biovolume, etc.)
Palmer Index	∑Palmer Index all taxa If the taxa don’t have an index, then it just sums zero.	Summed Value for either Species OR Genus, depending on taxonomic level of count, if Species, then anything with blank species is NOT summed (e.g., species level: *Ankistrodesmus falcatus* would have its value summed, but *Ankistrodesmus* would not, and for genus level: *Ankistrodesmus* would have its value summed, but *Ankistrodesmus falcatus* would not)
RA Sensitive Diatoms	$\sum p_i$ of taxa with PTClass=3	p_i is the relative proportion of each taxa (taxa/total sample taxa).
ACC:CMN	$\sum (n_{i\ \text{Achnanthes}}+n_{i\ \text{Cocconeis}}+n_{i\ \text{Cymbella}})/ \sum (n_{i\ \text{Cyclotella}}+n_{i\ \text{Aulocoseira}}+n_{i\ \text{Melosira}}+n_{i\ \text{Niztschia}})$	n_i is the concentration of each taxa specified
Nygaard’s Quotient (NQ)		
NQ Cyanophyte	# Species Cyanophyta/# Species Desmids	Divisions = Cyanophyta, Chlorophyta, Bacillariophyta, Euglenophyta, Desmids = (Families: Mesotaeniaceae + Desmidiaceae)

2. Diatom tolerance. Notes and acronym descriptions on following page. Summarized by PhycoTech 2015.

genus	**species**	**pH spec**	**nutrient spec**	**halo-bion**	**temp spec**	**DO require**	**N uptake**	**saprobien spec**	**flow**	**community**	**season**
Asterionella	*formosa*	P4	N1-N2	H8	.	O2	Y2	S4-S5	F1-F2	C1	D3
Aulacoseira	*ambigua*	P4	N1	H8	.	O3	Y2	S4	.	.	.
Aulacoseira	*granulata*	P4	N1	H8	.	O3	Y2	S4	.	.	.
Cyclotella	*bodanica*	**P2**	N5	H6	.	O1	Y1	S5	.	.	.
Cyclotella	*meneghiniana*	P4	N1	H8	.	O5	Y3	S3	F3	C1-C3	D4
Cyclotella	*ocellata*	P3-P4	N2	H8	.	O1	Y1	S5	F1	C3	.
Diatoma	*tenuis*	P4	N1	.	.	O3	Y2	S3	.	.	.
Fragilaria	*crotonensis*	P4	N1-N3	H8	.	O2	Y2	S4-S5	F3	C1	.
Navicula	*cryptocephala*	P4	N1	H8	T2-T3	O3	Y2	S4	F3	.	D2-D4
Navicula	*pupula*	P3	N1	H8	.	O3	Y2	S3	F3	C3	.
Navicula	*salinarum*	P3	N1	H5	.	O2	Y2	S4	.	.	.
Nitzschia	*acicularis*	P4	N1	H8	.	O4	Y4	S4	F2	C1	.
Nitzschia	*amphibia*	P4-P5	N1	H8	T2	O3	Y3	S3	F3	C3	.
Nitzschia	*gracilis*	P3	N3	H6	.	O2	.	S4	.	.	.
Nitzschia	*intermedia*	P3	N1	H8	.	.	.	S4	.	.	.
Nitzschia	*linearis*	P4	N1	H8	T2-T3	O2	Y2	S5	F5	C3	D3
Nitzschia	*palea*	P3	N1	H8	T6	O4	Y2	S1-S2	F3	C2-C3	D2-D4
Nitzschia	*socialis*	P3	N1	H8	.	.	.	S4	.	.	.
Stephanodiscus	*hantzschii*	P4-P5	N1	H8	.	O4	Y3	S4	F3-F4	C1	D2
Stephanodiscus	*parvus*	P5	N0	H8	.	.	.	.	.	.	.
Synedra	*delicatissima*	P3	N1	H8	.	.	.	.	F2	C1	.
Synedra	*filiformis*	P2	N5	H8	.	O1	.	S5	F4	.	.
Synedra	*ulna*	P4	N1	H8	T2-T3	.	.	S4-S5	F3	C1	D2-D4
Tabellaria	*flocculosa*	P2	N3	H9	.	O1	Y1	S3-S7	F1	C2-C3	D2/D4

