Top-down Trophic Cascades in Three Meromictic Lakes

Tanner J. Kraft, Caitlin T. Newman, Michael A. Smith, Bill J. Spohr
Ecology 3807, Itasca Biological Station, University of Minnesota

Abstract

Projections of tropic cascades from a top-down model suggest that biotic characteristics of a lake can be predicted by the presence of planktivorous fish. From the same perspective, the presence of planktivorous fish can theoretically be predicted based off of the sampled biotic factors. Under such theory, the presence of planktivorous fish contributes to low zooplankton abundances, increased zooplankton predator-avoidance techniques, and subsequent growth increases of algae. Lakes without planktivorous fish would theoretically experience zooplankton population booms and subsequent decreased algae growth. These assumptions were used to describe the tropic interactions of Arco, Deming, and Josephine Lakes; three relatively similar meromictic lakes differing primarily from their absence or presence of planktivorous fish. Due to the presence of several other physical, chemical, and environmental factors that were not sampled, these assumptions did not adequately predict the relative abundances of zooplankton and algae in a lake based solely on the fish status. However, the theory did successfully predict the depth preferences of zooplankton based on the presence or absence of fish.

Introduction

Trophic cascades play a major role in the ecological composition of lakes. One trophic cascade model predicts that the presence or absence of piscivorous fishes will affect the presence of planktivorous fishes, zooplankton size and abundance, algal biomass, and subsequent water clarity **(Fig. 1)** (Carpenter et al., 1987). The trophic nature of lakes also affects animal behavior, such as the distribution patterns of zooplankton as a predator avoidance technique (Loose and Dawidowicz, 1994). This measurable pattern of distribution can be attributed in part to fish kairomones exuded by predators (Loose and Dawidowicz, 1994). Zooplankton populations in lakes with planktivorous fishes demonstrate strong migration patterns of surface avoidance during the day and upward migration at night. Zooplankton populations in lakes without planktivorous fishes are more likely to stay in surface waters throughout the day, where food and ambient temperatures are more beneficial to overall fitness (Loose and Dawidowicz, 1994).

Lake stratification plays a role in animal population depth distribution. In heavily stratified meromictic lakes, the bottom layer remains relatively undisturbed year-round and does not mix with the layer above. This layer, called the monimolimnion, supports relatively few species in its oxygen-poor waters (Likens, 2008). The upper stratification level, called the mixolimnion, mixes at least once a year and supports a variety of life. The division between the monimolimnion and the mixolimnion is called the chemocline, which delineates the density difference between the dense, saline deep waters and the less dense upper surface (Likens, 2008). Sharp rises in conductivity mark the transition between these levels. Often, basins sheltered by steep slopes lead to conditions of meromixis, as is the case in the three lakes in this study.

This study hopes to find comparable data on the trophic communities in Arco and Deming Lakes. It has been documented that Arco Lake contains no piscivorous or planktivorous fishes (Reese and Brient, 1990), and prior observation by numerous researchers has confirmed the presence of fishes in Deming Lake, though it is unclear if these fishes are piscivores or planktivores. The fish status of Arco and Deming Lakes will be used in conjunction with collected data on all three trophic communities to infer the presence or absence of planktivorous fishes in Josephine Lake. In Arco Lake, we hypothesize that the absence of planktivorous fishes will correlate with large populations of zooplankton, low algal biomass, and high water transparency. In Deming Lake, we hypothesize that the presence of planktivorous fishes will correlate with small populations of zooplankton, sizeable algal biomass, and low water transparency.

Methods

Study Sites

Josephine, Arco, and Deming Lakes are single-basin, kettle lakes located within Itasca State Park (Clearwater County, MN). All three lakes are meromictic and are surrounded by steep moraine slopes that shelter their basins from wind, promoting strong summer stratification (Landon and Stasiak, 1983). Arco Lake, which is known to lack fishes, has a maximum depth of 10.5 m and is the shallowest of the three sample lakes. Lake Deming, which is known to have fish occupants, has a maximum depth of 16 m and is the deepest of the three lakes. Lake Josephine, whose fish status is unknown, has a maximum depth of 12 m.

Temperature, oxygen, and conductivity sampling & Determination of stratification layers

At each lake, the entire water column was sampled at one-meter increments for temperature (C), % oxygen saturation and mg/L, and conductivity levels (μS) using a YSI model 85 temperature, oxygen, conductivity meter. Based on this data the mixolimnion and monimolimnion stratification depths were determined. To divide the mixolimnion into the epilimnion, metalimnion, and hypolimnion layers, temperature was the examined variable. The saline monimolimnion was determined from the conductivity concentrations. These stratification levels helped to determine where zooplankton and water samples were obtained. All sampling occurred on 16 June 2008 for Arco and Josephine Lakes and on 22 June 2008 for Deming Lake.

