STUDY OF THE APPLICATION OF LIMNETIC ZOOPLANKTON AS A BIOASSESSMENT TOOL FOR LAKES OF SLEEPING BEAR DUNES NATIONAL LAKESHORE

By

Richard L. Whitman, Bruce Davis, and Maria L. Goodrich

USGS Lake Michigan Ecological Research Station
Porter, Indiana

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Table of Contents

LIST OF FIGURES

LIST OF TABLES

EXECUTIVE SUMMARY

Zooplankton—animals suspended in water with limited locomotion—tend to be widely distributed geographically, fulfill many functional roles, have short generation times, and are subject to both top-down and bottom-up trophic influences in a lake ecosystem (Carter et al. 1980, Carpenter et al. 1985, Shurin et al. 2000). All of these characteristics make them excellent candidates for use in lake monitoring and characterization. The lakes of Sleeping Bear Dunes National Lakeshore are popular recreation sites, and as such, they are vulnerable to anthropogenic impacts. In this study, we explored the usefulness of zooplankton as a monitoring tool for these inland lakes. Using biological indicators is a common practice; zooplankton have specifically been used in many ways to explore their usefulness in monitoring. In this study, both zooplankton and water chemistry were sampled to determine their interrelationships.

Ten lakes in Sleeping Bear Dunes National Lakeshore were selected for monitoring between April and October of 1998. Additionally, Crystal Lake, which lies outside of the park, was sampled during this time. Lakes were sampled biweekly for water chemistry, chlorophyll *a*, and zooplankton communities. Water samples were collected one meter below the surface and were tested in the Sleeping Bear Dunes laboratory for nitrate, ammonia, sulfate, alkalinity, total hardness, and calcium hardness. Samples for total phosphorus analysis were transported to an outside laboratory for analysis. Zooplankton were collected by vertical tows at the deepest point in each lake, using an 80 um-mesh Wisconsin net. Zooplankton were identified and enumerated by taxonomists at Lake Michigan Ecological Research Station and Great Lakes Science Center.

Data results were analyzed using statistical indices and multivariate analysis. According to calculations of trophic status, the lakes ranged from oligotrophic to eutrophic in both chlorophyll *a* and Secchi disk designations. Lake trophic status refers to the rate at which

organic matter is supplied to the lake over time. A eutrophic lake has a high rate of organic enrichment, and an oligotrophic lake has a low rate of organic enrichment; mesotrophic is between those two. A lake undergoing eutrophication becomes has an increasing rate of organic enrichment over time. Only Big Glen and Crystal lakes were oligotrophic using both chlorophyll *a* and Secchi disk indices. Chlorophyll *a* was high enough in most other lakes to identify them as eutrophic, but Secchi disk results identified most lakes as mesotrophic.

School Lake had the highest number of zooplankton organisms per liter (792), the majority of which were rotifers, and Glen Lake had the lowest number (7), with copepods dominating. Diversity was highest in Glen Lake, however, and lowest in Narada Lake. Throughout the season, there were periodic peaks in zooplankton groups. Most lakes showed a surge in rotifer abundance in late May. Glen Lake instead had a gradually increasing population of copepods throughout the season and a long-lived peak of branchipods in June and July. Other exceptions were Crystal Lake, which had a peak of branchiopods, copepods, and rotifers in early June. South Bar Lake had a branchiopod surge in mid-May, and Tucker Lake had periodic peaks of all three zooplankton groups.

In an analysis of multi-dimensional scaling, zooplankton communities were quite similar in all lakes except Glen and Crystal in the early spring. By June, the zooplankton community similarity diverged considerably and remained as such for the rest of the sampling period. Among water parameters that best explained variation in the zooplankton community were Secchi disk depth, chlorophyll *a*, and sulfate.

The lakes included in this study do not appear to be under immediate threat from excessive anthropogenic pollution. Many of the lakes had chlorophyll *a* and water chemistry results very similar to some collected in 1973-1974 (Stockwell and Gannon 1975), 1991-1993

(Boyle and Hoefs 1993), and 1994 (Last et al. 1995). The dominance of small zooplankters is characteristic with other studies of summer zooplankton in productive lakes (Gannon and Stemberger 1978). The abundance of smaller zooplankton may be the result of predation on the larger organisms by zooplanktivorous fish (Stemberger and Lazorchak 1994). Lake trophic status was the most significant environmental factor influencing zooplankton communities.

This study found substantial similarity among analyses of the zooplankton community based on overall abundance and many other levels of taxonomic, functional, and size classifications. This has significant meaning for using zooplankton as a method of lake monitoring because these types of classifications are far simpler and less time-consuming, and there is some evidence that an intermediate level of zooplankton aggregation may decrease natural variability and increase sensitivity (Frost et al. 1992).

The additional amount of time and expense required for detailed taxonomic identification and analysis may be unwarranted because a strong relationship was found between trophic status indicators and overall zooplankton abundance. Because of the large amount of temporal variation in the zooplankton community in lakes at SLBE, however, intensive bi-weekly sampling is likely warranted, although replication of samples may be less crucial.

A possible monitoring scheme for these SLBE lakes might be relatively frequent zooplankton sampling during the open-water period and subsequent organism counting. A scan of the samples for nonnative invasive species would be part of the counting. Zooplankton could be preserved and analyzed in the event of available funding. Sampling over several years is needed to provide a basis from which to monitor changes. The large-scale changes over individual sampling seasons indicates that changes between years are likely.

There were strong correlations between lake trophic status and zooplankton communities as measured by many different metrics and at many levels of aggregation. Zooplankton appear to be a useful indicator of trophic status for the inland lakes of Sleeping Bear Dunes National Lakeshore, but monitoring decisions will have to incorporate thorough consideration of costs and benefits of zooplankton sampling and analysis.

INTRODUCTION

The use of zooplankton for lake characterization and monitoring is attractive for a number of reasons. Zooplankton species tend to have wide geographic distributions (Carter et al. 1980, Shurin et al. 2000). For this reason, it is probable that local differences in zooplankton communities are not dominated by dispersal limitation. Also, the intermediate trophic position of the zooplankton community in the lacustrine food web makes it responsive to both top-down and bottom-up influences (Carpenter et al. 1985). The zooplankton community is composed of species that fill different ecosystem roles (predators, herbivores, omnivores). Also, zooplankton generation times may be short enough to respond quickly to acute stress but long enough to integrate the effects of chronic problems. These are favorable attributes for a community indicator of ecosystem health (Cairns et al. 1993). Finally, zooplankton are relatively easy to identify, particularly when community sensitivity can be detected based on zooplankton body sizes or gross taxonomic classifications.

Investigations of zooplankton to characterize lakes date back to at least the Birge-Juday era, 1879-1910 (Frey 1963). The combinations of metrics have been numerous and varied. Zooplankton community size structure has been used as an indicator of lake trophic status (Bays and Crisman 1983, Pace 1986, Beaver and Crisman 1990, Canfield and Jones 1996). Comparisons have been made between the abundance and biomass of micro- and macrozooplankton (Bays and Crisman 1983, Pace 1986, Sprules et al. 1988) to algal chlorophylls (Canfield and Jones 1996), Carlson's TSI (Bays and Crisman 1983), and nutrients (i.e., total phosphorus) (Sprules 1977, Pace 1986). In other studies, zooplankton indicator species have been used to determine shifts in trophic state (e.g., Fuller et al. 1977, Sprules 1977). Many studies have examined differences in rotifer communities in lakes of various trophic states

(Fuller et al. 1977, Gannon and Stemberger 1978, Beaver and Crisman 1990). Abundance of major zooplankton divisions (e.g., Rotifera, Copepoda) has also been used to show changes in trophic state (Gannon and Stemberger 1978, Pace 1986).

This study explored the usefulness of zooplankton as a monitoring tool for the inland lakes of Sleeping Bear Dunes. We considered issues of sampling frequency, natural variation, and data analysis methods. Also, we identified the environmental variables that appear to be most influential in shaping the zooplankton community, and we analyzed some of the community changes that took place along the most important environmental gradients.

SLEEPING BEAR DUNES

Sleeping Bear Dunes National Lakeshore (SLBE) occupies 28,800 hectares along 60 km of the eastern shore of Lake Michigan in the lower peninsula of Michigan. The lakeshore was established as part of the national park system in 1970. Most of the land in the lakeshore was cleared in logging activities prior to 1910, and the area has been reforested since that time. Many inland lakes of glacial origin (Calver 1942) are located within and around the lakeshore property. Small villages and private landholdings are also interspersed throughout SLBE. A number of the inland lakes in this area share shorelines and watersheds with both the national lakeshore and local villages or private landholders (including private homes with septic systems). Many of the lakes are also heavily used for recreation during the summer months. Consequently, the inland lake ecosystems of SLBE are vulnerable to anthropogenic impacts (such as accelerated eutrophication).

LAKE DESCRIPTIONS

Study lakes were located within five watersheds in the Sleeping Bear Dunes area. The watersheds were those of Shalda Creek, the Crystal River, Otter Creek, the Platte River, and the Betsie River. Two lakes (North Bar and South Bar) did not fall within any of these watersheds but are more directly linked to Lake Michigan.

Shalda Creek Watershed

The Shalda Creek watershed is located on the north end of the park near Good Harbor Bay. Study lakes in this watershed were School, Shell, and Narada.

Narada Lake has an area of 5.7 hectares and a maximum depth of 11 m. A small stream flows out through a cedar swamp on the east side and connects the lake to Shalda Creek. The west side of the lake is rimmed by black ash swamp. Flooding caused by a beaver dam killed off many trees along the shoreline. Bottom sediments are composed of soft mud covered with *Chara* sp. There are also large beds of white and yellow pond lily (*Nuphar* sp. and *Nymphaea sp*.) Fish species include rainbow trout, alewife, golden shiner, white sucker, brook stickleback, bluegill, pumpkinseed sunfish, largemouth bass, and yellow perch (Kelly and Price 1979).

School Lake has an area of 72 hectares. The maximum depth of 6.5 m is in a small cove in the southwest corner. The rest of the lake is approximately 1 m deep with mud sediments. A small inlet enters the southeast corner of the lake through a black ash swamp. Submerged and floating aquatic plants are particularly common on the east side of the lake near the inlet. Another small stream connects to Bass Lake. There is no surface water connection to Shalda Creek. Fish species include bluntnose minnow, white sucker, northern pike, yellow bullhead,

brown bullhead, bluegill, pumpkinseed sunfish, rock bass, and largemouth bass (Kelly and Price 1979).

Shell Lake occupies 40 hectares in the Shalda Creek watershed. A maximum depth of over 6 m occurs in a small cove in the southwest corner of the lake. Maximum depth in the main water body is 4 m. Bottom sediments are composed of sand and marl. There is no apparent surface inlet or outlet. Aquatic plants are sparse. Fish species include pumpkinseed sunfish, largemouth bass, smallmouth bass, bluntnose minnow, white sucker, banded killifish, bluegill, yellow perch, and Iowa darter (Kelly and Price 1979).

Crystal River Watershed

The Crystal River watershed is located near Sleeping Bear Bay and the town of Glen Arbor. Study lakes within this watershed include Big Glen and Tucker lakes.

Big Glen Lake is the largest lake in the Crystal River watershed with an area of 1,887 hectares and a maximum depth of 43 m. Only a small portion of the shoreline near the narrows (where Big Glen connects to Little Glen Lake) is within the park. Many homes surround the lake, and there is some indication of septic leaching (Curry 1973). Hatlam Creek flows into the south end of the lake. Fish species include brook trout, lake trout, splake, rainbow trout, Coho salmon, Chinook salmon, lake herring, white sucker, spottail shiner, sand shiner, rock bass, largemouth bass, smallmouth bass, bluegill, yellow perch, and Johnny darter (Kelly and Price 1979). A weir on the Crystal River is intended to protect Big Glen Lake from invasion by lamprey, alewife, and smelt.

Tucker Lake has an area of 6.3 hectares and a maximum depth of 3 m. Lake level is controlled by a beaver dam on the outlet. The outlet flows south to Fisher Lake. A black ash

swamp is located west of the lake. Most of the trees in the swamp died when flooded in 1986 and 1987 (Hazlett 1989). Bottom sediments are composed of soft organic material, and there is thick aquatic plant growth. Fish species include rock bass, largemouth bass, bluegill, pumpkinseed sunfish, yellow perch, northern pike, and darters (Kelly and Price 1979).

Isolated Lakes

North Bar and South Bar Lakes are separated from the other major watersheds included in the study. Both lakes are closely associated with Lake Michigan, although South Bar also has a surface inlet. The lakes lie northwest of the village of Empire.

North Bar Lake occupies 14 hectares adjacent to Lake Michigan and has a maximum depth of 8 m. The lake was once an embayment of Lake Michigan and is still periodically connected by a narrow channel through the sand dune between the two lakes. Bottom sediments are composed of sand and marl, with some brown mud in deeper waters. Open sand dominates the shoreline on the north end of the lake, and the largest concentration of submerged and floating plants is found on the south end. Northern hardwood forest rims the lake to the West. The east side is bordered by black ash swamp north of the access road and cedar swamp south of the access road (Hazlett 1989). Fish species include alewife, sand shiner, spottail shiner, northern pike, smallmouth bass, yellow perch, and Johnny darter (Kelly and Price, 1979).

South Bar Lake was also once a coastal embayment of Lake Michigan. It is now separated from that lake by a sand dune and no longer mixes with Lake Michigan. A small tributary enters South Bar from the northeast shore. Lake area is approximately 28 hectares, and the maximum depth is 4 m. Bottom sediments are composed of sand and mud. The lake is not within park boundaries and much of the shoreline is developed with homes. Recreational use is very heavy, and there is a public swimming beach on the west side of the lake. Fish species

include bluntnose minnow, largemouth bass, smallmouth bass, yellow perch, Johnny darter, and Iowa darter (Kelly and Price 1979).

Otter Creek Watershed

The Otter Creek watershed lies east of Platte Bay. The only study lake in this watershed is Otter Lake.

Otter Lake is the largest lake in the Otter Creek watershed. It occupies 26 hectares and has a maximum depth of 8 m. The bottom sediments are composed of marl, and large beds of *Chara* sp. are common (Kelly and Price 1979). An inlet flowing from Bass Lake is located on the south side, and Otter Creek leaves from the north side of the lake. Groundwater flow is the principal water source to both Otter Lake and Otter Creek. Fish species include bluntnose minnow, creek chub, sand shiner, common shiner, yellow perch, Johnny darter, largemouth bass, black crappie, and white sucker (Kelly and Price 1979).

Platte River Watershed

The Platte River watershed lies south and east of Platte Bay and encompasses Loon Lake.

Loon Lake has an area of 38 hectares and a maximum depth of 22 m. Bottom sediments are composed of marl, with sand and fine gravels near shore. A dense shrub zone borders the west and north sides of the lake, and an extensive tamarack bog borders the western shore. Floating and submerged aquatic macrophytes are most common on the south end of the lake. A small stream enters the lake on the southwest side, and the Platte River flows through the lake from the east to the north sides. Fish species include shorthead redhorse, pumpkinseed sunfish,

and rock bass (Kelly and Price 1979). Loon Lake is subject to point source pollution from a fish hatchery located upstream of Platte Lake (Boyle and Hoefs 1993).

Betsie River Watershed

The Betsie River watershed lies south of Platte Bay and is largely outside the boundaries of the park. Round and Crystal lakes lie within this watershed.

Round Lake is a small (6.6 hectares) lake with a maximum depth of 8 m. The sediments are composed of marl in the littoral zone and thick muck in the limnetic zone. There is a large floating sedge mat on the south side of the lake. An outlet flows through this mat to Crystal Lake. The sedge mat is composed largely of *Carex* sp. Fish species include bluntnose minnow, golden shiner, blacknose shiner, sand shiner, white sucker, banded killifish, largemouth bass, yellow perch, and Johnny darter (Kelly and Price 1979).

Crystal Lake is a large (4,236 hectare) lake located outside of the park and west of the villages of Beulah and Benzonia. Steep slopes surround the shoreline and isolate the lake within a relatively small and highly developed watershed. Homes are located densely within a narrow band along the shoreline. Water level is tightly controlled by a dam at the lake outlet. Maximum lake depth is 49 meters. Crystal Lake was sampled independently to improve the range of limnological conditions encompassed by this study.

