Effect of zebra mussels (*Dreissena polymorpha*) on trophic state in northern Michigan Lakes.

Danielle Stoermer

UMBS REU 2007

Abstract

Invasive species cause massive damage to the environment, human health, and the economy. Zebra mussels (*Dreissena polymorpha*) first invaded North America in 1988 and have had dramatic effects on many lake ecosystems. They are prolific filter feeders, effectively decreasing plankton densities and increasing water clarity, thereby altering the trophic state of lakes. I used Carlson's Trophic State Index to quantify changes in lake trophic state associated with zebra mussels. I examined the effect of zebra mussels on trophic state by comparing lake TSI values pre- and post-zebra-mussel invasion and the influence lake morphometry has on the zebra mussels' effect on trophic state. Secchi depth, chlorophyll-*a*, and total phosphorous data were collected at six lakes in northern lower Michigan. Sites were paired in each lake according to depth (<10 m and >15 m). No significant differences were found between shallow versus deep sites among any of the variables. Comparisons of trophic state variables showed no significant changes from data collected in 1973-1974. Zebra mussel density differed among lakes (0 – 3,600 m^{-2}) but showed no correlation with trophic state variables. TSI for Secchi was significantly greater than TSI for TP or chlorophyll. These results suggest that zebra mussel influences on trophic state variables were minor at this early stage in the invasion of these inland lakes.

Introduction

Invasive species can inflict enormous damage on the environment, human health, and the economy. Some affect ecosystem processes such as primary productivity, decomposition, hydrology, geomorphology, nutrient cycling, and disturbance regimes (Vitousek *et al.* 1997, Mack *et al.* 2000). Invasive pests and diseases cause massive perturbations world-wide. For example, the gypsy moth (*Lymantria dispar*) consumes a variety of species, causing as-yet unknown effects on forest diversity (Vitousek *et al.* 1997). Other invasive species degrade human health, such as the Asian tiger mosquito *Aedes albopictus*, which is a vector for eastern equine encephalitis, an often-fatal viral infection of people as well as horses (Craig 1993 cited in Vitousek *et al.* 1997). Invasive species also impact the economy: estimates of damages and control costs of invasive species in the U.S. alone equal approximately $120 billion per year (Pimentel *et al.* 2005).

Invasive species have had a huge impact on aquatic ecosystems. The invasion of the zebra mussel (*Dreissena polymorpha*) into North America may be one of the most dramatic examples. Zebra mussels were first discovered in North America in 1988 in Lake St. Clair near Detroit, Michigan, after having been inadvertently introduced from the release of ship ballast water (Hebert *et al.* 1989). They have since spread throughout the Great Lakes and Mississippi River drainage (USGS 2007). Zebra mussels are prolific filter-feeders (Fanslow *et al.* 1995), effectively filtering a wide size range of particles, from 750 μm (Ten Winkel and Davids 1982) to 1 μm (Silverman *et al.* 1996). Thus, high densities of zebra mussels can significantly decrease chlorophyll-*a* concentrations, total phosphorous (TP) concentrations, and plankton densities while also increasing water clarity (Holland 1993, Fahnenstiel *et al.* 1995, Heath *et al.* 1995). These changes indicate a reduction in trophic state.

The trophic state describes the general location of a lake on the lake succession continuum, ranging from oligotrophic lakes (cool and deep with little plant and animal life) to eutrophic lakes (warm and shallow supporting abundant aquatic plant growth) (CLMP 2006). Carlson (1977) developed a Trophic State Index (TSI) to help classify lakes according to any of three parameters: transparency, chlorophyll-*a*, and total phosphorous. TSI expresses lake productivity on a continuous numerical scale from 0 to 100, with increasing numbers indicating more eutrophic conditions (CLMP 2006). TSI variables measure ecosystem processes and as such provide indicators of important and large-scale changes, such as changes in a lake due to zebra mussel invasion. These indicators are relatively easy to measure and have been collected in historic surveys, so they provide an important way to measure zebra mussel effects on lake ecosystems both as a snapshot in time and over many years. For example, when pre-zebra-mussel invasion data (1979-1980) was compared to post-zebra-mussel invasion data (fall 1991-1993), Fahnenstiel *et al.* (1995) found a 59% and 43% decrease in chlorophyll-*a* and TP, respectively, and a 60% increase in transparency throughout inner Saginaw Bay, Lake Huron, indicating a major reduction in trophic state in the bay. Heath *et al.* (1995) found similar effects on phytoplankton abundance, water transparency, water chemistry, and phosphorous dynamics in a short-term enclosure experiment in Saginaw Bay.

There are several factors that could influence the effect of zebra mussels on TSI. Two related factors are zebra mussel colonization patterns and lake morphometry. Zebra mussels tend to colonize shallow, hard substrates first, such as bedrock deposits and woody debris in waters 2 to 12 m deep (Coakley *et al.* 1997), and subsequently reach their highest densities in similar areas (Mitchell *et al.* 1996). Thus, lakes with distinct shallow and deep regions might experience the effect of zebra mussels differently. Fahnenstiel *et al.* (1995) examined the effect of zebra mussels on TSI with respect to inner and outer Saginaw Bay, Lake Huron. The inner bay, which is relatively shallow (mean depth 5 m) and eutrophic, experienced a significant reduction in chlorophyll-*a* and TP concentrations as well as a significant increase in Secchi depth during the initial zebra mussel colonization and when compared to historic data (Fahnenstiel *et al.* 1995). However, the outer bay, which is deeper (mean depth 14 m) and oligotrophic, did not experience any significant changes during zebra mussel colonization nor when compared to historic data (Fahnenstiel *et al.* 1995).

