

A Statistical and Dynamic Modeling Analysis of Phytoplankton Changes in Saginaw Bay, Lake Huron During the Zebra Mussel Invasion

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Abstract

The introduction of the invasive freshwater bivalve Dreissena polymorpha altered the lower trophic levels of many North American aquatic ecosystems. In Saginaw Bay, zebra mussels became established during the late summer and fall of 1991, causing environmental changes and economic losses. Seven years of monitoring data characterizing the lower trophic levels of Saginaw Bay before, during, and after the zebra mussel invasion were collected between 1990-1996 by the National Oceanic and Atmospheric Administration Great Lakes Environmental Research Laboratory. In this study, I investigated shifts in the phytoplankton community composition over the seven-year period. Using multivariate statistics and a clustering analysis, five distinct phytoplankton assemblages were identified. Major shifts in community composition were identified in 1) the fall of 1991, 2) 1992-1993, and 3) the summer of 1994. A dynamic ecosystem model coupled to a zebra mussel bioenergetics model was used to analyze the forces driving these changes. After successfully calibrating the model to 1991 conditions, test scenarios were run to identify important zebra mussel mediated alterations to the phytoplankton community of inner Saginaw Bay. In addition to the direct filtration of phytoplankton, clearing of the water column and recycle of phosphorus were identified as causal mechanisms in the observed changes in the phytoplankton community composition. This study suggests that both direct (filtration) and indirect (nutrient cycling) mechanisms are important in understanding the long-term changes in the phytoplankton of Saginaw Bay induced by zebra mussels. This work describing the changes in an aquatic ecosystem resulting from the introduction of an invasive species is important for both ecosystem management and advancing the basic understanding of ecosystem response to disturbance.

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Overview

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). In the Laurentian Great Lakes, the economic, human health, and environmental risks associated with altered aquatic ecosystems drives research and management and underscores the need for long term ecological monitoring (Hartig et al. 1991). As the base of the pelagic food web, the phytoplankton community is one of the most responsive and easily measured indicators of the state of an aquatic ecosystem. In the Great Lakes, phytoplankton communities have been used widely for paleontological assessments of historical conditions and as rapid assessment tools for research and management (e.g. Stoermer et al. 1993, Makarewicz et al. 1998).

The character of phytoplankton communities in the Great Lakes is a product of the interaction between bottom-up growth limitations due to variable nutrient, light, and temperature regimes and top-down grazing pressure (Tilman et al. 1982, Scavia and Fahnenstiel 1987). While phytoplankton communities are sensitive to alterations at either level, identifying specific drivers is complicated not only by the landscape scale of confounding factors in aquatic ecosystems, but also by the complex and often nonlinear associations of environmental conditions and phytoplankton growth. Ecosystem and water quality modeling can be helpful for building conceptual understanding in this regard and, in the Great Lakes, a strategy that has been

frequently used to test theories of ecosystem function and the strength of linkages that operate on different scales (e.g. Canale 1976, Bierman and Dolan 1981, Scavia et al. 1981a, Scavia et al. 1988, Bierman et al. 2005, Higgins et al. 2006, Millie et al. 2006).

Invasive species, introduced as an unintended consequence of human economic activity, are a particularly pressing concern in Great Lake ecosystems as ocean going vessels transport and exchange large amounts of ballast water containing viable organisms (see Karatayev et al. 2007 for review). In the Laurentian Great Lakes, this has led to the introduction of numerous aquatic invasive species (Vanderploeg et al. 2002). The freshwater bivalve *Dreissena polymorpha* Pallas (the zebra mussel) became established in this manner in Lake St. Clair in 1988 and subsequently spread rapidly throughout the Laurentian watershed (Griffiths et al. 1991). The invasion was a potent environmental disturbance causing widespread economic damage and permanently altering the ecology of the Great Lakes (Vanderploeg et al. 2002). The zebra mussel continues to spread throughout the United States, travelling surprisingly long distances overland attached to the hulls of recreational boats, to the detriment of local and regional economies and native ecosystems (Bossenbroek et al. 2007).

The impact of zebra mussels on water quality is complicated by their dual role as a novel predator (Fanslow et al. 1995, Bailey et al. 1999) and as an ecosystem engineer (Strayer et al. 1999) and their impacts have varied among ecosystems in the Great Lakes (Sarnelle et al. 2005). Significant changes in phytoplankton community structure and composition have been identified

as a short and long-term effect of the zebra mussel invasion (Nicholls et al. 2002, Barbiero et al. 2006, Fernald et al. 2007). In Saginaw Bay, the return of summer cyanobacteria blooms after zebra mussels became established reversed years of successful water quality management (Vanderploeg et al. 2001, Bierman et al. 2005). 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* three years after the initial colonization of the bay. Since that observation, and many other similar observations in Great Lakes waters, there has been a renewed interest in understanding the mussel-mediated alterations to the complex interactions between top-down and bottom-up relationships driving phytoplankton communities (e.g. Vanderploeg et al. 2001, Vadeboncoeur et al. 2002, Hecky et al. 2004, Wilson et al. 2006).

Background

Zebra Mussels: Aquatic Invasive Species

The zebra mussel *Dreissena polymorpha* is an aquatic bivalve native to the Black and Caspian sea and introduced to the Great Lakes in 1986 via ballast water from trans-Atlantic shipping traffic (Griffiths et al. 1991). Following the first discovery of significant colonization of suitable hard substrates in Lake St. Claire in 1988, the zebra mussel spread rapidly throughout the watersheds of the Great Lakes (Hebert et al. 1989). Highly fecund, zebra mussels broadcast gametes for external fertilization which gives rise to pelagic larvae (veligers). After the pelagic stage, these veligers settle onto suitable hard substrates and form dense colonies (druses), often

displacing native bivalves (Ricciardi 2003). Settled mussels actively pump water across their feeding surfaces and remove suspended particles from the water column, retaining particles from 0.7-450 μm in diameter (Jorgensen et al. 1984). Edible particles, including phytoplankton and small zooplankton, are ingested while inedible or undesirable particles are consolidated and ejected as pseudo-feces (Dorgelo and Kraak 1993). 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). These community and ecosystem level effects are emergent phenomena derived from the life history, ecology, and feeding strategies of zebra mussels.

After the 1986 establishment of zebra mussels in the Great Lakes, a major ecological monitoring program in Saginaw Bay, Lake Huron, was undertaken from 1990 to 1996 with the goal of studying the ecological impact of zebra mussels at the lower trophic levels (Nalepa and Fahnenstiel 1995). Analyses of the data collected by this program have contributed greatly to the conceptual framework describing the impacts of zebra mussels in North America (Ricciardi 2001, Raikow et al. 2004, Bykova et al. 2006).

Nutrient Loadings

As set forth in the international Great Lakes Water Quality Agreement, Saginaw Bay was declared a Great Lakes International Joint Commission Area of Concern in 1978 because high

levels of pollution impaired “the beneficial use of the area’s ability to support aquatic life.”¹ Starting in the 1950s, inputs of phosphorus from point sources such as sewage treatment plants lead to hyper-eutrophy in Saginaw Bay (Beeton 1965). Mandated point source phosphorus reductions in the 1970s focused on controlling phosphorus discharges to improve Saginaw Bay water quality. Since investment in waste water treatment in the late 1970s, tributary loadings to the bay have been reduced (Bierman et al. 2005). Nonpoint sources of phosphorus are now the major component of the tributary loads; therefore yearly loadings are variable and correlated with river flows. The Saginaw River watershed accounts for the majority of the tributary inflow and thus phosphorus loads to Saginaw Bay.

Phytoplankton Communities

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). Phosphorus plays a determining role in the phytoplankton community composition of Saginaw Bay (Bierman and Dolan 1981), and was the limiting nutrient in Saginaw Bay in the 1990s (Heath et al. 1995). In Saginaw Bay, the reduction in phosphorus loadings in the 1970s diminished summer blooms of species of the nitrogen fixing cyanobacteria *Aphanizomenon*. This effectively addressed 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

¹ Great Lakes Water Quality Agreement of 1978, revised 1987

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).

Zebra mussels colonized Saginaw Bay in the fall of 1991 (Nalepa et al. 1995). A common occurrence in Great Lakes waters after zebra mussel invasions has been an increase in chroococcoid cyanobacteria (e.g. Makarewicz et al. 1999, Nicholls et al. 2002). Species of this type of cyanobacteria can form nuisance blooms and are potentially toxic to humans and other organisms. In Saginaw Bay, short term experiments have characterized the effects on the phytoplankton community and suggested that green algae and diatoms were diminished by the presence of zebra mussels while the cyanobacteria *Microcystis* spp. and *Aphanocapsa* spp. were either unaffected or promoted (Heath et al. 1995, Lavrentyev et al. 1995).

