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DISCERNING DIFFERENCES BETWEEN ZOOPLANKTON COMMUNITIES BASED ON LAKE TROPHIC STATUS

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**DISCERNING DIFFERENCES BETWEEN ZOOPLANKTON COMMUNITIES BASED
ON LAKE TROPHIC STATUS**

BY

**Jonathan Dufresne
B.S. University of New Hampshire, 2009**

THESIS

**Submitted to the University of New Hampshire
in Partial Fulfillment of
the Requirements for the Degree of**

**Master of Science
in
Zoology**

September, 2017

This thesis has been examined and approved in partial fulfillment of the requirements for the degree of Masters of Science in Zoology by:

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ABSTRACT

DISCERNING DIFFERENCES BETWEEN ZOOPLANKTON COMMUNITIES BASED ON LAKE TROPHIC STATUS

By

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University of New Hampshire, September, 2017

In 2007 the United States Environmental Protection Agency sampled 1157 lakes to determine the state of the nation's lakes. The data they collected provided a unique opportunity to study the effects of eutrophication on zooplankton community structure across a range of lakes from a large geographical area. Using this data set two main questions were assessed: 1) what level of taxonomic identification is necessary to detect differences in zooplankton community composition as it relates to patterns in water quality and 2) in a dataset that has extensive spatial and temporal variability, how does one account for regional differences in zooplankton seasonal succession?

Thirty lakes in the northeast United States were analyzed using non-metric multidimensional scaling (NMDS), multi-response permutation procedures (MRPP) and indicator species analysis (ISA) to assess zooplankton community composition with taxonomic resolution evaluated to species, genus and family. Detectable patterns were observed across all levels of taxonomic resolution with the NMDS and MRPP. Using ISA, the highest level of taxonomic resolution (species) resulted in the most consistent indicators of lake trophic status. Identifications to genus gave comparable results for small cladocerans but not for copepods.

To assess whether zooplankton seasonal succession has to be taken into account when relating zooplankton communities to water quality, three groups of 48 lakes were selected from across the country. Two groups of lakes were selected at random and the third group was selected using a model that predicted the date of *Daphnia* maximum abundance based on latitude. The NMDS using the model resulted in the best ordination with an R^2 of 0.94 and stress value of 10.49. Though these lakes had a detectable pattern in the zooplankton community, explaining the pattern based solely on lake trophic status may have been obscured by the state of seasonal succession indicating strong pressure by fish predation and or food limitation.

INTRODUCTION

Both natural and anthropogenic factors can influence how a lake functions physically and chemically and can exert strong pressures on the biological communities. One stressor in particular, human induced eutrophication, can cause biodiversity loss (Dudgeon et al. 2006), taste and odor issues (Smith et al. 2002), result in cyanobacteria blooms that can be toxic (Codd 2000; Giani et al. 2005; Beaver et al. 2014) and impact ecosystems services (Postel and Carpenter 1997; Zedler and Kercher 2005). The overall effects of these stressors are estimated to cost the United States \$2.2 billion annually (Dodds et al. 2009). To address cultural eutrophication and other anthropogenic pressures on lakes it is necessary to understand how integral components of lake ecosystems function and respond to stressors. In 2007 the United States Environmental Protection Agency (USEPA) completed its first survey to determine the condition of the nation's lakes by sampling 1157 lakes, ponds and reservoirs and analyzed them based on their physical, chemical and biological conditions (USEPA 2009). The USEPA published a report in 2009 summarizing their key findings regarding the health of our nation's lakes, but they also made the data they collected public so researchers could utilize the dataset to look for patterns among lakes. The dataset amassed by the USEPA in 2007 has been used to examine subjects such as cyanobacteria and cyanotoxins (Beaulieu et al. 2013; Rigosi et al. 2014; Beaver et al. 2014; Yuan et al. 2014; Loftin et al. 2016), development of near-shore physical habitat indices (Kaufmann et al. 2014), landscape limnology (Read et al. 2015), lake hydrology and how it relates to water quality (Brooks et al. 2014), CO₂ flux in lakes and reservoirs (McDonald et al. 2013), diatom communities (Winegardner et al. 2015) and algal biomass (Zimmerman and Cardinale 2014; Dolman and Wiedner 2015). To this author's

knowledge, no work has been completed that specifically analyzes zooplankton communities using the USEPA's 2007 National Lakes Assessment (NLA) dataset.

Zooplankton fulfill a key role in freshwater ecosystems as they represent the link between incoming solar radiation, nutrients, primary producers and higher trophic levels (e.g. fish). As zooplankton occupy this intermediary position, variation in the structure of the zooplankton community can be attributed to both changes in predation pressure and the phytoplankton community. Planktivory by fish can alter zooplankton species composition and decrease the biomass and the size distribution of the community (Brooks and Dodson 1965; Carpenter et al. 1985; Jeppesen et al. 2000). McQueen et al. (1986) suggested the bottom-up : top-down model to try to describe the interplay between the effects of predation and nutrient inputs on aquatic communities. In the model, nutrients ultimately determine the potential biomass at each trophic level, but the relative importance of nutrient inputs and predation varies with lake trophic status. Fish communities can be altered by the effects of eutrophication (Larkin and Northcote 1969), and the resulting change in fish composition (piscivores : planktivores) can influence zooplankton populations (Jeppesen et al. 2000). Gannon and Stemberger (1978) cautioned against making direct causal relationships between zooplankton community composition and trophic status due to the confounding effects of predation. However, they, along with other authors (Jeppesen et al. 2011), argued that because of their unique trophic position, zooplankton potentially have considerable value as indicators of water quality.

The pelagic zone of lakes is inhabited by four main groups of zooplankton: cladocerans, copepods, rotifers and protists. While increasing attention has been given to the role protists play in pelagic food webs (Pace and Orcutt 1981; Beaver and Crisman 1989; Havens et al. 2007; Sommer et al. 2012), they will not be discussed in detail further as the USEPA's 2007 National

Lake Assessment (NLA) did not contain data regarding them. Past research hypothesized that as lakes increase in productivity, calanoid copepods will become less abundant and small cladocerans, cyclopoid copepods and rotifers will increase in dominance (Brooks 1969; McNaught 1975; Maier 1998). Multiple studies confirm that, in general, there is a shift in the copepod community from calanoids to cyclopoids as lake trophic status increases (Pace 1986; Jeppesen et al. 2000; Pinto-Coelho et al. 2005). Hessen et al. (1995) found an increase in cyclopoid copepods with increasing lake productivity in 342 Norwegian lakes, but they did not find any relationship between calanoid copepods and trophic status. Haney (1987) noted that in New Zealand lakes, two genera of calanoid copepods *Boeckella* and *Calamoecia* are dominant in eutrophic lakes. Depending on the geographic region, morphometry of the lake and the composition of the fish community, various states of zooplankton assemblages can exist in eutrophic lakes.

One symptom of eutrophication is the phytoplankton community typically becomes dominated by cyanobacteria. Cyanobacteria colonies can potentially inhibit large zooplankton filter feeders by causing mechanical interference or by producing a variety of cyanotoxins which can have detrimental effects on the grazing community (Haney 1987; Lampert 1987). In eutrophic systems dominated by cyanobacteria, filter feeders >1.0 mm in body length can be reduced in numbers (Ghadouani et al. 2003) causing a shift in the size structure and composition of the zooplankton community. Small cladocerans such as *Bosmina* and *Ceriodaphnia* as well as rotifers are typically able to sustain high population densities during cyanobacterial blooms (de Bernardi and Giussani 1990). Porter and McDonough (1984) demonstrated that large cladocerans (*Daphnia*) have increased rejection and respiration rates in the presence of increasing amounts of the filamentous cyanobacteria, *Anabaena*. These increased rates imposed a higher energetic cost

on the larger cladocerans more so than on the small cladocerans (*Bosmina* and *Ceriodaphnia*). In some cases large crustaceans can coexist and or utilize cyanobacteria to a certain degree (de Bernardi and Giussani 1990). The effect of cyanobacteria on zooplankton communities can differ depending on the species of cyanobacteria, whether their form is colonial or single celled, the size and shape of the colonies and whether or not toxic strains of cyanobacteria are present (de Bernardi and Giussani 1990).

Another major component of pelagic zooplankton communities, rotifers, are also sensitive to anthropogenic disturbances such as eutrophication and salinization (Segers 2008). Their distribution and diversity can be influenced by changes in water quality (Segers 2008) and detailed lists by Sladeczek (1983) and Berzins and Pejler (1989) were created for European lakes that rank rotifers respectively by saprobity (pollution by organic matter measured by biological oxygen demand) and trophic degree. The general diet of filter-feeding rotifers consists of bacteria, detritus and small algae (Sladeczek 1983; Segers 2008). There is some overlap in the diet of rotifers when compared to crustacean zooplankton, but rotifers tend to feed on small particles that are between 1 to 20 μm in size (Allan 1976). Rotifers typically have a body length ranging from 100 μm to 500 μm (Sladeczek 1983). Due to their small size, rotifers can have a distinct advantage over the larger crustacean zooplankton when predation by planktivorous fish is intense (Brooks and Dodson 1965) and they are not as heavily impacted by large cyanobacteria colonies that can cause mechanical interference in larger grazers (de Bernardi and Giussani 1990). In 39 subtropical Florida lakes, as the trophic state increased, rotifer and ciliate biomass increased faster than the crustacean zooplankton until it accounted for 50 to 90% of the total zooplankton biomass in eutrophic lakes (Bays and Crisman 1983). In temperate lakes, an increase in rotifer biomass was observed with increasing total phosphorus, but an increase in rotifer biomass

relative to the crustacean biomass was not found (Pace 1986; Jeppesen et al. 2000). Rotifers have rapid turnover rates (Ruttner-Kolisko 1974) and a higher intrinsic growth rate (Allan 1976) compared with cladocerans or copepods; thus Gannon and Stemberger (1978) postulated that rotifers would be better indicators of water quality than crustaceans as they can respond quickly to environmental change.

Community datasets with numerous ecological and biological variables can be challenging to interpret as they generate vast amounts of noisy data (ter Braak and Verdonschot 1995). Multivariate statistics allows scientists to reduce and summarize complex datasets into manageable amounts of information. Redundancy analysis, canonical correspondence analysis and non-metric multidimensional scaling have all been used in aquatic ecology to determine how biological communities respond to environmental gradients. Non-metric multidimensional scaling (NMDS) was selected for this analysis as it is not constrained by the environmental variables and will give the optimal solution based on the patterns found in the species data (Peck 2016). Another benefit of using NMDS is it makes no distributional assumptions of the species response.

An increase in knowledge on how zooplankton communities respond to eutrophication can assist lake managers in determining trophic status, trend detection, decision-making and assessing the impacts of human activities (Attayde and Bozelli 1998; Stemberger et al. 2001). The overall goal of this study was to use the USEPA's 2007 NLA dataset to determine if patterns could be found between zooplankton community structure and lake trophic status. Within this framework four specific questions were examined:

- 1) What level of taxonomic resolution (family, genus or species) is needed to detect patterns between crustacean zooplankton assemblages and water quality? This question is salient

because identifying zooplankton to species is time-consuming and resource intensive, so there are clear advantages for agencies and lake managers to want to try to achieve similar results with higher levels of taxonomic resolution that are easier to classify (Whitman et al. 2004; Havens and Beaver 2011).

- 2) In a dataset with considerable spatial and temporal variability, does zooplankton seasonal succession need to be taken into account when looking for patterns between zooplankton communities and water quality? Zooplankton assemblages undergo seasonal shifts in biomass and community structure (Sommer et al. 1986, 2012). The 2007 NLA contains data from across the contiguous United States that were collected over a 6 month period (May to October). Taub and Wiseman (1998) suggested that for a sampling design that spanned the entire United States and where only one sample is collected per lake, that the timing of the sampling event will influence our interpretation of the results due to zooplankton seasonal succession. In particular, they note that *Daphnia*, an important grazer in pelagic communities, may decline markedly or does not persist throughout the summer months, particularly in warmer climates. To account for the variability within the NLA, a linear regression model developed by Gillooly and Dodson (2000) that predicts the date of *Daphnia* maximum abundance from degrees north latitude was used to try to normalize a portion of the dataset based on zooplankton seasonal succession.
- 3) Can zooplankton communities be used to differentiate lakes in different trophic states (oligotrophic, mesotrophic, eutrophic and hypereutrophic) from one another based on four common measures of lake trophic status: total phosphorus, total nitrogen, chlorophyll- α and Secchi disk depth?

- 4) In the crustacean and rotifer communities, are there any distinct taxonomic units that are consistent indicators of lake trophic status across multiple trophic parameters?

MATERIALS AND METHODS

Data were collected by the USEPA and their affiliates between May and October 2007, with the majority of the sampling occurring in June, July and August. During this sampling period, 1157 lakes across the contiguous United States were visited once and 95 lakes were revisited a second time for a total of 1252 sampling events (Figure 1). Field teams across the country followed the same protocols (USEPA 2007) and water chemistry was analyzed using standard methods (USEPA 2006). Water chemistry and zooplankton samples were collected at the deepest site in the lake the field crews could locate. Using two Wisconsin-style nets with a diameter of 13 cm and mesh sizes of 243 μm and 80 μm , a single vertical tow was taken 0.5 m off the bottom of the lake in order to collect microcrustaceans and rotifers, respectively. Zooplankton abundance was calculated as organisms per liter.

Only lakes with an original archived microcrustacean sample that had not been manipulated by the labs that completed the initial identifications were considered (N = 671). A number of samples were removed by this author to reduce potential error and variability between lakes. Plankton samples that had been flagged by the USEPA as potentially being compromised were removed from the study (N = 21). Shallow lakes with the maximum observed depth < 2.5m were removed (N = 99) to reduce background variability among the lakes, as lakes without a hypolimnetic refuge may differ in zooplankton abundance and diversity when compared to lakes with a refuge (Tessier and Welser 1991). Lakes with a pH < 6.0 were also removed (N = 3), due to the known effects of low pH on crustacean (Sprules 1975) and rotifer (Siegfried et al. 1989) communities, leaving 548 potential lakes which this study could draw upon.

This author removed benthic, meroplanktonic and planktonic organisms that would have been poorly sampled were removed from the analysis. As a result, the following organisms were

removed from the species list: *Argulus* spp., *Chaoborus* spp., *Ergasilus* spp., *Dreissena polymorpha*, *Leptodora kindti*, *Latona* spp., *Polyphemus pediculus*, organisms belonging to family Macrothricidae, members of family Chydoridae, except for specimens belonging to the *Chydorus sphaericus* group, water mites and bdelloid rotifers.

Northern Appalachians Ecoregion

Thirty lakes were selected to be analyzed from the Northern Appalachian ecoregion (NAP; Figure 2 & 3). The NAP ecoregion encompasses almost all of New England and New York as well as parts of Pennsylvania and Ohio (Figure 3; USEPA 2009). Lakes for the analysis were selected if they were consistent indicators of a trophic level based on four common measures of lake trophic status: total phosphorus (TP), total nitrogen (TN), chlorophyll- α and Secchi disk depth (Table 1). Based on the four trophic parameters, ten lakes were oligotrophic for all parameters, ten were mostly rated as mesotrophic with some designations as oligotrophic and ten lakes were classified eutrophic for chlorophyll- α , but the other three parameters could have ranged from oligotrophic to hypereutrophic. The ten lakes that were classified as eutrophic based on chlorophyll- α had two lakes where TP and TN were listed as hypereutrophic. Due to the low sample size for hypereutrophic conditions, those parameters were reclassified as eutrophic for this study.

Microcrustacean samples for the 30 lakes were re-identified by the author using the following keys: Wilson and Yeatman 1959; Pennak 1989; Hudson and Lesko 2003; Dodson et al. 2010; Reid and Williamson 2010; Haney et al. 2013. Juvenile calanoid copepods were designated as either a diaptomid or temorid copepodite. Male cyclopoid copepods and copepodites were both designated as one group: unknown cyclopoids. The cladoceran genus, *Diaphanosoma*, needs taxonomic revision at the species level in North America, as such all

specimens were identified as *Diaphanosoma* spp. (Korovchinsky 1992; Dodson et al. 2010). All other microcrustaceans were identified to species. Microcrustaceans were analyzed at three different levels of taxonomic scrutiny: family, genus and species to test if the level of taxonomic resolution was important in discerning differences between lakes based on the zooplankton communities. For the rotifer communities, the identifications compiled by the USEPA were used, but most taxa were aggregated to genus for consistency (Appendix A).

Contiguous United States

Three groups of 48 lakes were selected across the contiguous U.S. for the second study. A linear regression model ($y = 4.2x - 24.8$; $r^2 = 0.70$) from Gillooly and Dodson (2000) was used for the first group of 48 lakes to attempt to normalize lakes selected by their state of seasonal succession (Figure 4 & 5). Their model predicts the Julian date of the *Daphnia* maximum abundance from degrees north latitude. As a comparison to the 48 lakes selected by the Gillooly and Dodson model, the second and third groups of 48 lakes were chosen by using a random number generator to select lakes without regard to zooplankton succession. One group of randomly selected lakes was located above 40° latitude (Figure 6) and the other group was selected from across the entire contiguous U.S. (Figure 7).

The lakes included in the 2007 national lakes assessment (NLA) study were sampled from May to October across the lower 48 states. Over the course of the ice free period, in temperate regions, zooplankton communities can fluctuate widely in terms of biomass, size distribution and community composition (Sommer et al. 1986). During the 2007 NLA, only approximately 8% of the lakes were visited a second time, thus sample aggregation across seasons was not a feasible way to account for zooplankton seasonal succession. To account for seasonal zooplankton dynamics within the NLA dataset, an alternative method was used to

assess seasonal variation. A proxy for spring turnover was obtained by using the regression equation developed by Gillooly and Dodson (2000), where the date of maximum *Daphnia* abundance can be calculated as a function of latitude.

Using the equation by Gillooly and Dodson (2000) on the NLA lakes, the date of *Daphnia* maximum abundance across the contiguous United States occurs in February at the southern latitudes and the end of June at northern latitudes. The NLA samples were collected from May through October, with the majority of samples from the summer months of June, July and August; thus the equation predicts maximum *Daphnia* abundance for only a small subset of all samples. Time (30 to 100 days) was added to the predicted date of *Daphnia* maximum abundance for all lakes (Figure 5) to attempt to capture more lakes in the same state of succession. The majority of the southernmost lakes would not be accounted for, even with added time, therefore the study focused on lakes above 40° latitude. With a set amount of time added to all predicted dates, a seven day window was searched for that contained lakes in the same state of seasonal succession. Forty six days past the predicted date of *Daphnia* maximum abundance, 48 lakes were observed to be in the same state of seasonal succession and were selected for the analysis (Figure 5). The corresponding date range for when the 48 lakes were sampled was from July 10th to August 9, 2007.

Three different labs contracted by the USEPA counted and identified the zooplankton samples. The finest level of taxonomic resolution reported was variable and organisms had to be aggregated to an agreed upon taxonomic level. Eleven taxonomic units were then identified within the USEPA's dataset either to genus (*Ceriodaphnia*, *Daphnia*, *Diaphanosoma*, *Holopedium*, *Moina* and *Sida*) or family (Bosminidae, Chydoridae, Cyclopidae, Diaptomidae and Temoridae).

Statistical Methods

Prior to analysis, the species matrix was transformed using a generalized log procedure which helps to maintain the original order of magnitude in the data and will produce a value of zero if there was no species present (McCune and Grace 2002). Rare species, i.e., found in fewer than 5% of the lakes, were left in the analyses as removing them did not alter the results. Non-metric multidimensional scaling was used to evaluate similarities between sample units and to provide a graphical representation of the data; Sørensen distances were computed for the NMDS. For the NMDS, 250 runs with the real data and 250 randomized data runs were completed in PC-ORD for a Monte Carlo test of significance. A unique value in the interpretation of NMDS is stress, where lower values of stress indicate a better ordination. McCune and Grace (2002) summarized the work by Kruskal (1964) and Clarke (1993) on the interpretation of stress values and note that stress values below 10 are indicative of a good ordination and value above 20 will typically lead to a poor interpretation of the results. McCune and Grace (2002) further indicate that for ecological community data stress is typically between 10 to 20 and a NMDS output with stress values >35 should not be interpreted at all.

Four common indicators of lake trophic status: TP, TN, chlorophyll- α and Secchi disk depth (Table 1) were overlaid on the resulting NMDS ordinations and convex hulls were used to aid in the interpretation of groups (Appendices H to N). Multi-response permutation procedure (MRPP), a non-parametric test, was used to assess whether communities in lakes group by trophic status were significantly different from each other. Sørensen distances were used to calculate the distance matrix for the MRPP. If groups were significantly different, Dufrêne and Legendre (1997) indicator species analysis (ISA) was used to determine if any taxonomic unit (species, genus or family) were useful in indicating trophic conditions. The NMDS, MRPP and

ISA were all conducted using PC-ORD (McCune and Mefford 2011). Maps were prepared using ArcMap 10.3 and all other graphs were made using SigmaPlot 11 (Systat Software).

Table 1. Measures of lake trophic status, trophic designations follow USEPA (2009).

	TP ($\mu\text{g L}^{-1}$)	TN (mg L^{-1})	Chlor - a ($\mu\text{g L}^{-1}$)	Secchi (m)
Oligotrophic	≤ 10	≤ 0.35	≤ 2	> 4
Mesotrophic	$> 10 - 25$	$> 0.35 - 0.75$	$> 2 - 7$	2.1 - 4.0
Eutrophic	$> 25 - 50$	$> 0.75 - 1.40$	$> 7 - 30$	0.7 - 2.1
Hypereutrophic	> 50	> 1.40	> 30	≤ 0.7

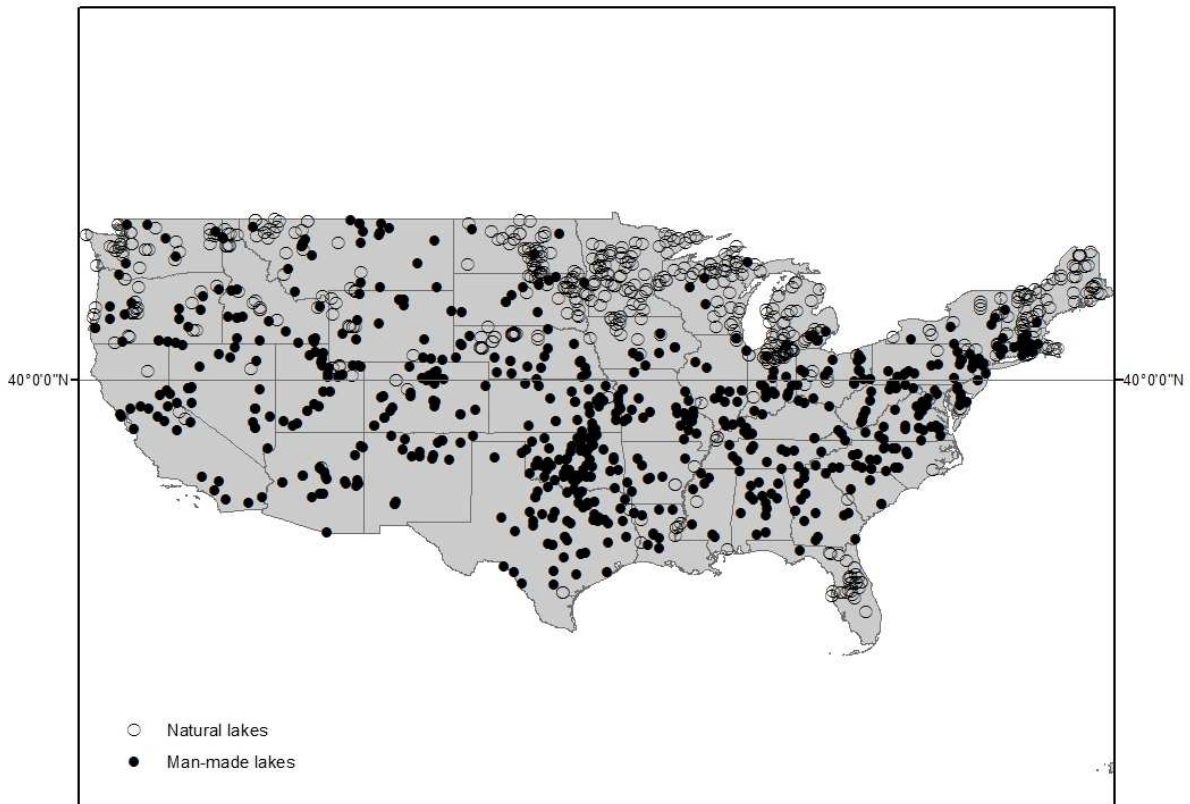


Figure 1. Location of the 1157 lakes sampled by the USEPA for the 2007 NLA. Open circles represent natural lakes, solid circles represent man-made lakes.