Several lakes in northern lower Michigan provide an ideal opportunity to study the effect of zebra mussels on TSI in general as well as the specific influence lake morphometry has on the effect of zebra mussels on TSI. The lakes were formed by retreating glaciers, which left large chunks of ice that created deep depressions in the land. These depressions eventually filled in with water to form lakes composed of deep basins, known as kettles, surrounded by shallow shoals of sand (Welch 1928). Zebra mussels have invaded these lakes within the last 15 years, expanding rapidly throughout the shallow regions but rarely if at all into the deep regions. The purpose of my study was to examine the effect of zebra mussels on trophic state by comparing lake TSI values pre- and post-zebra-mussel invasion and the influence lake morphometry has on the zebra mussels effect on trophic state. I hypothesized that the trophic state in these lakes now will be lower than it was prior to zebra mussel invasion and that the shallow regions will have experienced a greater reduction in TSI compared to the deep regions.

Methods and Materials

Study Sites

I studied six inland lakes in northern Michigan that have similar morphometic features (deep and shallow basins) and that were included in a University of Michigan Biological Station (UMBS) study in the 1970s (Gannon and Paddock 1974). Five of these lakes contain zebra mussels (Black, Burt, Douglas, Long, Mullett) and one does not (Munro) (Table 1, Fig. 1, Tip of the Mitt Watershed Council).

The lakes are similar in size (volumes range from 826,446,336 to 2,918,022 m^3), but range in depth from approximately a few meters in the littoral zone to anywhere between 18 and 50 m in the deep basins (Table 1). The substrate in the littoral zone is largely sand with scattered rock and woody debris, ideal for zebra mussel colonization, whereas the deep basins are primarily composed of fine, organic-rich sediment, which is poor substrate for zebra mussels (Coakley *et al.* 1997, Mitchell *et al.* 1996).

Data collection and lake sampling

I sampled at least one shallow (<10 m) and one deep (>15 m) site in each lake (Fig. 2). Sites were selected within lakes to minimize variation in distance from shore, fetch, basin size, and amount of boat activity. Locations were document sampled using WAAS enabled, handheld GPS (Table 2). Each site was visited once between July 20 and Aug. 6, 2007. Paired sites were sampled back-to-back on the same day.

At each site, water clarity was measured with a Secchi disk, and one water sample was collected 2 m below the surface using a horizontal Van Dorn sampler. One 125mL water sample was collected in a Nalgene poly bottle and refrigerated for analysis of TP. A measured volume of water was filtered through a 0.25 mm filter (Millipore HAWP 02500) which was wrapped in tinfoil and frozen for later chlorophyll-*a* analysis. To determine chlorophyll-*a* content that is corrected for phaeophyton, each filter was dissolved in 10.0 mL acetone, sonicated to disrupt cell walls, frozen for 48 hours to disrupt cell walls further, and then analyzed in a fluorimeter (Turner Designs TD-700), standardized against an acetone blank. Samples were then acidified and re-measured for phaeophytin content.

Secchi depth, chlorophyll-*a* concentration, and total phosphorous concentration were used to calculate TSI for each site (Carlson 1977), using the following equations:

$$\mathrm{TSI(SD)} = 10[6-\ln(\mathrm{SD})/\ln(2)]$$

$$\mathrm{TSI(Chl)} = 10\{6-[2.04-0.68\ln(\mathrm{Chl.})/\ln(2)]\}$$

$$\mathrm{TSI(TP)} = 10[6-\ln(48/\mathrm{TP})/\ln(2)]$$

As Secchi depth increases (gets deeper), Secchi TSI decreases. In other words, a deeper Secchi depth corresponds to a lower TSI value, indicating more oligotrophic conditions. Chlorophyll-*a* and TP are the opposite: higher concentrations of chlorophyll-*a* and TP result in higher TSI values, indicating more eutrophic conditions. Trophic state names are commonly associated with a range of TSI values: oligotrophic = 0-35, mesotrophic = 35-50, eutrophic = 50-65, hypereutrophic = 65-100 (CLMP 2006).

Adult zebra mussels were collected by divers from 1 m^2 PVC quadrates haphazardly placed in 0.8 to 1 m deep sites around each lake. Four sites were chosen at each lake close to the open water sampling sites (Fig. 3). Zebra mussels were separated from the substrate and all live zebra mussels were counted.

Data on historic trophic state measurements (e.g., Secchi depth for all lakes in the study; chlorophyll-*a* and TP for Douglas Lake only) were collected from papers from UMBS (Gannon and Paddock 1974, Wright 1979, Weaver 1988, Fenner 1989, Frost *et al.* 1992, Boven *et al.* 1993, Geddes *et al.* 1997, Conlon *et al.* 1998).

Data Analysis

Data were analyzed using paired t-tests and linear regression ($\alpha = 0.05$). Each trophic state parameter and each TSI value for each pair of sites were analyzed with a paired t-test. Linear regressions compared zebra mussel density and each of the trophic state parameters and TSI values. A one-way ANOVA tested for differences in mean zebra mussel density among lakes. A post-hoc test of paired differences compared zebra mussel densities between each lake and the other lakes. Secchi depth for pre- and post-zebra-mussel invasion for each of the lakes was analyzed using a paired t-test. Linear regression was used to examine the association between the trophic state parameters and time. TSI values for all data were compared using a paired t-test (paired either by lake pair for current data or by year for historic data). GIS maps were constructed with information regarding water depth, sampling site locations, zebra mussel sampling sites and densities, and chlorophyll-*a* concentrations.

Results

I found no evidence indicating differences in trophic state variables between shallow and deep pairs across all lakes. Secchi depth, chlorophyll-*a*, and TP and their associated TSI values showed no significant differences among paired sites (n=10). Secchi values varied considerably across lakes with values ranging from 1.40 to 5.45 m. Chlorophyll-*a* and TP values were generally low (<5 ug/L and <10 ug/L, respectively) indicating that most of these lakes are oligotrophic or mesotrophic (Figs. 4, 5). The highest chlorophyll-*a* and TP values were observed in Munro Lake, the only lake without zebra mussels.