FIELD 1: pH spectrum

P1	acidobiontic (< 5.5); rarely occurs naturally
P2	acidophilous (<7)
P3	indifferent (no apparent optimum)
P4	alkaliphilous (> 7 mainly)
P5	alkalibiontic (> 7 exclusively)
P6	circumneutral (at 7)

FIELD 2: Nutrient spectrum

N0	hypereutraphentic
N1	eutrophic (eutraphentic); high nutrient
N2	meso-eutraphenic
N3	mesotrophic (mesotraphentic); moderate
N4	oligo-mesotraphentic
N5	oligotrophic (oligotraphentic); low
N6	dystrophic (water rich in humic material)

FIELD 3: Halobion (mg/L)

H1	polyhalobous (over 40,000)
H2	euhalobous (30,000-40,000); marine
H3	mesohalobous (500-30,000); "brackish"
H4	mesohalobous alpha (10,000-30,000)
H5	mesohalobous beta (500-10,000)
H6	oligohalobous (<500); "freshwater"
H7	oligohalophilous (stimulated by small amounts)
H8	oligohalophilous indifferent (tolerates small amounts)
H9	oligohalophobus (does not tolerate small amounts)
H0	euryhalobus (broad ranges)

FIELD 4: Saprobien spectrum

S1	polsaprobic
S2	mesosaprobic (associated with detritus, swamps, bogs)
S3	mesosaprobic alpha
S4	mesosaprobic beta
S5	oligosaprobic
S6	saprophilic (usually in polluted waters but also in clean water habitats)
S7	saproxenous (occuring in clean water habitats but also in polluted ones)
S8	saprophobic (katharobic); not polluted

FIELD 5: Flow (Current spectrum)

F1	limnobiontic (standing water only)
F2	limnophilous
F3	indifferent
F4	rheophilous
F5	rheobiontic (running water only)

FIELD 6: Location (General habitat)

L1	marine
L2	estuary/ brackish
L3	lake
L4	pond
L5	river
L6	spring/stream
L7	aerophilous
L8	other

FIELD 7: Community (Specific habitat)

C1	euplanktonic	suspended in water
C2	tychoplanktonic	normally periphyticm, sometimes suspended
C3	periphyton	
C4	epipelic	mud/sediment
C5	epilithic	rock
C6	epidenric	on wood
C7	epiphytic	on plants
C8	epizooic	on animals
C9	attached	
C0	unattached	"metaphytic"

FIELD 8: Seasonal distribution

D1	winter
D2	spring
D3	summer
D4	autumn

FIELD 9: Temperature spectrum

T1	euthermal	> 30 degrees C
T2	mesothermal	15-30 degress C
T3	oligothermal	0-15 degrees C
T4	stenothermal	range ≤ 5 degrees
T5	metathermal	range 5-15 degrees
T6	eurythermal	range > 15 degrees
T7	undesignated	

FIELD 10: Oxygen requirements

O1	Con't high (100%)
O2	Fairly High (>75%)
O3	Moderate (>50%)
O4	Low (>30%)
O5	Very low (@ 10%)

FIELD 11: Nitrogen uptake metabolism

Y1	nitrogen-autotrophic taxa (tolerating very small conc. of organically bound nitrogen)
Y2	nitrogen-autotrophic taxa (tolerating elevated conc. of organically bound nitrogen)
Y3	facultative nitrogen-heterotrophic taxa (needing periodic elevated conc. of organically bound nitrogen)
Y4	obligately nitrogen-heterotrophic taxa (needing con't elevated conc. of organically bound nitrogen)