Journal of Great Lakes Research 36 (2010) 9–19

Contents lists available at ScienceDirect

Journal of Great Lakes Research

journal homepage: www.elsevier.com/locate/jglr

Phytoplankton community composition of Saginaw Bay, Lake Huron, during the zebra mussel (*Dreissena polymorpha*) invasion: A multivariate analysis

Daniel B. Fishman [a,*], Sara A. Adlerstein [a], Henry A. Vanderploeg [b], Gary L. Fahnenstiel [c], Donald Scavia [a]

[a] *University of Michigan School of Natural Resources and Environment, 440 Church Street, Ann Arbor, MI 48109-1041, USA*
[b] *NOAA/GLERL, 4840 S. State Rd., Ann Arbor, MI 48108-9719, USA*
[c] *NOAA/GLERL, Lake Michigan Field Station, 1431 Beach St., Muskegon, MI 49441-1098, USA*

ARTICLE INFO

Article history:
Received 19 August 2008
Accepted 15 October 2009

Communicated by Dr. Marley Waiser

Index words:
Saginaw Bay
Phytoplankton
Zebra mussels
Agglomerative hierarchical clustering
Community composition
Invasive species

ABSTRACT

The colonization of the zebra mussel (*Dreissena polymorpha*) in Saginaw Bay dramatically altered the phytoplankton community composition resulting in exclusion of light sensitive species and dominance of species with oligotrophic preferences and light resistance. In 1990, the NOAA Great Lakes Environmental Research Laboratory initiated a 7-year survey program to monitor changes in the lower food web of Saginaw Bay, where zebra mussels became established in the fall of 1991. To investigate shifts in the phytoplankton community composition over the 7-year period from 1990 to 1996 we searched for clusters of similar composition using multivariate principal component analysis (PCA) on proportions of 22 taxonomic groupings of the total phytoplankton density (cells per milliliter). We then used an agglomerative hierarchical clustering analysis of the PCA scores. We identified five characteristic phytoplankton communities in configurations that allowed recognizing four distinct periods in Saginaw Bay linked to the zebra mussel invasion. Significant changes were indicative of increased water clarity and eutrophic conditions being replaced by more oligotrophic conditions as clusters dominated by light sensitive species, such as the cyanobacteria *Oscillatoria redekii*, became immediately rare and clusters dominated by diatoms such as *Cyclotella* spp. became common. *Microcystis* spp., a light tolerant cyanobacteria not grazed by zebra mussel, dominated assemblages after 1994. The shifts in phytoplankton composition confirm that zebra mussels effects on phytoplankton communities are mediated by both direct (filtration) and indirect (nutrient cycling) mechanisms and also suggests that increased light penetration is an important mechanism behind some changes.

Introduction

Disturbance is a defining feature of many ecological systems and anthropogenic disturbance of aquatic ecosystems can result in widespread alterations to ecosystem structure and function. This motivates characterizations of aquatic ecosystem to assess both ecological stability and resilience (Folke et al., 2004; Dudgeon et al., 2006). The zebra mussel *Dreissena polymorpha* Pallas, a freshwater invasive bivalve, became established in Lake St. Clair around 1986, spread rapidly throughout the Laurentian watershed (Griffiths et al., 1991), and continues to spread through the United States (Bossenbroek et al., 2007). The invasion caused significant environmental disturbance and widespread economic damage, permanently altering the ecology of the Great Lakes (Vanderploeg et al., 2002). Zebra mussels are active grazers of phytoplankton (Holland, 1993), competitors for resources with other organisms such as the benthic macroinvertebrate *Diporeia* or herbivorous zooplankton (Vanderploeg et al., 2002), and energetic nutrient recyclers (Johengen et al., 1995). By filtering suspended particles (including phytoplankton, detritus, protozoa, small zooplankton, and bacterioplankton) from the water column, excreting available nutrients, and physically altering benthic habitat, zebra mussels are able to alter the community composition of the lower trophic levels and control ecosystem functions (Heath et al., 1995).

As the base of the pelagic food web, the phytoplankton community is responsive to disturbance and a convenient indicator of the state of an aquatic ecosystem. In the Great Lakes, phytoplankton communities have been used widely as rapid assessment tools for research and management and for assessments of paleontological conditions (e.g. Stoermer et al., 1993; Makarewicz et al., 1998). Phytoplankton communities are sensitive to nutrient loading levels and the ratio of available nitrogen to phosphorus can play a determining role in community composition (Tilman et al., 1982). Variation in the levels of phosphorus loadings plays a determining role community composition of Saginaw Bay phytoplankton. The reduction in phosphorus loadings in the 1970s diminished blooms of the nitrogen fixing cyanobacteria *Aphanizomenon* that occurred during summer and this effectively addressed

---

* Corresponding author. Tel.: +1 734 997 3845.
E-mail address: dbfish@umich.edu (D.B. Fishman).

0380-1330/$ – see front matter © 2009 Elsevier B.V. All rights reserved.
doi:10.1016/j.jglr.2009.10.004

water quality problems associated with the cultural eutrophication of Saginaw Bay (Bierman et al., 1984). After the phosphorus reductions were enacted, the community composition of Saginaw Bay was described as strongly seasonal, correlated to the eutrophication gradient of the bay, and dominated by three assemblages composed of a mix of diatoms, shade tolerant cyanobacteria and green algae (Stoermer and Theriot, 1985).

Significant changes in phytoplankton community structure and composition have also been identified as a short and long-term effect of zebra mussel invasions in North America (Nicholls et al., 2002; Barbiero et al., 2006; Fernald et al., 2007). Concern over the trajectory of zebra mussel-affected ecosystems towards nuisance-causing summer blooms of cyanobacteria was first prompted by the 1994 observation by Lavrentyev et al. (1995) of dense summer blooms of species of the toxic cyanobacteria *Microcystis* 3 years after the initial colonization of Saginaw Bay; this has been a common occurrence throughout affected North American ecosystems (Sarnelle et al., 2005). Long term phytoplankton responses in the Great Lakes to both phosphorus load reductions and zebra mussel invasions have been documented in the Eastern Basin of Lake Erie; the Bay of Quinte, Lake Ontario; and Lake Oneida, New York (Idrisi et al., 2001; Nicholls et al., 2002; Barbiero et al., 2006), but these studies are all limited by a combination of spatial, temporal, or taxonomic coverage by either focusing on a single season, one or two sampling locations, or limited descriptions of phytoplankton community composition.

In a modeling analysis of Saginaw Bay phytoplankton, Bierman et al. (2005) showed that altered nutrient cycling and selective feeding behavior were capable of driving changes in the phytoplankton community. However, no comprehensive description of the Saginaw Bay phytoplankton community composition immediately before the establishment of zebra mussels, during the initial colonization period, and after the zebra mussel populations stabilized has previously been available. Here, we describe the impacts of the zebra mussel invasion on the phytoplankton community in Saginaw Bay over a period of 7 years expanding from 1990 to 1996 by examining changes in composition using multivariate analysis and considering seasonal and spatial variation.

Methods

Study site: Saginaw Bay, Lake Huron

Saginaw Bay is a shallow, naturally eutrophic embayment of Lake Huron, one of the Laurentian Great Lakes. Expanses of hard substrate and high food availability in the bay facilitated the

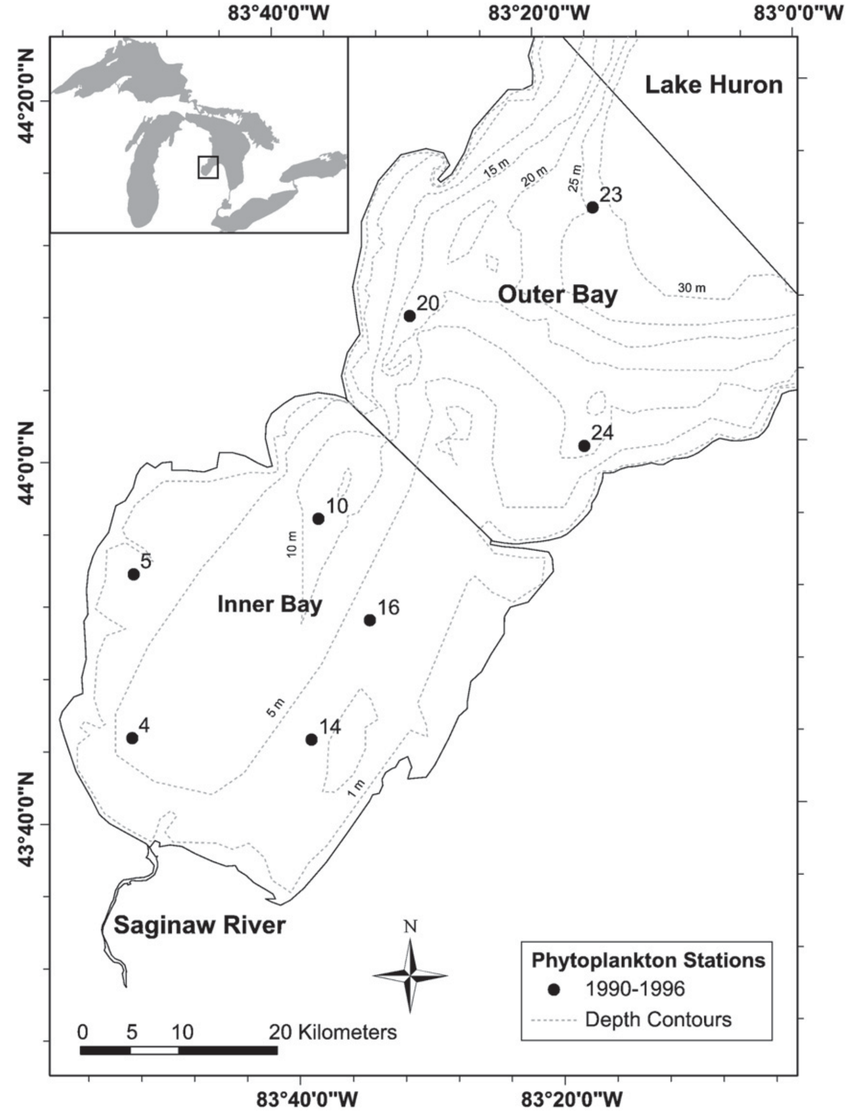

Fig. 1. Location of selected phytoplankton sampling sites in Saginaw Bay, Lake Huron, from NOAA GLERL monitoring 1990–1996.