Foodweb Interactions in the Lower Trophic Levels

Multi-year analyses from the Eastern Basin of Lake Erie; the Bay of Quinte, Lake Ontario; Lake Oneida, New York; and the Hudson River suggest that long-term changes in the phytoplankton community composition follow zebra mussel invasions (e.g. Strayer et al. 1999, Idrisi et al. 2001, Nicholls et al. 2002, Barbiero et al. 2006). The role of zebra mussels in foodwebs is both as an active grazer of phytoplankton (Holland 1993) and as a competitor for resources with other organisms such as the benthic macroinvertebrate *Diporeia* or herbivorous zooplankton (Vanderploeg et al. 2002). Phytoplankton communities are also sensitive to grazing. In typical foodwebs of the Great Lakes, zooplankton grazing and respiration are

important controls of the phytoplankton community (Scavia and Fahnenstiel 1987). While zooplankton filtration rates may turn over a water body in several weeks, zebra mussels filter the water column at a much higher rate; an individual zebra mussel may filter up to 1 L day⁻¹. In Saginaw Bay, during 1992, the collective filtration activity of the dense zebra mussel populations was enough to theoretically filter the entire volume of the 8.1 x 10⁹ m³ bay daily (Fahnenstiel et al. 1995b). This high filtration rate implies a capacity to strongly alter the ecology of the lower trophic levels. Additionally, the possibility of selective feeding has been suggested by Lavrentyev et al. (1995), who reported that in a 15 day bottle experiment using Saginaw Bay seston, zebra mussel treatment reduced the abundance of protozoans, *Cyclotella* spp, and *Cryptomonas* spp. while having no significant effect on *Microcystis* spp. The possibility of selective rejection of particles such as cyanobacteria cells and colonies has been suggested by Vanderploeg et al. (2001), who documented selective egestion of viable *Microcystis* colonies in pseudofeces. However, others have demonstrated no selective promotion of *Microcystis* in laboratory settings (Pires and Van Donk 2002).

Zebra Mussel Altered Ecology

Aside from its role as a novel predator and competitor in an aquatic system, the zebra mussel is also an ecosystem engineer that actively alters its surrounding habitat on a significant scale (Strayer et al. 1999, Vanderploeg et al. 2002). The removal of particulates from the water column increases light availability throughout the photic zone (Holland 1993). Altered nutrient cycling occurs as the metabolic activity of the mussels releases biologically available nutrients to

the water column (Heath et al. 1995, James et al. 1997). As zebra mussel biomass increases, nutrients including phosphorus are collected in the benthic environment and the growth of large populations acts as a benthic phosphorus sink (Johengen et al. 1995, Hecky et al. 2004). Finally, the physical effects of druses are associated with a localized structural complexity and enrichment of habitat beneficial for many benthic organisms (Botts et al. 1996, Beekey et al. 2004, Ward and Ricciardi 2007) and a deterioration of conditions for macroinvertebrates such as *Diporeia* (Nalepa et al. 2003).

These alterations, in concert with decreased pelagic production caused by removal of phytoplankton from the water column, affect the primary production of aquatic systems by shifting primary production from the pelagic zone to the benthos (Johannsson et al. 2000, Hecky et al. 2004, Bykova et al. 2006). The potential of altered food webs impacting Great Lakes fisheries remains unclear; although a pathway through the linkages to altered macro-invertebrate populations (i.e. the decline of *Diporeia* populations) has been proposed (McNickle et al. 2006). In Saginaw Bay, the immediate change in the ecosystem following the establishment of zebra mussels was so marked it was suggested that the trophic state (defined as the “organic production of the entire system”) began to shift from a largely eutrophic pelagic system to a more mesotrophic benthic-pelagic system as pelagic primary production rates fell and water clarity increased (Fahnenstiel et al. 1995a, Nalepa et al. 2003).

Objective

In this study, extensive field collections of phytoplankton from 1990 to 1996 allowed a multi-year analysis of the changes in the phytoplankton community composition resulting from the zebra mussel invasion. It is important to consider and describe changes in the phytoplankton community composition following the establishment of zebra mussel populations because the impacts of altered phytoplankton populations affect ecosystem function, food webs, and human health. The goal of this study is to describe the phytoplankton community of Saginaw Bay, Lake Huron, before, during, and after the zebra mussel invasion. By using multivariate statistical techniques to describe changes in the bay wide community composition (Chapter 1) and mathematical modeling to explore the mechanisms driving the observed changes in the inner bay (Chapter 2), this study complements earlier analyses of the impact of zebra mussels in Saginaw Bay from 1990 – 1996. I present an analysis of interactions between grazing, altered light regime and nutrient cycling, and environmental variability in promoting changes in the phytoplankton community as a response to the ecological disturbance created by the invasion of zebra mussels.

Chapter 1: Community Composition 1990-1996

*The establishment of zebra mussel populations has altered the lower trophic levels of many North American aquatic ecosystems. In 1990 the NOAA Great Lakes Environmental Research Laboratory initiated a seven-year survey program to monitor changes in the lower food web of Saginaw Bay, where zebra mussels became established in the fall of 1991. Monthly phytoplankton samples were collected and processed for species identification and cell counts. In this study, I investigated shifts in the phytoplankton community composition over the seven-year period and explored the resurgent summer blooms of cyanobacteria. Community composition was analyzed by using multivariate principal component analysis (PCA) on the relative abundance of identified species aggregated to 22 functional groupings as a proportion of the total phytoplankton density (cells/ml). PCA scores were used in an agglomerative hierarchical clustering analysis to identify clusters of similar composition by season and location in the bay. After the zebra mussel invasion, there were significant changes in the spatial and temporal distribution of the identified clusters. Some of these changes are indicative of eutrophic conditions being replaced by mesotrophic and oligotrophic conditions. Clusters dominated by light sensitive phytoplankton species such as the cyanobacteria *Oscillatoria redekei* became rare immediately after the mussel invasion and clusters dominated by *Cyclotella* spp. diatoms gradually became more common. While *Microcystis* spp. were present in many samples, clusters dominated by these species did not appear until 1994. Increased light penetration was a mechanism behind some immediate changes in the phytoplankton community composition. This study suggests that both direct (filtration) and indirect (nutrient cycling) mechanisms are also important in understanding the long-term changes in the phytoplankton of Saginaw Bay.*

Problem Statement

The phytoplankton community of Saginaw Bay was studied extensively when concern for water quality peaked with the cultural eutrophication of Great Lakes waters in the 1960s and 1970s. However, no comprehensive description of the 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 for Saginaw Bay. 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. I describe the long-term impacts of the zebra mussel invasion in Saginaw Bay by an examination of changes in the community composition of the phytoplankton, considering both 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 establishment of large populations of zebra mussels. Saginaw Bay is a significant

source of drinking water, recreation, and economic activity (Nalepa and Fahnenstiel 1995). Rates of primary production in Saginaw Bay are among the highest of any area in the Great Lakes region (Fahnenstiel et al. 1995a). The 2,960 km² bay receives flows from 28 fluvial systems, draining ~21,000 km² 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 meters in depth and an outer bay, averaging 13 meters in depth (Figure 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). 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). Previous work identified several major regions in the inner and outer bay that captured the relevant spatial variability in water quality and phytoplankton communities (Bierman and Dolan 1986, Bierman et al. 2005).