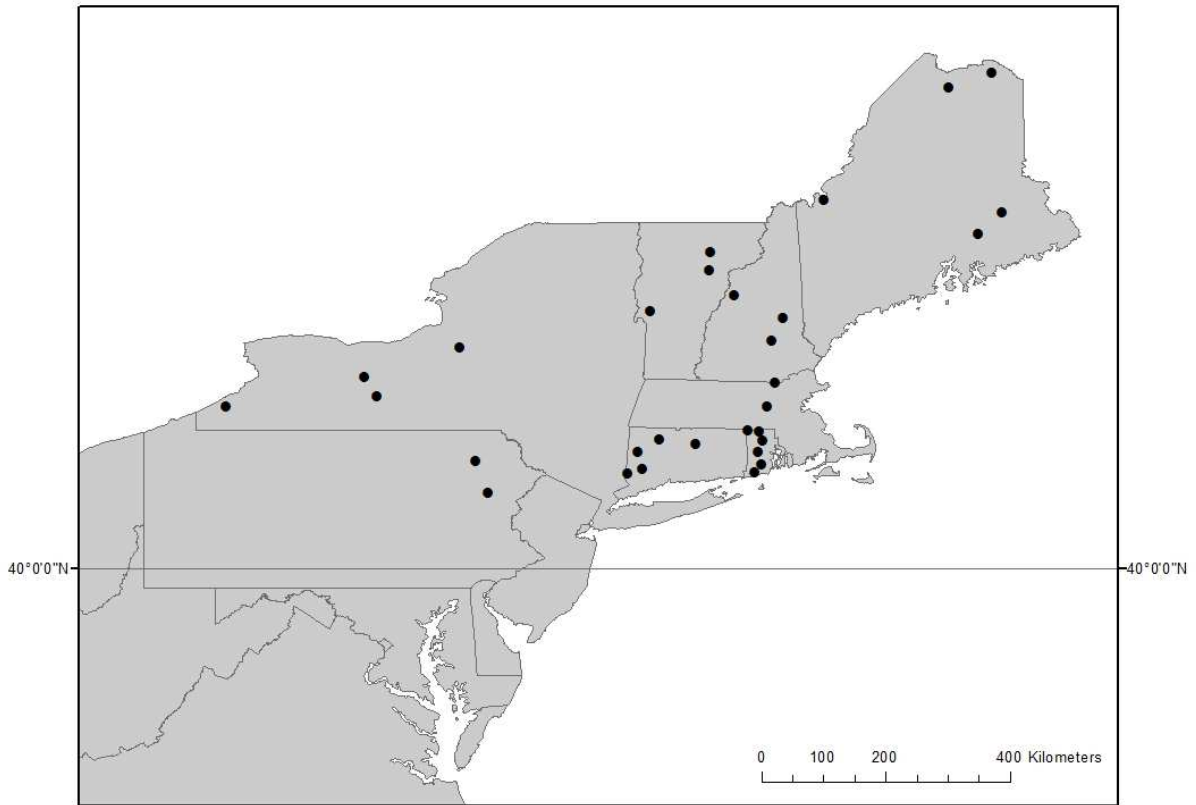


Figure 2. Location of the 30 lakes selected from the Northern Appalachian Ecoregion.

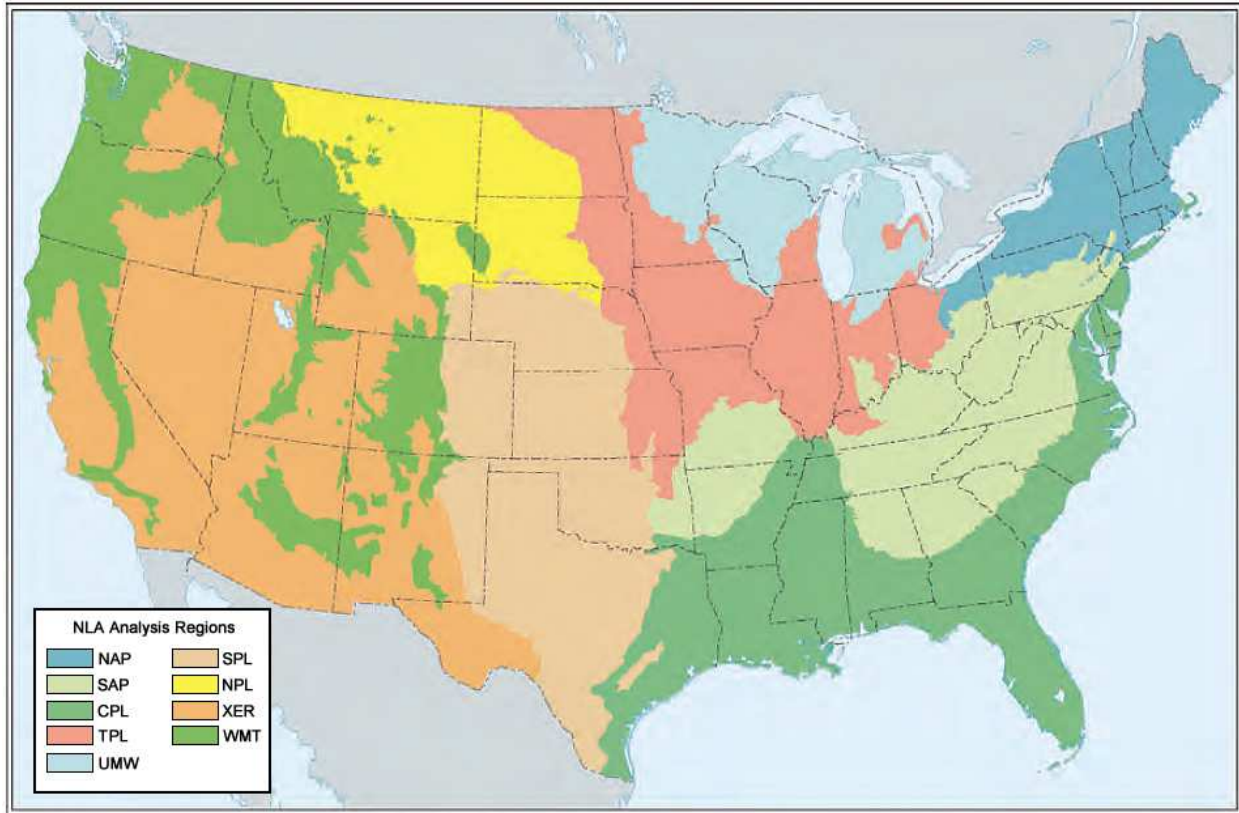


Figure 3. Aggregate ecoregions (based on Omernik Level III ecoregions) used in the NLA. Modified from USEPA (2009).



Figure 4. Location of the 48 lakes selected by using the linear regression model ($y = 4.2x - 24.8$; $r^2 = 0.70$) from Gillooly and Dodson (2000), where y = Julian date of the *Daphnia* maximum abundance and x = degrees north latitude.

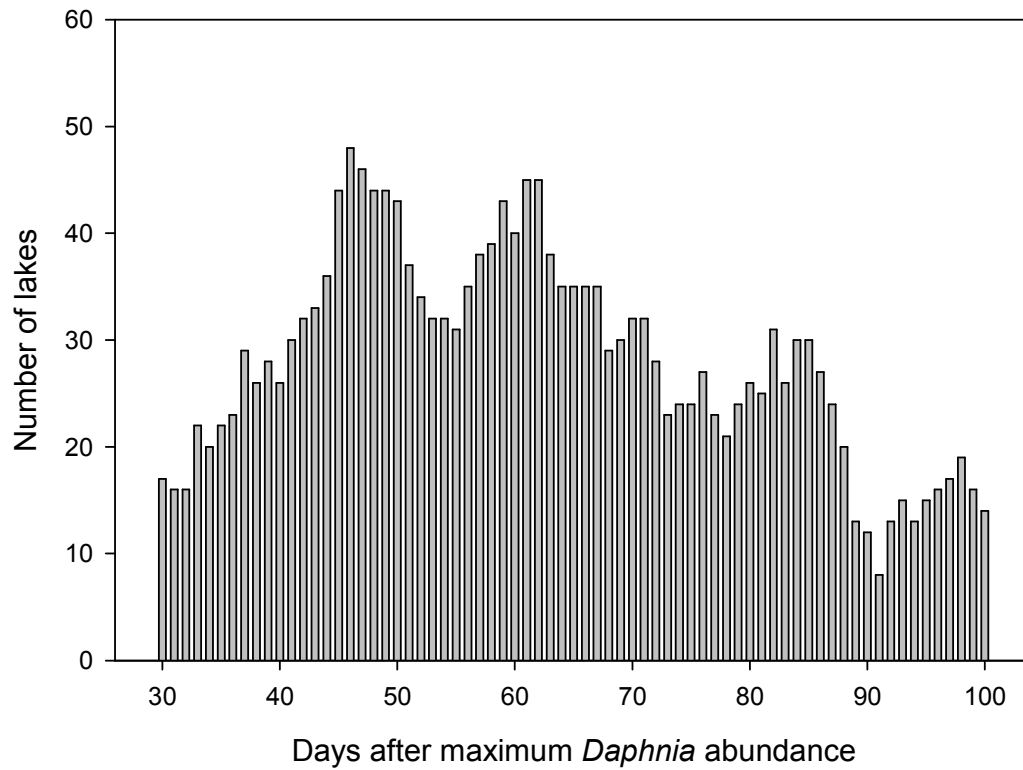


Figure 5. Predicted number of lakes above 40° latitude that are within a seven day window of being in the same state of seasonal succession based on days post maximum *Daphnia* abundance. *Daphnia* maximum abundance was calculated by the linear regression model ($y = 4.2x - 24.8$; $r^2 = 0.70$) from Gillooly and Dodson (2000).

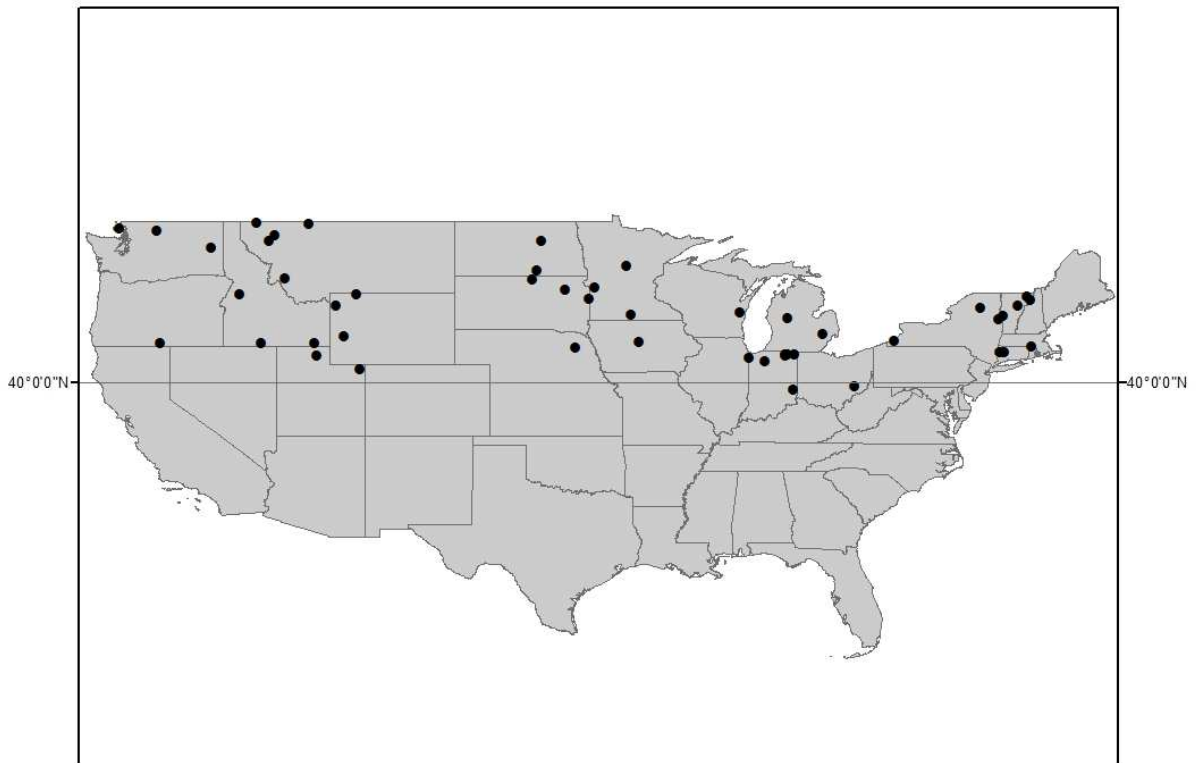


Figure 6. Location of the 48 lakes selected at random above 40° latitude.



Figure 7. Location of the 48 lakes selected at random across the contiguous United States.

RESULTS

MICROCRUSTACEANS

Northern Appalachians Ecoregion: Taxonomic Resolution

All three NMDS ordinations (species, genus and family) resulted in significant ($p < 0.05$) three-dimensional solutions with stress < 15.0 and $r^2 \geq 0.80$ (Table 2). The NMDS ordination with the least amount of stress (12.20) and highest r^2 (0.87) was when crustaceans were identified to family while the ordination with highest amount of stress (14.06) and lowest r^2 (0.80) was when they were identified to species (Table 2).

Three separate MRPP's, respectively using TP, TN and Secchi disk depth as a grouping factor, found that the microcrustacean communities in oligotrophic lakes were distinguishable from at least one other trophic level but were always significantly different from eutrophic lakes (Table 3). Using chlorophyll- α as the trophic parameter, microcrustacean communities in eutrophic lakes were significantly different from both oligotrophic and mesotrophic lakes (Table 3).

When zooplankton were identified to species, the ISA found that *Ceriodaphnia lacustris* and *Chydorus sphaericus* were indicators of eutrophic conditions based on TP, TN and chlorophyll- α , but not Secchi disk depth (Table 4). *Skistodiatomus pallidus* and *Bosmina longirostris* were consistent indicators of eutrophic conditions across all four trophic parameters (Table 4). Of the three levels of taxonomic resolution (species, genus and family), only *Epischura nordenskiöldi* was an indicator of mesotrophic conditions based on one environmental grouping variable, chlorophyll- α (Table 4).

When taxonomic resolution was reduced from species to genus, the genera *Ceriodaphnia*, *Chydorus*, and *Bosmina* all retained their same status as indicators of eutrophic conditions (Table 4). Aggregation to genus caused a reduction in the eutrophic indicator status of the copepod, *Skistodiaptomus*. At the genus level, *Skistodiaptomus*, was only an indicator for chlorophyll- α and Secchi disk depth (Table 4). When identifications were reduced to family, Chydoridae was the only family that was an indicator of eutrophic conditions across more than two parameters (Table 4).

Lower 48 States: Seasonal Succession

A pattern emerged in the NMDS stress and r^2 results along a gradient of spatial and temporal randomness in the three datasets (Table 5). For the lakes selected by the linear regression model from Gillooly and Dodson (2000), the NMDS resulted in a three-dimensional solution that had the lowest stress value (10.49) and highest r^2 (0.94) of all three datasets (Table 5). The NMDS for lakes selected randomly above 40° latitude came to a three-dimensional solution, had an intermediate stress value of 14.00 and a r^2 of 0.87 (Table 5). The dataset with the highest stress (21.42) and lowest r^2 (0.76) were the lakes selected randomly from across the contiguous U.S. (Table 5).

For lakes selected by the equation of Gillooly and Dodson (2000), the MRPP was only able to distinguish microcrustacean communities in hypereutrophic lakes apart from all other trophic levels based on TP and TN (Table 6). In the other two datasets (lakes randomly selected above 40° latitude and lakes selected randomly from across the contiguous U.S.) the MRPP was always able to differentiate microcrustacean communities in oligotrophic lakes from at least one other trophic level (Table 6).

The ISA for each of the three datasets did not find any clear and persistent patterns for any taxonomic unit across more than two trophic parameters (Table 7). In the dataset selected by the Gillooly and Dodson (2000) model, *Ceriodaphnia* was an indicator of eutrophic conditions based on TP and TN, but the genus was not a significant indicator in the other two datasets. In the lakes selected randomly above 40° latitude, family Chydoridae was an indicator of mesotrophic lakes for TP and Secchi disk depth while family Diaptomidae was an indicator of mesotrophic conditions based on TP and TN. For lakes selected across the contiguous U.S., family Cyclopidae was an indicator of oligotrophic condition using chlorophyll- α and Secchi disk depth as the trophic parameters. All other taxonomic units that were significant indicators were not consistent between the three datasets or across the four trophic parameters (Table 7).

Table 2. NMDS output for microcrustacean identifications to the species, genus and family level for 30 lakes in the Northern Appalachian ecoregion. Species: N = 44, genus: N = 23, family: N = 9.

	Dimensions	Cumulative r²	Axis 1 r²	Axis 2 r²	Axis 3 r²	Stress	p-value
Species	3	0.80	0.36	0.33	0.12	14.06	0.008
Genus	3	0.85	0.56	0.19	0.10	13.37	0.004
Family	3	0.87	0.31	0.40	0.16	12.20	0.048

Table 3. MRPP output for microcrustaceans comparing groups based on different levels of taxonomic identification in the Northern Appalachian ecoregion. Upper value is p = probability of a type I error and lower value is A = chance-corrected within-group agreement. Groups indicated in the pairwise comparisons (pair) have p < 0.05. Groups: O = oligotrophic, M = mesotrophic and E = eutrophic.

	TP	Pair TP	TN	Pair TN	Chlor-a	Pair Chlor-a	Secchi	Pair Secchi
Species	0.004 0.040	O vs. M, E	0.011 0.034	O vs. E	0.004 0.039	E vs. O, M	0.023 0.027	O vs. E
Genus	<0.001 0.072	O vs. M, E	0.002 0.053	O vs. M, E	0.001 0.064	E vs. O, M	0.002 0.053	O vs. E
Family	0.031 0.038	O vs. E	0.038 0.036	O vs. E	0.010 0.050	E vs. O, M	0.014 0.046	O vs. E

Table 4. ISA for taxonomic units in the Northern Appalachian ecoregion. Upper value is p = probability of a type I error and lower value is the indicator value. Groups: O = oligotrophic, M = mesotrophic, and E = eutrophic.

	TP	Group	TN	Group	Chlor – α	Group	Secchi	Group
Species								
<i>Chydorus sphaericus</i>	0.028 49.3	E	0.021 50.3	E	0.042 34.7	E		
<i>Ceriodaphnia lacustris</i>	0.018 51.2	E	0.028 50.4	E	0.050 35.5	E		
<i>Bosmina longirostris</i>	0.011 61.0	E	0.014 57.3	E	0.052 39.2	E	0.007 50.1	E
<i>Epischura nordenskiöldi</i>					0.005 45.6	M		
<i>Skistodiaptomus pallidus</i>	0.006 59.2	E	0.007 55.3	E	0.026 34.7	E	0.008 45.5	E
Genus								
<i>Chydorus</i>	0.026 49.3	E	0.020 50.3	E	0.037 34.7	E		
<i>Ceriodaphnia</i>	0.033 46.2	E	0.038 46.4	E	0.030 41.5	E		
<i>Bosmina</i>	0.009 61.0	E	0.015 57.3	E	0.046 39.2	E	0.007 50.1	E
<i>Leptodiaptomus</i>	0.042 49.1	O						
<i>Skistodiaptomus</i>					0.023 45.5	E	0.011 48.4	E
Family								
Chydoridae	0.028 49.2	E	0.023 50.2	E	0.037 34.7	E		
Daphniidae					0.009 38.4	E	0.055 37.3	E
Bosminidae					0.313 36.8		0.003 53.3	E

Table 5. NMDS output for microcrustaceans for the three datasets comparing seasonal succession. N= 48 for all 3 datasets.

	Dimensions	Cumulative r ²	Axis 1 r ²	Axis 2 r ²	Axis 3 r ²	Stress	p-value
G&D							
Equation > 40°	3	0.94	0.50	0.33	0.11	10.49	0.004
Random > 40°	3	0.87	0.57	0.18	0.12	14.00	0.024
Contiguous US	2	0.76	0.38	0.37	-	21.42	0.016

Table 6. MRPP output for microcrustaceans comparing groups based on the three ways lakes were selected to observe for differences between trophic level and zooplankton seasonal succession. Upper value is p = probability of a type I error (N.S. = not significant; p > 0.05) and lower value is A = chance-corrected within-group agreement. Groups indicated in the pairwise comparisons (pair) have p < 0.05. Groups: O = oligotrophic, M = mesotrophic, E = eutrophic and H = hypereutrophic.

	TP	Pair TP	TN	Pair TN	Chlor - α	Pair Chlor- α	Secchi	Pair Secchi
G&D								
Equation > 40°	0.003 0.048	H vs. O, M, E	0.002 0.050	H vs. O, M, E	N.S.	-	N.S.	-
Random > 40°	<0.001 0.078	O vs. E, H M vs. H	< 0.001 0.063	O vs. M, E, H M vs. H	<0.001 0.072	O vs. E, H M vs. E, H	<0.001 0.096	O vs M vs E vs H
Contiguous US	<0.001 0.063	O vs. M, E, H E vs. H	0.002 0.049	O vs. M, E, H	0.028 0.028	O vs. E, H	<0.001 0.069	O vs. E, H M vs. H

Table 7. ISA for microcrustacean taxonomic units across the three datasets comparing zooplankton seasonal succession. Upper value is p = probability of a type I error and lower value is the indicator value. Groups: O = oligotrophic, M = mesotrophic, and E = eutrophic.

	TP	Group	TN	Group	Chlor – α	Group	Secchi	Group
G&D Equation > 40°								
<i>Ceriodaphnia</i>	0.009 43.2	E	0.050 33.6	E				
<i>Moina</i>			0.026 28.6	E			Not Tested	
Random > 40°								
Bosminidae			0.027 35.6	O				
Chydoridae	0.007 36.1	M					0.021 36.4	M
Cyclopidae					0.017 30.6	E	0.032 30.6	M
<i>Daphnia</i>					0.041 29.2	M		
<i>Diaphanosoma</i>			0.032 34.7	M	0.003 44.4	E	0.002 49.2	M
Diaptomidae	< 0.001 36.1	M	0.017 33.3	M				
<i>Sida</i>	0.039 25.0	O						
Contiguous US								
Cyclopidae					0.004 30.8	O	0.029 29.5	O
<i>Daphnia</i>			0.008 31.1	O				
<i>Diaphanosoma</i>	0.013 41.6	E	0.050 36.8	O			0.002 43.9	O
<i>Holopedium</i>			0.015 42.1	E				
<i>Moina</i>	0.006 37.5	E					0.017 27.3	O

ROTIFERS

Northern Appalachians Ecoregion

The NMDS for rotifers in the NAP came to a significant ($p < 0.05$) one dimensional solution with an r^2 of 0.62, but the stress value (34.75) was too high to consider for further analysis.

Lower 48 States: Seasonal Succession

All three rotifer datasets had an NMDS which came to three-dimensional solutions that were significant ($p < 0.05$) and had stress values below 15.00 (Table 8). The NMDS solution with the highest stress (14.53) were the lakes selected by the Gillooly and Dodson (2000) model, while the solution with the lowest stress (11.08) were the lakes selected randomly above 40° latitude (Table 8). The r^2 values from all three rotifer datasets were comparable (approximately 0.85; Table 8).

The MRPP revealed that rotifer communities in oligotrophic lakes were always significantly different from hypereutrophic lakes and except for one instance, were different from eutrophic lakes (Table 9). Rotifer communities in mesotrophic lakes were distinguishable from hypereutrophic lakes in all but two cases. In general, oligotrophic and mesotrophic communities were not significantly different from each other and eutrophic and hypereutrophic lakes were not discernable apart from each other based on their rotifer communities (Table 9).

For lakes selected by the Gillooly and Dodson (2000) model, the genus *Brachionus* was an indicator of eutrophic to hypereutrophic conditions across all four trophic parameters (Table 10). In the other two datasets, *Brachionus* was an indicator of either oligotrophic or mesotrophic conditions. The species *Kellicottia longispina* was a consistent indicator of mesotrophic

conditions in the lakes selected randomly from across the contiguous U.S., but it was either not an indicator or exhibited variation as an indicator within the other two datasets. Across the three datasets, the genus *Polyarthra* was an indicator of eutrophic to hypereutrophic conditions based on at least one parameter. All other taxonomic units that were significant indicators were either not consistent or appeared as an indicator for less than two parameters across all datasets.

Table 8. NMDS output for aggregated rotifer identifications. G&D Equation > 40°: N = 43, random > 40°: N = 32, contiguous US: N = 31.

	Dimensions	Cumulative r ²	Axis 1 r ²	Axis 2 r ²	Axis 3 r ²	Stress	p-value
G&D							
Equation > 40°	3	0.85	0.42	0.27	0.16	14.53	0.004
Random > 40°	3	0.86	0.39	0.39	0.16	11.08	0.008
Contiguous US	3	0.84	0.43	0.30	0.12	13.26	0.004

Table 9. MRPP rotifer output comparing groups based on the three ways lakes were selected to observe for differences between trophic level and zooplankton seasonal succession. Upper value is p = probability of a type I error and lower value is A = chance-corrected within-group agreement. Groups indicated in the pairwise comparisons (pair) have p < 0.05. Groups: O = oligotrophic, M = mesotrophic, E = eutrophic and H = hypereutrophic.

	TP	Pair TP	TN	Pair TN	Chlor - α	Pair Chlor- α	Secchi	Pair Secchi
G&D								
Equation > 40°	<0.001 0.055	O vs. E, H M vs. H	0.005 0.037	H vs. O, M O vs. E, H	<0.001 0.049	O vs. E, H M vs. H	<0.001 0.056	O vs. E, H M vs. E, H
Random > 40°	0.010 0.043	O vs. E, H M vs. H	<0.001 0.072	M vs. E, H E vs. H	0.018 0.038	O vs. M, E, H	0.003 0.054	O vs. E, H M vs. H
Contiguous US	<0.001 0.110	O vs. M, E, H M vs. E, H	<0.001 0.083	O vs. M, E, H M vs. H	<0.001 0.089	O vs. E, H M vs. E, H E vs. H	<0.001 0.079	O vs. E, H M vs. E, H E vs. H

Table 10. ISA for rotifer groups identified as significantly different by the MRPP. Upper value is p = probability of a type I error and lower value is the indicator value. Groups: O = oligotrophic, M = mesotrophic, E = eutrophic and H = hypereutrophic.