METHODS

Field Methods

All samples were collected at the deepest location on each lake as determined by sonar soundings or by pre-determined GPS readings. Lakes were sampled at approximately bi-weekly intervals from late April to early October. On most lake visits, a depth profile was taken with a Hydrolab Surveyor 4 datalogger and a Hydrolab Datasonde 3 multi-probe that measured dissolved oxygen, temperature, specific conductance, pH, and depth. Secchi transparency was also measured.

Samples for water chemistry and chlorophyll *a* analysis were collected one meter below the surface with a 2-liter horizontal VanDorn-style water sampler. One collection was made for chlorophyll *a* analysis, one for total phosphorus, and a third for all other water chemistry tests. Water chemistry samples were stored in sterile polyethylene bags (or sample jars for total phosphorus analysis) and placed in a cooler for transport to the laboratory. Chlorophyll *a* samples were pre-processed in the field. A Nalgene filtering apparatus and hand pump were used to filter water on a 45µm Millipore membrane filter. The filter was wrapped in aluminum foil and placed in a cooler. Filters were frozen in the lab and transported to Lake Michigan Ecological Research Station (LMERS) for analysis.

Zooplankton samples were collected by vertical tows using a Wisconsin net with 80 µm mesh. Tows started one meter above the lake bottom, and the net was pulled at a rate of approximately 0.5 $m \cdot s^{-1}$. The outside of the net was rinsed to concentrate zooplankton in the collecting bucket, and the bucket was placed in a container of carbonated water for one minute to narcotize the organisms (Gannon and Gannon 1975). Contents of the bucket were then rinsed

into a sample jar using filtered water. Samples were fixed with Lugol's solution. Three such samples were collected from the same location on each visit to the lake.

Laboratory Methods

All chemical analyses except total phosphorus were conducted by staff at SLBE. Total phosphorus was analyzed by a contracted laboratory according to EPA method 365.1 (US EPA 1983), with a minimum detection limit of 0.015 $mg \cdot l^{-1}$. Nitrate nitrogen, ammonia nitrogen, and sulfate sulfur were measured using a Hach DR/2000 spectrophotometer. Nitrate nitrogen was measured by the cadmium reduction method (0.01 to 0.40 $mg \cdot l^{-1}$ as NO_3^--N), ammonia nitrogen by the salicylate method (0.01 to 0.50 $mg \cdot l^{-1}$ as NH_3-N), and sulfate sulfur by the Sulfa Ver 4 method (1 to 65 $mg \cdot l^{-1}$ as SO_4^{2-}-S) (Hach 1993). Samples that exceeded the maximum detection limit for a test were diluted to half-concentration and re-tested. Alkalinity (10 to 4000 $mg \cdot l^{-1}$ as $CaCO_3$), total hardness (10 to 4000 $mg \cdot l^{-1}$ as $CaCO_3$), and calcium hardness (10 to 4000 $mg \cdot l^{-1}$ as $CaCO_3$) were analyzed by digital titration methods (Hach 1993). Magnesium and calcium concentrations were calculated from values for total and calcium hardness.

Chlorophyll *a* determination followed the methods of Wetzel and Likens (1979) and Standard Methods (APHA 1992). Filters were removed from the freezer, unwrapped, and placed in 10 ml of 90% acetone. The filters were extracted for 22-24 hours in a dark refrigerator. Extracts were poured into a cuvette and fluorescence was measured on a Sequoia-Turner model 450 fluorometer. Fluorometric readings were entered into a spreadsheet, and chlorophyll *a* concentration was calculated.

Zooplankton identification and enumeration were performed by staff at LMERS and Great Lakes Science Center (GLSC) in Ann Arbor. Macrozooplankton for Tucker, North Bar, Round, and Big Glen lakes were identified at LMERS, whereas rotifers for those lakes were identified at GLSC. All zooplankton samples for the remaining lakes were identified at GLSC. Counting and identification were conducted as follows: the sample was stirred in a figure-eight motion to suspend organisms. Six milliliters of sample were removed in multiple aliquots using a Hensen-Stempel pipette. This subsample was placed into a Ward counting wheel for enumeration and identification of zooplankton taxa under a dissecting microscope. Some individuals were removed from the counting wheel for identification and confirmation at higher magnification. Specimens were identified according to Edmondson (1959), Stemberger (1979), Balcer et al. (1984), Pennak (1989), and Thorp and Covich (1991). Most mature individuals were identified to genus- or species-level. Copepod nauplii were simply identified as such, and copepodids were classified as cyclopoid or calanoid. Rotifers were identified to genus.

Statistics

Statistical procedures used in this report employed a variety of multivariate techniques. All statistical analyses were carried out using SPSS 10.0.5 (SPSS Inc. 1999) and PRIMER 5.1.2 (Clark and Warwick 1994).

Taxon-independent indices

Five taxon-independent indices were employed in this study. The two simplest were N = zooplankton individuals per liter and S = total number of taxa. In this study, S was expressed at the lowest identified taxonomic level or at the genus level. The remaining indices

were calculated using these two parameters. Shannon diversity (Appendix 1, equation 1) is a measure of the distribution of individuals among taxa where p_i = the proportion of individuals belonging to taxon *i*. Shannon diversity is increased when individuals are evenly distributed among taxa, and decreases when relatively few taxa dominate the overall abundance (*N*). Shannon diversity is affected by the number of categories as well as the distribution of data. To remove this effect, Pielou evenness was calculated where $H'_{max} = \log S$ (Appendix 1, equation 2). This gives a measure of the relative diversity based on the maximum Shannon diversity value for that number of taxa.

Finally, Margalef richness was also calculated (Appendix 1, equation 3). This measure relies only on zooplankton abundance and the number of taxa. Richness increases when abundance is spread over a greater number of categories, but it does not take into account the evenness of that distribution. Also, between two samples with the same *S*, richness will be higher in the one with the lower abundance.

Multivariate analyses

The multivariate techniques were based on measures of sample similarity or dissimilarity (for the analyses in this report "sample" generally refers to lake average). Normalized Euclidean distance was used to make comparisons based on environmental data (Appendix 1, equation 4) in which *y* is the normalized value of the *i*th variable for the *j*th or *k*th sample. Larger *d* values indicated greater dissimilarity between samples. Environmental variables were transformed as needed to achieve approximate normality prior to analysis. Log-transformations were employed to normalize data for sulfate, nitrate, ammonia, chlorophyll *a*, depth, and area. All variables

were then transformed to zero mean and unit standard deviation so that each variable had equal weight in the analysis.

Comparisons based on zooplankton community data were performed using Bray-Curtis similarity (Appendix 1, equation 5) in which y is the abundance of the ith taxon in the jth or kth sample. S=0 indicates total dissimilarity between samples (no taxa in common), while S=100 indicates total similarity (the two samples contain all the same taxa in the same abundances). Joint absences do not increase the value of S, which makes it appropriate for this sort of biological data. Abundance data were log(y+1)-transformed prior to analysis to give less-dominant taxa a greater role in determining similarity between samples.

In short, a pairwise comparison of lakes that yielded a high Euclidean distance indicated that the lakes were relatively dissimilar on the basis of the environmental parameters used in the equation. Pairwise comparisons of lakes with high Bray-Curtis similarities showed relatively high zooplankton community similarity between the two lakes under consideration. Euclidean distance and Bray-Curtis similarity both gave us the ability to reduce a complex set of data to a single number for the sake of comparing two lakes. Similarity matrices were constructed from each of these values so that every possible pair-wise comparison was represented. These similarity matrices were the basis for the following analyses.

Sample groupings were identified by group average hierarchical agglomerative clustering. This method was used with Euclidean distances or Bray-Curtis similarities to join samples successively into groups based on mutual similarities. After the formation of each group, similarities are recomputed based on the weighted average of mutual similarities between members of that group and other samples or groups. The resulting dendrogram depicts the similarity (Bray-Curtis) or distance (Euclidean) among lakes by showing the location and order

of joining for the different lakes "branches". Groupings were identified by observing which lakes were joined together at different points along the scale of similarity or distance in the dendrogram.

Ordinations were used to map samples based upon their similarity/dissimilarity, such that the distance between any two samples in the ordination picture is representative of their dissimilarity. The ideal result is a low-dimensional depiction of sample dissimilarities based on high-dimensional taxon or environmental data.

Principal components analysis (PCA) was the ordination method employed for environmental data. PCA is based on Euclidean distance measures. The first component (axis) is constructed along the direction in *n*-dimensional space (*n*=the number of variables in the ordination) where the variance of sample points is maximized. The second component is constrained to be perpendicular to the first, again in the direction of maximum sample point variation. Additional components can be constructed until a satisfactory proportion of the sample variation is "explained" by the ordination, although limiting analyses to two or three axes is attractive for ease of visualization and interpretation. Each axis is defined by a linear combination of the original variables.

Non-metric multi-dimensional scaling (MDS) creates an ordination picture from a matrix of similarities among samples. Here it was used with Bray-Curtis similarities to compare zooplankton community composition among samples. Distances in the MDS ordination are calculated by ranking similarities between samples from 1 to $n(n-1)/2$ so that the highest similarities have the lowest ranks. The MDS algorithm is then used to construct a picture in which rank similarities are preserved as Euclidean distance between samples. Stress is a measure of the distortion between rank similarities and distances in the ordination plot. The goal

of the MDS algorithm is to construct an ordination configuration that minimizes this stress by iteratively converging on the solution that gives the lowest stress values.

Both PCA and MDS produce a "map" of the lakes in which the distance between any two lakes is representative of their dissimilarity based on the data under analysis. PCA is a parametric procedure more appropriate to the variables in the environmental data. MDS is a non-parametric method, and the axes and distances produced by MDS cannot be directly interpreted as in PCA.

The BIOENV procedure was used to identify those environmental variables that best "explained" the patterns of variation seen on the community data. BIOENV is a non-parametric method that measures the correlation between biological and environmental similarity matrices. The similarity matrices are composed of pair-wise comparisons of every lake or sample. For this study, Euclidean distances based on environmental data and Bray-Curtis similarities based on community data were used as a measure of similarity (Bray-Curtis) or dissimilarity (Euclidean distance). Results from BIOENV are expressed as Spearman coefficients (Appendix 1, equation 6), where $N=n(n-1)/2$ (n being the number of samples), and r_i and s_i being the rank similarities the same sample pair in each matrix. The constants are defined such that ρ lies in the range –1 to 1 (total dissimilarity to total similarity). BIOENV tests the community matrix against environmental matrices constructed from different combinations of environmental variables, and the combinations giving the highest correlation coefficients are reported.

Essentially, BIOENV compares a chosen biological similarity matrix with a number of different environmental similarity matrices. Different combinations of environmental variables are used to find the set that yields a similarity matrix that closely matches the relative similarities

in the zooplankton matrix. If a variable improves the correlation with the zooplankton matrix, it is presumed to have some relation to the zooplankton community features. If the variable degrades the correlation, then it is omitted from the analysis and likely has little influence on the zooplankton community.

RESULTS

Environmental/Limnological

Specific conductance Specific conductance is the reciprocal of the resistance of water to electrical flow. Pure water is a poor conductor of electricity and has low conductance. As the ion content of water increases, so does conductance. Specific conductance is generally proportional to the concentrations of major ions in bicarbonate lakes.

All the study lakes had high mean specific conductance values (Fig. 1). School and Shell lakes had the lowest mean specific conductance with 235 $\pm$ 2 and 235 $\pm$ 5 $\mu s \cdot cm^{-1}$. Crystal and South Bar lakes had the highest mean specific conductance (363 $\pm$ 5 and 363 $\pm$ 3 $\mu s \cdot cm^{-1}$). Mean specific conductance fell between 280 and 340 $\mu g \cdot cm^{-1}$ for most of the study lakes.

Total alkalinity The resistance of water to downward pH shifts (buffering capacity) is controlled by dissolved compounds measured as alkalinity. Alkalinity usually arises from the presence of carbonates, bicarbonates, and hydroxides. These compounds buffer water bodies from the pH shifts associated with acid precipitation. The range of alkalinity in natural waters is quite large. Surface water alkalinity may drop during periods of high algal production as carbon dioxide is removed from the carbonate-bicarbonate buffering complex.

Mean alkalinity in the study lakes ranged from 109 $\pm$ 2 $mg \cdot l^{-1}$ in School Lake to 169 $\pm$ 5 $mg \cdot l^{-1}$ in South Bar Lake (Fig. 1).

Hardness The concentration of calcium and magnesium salts combined with various anions (usually carbonates) constitutes the total hardness of water. Calcium and magnesium can bind and precipitate various nutrients such as iron, manganese, and phosphorus. Co-precipitation of

phosphorus with calcium can contribute significantly to phosphorus scarcity in marl lakes (Wetzel 1983).

All the study lakes are hard-water lakes. Mean hardness ranged from 117 $\pm$ 5 $mg \cdot l^{-1}$ in School Lake to 170 $\pm$ 3 $mg \cdot l^{-1}$ in North Bar Lake (Fig. 1). In most lakes mean hardness fell between 135 and 170 $mg \cdot l^{-1}$.

pH The pH of water is representative of the relative concentration of hydrogen ions in solution. Pure water has a pH of 7, with acidic waters falling below and alkaline above that value. Most lakes have pH values between 6 and 9 (Wetzel 1983). Some systems are naturally quite acidic, but the majority of freshwater aquatic habitats are negatively affected by extremely low pH. Industrial pollution may cause acid precipitation that can lower the pH of poorly buffered lakes. Hard-water lakes are generally well-buffered and tend to have pH values above 8.

Since the study lakes all had relatively high alkalinity and hardness, it is not surprising that all had median pH values above 8. Mean pH ranged from a median of 8.06 in Narada Lake to 8.65 in Round Lake (Fig. 1). School Lake also had a lower pH (median 8.30 with a low of 7.71) consistent with its low hardness and alkalinity relative to the other study lakes.

Secchi disk transparency Water transparency is frequently measured in terms of Secchi disk transparency. This is the mean of the depth at which a weighted white (Secchi) disk disappears from sight when lowered into the water and reappears when it is raised. Usually, Secchi disk transparency is a function of the suspended particulates in the water, although the measure may also be affected somewhat by dissolved organic matter. Frequently, there is a good relationship between increased lake productivity and lower Secchi disk transparency due to increased

phytoplankton populations. Caution should be used when applying Secchi disk transparency to infer productivity for lakes of the Sleeping Bear Dunes area. Occasionally during the summer months, a suspension of white calcium carbonate precipitates may occur in hard-water lakes, drastically reducing Secchi transparency.

Secchi disk transparencies were quite variable within and among sample lakes. Largest mean Secchi disk transparencies were 5.7 $\pm$ 0.2 m in Crystal Lake and 5.9 $\pm$ 0.6 m in Big Glen Lake (Fig. 1). Big Glen Lake also displayed a large range throughout the season (3.7-12.5 m). The lowest mean Secchi disk transparencies were seen in School Lake (1.5 $\pm$ 0.2 m) and South Bar Lake (1.4 $\pm$ 0.2 m).

Chlorophyll *a* Another measure of lake productivity is the chlorophyll *a* concentration of unfiltered water. Chlorophyll *a* concentration gives some measure of standing phytoplankton biomass, which is generally correlated with concentrations of the limiting nutrient(s) for a system. Increased loading of limiting nutrients produces a corresponding increase in phytoplankton production and subsequently biomass until another nutrient becomes relatively scarce and limits production. Chlorophyll *a* concentration is usually a reliable way to track such changes in nutrient loading, though top-down control by herbivores may prevent standing biomass from increasing with increased productivity.

Chlorophyll *a* concentrations throughout the study were quite varied. The lowest mean concentrations were in Crystal Lake (3.99 $\pm$ 1.52 $\mu g \cdot l^{-1}$) and Big Glen Lake (3.74 $\pm$ 1.08 $\mu g \cdot l^{-1}$) (Fig. 1). Highest mean chlorophyll *a* concentration was in School Lake (51.00 $\pm$ 12.31 $\mu g \cdot l^{-1}$). However, concentrations were quite variable in this and other lakes over the course of the study; School Lake actually ranged from 3.59 to 130.14 $\mu g \cdot l^{-1}$, with several high concentrations

occurring from August through October. Every lake except Tucker Lake experienced the highest chlorophyll *a* peaks toward the end of the study season.