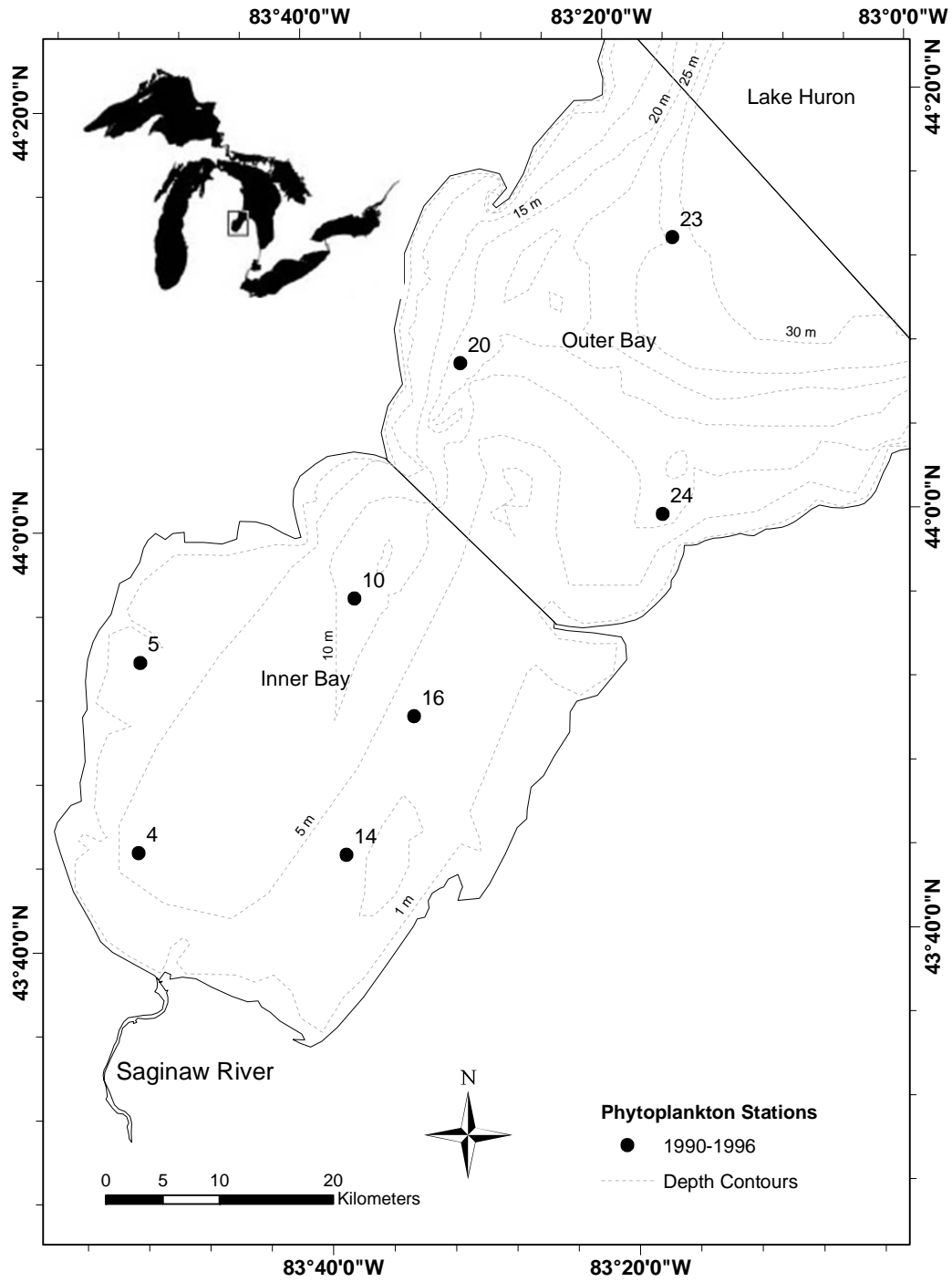


Figure 1: Location of selected phytoplankton sampling sites in Saginaw Bay, Lake Huron from NOAA GLERL monitoring 1990-1996.

Data Collection

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 by NOAA personnel at eight stations located throughout the inner and outer bay on monthly cruises, April – October, except July 1990, May 1994, and October 1996 (Figure 1, Table 1). Selected samples were collected using a Niskin bottle at 1m depth at all stations except in 1990, when some samples were collected at depths of 2-5 m. Phytoplankton identification and cell counts were conducted by NOAA personnel and provided by Henry Vanderploeg (pers comm.). Phytoplankton were preserved in 0.5% Lugols solutions. Slides were prepared with variable water volumes and cell counts were conducted in two passes with a light microscope at high and low magnification. The general method for sample processing is described in detail by Fahnenstiel et al. (1998). Recorded data consist of phytoplankton species cell counts, as well as sample location, depth, and date. Biovolume was also calculated using geometric relationships and standard species cell sizes.

Table 1: Number of samples used in the analysis of phytoplankton composition

Station	1990	1991	1992	1993	1994	1995	1996
4	4	5	6	5	5	6	4
5	1	7	5	6	5	11	11
10	4	7	6	7	7	10	6
14	4	6	5	5	4	8	5
16	3	7	5	5	4	6	5
20	3	7	7	8	6	7	7
23	4	7	7	8	4	6	6
24	4	7	6	6	6	6	5
Total	27	53	46	51	41	61	48

Phytoplankton Species Identification

228 phytoplankton species were identified within the selected samples. At most, 47 species were identified in any one sample while on average there were 21 species per sample. More than half of the species (128) were identified in 10 or fewer samples. Of these species, 42 were identified only once. Ten species were found in more than half of the samples and 30 species were present in more than a third of the samples (Table 1).

Table 2: Species identified in more than 1/3 of samples used in the analysis. Prevalence is the proportion of samples in which at least one cell of the species was present.

Division	Species	Prevalence
Bacillariophyta	<i>Asterionella formosa</i>	51%
	<i>Actinocyclus normanii f. subsalsa</i>	51%
	<i>Cyclotella comensis</i>	63%
	<i>Cyclotella comta</i>	39%
	<i>Cyclotella ocellata</i>	82%
	<i>Fragilaria capucina</i>	63%
	<i>Fragilaria crotonensis</i>	75%
	<i>Fragilaria pinnata</i>	44%
	<i>Aulacoseira islandica</i>	34%
	<i>Aulacoseira ambigua</i>	73%
	<i>Stephanodiscus sp.</i>	40%
	<i>Synedra filiformis</i>	44%
	<i>Tabellaria fenestrata</i>	64%
	Cyanobacteria	<i>Aphanocapsa incerta</i>
<i>Anacystis thermales</i>		47%
<i>Microcystis sp.</i>		35%
Chlorophyta	<i>Pediastrum sp.</i>	34%
	<i>Scenedesmus sp.</i>	34%
Cryptophyta	<i>Cryptomonas erosa</i>	67%
	<i>Rhodomonas minuta</i>	76%
Chrysophyta	<i>Dinobryon divergens</i>	37%

Multivariate Analysis

For the analysis of community composition I used multivariate techniques. I performed a Principal Component Analysis (PCA) and used the PCA standardized scores as input variables to conduct an agglomerative hierarchical cluster analysis. This clustering technique groups cases by their similarity and provides a hierarchical clustering tree or dendrogram plot (Kaufman and

Rousseeuw 2005). The analysis was implemented using the *agnes* routine, an agglomerative hierarchical method in the statistical software package S-PLUS 2000 (Struyf et al. 1997). I used the clustering tree to identify distinct phytoplankton community assemblages by defining clusters based on a chosen threshold separation on the y-axis.

Phytoplankton species densities (number of cells per ml) were used as input data for the multivariate analysis. Although similar studies of phytoplankton community composition have used biovolume, previous studies in Saginaw Bay used densities (Stoermer and Theriot 1985). Species density data from the 357 selected samples were combined into four time periods: April-May, June, July-September, and October resulting in 199 station/season cases for the analysis. To create response variables for the multivariate analysis, species densities were aggregated into taxonomic groups. Following the methods described by Nicholls et al. (2002), aggregation was performed at two taxonomic levels: 1) divisions and 2) common genera. To identify common genera within the diatoms and the cyanobacteria, a cutoff of >5% of cells/ml of any sample was used. For all the remaining less abundant diatoms and cyanobacteria as well as the other five divisions, division level classifications were used. This provided 22 taxonomic categories as input variables: the cyanobacteria *Anabaena*, *Aphanocapsa*, *Gomphosphaeria*, *Microcystis*, *Oscillatoria*, and other cyanobacteria; the diatoms *Aulacoseira*, *Asterionella*, *Coscinodiscus*, *Cyclotella*, *Fragilariaria*, *Navicula*, *Nitzschia*, *Stephanodiscus*, *Synedra*, *Tabellaria*, and other diatoms; Chlorophyta, Cryptophyta, Chrysophyta, Pyrrophyta, and unidentified protozoan flagellates. The response variables for the analysis were the densities of each of the 22

categories scaled by the total densities in each station and season. Species names were revised from the original classification to reflect modern taxonomy. In the *Aphanocapsa* genus, the majority of cells were originally identified as *Anacystis incerta* Drouet & Daily 1952. The current taxonomy generally does not recognize *Anacystis* as a valid genus and in many cases *Anacystis spp.* have been rolled into the *Microcystis* genus (Komarek and Anagnostidis 1986). However, this common colony forming chroococcoid cyanobacteria was reclassified as *Aphanocapsa incerta* Cronberg & Komarek 1994 (Komarek and Anagnostidis 1999). These revisions do not affect the analysis because *Anacystis incerta* was revised as a separate genus from *Microcystis*.