	TP	Group	TN	Group	Chlor – α	Group	Secchi	Group
G&D Equation > 40°								
<i>Brachionus</i>	0.028 37.5	E	0.021 42.1	E	0.001 67.5	H	0.013 45.5	H
Conochilidae							0.030 39.4	O
<i>Gastropus</i>					0.036 39.5	E		
<i>Kellicottia longispina</i>	0.001 44.5	H					0.039 38.1	O
<i>Polyarthra</i>					0.019 37.3	H		
Random > 40°								
<i>Brachionus</i>			0.001 71.1	M			0.004 55.6	M
<i>Gastropus</i>			0.012 51.8	E				
<i>Kellicottia bostoniensis</i>							0.011 48.6	H
<i>Keratella</i>			0.002 37.2	E				
<i>Polyarthra</i>			0.036 39.9	E			0.044 39.1	H
<i>Trichocerca</i>			0.013 49.6	E				
Contiguous US								
<i>Brachionus</i>					0.025 46.8	O	<0.001 65.6	O
Conochilidae					0.022 40.1	H		
<i>Filinia</i>							0.045 37.3	O
<i>Hexarthra</i>					0.023 46.4	O		
<i>Kellicottia longispina</i>	0.038 44.0	M	0.001 60.9	M	0.002 58.0	M	0.002 54.0	M
<i>Platyias</i>			0.025 50.0	H				
<i>Polyarthra</i>	0.028 43.3	H						
<i>Pompholyx</i>	0.001 65.5	H						

DISCUSSION

MICROCRUSTACEANS

Northern Appalachians Ecoregion: Taxonomic Resolution

The slight increase in stress in the NMDS datasets moving from family (N = 9, stress = 12.20) to genus (N = 23, stress = 13.37) then to species (N = 44, stress = 14.06) is likely due to the increased number of starting dimensions in the species dataset. Removing rare species, in this case by taxonomic aggregation, can improve the final stress value in a NMDS (McCune and Grace 2002).

Crustacean communities grouped to any of the three different levels of taxonomic resolution: species, genus and family, for the 30 lakes selected in the NAP, were always able to differentiate lakes at the extremes of the trophic gradient (oligotrophic from eutrophic) apart from each based on all four trophic parameters (Table 3). Three small cladoceran species: *Ceriodaphnia lacustris*, *Chydorus sphaericus*, *Bosmina longirostris* and the calanoid copepod, *Skistodiaptomus pallidus*, were all consistent indicators of eutrophic conditions for at least three trophic parameters (Table 4). It should be noted that the taxonomic status for the three cladoceran indicator species, *Ceriodaphnia lacustris*, *Chydorus sphaericus* and *Bosmina longirostris*, has undergone recent scrutiny and each organism may be a part of cryptic species complex within their respective genus. For general comments on their taxonomy refer to the dichotomous key by Dodson et al. (2010).

Aggregated to genus, *Chydorus*, *Bosmina*, and *Ceriodaphnia* all maintained their designation as indicators of eutrophic conditions (Table 4). The genera *Chydorus* and *Bosmina* only contained one species therefore their indicator value was not subjected to change. The genus *Ceriodaphnia* was an aggregation of four species (*C. dubia*, *C. lacustris* *C. laticaudata*

and *C. reticulata*). *Ceriodaphnia lacustris*, an indicator at the species level, was the most abundant organism, occurring in nine lakes, while each of the other three species only occurred in one lake (Appendix B). Thus the indicator values for eutrophic conditions for the genus as a whole compared to just *C. lacustris* did not vary widely (Table 4). In small urban lakes Shahady and Redfield (1994) noted when *Ceriodaphnia* abundance increased, chlorophyll-*a* increased and Secchi disk depth decreased. They found the exact opposite relationship with the two trophic parameters when a large cladoceran, *Daphnia*, increased in abundance. Evidence suggests that *Ceriodaphnia*, *Bosmina* and rotifers are able to sustain high population densities during cyanobacterial blooms that occur in eutrophic conditions (de Bernardi and Giussani 1990). As human land use disturbance increased within a watershed, G elinas and Pinel-Alloul (2008) found that body length of the crustacean community decreased and biomass of organisms such as *Ceriodaphnia* and *Bosmina* increased. *Bosmina longirostris* can be used as an indicator of nutrient enrichment, but (Brooks 1969) cautioned that the increase in abundance of *Bosmina longirostris* is indirect and probably due to the effects of eutrophication acting on fish populations. The alteration of trophic structure in the fish assemblages then manifests itself in the zooplankton community with small bodied *B. longirostris* becoming more prevalent in the community.

The calanoid genus, *Skistodiaptomus*, had less predictive power as an indicator when compared to just *S. pallidus* (Table 4). Four calanoid copepod species, each found in multiple lakes were aggregated into the genus: *S. oregonensis* (N = 4), *S. pallidus* (N = 5), *S. pygmaeus* (N = 7) and *S. reighardi* (N = 2; Appendix B). Of those four species, only *S. pallidus* has been reported as an indicator of eutrophic conditions (Byron and Saunders 1981; Torke 2001; Thum and Stemberger 2006; Van Egeren et al. 2011). Torke (2001) reported *S. oregonensis* inhabits

lakes of all trophic types in Wisconsin lakes, and Thum and Stemberger (2006) postulated the range of *S. oregonensis* and *S. reighardi* was more dependent on their biogeographic histories rather than lake productivity. For *Skistodiaptomus*, the reduction of taxonomic resolution from species to genus caused a loss of information and usefulness as a predictor of trophic condition.

Family Chydoridae remained a consistent indicator because it only contained one species, *Chydorus sphaericus*. It would be misleading to characterize the entire family as an indicator of eutrophic conditions as all other chydorids found in the samples were excluded due to their littoral and benthic lifestyle. Other members of family Chydoridae found in pelagic plankton tows were probably there because the plankton net either hit the bottom or passed through macrophytes that some members of the family utilize for habitat. When examining 585 waterbodies in Sweden, Berzins and Bertilsson (1989) noted that *C. sphaericus* has maximum abundance in waterbodies with $> 50 \mu\text{g L}^{-1}$ TP; a value considered hypereutrophic by the USEPA (2009). As trophic degree increases to eutrophy, the phytoplankton community will come to be dominated by large, potentially inedible colonies of cyanobacteria (de Bernardi and Giussani 1990). Blooms of large colonial cyanobacteria provide a substrate for the normally bottom dwelling *C. sphaericus* to perch on in the pelagic zone (Brooks 1969). Organisms that are efficient at feeding on small particles will become favored during these conditions and Pejler (1983) noted that *C. sphaericus* is a high-efficiency bacteria feeder. He and Brooks (1969) further suggested that the occurrence of *C. sphaericus* in the pelagic zone should be considered an indicator of eutrophic conditions.

The results for the NAP agree with general assumption that as lakes become more eutrophic there will be a shift in body size and species composition to smaller cladocerans (Brooks 1969; McNaught 1975). The average body size of *Chydorus* is 0.40 mm, *Bosmina* (0.40

mm) and *Ceriodaphnia* (0.75 mm), whereas the average body length of the important pelagic grazer, *Daphnia*, that was not found as an indicator of any trophic state, is 1.55 mm (Gillooly and Dodson 2000). Body length data were not included in this current study, so changes in body lengths could not be analyzed for differences within a species or genus. *Daphnia* did not appear to be sensitive to trophic status as they were ubiquitous and were found in 29 of the 30 lakes. In contrast, *Chydorus* were found in 7, *Bosmina* in 12 and *Ceriodaphnia* in 11 lakes (Appendix C). The shift toward smaller cladocerans could be due to either size selective predation (Brooks and Dodson 1965) or mechanical interference by large cyanobacterial colonies that promote smaller species (Gliwicz 1977; Gliwicz and Siedlar 1980).

In the NAP ecoregion *Ceriodaphnia lacustris*, *Chydorus sphaericus*, *Bosmina longirostris* and *Skistodiaptomus pallidus* were all consistent indicators of eutrophy. The genera *Ceriodaphnia*, *Chydorus* and *Bosmina* were equal to or comparable indicators, but this was mainly either because the genera contained only one species or if more than one species were present it occurred very infrequently. Species in the calanoid genus *Skistodiaptomus* have much better potential as indicators when identified to species. Aggregations to family were the least sensitive and in the case of family Chydoridae produce misleading results. These results agree with the conclusions of both Whitman et al. (2004) and Havens and Beaver (2011) that identifications to the lowest taxonomic level produce the best results when relating zooplankton to water quality.

Lower 48 States: Seasonal Succession

Across the three datasets there was an evident pattern in the NMDS stress and r^2 results along a gradient of spatial and temporal randomness (Table 5). The lakes selected via the Gillooly and Dodson (2000) model, were all located above 40° latitude (space) and the equation

was used to control for temporal zooplankton seasonal succession. The lakes selected randomly above 40° latitude, were controlled via space but not time and lastly the lakes selected randomly across the contiguous US varied widely spatially and temporally. Along the gradient of increasing spatial and temporal randomness in the datasets (G&D equation > 40°, random > 40° and contiguous US), r^2 respectively decreased 0.94, 0.87, 0.76 and stress increased 10.49, 14.00, 21.42 (Table 5).

Similar to the results for the NAP, the MRPP for the three datasets (G&D equation > 40°, random > 40° and contiguous US) were able to differentiate lakes at the extremes of the trophic gradient (oligotrophic from eutrophic and hypereutrophic) apart from one another using zooplankton communities (Table 6). The only exception was the MRPP was unable to distinguish communities apart using chlorophyll- α and Secchi disk depth as the grouping factors in the G&D equation > 40° dataset. This was an interesting exception because the G&D equation > 40° dataset had the best r^2 and stress values and thus of the three dataset, had the strongest underlying structure. A possible factor for being unable to discern communities apart using chlorophyll- α and Secchi disk depth was the state of seasonal succession the lakes were in at the time of sampling. Lakes were selected 46 ± 3 days after the date of predicted *Daphnia* maximum abundance because that was the time located with the most amount of lakes (N=48) in a similar state of seasonal succession (Figure 5). Referencing the time frame selected to the PEG model of seasonal succession (Sommer et al. 1986, 2012) indicates that 46 ± 3 days after *Daphnia* maximum abundance is approximately just after the clear water phase in lakes. At this point in time, zooplankton communities should be undergoing compositional change and are probably at their lowest summer biomass level because fish predation just reached its maximum intensity and grazeable phytoplankton are at their lowest density for the summer months. During the

spring clear water phase in lakes, chlorophyll- α and Secchi disk depth can be at their lowest and highest respectively for the warmer months and not representative of more typical conditions in the lakes. This “clear-water effect” may be one explanation for why chlorophyll- α and Secchi disk depth could not discern differences between zooplankton communities.

There was no consistent pattern (i.e. > 2 agreements on trophic status) within or between the datasets using ISA (Table 7). The potential reasons for the overall lack of agreement could be 1) large amounts of temporal and spatial variability and 2) the reduced taxonomic resolution within the datasets (6 genera and 5 families), was simply too coarse to predictably detect patterns.

ROTIFERS

Northern Appalachians Ecoregion

It is unknown why the NMDS for the rotifers in the NAP did not result in an interpretable solution (stress = 34.75). Removing lakes that were outliers (> 2 standard deviations from the overall mean) and removing species that were in < 5% of the samples did not improve the results. The lakes in the NAP were selected non-randomly by choosing lakes that had a strong fidelity to trophic level across all four trophic parameters. Selecting lakes in this fashion was intended to reduce chemical and biotic (i.e. chlorophyll- α) variability between lakes, but could have potentially obscured patterns in the rotifer data. This method of selecting lakes did not seem to affect the interpretability of the crustacean zooplankton (Table 2), therefore it could be that there was no relationship between rotifer communities and water quality in the NAP ecoregion. These results contradict studies by Gannon and Stemberger (1978), Siegfried et al. (1989) and

Barbiero and Warren (2011) who were able to detect patterns in rotifer communities with regards to lake trophic status in the northeastern US.

Lower 48 States: Seasonal Succession

The NMDS results (p-values, stress and r^2) were all comparable across the three datasets: G&D equation $> 40^\circ$, random $> 40^\circ$ and contiguous US (Table 8). It is worth noting that of the 48 potential lakes in each dataset, lakes had to be removed from the rotifer analysis because samples did not have an adequate number (< 190) of organisms (Appendices E, F, G). The number of lakes per rotifer dataset were: G&D Equation $> 40^\circ$ (N = 43), random $> 40^\circ$ (N = 32) and contiguous US (N = 31). Thus the dataset selected via the equation by Gillooly and Dodson (2000) retained 11 to 12 more lakes than the two groups of randomly selected lakes. The G&D Equation $> 40^\circ$ lakes did have a slightly higher stress value when compared to the other two datasets (Table 8). McCune and Grace (2002) demonstrated that as sample units are removed from an analysis, the stress value will begin to decline. Hence the higher stress in the G&D Equation $> 40^\circ$ lakes may just be because of sample size. A potential reason why the equation retained more lakes as compared to the two random datasets is because, as discussed in detail for the crustacean zooplankton, the lakes selected by the equation were approximately in the seasonal cycle that matched the clear water phase. Crustacean biomass could have been reduced due to food limitation and or fish predation, which freed the rotifers from competition and allowed their biomass to increase (Sommer et al. 1986, 2012).

As with the crustacean zooplankton data, the MRPP for rotifers were effective at distinguishing lakes at the trophic extremes across all four trophic parameters (Table 9). Using rotifers, oligotrophic lakes were distinguishable from eutrophic lakes in all instances except one: G&D Equation $> 40^\circ$, with a grouping variable of TN. Oligotrophic and mesotrophic lakes were

always different from hypereutrophic lakes. The ISA did locate some potential rotifer indicators within the three datasets. The genus *Brachionus* was an indicator of eutrophic to hypereutrophic conditions for all four trophic parameters in the G&D Equation $> 40^\circ$ lakes, but in the other datasets it was an indicator of either oligotrophic or mesotrophic conditions for two parameters (Table 10). Previous studies have mentioned that *Brachionus* is typically associated with eutrophic conditions (Stemberger 1979; Sladeczek 1983; Attayde and Bozelli 1998; Segers 2008). The genus *Polyarthra* was an indicator of eutrophic to hypereutrophic based on only one trophic parameter across all three datasets (Table 10). A study by Barbiero and Warren (2011) that looked at the distribution of rotifer genera along a trophic gradient in the Great Lakes noted shifts in community composition across time and trophic degree. The shifts in community structure indicated a general trend where the genus *Polyarthra* indicated eutrophy, *Keratella* (mesotrophy), *Conochilus* (mainly oligotrophy) and *Kellicottia* (oligotrophy).

GENERAL DISCUSSION

It is interesting to note that no consistent indicators of mesotrophic conditions were found for rotifers or crustaceans across all the datasets (Tables 4, 7, 10). This may indicate that the data are in agreement with two general hypotheses in ecology: the intermediate disturbance (Connell 1978) and or the trophic cascade hypothesis (Carpenter et al. 1985). Both predict respectively, that the highest diversity or productivity will be found at intermediate levels of disturbance, stress or predation. At the extremes of these gradients, specialist and opportunistic organisms can become more important and dominate the system. Thus intermediate levels of stress, disturbance and or predation allow more organisms to coexist and an overlap in organisms with varying tolerances is more likely to occur. Mesotrophic lakes may also lack indicator species since many cladocerans and rotifers are generalist filter feeders (Allan 1976), have high dispersal potential,

growth rates, reproduction rates and can have large geographical distributions. Without a strong stressor to act as a filter, many species of zooplankton should be able to colonize and inhabit a wide range of lakes. Anas et al. (2013) looked at the susceptibility of zooplankton to acid stress in 244 boreal lakes. They found zooplankton indicators of high and low acid stress, but no indicators in intermediate lakes. Overall the results from this and previous studies indicate that zooplankton can be used to detect coarse changes in lake trophic (e.g. oligotrophic to eutrophic) rather than fine changes between trophic levels (e.g. oligotrophic to mesotrophic).

One experimental design flaw in the study was the use of a Wisconsin-style net with a 243 μm mesh to collect the crustacean zooplankton. The average body size of adult *Bosmina longirostris* is 400 μm (Gillooly and Dodson 2000), but juvenile *Bosmina* can be smaller than the mesh size used by the USEPA. This author observed that when concentrating samples using a ring net with a 240 μm mesh in the lab, some juvenile bosminids passed through the mesh. A potential loss of juveniles during field sampling or laboratory processing could have resulted in an underestimation of the abundance and distribution of *Bosmina*. Also, when analyzing the plankton samples in this study, many zooplankton samples fell below the target enumeration range of 200 to 400 organisms and thus could not be used in the analyses. The relatively small diameter (13 cm) opening on the plankton nets resulted in some samples from low productivity oligotrophic lakes and shallow lakes having too few organisms for analysis. For the crustacean zooplankton, utilizing a plankton net with an opening diameter of 20 cm and mesh size closer to 200 μm would help alleviate some of the problems discussed above.

The overall results of this study support the conclusions of past research suggesting freshwater zooplankton have potential as indicators of water quality (Gannon and Stemberger

1978; Stemberger and Miller 2003; Whitman et al. 2004; Gélinas and Pinel-Alloul 2008; Jeppesen et al. 2011). The general findings of this study indicate that:

- 1) There are consistent zooplankton indicator species that reflect eutrophic conditions in lakes.
- 2) The highest level of taxonomic resolution (species) gave the best results when looking for indicator organisms. Identifications to genus were comparable for small cladocerans (*Bosmina*, *Ceriodaphnia* and *Chydorus*), but for a calanoid copepod (*Skistodiaptomus*) it resulted in a loss of predictive power as an indicator.
- 3) Trophic status of lakes can be determined by zooplankton communities; they are most effective at differentiating lakes at extremes of the trophic gradient (oligotrophic compared to eutrophic/hypereutrophic).
- 4) There is a need to account for zooplankton seasonal succession when lakes are sampled over a large spatial and temporal gradient.
- 5) The linear regression model by Gillooly and Dodson (2000) shows promise as a method to account for zooplankton seasonal succession, but further analyses should be completed to determine the optimal sampling time for when zooplankton community composition reflects lake trophic status.

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APPENDICES

APPENDIX A

Table 1: Aggregated rotifers identifications compiled from the 2007 USEPA NLA. Twenty six distinct taxonomic units were identified: species (N = 2), genera (N = 22) and families (N = 2). Includes identifications from all 4 datasets used in this study: Northern Appalachian Ecoregion, lakes selected by using the linear regression model ($y = 4.2x - 24.8$; $r^2 = 0.70$) from Gillooly and Dodson (2000), lakes selected randomly above 40° latitude and the lakes selected randomly from across the country. There were a total of 111 different lakes from 114 distinct sampling events.

Taxonomic Rank	Identification
Species	<i>Kellicottia bostoniensis</i> <i>Kellicottia longispina</i>
Genus	<i>Anuraeopsis</i> <i>Ascomorpha</i> <i>Asplanchna</i> <i>Brachionus</i> <i>Collotheca</i> <i>Colurella</i> <i>Euchlanis</i> <i>Filinia</i> <i>Gastropus</i> <i>Hexarthra</i> <i>Keratella</i> <i>Lepadella</i> <i>Lophocharis</i> <i>Notholca</i> <i>Platyias</i> <i>Ploesoma</i> <i>Polyarthra</i> <i>Pompholyx</i> <i>Ptygura</i> <i>Synchaeta</i> <i>Testudinella</i> <i>Trichocerca</i>
Family	Conochilidae Lecanidae

APPENDIX B

Table 1: Species level identifications completed by the author for microcrustaceans from 30 lakes in the Northern Appalachian ecoregion. Forty four distinct taxonomic units were identified. Numbers in parenthesis indicate the number of lakes an organism was found in.

Copepoda	Cladocera
Cyclopoida	<i>Bosmina longirostris</i> (12)
<i>Acanthocyclops brevispinosus</i> (2)	<i>Ceriodaphnia dubia</i> (1)
<i>Acanthocyclops robustus</i> (1)	<i>Ceriodaphnia lacustris</i> (9)
<i>Cyclops scutifer</i> (5)	<i>Ceriodaphnia laticaudata</i> (1)
cyclopoid copepodite / male (28)	<i>Ceriodaphnia reticulata</i> (1)
<i>Diacyclops thomasi</i> (7)	<i>Chydorus sphaericus</i> (7)
<i>Eucyclops elegans</i> (1)	<i>Daphnia ambigua</i> (9)
<i>Macrocyclops albidus</i> (1)	<i>Daphnia catawba</i> (11)
<i>Mesocyclops edax</i> (22)	<i>Daphnia dubia</i> (2)
<i>Orthocyclops modestus</i> (3)	<i>Daphnia mendotae</i> (15)
	<i>Daphnia longiremis</i> (5)
Calanoida	<i>Daphnia parvula</i> (6)
<i>Aglaodiaptomus spatulocrenatus</i> (1)	<i>Daphnia pulex</i> (7)
Diaptomidae copepodite (20)	<i>Daphnia retrocurva</i> (6)
<i>Epischura</i> copepodite (7)	<i>Diaphanosoma</i> spp. (21)
<i>Epischura lacustris</i> (5)	<i>Eubosmina coregoni</i> (4)
<i>Epischura nordenskioldi</i> (6)	<i>Eubosmina hagmanni</i> (3)
<i>Leptodiaptomus minutus</i> (11)	<i>Eubosmina longispina</i> (7)
<i>Leptodiaptomus nudus</i> (1)	<i>Eubosmina tubicen</i> (6)
<i>Leptodiaptomus sicilis</i> (2)	<i>Holopedium gibberum</i> (16)
<i>Limnocalanus macrurus</i> (1)	<i>Sida crystalline</i> (2)
<i>Onychodiaptomus sanguineus</i> (1)	
<i>Skistodiaptomus oregonensis</i> (3)	
<i>Skistodiaptomus pallidus</i> (5)	
<i>Skistodiaptomus pygmaeus</i> (7)	
<i>Skistodiaptomus reighardi</i> (2)	

APPENDIX C

Table 1: Aggregated identifications completed by the author for microcrustaceans from 30 lakes in the Northern Appalachian ecoregion. Twenty three genera and nine families were identified. Numbers in parenthesis indicate the number of lakes a group was found in.

Genus	Family
<i>Acathanocyclops</i> (3)	Bosminidae (23)
<i>Aglaodiaptomus</i> (1)	Centropagidae (1)
<i>Bosmina</i> (12)	Chydoridae (7)
<i>Ceriodaphnia</i> (11)	Cyclopidae (30)
<i>Chydorus</i> (7)	Daphniidae (30)
<i>Cyclops</i> (5)	Diaptomidae (29)
cyclopoid copepodite / male (28)	Holopedidae (16)
<i>Daphnia</i> (29)	Temoridae (12)
<i>Diacyclops</i> (7)	Sididae (21)
<i>Diaphanosoma</i> (21)	
Diaptomidae copepodite (20)	
<i>Epischura</i> (12)	
<i>Eubosmina</i> (16)	
<i>Eucyclops</i> (1)	
<i>Holopedium</i> (16)	
<i>Leptodiaptomus</i> (14)	
<i>Limnocalanus</i> (1)	
<i>Macrocyclus</i> (1)	
<i>Mesocyclops</i> (22)	
<i>Onchyodiaptomus</i> (1)	
<i>Orthocyclops</i> (3)	
<i>Sida</i> (2)	
<i>Skistodiaptomus</i> (17)	

APPENDIX D

Table 1: Site identification numbers and sampling date for 30 lakes from the Northern Appalachian ecoregion. All sites microcrustacean communities were analyzed, a NI indicates the site was not included in the rotifer analysis. Rotifers (N = 29).

Site ID	Date	Rotifer
NLA06608-0134	7/24/2007	
NLA06608-0369	7/26/2007	
NLA06608-0470	7/24/2007	
NLA06608-0550	8/1/2007	
NLA06608-0997	8/3/2007	
NLA06608-1045	8/29/2007	
NLA06608-3846	7/12/2007	
NLA06608-NELP-0253	8/8/2007	
NLA06608-NELP-0955	8/29/2007	
NLA06608-0754	7/2/2007	
NLA06608-0021	8/30/2007	
NLA06608-0341	9/18/2007	NI
NLA06608-0610	8/2/2007	
NLA06608-0690	8/22/2007	
NLA06608-1209	8/15/2007	
NLA06608-1906	7/20/2007	
NLA06608-ELS:1E1-128	8/10/2007	
NLA06608-2162	7/9/2007	
NLA06608-0562	8/21/2007	
NLA06608-1174	8/15/2007	
NLA06608-0037	7/13/2007	
NLA06608-0293	7/25/2007	
NLA06608-0401	8/27/2007	
NLA06608-0546	7/18/2007	
NLA06608-0582	7/19/2007	
NLA06608-0661	8/8/2007	
NLA06608-0753	7/19/2007	
NLA06608-0806	9/7/2007	
NLA06608-1010	8/9/2007	
NLA06608-ELS:1C2-032	7/12/2007	

APPENDIX E

Table 1: Site identification numbers and sampling date for the 48 lakes selected randomly from across the continental United States. All sites microcrustacean communities were analyzed, a NI indicates the site was not included in the rotifer analysis. Rotifers (N = 31).