Littoral zebra mussel densities were variable among sites within lakes and between lakes. Average values for the six lakes varied from zero in Lake Munro to 2,247 in Douglas Lake (Table 1). Average zebra mussel densities were significantly different between the lakes (excluding Munro, n=5, p=0.011). Specifically, the average zebra mussel density in Black Lake was significantly different from the average densities in Burt, Douglas, and Long lakes (p=0.008, p=0.002, p=0.030, respectively). Average zebra mussel densities in Douglas and Mullett lakes were also significantly different from each other (p=0.021). No significant correlation between average zebra mussel density and average lake trophic state parameters (Secchi, chlorophyll-*a*, and TP) existed in any of the lakes (n=6).

Analysis of historic data revealed no significant change in trophic state across the 5 lakes with zebra mussels. Only data for Secchi depth were available for all of the lakes included in this analysis. Secchi depth and its associated TSI value were not significantly different compared to 1973-1974 (n=6). Because historic chlorophyll-*a* and TP data were available for Douglas Lake, regression analysis was used to determine whether there was a significant change through time in either of these trophic state variables. No change in chlorophyll-*a* and TP concentrations, as well as their TSI values, were found in Douglas Lake since 1973 (Fig. 6).

A comparison of trophic state indicators can be used to infer factors regulating production. In order to determine whether Secchi, chlorophyll-*a*, and TP data predicted similar trophic states for the lakes, I compared TSI among all of these variables (Fig. 7). Secchi TSI predicted a greater trophic state than did either chlorophyll-*a* or TP (n=19, p<0.001 for both). The analysis also revealed that the trophic state predicted by chlorophyll-*a* was significantly greater than that predicted by TP (n=19, p=0.0272, Fig. 7).

Discussion

Zebra mussels have been shown to cause reductions in trophic state because of their large filtering capacity (Holland 1993, Fahnenstiel *et al.* 1995, Heath *et al.* 1995). Trophic state variables, namely transparency, chlorophyll-*a*, and TP, are one relatively easy way to quantify changes in the state of a lake. Thus, comparisons of historic TSI to current TSI for lakes that have been recently invaded by zebra mussels should reveal a reduction in TSI over time. Since lakes have variable morphometry and zebra mussels typically colonize shallow basins first (Coakley *et al.* 1997), TSI for shallow regions should be lower than deep regions. My study contradicted both of these hypotheses: the trophic state did not decrease after zebra mussels invaded, and the trophic state was not lower in shallow regions compared to deep regions.

None of the lake pairs had significant differences in any of the trophic state variables. This result could be explained because wind events mix the epilimnetic water throughout the lake. We sampled chlorophyll-*a* and phosphorous at 2 m so mixing could be masking any differences in trophic state between the different sites in each lake. We also did not detect significant changes in trophic state between pre- and post-zebra mussel invasion. This finding contradicts the published literature on trophic state effects of zebra mussels (e.g., Holland 1993, Fahnenstiel *et al.* 1995, Heath *et al.* 1995). My results showed no significant relationship between zebra mussel density and whole lake TSI as well. These results taken together suggest that zebra mussels are not yet altering summer TSI values for these lakes.

There are several potential reasons for the discrepancy between my findings and previously published results. First, the lakes in this study have different morphometry compared to the majority of lakes where zebra mussel effects have been studied. I sampled moderate-sized, kettle lakes, whereas other studies focused on lakes with large, shallow, eutrophic bays such as the Laurentian Great Lakes (Pillsbury *et al.* 2002). Northern Michigan lakes tended to be oligotrophic to mesotrophic before zebra mussels invaded. Lower productivity could reduce the filtering efficiency of the zebra mussels since there are lower plankton densities compared to more productive systems. Second, the lakes in this study have different substrates than most other lakes studied. These lakes have primarily sandy shallows, with only limited cobble substrates with muck bottoms in the deep basins. Other lake bottoms are composed of more cobble and gravel (Nalepa *et al.* 1995), which support the highest densities of zebra mussels (Mitchell *et al.* 1996). My sampling revealed that the zebra mussel density was lower than reported in earlier studies (Galligan 2005). Exempting Lake Munro since it has not been invaded by zebra mussels, zebra mussel densities in the lakes I studied were an order of magnitude lower than typical densities of zebra mussels (1,300 m^{-2} compared to 30,000 m^{-2}, this study and Nalepa *et al.* 1995, respectively). Low densities of zebra mussels would filter less plankton, limiting the magnitude of trophic state reduction. Reeders and Bij de Vaate (1990) found that a zebra mussel density of 675 zebra mussels$\cdot m^{-2}$ in Lake Wolderwijd in the Netherlands was required to reduce phytoplankton growth by grazing. This low density requirement could be related to the hypereutrophic state of the lake (Reeders and Bij de Vaate 1990). Since the lakes in this study are mesotrophic, a higher zebra mussel density might be required to reduce phytoplankton growth. Another possible reason for the low zebra mussel density requirement in Lake Wolderwijd is that the lake has a mean depth of only 1.50 m, and shallow lakes tend to be more susceptible to zebra mussel effects (Reeders and Bij de Vaate 1990). The lack of significant correlation between zebra mussel density and any of the trophic state parameters in my study suggests that zebra mussel densities in these lakes are within a range in which zebra mussels have a minimal impact on trophic state.