Sulfate The main form of sulfur in natural waters is sulfate. Sulfate may enter natural waters from rocks, fertilizers, precipitation, or dry deposition. Given the rural nature of Sleeping Bear Dunes and the surrounding area, fertilizer might be a sulfur source for the study lakes, and industrial sulfur may travel long distances in the atmosphere. Sulfur is a major component in protein synthesis and is used by all living organisms. Organic sulfur compounds degrade slowly, so large amounts of sulfur may be sequestered in organic matter. Bacterial degradation releases sulfur as H_2S, and under oxygen conditions it is quickly oxidized to sulfate. Most biological assimilation of sulfur is as sulfate. As a result, availability of sulfate has the potential to limit lake productivity.

Most of the study lakes had mean sulfate concentrations between 10 and 18 $mg \cdot l^{-1}$ (Fig. 1). The major exception was Crystal Lake, which had a mean sulfate concentration of 61 ± 1 $mg \cdot l^{-1}$. Crystal Lake is oligotrophic, and low sulfur demand may allow more sulfate to remain dissolved in the water column. Additionally, Crystal Lake has a rather high density of home and road development in its watershed, and this may result in additional sulfur input from anthropogenic sources. Lakes on the lower end of the spectrum were School Lake and Tucker Lake, both with a mean concentration of 1 ± 0 $mg \cdot l^{-1}$. These are relatively productive lakes, as indicated by chlorophyll *a* levels. Both lakes are also fairly isolated and located in a less developed watershed. It is possible that low sulfur input and high productivity (with large amounts of sulfur sequestered organically) may contribute to these much lower sulfate concentrations.

Nitrate As with sulfur, nitrogen is a major protein component and may be sequestered in organic material. One major form of dissolved nitrogen is nitrate. Nitrogen can enter a water body through precipitation, dry deposition, and elemental nitrogen fixation by bacteria and plants. However, runoff and groundwater may also be major nitrogen sources. High nitrogen loading rates have been linked to high lake productivity, and nitrogen may be a productivity-limiting nutrient under certain conditions. Expected nitrate concentrations in unpolluted fresh water range from undetectable levels to 10 $mg \cdot l^{-1}$ (Wetzel 1983). Plants must reduce nitrate to ammonia before it can be utilized.

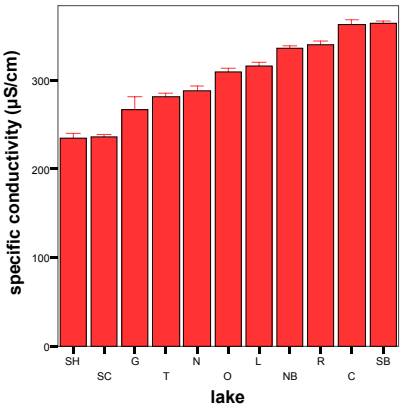
Nitrate levels were generally low in the study lakes. Mean nitrate concentrations fell between 0.03 and 0.06 $mg \cdot l^{-1}$ for most lakes (Fig. 1). Slightly higher levels were seen in Otter and North Bar lakes, with levels of 0.12 ± 0.02 and 0.18 ± 0.03 $mg \cdot l^{-1}$. The highest mean nitrate concentration was seen in South Bar Lake, with 0.49 ± 0.03 $mg \cdot l^{-1}$. This is still well within the expected range for unpolluted fresh waters. Close proximity to the village of Empire and heavy recreational use may contribute to higher nitrate concentrations in South Bar Lake relative to other studied lakes.

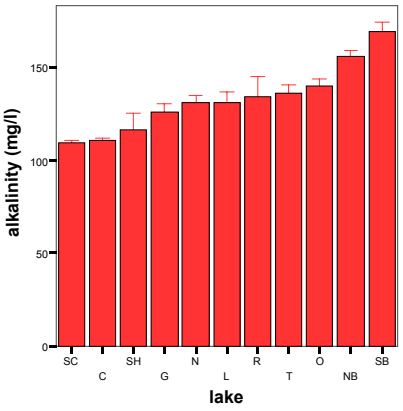
Ammonia Dissolved nitrogen may also be present as ammonia. Ammonia is generated as an excretory product of aquatic animals, but the major source in most systems is the decomposition of plant and animal material by bacteria. Because plants must reduce nitrate to ammonia prior to utilization, ammonia is a more energy efficient nitrogen source. However, under high pH conditions ammonia becomes toxic to many organisms. Ammonia concentrations in well-oxygenated, unpolluted natural waters tend to remain low (0-5 $mg \cdot l^{-1}$) (Wetzel 1983).

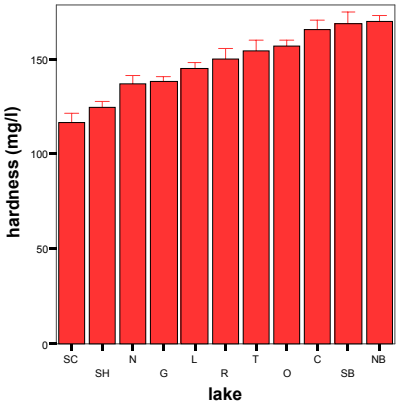
Ammonia levels in all study lakes were quite low, and well within the range for unpolluted waters. Mean concentrations ranged from 0.02 $\pm$ 0.00 $mg \cdot l^{-1}$ in Big Glen Lake to 0.093 $\pm$ 0.034 $mg \cdot l^{-1}$ in School Lake (Fig. 1).

Total phosphorus The concentration of phosphorus in both particulate and dissolved forms is measured as total phosphorus. Phosphorus is a critical component of proteins, nucleic acids, nucleotide phosphates, and other organic compounds. Much particulate phosphorus may be in this form, or adsorbed to organic or mineral materials. Dissolved phosphorus may be present in a number of organic and inorganic forms. Phosphorus may enter a lake from organic matter, rock and sediments, and anthropogenic pollution from synthetic detergents. Large amounts of phosphorus may also be sequestered in lake sediments, and internal phosphorus loading can take place during lake turnover. Phosphorus is often the limiting nutrient for algal productivity in lake water, and high total phosphorus concentrations are associated with high productivity and eutrophy. Unpolluted lakes generally have phosphorus concentrations between 0.01 and 0.05 $mg \cdot l^{-1}$ (Wetzel 1983).

The lower detection limit for the total phosphorus test was 0.015 $mg \cdot l^{-1}$, and many samples from the study lakes did not exceed that value. Mean phosphorus concentration in the study lakes ranged from 0.017 $\pm$ 0.002 $mg \cdot l^{-1}$ in Crystal Lake to 0.061 $\pm$ 0.010 $mg \cdot l^{-1}$ in School Lake (Fig. 1). Phosphorus concentrations varied considerably over time in some lakes, such as Otter Lake (0.028 to 0.171 $mg \cdot l^{-1}$).


specific conductivity (µS/cm)
0
100
200
300
SH SC G T N O L NB R C SB
lake


alkalinity (mg/l)
0
50
100
150
SC C SH G N L R T O NB SB
lake


hardness (mg/l)
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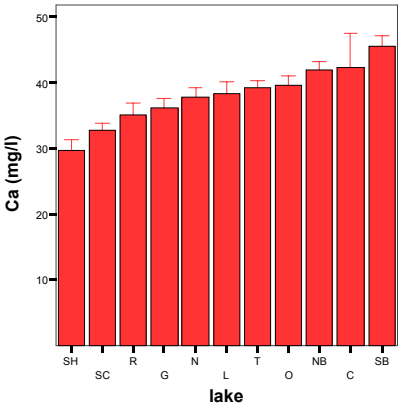
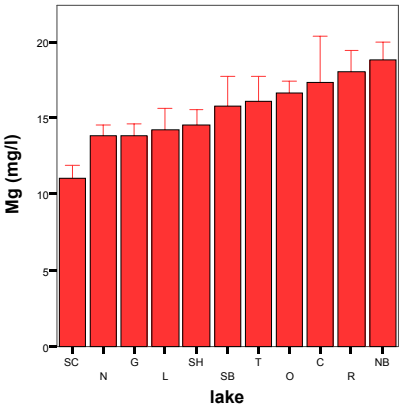
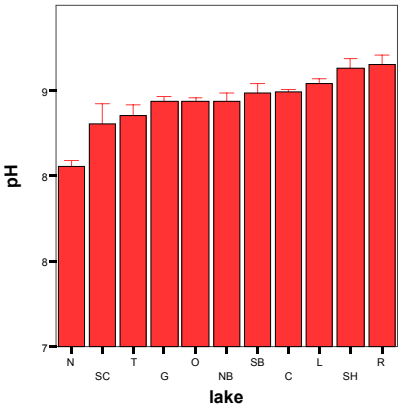
50
100
150
SC SH N G L R T O C SB NB
lake


Ca (mg/l)
10
20
30
40
50
SH SC R G N L T O NB C SB
lake


Mg (mg/l)
0
5
10
15
20
SC N G L SH SB T O C R NB
lake


pH
7
8
9
N SC T G O NB SB C L SH R
lake

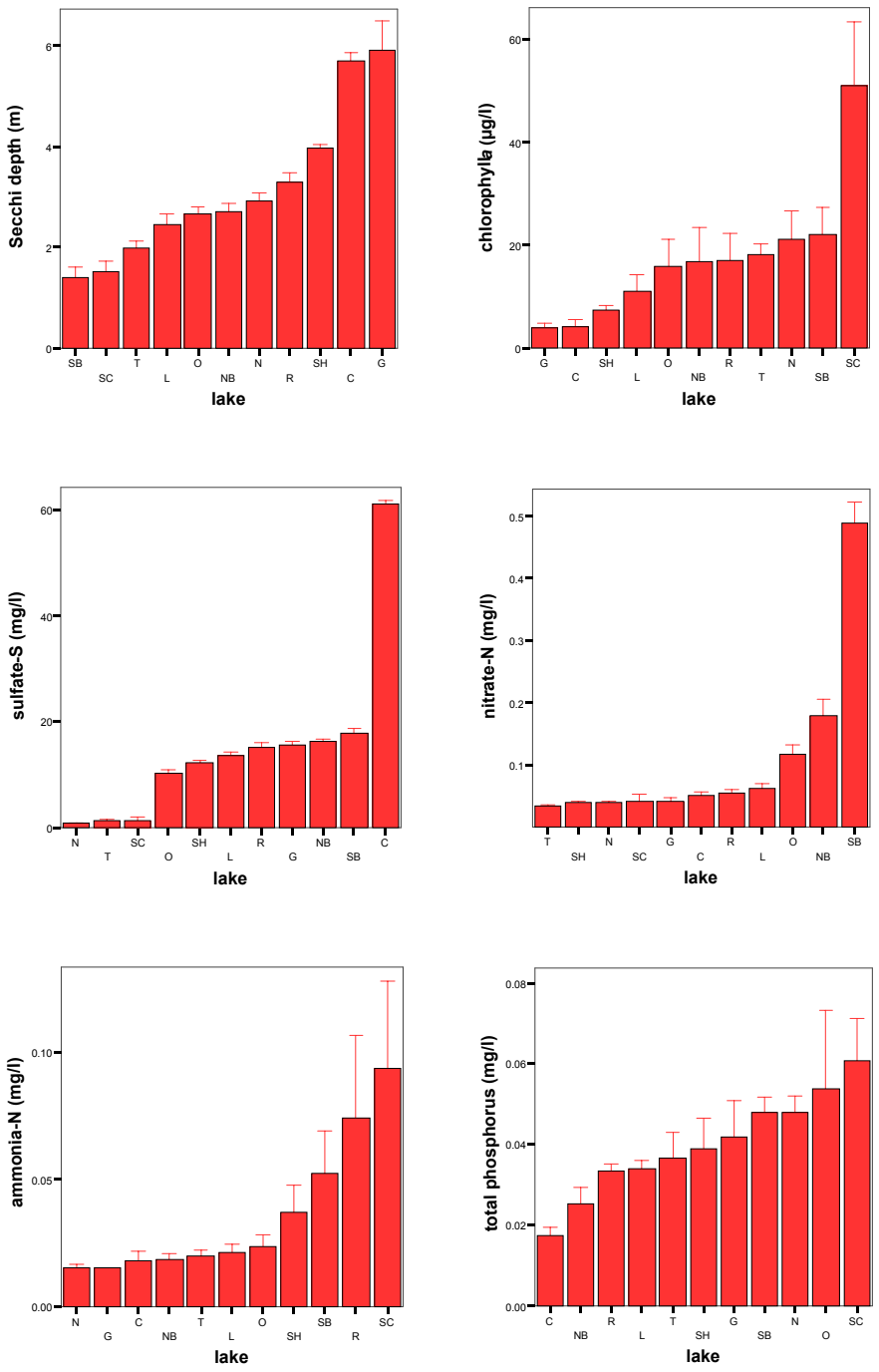


Figure 1. Average values of environmental variables in each of the lakes over the course of the study. Error bars = 1 standard error of the mean. Lakes identified by abbreviation as: Crystal (C), Big Glen (G), Loon (L), Narada (N), North Bar (NB), Otter (O), Round (R), South Bar (SB), School (SC), Shell (SH), and Tucker (T).

The study lakes experienced a range of stratification regimes. Big Glen, Crystal, Loon, and Narada were dimictic lakes that were stratified for the entire study period; initial stratification occurred in these lakes prior to mid-April, and fall turnover occurred after mid-October. Hypolimnetic oxygen depletion occurred in all four lakes.

Round, North Bar, and School lakes were also dimctic but had shorter periods of stratification. School Lake was stratified before the first sample date, and turnover occurred in late September or early October. Round and North Bar lakes stratified in mid- to late April. Turnover occurred in Round Lake in mid- to late September, whereas North Bar Lake turned over in late September or early October. Hypolimnetic oxygen depletion occurred in these lakes as well.

The remaining lakes were polymictic. Otter and South Bar lakes stratified periodically but did not maintain stratification throughout the summer. A degree of hypolimnetic oxygen depletion was present at times in Otter Lake but not in South Bar. Shallow water depth prevented stratification in Shell and Tucker lakes.

The trophic status of each lake was evaluated using Carlson's Trophic State Index (Carlson 1977) and the trophic state designations assigned by Kratzer and Brezonik (1981) (Table 1). Although calcium carbonate precipitation can occasionally reduce Secchi transparency in some Sleeping Bear Dunes lakes, the Secchi-based TSI was consistently lower than the chlorophyll *a*-based calculation. The majority of study lakes were mesotrophic to eutrophic according to the two indices. Big Glen and Crystal lakes were oligotrophic based on Secchi transparency and chlorophyll *a*. Shell Lake was more mesotrophic but had TSI values lower than the remaining lakes. Round Lake was almost oligotrophic based on Secchi

transparency but eutrophic on the basis of chlorophyll *a*. School Lake was nearly hypereutrophic in chlorophyll *a* concentration but barely eutrophic based on Secchi transparency.

Table 1.Carlson's TSI values and associated trophic status as calculated from mean Secchi transparency and chlorophyll a concentration (chl a). Trophic status (TS): o=oligotrophic, m=mesotrophic, e=eutrophic, h=hypereutrophic. Lakes identified by abbreviation as: Crystal (C), Big Glen (G), Loon (L), Narada (N), North Bar (NB), Otter (O), Round (R), South Bar (SB), School (SC), Shell (SH), and Tucker (T).

Lake	Secchi	TS	chl *a*	TS
G	39	o	44	o
C	39	o	44	o-m
SH	43	o	50	m
L	47	m	54	e
O	47	m	58	e
NB	46	m	58	e
R	44	o-m	58	e
T	50	m	59	e
N	46	m	60	e
SB	53	e	61	e
SC	52	m-e	69	e-h

Zooplankton Community Features of Study Lakes

Of the 85 taxa identified among all samples, only 32 comprised 1% or greater of the average abundance for any lake (Table 2). Copepod nauplii and copepodids (particularly cyclopoid copepodids) were quite common in most lakes. These groups are influential in multivariate analysis at the "lowest identified taxon" level since separations to genus or species level were not possible for these immature organisms and they are reported as a group (with larger numbers of individuals than most other taxa). The cladoceran *Bosmina longirostris* was also relatively common in all study lakes, ranging from 2-13% of the average total zooplankton abundance in a lake. The only other taxon found in at least 1% abundance in all lakes was the rotifer genus *Kellicottia,* although *Keratella* was also relatively abundant in all lakes but Crystal and Big Glen (the two largest and most oligotrophic lakes). Rotifer genera *Conochilus* and *Polyarthra* were each found in abundance: >1% in all but one study lake. Only two calanoid copepod species contributed to 1% or greater of the zooplankton abundance, and these only in the three most sparsely-populated and least productive lakes (Crystal, Big Glen, and Shell).