Table 1
Mean proportion of the densities of the 22 variables (in cells per milliliter) used in the principal components analysis. The 22 variables represent an aggregation of species data to genera or division and the mean is a global mean using the complete dataset from 1990 to 1996. The variables were identified at two taxonomic levels: division and common genera.

Division	Common genera	Inner bay	Outer bay	Total
Bacillariophyta	*Asterionella*	0.4%	1.7%	0.9%
	Coscinodiscus	0.1%	0.0%	0.1%
	Cyclotella	25.3%	44.0%	32.5%
	Fragilaria	6.8%	5.4%	6.3%
	Aulacoseira	5.1%	2.4%	4.0%
	Navicula	0.2%	0.2%	0.2%
	Nitzschia	0.5%	0.3%	0.4%
	Stephanodiscus	2.1%	0.4%	1.4%
	Synedra	0.4%	3.5%	1.6%
	Tabellaria	0.4%	2.3%	1.1%
	Other diatoms	1.2%	1.2%	1.2%
Cyanobacteria	*Anabaena*	0.5%	0.5%	0.5%
	Aphanocapsa	15.5%	9.4%	13.1%
	Microcystis	7.1%	1.4%	4.9%
	Oscillatoria	5.0%	5.2%	5.1%
	Gomphosphaeria	4.5%	2.6%	3.8%
	Other cyanobacteria	1.2%	1.2%	1.2%
Others	Chlorophytes	4.5%	1.9%	3.5%
	Cryptophytes	7.1%	3.0%	5.5%
	Chrysophytes	0.3%	1.9%	0.9%
	Pyrrophytes	0.0%	0.0%	0.0%
	Flagellates	11.8%	11.8%	11.8%

establishment of large populations of zebra mussels. Rates of primary production in Saginaw Bay are among the highest of any area in the Great Lakes region (Fahnenstiel et al., 1995a). Saginaw Bay is a significant source of drinking water, recreation, and economic activity (Nalepa and Fahnenstiel, 1995). The 2960 km^2 bay receives flows from 28 fluvial systems, draining ~21,000 km^2 of southeast Michigan (Nalepa et al., 2003). Anthropogenic inputs of nutrients result from both point and nonpoint sources of nitrogen and phosphorus are attributable to the intensive agricultural, industrial, and wastewater discharges from the surrounding region (Beeton, 1965). The bay is generally considered as two related entities: an inner bay, averaging 5 m in depth and an outer bay, averaging 13 m in depth (Fig. 1). A gradient in water quality exists between the two areas because the inner bay is influenced by enriched runoff from the Saginaw River while the outer bay is influenced by generally nutrient-poor oligotrophic influxes of water from Lake Huron (Stoermer, 1978). Bierman et al. (2005) break the bay into seven spatial regions, based first on a split between the inner and outer bay and second on circulation patterns within these regions. The interactions of variable winds, currents, and anthropogenic pollution and enrichment drive the ecology of the lower trophic levels in the bay (Bierman and Dolan, 1981). While representing 10% of the volume of Lake Huron, the outflow of highly nutrient rich Saginaw Bay waters into the greater lake basin is an important determinant for the ecology of the lake system (Beeton and Saylor, 1995).

Data for the analysis

We used data from 357 phytoplankton samples collected during the multi-year survey program conducted by the National Oceanic & Atmospheric Administration (NOAA) Great Lakes Environmental Research Laboratory (GLERL). Samples were obtained at eight stations located throughout the inner and outer bay on monthly cruises, April–October, except June 1990, May 1994, and October 1996 (Fig. 1). Selected samples were collected using a Niskin bottle at 1 m depth at all stations except in 1990, when some samples were collected at depths of 2–5 m. Phytoplankton were preserved in 0.5% Lugols solutions, enumerated, and identified to species levels; as described by Fahnenstiel et al. (1998). Within the selected samples, 228 phytoplankton species were identified.

To create the input data for the multivariate analysis we identified main taxonomic groups and calculated proportions based on species densities (number of cells per milliliter). Although similar studies of community composition have used biovolume, the previous study for Saginaw Bay was based on densities (Stoermer and Theriot, 1985). Following the aggregation method described by Nicholls et al. (2002), we aggregated data at two taxonomic levels: (1) common genera and (2) divisions. We defined common genera within diatoms and cyanobacteria as those that constituted over 5% of cells per milliliter of any sample. Other genera and less abundant diatoms and cyanobacteria were aggregated within divisions. The process resulted in 22 taxonomic categories within the three main groups (Table 1). The first group was dominated by diatoms: *Aulacoseira*, *Asterionella*, *Coscinodiscus*, *Cyclotella*, *Fragiliaria*, *Navicula*, *Nitschia*, *Stephanodiscus*, *Synedra*, and *Tabellaria*. The second group was dominated by cyanobacteria: *Anabaena*, *Aphanocapsa*, *Gomphosphaeria*, *Microcystis*, and *Oscillatoria*. The third group was dominated by Chlorophyta, Cryptophyta, Chrysophyta, Pyrrophyta, and unidentified protozoan flagellates.

To calculate proportions we aggregated densities of individual species by year, taxonomic category, and station within four time periods: April–May, June, July–September, and October. These time periods were selected because preliminary analysis suggested distinct phytoplankton community seasonality in Saginaw Bay. We also calculated proportions by categories and year to compare overall annual phytoplankton community assemblages.

Species names were revised from the original classification to reflect modern taxonomy. Many cells of chrococcoid cyanobacteria were classified as *Anacystis incerta* Drouet & Daily 1952. The current taxonomy generally does not recognize *Anacystis* as a valid genus and although many *Anacystis* spp. have been reclassified as *Microcystis* (Komarek and Anagnostidis, 1986), *Anacystis incerta* was reclassified as *Aphanocapsa incerta* Cronberg & Komarek 1994 (Komarek and Anagnostidis, 1999). This revision does not affect the analysis.

Multivariate analysis

For the analysis of community composition we used multivariate techniques. Briefly, we performed principal component analysis

Table 2
Loadings of the principal component analysis of the phytoplankton community data using 22 phytoplankton input variables based on proportions of total densities.

	Variable	Comp 1	Comp 2	Comp 3	Comp 4	Comp 5
Cyanobacteria	Anabaena	0.01	−0.01	−0.01	−0.01	0.00
	Aphanocapsa	0.08	0.90	−0.03	0.14	0.27
	Microcystis	0.05	0.17	−0.05	−0.01	−0.93
	Oscillatoria	0.17	−0.17	0.83	0.37	0.04
	Gomphosphaeria	0.09	−0.03	0.15	−0.73	0.13
	Other cyanobacteria	0.01	0.04	−0.01	0.01	−0.02
Diatoms	Asterionella	0.01	−0.02	0.00	−0.01	0.00
	Coscinodiscus	0.00	0.00	0.00	0.00	0.00
	Cyclotella	−0.95	−0.02	0.06	0.03	0.03
	Fragilaria	0.11	−0.16	−0.09	−0.29	0.12
	Aulacoseira	0.10	−0.09	−0.11	−0.07	0.10
	Navicula	0.00	−0.01	−0.01	0.01	0.00
	Nitzschia	0.01	−0.01	−0.02	0.02	0.01
	Stephanodiscus	0.01	−0.04	−0.04	−0.01	0.03
	Synedra	0.00	−0.04	0.01	0.04	0.02
	Tabellaria	0.01	−0.03	0.00	0.00	0.03
	Other diatoms	0.01	−0.03	0.00	0.03	0.02
Others	Chrysophytes	0.00	−0.02	−0.01	0.01	0.02
	Cryptophytes	0.12	−0.12	−0.22	0.21	0.01
	Chlorophytes	0.08	−0.03	0.00	−0.14	−0.04
	Pyrrophytes	0.00	0.00	0.00	0.00	0.00
	Flagellates	0.10	−0.27	−0.45	0.40	0.15

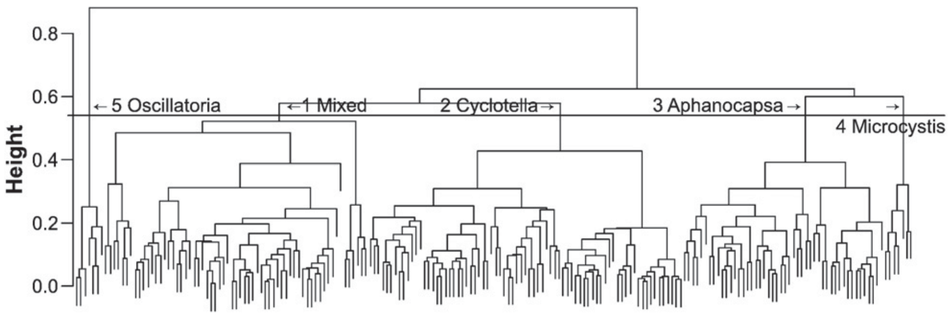

Fig. 2. Agglomerative hierarchical clustering tree showing the five cluster classifications selected based on dominant phytoplankton variable. The dendrogram shows the linkages between the aggregated samples in the analysis.