To compare phytoplankton community assemblages among years, a PCA was performed by using yearly mean densities of each of the 22 phytoplankton variables as input variables. The standardized scores were used to generate a clustering tree for each of the seven years from the study period. I identified distinct yearly periods by defining clusters based on the separation distances between each year.

Following the methods of Barbiero et al. (2006), the species richness of the phytoplankton community assemblages identified through the cluster analysis was analyzed using the Shannon diversity index:

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

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

Scaling by the maximum diversity gives an evenness index:

$$J = \frac{H'}{H_{max}}$$

Where:

$$H_{max} = \log s$$

Results of the community assemblage analysis were mapped 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.

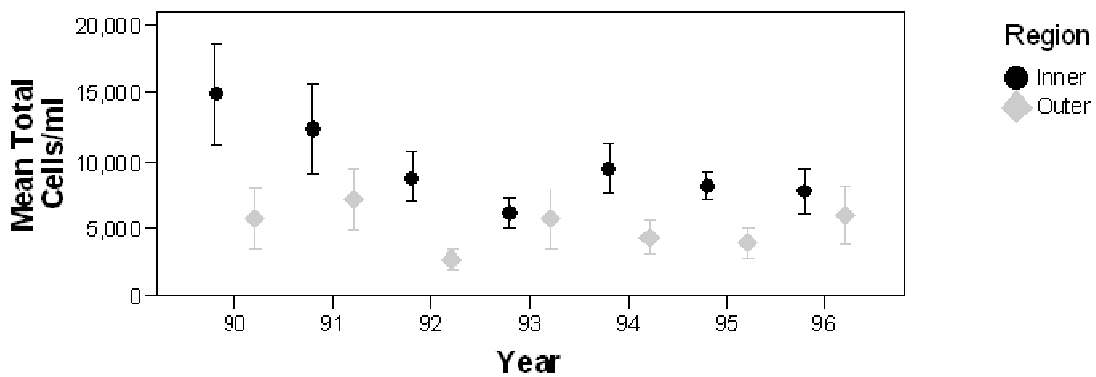
Results

Over the seven-year period of the study, mean annual (April-October) phytoplankton density was higher in the inner bay (9,331 cells/ml) than the outer bay (4,862 cells/ml) (Figure 2a). Following the widespread establishment of zebra mussels throughout the inner and outer bays in the fall of 1991 (see Nalepa et al. 1995), both the inner and outer bay total phytoplankton density declined by 40% from 1991 to 1992 (Figure 2a). While the inner bay density declined a further 25% in 1993, the outer bay density recovered. The total density in the inner bay remained stable 1994-1996 at approximately 40% of pre-invasion levels while the outer bay continued to fluctuate (Figure 2a). Phytoplankton density was strongly seasonal, with a seven year mean peak density in August (Figure 2b).

Over the study period, either Bacillariophyta or cyanobacteria dominated the bay-wide phytoplankton assemblage (Table 3). Changes in the abundances of the phytoplankton divisions between the inner and outer bay varied. In both regions, all divisions except cyanobacteria increased in density from 1990 to 1991 (Table 3). Cyanobacteria were always dominant in the inner bay and were dominant in the outer bay in 1990 and 1996. Bacillariophyta were the most abundant group in the outer bay 1991-1995. In 1992 the Bacillariophyta and cyanobacteria densities decreased by about 50% from 1990 to 1991 (Table 3). In both regions, cyanobacteria densities continued to decline through 1993 but returned to close to the seven-year average in 1994 - 1996. Bacillariophytes increased from the 1992 minimum and fluctuated around the seven-year average density from 1993-1996. There were marked reductions in the abundance of

chlorophytes, chrysophytes, and pyrrophytes from 1993 onwards; abundances for these divisions decreased by more than 70% in 1993-1996 when compared to average abundances over the seven-year period. Abundances of flagellates and cryptophytes fluctuated from year to year but there were no sustained trends (Table 3).

a)



b)

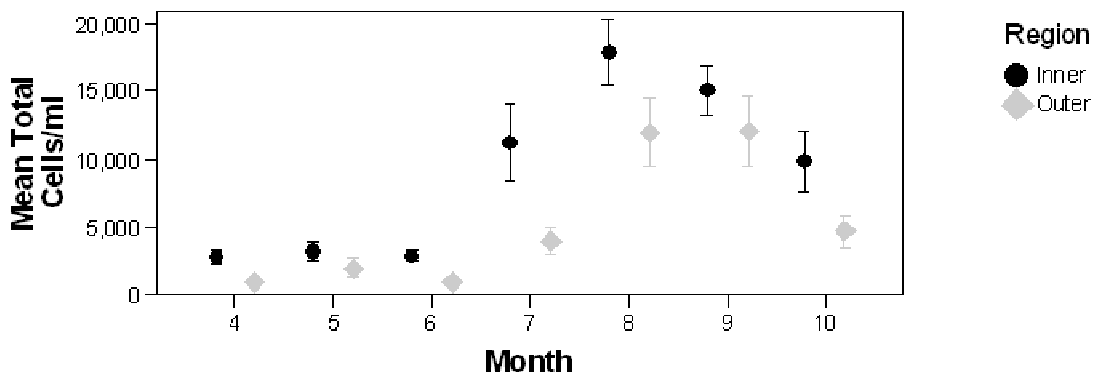


Figure 2: Total phytoplankton densities in Saginaw Bay \pm standard error of the mean by a) year (1990-1996) and b) month (April-October).

Table 3: Annual mean phytoplankton densities (cells/ml ± standard error of the mean) in Saginaw Bay by major taxonomic division in selected samples for the analysis

Region	Year	<u>Bacillariophyta</u>		<u>Cyanobacteria</u>		<u>Chlorophyta</u>		<u>Chrysophyta</u>		<u>Cryptophyta</u>		<u>Pyrrophyta</u>		<u>Flagellates</u>	
		Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
Inner Bay	1990	2,487	456	11,412	3,572	460	80	17	10	268	51	1	0	327	71
	1991	3,583	788	6,649	2,686	1,112	325	13	5	343	94	5	2	762	157
	1992	1,530	233	6,095	1,844	519	271	25	14	337	74	0	0	324	64
	1993	2,942	756	2,215	655	48	14	1	1	481	194	0	0	430	85
	1994	2,539	387	6,368	1,683	119	44	5	3	136	40	1	0	331	72
	1995	3,591	698	3,996	761	108	23	1	1	206	109	0	0	286	52
	1996	2,217	329	4,398	1,433	111	27	2	1	313	180	0	0	728	128
Total		2,698	521	5,876	1,805	354	112	9	5	298	106	1	0	455	90
Outer Bay	1990	1,816	766	3,374	1,671	207	87	16	6	48	20	1	1	239	91
	1991	5,058	2,091	1,073	444	320	94	28	14	93	23	3	2	506	134
	1992	1,360	376	956	455	84	38	45	16	73	16	0	0	188	39
	1993	3,574	1,329	1,766	1,063	9	3	22	9	76	19	0	0	234	55
	1994	2,743	785	1,445	700	15	6	2	1	10	5	1	0	63	18
	1995	2,329	656	1,393	511	19	5	8	3	49	27	0	0	101	30
	1996	2,315	555	3,142	1,836	51	41	7	2	22	9	0	0	391	129
Total		2,742	937	1,878	954	101	39	18	7	53	17	1	0	246	71

Community Composition Analysis

The principal component analysis (PCA) identified five significant axes of variation. The first two components explained 58% of the total variance in the phytoplankton community data, while the remaining three explained a further 21%. The *Cyclotella* variable 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 4). Other important variables in the remaining three components were *Oscillatoria*, *Microcystis*, and *Gomphosphaeria*.

The agglomerative hierarchical analysis revealed that the phytoplankton data can be separated in five clusters (Figure 3). These five clusters represent distinct phytoplankton community assemblages in Saginaw Bay. The clusters were named for the dominant phytoplankton variable: Cluster 1 was named “Mixed”; Cluster 2 “*Cyclotella*”; Cluster 3 “*Aphanocapsa*”; Cluster 4 “*Microcystis*”; and Cluster 5 “*Oscillatoria*” (Table 5). The Mixed cluster was an even mix of the phytoplankton variables. The *Cyclotella* cluster was the most prevalent cluster 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. While the individual cases in a cluster vary, the overall proportion of the phytoplankton variables in each cluster is indicative of the community assemblage.

Table 4: Component Loadings of the phytoplankton variables from the Principal Component Analysis of the phytoplankton community data.