Even though there was no significant change in trophic state over time or between paired sites, zebra mussels could still be having an effect on these lake ecosystems. For example, plankton communities could have changed in composition even though they have not changed enough in density to cause a significant reduction in trophic state (Lavrentyev *et al.* 1995). Zebra mussel filtering reduces planktonic diatom densities but often results in compensatory growth of cyanobacteria (Pillsbury *et al.* 2002, Cotner *et al.* 1995, Lavrentyev *et al.* 1995). This change may not register in any of the TSI parameters since phytoplankton community composition is not characterized directly. This community composition shift has significant implications for management. Some species of cyanobacteria (such as *Microcystis* and *Cylindrospermopsis*) produce toxins that can be harmful to fish, wildlife and humans. Measuring the trophic state of a lake with any of the three parameters, but especially with Secchi disk transparency, is a quick and easy way to determine the status of a lake. But, if zebra mussels are having an effect on lake ecosystems while not affecting the trophic state, then managers may not meet their goals of detecting changes in lakes.

Useful information about the factors controlling the overall trophic status of a lake can be inferred by comparing the TSI_{SD}, TSI_{CHL}, and TSI_{TP} values for the lake (Carlson and Simpson 1996 cited in CLMP 2006). Lakes with phosphorous as their limiting factor for algae growth typically have nearly equal Secchi, chlorophyll and phosphorus TSI values (CLMP 2006). Our results showed a significantly greater Secchi TSI value than chlorophyll or phosphorus. This suggests that some non-algal material is reducing water clarity. One potential mechanism may involve calcium precipitation, scattering light and reducing Secchi disk transparency (CLMP 2006). Suspended calcium particles may bind phosphorous and cause nutrient limitation (CLMP

2006). Since marl was found to some extent in every lake, it seems plausible that marl precipitation is at least part of the reason TSI_{SD} is significantly higher than TSI_{CHL} and TSI_{TP}.

Significant differences between each of the TSI values also raise concerns about the reliability of these parameters to accurately reflect the true trophic status of a lake. Like the shift in algal composition, these differences have implications for management. Not only could managers be missing changes in lake ecosystems, but they could also be assigning the trophic state of the lakes incorrectly. This might affect management decisions, such as limitations on development and recreational activities.

Zebra mussels appear to not be affecting the trophic state of these lakes differently between shallow and deep regions nor over time. Most of the literature supports the hypothesis that these differences should be occurring (Holland 1993, Fahnenstiel *et al.* 1995, Heath *et al.* 1995). The lack of a strong zebra mussel effect on summer epilimnetic trophic state may be partially explained by the relatively recent introduction of these exotic mussels, as well as by the mesotrophic state of the lakes prior to zebra mussel invasion. More research should be conducted to determine how zebra mussels are affecting these lake ecosystems without changing their trophic states.

Acknowledgements

This study was part of the Research Experiences for Undergraduates (REU) program funded by the National Science Foundation at the University of Michigan Biological Station (UMBS). Special thanks to my mentor Dr. Troy Keller for invaluable assistance throughout this study. Thanks to the REU co-directors at UMBS, Drs. Dave Karowe and Mary Anne Carroll, the UMBS staff, especially Bob Vande Kopple, Mike Grant, Tony Sutterly, and Richard Spray, everyone who helped with data collection, especially Lisa Fineman, and my REU family.

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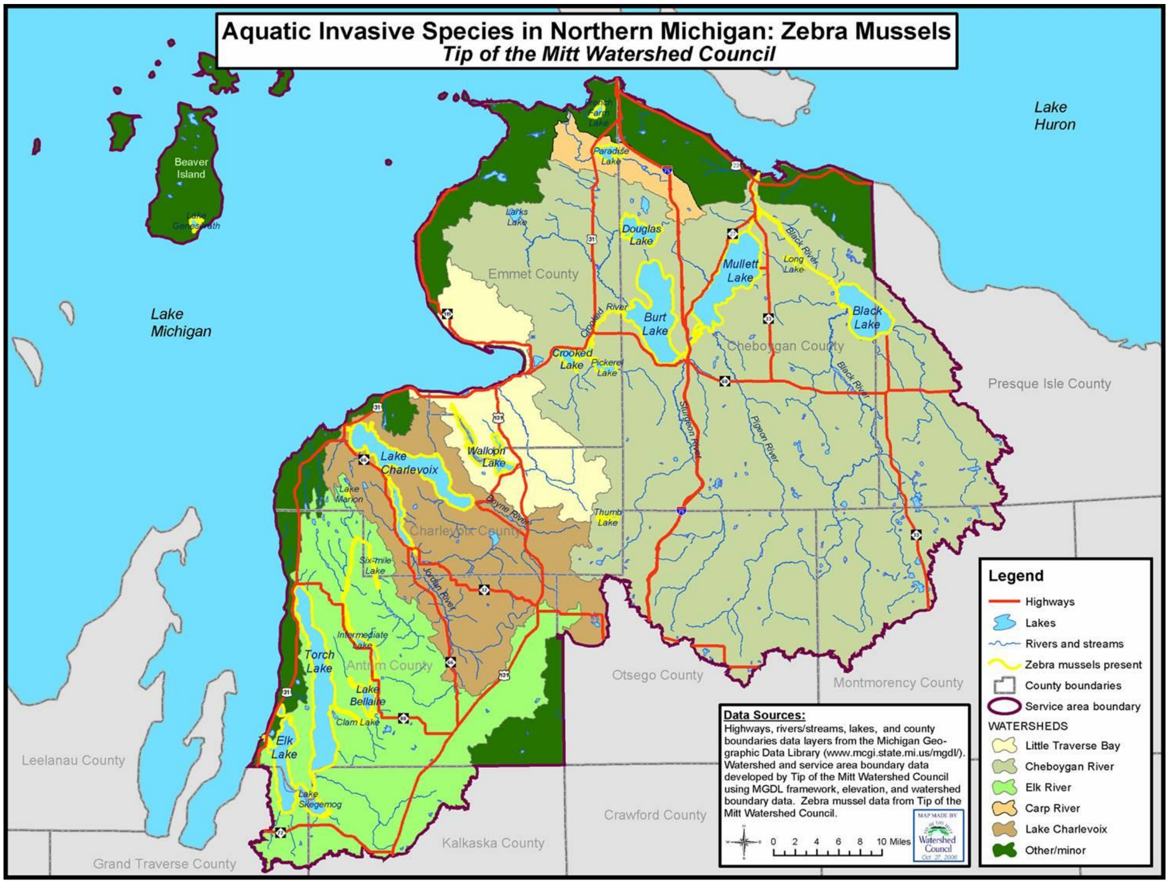
Table 1. Basic morphometric data for the six Michigan lakes in this study, as well as the year zebra mussels were first documented and the average littoral zebra mussel density in each lake.