(covariance-based PCA), on a matrix of species proportions and used the scores of the PC axis that explained more than 80% of the variation as input variables to implement agglomerative hierarchical clustering (AHC) and classify the phytoplankton records into groups. The criteria for selecting the number of PC axis deviates from standards in Legendre and Legendre (1983) as the PCA was part of a multivariate combined approach. The absolute density representing abundance based on the 22 taxa selected was transformed into a profile of relative species composition proportions by dividing the density by group by the total density. The AHC clustering technique grouped cases by their group average similarity and provides a tree or dendrogram plot (Kaufman and Rousseeuw, 2005). There are several reasons for performing a combined factorial (PCA) classification (AHC) analysis. The factorial analyses provide a geometric representation of variables, easier to interpret than the initial data and allow reduction of the dimensions of the data table by retaining only the axes that explain up to a given part of the variation helpful in eliminating marginal effects that might blur the structure of interest in the data set. On the other hand, classification alleviates interpreting factorial axes, palliates individual influences in the construction of axes that can dominate the results, and makes the analysis robust. The approach we followed was based on ordination and classification techniques described in detail in Pelletier and Ferraris (2000) and widely used in applications to identify spatial and temporal patterns in community composition (among others Goñi et al., 2004; Ulrich and Anderson, 2004; Yañez et al., 2009). The PCA and HAC analysis were implemented using the princomp and the agnes routines respectively, available in the statistical software package S-PLUS 2000 (Becker et al., 1988). Clusters were built by successive pairwise agglomerations of elements, using the Euclidean distance as the metric of dissimilarity and Ward's minimum variance linkage as the clustering method (Struyf et al., 1997). We used the clustering tree to identify clusters that represent distinct phytoplankton community assemblages. In general, the selection of the appropriate number of clusters depends on the purpose of the analysis and cluster interpretability (Lewy and Vinther, 1994; Pelletier and Ferraris, 2000) rather than on a standard objective procedure (McGarigal et al., 2000). We used the separation on the height of the y-axis, which is a measure of the dissimilarity between samples separation on the height of the y-axis (where the dendrogram showed the highest distance between alternative clustering (Afifi and Clark, 1984). We used alternative selection in the number of clusters and looked at the phytoplankton composition before making a final decision.

Table 3
Composition of the five clusters identified in the analysis. The overall proportion of phytoplankton cells per milliliter of each variable is shown.

Phytoplankton variable	*Cluster*				
	1 Mixed	2 Cyclotella	3 Aphanocapsa	4 Microcystis	5 Oscillatoria
Anabaena	0.90%	0.50%	0.10%	0.30%	0.00%
Aphanocapsa	0.70%	3.80%	45.20%	14.50%	2.00%
Gomphosphaeria	8.10%	1.00%	2.70%	3.30%	3.90%
Microcystis	1.30%	1.70%	8.60%	51.10%	0.00%
Oscillatoria	6.50%	0.90%	0.60%	0.70%	73.80%
Other cyanobacteria	0.60%	1.10%	2.20%	1.50%	0.00%
Asterionella	1.20%	1.40%	0.00%	0.00%	0.10%
Aulacoseira	8.60%	2.30%	1.80%	0.70%	1.50%
Coscinodiscus	0.10%	0.00%	0.00%	0.10%	0.00%
Cyclotella	11.60%	57.90%	27.30%	11.90%	2.00%
Fragilaria	12.10%	5.10%	1.70%	1.50%	3.50%
Navicula	0.40%	0.10%	0.00%	0.10%	0.00%
Nitzschia	0.90%	0.40%	0.10%	0.00%	0.10%
Stephanodiscus	2.70%	1.20%	0.40%	0.10%	0.30%
Synedra	2.30%	2.10%	0.10%	0.00%	0.60%
Tabellaria	2.40%	1.00%	0.00%	0.00%	0.40%
Other diatoms	1.60%	1.40%	0.10%	0.30%	3.10%
Chlorophytes	5.90%	2.00%	2.50%	4.90%	3.40%
Cryptophytes	11.60%	3.30%	2.10%	2.00%	3.30%
Chrysophytes	1.53%	1.10%	0.07%	0.01%	0.07%
Pyrrophytes	0.10%	0.00%	0.00%	0.00%	0.00%
Flagellates	19.00%	11.80%	4.40%	7.00%	1.90%

We calculated species diversity of the phytoplankton community assemblages, identified through the cluster analysis, using evenness score which is the Shannon diversity index H' scaled to log of the maximum number of species in all assemblages as in Barbiero et al. (2006):

$$H' = -\sum_{i=1}^{s} p_i log p_i$$

where s is the number of species and p is proportion of cells of species i.

We mapped results of the community assemblage analysis in a geographic information system (GIS) using ArcGIS. Because the number of sampling stations was limited (only 8), Thiessen polygons were calculated around each station to interpolate the spatial range of influence based on the geometry of the sampling network.

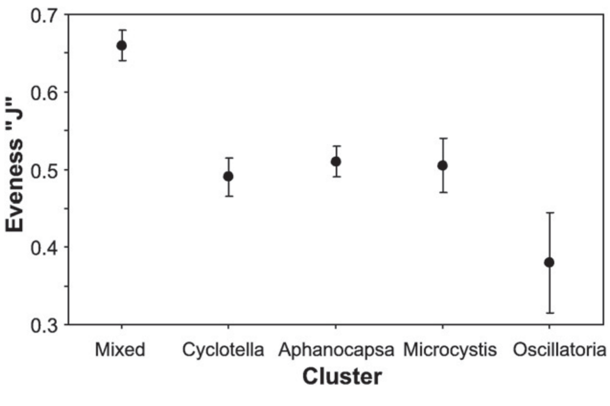

Fig. 3. Diversity of identified phytoplankton assemblage clusters from the Agglomerative Hierarchical Cluster analysis. Error bars represent 95% Confidence intervals.

Results

Over the 7-year study, mean annual (April–October) phytoplankton density was higher in the inner bay (9331 cells/ml) than the outer bay (4862 cells/ml). See Fishman (2008) for a more comprehensive and quantitative description of the Saginaw Bay phytoplankton density from 1990 to 1996. Following the 1991 widespread establishment of zebra mussels in the fall (see Nalepa et al., 1995), total phytoplankton density steadily declined up to 1994 at approximately 40% of pre-invasion levels and remained stable through 1996 with some differences in patterns between the inner and outer bay. Phytoplankton density was strongly seasonal, with a 7 year mean peak density during August. Detailed information on species composition and regression analysis on density trends by major taxonomic groups will be given in a separate publication.

Over the study period and bay-wide the mean composition of the phytoplankton was dominated by taxonomic categories with high proportions of Bacillariophyta or cyanobacteria which reached over 50% of the total densities (Table 1). Categories with high proportion of cyanobacteria were always dominant in the inner bay and during 1990 and 1996 also in the outer bay, while Bacillariophyta categories were dominant in the outer bay from 1991 to 1995.

Community composition analysis

Based on our selection criteria we identified five PCA axes of variation in the phytoplankton community data. The first two components explained 36% and 22% of the total variance respectively, while the remaining three explained 12%, 6%, and 5% respectively. The *Cyclotella* variable (category) had the strongest impact on the first axis (loading of −0.95) while the *Aphanocapsa* variable strongly impacted the second axis (loading of 0.90) (Table 2). Other important variables in the remaining three components were *Oscillatoria*, *Microcystis*, and *Gomphosphaeria*.