	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
	Melosira	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

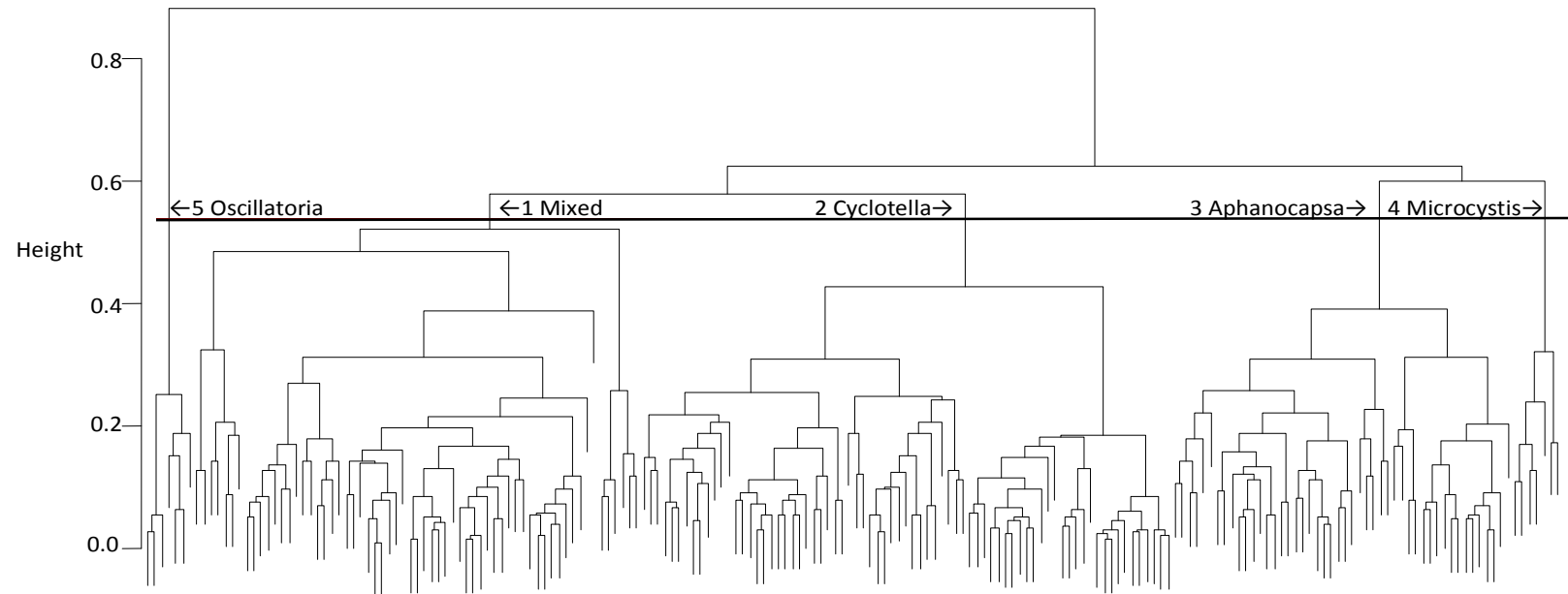


Figure 3: Agglomerative hierarchical clustering tree showing the five cluster classifications selected based on dominant phytoplankton variable.

Cluster 1 corresponds to an assemblage characterized by a mix of taxa made up by about 10% each of the following variables: *Fragiliaria* spp. (including *F. crotonensis*, *F. capucina*, and *F. intermida*), *Aulacoseira* spp. (*A. italic* (= *ambigua*), *A. granulata*, and *A. islandica*), and *Cyclotella* spp. (*C. atomus*, *C. ocellata*, and *C. comensis*); Cyanobacteria (*Gomphosphaeria lacustris* and *Oscillatoria redekii* (= *Limnothrix redekei*)); Cryptophytes (mostly *Rhodomonus minuta*); and chlorophytes (a diverse mix of 60 species in 28 genera, of which the most abundant were *Scenedesmus quadricula* and *Pediastrum duplex*) (Table 5). Unidentified flagellates made up a further 20% of the cells in this cluster. Other diatoms made up the rest of the difference.

Cluster 2 was dominated by *Cyclotella* spp (Table 5). Within this cluster, several species dominated the *Cyclotella* genus at different times. Species dominance shifted from *Cyclotella comensis* in 1991-1993 to *C. atomus* and *C. ocellata* in 1994-1996. The cyanobacteria *Aphanocapsa incerta* was also a significant component of this cluster. Cluster 3 was dominated by *Aphanocapsa incerta*, which made up 45% of this assemblage (Table 5). The other major component of this cluster was *Cyclotella* spp. which made up another 27% of the assemblage.

Cluster 4 was only present from 1994-1996. This cluster was dominated by the *Microcystis* sp. (Table 5). *Anacystis* spp, *Cyclotella* spp. and *Chlorophyta* spp. were also minor contributors to this assemblage. Cluster 5 was strongly dominated (> 75% of the cells) by *Oscillatoria* spp. The most common species identified was *Oscillatoria redekei* (= *Limnothrix redekei*) (Table 5).

Table 5: Composition of the five clusters identified in the analysis (Figure 3). The overall proportion of phytoplankton cells/ml of each variable is shown.

Phytoplankton Variable	<u>Cluster</u>				
	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%
Cryptophytes	11.60%	3.30%	2.10%	2.00%	3.30%
Chlorophytes	5.90%	2.00%	2.50%	4.90%	3.40%
Pyrrophytes	0.10%	0.00%	0.00%	0.00%	0.00%
Flagellates	19.00%	11.80%	4.40%	7.00%	1.90%

The diversity of the phytoplankton species in each assemblage varied. The mixed cluster was the most diverse, with an evenness score of 0.68, while the *Oscillatoria* cluster was significantly less diverse, with an evenness score of 0.38 (Figure 4). The remaining three clusters were similar in their diversity, with evenness scores of around 0.5.

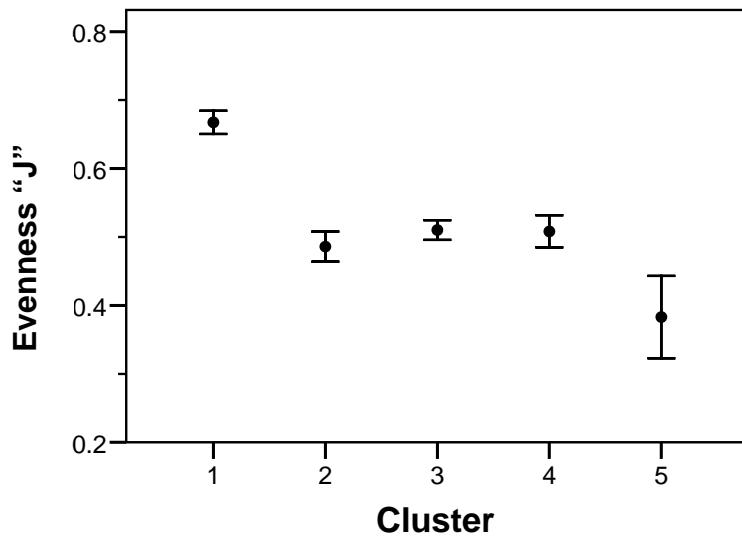


Figure 4: Diversity of each cluster from the AHC analysis.

Temporal and Spatial Distribution

Based on the multivariate analysis results, the distribution of phytoplankton community assemblages changed over the seven-year study period. Three major changes occurred: 1) the rapid disappearance of assemblages dominated by *Oscillatoria* between 1990 and 1991; 2) the gradual replacement of the mixed assemblage with *Cyclotella* dominated assemblages from 1991-1992; and 3) the appearance of *Microcystis* and *Aphanocapsa* dominated assemblages from 1994 onwards (Figure 5).