Site ID	Date	Rotifer
NLA06608-1992	9/20/2007	
NLA06608-0993	9/20/2007	NI
NLA06608-3846	7/12/2007	
NLA06608-0038	8/27/2007	
NLA06608-0421	6/28/2007	
NLA06608-0401	8/27/2007	
NLA06608-0367	8/23/2007	NI
NLA06608-0378	6/26/2007	
NLA06608-0126	6/21/2007	
NLA06608-0480	8/24/2007	NI
NLA06608-1348	8/8/2007	
NLA06608-0031	6/13/2007	
NLA06608-0319	7/22/2007	
NLA06608-0459	7/16/2007	
NLA06608-R322	9/4/2007	
NLA06608-1775	8/24/2007	
NLA06608-3320	9/17/2007	
NLA06608-3616	7/30/2007	NI
NLA06608-0456	8/9/2007	
NLA06608-2332	8/9/2007	NI
NLA06608-0804	8/19/2007	
NLA06608-0659	6/26/2007	
NLA06608-R723	8/23/2007	
NLA06608-0254	6/21/2007	
NLA06608-0744	7/18/2007	
NLA06608-1015	8/14/2007	NI
NLA06608-1108	6/21/2007	
NLA06608-1840	8/15/2007	
NLA06608-1390	7/19/2007	
NLA06608-1771	8/28/2007	
NLA06608-MN:56-0306	9/17/2007	
NLA06608-1303	8/8/2007	NI
NLA06608-0079	8/16/2007	NI
NLA06608-0614	6/27/2007	NI
NLA06608-1748	7/31/2007	
NLA06608-2450	7/24/2007	NI
NLA06608-2726	9/12/2007	NI
NLA06608-R10COUNCI	8/22/2007	NI
NLA06608-0209	9/27/2007	NI

NLA06608-0449	7/26/2007	NI
NLA06608-1190	6/25/2007	NI
NLA06608-2685	9/14/2007	
NLA06608-3157	7/11/2007	
NLA06608-0770	5/8/2007	NI
NLA06608-2345	8/16/2007	
NLA06608-NV:3	9/20/2007	
NLA06608-1521	8/14/2007	
NLA06608-1151	7/17/2007	NI

APPENDIX F

Table 1: Site identification numbers and sampling date for the 48 lakes selected by using the linear regression model ($y = 4.2x - 24.8$; $r^2 = 0.70$) from Gillooly and Dodson (2000). All sites microcrustacean communities were analyzed, a NI indicates the site was not included in the rotifer analysis. Rotifers (N = 43).

Site ID	Date	Rotifer
NLA06608-1617	8/8/2007	
NLA06608-0403	8/6/2007	
NLA06608-0062	8/9/2007	
NLA06608-MN:15-0010	8/9/2007	
NLA06608-MN:03-0029	8/8/2007	
NLA06608-1998	8/6/2007	
NLA06608-0878	8/1/2007	NI
NLA06608-2134	8/1/2007	
NLA06608-0086	8/2/2007	
NLA06608-1334	7/31/2007	
NLA06608-0842	8/1/2007	
NLA06608-2634	7/30/2007	NI
NLA06608-0881	7/30/2007	
NLA06608-9999	7/31/2007	
NLA06608-0369	7/26/2007	
NLA06608-1674	7/27/2007	
NLA06608-2250	7/29/2007	
NLA06608-0658	7/26/2007	NI
NLA06608-2450	7/24/2007	NI
NLA06608-0470	7/24/2007	
NLA06608-1450	7/24/2007	
NLA06608-0837	7/19/2007	
NLA06608-0677	7/17/2007	
NLA06608-0010	7/17/2007	
NLA06608-1643	7/19/2007	
NLA06608-0546	7/18/2007	
NLA06608-0753	7/19/2007	
NLA06608-0619	7/18/2007	
NLA06608-1679	7/15/2007	
NLA06608-4413	7/18/2007	
NLA06608-0582	7/19/2007	
NLA06608-1884	7/18/2007	
NLA06608-0860	7/19/2007	
NLA06608-0037	7/13/2007	
NLA06608-0562	7/13/2007	
NLA06608-0006	7/17/2007	
NLA06608-0149	7/18/2007	
NLA06608-0962	7/17/2007	

NLA06608-1268	7/17/2007	
NLA06608-2036	7/11/2007	
NLA06608-3846	7/12/2007	
NLA06608-0235	7/16/2007	
NLA06608-2283	7/17/2007	
NLA06608-2891	7/16/2007	
NLA06608-0016	7/11/2007	
NLA06608-1401	7/11/2007	
NLA06608-0692	7/10/2007	NI
NLA06608-2507	7/11/2007	

APPENDIX G

Table 1: Site identification numbers and sampling date for the 48 lakes selected randomly above 40° latitude. All sites microcrustacean communities were analyzed, a NI indicates the site was not included in the rotifer analysis. Rotifers (N = 32).

Site ID	Date	Rotifer
NLA06608-0065	7/17/2007	
NLA06608-0064	6/18/2007	NI
NLA06608-3153	9/25/2007	
NLA06608-R10RAINYL	8/19/2007	
NLA06608-1857	7/25/2007	NI
NLA06608-0254	6/21/2007	
NLA06608-1089	7/20/2007	
NLA06608-2753	8/30/2007	
NLA06608-1262	7/9/2007	
NLA06608-0275	6/21/2007	NI
NLA06608-1377	7/22/2007	
NLA06608-0851	6/5/2007	NI
NLA06608-MN:06-0002	9/6/2007	NI
NLA06608-1575	7/24/2007	NI
NLA06608-0561	8/9/2007	NI
NLA06608-2634	7/30/2007	NI
NLA06608-0038	8/27/2007	
NLA06608-2135	8/20/2007	NI
NLA06608-9999	7/31/2007	
NLA06608-0806	9/7/2007	
NLA06608-2250	7/29/2007	
NLA06608-0993	9/20/2007	NI
NLA06608-WI:SY	7/17/2007	
NLA06608-0997	8/3/2007	
NLA06608-1450	7/24/2007	
NLA06608-0053	9/27/2007	NI
NLA06608-1034	8/16/2007	
NLA06608-1562	6/11/2007	NI
NLA06608-0753	7/19/2007	
NLA06608-1544	7/25/2007	
NLA06608-1521	8/14/2007	
NLA06608-1989	8/2/2007	NI
NLA06608-0290	7/11/2007	
NLA06608-0690	8/22/2007	
NLA06608-3608	8/16/2007	
NLA06608-0037	9/5/2007	
NLA06608-0006	8/30/2007	
NLA06608-1835	7/24/2007	
NLA06608-0043	8/15/2007	

NLA06608-3035	7/25/2007	
NLA06608-1243	8/7/2007	NI
NLA06608-0587	7/9/2007	NI
NLA06608-1631	8/8/2007	
NLA06608-0031	6/13/2007	
NLA06608-1199	8/15/2007	NI
NLA06608-MN:22-0074	9/11/2007	
NLA06608-0962	7/17/2007	
NLA06608-0091	7/10/2007	

APPENDIX H

Microcrustacean NMDS ordinations with graphical overlays for lakes in the Northern Appalachian ecoregion. Contains ordinations for species, genus and family. The five strongest environmental vectors were retained on the figure if their R^2 was ≥ 0.20 .

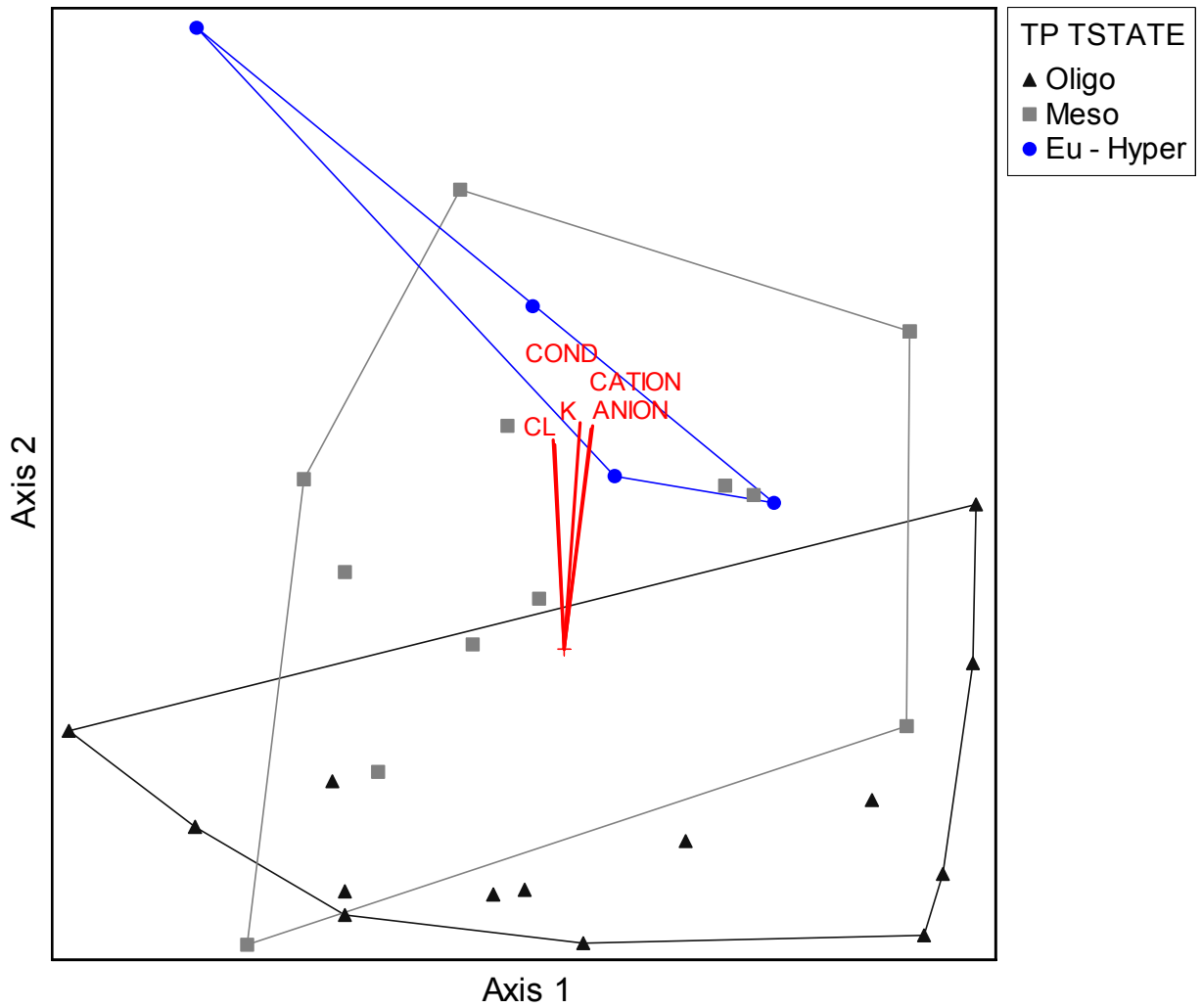


Figure 1: NMDS ordination with identifications to species and total phosphorus as the overlay.

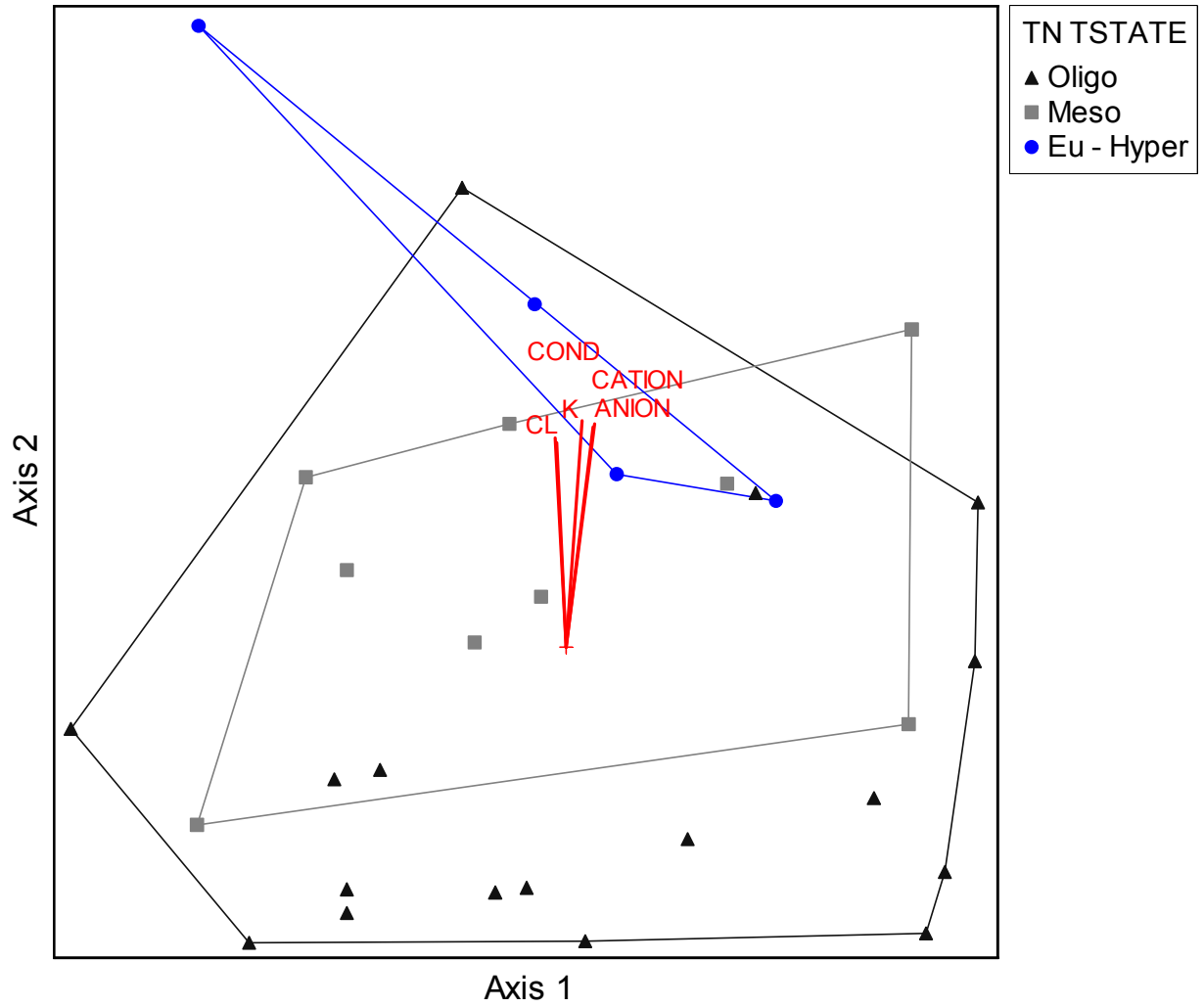


Figure 2: NMDS ordination with identifications to species and total nitrogen as the overlay.

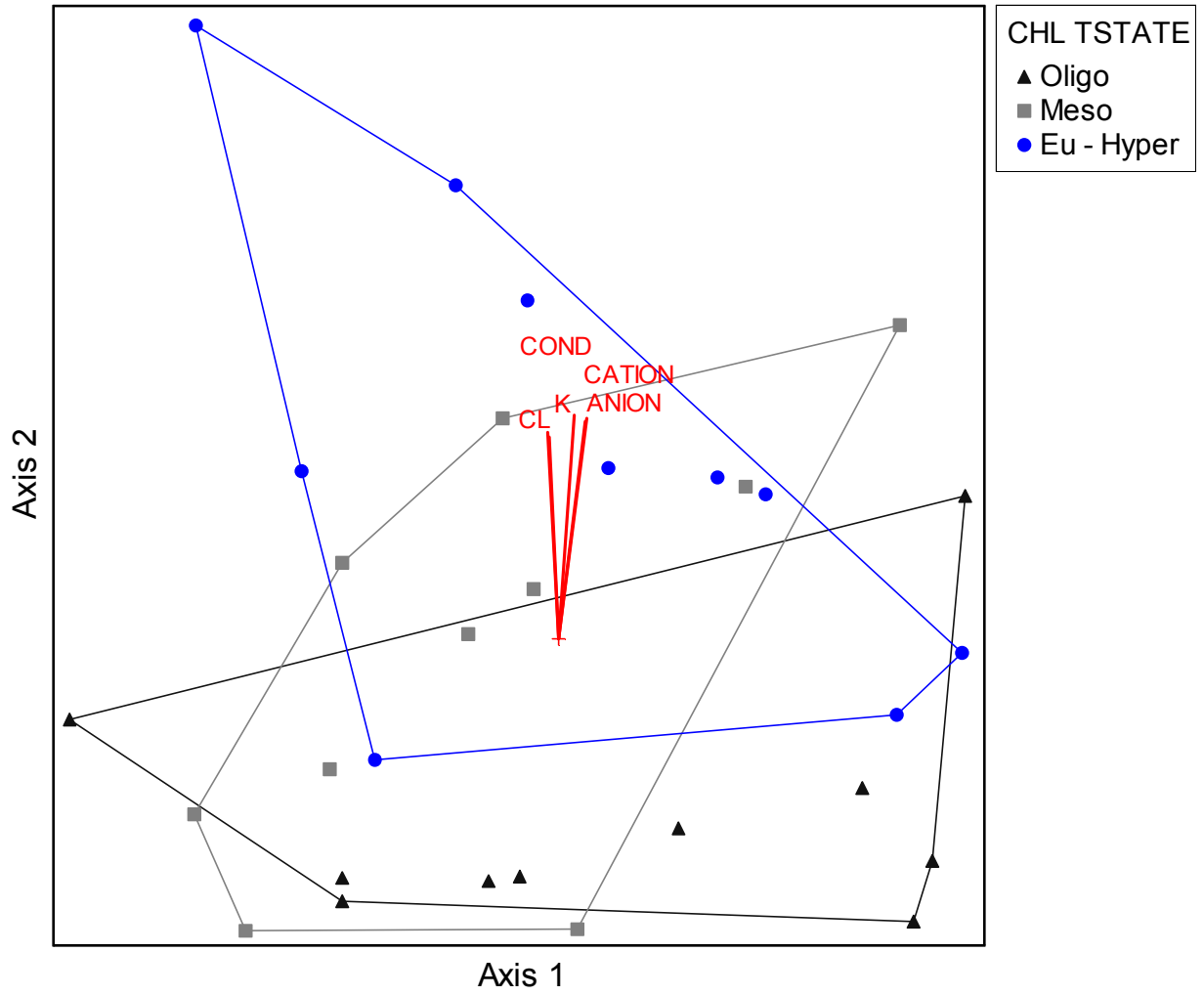


Figure 3: NMDS ordination with identifications to species and chlorophyll- α as the overlay.

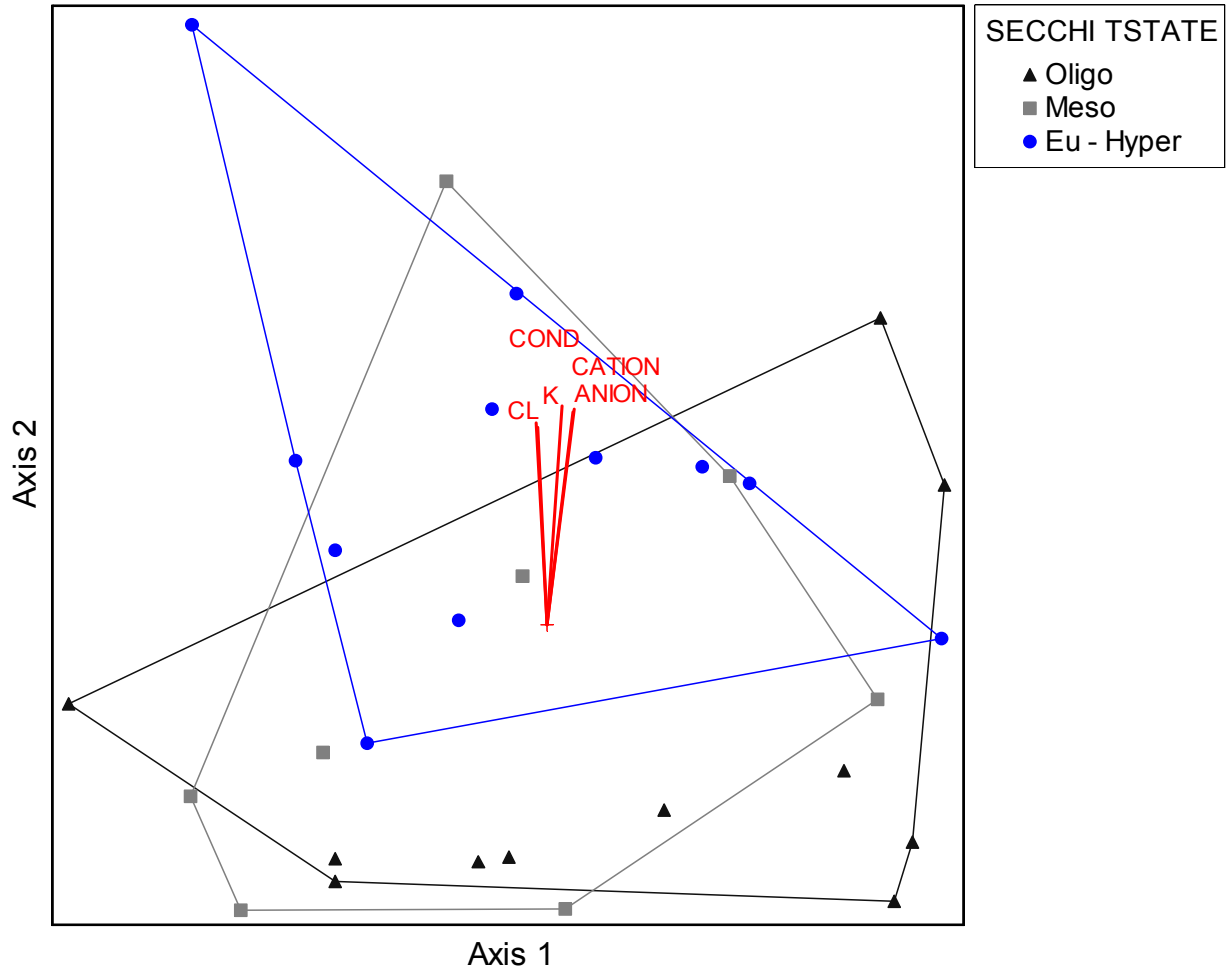


Figure 4: NMDS ordination with identifications to species and Secchi disk depth as the overlay.

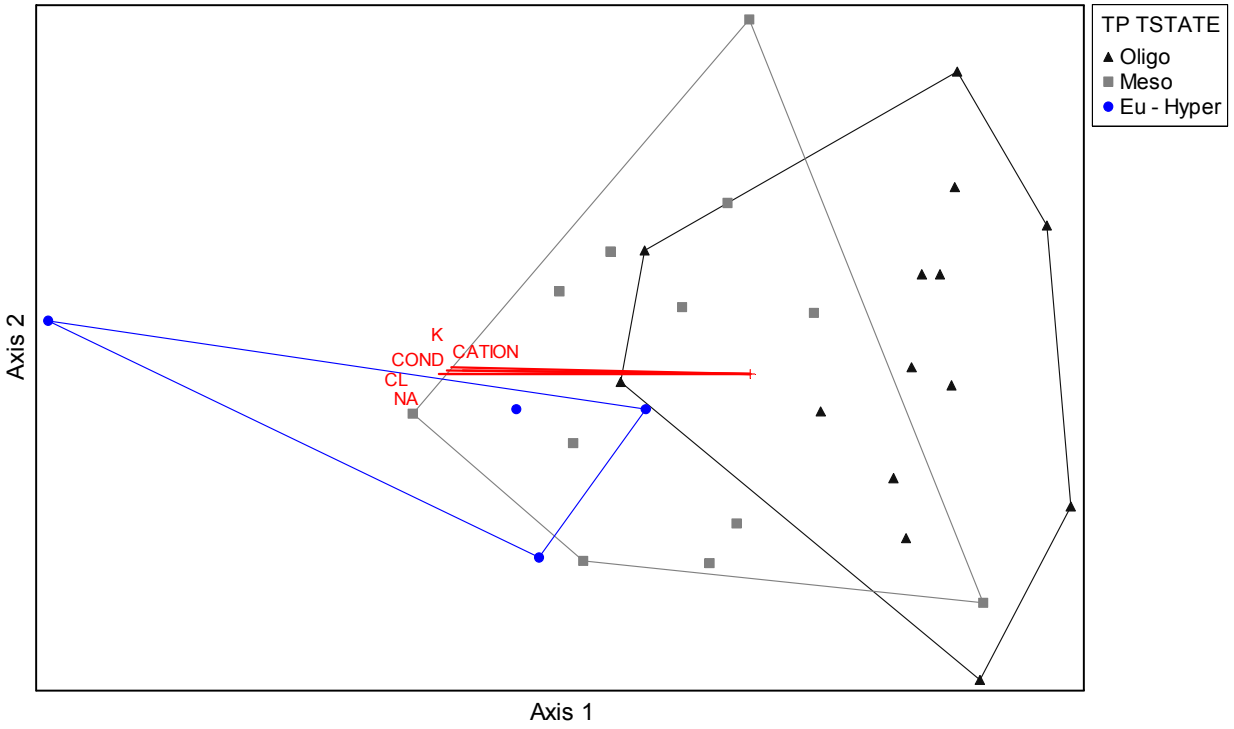


Figure 5: NMDS ordination with identifications to genus and total phosphorus as the overlay.