The AHC analysis revealed that the phytoplankton data can be separated in five clusters representative of distinct phytoplankton community assemblages in Saginaw Bay (Fig. 2). Cluster 1, a mixed assemblage was composed of 19% unidentified flagellates and over 5% of each of the following genera and divisions: the diatoms *Fragilaria* (including *F. crotonensis*, *F. capucina*, and *F. intermida*), *Aulacoseira* (*A. italica* (= *ambigua*), *A. granulata*, and *A. islandica*), and *Cyclotella* (*C. atomus*, *C. ocellata*, and *C. comensis*); the cyanobacteria *Gomphosphaeria* (*G. lacustris*) and *Oscillatoria* (*O. redekii* = *Limnothrix redekii*); cryptophytes (mostly *Rhodomonus minuta*); and chlorophytes (60 species in 28 genera, primarily *Scenedesmus quadricula* and *Pediastrum duplex*) (Table 3). Cluster 2 was 57% *Cyclotella* (*C. comensis* was dominant from 1991 to 1993 and *C. atomus and C. ocellata* from 1994

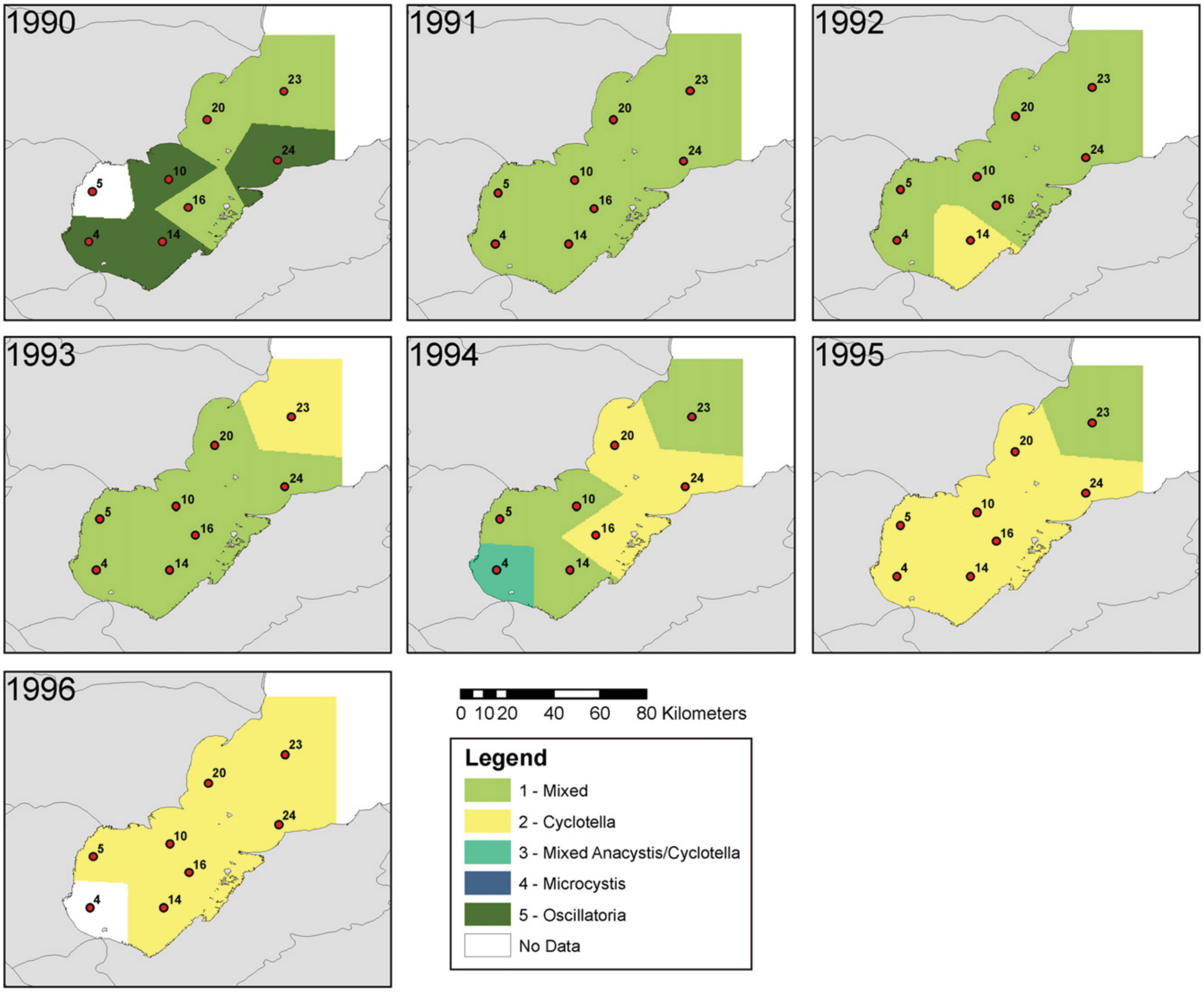

Fig. 4. Phytoplankton community composition during spring (April–May) based on cluster results from the multivariate analysis of the proportions of phytoplankton densities from selected samples.

to 1996) and 12% flagellates (Table 3). Cluster 3 was 45% *Aphanocapsa* (*A. incerta*) and 27% *Cyclotella* (several species) (Table 3). Cluster 4 was 51% *Microcystis*, 15% *Aphanocapsa*, and 12% *Cyclotella* (Table 3). Cluster 5 was strongly dominated by *Oscillatoria* (>75% of the cells mostly *O. redekii* (= *L. redekii*) (Table 3). Clusters were named by the dominant variable.

The *Cyclotella* cluster was the most prevalent with 75 station/season occurrences. The Mixed and *Aphanocapsa* clusters were also common, representing 62 and 48 cases respectively. The *Microcystis* and *Oscillatoria* clusters were uncommon and represented seven cases each.

The diversity of the phytoplankton varied among cluster assemblages. Evenness scores ranged between 0.68 and 0.38 and was highest for the Mixed cluster, lowest for the *Oscillatoria* cluster and intermediate and similar for the *Aphanocapsa*, *Microcystis* and *Cyclotella* clusters with scores around 0.5 (Fig. 3).

The phytoplankton community varied seasonally and spatially. During 1990, in spring most of the inner bay and portions of the outer bay were characterized by the *Oscillatoria* cluster while the outer bay was mostly characterized by the Mixed cluster (Fig. 4). In the summer of 1990, the bay was dominated by the Mixed cluster (Fig. 6), while in the fall the community was similar to that in spring (Fig. 7). Changes in the community composition became apparent in the spring and summer of 1991: The *Oscillatoria* cluster was absent and the Mixed cluster was now common throughout the bay from April to June (Figs. 4 and 5), but in summer and fall it was displaced by the previously uncommon *Cyclotella* cluster (Fig. 6). Between 1992 and 1993, the *Cyclotella* cluster became increasingly prevalent throughout the bay especially in the summer of 1993 and from April to June of 1994–1996. But starting during the summer of 1992 the *Aphanocapsa* cluster, composed mainly of chrococcoid cyanobacteria, dominated the bay in most years (Fig. 6) and in 1994 the *Microcystis* cluster appeared in the inner bay during the summer and was present in the subsequent years (Figs. 5 and 6).

Three major changes in the phytoplankton community occurred over the 7-year study period based on cluster assemblages: (1) assemblages were dominated by *Oscillatoria* in 1990 and disappeared in 1991; (2) the Mixed assemblages that dominated during 1991–1992 were gradually replaced by Cyclotella assemblages; and (3) *Microcystis* appeared in 1994 and *Aphanocapsa* and *Microcystis* dominated assemblages from 1994 to 1996 (Figs. 7 and 8). The clustering analysis distinguished four distinct time periods in the bay (Fig. 9): 1990, 1991, 1992–1993, and 1994–1996. A case for considering 1996 as a fifth separate timer period could be made, however the separation distance between it and 1994/1995 is minimal and, as noted in the methods, data collection ceased mid-summer in 1996. The annual community assemblage in 1990, the