Lake	Max Depth (m)[1]	Mean Depth (m)[1]	Volume (m^3)[1]	Year Documented	Density ($\#\cdot m^{-2}$)
Burt	22.2	15.7	826,446,336	1993[2]	1,908
Mullett	42.7	11.2	756,373,248	1998[2]	685
Black	15.2	7.7	313,882,624	2002[3]*	132
Douglas	27.1	5.47	82,671,888	2001[4]	2,247
Long	19.5	7	11,311,422	2005[2]	1,531
Munro	4.6	1	2,948,022	N/A	0

[1] Gannon and Paddock 1974. [2] Michigan Sea Grant 2001. [3] Hopkins 2007. [4] Galligan 2005.
*Data unsubstantiated and based on personal observation.

Table 2. Latitude and longitude coordinates for each of the 20 sites in this study, organized by lake pair. Lake Munro does not have any deep basins, so only shallow sites were sampled.

	Shallow		Deep	
Lake Pair	Latitude	Longitude	Latitude	Longitude
Burt 1	45°31"32.3	84°39"50.4	45°29"02.0	84°39"29.6
Burt 2	45°27"46.1	84°41"54.3	45°33"52.7	84°40"22.8
Mullett 1	45°32"39.0	84°29"08.6	45°32"36.7	84°31"06.5
Mullett 2	45°27"34.5	84°34"58.8	45°27"46.7	84°33"13.4
Black	45°29"01.0	84°17"44.2	45°27"01.5	84°16"17.1
Douglas 1	45°35"46.7	84°42"50.7	45°35"46.7	84°42"42.3
Douglas 2	45°35"01.2	84°39"43.4	45°33"52.7	84°40"22.8
Douglas 3	45°34"64.2	84°41"34.0	45°34"39.3	84°41"25.6
Long	45°32"18.7	84°24"20.9	45°31"55.0	84°24"20.9
Munro 1	45°36"56.0	84°40"58.6		
Munro 2	45°36"55.6	84°40"59.3		



Data Sources:
Highways, rivers/streams, lakes, and county boundaries data layers from the Michigan Geographic Data Library (www.mcgi.state.mi.us/mgdl/). Watershed and service area boundary data developed by Tip of the Mitt Watershed Council using MGDL framework, elevation, and watershed boundary data. Zebra mussel data from Tip of the Mitt Watershed Council.

Figure 1. Lakes and rivers in northern lower Michigan with documented zebra mussel populations (Tip of the Mitt Watershed Council 2007).

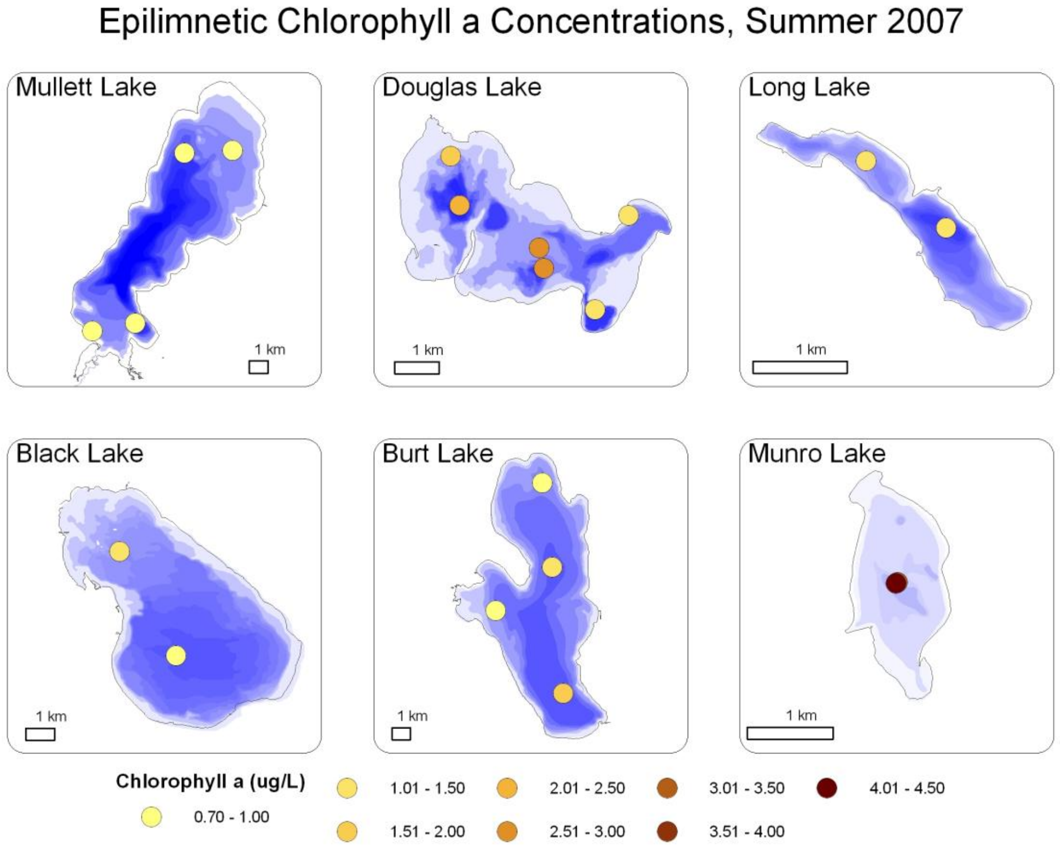


Figure 2. Epilimnetic chlorophyll-*a* concentrations at each site sampled in 2007. Points represent sample sites and are colored by chlorophyll-*a* (ug/L); points closest together are paired sites. Depth of the lakes is represented by color intensity with darker colors indicating the deeper areas. Lakes are not set to the same scale and are not in the same North to South orientation.