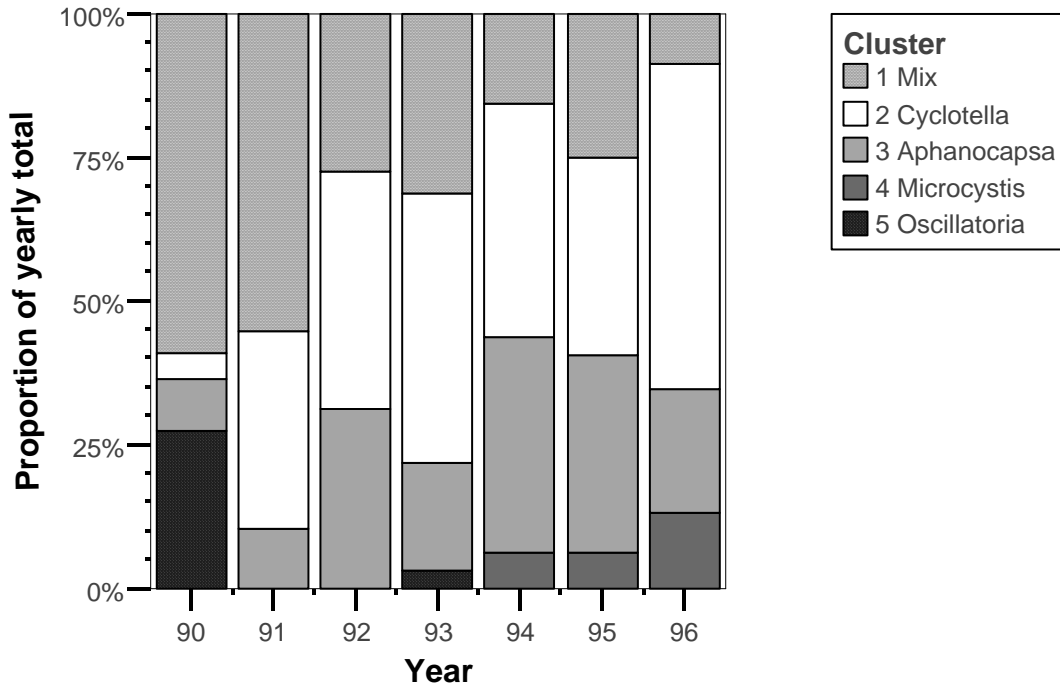


Figure 5: The prevalence of the phytoplankton community assemblages (clusters) by year.

The phytoplankton composition varied seasonally and spatially. In 1990 the spring phytoplankton community of the inner bay and portions of the outer bay were characterized by the *Oscillatoria* cluster while the Mixed cluster was common throughout the rest of the bay; spring 1991 was similar (Figure 6). While no samples were collected in June of 1990, the Mixed cluster was common throughout the bay in 1991 (Figure 7). The summer (July-September) phytoplankton composition of 1990 varied spatially with the inner bay dominated by the Mixed cluster and the *Cyclotella* cluster present in the outer bay (Figure 8). Fall 1990 was similar to the

spring community, with the Oscillatoria cluster prevalent throughout the inner bay and the Mixed cluster spread throughout the entire bay (Figure 9). Changes in the community composition became apparent in the summer of 1991, when the previously uncommon Cyclotella cluster displaced the Mixed assemblage throughout the inner and outer bay (Figure 8). Change was more dramatic in the fall of 1991, when both the Mixed and the Oscillatoria cluster were absent in the fall (Figure 9). As the total phytoplankton abundance decreased from 1992 to 1993, the Cyclotella cluster became increasingly prevalent throughout the bay especially throughout the summers of 1992 and 1993 and the spring (April – June) of 1994-1996 (Figure 7, Figure 8). The Aphanocapsa cluster, composed mainly of chroococcoid cyanobacteria *Aphanocapsa incerta* with some *Cyclotella* spp., displaced the Mixed cluster in the inner bay in the summer of 1992 (Figure 8). In 1994 the Microcystis cluster appeared in the inner bay during the summer and was present in the subsequent years (Figure 8).

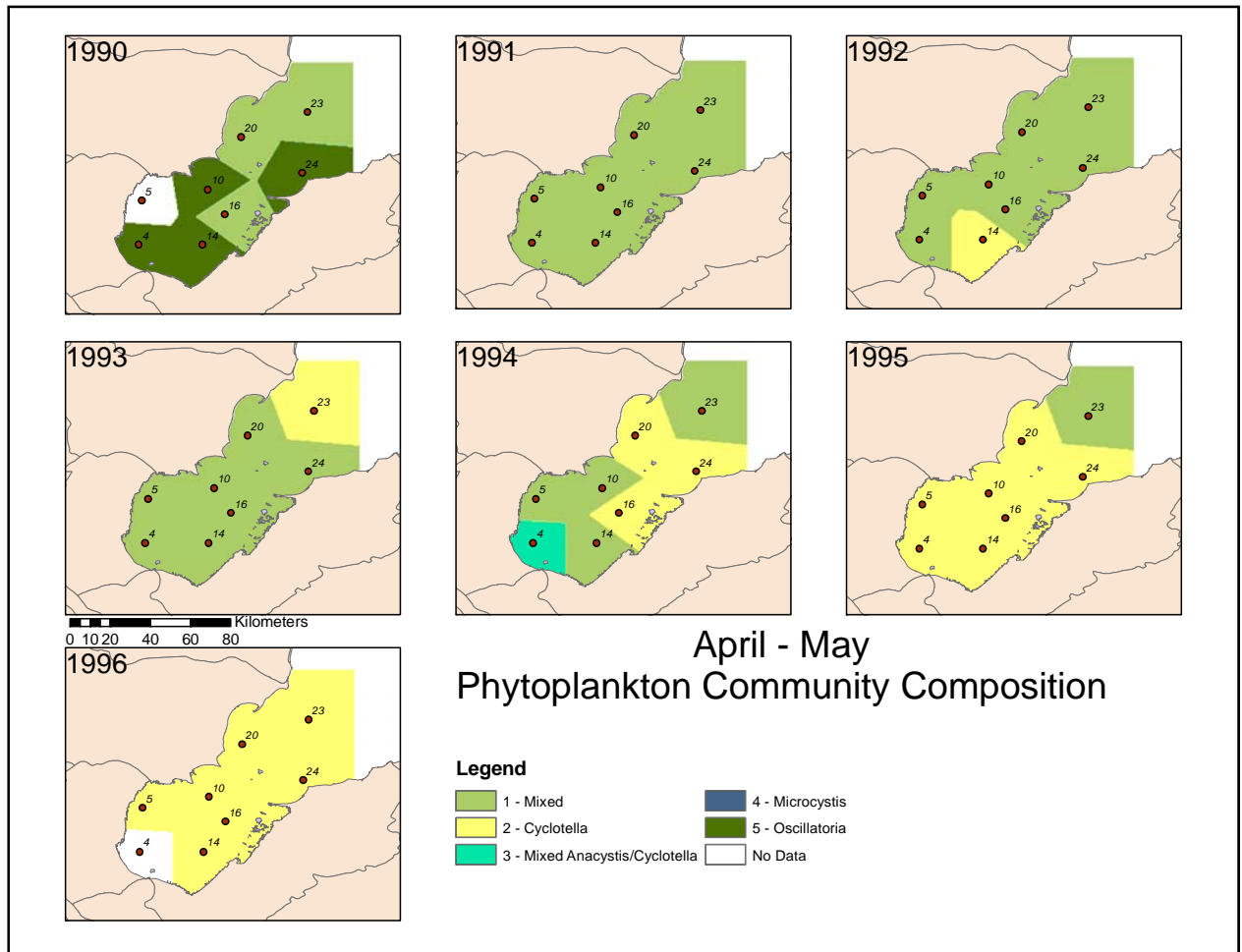


Figure 6: Phytoplankton community composition during the spring (April –May) based on cluster results from the multivariate analysis of the proportions of phytoplankton densities from select samples. By calculating the spatial neighborhood of influence of each station based on the proximity to the other stations, an interpolation surface was created.