Table 2. Taxa comprising > 1% of average zooplankton abundance in each of the study lakes (numbers represent % of average abundance). Lakes identified by abbreviation as: Crystal (C), Big Glen (G), Loon (L), Narada (N), North Bar (NB), Otter (O), Round (R), South Bar (SB), School (SC), Shell (SH), and Tucker (T).

Class	Order	Family	Genus	Species	C	G	SH	L	O	R	NB	SB	N	T	SC
Branchiopoda	Anomopoda	Bosminidae	*Bosmina*	*longirostris*	5	11	4	5	4	2	12	2	7	10	13
Branchiopoda	Anomopoda	Bosminidae	*Eubosmina*	*coregoni*							2	26			
Branchiopoda	Anomopoda	Daphniidae	*Ceriodaphnia*	*dubia*									1		
Branchiopoda	Anomopoda	Daphniidae	*Ceriodaphnia*	*lacustris*										2	3
Branchiopoda	Anomopoda	Daphniidae	*Daphnia*	*dentifera*									1		
Branchiopoda	Anomopoda	Daphniidae	*Daphnia*	*galeata mendotae*	3	2	2								
Branchiopoda	Anomopoda	Daphniidae	*Daphnia*	*longiremis*		2									2
Branchiopoda	Anomopoda	Daphniidae	*Daphnia*	*retrocurva*		2		3		1	2	3			
Branchiopoda	Ctenopoda	Holopediidae	*Holopedium*	*gibberum*		4									
Branchiopoda	Ctenopoda	Sididae	*Diaphanosoma*	*birgei*						3				1	
Copepoda	Calanoida	Diaptomidae	*Leptodiaptomus*	*minutus*	1	3									
Copepoda	Calanoida	Diaptomidae	*Skistodiaptomus*	*oregonensis*			2								
Copepoda	Calanoida		calanoid	copepodids	24	4	7					3	3	2	
Copepoda	Cyclopoida	Cyclopidae	*Diacyclops*	*thomasi*	2	3		2							
Copepoda	Cyclopoida	Cyclopidae	*Mesocyclops*	*edax*		2									
Copepoda	Cyclopoida	Cyclopidae	*Tropocyclops*	*prasinus mexicanus*					4	4	1			3	1
Copepoda	Cyclopoida		cyclopoid	copepodids	21	20	7	7	18	11	10	8	3	6	6
Copepoda			nauplii		16	34	26	22	20	24	18	21	13	20	11
Monogononta	Collothecacea	Collothecidae	*Collotheca*	*spp.*	3		4		6	2					
Monogononta	Floscullariacea	Conochilidae	*Conochilus*	*spp.*	9	4	18	5	4	4	2		7	12	4
Monogononta	Floscullariacea	Filiniidae	*Filinia*	*spp.*				2					1		
Monogononta	Floscullariacea	Testudinellidae	*Pompholyx*	*spp.*								5			2
Monogononta	Ploima	Asplanchnidae	*Asplanchna*	*spp.*			1	1	4	2	1			1	3
Monogononta	Ploima	Brachionidae	*Kellicottia*	*spp.*	10	4	20	21	5	17	15	1	23	4	13
Monogononta	Ploima	Brachionidae	*Keratella*	*spp.*			4	19	30	22	19	19	33	26	33
Monogononta	Ploima	Brachionidae	*Notholca*	*spp.*				1							
Monogononta	Ploima	Gastropodidae	*Gastropus*	*spp.*									1		1
Monogononta	Ploima	Synchaetidae	*Ploesoma*	*spp.*				2							
Monogononta	Ploima	Synchaetidae	*Polyarthra*	*spp.*		1	1	7	2	1	11	5	2	5	3
Monogononta	Ploima	Synchaetidae	*Synchaeta*	*spp.*	3	2		2							
Monogononta	Ploima	Trichoceridae	*Trichocerca*	*spp.*					1	2	3	1		5	

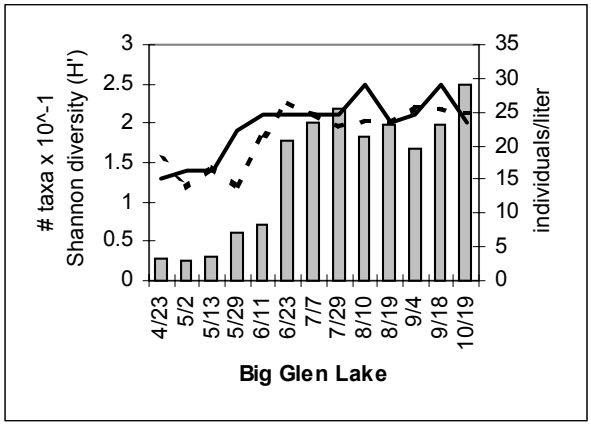
Taxon-independent indices were calculated from lake means for each genus (Table 3), since the majority of taxa were identified to at least that level. Nauplii and copepodids were not included in those analyses. The total number of genera was relatively similar among the lakes, generally falling between 30 and 40. Crystal Lake may have had an artificially low number of genera since this lake was sampled on fewer dates than the others. Total zooplankton density, however, varied greatly among lakes. The highest average zooplankton abundance (in School Lake) was over 100x the average abundance in the most sparsely populated lake (Big Glen Lake). In general, genus richness, evenness, and diversity among lakes declined as average abundance increased.

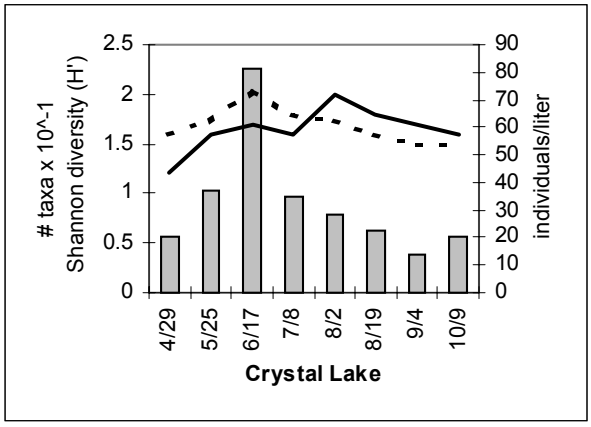
Table 3. Total genera (S), total individuals (N), Margalef richness (d), Pielou evenness (J'), and Shannon diversity (H') for each lake averaged over all sampling dates. Lakes identified by abbreviation as: Crystal (C), Big Glen (G), Loon (L), Narada (N), North Bar (NB), Otter (O), Round (R), South Bar (SB), School (SC), Shell (SH), and Tucker (T).

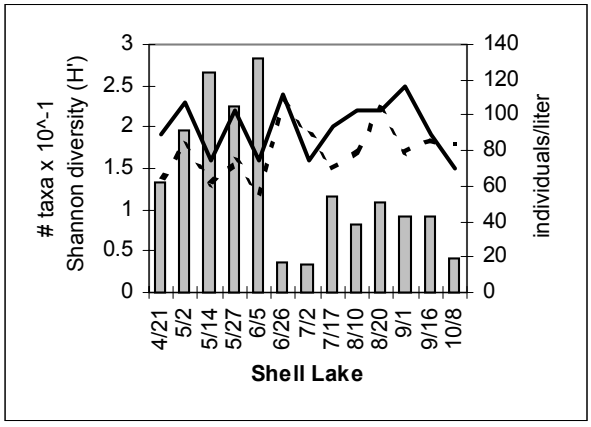
	S	N	d	J'	H'
G	28	7	13.9	0.69	2.30
C	23	12	8.7	0.67	2.11
SH	40	37	10.8	0.54	1.98
L	34	62	8.0	0.59	2.10
O	33	65	7.7	0.53	1.86
R	29	114	5.9	0.60	2.02
NB	34	140	6.7	0.59	2.08
SB	39	144	7.6	0.52	1.90
N	35	193	6.5	0.49	1.75
T	37	496	5.8	0.56	2.04
SC	33	792	4.8	0.56	1.97

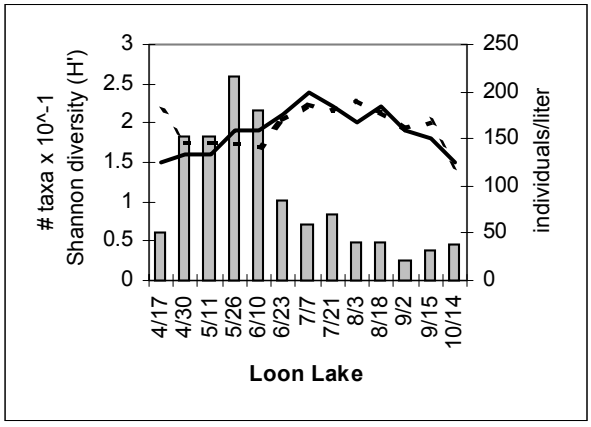
Temporal trends in zooplankton abundance, number of taxa (at lowest identified taxonomic level), and Shannon diversity (based on lowest identified taxonomic level) were different among the study lakes (Fig. 2). Abundance often peaked in April-June for most lakes, although Otter and Tucker lakes peaked in July and Narada, and Big Glen lakes reached their zooplankton abundance maxima in September-October. In Big Glen Lake, diversity and the number of taxa rose in rough correspondence with overall zooplankton abundance, although in most lakes, diversity and number of taxa appeared to be independent of abundance. In some instances, most notably the July abundance peak in Otter Lake, abundance and diversity appeared to be inversely related. This is probably because the sharp rise in zooplankton abundance was dominated by an increase in *Keratella* sp. that drove down the Shannon diversity value. To some extent, it appears that the more heavily populated lakes exhibited a weak inverse relationship between increases in zooplankton abundance and greater zooplankton taxa numbers and diversity. In the more sparsely populated Crystal and Big Glen lakes, abundance and

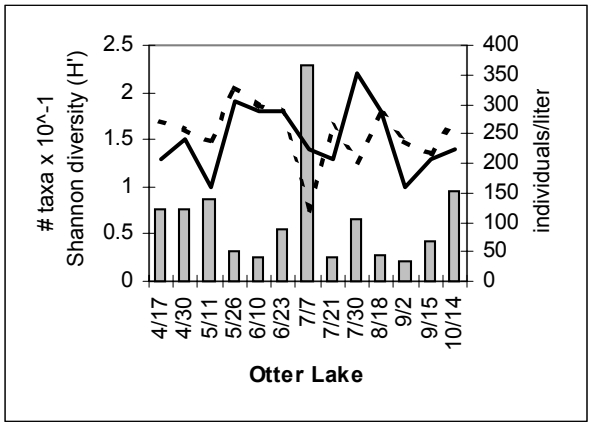
diversity appeared to rise together. Overall, the extent of temporal variation in abundance, number of taxa, and Shannon diversity emphasizes the necessity of taking samples several times within a season.

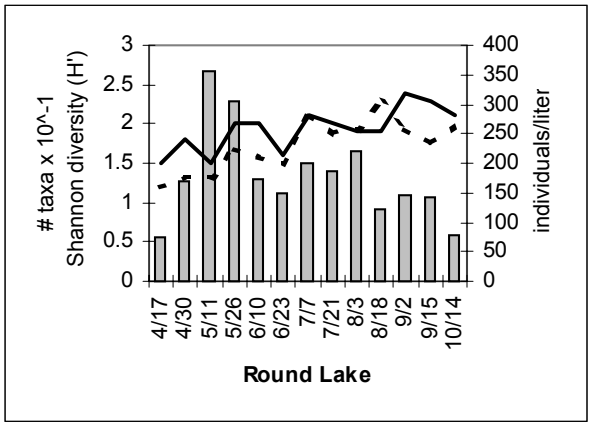












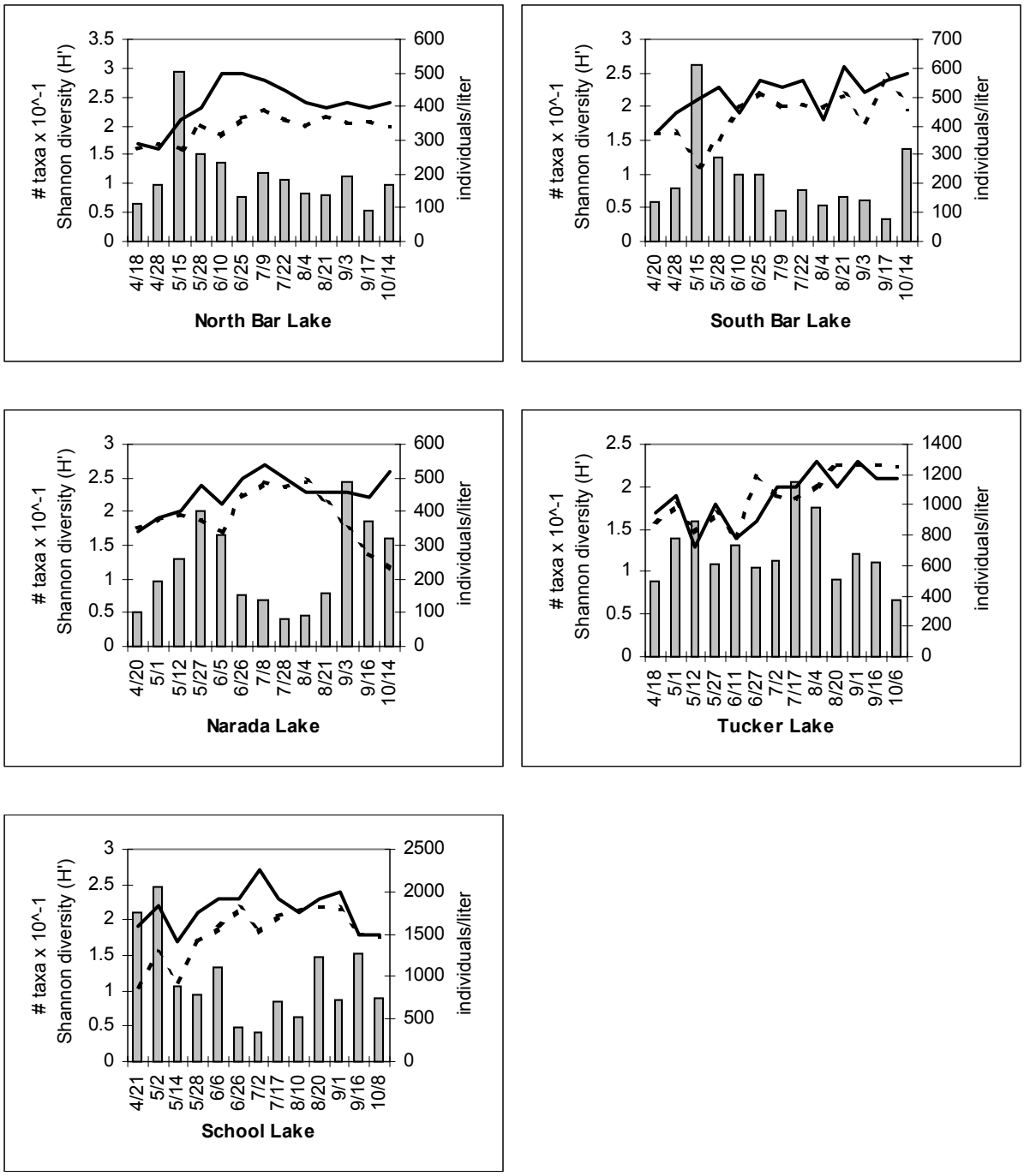


Figure 2. Number of taxa, Shannon diversity, and zooplankton abundance from May-October, 1998. Bars represent zooplankton individuals / liter. Solid lines show the # of zooplankton taxa at the lowest identified level. Dotted lines show Shannon diversity calculated from lowest identified taxonomic level.

Average zooplankton abundance in Big Glen Lake was the lowest of all the study lakes, whereas Margalef richness, Pielou evenness, and Shannon diversity were the highest (Table 3). Big Glen Lake also had one of the few zooplankton communities dominated by copepods on average (Fig. 3). Copepod abundance rose rapidly from late May to early July (Fig. 4), driven mostly by increases in nauplii and cyclopoid copepodids. Branchiopods were second to copepods in average abundance, although they were surpassed by rotifers in September and October samples. Highest branchiopod abundance occurred in June and July samples. The dominant branchiopod was generally *B. longirostris*. *Holopedium gibberum, Daphnia galeata mendotae, D. longiremis,* and *D. retrocurva* were also represented on most sample dates. Rotifer abundance was very low for most of the study period. A marked rise in September and October was driven by increases in the genera *Conochilus, Kellicottia, Synchaeta,* and to a lesser degree, *Keratella.*

Crystal Lake also had low zooplankton abundance dominated by copepods (Fig. 3). Abundance in all three major zooplankton groups was low in April, spiked in mid-June, and returned to near early-season abundance by September (Fig. 4). The mid-June rise in copepods was driven by increases in calanoid and cyclopoid copepodids; this was preceded by high numbers of copepod naulplii in May. High rotifer abundance in June was primarily the result of increases in the genera *Collotheca, Conochilus,* and *Kellicottia. Bosmina longirostris* dominated a weaker simultaneous rise in branchiopod abundance.