Zooplankton sampling & analysis

Zooplankton samples were obtained using a closing plankton net (27 cm diameter, 130 μm mesh size). Depths for sampling were determined by prior assessment of lake stratification; on each lake, samples were obtained from within the epilimnion, metalimnion, hypolimnion, and monimolimnion levels. Duplicate samples were taken at each sample site, so that eight zooplankton samples total were obtained from each lake. Samples were preserved in the field with ethanol and refrigerated until analysis.

To obtain community composition and zooplankton densities per liter of lake water, each zooplankton sample was diluted to between 100-150 mL with tap water. For each sample, animals in three 1 mL subsamples were counted and identified under a compound microscope in Sedgewick-Rafter cells. Zooplankton were taxonomically identified as

Daphnia, Calanoid copepods, Cyclopoid copepods, nauplii, *Bosmina, Diaphanosoma*, or as other animals, *Chaoborus* or Rotifera. *Chaoborus* were removed from the larger samples and counted prior to subsampling. Rotifera individuals were grouped into a larger category 'Rotifera', unless a large abundance of species prompted further identification. *Kellicottia* and *Asplancha* individuals were the only Rotifers abundant enough to require new categories. Total zooplankton counts were averaged across the three subsamples and then across duplicate samples for each limnion.

Algae sampling & analysis

Phytoplankton samples for chlorophyll *a* concentrations in each lake were obtained with a Van Dorn sampler pulled at the epilimnion, metalimnion, and hypolimnion levels. Each pull yielded two bottles of lake water, which were analyzed separately for chlorophyll *a* concentrations. Samples were filtered through glass fiber filters (47 mm) and chlorophyll *a* pigments were removed using ethanol. Filters were frozen for one day before analysis. Pigment concentration was obtained from filters using a spectrophometer according to the methods of O. Hold-Hansen and B. Reimann (1978). Additional information on algae abundance was obtained using a Secchi disc to determine water clarity depth.

Fish

Determination of fish presence in Deming Lake was based on observations at the time of sampling as well as observations in prior years. Arco Lake has been documented to lack fish (Reese and Brient, 1990) and prior research and observation supports this documentation (Hembre, pers. com.). No known documentation was available detailing the presence or absence of fish in Josephine Lake.

Results

Oxygen concentrations, temperature, and conductivity

To determine the stratification of each lake, temperature changes, oxygen gradients, and conductivity spikes were measured and analyzed. The epilimnion in Arco was determined to be 0-2 m, metalimnion 2-6.5 m, hypolimnion 6.5-8 m, and monimolimnion 8-10 m. In Deming, the epilimnion was from 0-2 m, metalimnion 2-7 m, hypolimnion 7-12 m, and monimolimnion 13-16 m. In Josephine, the epilimnion was 1-3 m, metalimnion 3-7 m, hypolimnion 7-10 m, and monimolimnion 10-12 m.

Oxygen concentrations in Arco Lake fell from 12.57 mg/L at 135% in the epilimnion to 3.57 g/ml and 28% in the monimolimnion. **(Fig. 2)** Surface temperatures were 18.6 ºC and dropped to 4.7º C in the monimolimnion. Conductivity at the epilimnion was 93 μS and gradually and consistently rose to 225 μS in the monimolimnion. Surface conductivity in Arco measured higher than that of any other lake. Oxygen concentrations in Josephine Lake fell from 9.2 mg/L at 97.5% in the epilimnion to 2.07 g/ml at 16.4% in the monimolimnion. (**Fig. 2**) Temperatures in the epilimnion were at 18 ºC and fell to 5.3ºC in the monimolimnion. Conductivity at the epilimnion was 68.7 μS and rose to 101.6 μS in the monimolimnion. Oxygen concentrations in Deming Lake fell from 13.61 mg/L at 93.6% in the epilimnion to 2.39 g/ml at 18.5% in the monimolimnion (**Fig. 2).** Temperatures in the epilimnion were measured at 22.6ºC and fell to 4.6ºC in the monimolimnion. Conductivity at the epilimnion was measured at 52.5 μS and increased to 486.9 μS in the monimolimnion. Compared to Arco and Josephine Lakes, Deming had high saline concentrations in the monimolimnion, with a difference of 261.9 μS between Arco and Deming and 385.3 μS between Josephine and Deming.