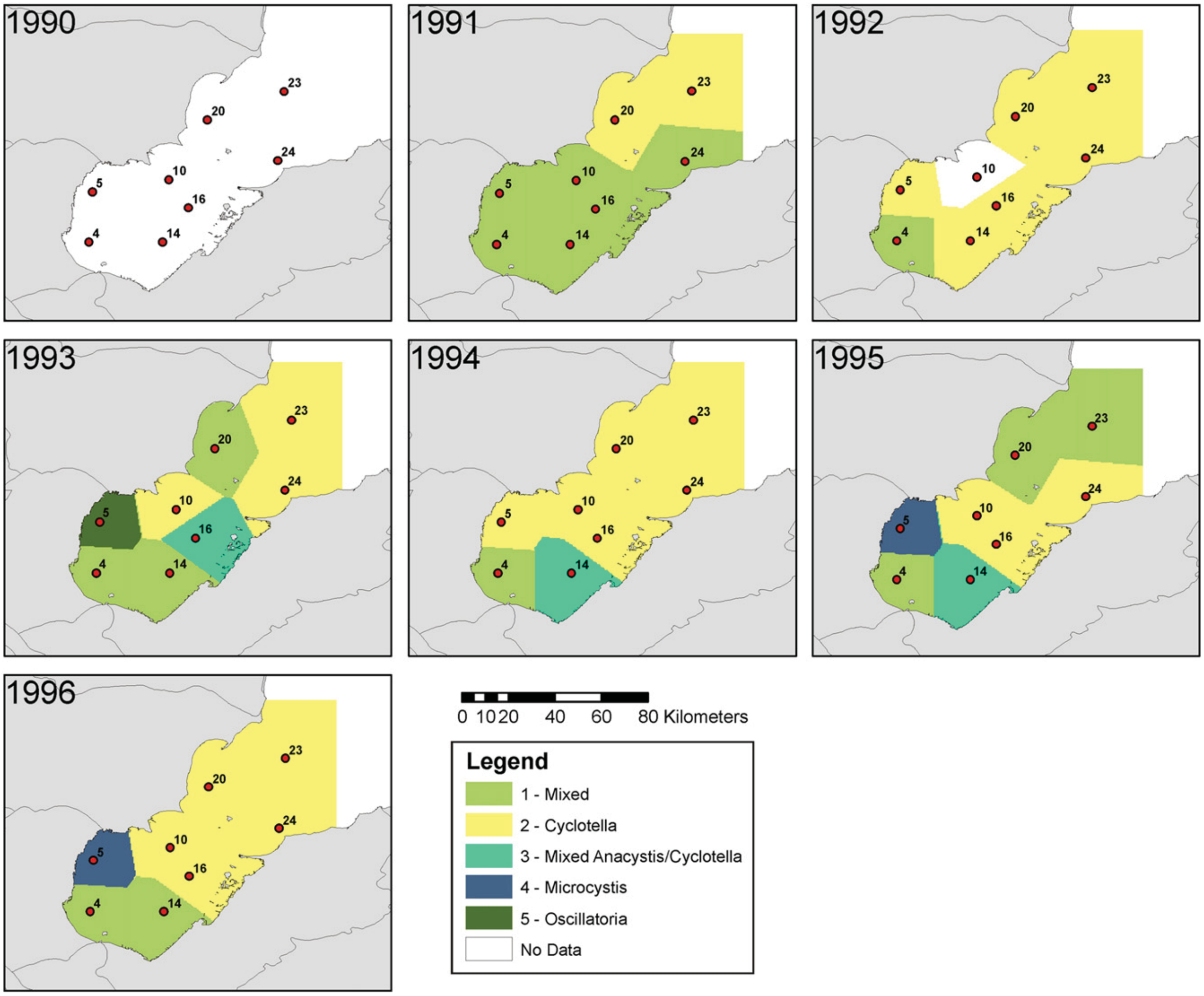

Fig. 5. Phytoplankton community composition during June based on clusters from the multivariate analysis of the proportions of phytoplankton densities from select samples.

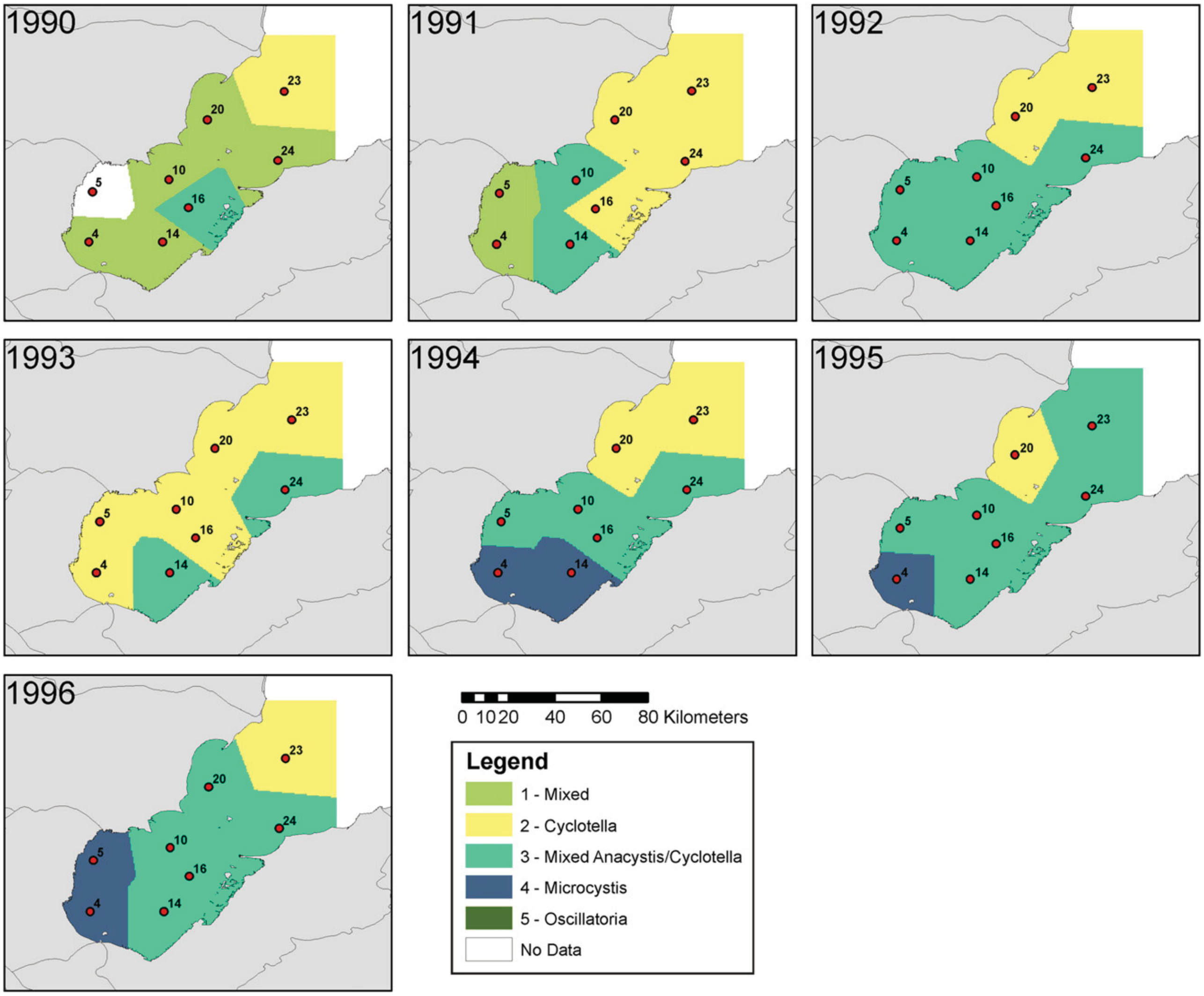

Fig. 6. Phytoplankton community composition during the summer (July–September) based on clusters from the multivariate analysis of the proportions of phytoplankton densities from select samples.

only year prior to the establishment of zebra mussels was the most different among the 7 years.

Discussion

We identified four configurations of the Saginaw Bay phytoplankton community in the 7-year period that corresponded to changes linked to the zebra mussel invasion based on five characteristic phytoplankton cluster assemblages. Overall, clusters dominated by cyanobacteria and indicative of highly eutrophic conditions were more common in the inner bay and assemblages dominated by diatoms indicative of more oligotrophic were more common in the outer bay, leading to the conclusion that the spatial distribution of the phytoplankton communities was linked to the trophic gradient from the inner to outer bay. This spatial gradient did not change over the 7-year period but communities changed on seasonal and annual temporal scales.

In 1990, the phytoplankton community was similar to the configuration described in 1980 (Stoermer and Theriot, 1985) as having three main assemblages: (1) species indicative of light limited, highly eutrophic conditions influenced by the Saginaw River (including riverine diatoms, filamentous cyanobacteria, and cryptophytes) in the inner bay; (2) two groupings of generally eurytopic diatoms (including *Melosira granulata* (= *Aulacoseira granulata*), *Tabellaria* spp., *Nitschia* spp., *Synedra* spp., and *C. comensis*), chlorophytes, and cryptophytes in the mid bay; and (3) more mesotrophic diatoms (including *Cyclotella ocellata*, *Melosira italica* (= *Aulacoseira ambigua*), and *M. islandica* (= *A. islandica*) in the outer bay (Figs. 4–6 and Table 3). Although the communities in 1990 and 1980 were generally similar, chlorophytes were 50% less abundant even before the zebra mussel colonization (Stoermer and Theriot, 1985; Fishman, 2008). A major transition occurred within the year of the zebra mussel colonization in 1991. The filamentous *O. redekii* (= *L. redekii*), characteristic of one of the cluster assemblages, dominated in 1990 and subsequently disappeared from the inner bay. *Oscillatoria* are light-sensitive planktonic cyanobacteria common in the spring and fall metalimnion of temperate eutrophic lakes (Komarek et al., 2003) and were probably affected by the increased water transparency in the bay induced by the zebra mussel.