The largest number of zooplankton genera was collected from Shell Lake (Table 3). Copepods generally dominated the zooplankton community throughout the study (Fig. 4), mostly in the form of nauplii and calanoid and cyclopoid copepodids. However, on average, rotifers were slightly more abundant than copepods (Fig. 3) due to elevated abundance from late May

through June. This was driven by >10-fold increases in abundance within the genera *Kellicottia* and *Conochilus*. Branchiopod abundance was consistently low, with only two small peaks in May and August that were dominated by *B. longirostris*.

Loon Lake zooplankton were consistently dominated by rotifers (Fig. 4). In mid-April and mid-July, rotifer and copepod abundances were comparable, but rotifer abundance peaked well above the other zooplankton groups in late May due to increases in *Kellicottia* sp., *Keratella* sp., and to a lesser extent, *Conochilus* sp. Copepod abundance was highest in late April, dominated by nauplii. Cyclopoid copepodids peaked in early June, but overall copepod abundance fell gradually from May until September. Branchiopod abundance was generally low; a small peak in early June was driven by increases in *B. longirostris* and *D. retrocurva*.

Average zooplankton abundance in Otter Lake was weakly dominated by rotifers (Fig. 3), although on the majority of sample dates, copepod abundance was highest (Fig. 4). Rotifer abundance spiked sharply in early July as the dominant genus switched from *Kellicottia* to *Keratella*, and *Keratella* sp. abundance alone rose to 300 organisms per liter. A smaller late-July rotifer spike was caused by an increase in *Collotheca* sp. Copepods dominated early and late in the study period. In April and May, the copepod community was composed mainly of nauplii and cyclopoid copepodids, but the resurgence of copepod abundance in September and October was also influenced by increases in *Tropocyclops prasinus mexicanus*. Branchiopod abundance remained relatively low throughout the study period. One small peak in early May was caused by increases in *B. longirostris* and *D. retrocurva*.

The average zooplankton abundance of Round Lake was also dominated by rotifers (Fig. 3), although copepods were more numerous on over half of the sample dates (Fig. 4). Rotifer abundance peaked strongly in late May, driven by increased abundance in *Kellicottia* sp. and

Keratella sp. A smaller peak occurred in late June with a surge in *Keratella* sp. numbers, and again in early August when *Keratella* sp. and *Collotheca* sp. increased. Copepods peaked in early May with large numbers of nauplii and cyclopoid copepodids. Slightly smaller peaks in mid-July and mid-September showed increases in nauplii and *T. prasinus mexicanus.* Branchiopod abundance generally remained low relative to the other two groups, although a rise in *Diaphanosoma birgei* in early September drove branchiopod abundance above rotifer abundance. A smaller peak in early July resulted from an increase in *B. longirostris.*

Average zooplankton abundance in North Bar Lake was dominated by rotifers (Fig. 3), due in large part to a high peak in mid-May (Fig. 4) caused by the genera *Kellicotia* and *Keratella*. April rotifer populations were composed mainly of *Polyarthra* sp., and fluctuations in *Polyarthra* sp. and *Keratella* sp. caused a small rotifer peak in mid- to late July. The copepod community was primarily composed of nauplii and cyclopoid copepods throughout the study period, with small peaks in mid-May, early July, and early September. Branchiopods were of relatively low average abundance, but a rise in *B. longirostris* and (to a lesser degree) *D. retrocurva* through late May and early June caused branchiopod abundance to exceed falling rotifer and copepod numbers on one sample date. A smaller peak in early July was caused by the same two species in addition to a large rise in *Eubosmina coregoni* abundance.

The average zooplankton abundance of South Bar Lake was very evenly distributed among the three major zooplankton groups (Fig. 3). Generally, copepods or rotifers were dominant on any given date (Fig. 4), but a sharp increase in *E. coregoni* drove branchiopod abundance far above that of the other two groups in mid- to late May. *D. retrocurva* also peaked strongly, although less dramatically, in late June. The majority of copepods on any date were nauplii, along with calanoid and cyclopoid copepodids. These peaked in mid-May and again in

late June. The rotifers were comprised primarily of *Keratella* sp. *Pompholyx* sp. and *Polyarthra* sp. contributed to a rotifer peak in early June, whereas another peak in mid-July resulted from increases in *Keratella* sp., *Pompholyx* sp., and *Trichocerca* sp. The largest rotifer peak was driven by a sharp rise in *Keratella* sp. in mid-October.

Narada Lake had the lowest scores for Pielou evenness and Shannon diversity among all the study lakes (Table 3). Rotifers dominated the zooplankton community of Narada Lake for most of the study period (Fig. 3). There was a strong peak in rotifer abundance in late May brought on by increases in the genera *Conochilus*, *Kellicottia,* and *Keratella.* A second rise in rotifer abundance from early September to the end of the study was driven by *Kellicottia* and *Keratella*. Copepod and branchiopod abundance remained much lower than rotifer abundance for most of the study. These two groups appeared to rise and fall together, with copepods dominated by nauplii and cyclopoid copepodids, and branchiopod abundance primarily determined by *B. longirostris*.

The zooplankton community of Tucker Lake was strongly dominated by rotifers from early May to mid-August (Fig. 4). Dominance within the rotifers shifted among genera. The first sample was composed mostly of *Kellicottia* sp., which declined as the overall population approached a mid-May peak driven by increasing *Keratella* sp. *Conochilus* sp. and *Polyarthra* sp. numbers rose strongly on the next sample date, but overall rotifer abundance declined with *Keratella* sp. The early June rotifer peak coincided with increased *Keratella* sp. and *Trichocerca* sp. The last large peak was characterized by high numbers of *Conochilus* sp. in mid-July that gave way to a rise in *Keratella* sp. in early August. Copepod abundance was dominated by nauplii and cyclopoid copepodids in the early part of the study period. A mid-July peak resulted from increases in these two taxa and (to a lesser extent) calanoid copepodids and *T. prasinus*

mexicanus. The early September peak was similarly affected by these four taxa. Branchiopod abundance was generally linked to fluctuations in *B. longirostris*, although *C. sphaericus* had a high in early May and *Ceriodaphnia lacustris* and *Diaphanosoma birgei* were common in the second half of the study period.

School Lake had the highest average zooplankton abundance among all the study lakes (Table 3). The zooplankton community was dominated by rotifers on average (Fig. 3), although branchiopods or copepods were in greater abundance on some dates (Fig. 4). From late April through May, *Keratella* sp. was clearly the dominant rotifer, although *Asplanchna* sp. was also relatively abundant in April. A rotifer peak in early June was caused by high numbers of *Keratella* sp. and *Kellicottia* sp., and a mid-July peak came from increases in *Kellicottia* sp. and *Conochilus* sp. *Pompholyx* sp. was the most numerous rotifer in late August (although *Kellicottia* sp. and *Conochilus* sp. were also abundant), and the final rotifer peak in mid-September was driven by a large increase in *Kellicottia sp*. Copepods and branchiopods were of comparable abundance on average, with copepods more common in the first half of the study period and branchiopods more common in the second half. The copepods were primarily nauplii and cyclopoid copepodids. Calanoid copepodids and *S. oregonensis* were also common in May and June. *T. prasinus mexicanus* and *Mesocyclops edax* dominated adult forms in the second half of the study period. Branchiopod abundance peaked in mid-August with large numbers of *B. longirostris* and *C. lacustris. D. parvula* was abundant in early June and *D. longiremis* was common for most of the study period.

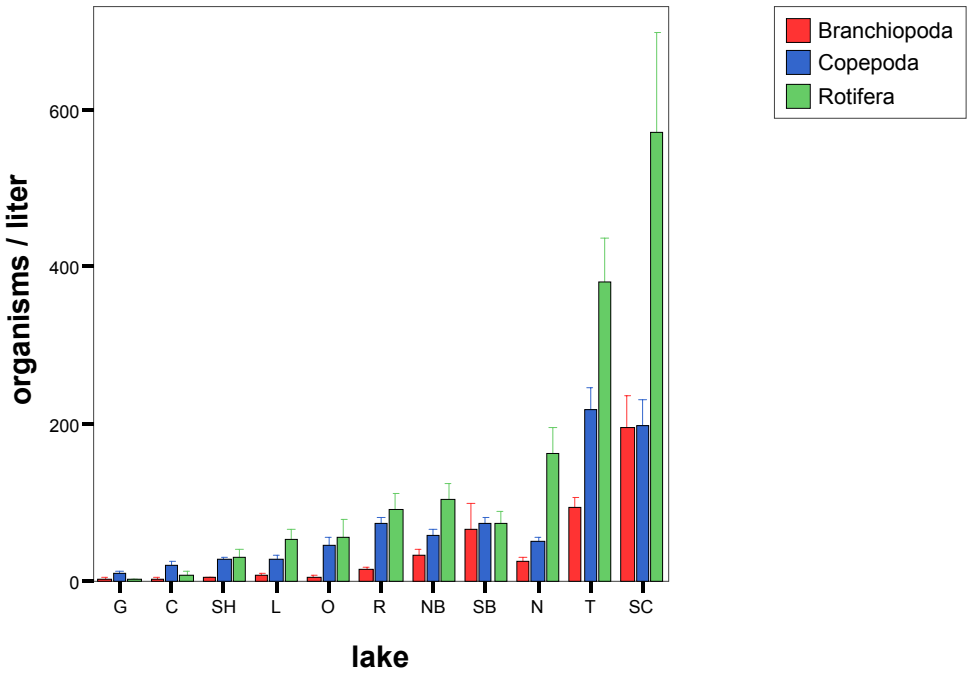
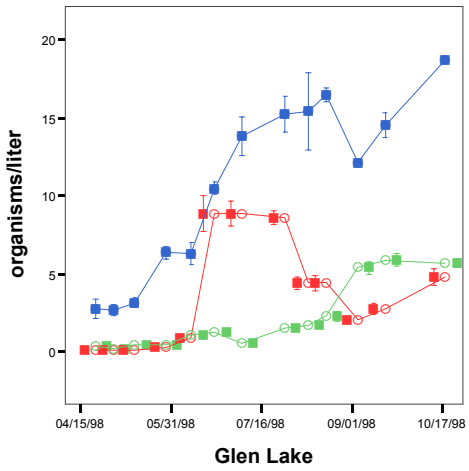
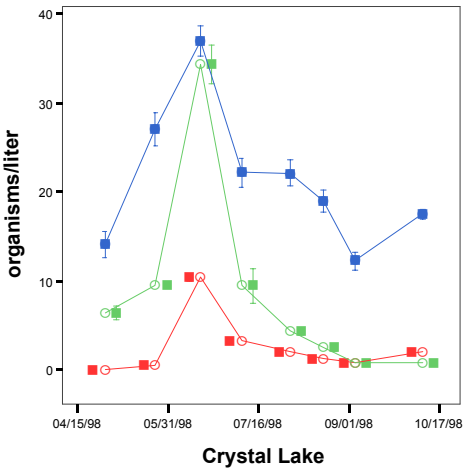


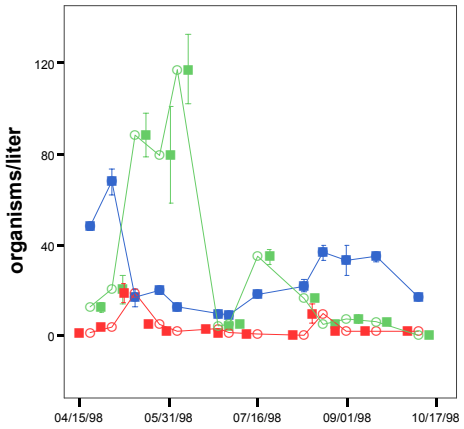
Figure 3. Mean abundance of major zooplankton groups for each study lake. Error bars = 1 standard error of the mean. Lakes identified by abbreviation as: Crystal (C), Big Glen (G), Loon (L), Narada (N), North Bar (NB), Otter (O), Round (R), South Bar (SB), School (SC), Shell (SH), and Tucker (T).



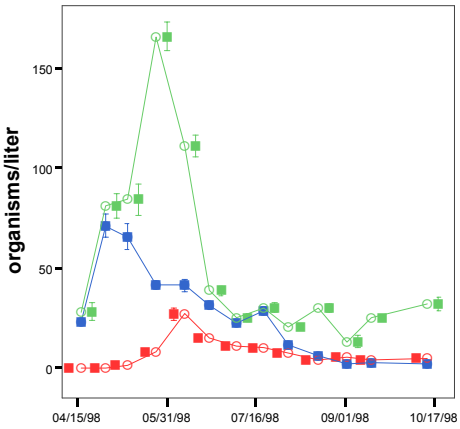
Glen Lake



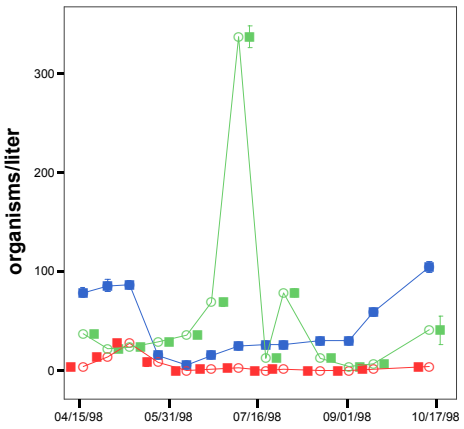
Crystal Lake



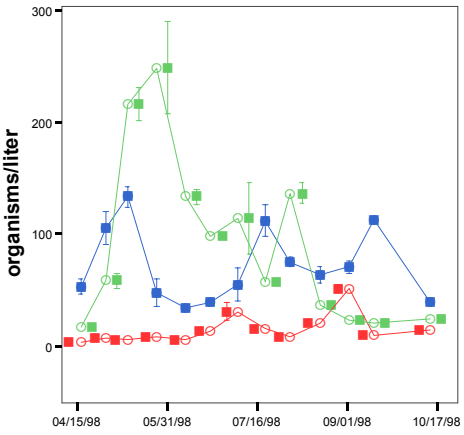
Shell Lake



Loon Lake



Otter Lake



Round Lake

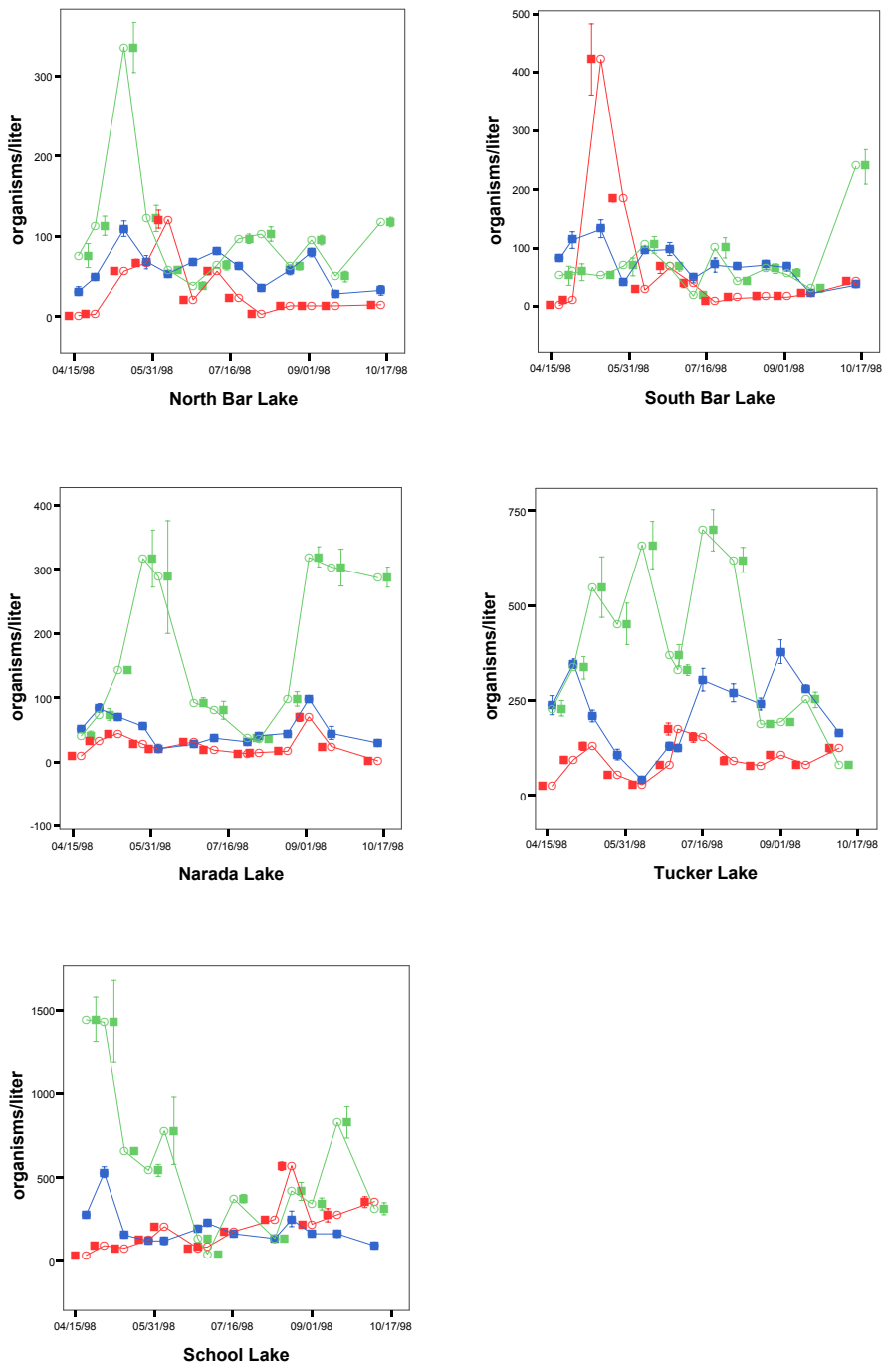


Figure 4. Mean abundance of major zooplankton groups on each sample date: red = branchiopods, blue = copepods, green = rotifers. Error bars = 1 standard error of the mean.