Zooplankton community composition

Between the three sampled lakes, zooplankton community composition and abundances at respective layers varied. Arco Lake contained individuals of *Daphnia,* Calanoid and Cyclopoid copepods, nauplii, *Chaoborus*, and the rotifer *Kellicottia*. The epilimion contained higher numbers of most animals than any deeper levels, excluding *Chaoborus*, which was found only in the metalimnion, and *Kellicottia*, which was found in higher average numbers in the metalimnion (1.65 #/L) than the epilimnion (1.24 #/L) (**Fig. 3).** The monimolimnion contained only Cyclopoids (2.48 #/L). Josephine Lake also contained individuals of *Daphnia*, Calanoid and Cyclopoid copepods, nauplii, *Chaoborus*, and the rotifer *Kellicottia*. An additional 'other' category was created for Josephine Lake to include individuals of *Bosmina* and *Diaphanosoma*, which were found in small quantities in the hypolimnion, and *Asplanchna*, which were found in small quantities in the metalimnion. Excluding *Chaoborus*, which was found only in the epilimnion (0.8 #/L), and nauplii, which were not found in the hypolimnion, all animals were found in every stratification level. **(Fig. 4)** All other species were found in highest numbers in the monimolimnion. *Kellicottia* rotifers make up the largest portion of the zooplankton population in every stratification layer. Deming Lake also contained individuals of *Daphnia*, Calanoid and Cyclopoid copepods, nauplii, and the rotifer

Kellicottia (**Fig. 5***)*. Unlike Arco and Josephine Lakes, *Chaoborus* was not present in the lake. Cyclopoid copepods and nauplii were distributed throughout the water column at various densities in each layer, while *Daphnia* were found only in the epilimion and metalimnion, and Calanoids in the epilimnion, metalimnion, and hypolimnion. *Kellicottia* was detected in the metalimnion (6.6 #/L), hypolimnion (5 #/L), and the monimolimnion (1.65 #/L).

Fish

During the time of sampling, visual observation by researchers confirmed the existence of fish in both Deming Lake and Josephine Lake. Planktivores (minnows) were present in Deming Lake, but presence of piscivores was not determined. Rock bass, which are both planktivores and piscivores, were observed in Josephine Lake. Visual observations could not positively confirm the status of fish in Arco Lake, though no fish were observed.

Algal concentrations

Phytoplankton concentrations from each lake were obtained from the epilimnion, metalimnion, and hypolimnion levels of the mixolimnion. Chlorophyll *a* concentrations in each lake were highest in the hypolimnions of Arco Lake (55.13 μg/L) and Josephine Lake (89.47 μg/L) and highest in the metalimnion of Deming Lake (27.61 μg/L). Algal concentrations in the epilimnions were 12.37 μg/L in Arco Lake, 1.38 μg/L in Josephine Lake, and 4.29 μg/L in Deming lake (**Fig. 6**).

Algal concentrations correlate with water transparency as measured by Secchi depths. In Arco Lake, Secchi depth measured 2.8 m, which fell in the determined transition between the epilimnion and metalimnion depths. In Josephine Lake, Secchi depth measured 5.0 m, which was within the metalimnion. Secchi depth in Deming Lake was 1.8 m, which was within the epilimnion.

Discussion

Oxygen concentrations, temperature, and conductivity

Oxygen, temperature, and conductivity measurements were used to determine the stratification of the lakes. We did not expect significant correlations between this data and our hypothesis. However, some interesting results are worth noting. Super-saturation of oxygen in the epilimnion of Arco and Josephine Lakes, and saturation of Deming Lake, was peculiar and surprising. The reason for this surplus of oxygen is hard to determine, but could be due to a high photosynthesis to respiration ratio by phytoplankton (Hembre, pers. com.).

Algal Concentrations

The data we collected on chlorophyll *a* concentrations was quite interesting. Chlorophyll *a* levels in each lake corresponded to total zooplankton numbers only in the epilimnion, where Arco Lake had the chlorophyll *a* concentrations and the lowest number of zooplankton. Hypolimnion results were drastically higher than expected, likely due to dead biomass that absorbs the same wavelength of light from the spectrophotometer (Hembre, pers. com.). The chlorophyll *a* concentrations in Josephine Lake were quite low and correlated to high water transparency (5m). This may be due to consumption of algae by zooplankton, but this trend was not observed in the other two sample lakes. No apparent trend exists within our sample sites, suggesting that algae abundance is not directly linked to zooplankton abundance, though phytoplanktivory does play a notable role (Hembre, pers. com.).