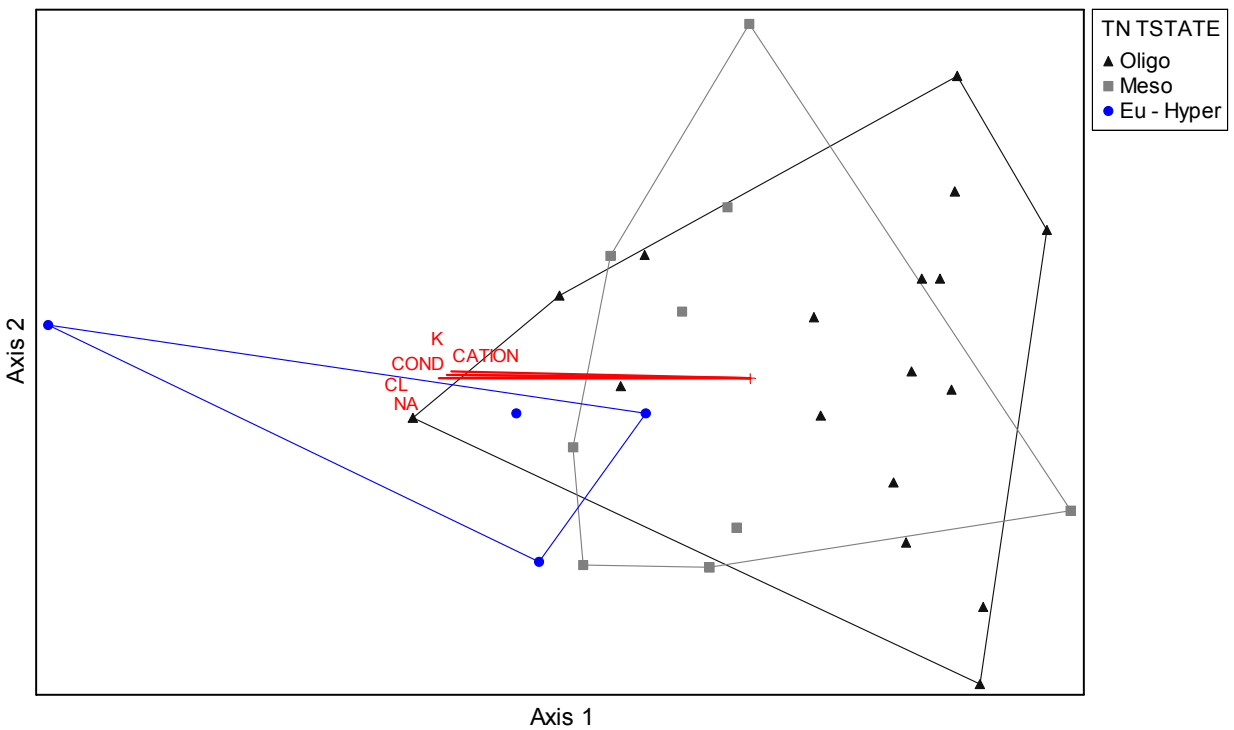


Figure 6: NMDS ordination with identifications to genus and total nitrogen as the overlay.

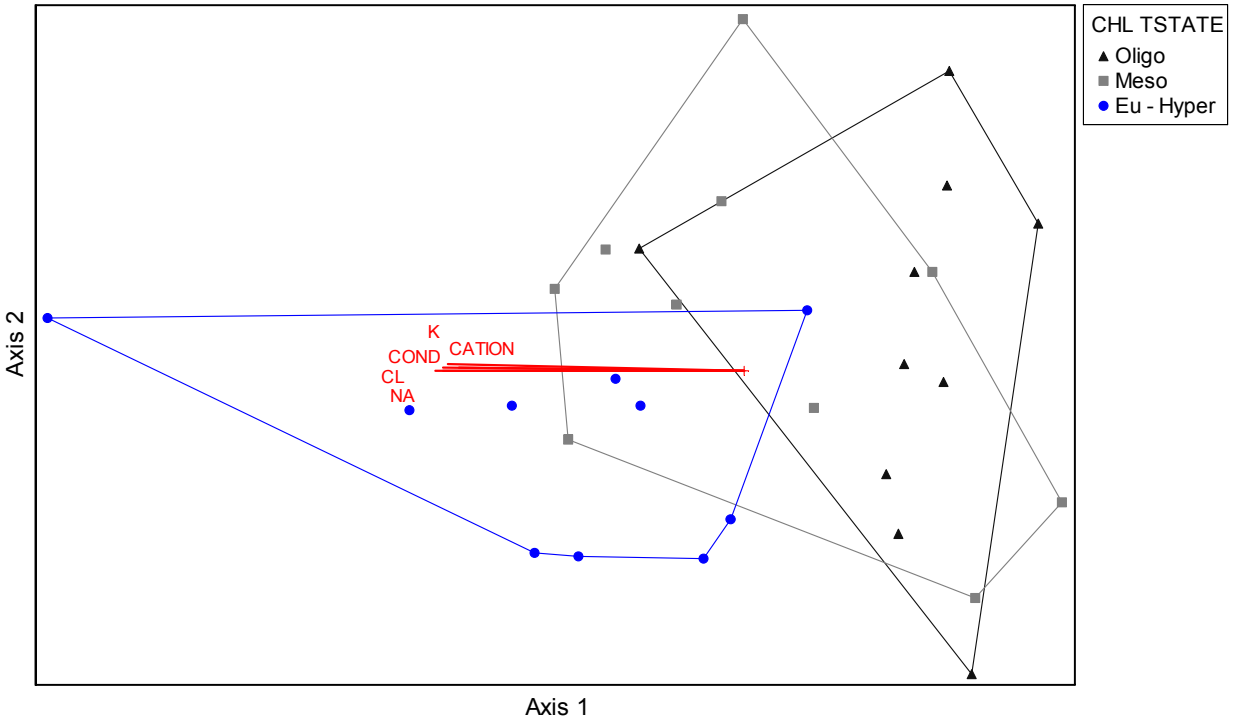


Figure 7: NMDS ordination with identifications to genus and chlorophyll- α as the overlay.

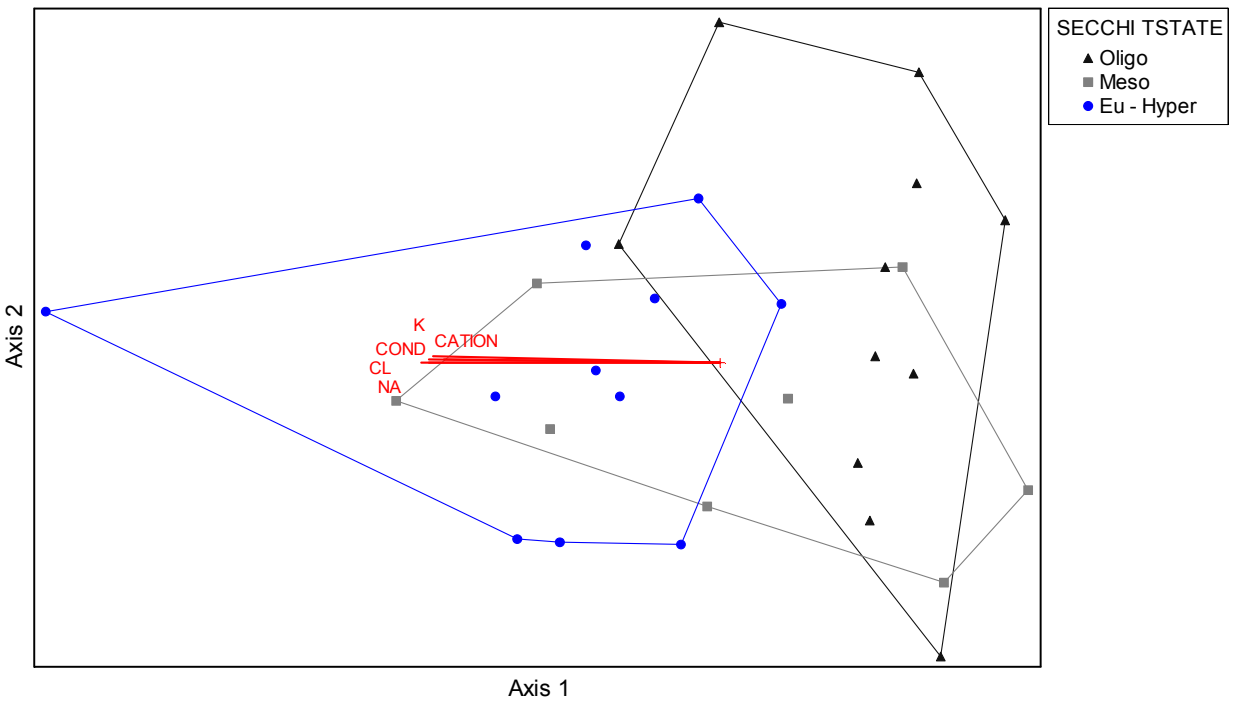


Figure 8: NMDS ordination with identifications to genus and Secchi disk depth as the overlay.

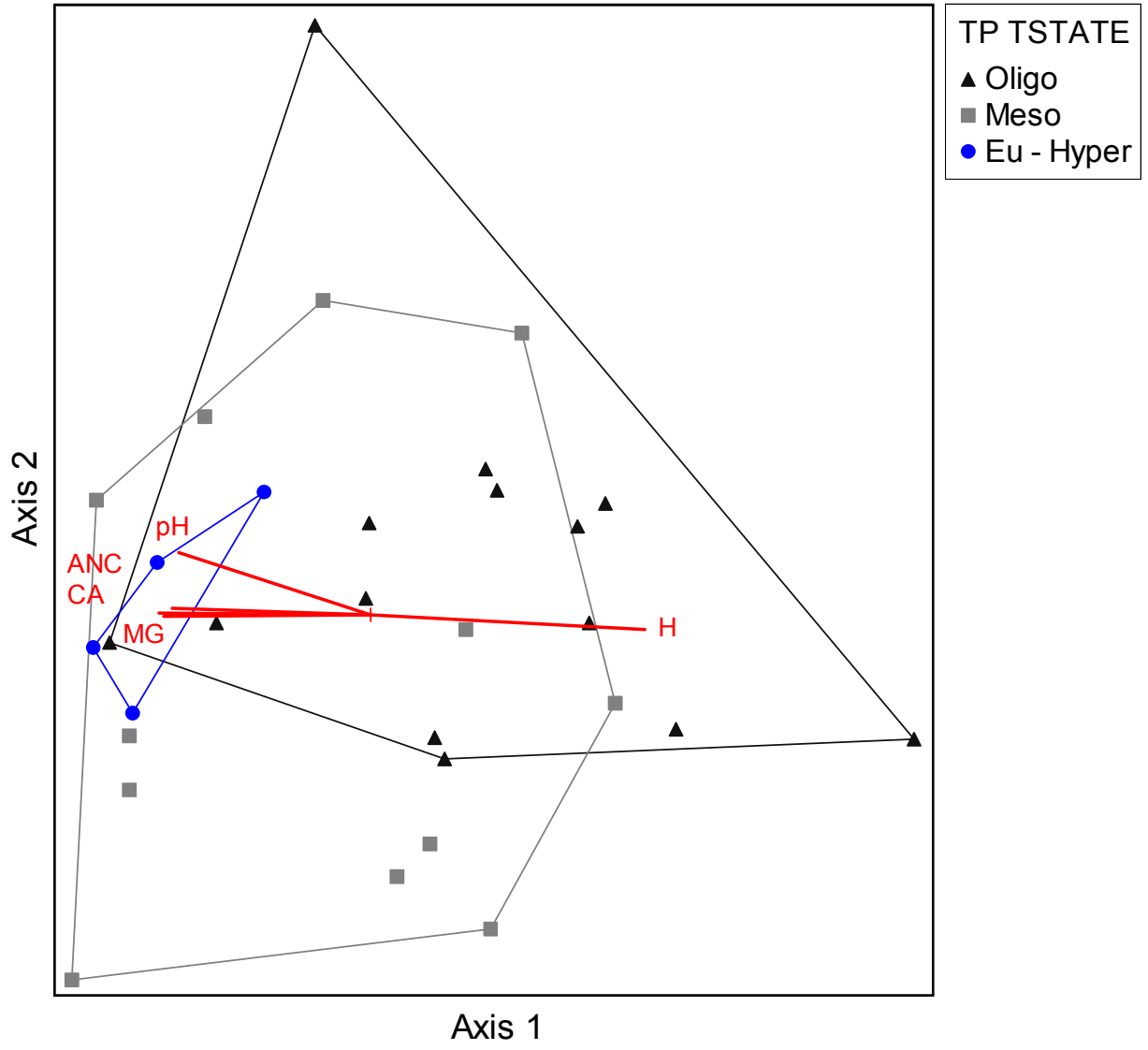


Figure 9: NMDS ordination with identifications to family and total phosphorus as the overlay.

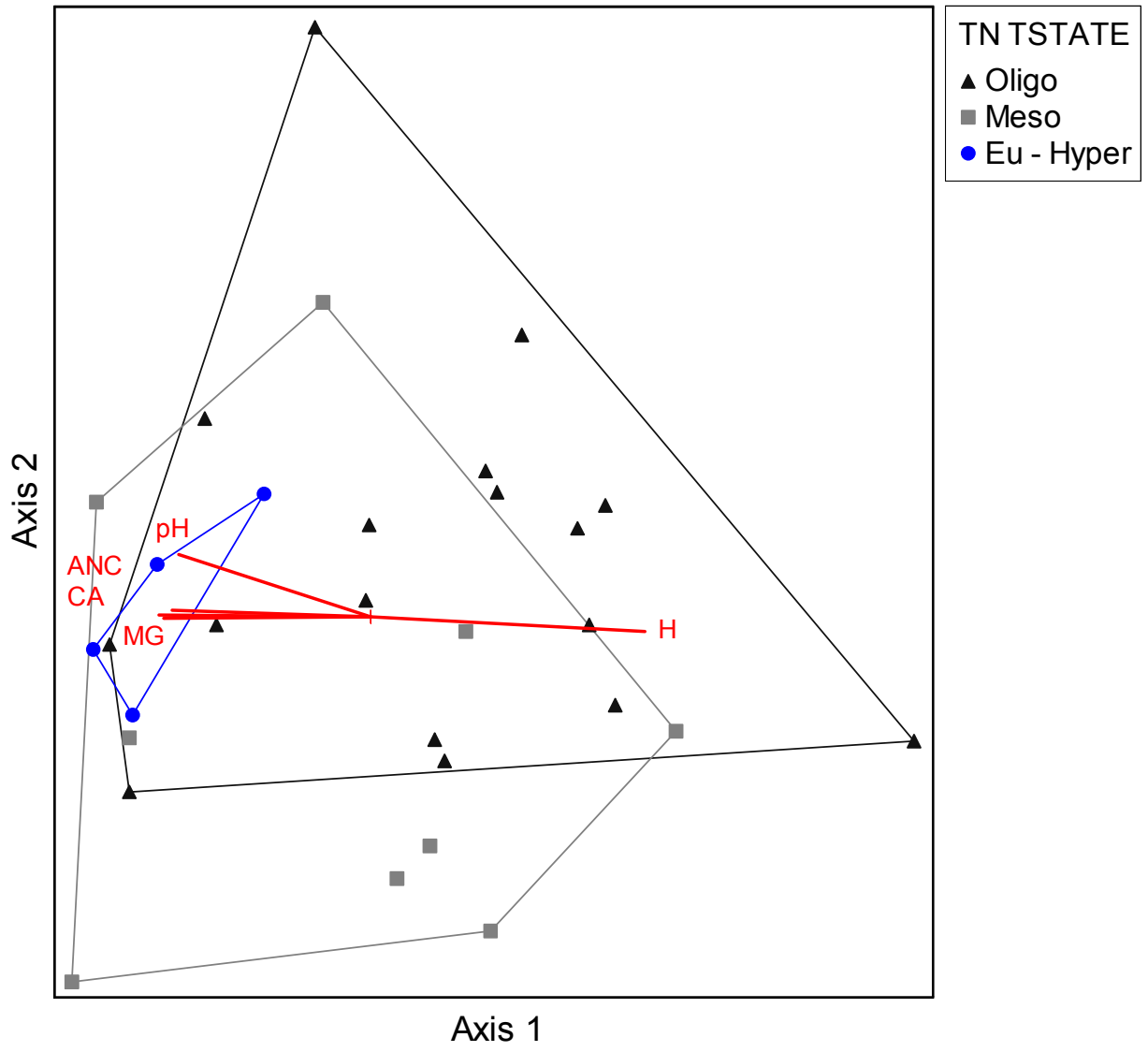


Figure 10: NMDS ordination with identifications to family and total nitrogen as the overlay.

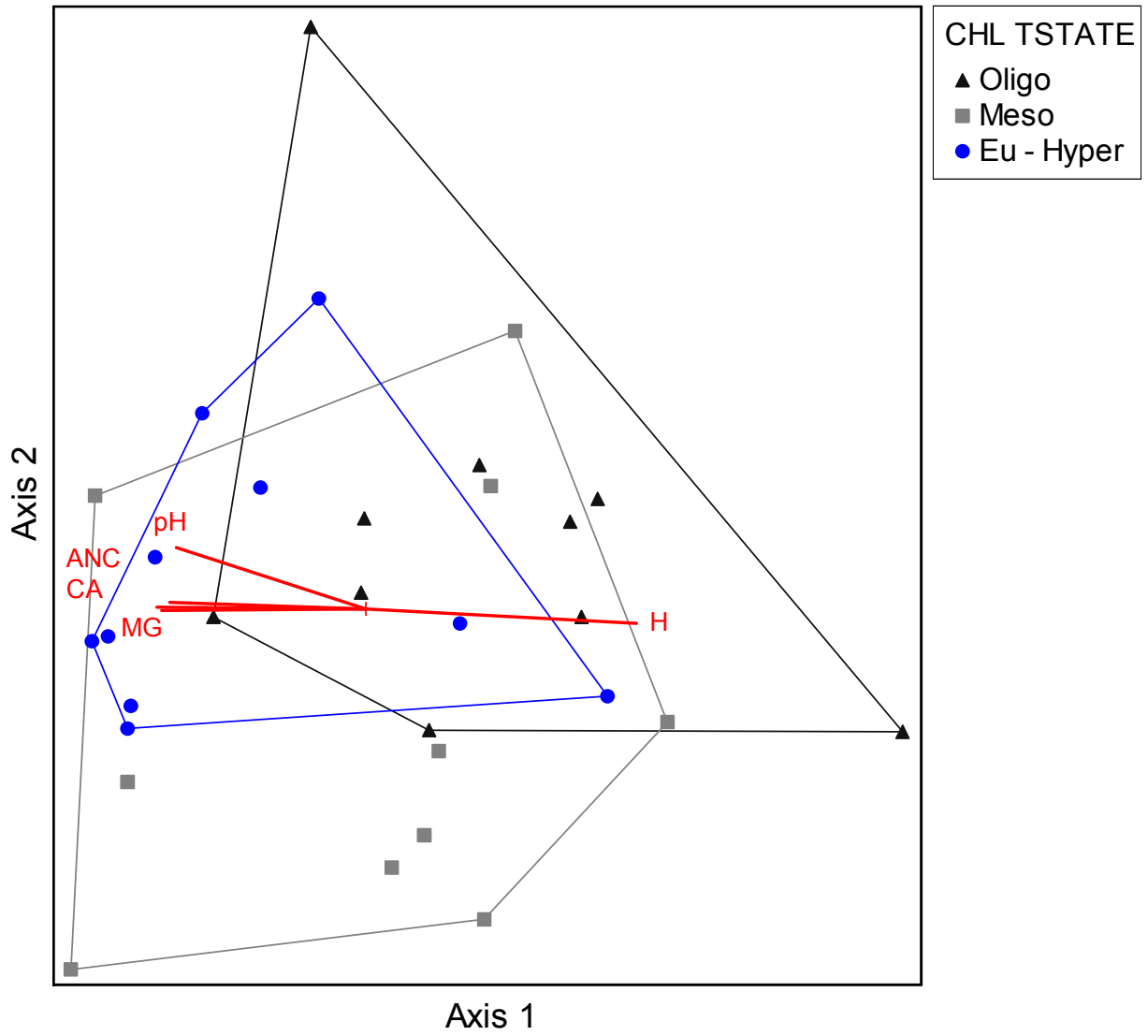


Figure 11: NMDS ordination with identifications to family and chlorophyll- α as the overlay.

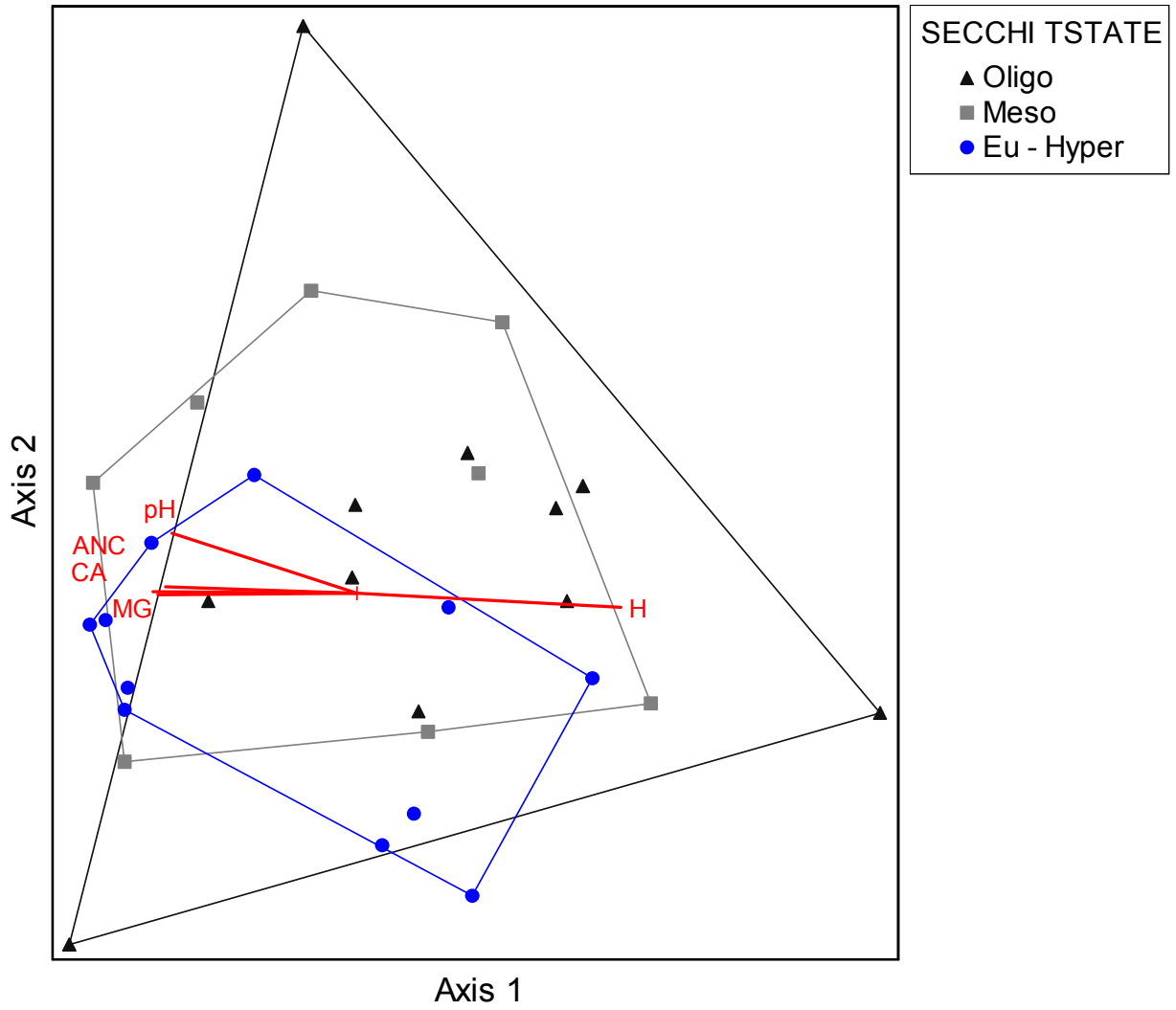


Figure 12: NMDS ordination with identifications to family and Secchi disk depth as the overlay.

APPENDIX I

Microcrustacean NMDS ordinations with graphical overlays for lakes selected via the linear regression model developed by Gillooly and Dodson (2000). The five strongest environmental vectors were retained on the figure if their R^2 was ≥ 0.20 .