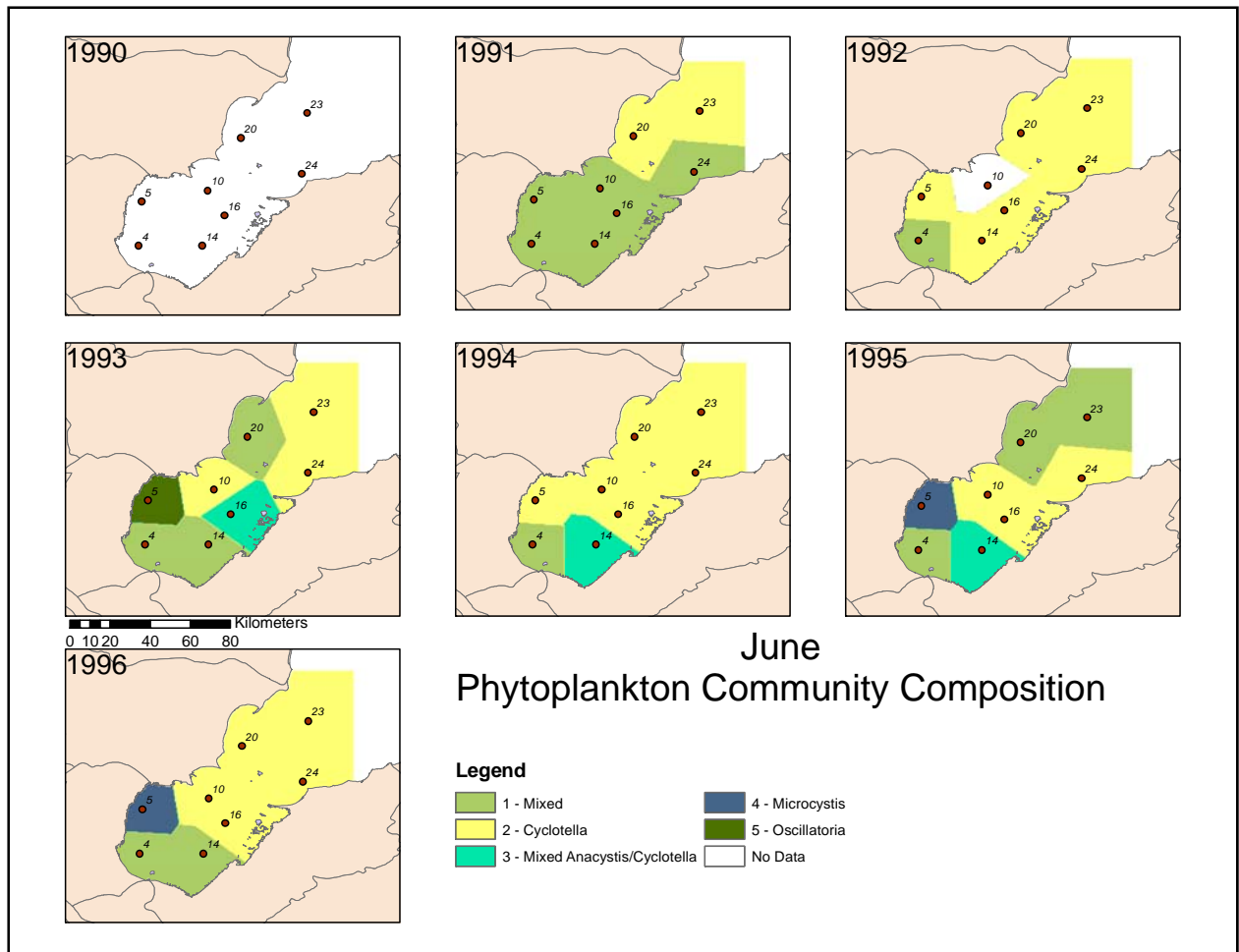


Figure 7: Phytoplankton community composition during June based on cluster results from the multivariate analysis of the proportions of phytoplankton densities from select samples. By calculating the spatial neighborhood of influence of each station based on the proximity to the other stations, an interpolation surface was created.

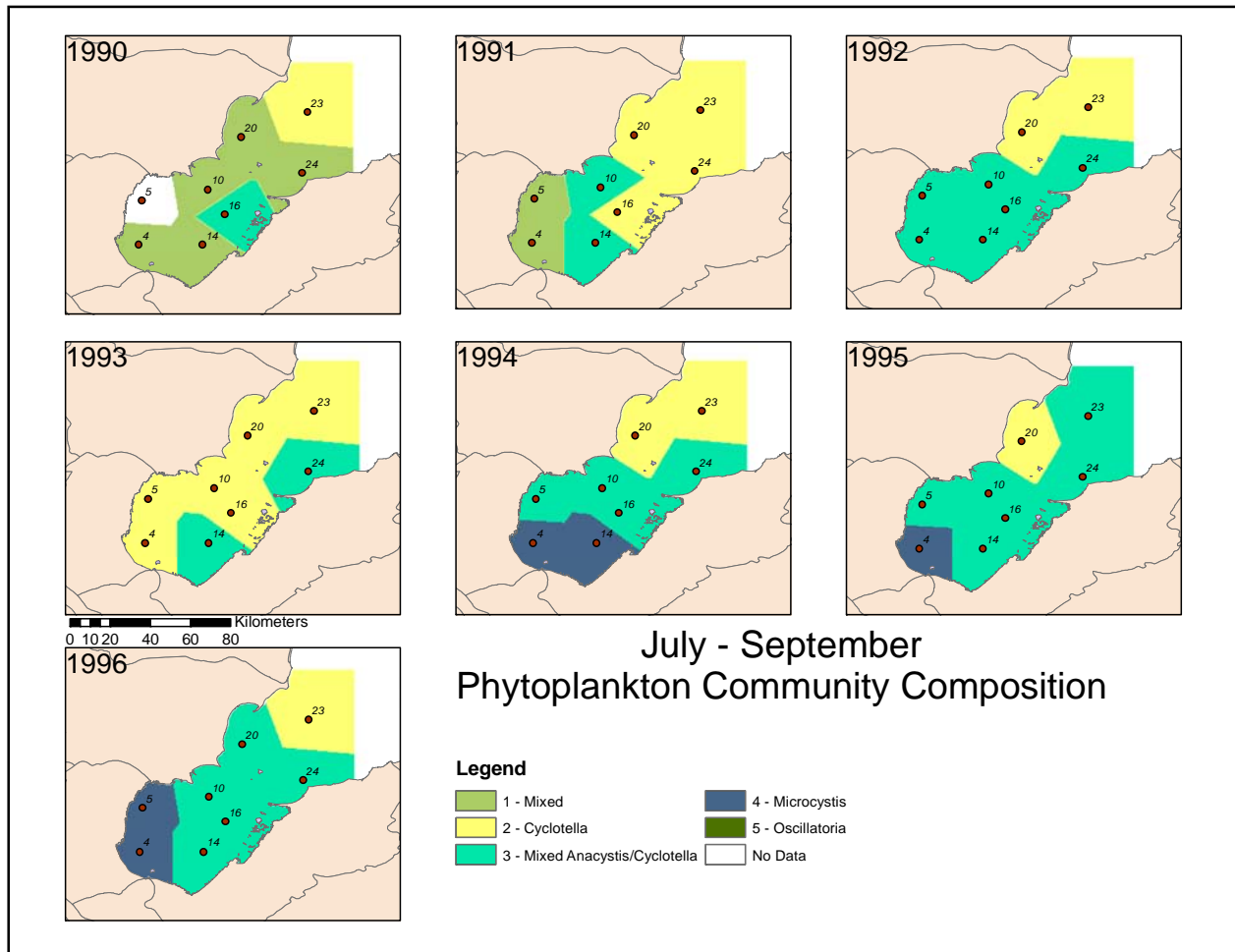


Figure 8: Phytoplankton community composition during the summer (July – September) based on cluster results from the multivariate analysis of the proportions of phytoplankton densities from select samples. By calculating the spatial neighborhood of influence of each station based on the proximity to the other stations, an interpolation surface was created.