Zooplankton Abundance and Distribution

Only one of our sampled lakes matched our expected results of zooplankton abundance. In Deming Lake, we found low densities of zooplankton, which contributed to its murky nature. In Arco Lake and Josephine Lake, zooplankton abundance did not match the expected results. When considering trophic cascade alone, Arco exhibits far too few zooplankton to expect a fishless lake when past zooplankton booms have been recorded. This phenomenon has been highly variable since its first exploration in the 1970s, which showed quite large populations of *Daphnia* (Landon and Stasiak, 1973). It is probable that the zooplankton carrying capacity is limited not by biotic factors, but by abiotic factors. For example, Arco Lake's phosphate supply is almost entirely locked and unavailable in the monimolimnion, due to the lack of mixing at lower depths (Loeffler, 1979). Also, Arco's small size, and consequent winter fish kills, may be a contributing factor to its fishless nature (Reese and Brient, 1990).

Zooplankton in Josephine Lake were distributed at greater depths. This is likely due to Josephine's increased water clarity and the subsequent need for zooplankton to remain at lower depths to avoid predation. Zooplankton were sampled all the way to the monimolimnion and were unseen in the two other lakes. This is feasible due to Josephine's very low saline concentrations, even in the monimolimnion. Deming Lake's zooplankton population was also found in deeper water suggesting predator avoidance. However, due to Deming's murky waters, there is little need for zooplankton to be at excessively low depths to avoid predation. Arco, being the only lake with no fish, showed no signs of zooplankton predator avoidance. The vast majority of samples in this lake were in the epilimnion and metalimnion, with almost nonexistent numbers in the hypolimnion. The effect of fish presence on zooplankton depth distribution seems to be strong. Water clarity also seems to play an important role on depth distribution of zooplankton when fish are present.

Summary

Our results were unexpected. This study in many ways provided more questions than answers. Further study of these meromictic lakes is necessary. Particularly, the reasons for Arco's variability of zooplankton should be firmly established. One possible hypothesis is that the lake's chemical properties are not particularly conducive to the growth of any zooplankton (Brient and Reese, 1990) Perhaps the dormancy of zooplankton egg capsules caused by the highly saline monimolimnion inhibit population growth and relegate the fewer marginally planted eggs as the main progenitors of the lake

(Hembre, pers. com.). Data study of the differing chemical qualities of each lake, as well as progenitor population demography and success rates, should be uncovered.

Acknowledgements

We would like to thank Dr. Hembre for his insights and assistance, as well as patience. A special thanks to Mark Dube' for so many things, and the IBS 2008 ecology class for their assistance in data gathering and analysis.