A different phytoplankton community, identified in 1992–1993, was dominated by light-tolerant and typically oligotrophic species. The *Cyclotella* cluster in this time period was dominated by *C. comensis*, a centric diatom often associated with clear water (Reynolds, 2006) and oligotrophic conditions (Stoermer, 1978) while the Aphanocapsa cluster was dominated by *Aphanocapsa incerta* (previously *Anacystis incerta*), and *C. comensis*, an assemblage described by Stoermer (1978) as indigenous to the oligotrophic waters of Lake Huron. The dominance of the bay by these assemblages

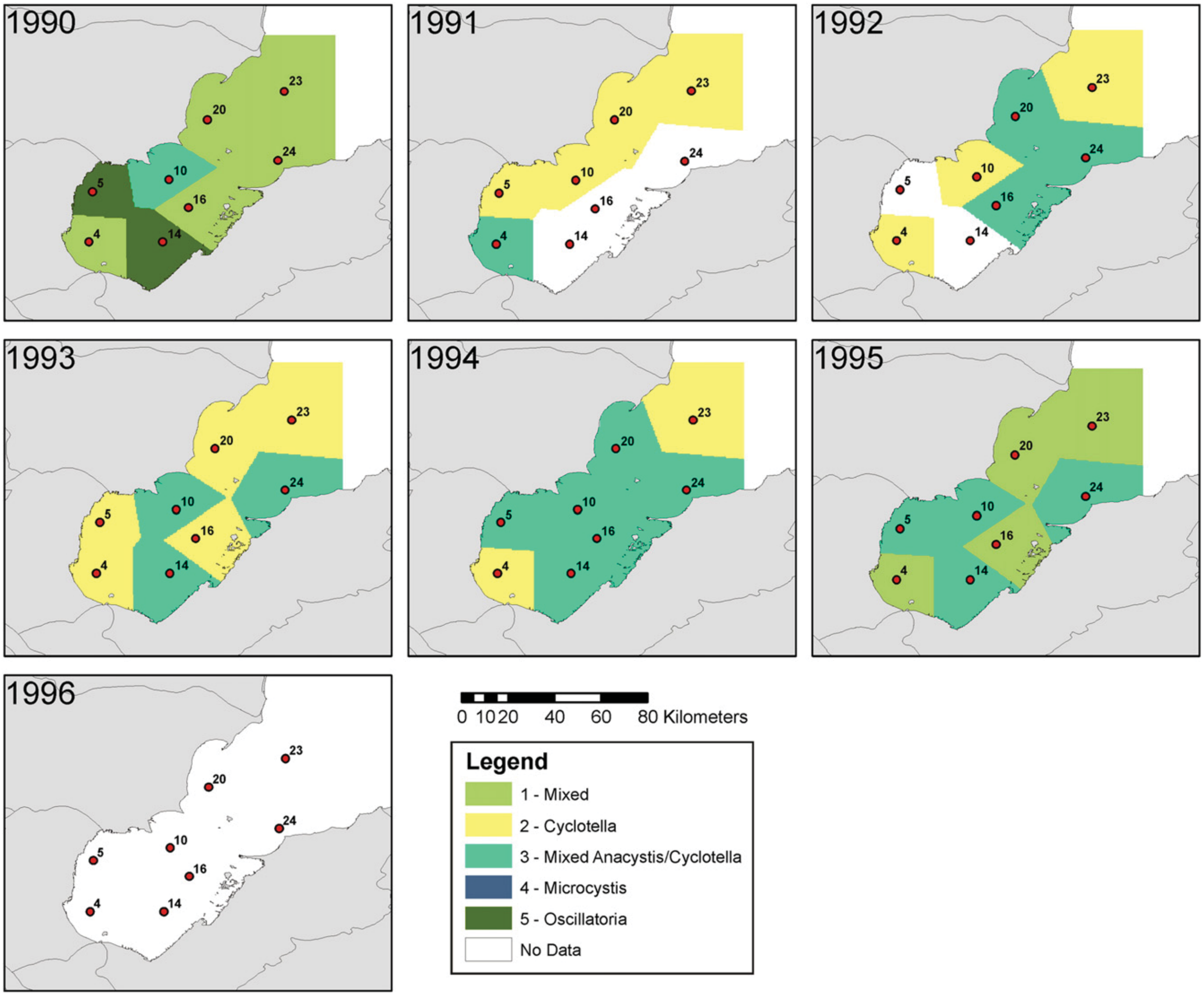

Fig. 7. Phytoplankton community composition during October based on clusters from the multivariate analysis of the proportions of phytoplankton densities from select samples.

was coupled with the decline in the Mixed cluster, which was partly composed of pennate diatom species typically associated with low light conditions and eutrophic environments (Tables 3 and 4). From a functional association standpoint, this is indicative of a shift towards mesotrophic or even oligotrophic conditions, a conclusion supported by the markedly decreased pelagic primary production reported for 1992 and 1993 by Fahnenstiel et al. (1995a).

A second set of changes occurred in 1994 with a shift in species among *Cyclotella* species, where *C. comensis* was replaced by *C. ocellata*, a species characteristic of the nutrient-poor Lake Huron waters and common in the outer bay during 1980 (Stoermer and Theriot, 1985). *Cyclotella* spp. are known to respond morphologically to subtle environmental shifts (Stoermer and Julius, 2003). During the summer of 1994, when *C. ocellata* were extremely abundant, cells appeared to vary greatly in size. This abrupt change in size and species and composition may be attributable to increased light penetration caused by removal of particles from the water column by zebra mussels, which resulted in a significant

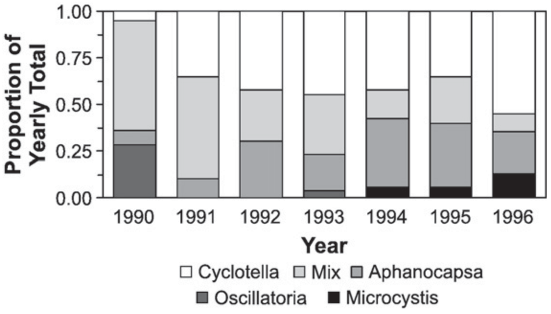

Fig. 8. Composition of phytoplankton community assemblages based on identified clusters.

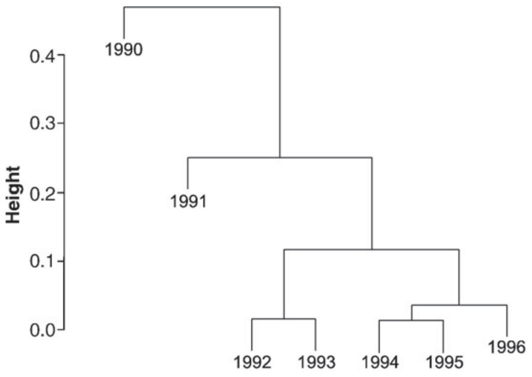

Fig. 9. Cluster analysis tree of phytoplankton composition based on annual mean proportion of total densities.

Table 4
Mean cells per milliliter of diatom genera and or species from the sample variables used in the analysis, where $n = $ number of samples collected by NOAA GLERL from the selected stations in a given year (see Fig. 1).

Diatom species	1990 $n = 27$	1991 $n = 54$	1992 $n = 55$	1993 $n = 52$	1994 $n = 48$	1995 $n = 66$	1996 $n = 55$
All other diatoms	21	26	8	7	11	9	5
Asterionella formosa	27	27	6	4	4	2	3
Aulacoseira ambigua	221	28	53	47	17	88	52
Aulacoseira granulata	8	0	2	1	0	1	1
Aulacoseira islandica	4	293	5	3	19	2	4
Aulacoseira spp.	1	3	0	1	4	0	3
Coscinodiscus subsalsa	1	6	4	1	5	2	1
Cyclotella atomus	0	0	0	0	28	195	987
Cyclotella comensis	1,214	2,991	1,083	2,929	205	558	213
Cyclotella ocellata	17	191	171	389	2,156	2,212	774
Cyclotella spp.	23	17	4	7	6	155	20
Diatoma	81	4	4	2	3	1	2
Fragilaria	466	489	134	108	87	77	146
Navicula	4	4	5	2	1	2	1
Nitzschia	10	23	14	4	5	3	1
Stephanodiscus	36	85	4	4	38	51	26
Synedra	45	101	13	11	7	8	9
Tabellaria	37	52	16	7	3	3	2

increase in Secchi depths (Fahnenstiel et al., 1995b; Fishman et al., 2009), or by the influence of Lake Huron waters transporting cells into the bay that find ample available nutrients and little competition or zooplankton grazing pressures. Shifts were also found in the cyanobacteria community composition that culminated with the onset of summer blooms of *Microcystis* sp. in 1994–1996. After the disappearance of the 1980–1990 typical spring/fall *Oscillatoria* dominated community, there were three intervening years when cyanobacteria were only represented by the *Aphanocapsa* cluster and overall abundances was low. In 1994, the dominance of the *Microcystis* cluster was due to increased densities of *Microcystis* sp. throughout the inner bay.

A framework is emerging to explain the role of zebra mussels in promoting cyanobacteria blooms in waters that have been largely free of nuisance blooms since the advent of water quality controls (Bierman et al., 2005; Sarnelle et al., 2005; Bykova et al., 2006). The indirect effect of altered nutrient cycling associated with zebra mussel populations, particularly the recycle of available phosphorus to the water column, is thought to play an important role in stimulating summer blooms of cyanobacteria. Another mechanism is that zebra mussel colonies may selectively reject *Microcystis* spp. and egests viable colonies back into the water column, thus directly promoting blooms (Vanderploeg et al., 2001). While laboratory feeding experimental results suggest that zebra mussels may show a slight preference for some cyanobacteria cells as a food sources (Pires and Van Donk, 2002; Sarnelle et al., 2005), direct video observations of zebra mussels feeding on natural seston from the Great Lakes indicate that after filtration but before ingestion, zebra mussels reject certain phytoplankton cells, particularly strains of *Microcystis aeruginosa* (Vanderploeg et al., 2001).