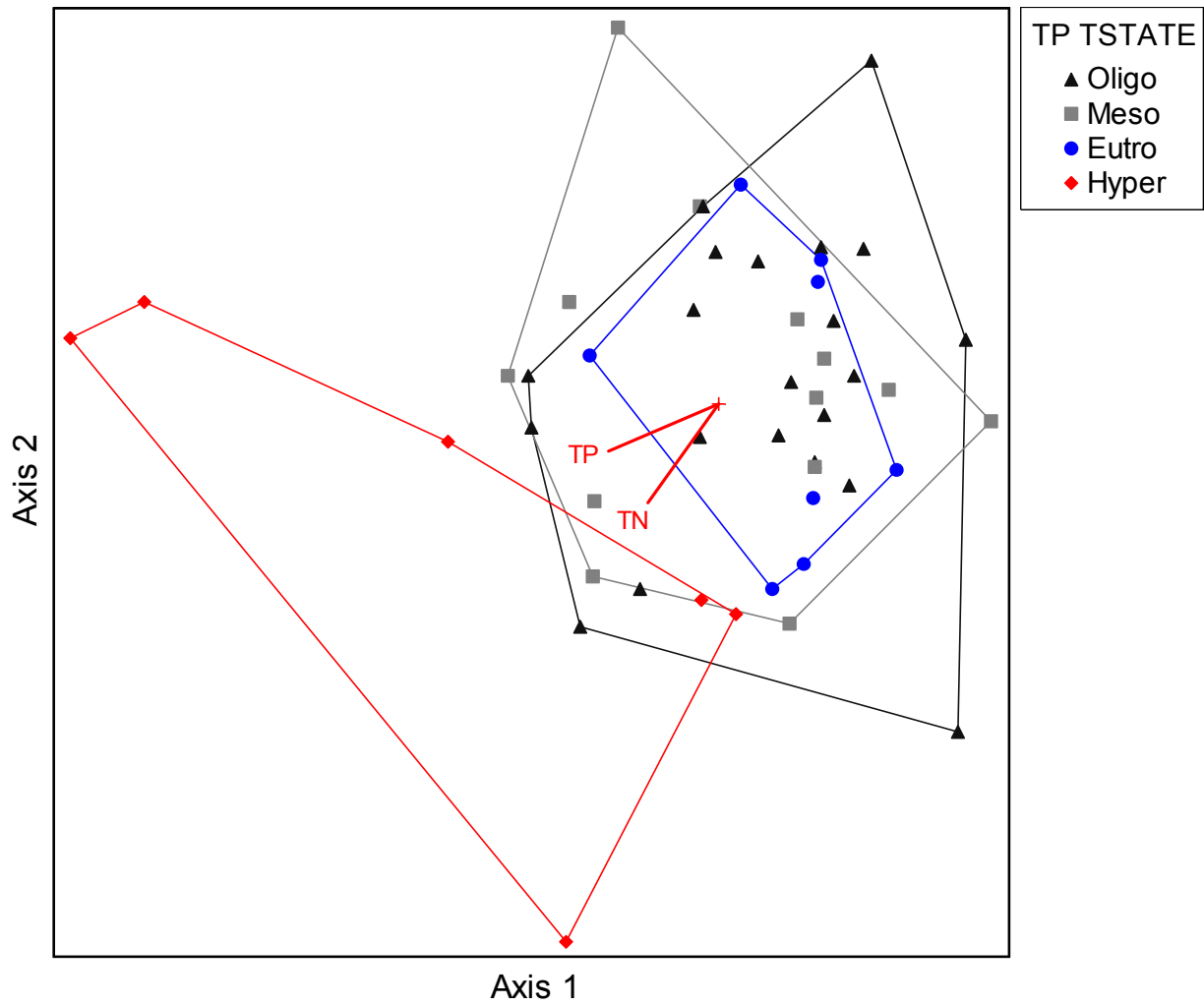


Figure 1: Microcrustacean NMDS ordination for lakes selected by the Gillooly and Dodson (2000) model with total phosphorus as the overlay.

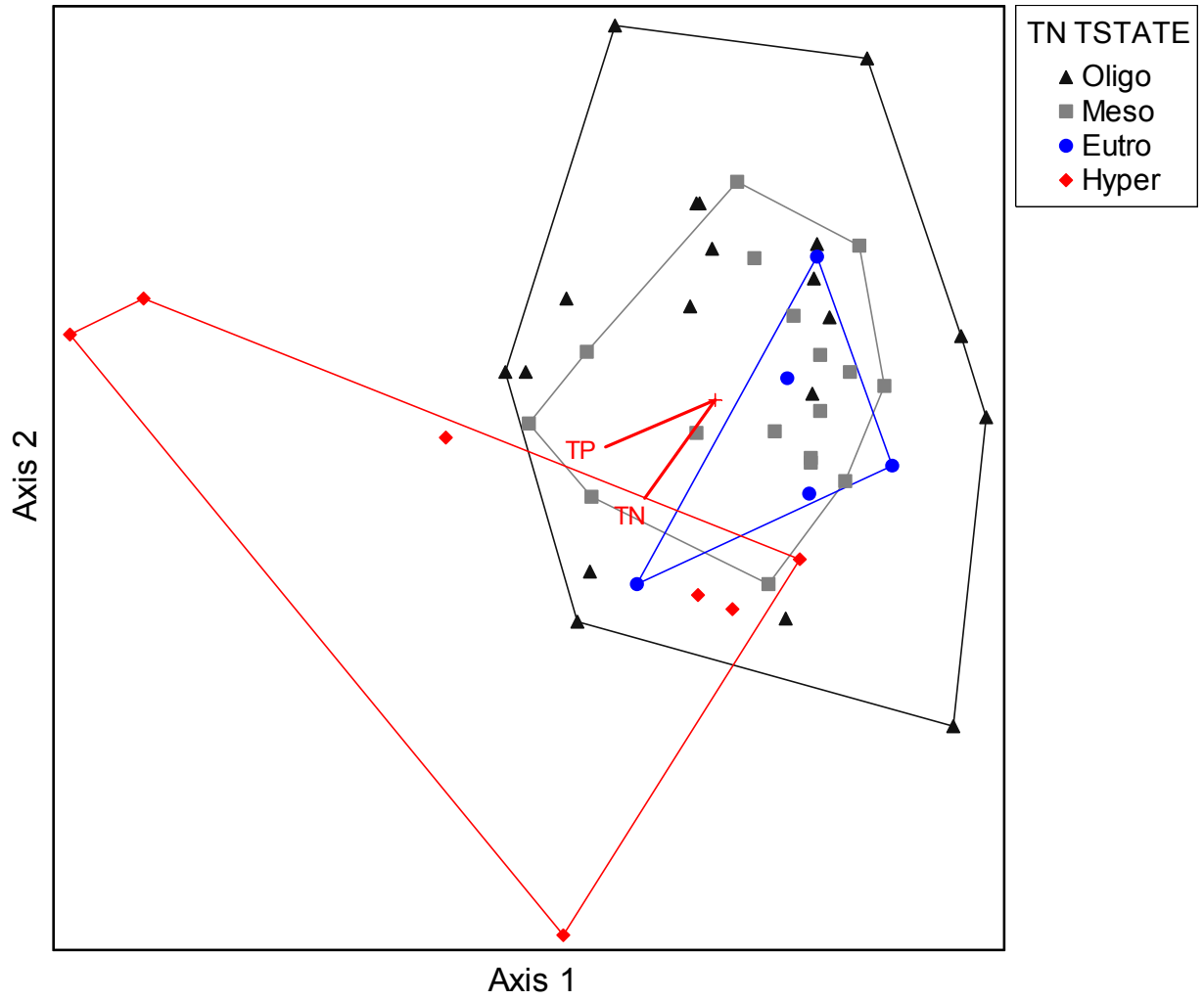


Figure 2: Microcrustacean NMDS ordination for lakes selected by the Gillooly and Dodson (2000) model with total nitrogen as the overlay.

APPENDIX J

Microcrustacean NMDS ordinations with graphical overlays for lakes selected randomly above 40° latitude. The five strongest environmental vectors were retained on the figure if their R^2 was ≥ 0.20 .

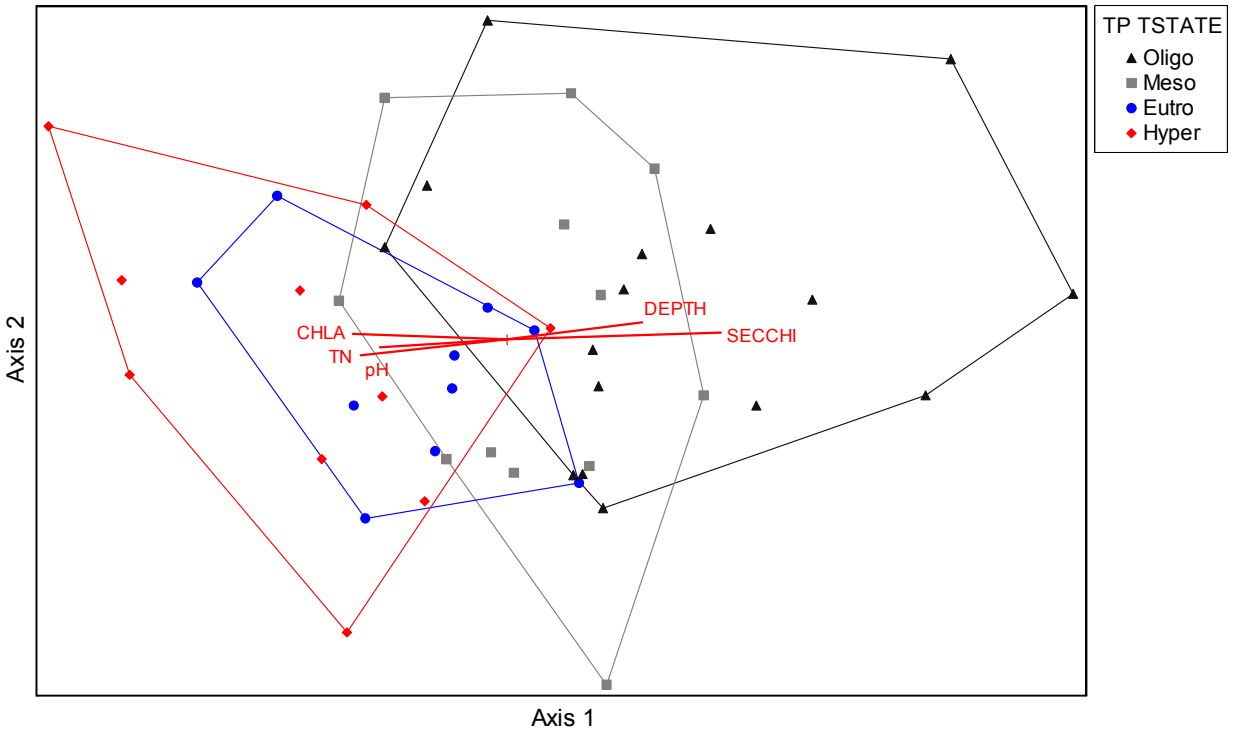


Figure 1: Microcrustacean NMDS ordination for lakes selected randomly above 40° latitude with total phosphorus as the overlay.

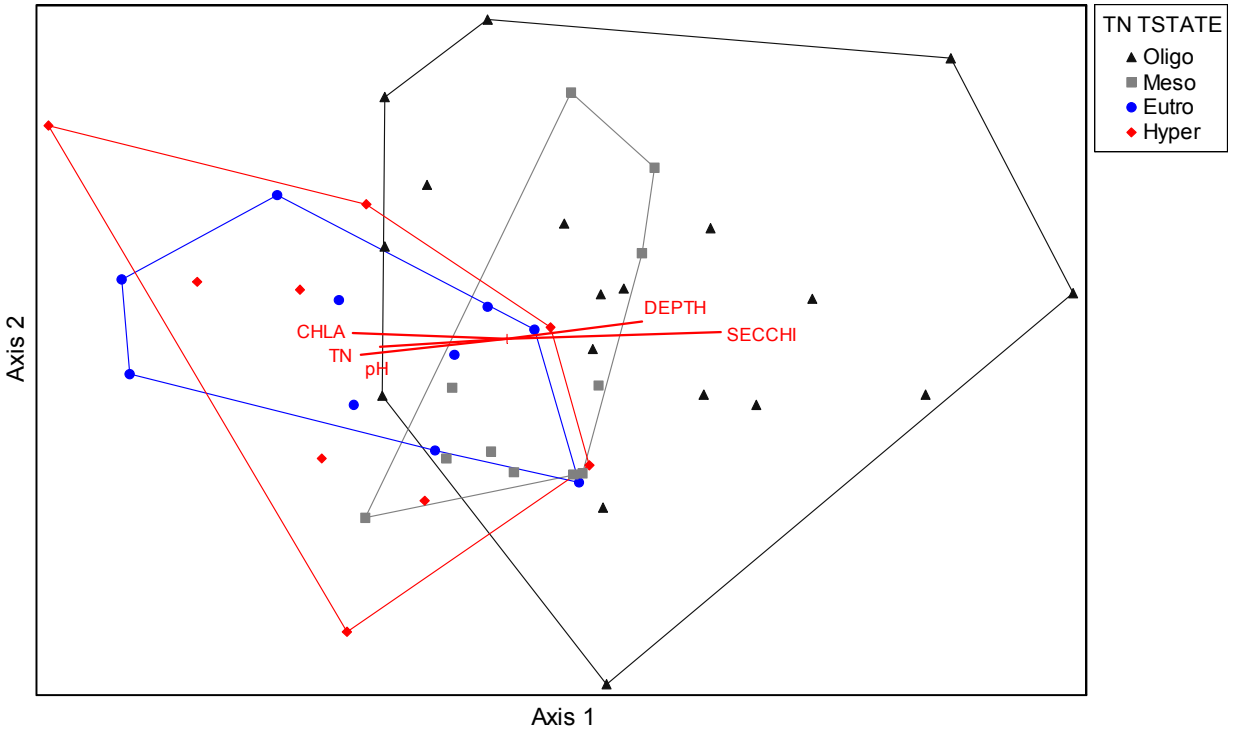


Figure 2: Microcrustacean NMDS ordination for lakes selected randomly above 40° latitude with total nitrogen as the overlay.

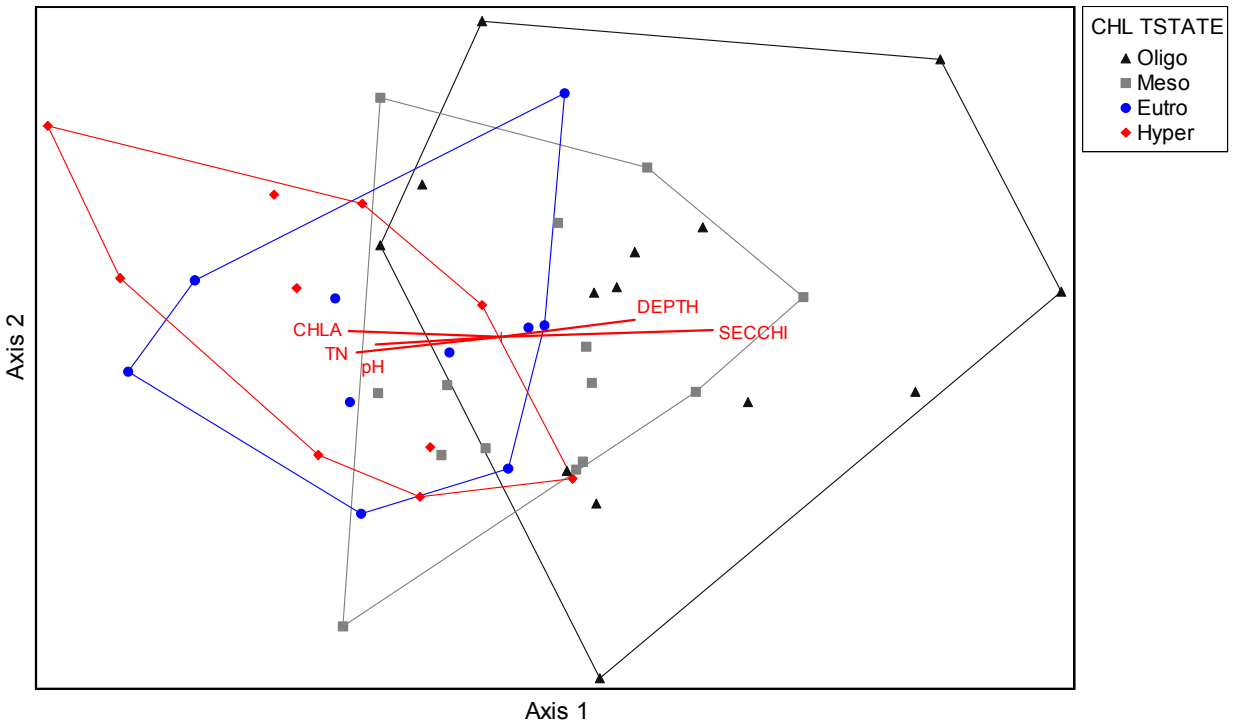


Figure 3: Microcrustacean NMDS ordination for lakes selected randomly above 40° latitude with chlorophyll- α as the overlay.

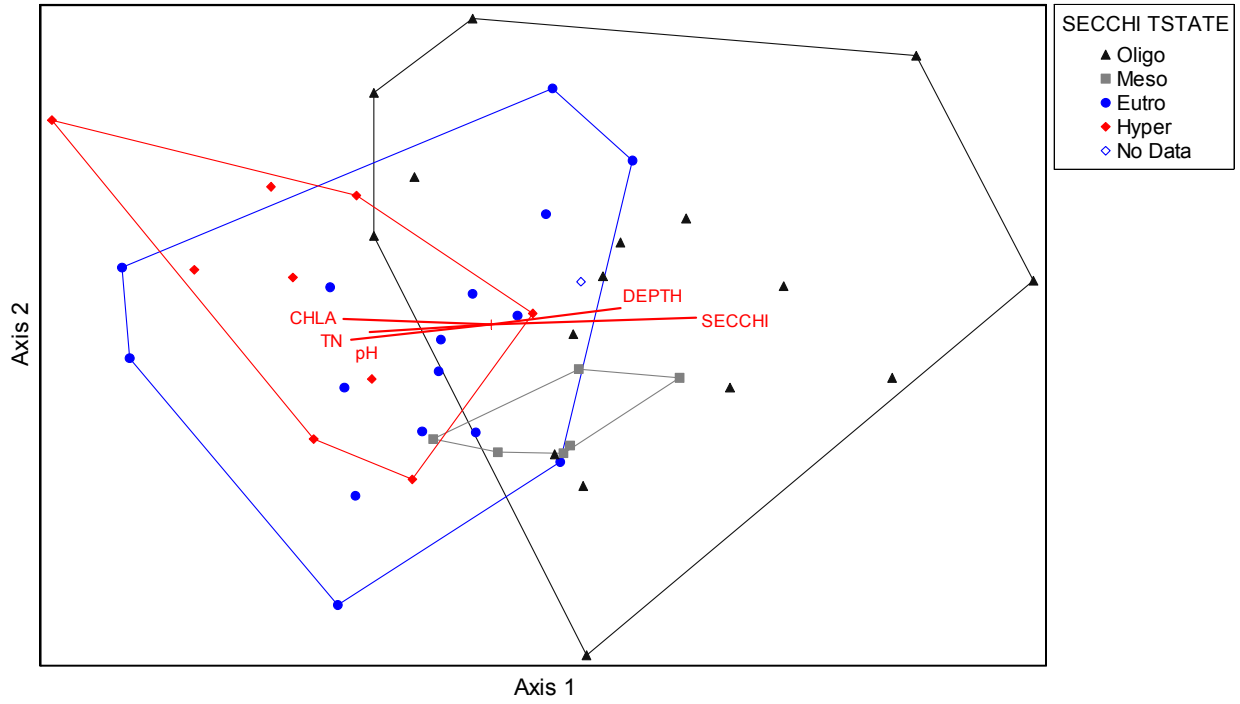


Figure 4: Microcrustacean NMDS ordination for lakes selected randomly above 40° latitude with Secchi disk depth as the overlay.

APPENDIX K

Microcrustacean NMDS ordinations with graphical overlays for lakes selected randomly from across the contiguous United States. The five strongest environmental vectors were retained on the figure if their R^2 was ≥ 0.20 .

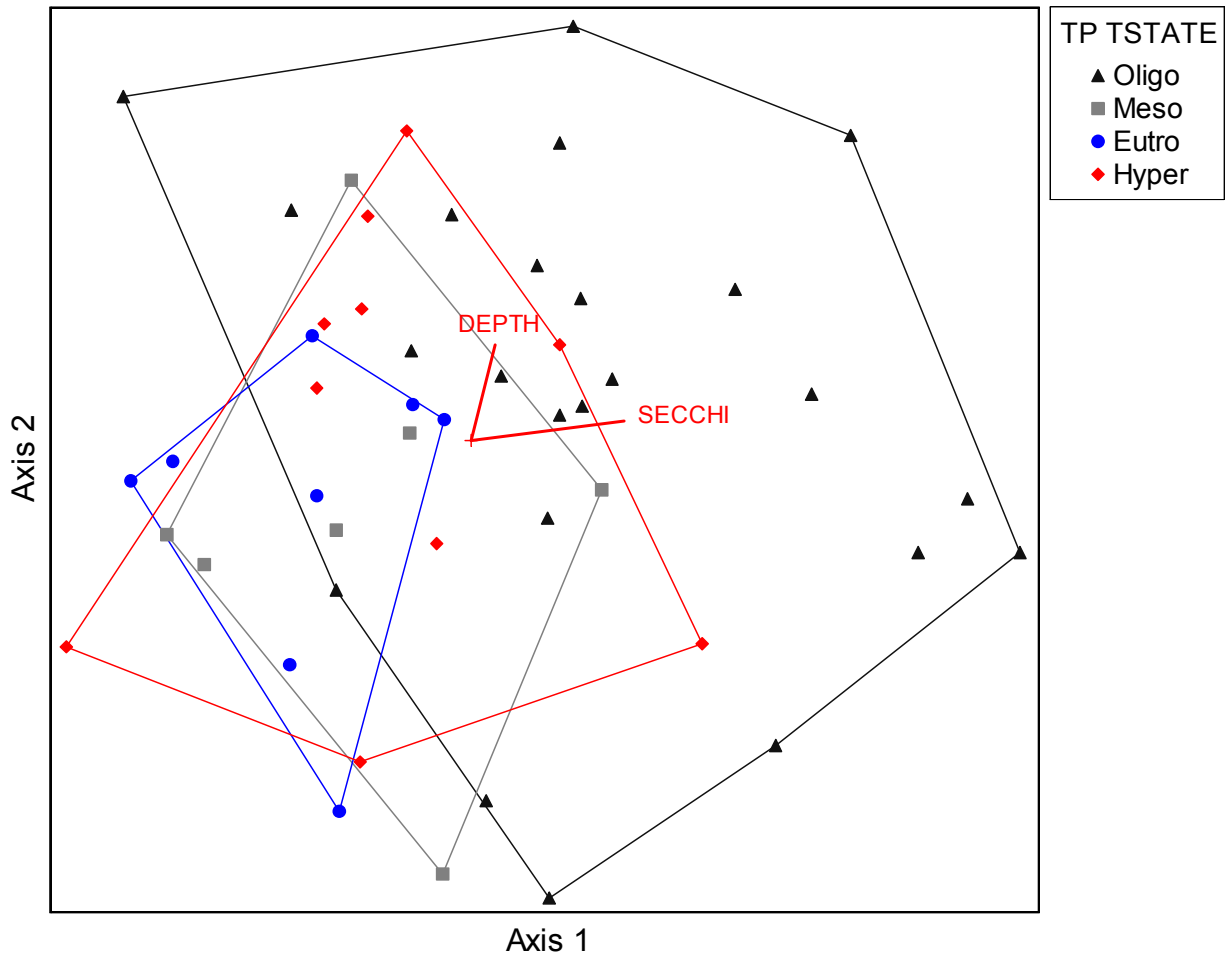


Figure 1: Microcrustacean NMDS ordination for lakes selected randomly from across the contiguous United States with total phosphorus as the overlay.

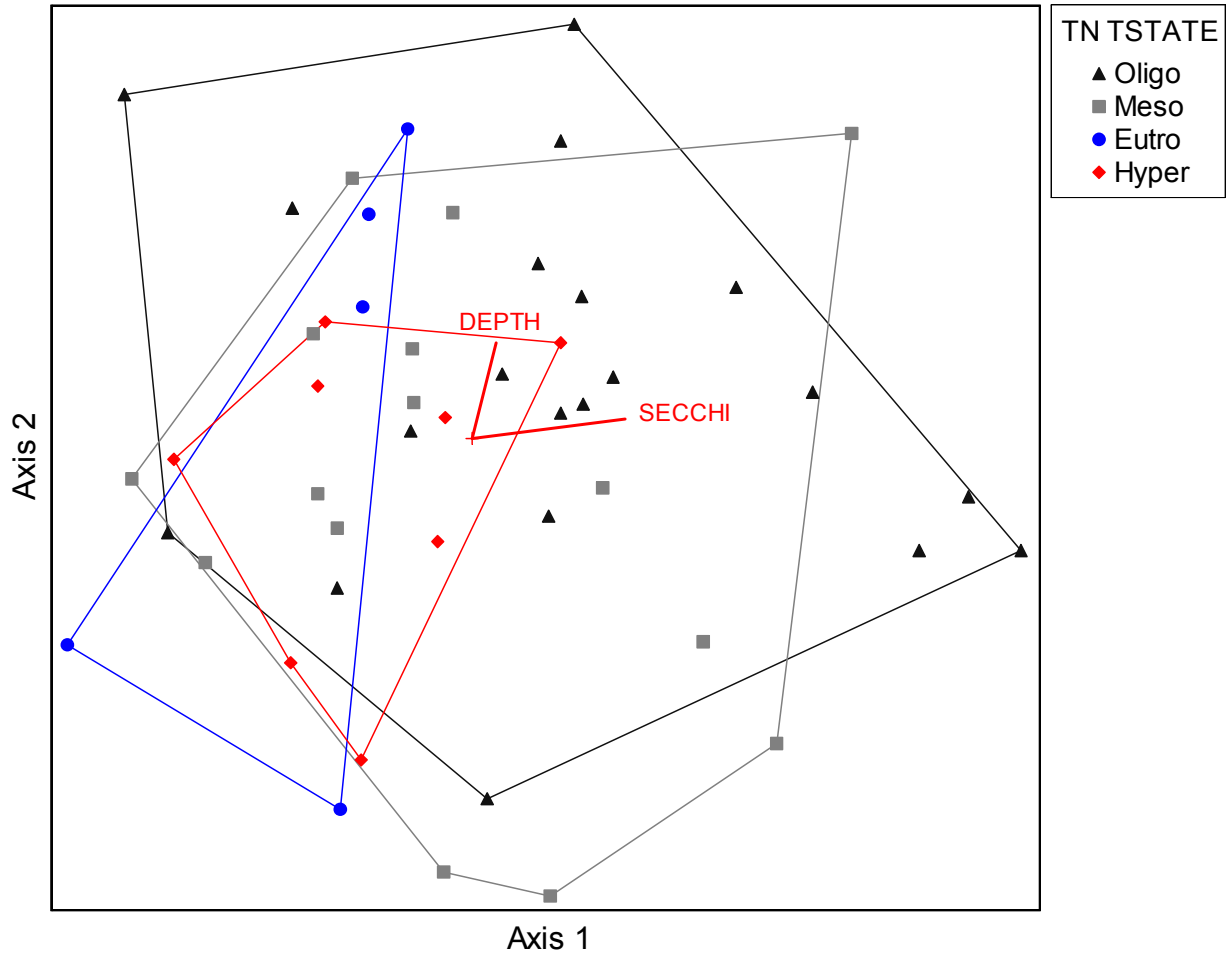


Figure 2: Microcrustacean NMDS ordination for lakes selected randomly from across the contiguous United States with total nitrogen as the overlay.