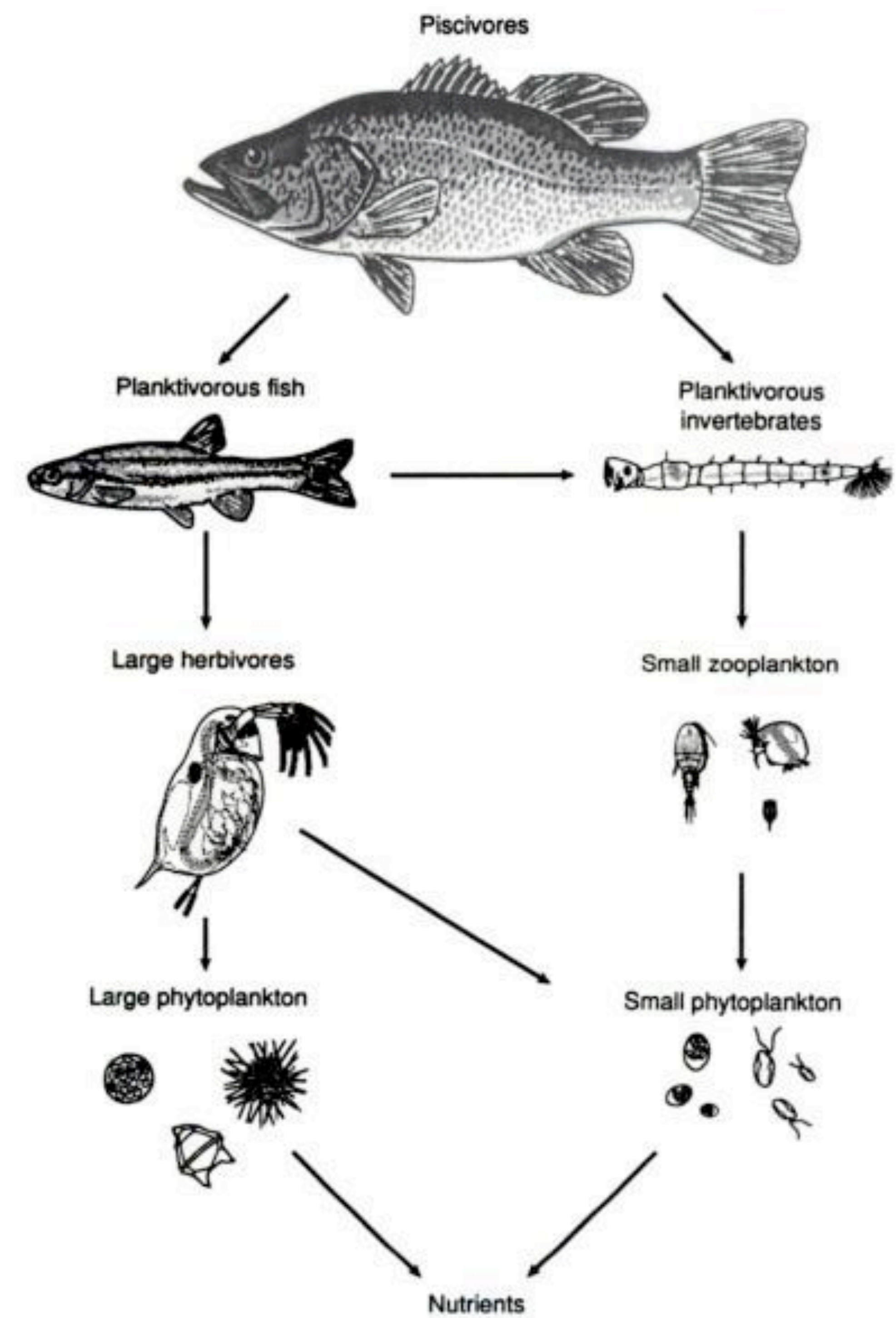

Fig 1: Basic interactions among commonly found freshwater communities. Major nutrient components are inorganic Nitrogen (N) and Phosphorus (P). Inputs from our study lakes include runoff from land and groundwater. (Kitchel, Carpenter)