Agreement among replicate samples was good (Table 4), with overall average Bray-Curtis similarity among replicates at 88. Replicates from Crystal, North Bar, and Tucker lakes were particularly consistent, while Shell Lake had much lower average similarity among replicates than any of the other study lakes. Similarity among samples taken at different times was much lower than similarity among replicates. The average similarity among sample times within a lake was 61. Narada Lake appeared to have the least temporal variation in the zooplankton community with average similarity among sample times approaching 70.

Table 4. Average Bray-Curtis similarities based on log-transformed community data (lowest identified taxa) in each lake among replicates (rep) and sampling times (time). Lakes identified by abbreviation as: Crystal (C), Big Glen (G), Loon (L), Narada (N), North Bar (NB), Otter (O), Round (R), South Bar (SB), School (SC), Shell (SH), and Tucker (T).

lake	rep	time
C	91.4	55.4
G	88.1	55.2
L	90.3	57.6
N	88.7	69.5
NB	90.3	67.3
O	89.1	53.9
R	89.5	60.4
SB	86.2	66.2
SC	88.3	65.4
SH	79.3	52.3
T	90.2	68.1

Due to temporal variations, the lake comparisons were rather different from one another depending upon which sample time was analyzed. The MDS ordination based on late April samples placed Crystal and Big Glen lakes very far from the other study lakes and very far from each other (Fig. 5). In contrast, early June samples place Crystal Lake closer to the center of the ordination and suggest that Big Glen Lake is most similar to Otter Lake. Loon and North Bar lakes are closely associated in the early June MDS but far more distant in the late August

ordination. Round, Otter, and Narada lakes are not particularly closely associated in the late August MDS but appear to be quite similar in early October. Therefore, if basing zooplankton community comparisons on only one sample time, the choice of sample time may have a large effect on the apparent similarities among lakes.

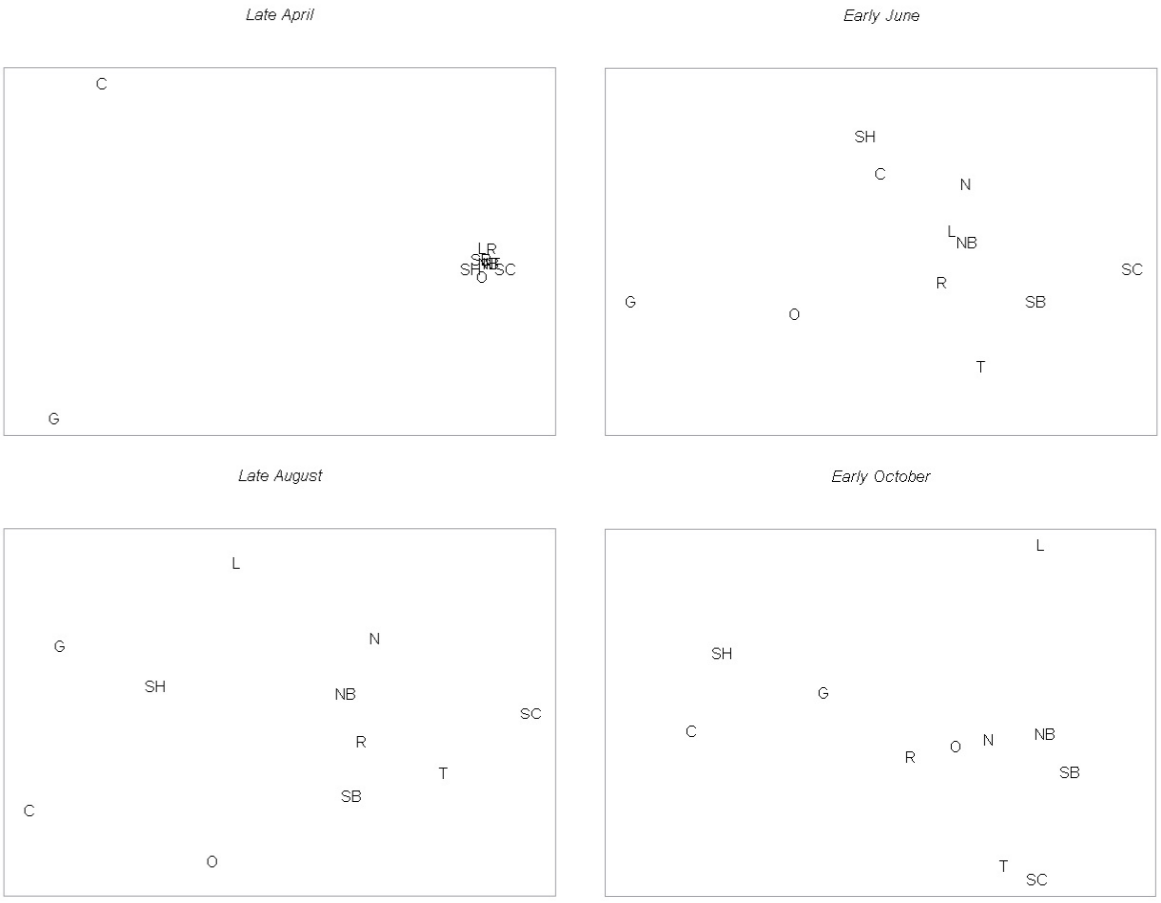


Figure 5. MDS ordinations of zooplankton community data from four different sampling times: late April (stress = 0.01), early June (stress = 0.09), late August (stress = 0.09), early October (stress = 0.09). MDS based on Bray-Curtis similarities computed from log-transformed data at lowest identified taxonomic level. Lakes identified by abbreviation as: Crystal (C), Big Glen (G), Loon (L), Narada (N), North Bar (NB), Otter (O), Round (R), South Bar (SB), School (SC), Shell (SH), and Tucker (T).

The MDS ordination of the six mid-summer sampling dates (June-August) for each of the study lakes illustrates the patterns of temporal variation in the zooplankton communities (Fig. 6).

Earlier and later sampling dates were omitted from the ordination; early- and late-season extremes in the zooplankton community caused the central portion of the ordination to cluster too tightly for interpretation. Temporal variation in certain lakes was very large, and many lakes overlapped one another in the ordination space. Crystal Lake and Big Glen Lake were each distinct from the other study lakes, but Crystal Lake in particular showed a broad range of temporal variation. The Shell Lake zooplankton community was variable but generally was confined to an area between the two large oligotrophic lakes and the rest of the study lakes. Loon Lake zooplankton shifted very strongly and consistently over the dates shown. Otter Lake showed no clear temporal patterns but did overlap with the late August sample from Loon Lake. Round and North Bar lakes clustered rather tightly together and overlapped strongly. They also appeared to have similar temporal tendencies, with early and late samples oriented much the same way. Narada Lake zooplankton samples overlapped with the earliest North Bar Lake sample in the ordination, but Narada Lake samples were generally tightly clustered and showed a strong temporal trend. Zooplankton samples from South Bar Lake varied substantially and were oriented around the perimeter of the Round and North Bar lakes cluster. Tucker and School Lake zooplankton communities were each distinct from the other lakes during the sample times shown.

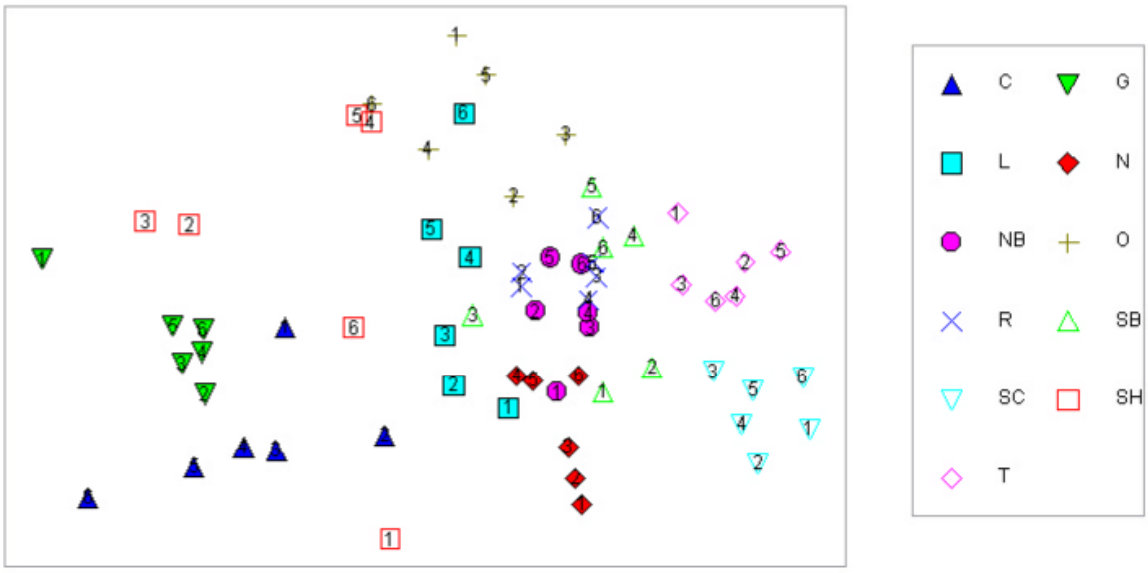


Figure 6. MDS of zooplankton community samples from six mid-summer sampling dates (stress = 0.17). Numbers are relative to sample times within each lake. MDS based on Bray-Curtis similarities computed from log-transformed data at lowest identified taxonomic level. Lakes identified by abbreviation as: Crystal (C), Big Glen (G), Loon (L), Narada (N), North Bar (NB), Otter (O), Round (R), South Bar (SB), School (SC), Shell (SH), and Tucker (T).

MDS ordination and hierarchical cluster analysis of mean zooplankton data for the entire study period placed the lakes into four groups at Bray-Curtis similarity of 60 (Fig. 7). The order of the lakes from left to right matched the order of increasing mean zooplankton abundance (Table 3). Crystal and Big Glen lakes had the smallest zooplankton densities and remained clustered apart from the other study lakes at Bray-Curtis similarity of 50. Shell Lake also had low zooplankton abundance and grouped with no other lakes in the first cluster but was joined with the remaining study lakes at Bray-Curtis similarity of 50. The rest of the study lakes were split into two groups. However, the lakes were fairly consistently spaced across the ordination, and the clusters did not look particularly strong on the MDS. It appears that, for the most part, the zooplankton communities of these lakes did not form strongly distinct groups but rather a gradient of differences in zooplankton community composition and abundance.

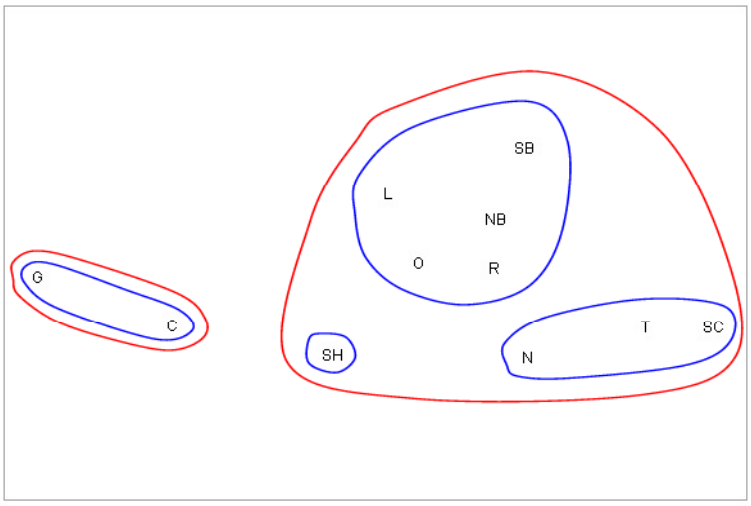


Figure 7. MDS of lake averages for all zooplankton taxa (stress = 0.05). Blue and red lines indicate hierarchical group average clusters at Bray-Curtis similarity = 60 and 50. Lakes identified by abbreviation as: Crystal (C), Big Glen (G), Loon (L), Narada (N), North Bar (NB), Otter (O), Round (R), South Bar (SB), School (SC), Shell (SH), and Tucker (T).

Relationships Between Environmental Variables and Community Patterns

Bio-Env analysis indicated that the rank similarities of lakes based on zooplankton community structure related quite well to a small suite of environmental variables (Table 5). The best correlation was for all taxa at the lowest identified level; the correlation coefficient was 0.87 when environmental similarities were calculated form Secchi transparency, chlorophyll *a,* and sulfate. Genus-level analysis gave only a slight reduction in correlation for the best combination of variables and also included maximum depth in addition to Secchi transparency, chlorophyll *a,* and sulfate. Zooplankton aggregation to family and order achieved lower maximum correlations (0.79 and 0.76), but major group (rotifers, copepods, and branchiopods), the coarsest taxonomic aggregation, exceeded them with a correlation of 0.81. The suite of environmental variables giving the best correlation varied slightly depending upon aggregation level, although all included Secchi depth and chlorophyll *a* concentration. When analysis was restricted to the single best variable, correlations remained high (>0.70) and the best variable was chlorophyll *a* concentration.

When community analysis is limited to certain taxonomic groups, it may give a better representation of environmental heterogeneity (Sladecek 1983, Attayde et al. 1998). With this in mind, we examined the relationship between environmental variables and community structure at the lowest taxonomic level separately for the rotifers, copepods, and branchiopods. Overall, correlations indicated a similar set of environmental variables and lower maximum correlations than the first analysis (which included all taxa). Analysis using the branchiopod taxa alone was the only one to include alkalinity in the best correlation, and it showed the largest decrease in correlation when reduced to the single best variable (0.80 for chlorophyll *a,* sulfate, and

Table 5. Results from Bio-Env analysis of zooplankton and environmental variables at different levels of zooplankton aggregation. Correlation coefficients are given for the best combination of environmental variables (marked columns) and the single best environmental variable (large "X").

aggregation level	best	single	Secchi	chl *a*	sulfate	nitrate	alkalinity	max depth	area	spcond	Ca
all taxa	0.87	0.83	x	X	x						
genus	0.86	0.80	x	**X**	x			x			
family	0.79	0.76	x	**X**	x						
order	0.76	0.73	x	**X**	x			x	x		
major group	0.81	0.80	x	**X**							
branchiopoda taxa	0.80	0.60		**X**	x		x				
copepod taxa	0.75	0.75		**X**							
rotifer taxa	0.86	0.78	X	x				x			
functional - 2	0.81	0.81		X							
functional - 5	0.71	0.71		**X**							
rotifer trophi	0.80	0.70	x	**X**	x			x	x	x	
major group standardized	0.78	0.71	X	x		x			x		
functional - 2 standardized	0.45	0.45							X		
functional - 5 standardized	0.68	0.65	X		x				x		
rotifer trophi standardized	0.55	0.55	**X**	x				x	x		x
total abundance	0.83	0.83		X							

alkalinity, 0.60 for chlorophyll *a* alone). The rotifer taxa alone gave best-combination and single-variable correlations similar to those for genus-level aggregation of the entire data set, although sulfate did not enter the best variable combination for rotifers. The best single variable explaining rotifer variation was Secchi transparency instead of chlorophyll *a.* These two variables are both closely related to trophic status, so the implications are essentially the same.