Peak zebra mussel densities occurred throughout Saginaw Bay in 1992 (Nalepa et al., 2003) coinciding with a period of low phosphorus loads (Bierman et al., 2005). Primary production fell (Fahnenstiel et al., 1995a) and water clarity increased (Pillsbury et al., 2002). These trends, combined with the changes in the prevalence and distribution of phytoplankton assemblages described here, suggest a move towards a more meso-to-oligotrophic type community from 1992 to 1993 in response to the changing ecological conditions.

The use of functional groups to describe lake phytoplankton communities can reveal associations between community composition and ecological conditions (Stoermer, 1978; Reynolds et al., 2002; Reavie et al., 2006). The Saginaw Bay species composition in 1980, 1990, and early 1991 with abundant *F. crotonensis*, *A. italica* (= *ambigua*), *A. islandica*, *Asterionella formosa*, and *O. redekii* (= *L. redekii*), correspond to functional groups C, P, and S1 proposed by Reynolds et al. (2002). These functional groups are associated with eutrophic, light limited conditions in temperate shallow lakes (Reynolds et al., 2002; Reynolds, 2006). The S1 group, defined as common to turbid mixed layers, tolerant of highly light deficient conditions, and characterized by species such as *L. redekii*, is similar to the phytoplankton community of 1980 and 1990 to 1991 in inner Saginaw Bay, where the effect of the Saginaw River was the greatest and the community was dominated by *O. redekii* (= *L. redekii*). The P group, defined as common to eutrophic epilimnia, composed of species tolerant of light deficiency, and characterized by diatoms including *F. crotonensis* and *Aulacoseira* spp. and the C group, defined as common to mixed, small to midsized eutrophic lakes, also tolerant of light deficiencies and characterized by diatoms including *A. formosa* and *Aulocoseira* spp., are similar to the outer bay Saginaw Bay phytoplankton communities of 1980 (see Stoermer and Theriot, 1985) and 1990 through 1991 (see Table 4 for diatom genera and species densities).

A shift in cyanobacterial cell phenotype was noted in 1993 samples, when two types of *Microcystis* were found: *M. aeruginosa*, present from 1990 to 1993 (50 $\mu m^3\ cell^{-1}$) while *Microcystis* sp., was present from 1993 to 1996 (34 $\mu m^3\ cell^{-1}$). The preservation and identification technique used with the Saginaw Bay survey program did not note colonial forms, nor were any genetic analyses undertaken. Therefore it is unknown what characteristics such as colonial structure, toxicity, or ecological affinity may be associated with these taxa, though a smaller individual cell size may be indicative of a colony forming phenotype. The change in size coincides with increased *Microcystis* dominance. *Microcystis* phenotypes vary greatly, as evidenced by the variable propensity to produce toxins or form gelatinous colonies (Wilson et al., 2005). The diversity of *Microcystis* is an emerging topic; the use of genetic analyses of *Microcystis* blooms suggest that blooms, which were previously thought to be single species, may actually be composed of a mix of genetically distinct species with different toxicity, morphology, and ecological affinities (Bittencourt-Oliveira et al., 2001; Wilson et al., 2005; Wilson et al., 2006). If zebra mussels in Saginaw Bay selectively rejected unpalatable *Microcystis* strains and returned viable cells to the water column, they could have promoted shifting dominance within a heterogeneous mix of species.

In summary, the zebra mussel colonization introduced dramatic changes in phytoplankton community composition in Saginaw Bay.

The description of *Microcystis* assemblages dominating the inner bay assemblages helps to confirm the framework suggested by Bierman et al. (2005) of selective feeding and altered nutrient availability in promoting summer cyanobacteria blooms. However, the disappearance of shade tolerant phytoplankton assemblages and their replacement with light tolerant assemblages also highlights the role of the altered light regimes associated with zebra mussel invasions in disrupting the phytoplankton community composition.

Acknowledgments

Thanks to Tom Nalepa at NOAA GLERL for providing access to sampling data. Eugene Stoermer and Richard P. Barbiero were very helpful in working with the phytoplankton identifications and reviewing selected original phytoplankton slides. The comments and revisions to diatom taxonomy by Mark Edlund at the Science Museum of Minnesota were especially valuable. We also thank an anonymous reviewer for helpful comments particularly in reference to the data analysis. This is GLERL contribution number 1539.

References

Afifi, A.A., Clark, V., 1984. Computerized multivariate analysis. Lifetime Learning, Belmont, CA.

Barbiero, R.P., Rockwell, D.C., Warren, G.J., Tuchman, M.L., 2006 Jull. Changes in spring phytoplankton communities and nutrient dynamics in the eastern basin of Lake Erie since the invasion of *Dreissena* spp. Can. J. Fish. Aquat. Sci. 63 (7), 1549–1563.

Becker, R.A., Chambers, J.M., Wilks, A.R., 1988. The new S language. A programming environment for data analysis and graphics. Wadsworth & Brooks/Cole Advanced Books & Software, Pacific Grove, CA.

Beeton, A.M., 1965 Aprill. Eutrophication of the St. Lawrence Great Lakes. Limnol. Oceanogr. 10 (2), 1965.

Beeton, A.M., Saylor, J., 1995. Limnology of Lake Huron: the Lake Huron ecosystem: ecology, fisheries and management. SPB Academic Publishing, Amsterdam.

Bierman, V.J., Dolan, D.M., 1981. Modeling of the phytoplankton-nutrient dynamics in Saginaw Bay, Lake Huron. J. Great Lakes Res. 7 (4), 409–439.

Bierman, V.J., Dolan, D.M., Kasprzyk, R., 1984. Retrospective analysis of the response of Saginaw Bay, Lake Huron, to reductions in phosphorus loadings. Environ. Sci. Technol. 18 (1), 23–31.

Bierman, V.J., Kaur, J., DePinto, J.V., Feist, T.J., Dilks, D.W., 2005. Modeling the role of zebra mussels in the proliferation of blue-green algae in Saginaw Bay, Lake Huron. J. Great Lakes Res. 31 (1), 32–55.

Bittencourt-Oliveira, M.D., de Oliveira, M.C., Bolch, C.J.S., 2001 Octt. Genetic variability of Brazilian strains of the *Microcystis aeruginosa* complex (Cyanobacteria/Cyanophyceae) using the phycocyanin intergenic spacer and flanking regions (cpcBA). J. Phycol. 37 (5), 810–818.

Bossenbroek, J.M., Johnson, L.E., Peters, B., Lodge, D.M., 2007 Junn. Forecasting the expansion of zebra mussels in the United States. Conserv. Biol. 21 (3), 800–810.

Bykova, O., Laursen, A., Bostan, V., Bautista, J., McCarthy, L., 2006 Dec 1. Do zebra mussels (*Dreissena polymorpha*) alter lake water chemistry in a way that favours Microcystis growth? Sci. Total Environ. 371 (1–3), 362–372.

Dudgeon, D., Arthington, A.H., Gessner, M.O., et al., 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. Biol. Rev. 81 (2), 163–182.

Fahnenstiel, G.L., Bridgeman, T.B., Lang, G.A., McCormick, M.J., Nalepa, T.F., 1995a. Phytoplankton productivity in Saginaw Bay, Lake Huron: effects of zebra mussel (*Dreissena polymorpha*) colonization. J. Great Lakes Res. 21 (4), 465–475.

Fahnenstiel, G.L., Lang, G.A., Nalepa, T.F., Johengen, T.H., 1995b. Effects of zebra mussel (*Dreissena polymorpha*) colonization on water quality parameters in Saginaw Bay, Lake Huron. J. Great Lakes Res. 21 (4), 435–448.

Fahnenstiel, G.L., Krause, A.E., McCormick, M.J., Carrick, H.J., Schelske, C.L., 1998. The structure of the planktonic food-web in the St. Lawrence Great Lakes. J. Great Lakes Res. 24 (3), 531–554.

Fernald, S.H., Caraco, N.F., Cole, J.J., 2007 Febb. Changes in cyanobacterial dominance following the invasion of the zebra mussel *Dreissena polymorpha*: long-term results from the Hudson River Estuary. Estuar. Coast. 30 (1), 163–170.

Fishman, D.B., 2008. A statistical and dynamic modeling analysis of phytoplankton changes in Saginaw Bay, Lake Huron during the zebra mussel invasion. University of Michigan, Ann Arbor, MI.

Fishman, D.F., Adlerstein, S., Vanderploeg, H.A., Fahnenstiel, G.L., Scavia, D., 2009. Causes of phytoplankton changes in Saginaw Bay, Lake Huron during the zebra mussel invasion. J. Great Lakes Res. (3), 35.

Folke, C., Carpenter, S., Walker, B., et al., 2004. Regime shifts, resilience, and biodiversity in ecosystem management. Ann. Rev. Ecolog. Evol. Syst. 35, 557–581.