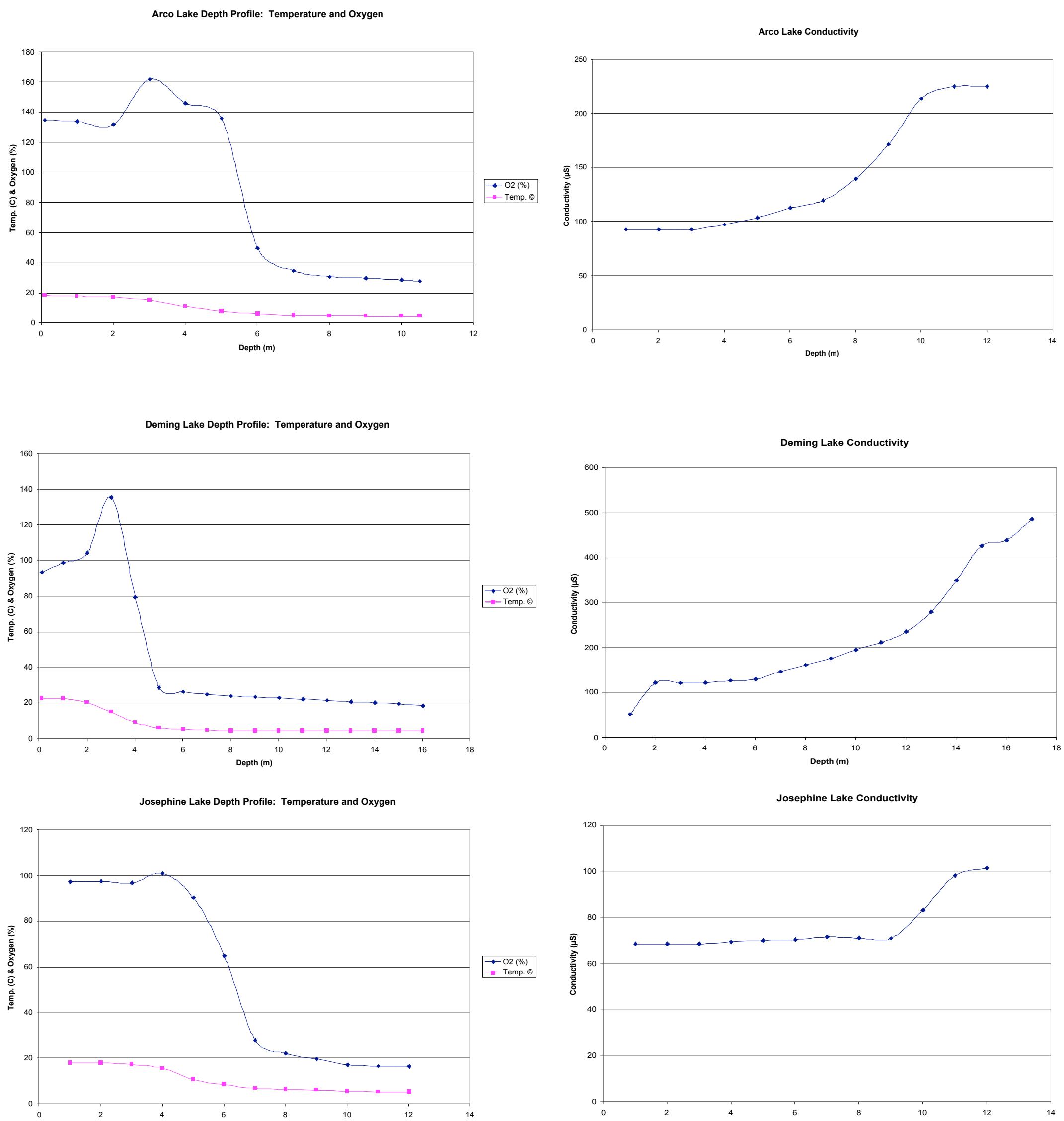

Figure 2: Temperature (C), oxygen (%), and conductivity (µS) for Arco, Deming, and Josephine Lakes.

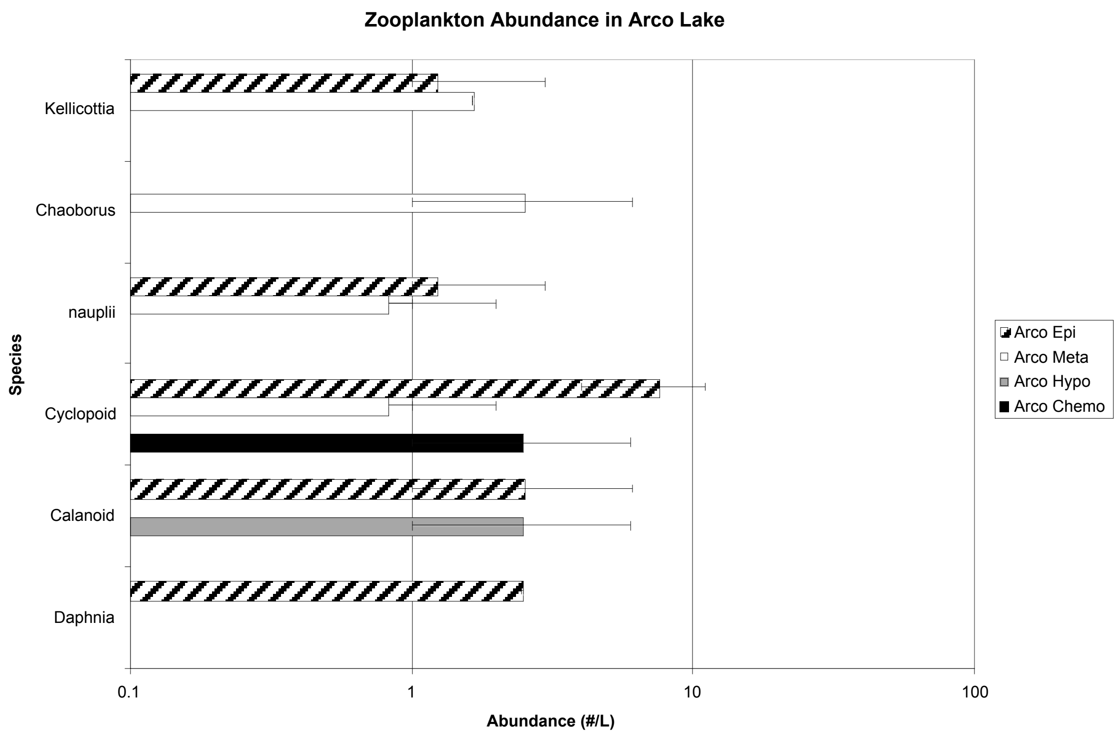

Figure 3: Zooplankton abundance for Arco Lake. Abundance was measured in of organisms per liter of lake water. Standard deviation for *Daphnia* (epilimnion) equaled zero.