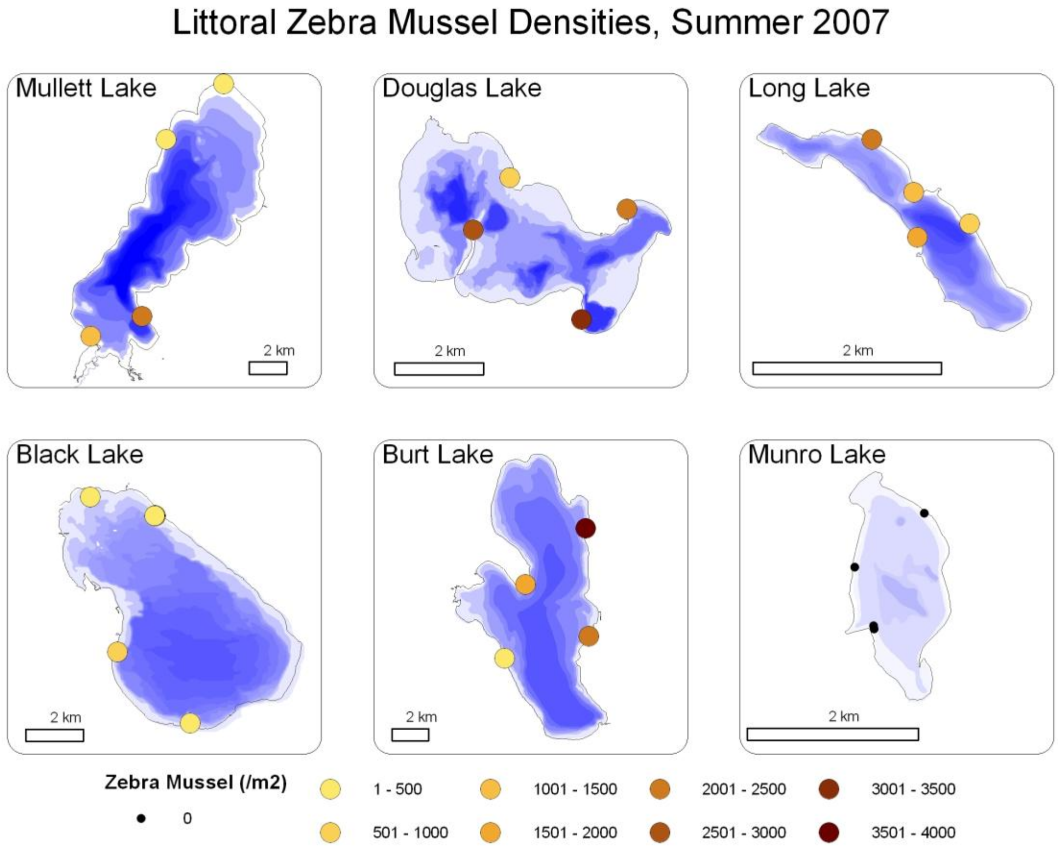


Figure 3. Littoral zebra mussel densities (#·m^{-2}) at each site sampled in 2007. Depth of the lakes is represented by color intensity with darker colors indicating the deeper areas. Lakes are not set to the same scale and are not in the same North to South orientation.