Goñi, R., Adlerstein, S., Alvarez, M., et al., 2004. Recruitment indices of European hake, *Mercluccius merluccius* (Linnaeus 1758), in the Northwestern Mediterranean based on landings from bottom trawl multispecies fisheries. ICES J. Mar. Sci. 61, 760–773.

Griffiths, R.W., Schloesser, D.W., Leach, J.H., Kovalak, W.P., 1991 Augg. Distribution and dispersal of the zebra mussel (*Dreissena polymorpha*) in the Great-Lakes Region. Can. J. Fish. Aquat. Sci. 48 (8), 1381–1388.

Heath, R.T., Fahnenstiel, G.L., Gardner, W.S., Cavaletto, J.F., Hwang, S.J., 1995. Ecosystem-level effects of zebra mussels (*Dreissena polymorpha*): an enclosure experiment in Saginaw Bay, Lake Huron. J. Great Lakes Res. 21 (4), 501–516.

Holland, R.E., 1993. Changes in planktonic diatoms and water transparency in Hatchery Bay, Bass-Island Area, Western Lake Erie since the establishment of the zebra mussel. J. Great Lakes Res. 19 (3), 617–624.

Idrisi, N., Mills, E.L., Rudstam, L.G., Stewart, D.J., 2001 Jull. Impact of zebra mussels (*Dreissena polymorpha*) on the pelagic lower trophic levels of Oneida Lake, New York. Can. J. Fish. Aquat. Sci. 58 (7), 1430–1441.

Johengen, T.H., Nalepa, T.F., Fahnenstiel, G.L., Goudy, G., 1995. Nutrient changes in Saginaw Bay, Lake Huron, after the establishment of the zebra mussel (*Dreissena polymorpha*). J. Great Lakes Res. 21 (4), 449–464.

Kaufman, L., Rousseeuw, P., 2005. Finding groups in data: an introduction to cluster analysis. Wiley, New York.

Komarek, J., Anagnostidis, K., 1986. Modern approach to the classification system of cyanophytes: 2. Chroococcales. Arch. Hydrobiol. Suppl. 73, 157–226.

Komarek, J., Anagnostidis, K., 1999. Susswasserflora von Mitteleuropa Band 19/1 Cyanoprokaryota: I. Chroococcales. Gustav Fischer Verlag.

Komarek, J., Kling, H., Komarkova, J., 2003. In: Wehr, J.D., Sheath, R.G. (Eds.), 4 - Filamentous Cyanobacteria. Freshwater Algae of North America Ecology and Classification. Academic Press, New York, pp. 126–155.

Lavrentyev, P.J., Gardner, W.S., Cavaletto, J.F., Beaver, J.R., 1995. Effects of the zebra mussel (*Dreissena polymorpha* Pallas) on protozoa and phytoplankton from Saginaw Bay, Lake Huron. J. Great Lakes Res. 21 (4), 545–557.

Legendre, L., Legendre, P., 1983. Numerical ecology; develop. environ. model V3. Elsevier, Amsterdam.

Lewy, P., Vinther, M., 1994. Identification of Danish North Sea trawl fisheries. ICES. J. Mar. Sci. 51, 263–272.

Makarewicz, J.C., Bertram, P., Lewis, T.W., 1998. Changes in phytoplankton size-class abundance and species composition coinciding with changes in water chemistry and zooplankton community structure of Lake Michigan, 1983 to 1992. J. Great Lakes Res. 24 (3), 637–657.

McGarigal, K., Cushman, S.A., Stafford, S., 2000. Multivariate statistics for wildlife and ecology research. Springer Verlag, New York.

Nalepa, T.F., Fahnenstiel, G.L., 1995. Preface. *Dreissena polymorpha* in the Saginaw Bay, Lake Huron ecosystem: overview and perspective. J. Great Lakes Res. 21 (4), 411–416.

Nalepa, T.F., Wojcik, J.A., Fanslow, D.L., Lang, G.A., 1995. Initial colonization of the zebra mussel (*Dreissena polymorpha*) in Saginaw Bay, Lake Huron: population recruitment, density, and size structure. J. Great Lakes Res. 21 (4), 417–434.

Nalepa, T.F., Fanslow, D.L., Lansing, M.B., Lang, G.A., 2003. Trends in the benthic macroinvertebrate community of Saginaw Bay, Lake Huron, 1987 to 1996: responses to phosphorus abatement and the zebra mussel, *Dreissena polymorpha*. J. Great Lakes Res.. 29 (1), 14–33.

Nicholls, K.H., Heintsch, L., Carney, E., 2002. Univariate step-trend and multivariate assessments of the apparent effects of P loading reductions and zebra mussels on the phytoplankton of the Bay of Quinte, Lake Ontario. J. Great Lakes Res. 28 (1), 15–31.

Pelletier, D., Ferraris, J., 2000. A Multivariate approach for defining fishing tactics from commercial catch and effort data. Can. J. Fish. Aquat. Sci. 57, 51–65.

Pillsbury, R.W., Lowe, R.L., Pan, Y.D., Greenwood, J.L., 2002 Junn. Changes in the benthic algal community and nutrient limitation in Saginaw Bay, Lake Huron, during the invasion of the zebra mussel (*Dreissena polymorpha*). J. North. Am. Benthol. Soc. 21 (2), 238–252.

Pires, L.M.D., Van Donk, E., 2002 Octt. Comparing grazing by *Dreissena polymorpha* on phytoplankton in the presence of toxic and non-toxic cyanobacteria. Freshw. Biol. 47 (10), 1855–1865.

Reavie, E.D., Axler, R.P., Sgro, G.V., et al., 2006. Diatom-based weighted-averaging transfer functions for great lakes coastal water quality: relationships to watershed characteristics. J. Great Lakes Res. 32 (2), 321–347.

Reynolds, C.S., 2006. The ecology of phytoplankton. Cambridge University Press, Cambridge.

Reynolds, C.S., Huszar, V., Kruk, C., Naselli-Flores, L., Melo, S., 2002 Mayy. Towards a functional classification of the freshwater phytoplankton. J. Plankton. Res. 24 (5), 417–428.

Sarnelle, O., Wilson, A.E., Hamilton, S.K., Knoll, L.B., Raikow, D.F., 2005 Mayy. Complex interactions between the zebra mussel, *Dreissena polymorpha*, and the harmful phytoplankton, *Microcystis aeruginosa*. Limnol. Oceanogr. 50 (3), 896–904.

Stoermer, E.F., 1978. Phytoplankton assemblages as indicators of water-quality in Laurentian Great Lakes. Trans. Am. Microsc. Soc. 97 (1), 2–16.

Stoermer, E.F., Julius, M., 2003. Centric diatoms. In: Wehr, J.D., Sheath, R.G. (Eds.), Freshwater algae of North America ecology and classification. Academic Press, New York, pp. 559–594.

Stoermer, E.F., Theriot, E., 1985. Phytoplankton distribution in Saginaw Bay. J. Great Lakes Res. 11 (2), 132–142.

Stoermer, E.F., Wolin, J.A., Schelske, C.L., 1993 Sepp. Paleolimnological comparison of the Laurentian Great-Lakes based on diatoms. Limnol. Oceanogr. 38 (6), 1311–1316.

Struyf, A., Hubert, M., Rousseeuw, P.J., 1997 Nov 6. Integrating robust clustering techniques in S-PLUS. Comput. Stat. Data Anal. 26 (1), 17–37.

Tilman, D., Kilham, S.S., Kilham, P., 1982. Phytoplankton community ecology—the role of limiting nutrients. Ann. Rev. Ecolog. Syst. 13, 349–372.

Ulrich, U., Anderson, B.S., 2004. Dynamics of fisheries, and the flexibility of vessel activity in Denmark between 1989 and 2001. ICES J. Mar. Sci. 308–322.

Vanderploeg, H.A., Liebig, J.R., Carmichael, W.W., et al., 2001 Junn. Zebra mussel (*Dreissena polymorpha*) selective filtration promoted toxic Microcystis blooms in Saginaw Bay (Lake Huron) and Lake Erie. Can. J. Fish. Aquat. Sci. 58 (6), 1208–1221.

Vanderploeg, H.A., Nalepa, T.F., Jude, D.J., et al., 2002 Jull. Dispersal and emerging ecological impacts of Ponto-Caspian species in the Laurentian Great Lakes. Can. J. Fish. Aquat. Sci. 59 (7), 1209–1228.

Wilson, A.E., Sarnelle, O., Neilan, B.A., Salmon, T.P., Gehringer, M.M., Hay, M.E., 2005 Octt. Genetic variation of the bloom-forming cyanobacterium *Microcystis aeruginosa* within and among lakes: implications for harmful algal blooms. Appl. Environ. Microbiol. 71 (10), 6126–6133.

Wilson, A.E., Wilson, W.A., Hay, M.E., 2006 Novv. Intraspecific variation in growth and morphology of the bloom-forming cyanobacterium *Microcystis aeruginosa*. Appl. Environ. Microbiol. 72 (11), 7386–7389.

Yañez, E., Silva, C., Barbieri, M.A., Órdenes, A., Vega, R., 2009. Environmental conditions associated with swordfish size and catches in front of the Chilean coast. Lat. Am. J. Aquat. Res. 37 (1), 71–81.