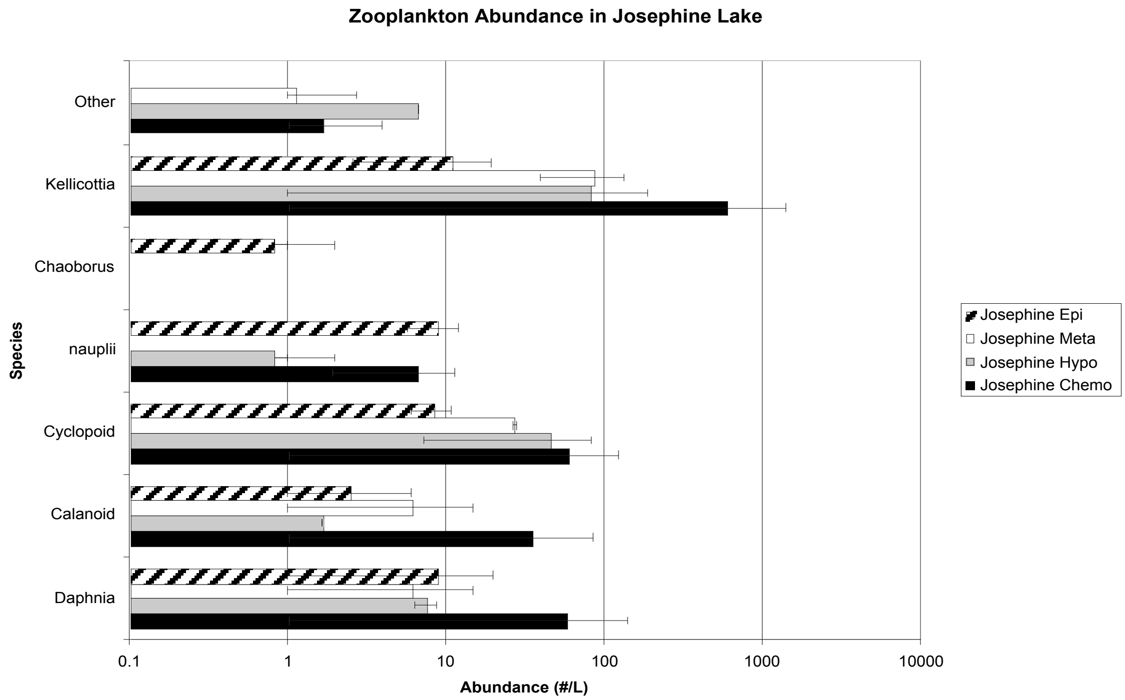

Figure 4: Zooplankton abundance for Josephine Lake (#/L). Standard deviation for Calanoid (hypolimnion) and 'other' (hypolimnion) equaled zero. The 'other' category includes species *Bosmina*, *Diaphanosoma* , and *Asplanchna*, which were present in small, but notable, abundances.

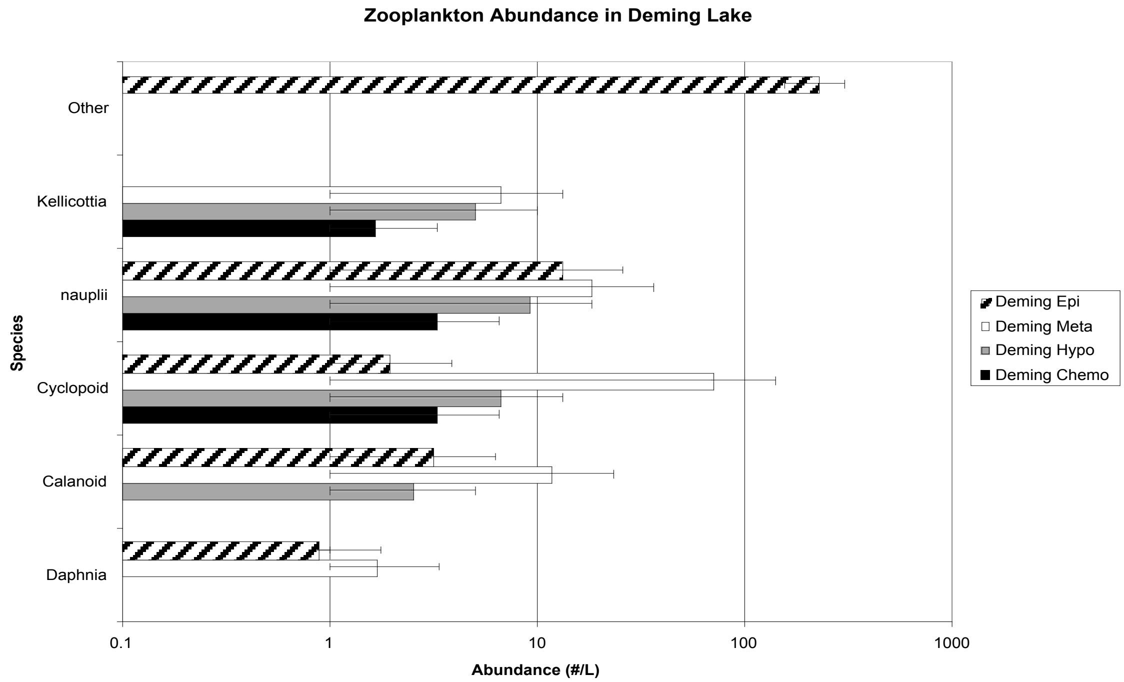

Figure 5: Deming zooplankton abundance measured in number per liter of lake water. The other category (epilimnion) included an unidentified algae that was included because of its high sample size.