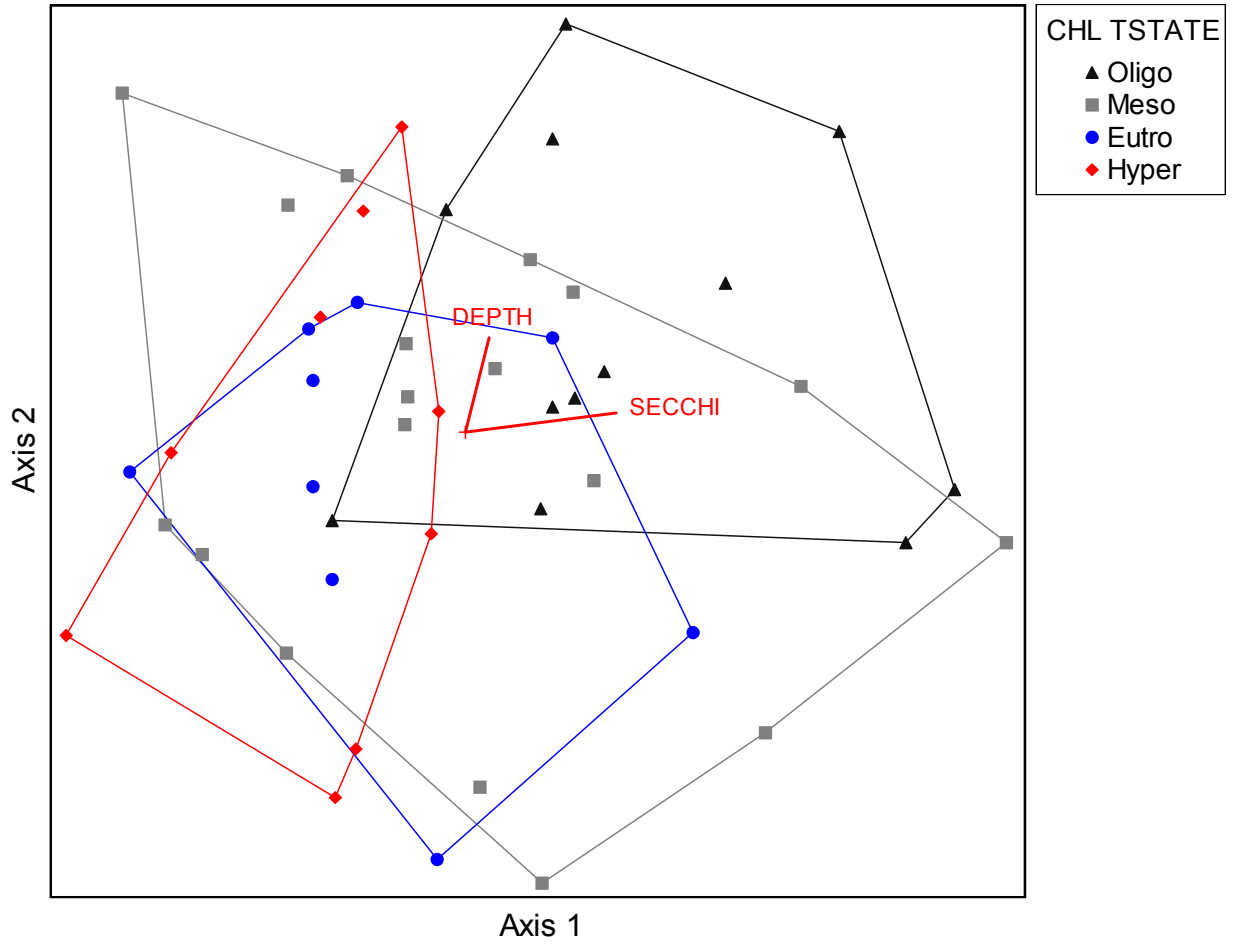


Figure 3: Microcrustacean NMDS ordination for lakes selected randomly from across the contiguous United States with chlorophyll- α as the overlay.

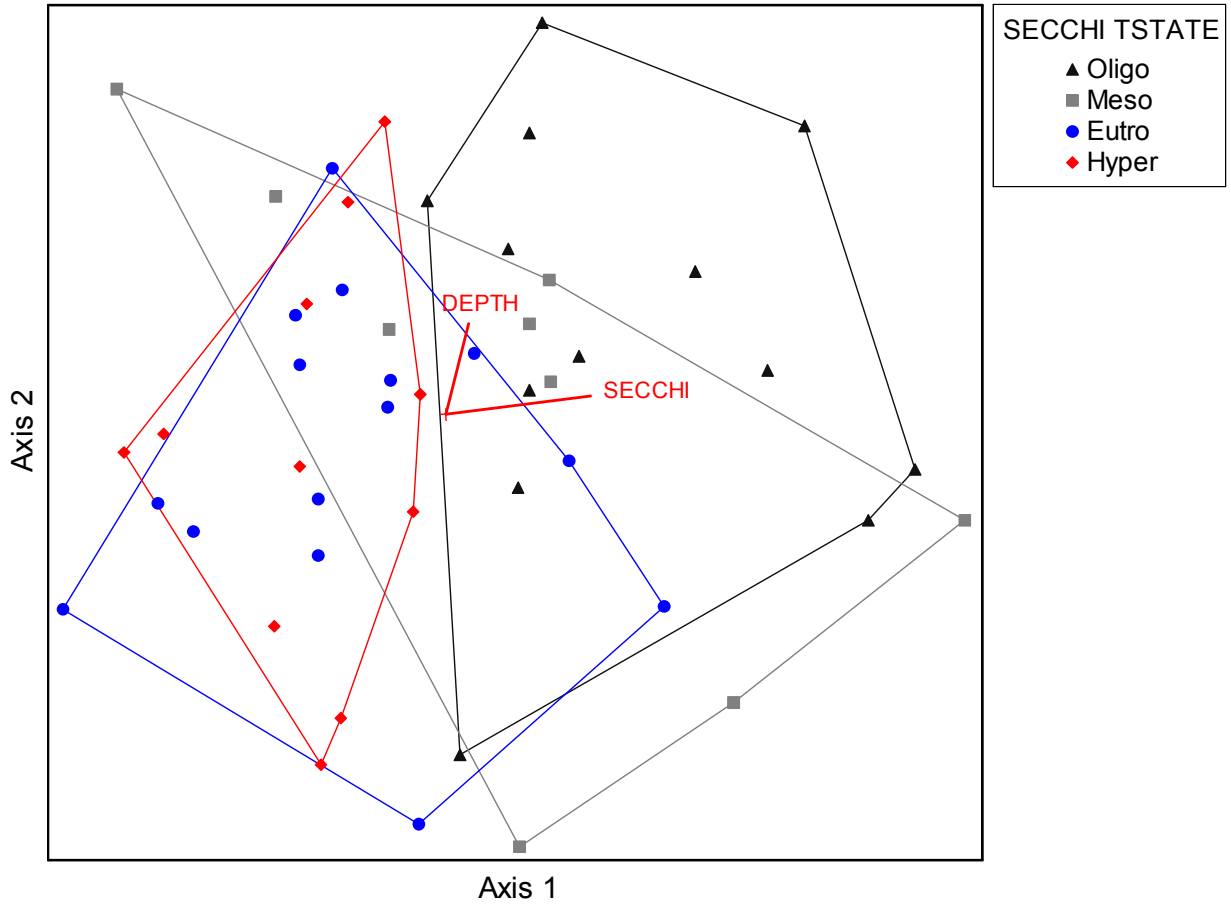


Figure 4: Microcrustacean NMDS ordination for lakes selected randomly from across the contiguous United States with Secchi disk depth as the overlay.

APPENDIX L

Rotifer NMDS ordinations with graphical overlays for lakes selected via the linear regression model developed by Gillooly and Dodson (2000). The five strongest environmental vectors were retained on the figure if their R^2 was ≥ 0.20 .

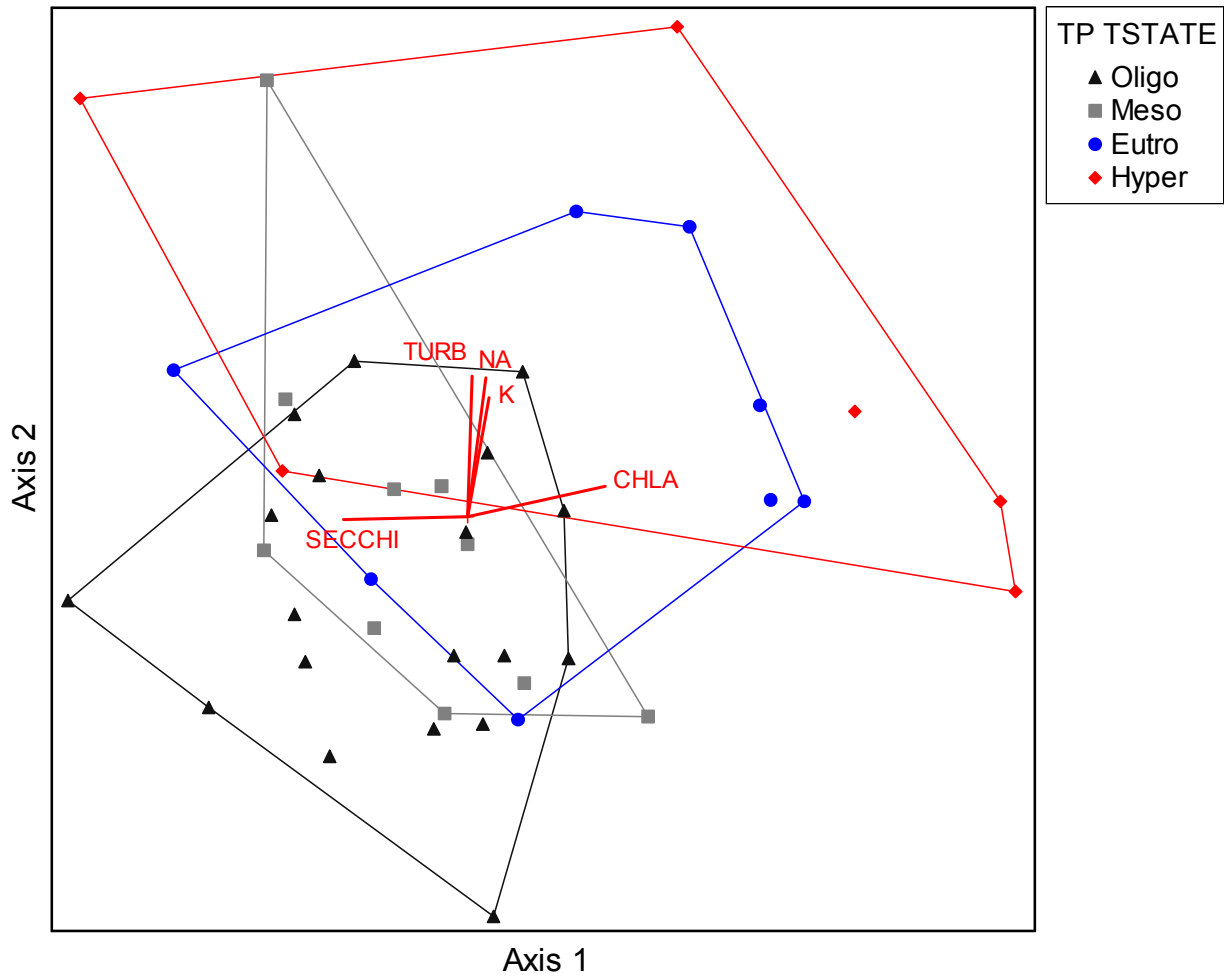


Figure 1: Rotifer NMDS ordination with total phosphorus as the graphical overlay for lakes selected via the linear regression model developed by Gillooly and Dodson (2000).

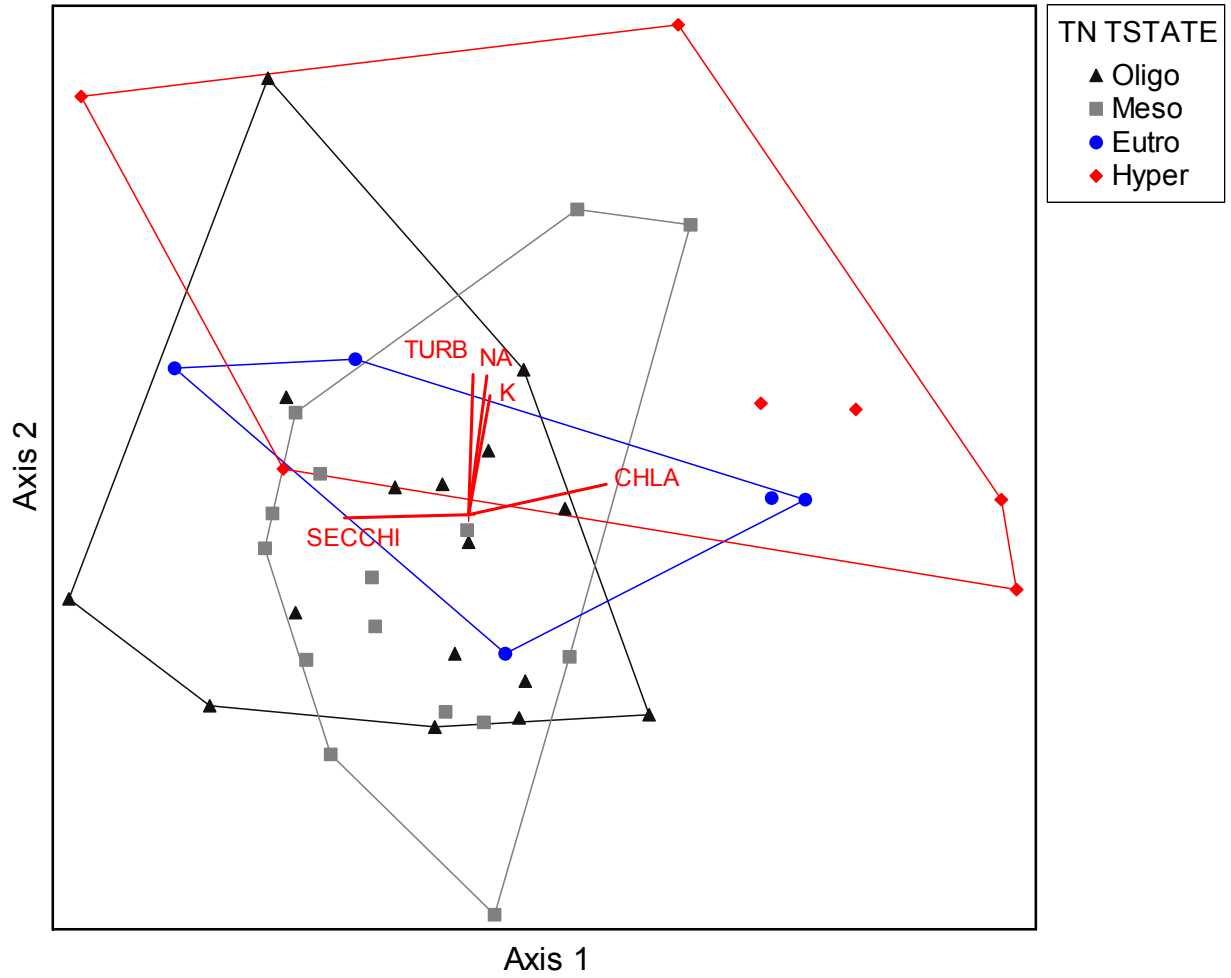


Figure 2: Rotifer NMDS ordination with total nitrogen as the graphical overlay for lakes selected via the linear regression model developed by Gillooly and Dodson (2000).

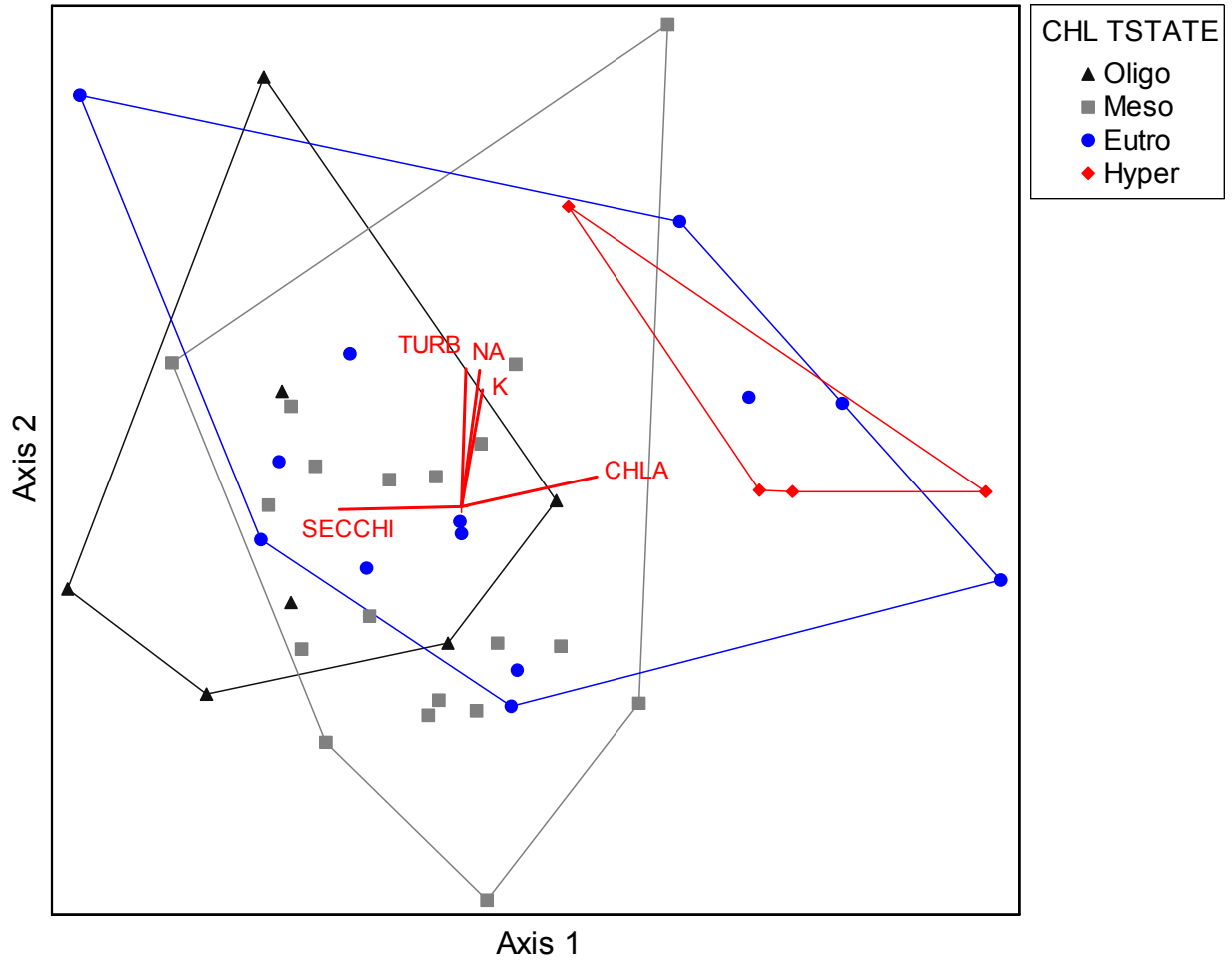


Figure 3: Rotifer NMDS ordination with chlorophyll- α as the graphical overlay for lakes selected via the linear regression model developed by Gilooley and Dodson (2000).

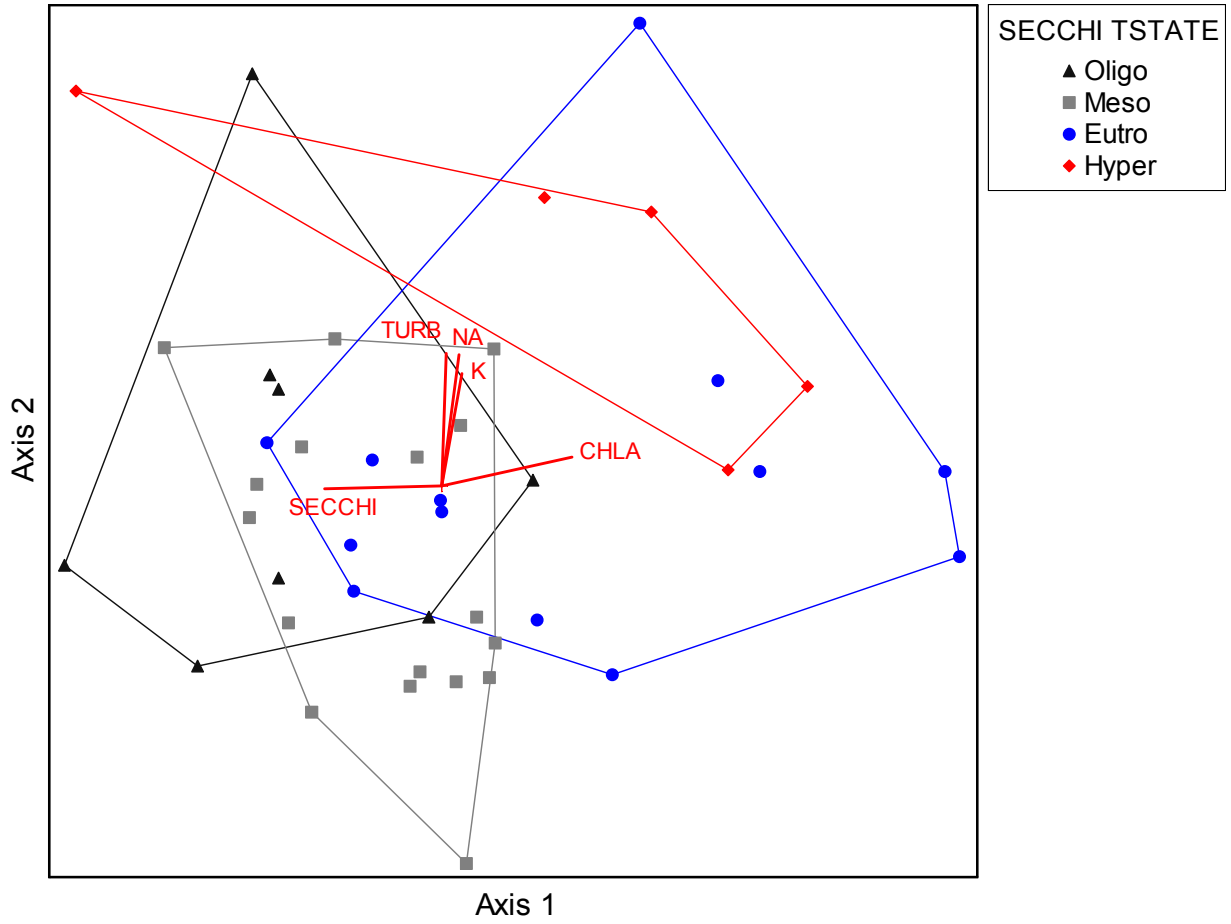


Figure 4: Rotifer NMDS ordination with Secchi disk depth as the graphical overlay for lakes selected via the linear regression model developed by Gillooly and Dodson (2000).

APPENDIX M

Rotifer NMDS ordinations with graphical overlays for lakes selected randomly above 40° latitude. The five strongest environmental vectors were retained on the figure if their R^2 was ≥ 0.20 .