In some cases, functional rather than taxonomic groupings may be more effective in discerning ecologically relevant community shifts (Sprules and Holtby 1979); we repeated Bio-Env analysis using three different functional aggregations of zooplankton data. The first two aggregations were constructed according to the functional zooplankton classifications of Sprules (1984). Functional – 2 separated herbivores/grazers from carnivores. This low-complexity functional representation of the zooplankton data yielded a 0.81 correlation with chlorophyll *a*

concentrations (Table 5). The next level of analysis included a size component with the functional classification (functional – 5). Zooplankton were separated into small grazers (<0.4 mm, including all rotifers), large grazers (1.0-1.7 mm), herbivorous calanoid copepods (1.0-1.7 mm), cyclopoid copepods (0.8-1.3 mm), and large predators (up to 5.0 mm, including carnivorous calanoid copepods). Again, the best correlation was with similarities based on chlorophyll *a* concentration, but the correlation was lower (0.71). Finally, since rotifer taxa had a very high correlation with environmental variables, we grouped them according to trophi morphology (since trophi are often indicative of functional feeding ecology). The best correlation coefficient was reasonably high (0.80) and incorporated the largest number of environmental variables. However, the correlation only decreased moderately when limited to the single best variable (chlorophyll *a*).

To remove the effect of total zooplankton abundance in the similarity measures, we performed Bio-Env on selected aggregations after standardizing taxon abundances to their percentage of the total community. In this manner, changes in the relative abundance of various groups within a lake might show environmental sensitivities that were overwhelmed by the great differences in overall abundance among the zooplankton communities. Analysis of standardized major group data was the only instance when nitrate figured into the best environmental correlation. However, trophic status as indicated by Secchi transparency alone gave a correlation coefficient only 0.07 lower, so it appears that the strongest gradient in the analysis is still trophic status. In the two-functional-group aggregation the similarities based on standardized abundances had a poor relationship to any combination of the environmental variables measured, with the best correlation at 0.45 for lake area alone. The increased detail provided by standardized data from the five-functional-group aggregation gave a better correlation with the

environmental data than the two-functional-group aggregation, but the most influential single variable was still Secchi transparency.

It appears that removing overall zooplankton abundance from the mutivariate analysis did not do much to improve sensitivity to other environmental variables, since the best correlations consistently decreased when a data set was standardized and the driving variables did not change appreciably. In fact, Bio-Env analysis of Bray-Curtis similarities computed from total zooplankton density alone yielded a higher correlation than any of the standardized aggregations (0.83), with the best variable combination including only chlorophyll *a* concentration.

Most taxonomic aggregations were related to a similar suite of variables at comparable levels of correlation. However, analysis based on all taxa at the lowest identified level provided the highest correlation and allowed us to take full advantage of the complexity of the data set. For this reason, further analysis was focused on the environmental variables identified by Bio-Env analysis of all taxa at the lowest identified levels: Secchi transparency, chlorophyll *a* concentration, and sulfate concentration (Table 5). Relative values of these environmental variables can be seen superimposed on the taxa MDS ordination in Figure 8. Secchi depth and chlorophyll *a* concentrations identify the pattern of trophic status over the zooplankton ordination, with oligotrophic Crystal and Big Glen lakes defining one end of the spectrum, and eutrophic School Lake at the other extreme. However, there is a split on the eutrophic end of the ordination, with South Bar Lake on the end of the other branch. Sulfate levels appear to differentiate these two branches. School, Tucker, and Narada lakes have markedly lower sulfate levels than any of the other study lakes. These three lakes are located near each other in the zooplankton ordination space and were grouped together at 60% similarity in hierarchical cluster analysis (Fig. 7).

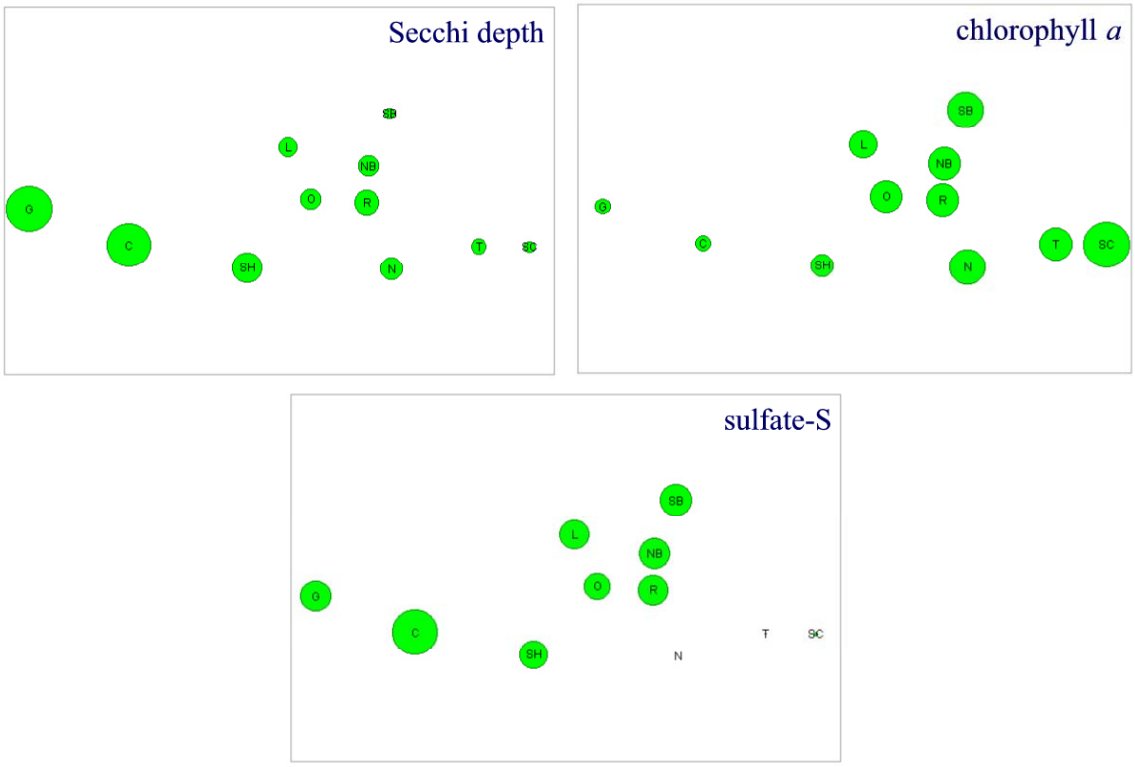


Figure 8. MDS of lake averages for all zooplankton taxa (stress = 0.05) with bubbles representing average values for Secchi depth, chlorophyll a (log-transformed), and sulfate-S (log-transformed). Lakes identified by abbreviation as: Crystal (C), Big Glen (G), Loon (L), Narada (N), North Bar (NB), Otter (O), Round (R), South Bar (SB), School (SC), Shell (SH), and Tucker (T).

Correlation-based PCA of the study lakes from these three environmental variables placed the lakes in relative positions similar to those in the zooplankton MDS (Fig. 9). The first PC axis summarizes 80.5% of the variation. The coefficients were positive for chlorophyll *a* and negative for Secchi depth and sulfate. All three variables correlated strongly with PC1 (Table 6), and the distribution of lakes along that axis described a gradient of increasing eutrophy. The second PC axis (17.0% of the variation) was not highly correlated with any of the original PCA components, and among the original component variables, its only significant correlation was with sulfate (0.60).

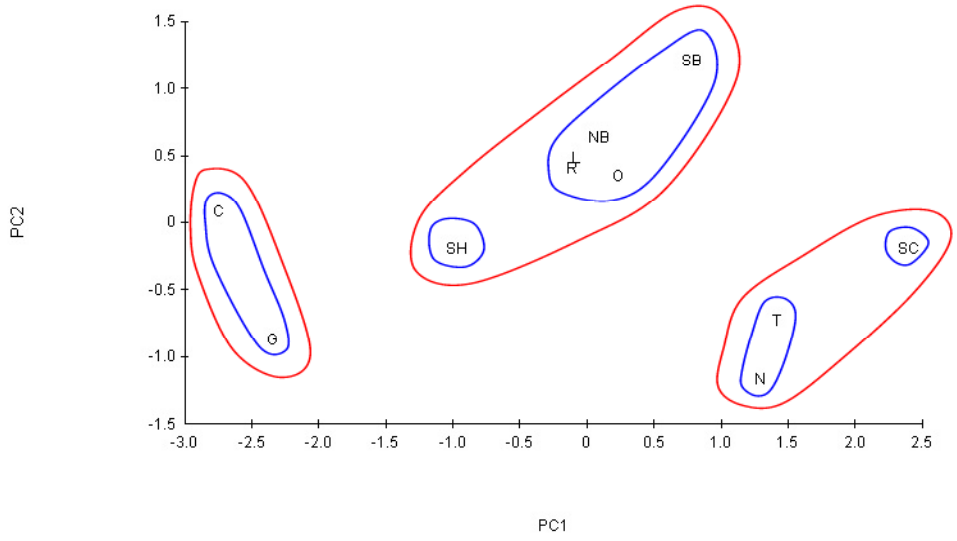


Figure 9. PCA of lake averages for sulfate-S, chlorophyll a, and Secchi depth. Blue and red lines indicate hierarchical group average clusters at normalized Euclidean distance = 1.25 and 2.00. PC1 (80.5% of variation) = -0.513 x sulfate-S – 0.593 x Secchi depth + 0.621 x chlorophyll *a*. PC2 (17.0% of variation) = 0.843 x sulfate-S – 0.485 x Secchi depth +0.233 chlorophyll *a*. Lakes identified by abbreviation as: Crystal (C), Big Glen (G), Loon (L), Narada (N), North Bar (NB), Otter (O), Round (R), South Bar (SB), School (SC), Shell (SH), and Tucker (T).

Although only three environmental variables contributed to the optimal correlation, the axes identified by the PCA ordination were correlated with other variables (Table 6). PC1 was positively (though relatively weakly) correlated with total phosphorus, which further supports the conclusion that the first axis is one of increasing eutrophication. However, trophic status was not entirely independent of lake morphology. Lake area and maximum depth were negatively correlated with PC1: the more eutrophic lakes tended to be smaller and shallower. Mean surface temperature and dissolved oxygen also correlated with this axis. These additional factors may influence the zooplankton community directly through the physiological requirements of particular zooplankton taxa (Gannon and Stemberger 1978). Additionally, these factors may significantly affect the structure of the fish community. Cascading trophic interactions initiated in the fish community can significantly affect both zooplankton community structure and overall

lake trophic status (Carpenter et al. 1985). Therefore, caution must be used in attributing the differences in zooplankton community along PC1 exclusively to trophic status, since this study included neither large, deep, eutrophic lakes, nor small, shallow, oligotrophic lakes.

The second PC axis was positively correlated with specific conductivity and nitrate in addition to sulfate. Since phosphorus is the limiting nutrient for most Sleeping Bear lakes (Boyle and Hoefs 1993), nitrate may be more significant in this context as an ion than as a limiting nutrient. This suggests that PC2 is primarily an axis of increasing ion concentration. This may separate eutrophic lakes from those that are tending towards dystrophy, and it could explain the split at the right-hand side of the zooplankton MDS ordination.

Nitrate concentrations may also be positively related to the nitrogen to phosphorus (N:P) ratio (Stemberger and Miller 1998). This study did not measure total nitrogen, so the relationship cannot be confirmed for these lakes. However, if this is the case and the lakes toward the lower end of PC2 also had lower N:P ratios, this could be another factor that causes differences in the zooplankton communities along this axis. If these lakes were actually approaching nitrogen limitation that would give a competitive advantage to nitrogen-fixing blue-greens, which could in turn affect the community of zooplankton herbivores (Kerfoot and DeAngelis 1989).

Table 6. Pearson correlation coefficients (p<0.05) between PCA axes and environmental variables (* denotes component of PCA ordination).

environmental variable	PC1	PC2
Secchi depth *	-0.92	
sulfate-S *	-0.80	0.60
area	-0.76	
surface dissolved oxygen	-0.72	
maximum depth	-0.71	
total phosphorus	0.64	
surface temperature	0.79	
chlorophyll *a* *	0.96	
specific conductivity		0.65
nitrate-N		0.81

To examine how individual taxa abundances were aligned with most biologically relevant environmental gradients, we tested Spearman correlations between each identified taxon and the first two PCA axes. Significant correlations are reported in Table 7. Taxa giving the highest correlation with PC1 were primarily small grazers, particularly rotifers. Individuals of the genera *Keratella, Asplanchna,* and *Conochilus* are abundant and generally distributed (Pennak 1989), and these genera were found in all of the study lakes, but abundances were higher in more eutrophic lakes. Similarly, *B. longirostris* was the dominant branchiopod in most of the study lakes, but its densities were higher in the more eutrophic lakes, causing it to correlate positively with PC1.

Leptodiaptomus minutus was the only taxon that was negatively correlated with PC1 (Table 7). *L. minutus* is a cold-water species more typical of deep lakes (Pennak 1989), and only in Crystal and Big Glen lakes did it comprise more than 1% of the zooplankton individuals. However, this species was also found in Shell Lake, which has a maximum depth of only four meters and posted hypolimnetic temperatures exceeding 25° C in July.

Table 7. Spearman correlation coefficients ($p<0.05$) between PCA axes and lowest identified taxa means.

taxon	PC1	PC2
Leptodiaptomus minutus	-0.63	
Conochilus spp.	0.61	
Euchlanis spp.	0.61	
Orthocyclops modestus	0.62	
Ascomorpha spp.	0.65	
Trichocerca spp.	0.65	
Lecane spp.	0.68	
Skistodiaptomus oregonensis	0.69	
Cyclopoid Copepodids	0.72	
Acroperus harpae	0.72	
Diaphanosoma birgei	0.73	
Mytilina spp.	0.73	
Testudinella spp.	0.76	
Tropocyclops prasinus mexicanus	0.76	
Asplanchna spp.	0.81	
Pompholyx spp.	0.82	
Bosmina longirostris	0.84	
Nauplius	0.85	
Polyarthra spp.	0.85	
Chydorus sphaericus	0.85	
Gastropus spp.	0.86	
Keratella spp.	0.94	
Acanthocyclops brevispinosus		0.61
Synchaeta spp.		0.64
Trichotria spp.		0.67
Eubosmina coregoni		0.70
Daphnia retrocurva		0.87

All significant correlations among zooplankton families were positive along PC1 (Table 8). The strongest correlation was with the family Testudinellidae. This family as a whole correlated better with PC1 than its major constituents (*Pompholyx* sp. and *Testudinella* sp.) Since these two genera fill a similar functional role in the ecosystem, the fluctuations of the entire family may be more ecologically significant than changes in abundance within an individual genus. However, the family aggregation did not always improve correlations. The rotifer family Brachionidae correlated positively with PC1 but not as strongly as the genus

Keratella within that family. This is because the other abundant Brachionidae genus, *Kellicottia*, was common enough in some of the more oligotrophic lakes to degrade the rank correlation of Brachionidae abundance with PC1. Synchaetidae had a lower correlation with PC1 than *Polyarthra* for the same reason. Asplanchnidae, on the other hand, was only represented by one genus (*Asplanchna*), so the correlation remained the same.

Total zooplankton abundance in each of the major zooplankton groups (rotifers, copepods, and branchiopods) correlated positively with PC1 (Table 8). This is likely related to the increase in overall zooplankton abundance with increasing eutrophy among the study lakes. In fact, the correlation between PC1 and overall zooplankton abundance was higher than for any taxon or metric. Richness, evenness, and diversity were negatively correlated with PC1; the most eutrophic and densely populated lakes had a greater tendency to be dominated by relatively few taxa. Although total copepod abundance correlated positively with PC1, there was a strong negative correlation between PC1 and the percentage of copepods in the zooplankton community. Of the zooplankton metrics summarized by Andronikova (1996), only two were significantly correlated with a PC axis: the ratio of branchiopods to copepods (PC1) and the ratio of calanoid copepods to cyclopoid copepods and branchiopods.