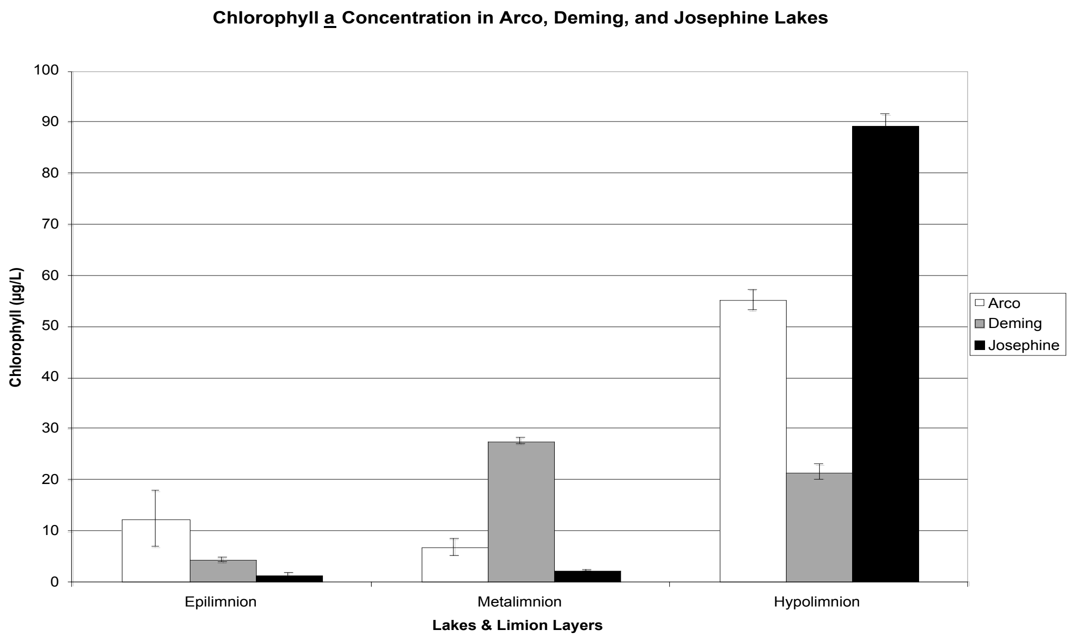

Figure 6: Chlorophyll *a* concentrations for Arco, Deming, and Josephine Lakes. Replicate samples were taken from the epilimnion, metalimnion, and hypolimnion for each lake.

Works Cited

Brient, H. L., and E. O. Reese III. "It's Still There! Arco Lake: a Limnological Study of the Disappearance of Daphnia Pulex." (1990).

Carpenter, S. R., J. F. Kitchell, J. R. Hodgson, P. A. Cochran, J. J. Elser, M. M. Elser, D. M. Lodge, D. Kretchmer, X. He, and C. N. Von Ende. "Regulation of Lake Primary Productivity by Food Web Structure." Ecology 68 (1987): 1863-1876. JSTOR. JSTOR. University of MN. 27 June 2008.

Hembre, L.K. "Super-saturation of Oxygen." Biology 3807. University of Minnesota. Itasca State Park, 25 June 2008.

Hembre, L. K., and R. O. Megard. "Timing of Predation by Rainbow Trout Controls Daphnia Demography and the Trophic Status of a Minnesota Lake." Freshwater Biology 50 (2005): 1064-1080.

Kitchel, J.F., Carpenter, S.R. “Cascading trophic interactions”. The Trophic Cascade in Lakes.
Cambridge study of ecology. (2000) 14.

Likens, Gene E. "Meromictic Lake." AccessScience. JSTOR. JSTOR. University of MN. <http://www.accessscience.com.floyd.lib.umn.edu, DOI 10.1036/1097-8542.416400>.

Loeffler, Elaine. “A Limnological Survey of Arco Lake.” (1979) IBS 1288

Loose, Carsten J., and Piotr Dawiowicz. "Trade-Offs in Diel Vertical Migration by Zooplankton: the Costs of Predator Avoidance." Ecology 75 (1994): 2255-2263. JSTOR. JSTOR. University of MN.