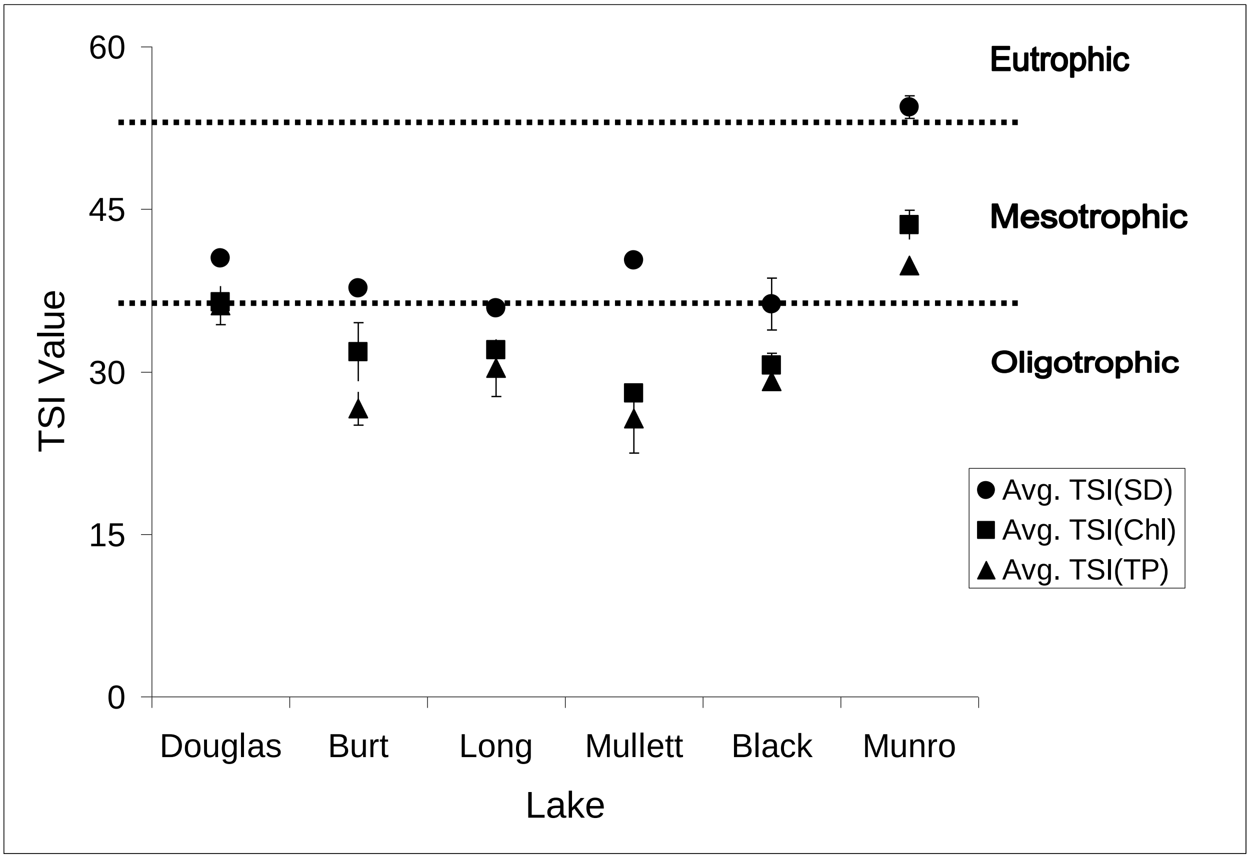


Figure 4. Average Trophic State Index (TSI) value for Secchi disk (SD), chlorophyll-*a* (Chl), and total phophorus (TP) for six northern Michigan lakes during July/August 2007. Horizontal, dotted lines represent approximate separation between the three major trophic states (CLMP 2006).

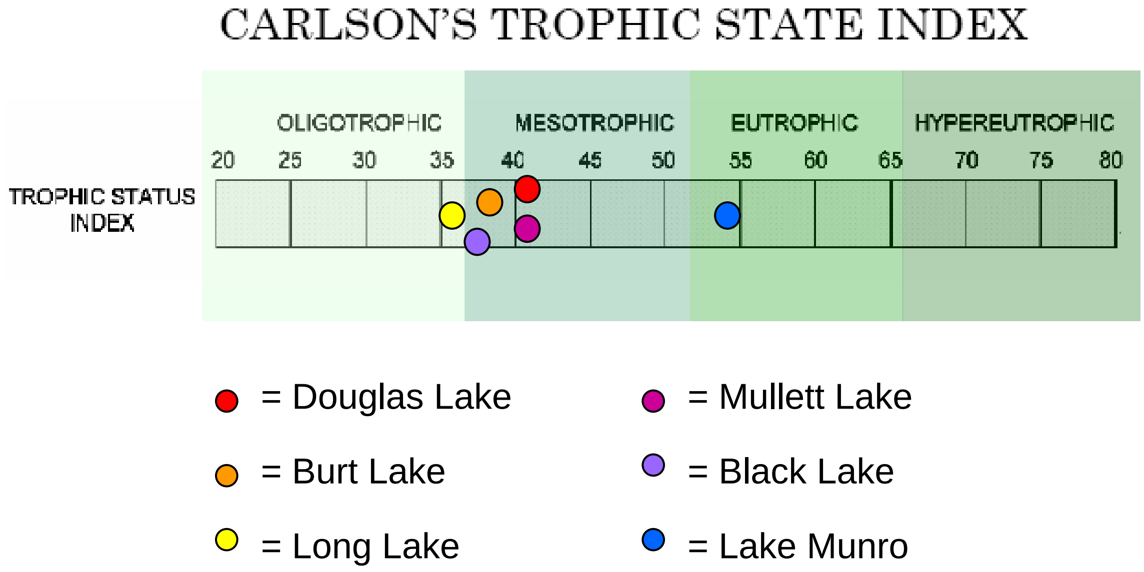


Figure 5. Average summer lake chlorophyll-*a* TSI values for six lakes in northern Michigan. TSI values calculated from Carlson's (1977) equations. Diagram from CLMP (2006).