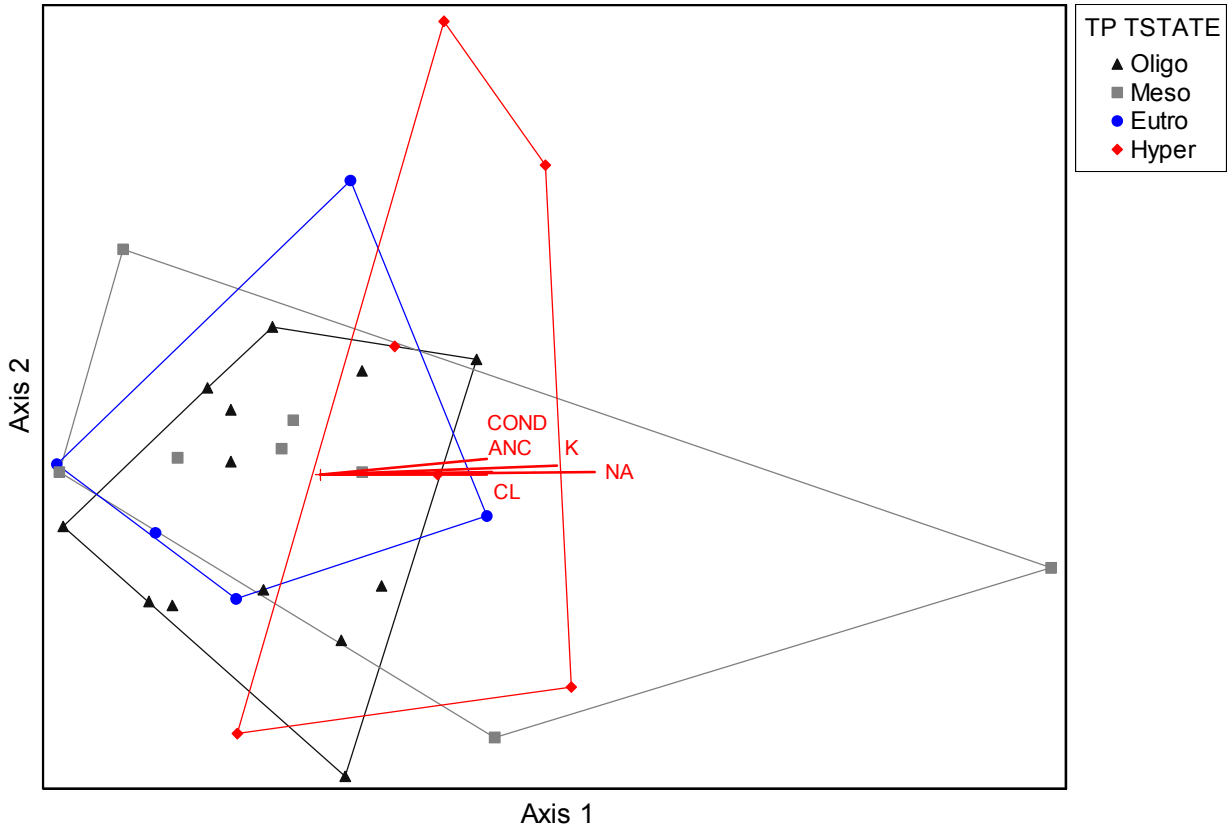


Figure 1: Rotifer NMDS ordination with total phosphorus as the graphical overlay for lakes selected randomly above 40° latitude.

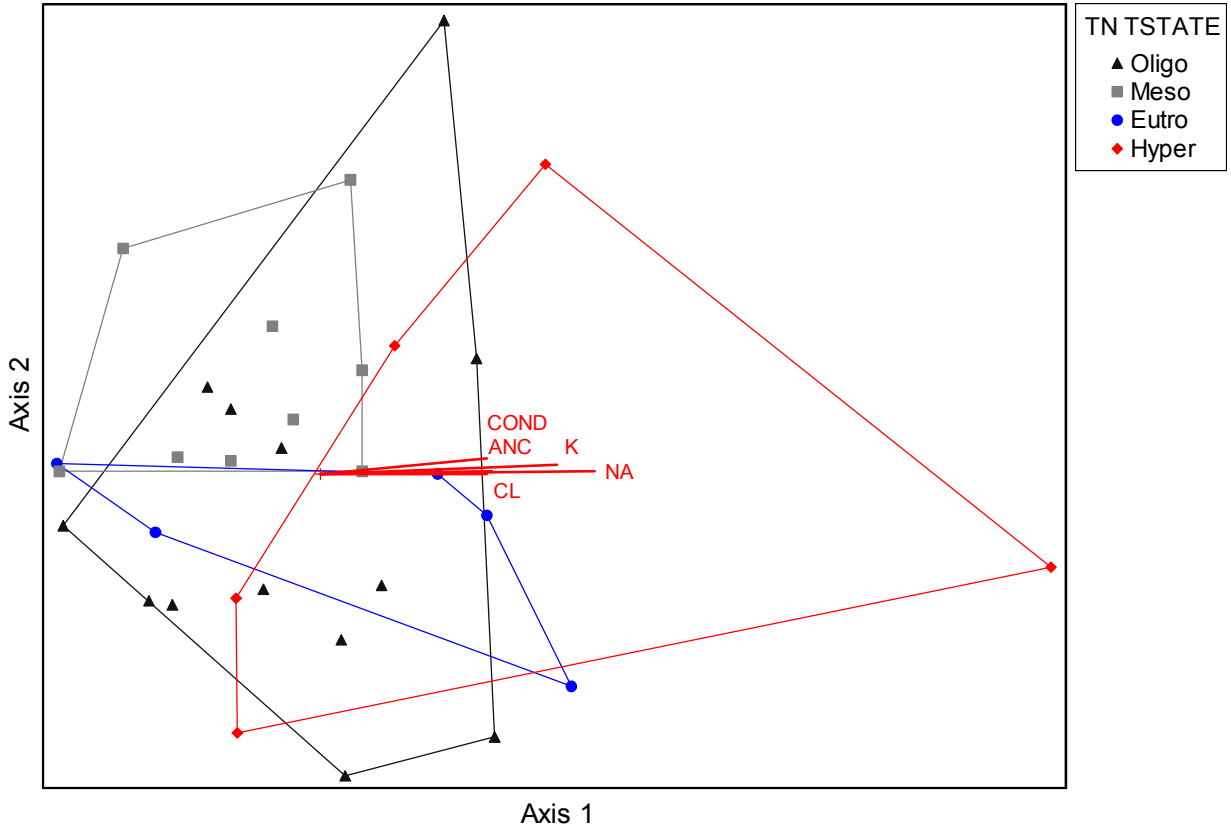


Figure 2: Rotifer NMDS ordination with total nitrogen as the graphical overlay for lakes selected randomly above 40° latitude.

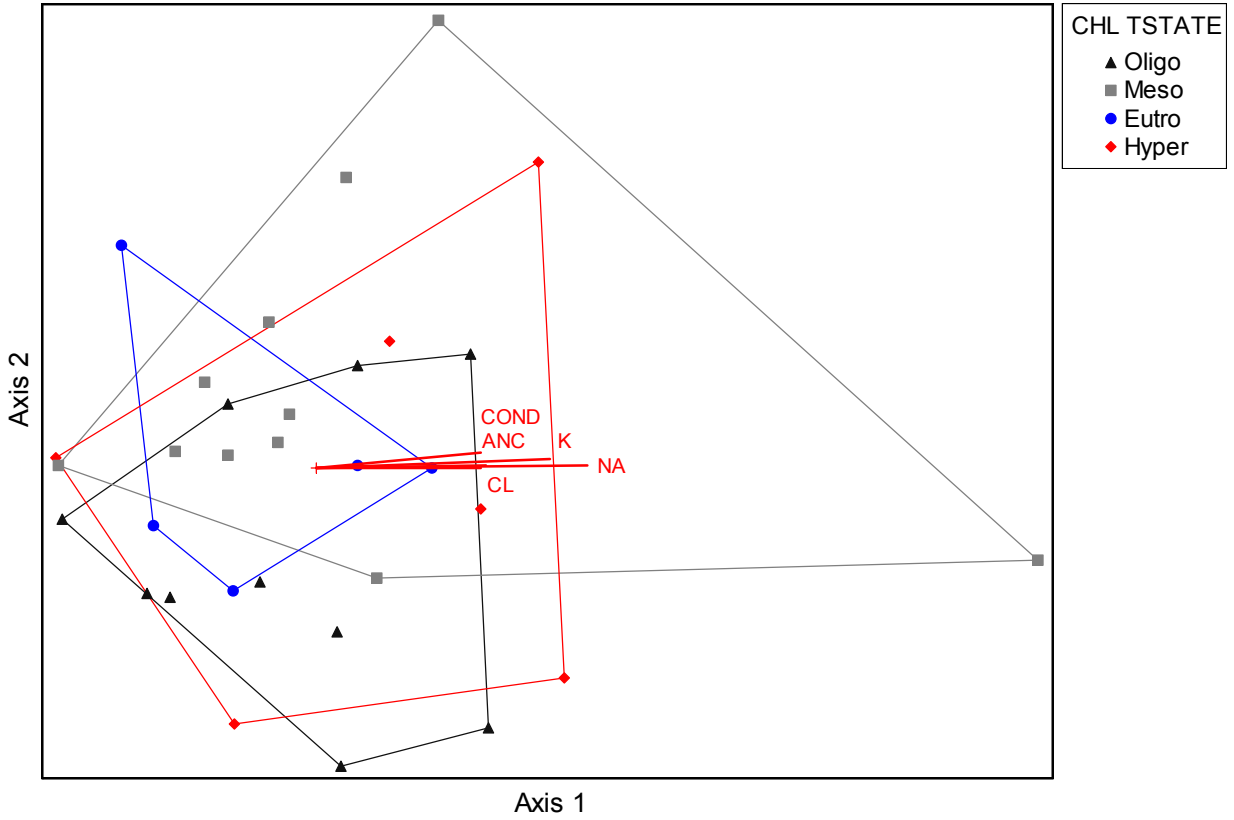


Figure 3: Rotifer NMDS ordination with chlorophyll- α as the graphical overlay for lakes selected randomly above 40° latitude.

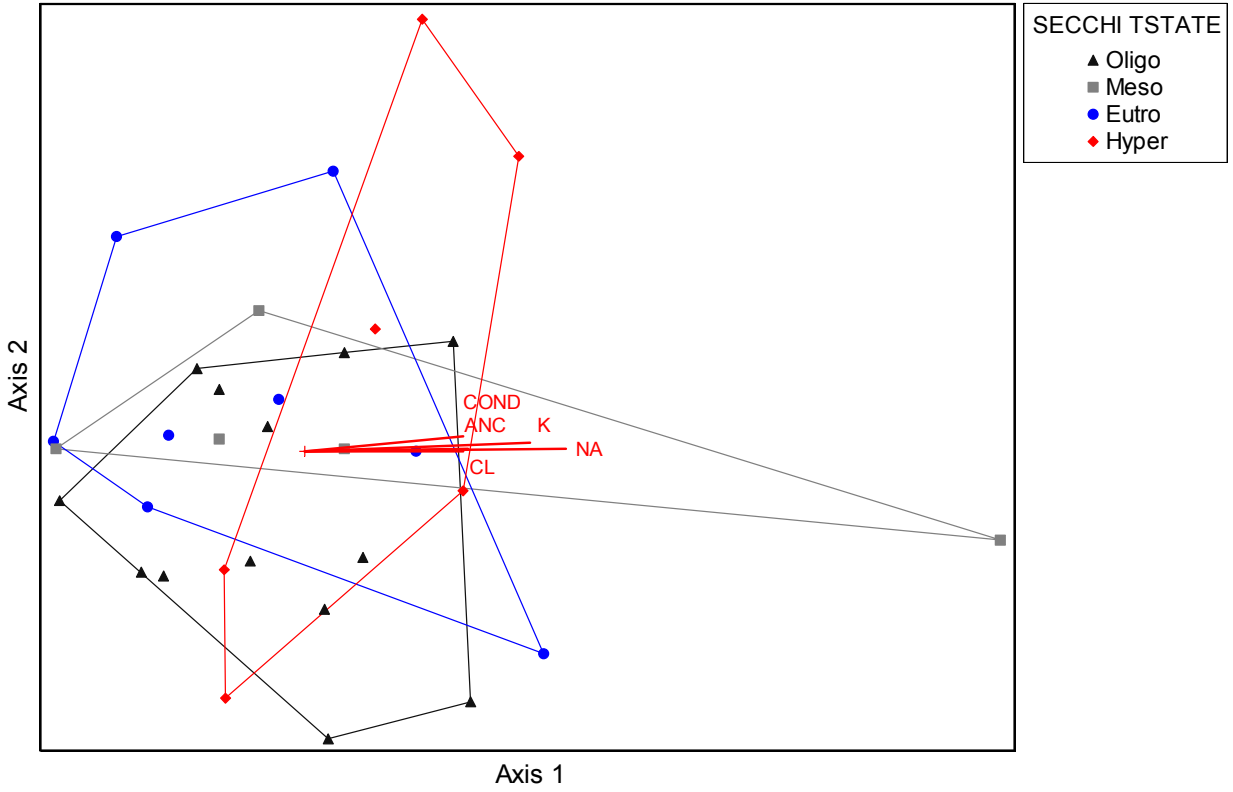


Figure 4: Rotifer NMDS ordination with Secchi disk depth as the graphical overlay for lakes selected randomly above 40° latitude.

APPENDIX N

Rotifer NMDS ordinations with graphical overlays for lakes selected randomly from across the contiguous United States. The five strongest environmental vectors were retained on the figure if their R^2 was ≥ 0.20 .

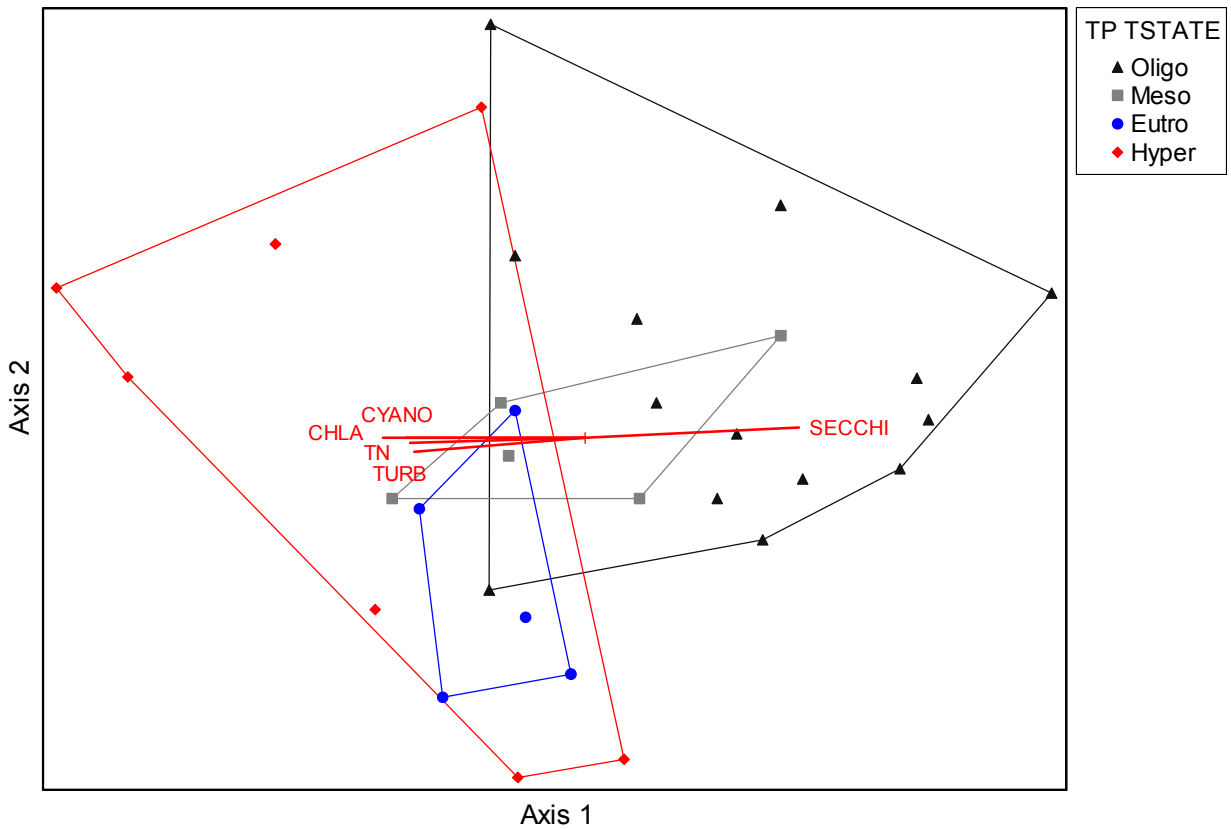


Figure 1: Rotifer NMDS ordination with total phosphorus as the graphical overlay for lakes selected randomly across the contiguous United States.

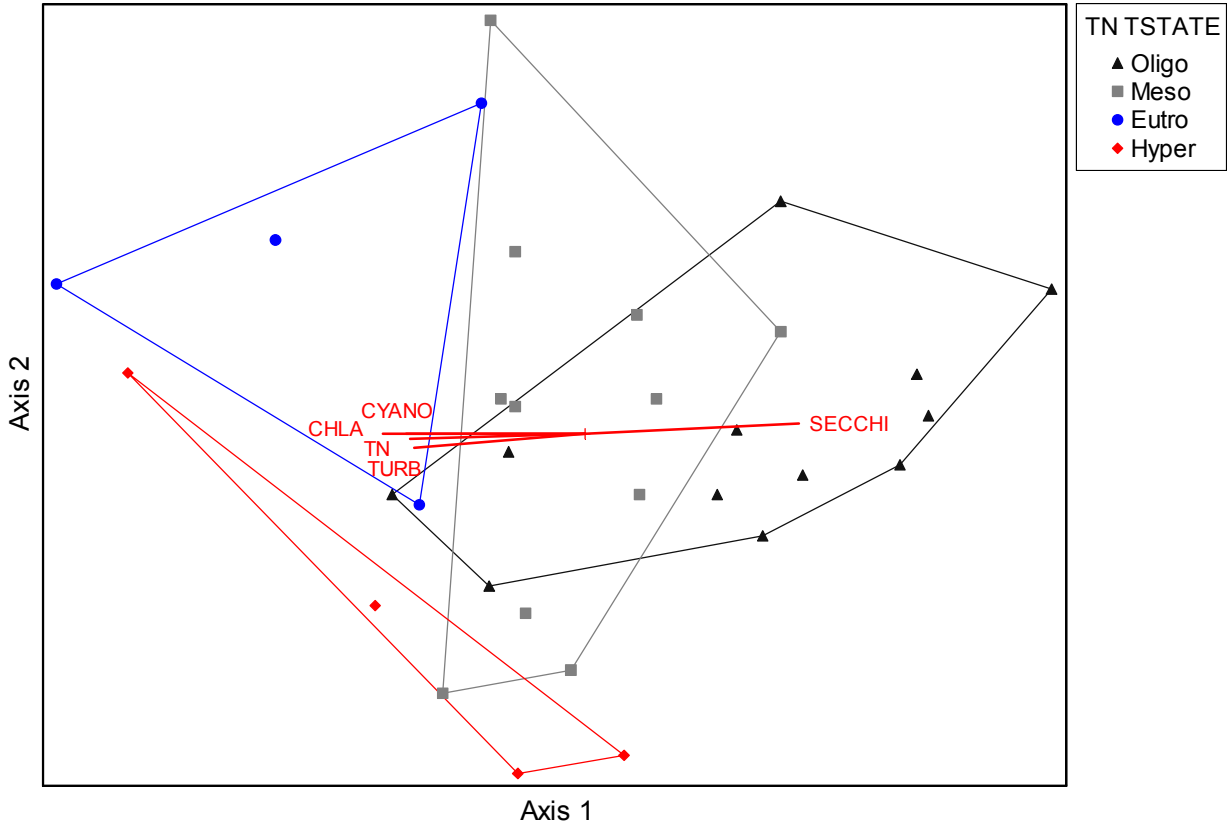


Figure 2: Rotifer NMDS ordination with total nitrogen as the graphical overlay for lakes selected randomly across the contiguous United States.

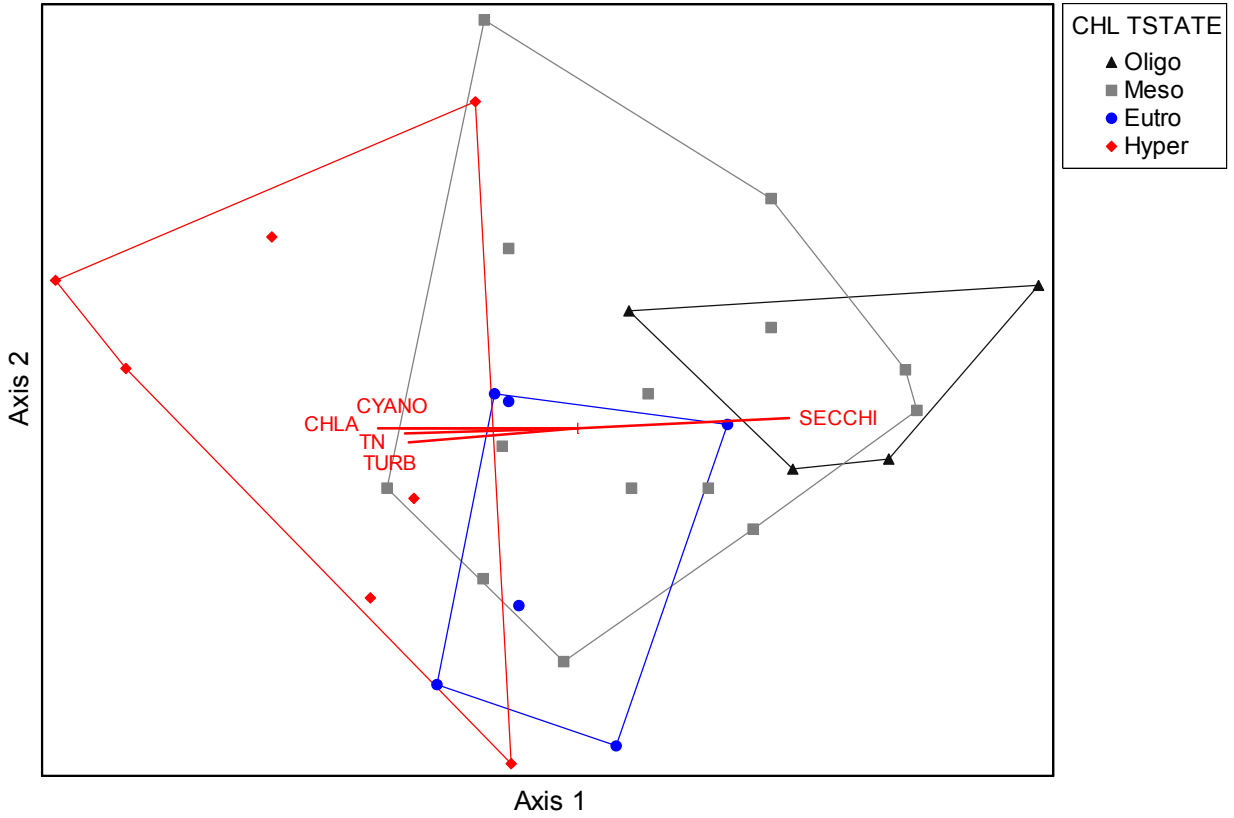


Figure 3: Rotifer NMDS ordination with chlorophyll- α as the graphical overlay for lakes selected randomly across the contiguous United States.

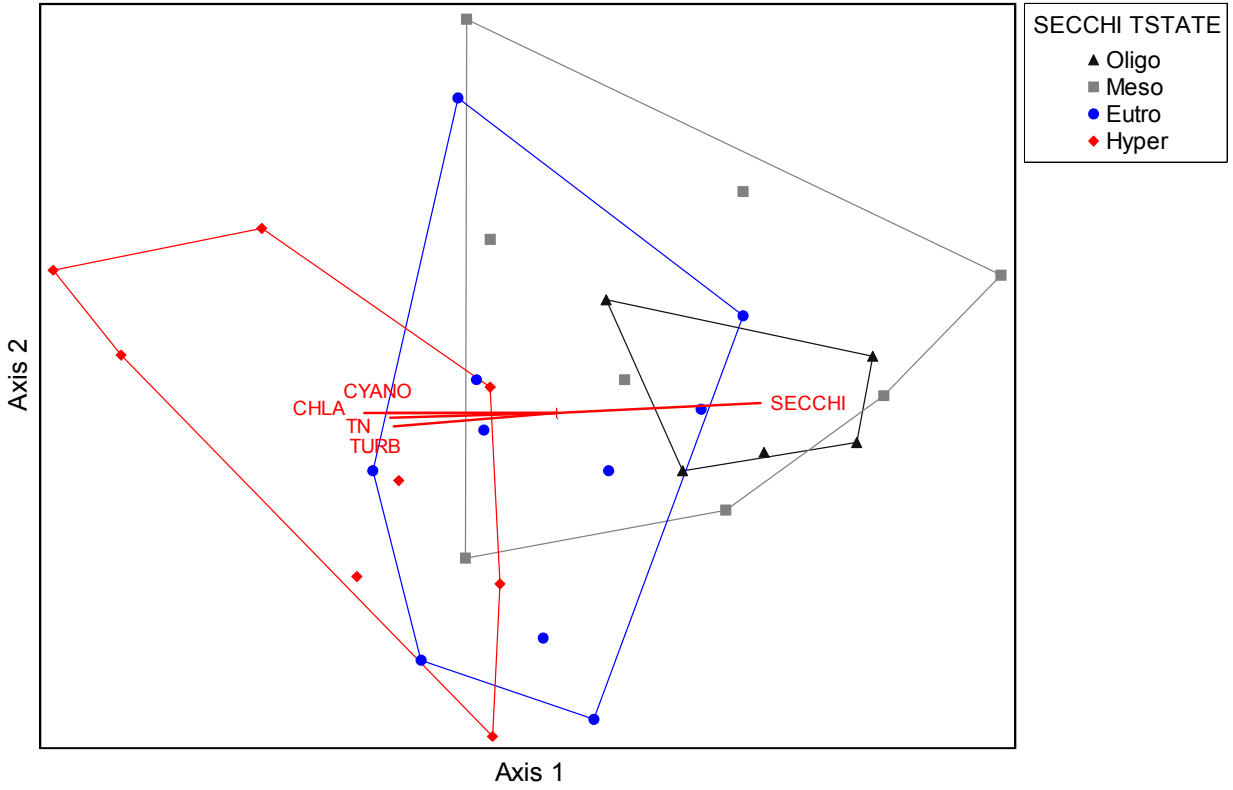


Figure 4: Rotifer NMDS ordination with Secchi disk depth as the graphical overlay for lakes selected randomly across the contiguous United States.