Table 8. Spearman correlation coefficients ($p<0.05$) between PCA axes and various zooplankton aggregation groups or metrics. Nbran/Ncop = ratio of brachiopods to copepods; Ncal/Nbran+cycl = ratio of calanoid copepods to cyclopoid copepods + branchiopods

FAMILY	PC1	PC2
Conochilidae	0.61	
Euchlanidae	0.61	
Trichoceridae	0.65	
Sididae	0.73	
Lecanidae	0.73	
Mytilinidae	0.73	
Cyclopidae	0.75	
Chydoridae	0.76	
Daphniidae	0.77	
Asplanchnidae	0.81	
Synchaetidae	0.82	
Bosminidae	0.84	
Brachionidae	0.87	
Testudinellidae	0.88	
MAJOR GROUP		
Branchiopoda	0.90	
Copepoda	0.84	
Rotifera	0.89	
OTHER METRICS		
Margalef Richness (d)	-0.81	
Pielou Evenness (J')	-0.66	
Shannon Diversity (H')	-0.65	
# of individuals (N)	0.95	
% Copepoda	-0.81	
% Rotifera	0.69	
N_{bran}/N_{cop}	0.65	
$N_{cal}/N_{bran+cycl}$		-0.62

DISCUSSION

In general, the lakes in this study do not appear to be under immediate threat from excessive anthropogenic pollution. Chlorophyll *a* concentrations in Loon Lake were similar to those found in 1973 and 1974 (Stockwell and Gannon 1975). Secchi disk, alkalinity, and pH measurements in Big Glen, Loon, North Bar, Narada, Otter, Round, South Bar, School, Shell, and Tucker lakes were comparable to those found in 1991-93 (Boyle and Hoefs 1993), although total phosphorus may have increased somewhat in Loon, Narada, Otter, Round, and Shell lakes. Specific conductance, total phosphorus, and chlorophyll *a* were tested in Loon, Otter, North Bar, Big Glen, Tucker, School, Narada, and Shell lakes in 1994 (Last et al. 1995). Those results were similar to the values seen in this study. Overall, the study lakes do not appear to have experienced any drastic chemical or trophic changes in the last decade.

Comparisons with previous data are difficult due to differences in methods and low sampling frequency in earlier studies. For instance, the assessment of lake trophic states by Boyle and Hoefs (1993) generally found the SLBE lakes to be less eutrophic than did this study. The basis for their trophic state assignment was Carlson's TSI derived from chlorophyll *a* concentrations. However, the chlorophyll *a* values from that 1991-93 study were substantially lower than those seen in 1998, and samples were taken only once per year for three years. This study incorporates many more samples over the entire summer (although only for one year), including chlorophyll *a* peaks in late summer and early autumn. Additionally, chlorophyll *a* analysis methods differed between the two studies. Therefore, it seems likely that the differences in trophic state assignments result from differences in the sampling and analysis methods of the two studies and do not indicate rapid lake eutrophication between 1993 and 1998.

Most of the studied lakes were dominated by small zooplankters such as nauplii and rotifers. This is a characteristic consistent with previous studies of summer zooplankton communities in productive lakes (Gannon and Stemberger 1978, Bays and Crisman 1983, Canfield and Jones 1996). Predation by zooplanktivorous fish may contribute to the dominance of small zooplankton forms (Carpenter et al. 1985, Stemberger and Lazorchak 1994), and current, quantitative data on the fish community structure of the SLBE lakes would likely improve our ability to explain variation among their zooplankton communities.

The pattern of seasonal change in the limnetic zone of temperate lakes generally follows a particular series of events. This includes spring algal bloom, followed by spring increases in zooplankton abundance. The rise in zooplankton abundance starts with a pulse of copepods and rotifers and is followed later by the development of cladoceran populations that typically result in a depression of phytoplankton (Brandl et al. 1989). However, the study lakes did not adhere strictly to this temporal pattern. In fact, the three lakes (School, Tucker, Narada) that consistently cluster together and appear to be the most eutrophic show different patterns in abundances of major zooplankton groups throughout the study. Although most of the SLBE lakes appear to be mesotrophic to eutrophic, other factors such as water temperature, physico-chemical parameters, lake morphology, competition, and predation, are all part of a complex of variables influencing the community response and determining which specific taxa are ultimately successful. Certainly predation, both invertebrate and vertebrate, must be considered as a strong factor influencing the characteristics of the zooplankton community.

Typically, in a limnetic zooplankton community controlled by invertebrate predators, one would find higher densities of larger zooplankton, as smaller species are selected for consumption (Black and Hairston 1988, Christoffersen 1990). Some of the most important

invertebrate predators were found during this study; *Chaoborus* and *Leptodora* in six of the lakes, and *Asplanchna* and *Mesocyclops* in all lakes. However, they were only fairly abundant in School Lake and only for a limited time during the study period. These invertebrate predators are somewhat large, and although they may employ certain strategies (transparency and limited motion) to appear less noticeable, they are susceptible to predation from fish (Christoffersen 1990). Planktivorous fish typically crop off the larger zooplankton leaving smaller species as the dominant taxa, although predation must be intensive to have this effect (Stemberger 1990, Mazumder et al. 1992, Taylor and Carter 1997). Fish have been found in all of the study lakes (Kelly and Price 1979), and whether in larval form or as adults (cyprinids and alewives), there were potential zooplankton predators. Bosminids and rotifers were the most abundant zooplankton in the majority of study lakes. This may be because the larger zooplankton taxa were preferentially consumed by zooplanktivorous fish.

Smaller zooplankton species may also be better adapted to living in eutrophic lakes due to enhanced availability of smaller food particles (Gannon 1972). However, this only holds true when the food particles are suitable for consumption. Much of the productivity in eutrophic lakes may consist of certain filamentous blue-green algae that are not a preferred food for cladocerans or rotifers based on ease of handling or taste (Kerfoot and DeAngelis 1989). Both groups feed more efficiently on diatoms, detritus, chlorophytes, bacteria, protozoans, and other rotifers (Stemberger 1979, McNaught et al. 1980, Balcer et al. 1984). Size of zooplankton has been suggested as a robust indicator of energy transfer efficiency of an ecosystem; ecosystems dominated by small zooplankton may transfer energy inefficiently from producers to zooplankton and fish (Mazumder et al. 1992). Energy transfer from producers to fish is most efficient when large herbivores are the major consumers of primary producers and energy moves

through fewer trophic levels. The more eutrophic SLBE lakes dominated by rotifers and small cladocerans may be highly productive, but energy transfer through the food web to the top consumers is inefficient.

Rotifers play a major role in energy transfer in lakes of varying trophic status (Makarewicz and Likens 1979). Rotifers greatly dominated zooplankton densities in the more eutrophic study lakes, but their abundance may have been much greater than it appeared. Mazumder et al. (1992) determined that tow nets using 64-µm screens collected substantially fewer rotifers than those with 30-µm screens. Since this study used 80-µm screens, the true abundance of rotifers may have been greatly underestimated, which in turn would greatly underestimate their contribution to the biomass of these lakes and their importance to the food web. Soft-bodied (non-loricate) forms would be more likely to pass through the screen; the vast majority of those retained in this study were loricate or semi-loricate. Despite the probable loss of some forms, over 50 genera were identified. Stemberger (1990) found 75 planktonic species in his more comprehensive study of northern Michigan inland lakes. Both studies found similar species to be dominant in the pelagic zone. It may be possible that in the relatively shallow SLBE lakes short tow duration reduced the rate of rotifer loss compared to Mazumder's (1992) study of Lake Ontario.

The environmental factor with the strongest relationship to differences among zooplankton communities in the SLBE lakes was lake trophic status. Chlorophyll *a* concentration or Secchi disk depth was consistently the most influential single environmental variable in Bio-Env correlations, regardless of how the zooplankton community data were aggregated or transformed. This study included only eleven lakes from a relatively small geographic area. All of the lakes were of similar origin and generally had similar water

chemistry characteristics. As a result, potentially important parameters such as pH may not have been represented in a range wide enough to reveal their influence. However, Stemberger and Lazorchak (1994) found that lake trophic state had the greatest explanatory power in examinations of zooplankton body size, taxonomic groups, and feeding guilds in 19 New England lakes from a much larger geographic area.

This study showed a positive relationship between lake trophic status and zooplankton abundance. Such a relationship has been observed in a number of previous studies as well (Bays and Crisman 1983, Pace 1986, Canfield and Jones 1996, Attayde et al. 1998). Attayde et al. (1998) found that total zooplankton density significantly discriminated between mesotrophic and eutrophic study sites in a tropical lagoon undergoing cultural eutrophication. Similarly, Bays and Crisman (1983) found positive relationships between zooplankton biomass and increased eutrophy in Florida lakes. Zooplankton abundance and biomass in mid-western lakes were also positively correlated with measurements of algal chlorophyll, and correlations increased when compared to data from Canfield and Jones (1996) that included a broader spectrum of lakes. Pace (1986) found a positive relationship between lake trophy and zooplankton biomass in Quebec lakes, although there appeared to be no relationship to the size structure of the zooplankton community.

This study found substantial similarity among analyses of the zooplankton community based on overall abundance and a range of other levels of taxonomic, functional, and size classifications. Analysis of zooplankton data by means other than species-level identification is attractive for a number of reasons. The first is that gross taxonomic or size-based classifications are much simpler and less time-consuming to perform, allowing managers to devote more resources to frequent and widespread monitoring. The second, as suggested by Frost et al.

(1992), is that an intermediate level of zooplankton aggregation may decrease natural variability and increase sensitivity. Competition may cause ecologically similar species to exclude one another without any significant difference in the overall state of the lake ecosystem. Some intermediate level of aggregation has the potential to increase sensitivity to changes in water quality by removing the community differences introduced by compensatory variation, thereby revealing the more significant trends in lake status. However, the loss of information produced by excessive simplification may also be severe enough to degrade sensitivity.

Studies evaluating the sensitivity of various zooplankton aggregations to limnological variables have provided mixed results (Sprules and Holtby 1979, Sprules 1984, Stemberger and Lazorchak 1994). Zooplankton were usually characterized based on one or a combination of these three criteria: taxonomy, ecology, and size. Sprules and Holtby (1979) found that the amount of variation in community structure that could be attributed to limnological variables was greatest when zooplankton were characterized ecologically, followed by size and taxonomic characterizations. However, later work by Sprules (1984) found that zooplankton size designations had the strongest relationship to limnological variables, while functional classifications performed least well (taxonomic aggregations were intermediate). Stemberger and Lazorchak (1994) found that although aggregate variables and species analyses gave similar results, species data gave a more refined separation of lake types.

There are a number of difficulties in trying to determine which method of zooplankton classification or aggregation is most appropriate for lake classification or long-term monitoring. First, the suite of environmental variables varies from study to study. The strength of the relationship between these variables and the zooplankton data may be very significantly affected by the variables included in the analysis. In this study and others (Sprules 1977, Sprules 1984,

Tessier and Horowitz 1991, Stemberger and Lazorchak 1994), water chemistry and trophic state data were supplemented with information on lake size and depth. One study included data on the fish community (Stemberger and Lazorchak 1994), thereby incorporating a more complete measure of the top-down forces acting on the zooplankton community. Determination of the ideal zooplankton classification method (or even the general usefulness of zooplankton as bioindicators) may be strongly dependent upon which of an infinite number of independent variables are measured in a particular study.

Another problem in determining the optimal zooplankton classification method is that there is a limitless number of ways to group and classify the zooplankton community constituents based on taxonomy, morphology, feeding ecology, size, or any combination of these characteristics. To determine which classification most accurately represents environmentally relevant changes in the zooplankton community, one would need to test every possible aggregation configuration against the environmental variables of interest.

Added to these difficulties are the wide range of parametric and non-parametric univariate and multivariate statistical techniques employed in exploring these problems. These techniques give researchers a great deal of flexibility and power to explore relationships, but they also make it very difficult to compare two studies that employ different techniques and arrive at contrasting conclusions. Therefore, only intense and large-scale research and a great deal of professional consensus on analysis methods will allow for the development of generally applicable zooplankton metrics for lake monitoring.

That said, this study offers some useful information for local monitoring decisions at SLBE. Multivariate analysis of zooplankton data at the lowest level of taxonomic identification appeared to be the most sensitive indicator for classification of lake trophic state among the

study lakes. Further, it has been shown that multivariate analysis of zooplankton community data can also be successfully used to detect the effects of contaminants such as pesticides (Kreutzweiser and Faber 1999). Finally, detailed taxonomic identification of zooplankton samples could allow early detection of invasion by exotic zooplankton species.

Although analysis at the lowest level of taxonomic aggregation appeared to give the strongest relationship to environmental differences among lakes, a comparably strong correlation was seen between trophic status indicators and overall zooplankton abundance. This suggests that the additional time and expense required for detailed taxonomic identification and analysis may be unwarranted if zooplankton are going to be employed for monitoring at SLBE. The large amount of temporal variation in the zooplankton community, however, suggests that the intensive bi-weekly sampling of lakes over the study period was warranted, although replication of samples may be less crucial.

One possible monitoring scheme that would take these considerations into account could incorporate relatively frequent sampling during the open-water period, but little or no identification of zooplankton individuals. Total zooplankton abundance could be used to supplement other data on trophic status. Samples could be preserved and maintained so that if future funding or interest allow, further analysis might be conducted. In addition, it might be useful to scan a certain number of samples from each lake to track the spread of exotics if there are known invasive species of concern to the park.

Even if a relatively low level of effort were given to zooplankton monitoring, the fact remains that in this study, zooplankton were consistently most sensitive as indicators of lake trophic status. Trophic status could be much more quickly, cheaply, and reliably tracked by simple Secchi disk readings or, when marl precipitation is a concern, chlorophyll *a*

concentrations. For this reason, managers may determine that the time and effort required for collection and counting of zooplankton individuals would not be worth the information gained. Certainly, for simple trophic status determination, this may be the case.

What we have presented here are possibilities for using zooplankton community data to identify differences among lakes. Independent samples of other lakes in the region, along with samples of these lakes from other years, are needed to discern the reliability of the relationships we have laid out. This is only a preliminary attempt to identify promising zooplankton metrics for monitoring at SLBE. The most critical information missing from the scope of this study is comparably rigorous zooplankton data from a number of years. We have already seen that the zooplankton community may fluctuate a great deal in abundance and composition over two-week intervals. It stands to reason that natural variation from year to year may be comparably large. Without data on the magnitude and character of this natural variation, we have no means to assess the potential for using zooplankton data to monitor changes within individual lakes. It is also possible that multi-year data within individual lakes would reveal zooplankton sensitivities to variables that were not emphasized by the multi-lake analyses.

In conclusion, we saw strong correlations between differences in lake trophic status and zooplankton community differences as measured by a number of different metrics and at a number of different levels of aggregation. There was some suggestion that the zooplankton communities in this study were sensitive to other environmental variables, but these sensitivities were largely overwhelmed by differences in trophic status. Temporal variation within the study period was substantial, and any attempt to assess lakes using zooplankton community data should incorporate frequent sampling during the period of interest. Zooplankton appear to be a useful indicator of trophic status for the inland lakes of Sleeping Bear Dunes, but monitoring

decisions will naturally have to incorporate a thorough consideration of the costs and benefits of zooplankton sampling and analysis.

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Appendix 1. Equations for statistical analyses.

$$H' = -\sum_{i=1}^{S} p_i \log p_i$$ (1) Shannon diversity

$$J' = \frac{H'}{H'_{\max}}$$ (2) Pielou evenness

$$d = (S-1)/\log(N)$$ (3) Margalef richness

$$d_{jk} = \sqrt{\sum_{i=1}^{p} (y_{ij} - y_{ik})^2}$$ (4) Euclidean distance

$$S_{jk} = 100\left\{1 - \frac{\sum_{i=1}^{p} |y_{ij} - y_{ik}|}{\sum_{i=1}^{p} (y_{ij} + y_{ik})}\right\}$$ (5) Bray-Curtis similarity

$$\rho_s = 1 - \frac{6}{N(N^2-1)} \sum_{i=1}^{N} (r_i - s_i)^2$$ (6) Spearman coefficient for BIOENV procedure