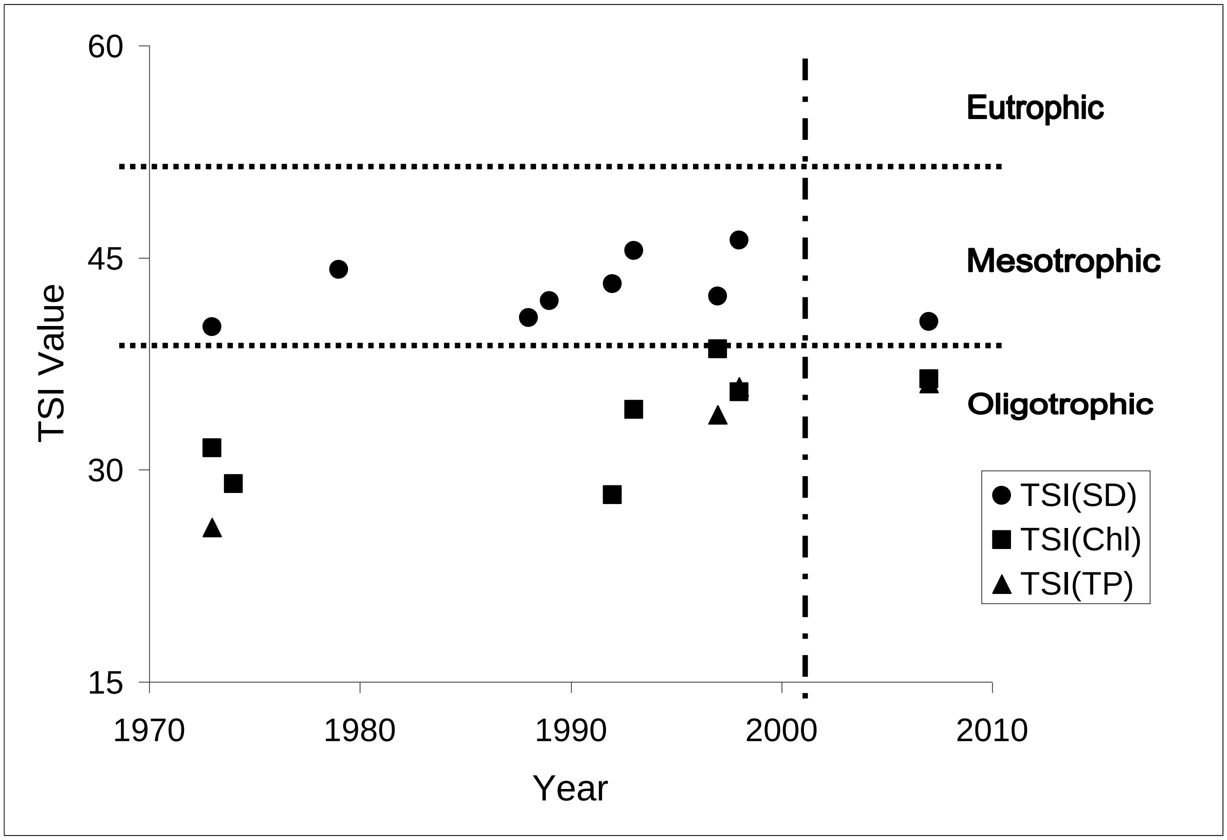


Figure 6. Douglas Lake TSI for each parameter over time (Gannon and Paddock 1974, Wright 1979, Weaver 1988, Fenner 1989, Frost et al. 1992, Boven et al. 1993, Geddes et al. 1997, Conlon et al. 1998). Samples were taken at various sites throughout Douglas Lake, though most are from South Fishtail Bay and Pells Island (Fairy Island) Depression. Vertical, dashed line represents year zebra mussels were first documented: 2001 (Galligan 2005). Horizontal, dotted lines represent approximate separation between the three major trophic states (CLMP 2006).

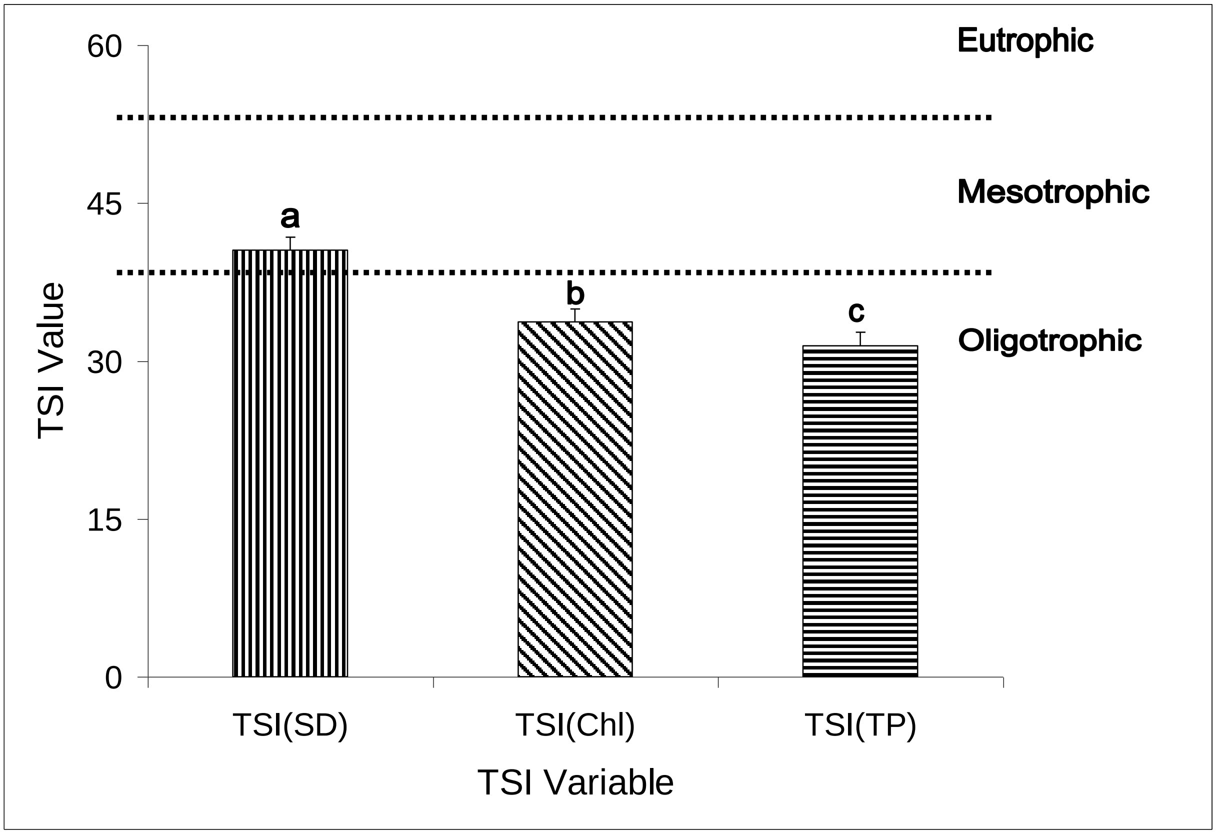


Figure 7. Average summer 2007 Secchi disk (SD), chlorophyll-*a* (Chl), and total phosphorus (TP) TSI values (+ 1 standard error) grouped across all lake sites (n=19). Bars not sharing the same letter differ statistically ($p<0.05$). Horizontal, dotted lines represent approximate separation between the three major trophic states (CLMP 2006).