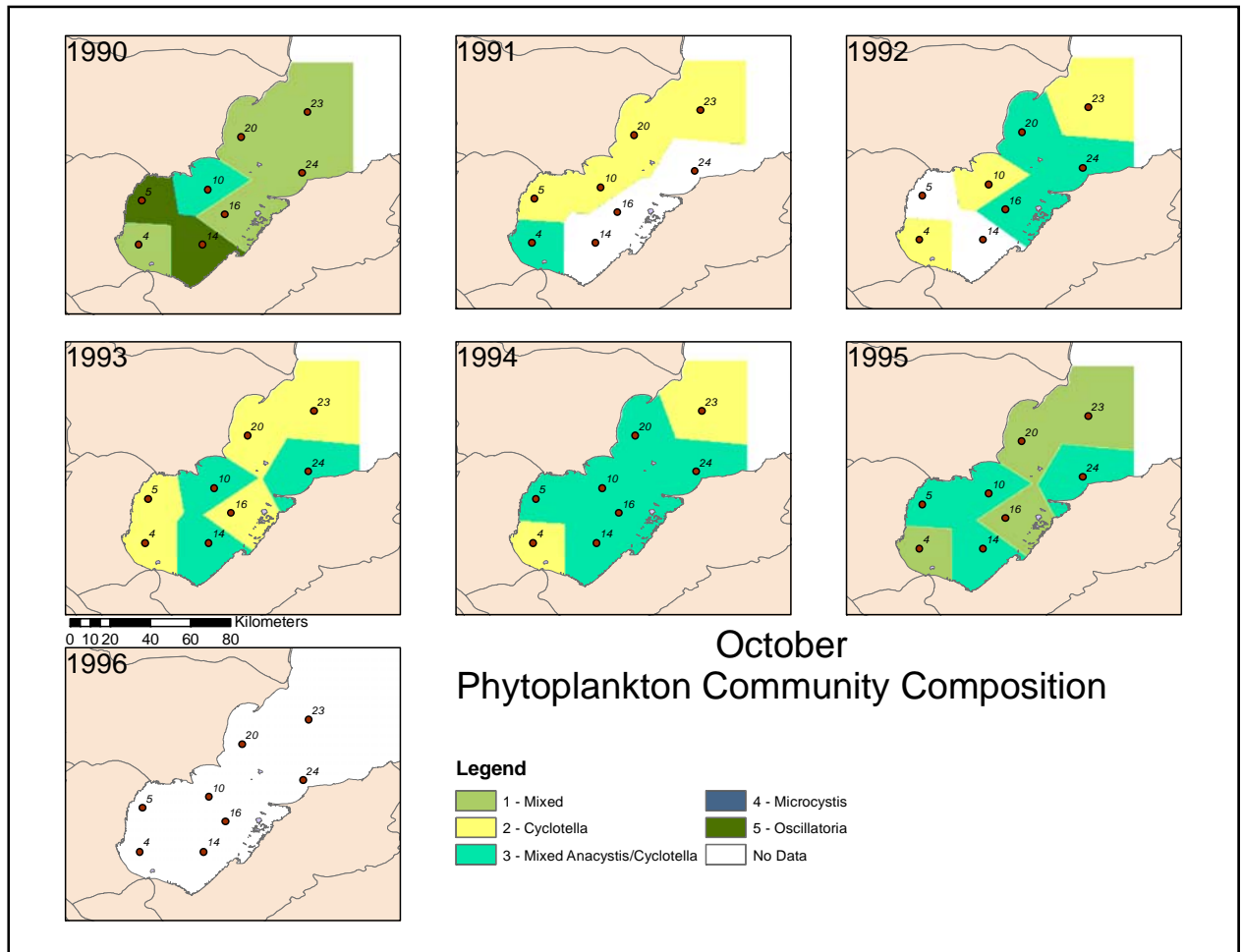


Figure 9: Phytoplankton community composition during October based on cluster results from the multivariate analysis of the proportions of phytoplankton densities from select samples. By calculating the spatial neighborhood of influence of each station based on the proximity to the other stations, an interpolation surface was created.

The results of the yearly mean cells/ml clustering analysis distinguished four distinct time periods in the bay (Figure 10). The annual community assemblage in 1990 was least similar to the other 6 years. With a mid range separation height, 1991 was not similar to either 1990 or 1992-1996. 1992 and 1993 clustered together and 1994-1996 clustered together, but all four years were more similar to each other than to 1990 or 1991.

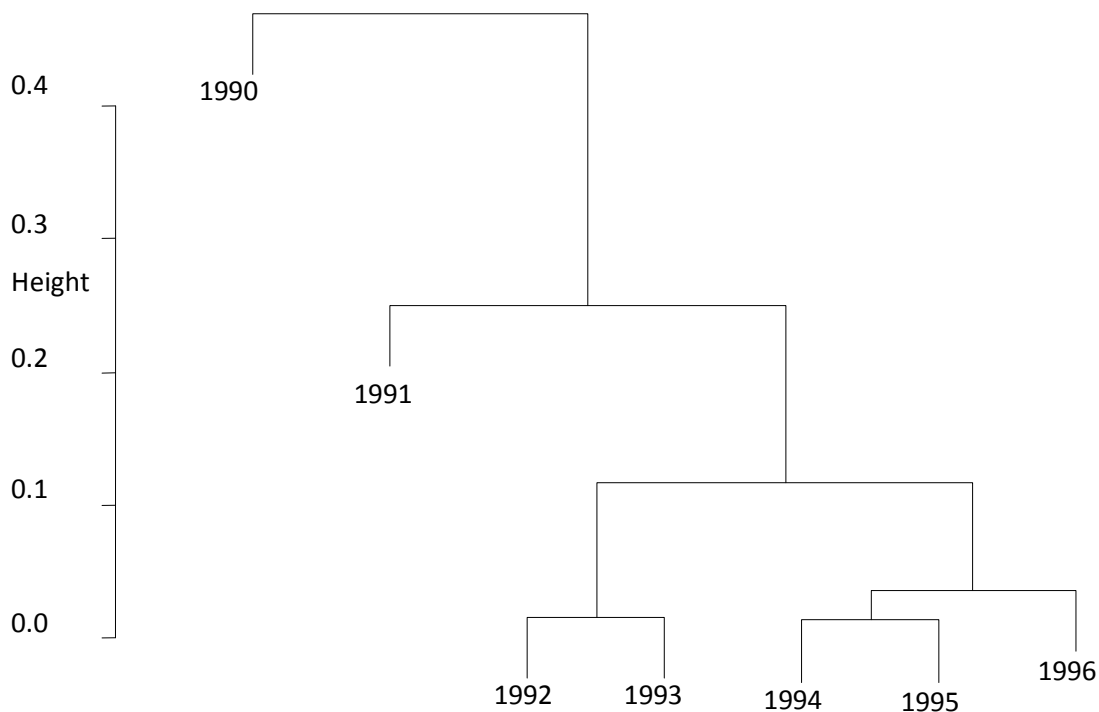


Figure 10: Results of the cluster analysis by yearly assemblage, based on annual mean proportion of cells/ml of the 22 phytoplankton variables.

Discussion

Using multivariate techniques, 5 characteristic phytoplankton communities were identified in Saginaw Bay from 1990-1996. Overall, assemblages indicative of highly eutrophic conditions were more common in the inner bay and assemblages dominated by diatoms were more common in the outer bay, leading to the conclusion that the spatial distribution of the phytoplankton community was linked to the eutrophic gradient from the inner to outer bay. This gradient did not change over the seven-year period. However, the shifts in the type and prevalence of clusters did change on seasonal and annual temporal scales. I identified four configurations of the Saginaw Bay phytoplankton community in the seven-year period that corresponded to a trajectory of change linked to the zebra mussel invasion.

In 1990, the phytoplankton community composition was very similar to the last reported configuration of the Saginaw Bay phytoplankton community described by Stoermer and Theriot (1985), suggesting that there was little change in community composition from 1980 – 1990. In 1980, the phytoplankton community was represented by three main assemblages (Stoermer and Theriot 1985): 1) In the inner bay, highly eutrophic species influenced by the Saginaw River fell into one community type (including riverine diatoms, filamentous cyanobacteria, and cryptophytes), 2) the mid bay hosted two groupings of generally eurytopic diatoms (including *Melosira granulata* (= *Aulacoseira granulata*), *Tabellaria* spp., *Nitzschia* spp., *Synedra* spp., and *Cyclotella comensis*), chlorophytes, and cryptophytes, and 3) the outer bay was dominated by more mesotrophic diatoms (including *Cyclotella ocellata*, *Melosira italic* (= *Aulacoseira*

ambigua), and *M. islandica* (= *A. islandica*). The community in 1990 was generally similar in density, composition, and distribution to this post phosphorus load-reduction community of 1980, although chlorophytes were 50% less abundant.

1991 was a transition year and generally similar to 1990 throughout the first half of the year. However changes were observed immediately after the zebra mussels became established in the late summer. The characteristic filamentous *Oscillatoria redekei*, a light-sensitive planktonic filamentous cyanobacteria abundant in 1990 and common in the spring and fall metalimnion of temperate eutrophic lakes (Komarek et al. 2003), disappeared from the inner bay and *Cyclotella comensis* dominated the baywide assemblage.

A new phytoplankton community configuration was identified in 1992-1993 that was very different than the conditions described in 1980 through the first half of 1991. While cell density was used to describe changes in phytoplankton community composition using multivariate statistical analysis, the specific changes identified are further discussed below using calculated biovolume. Biovolume can be used to find biomass and thus is useful when considering the identified changes community composition. Biovolume and biomass were also used in similar studies characterizing the zebra mussel invasion in the Great Lakes. The rise of *Cyclotella comensis*, a centric diatom often associated with clear water (Reynolds 2006) and oligotrophic conditions (Stoermer 1978), is coupled with decreased biovolume of diatoms typical of functional groups associated eutrophy and low light (Figure 11). From a functional association

standpoint, this is indicative of a shift towards mesotrophic or even oligotrophic conditions, a conclusion supported by the markedly decreased primary pelagic production reported for 1992 and 1993 by Fahnenstiel et al. (1995a).

The use of functional groups to describe lake phytoplankton communities can reveal interesting 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 *Fragilaria crotonensis*, *Aulacoseira italica* (= *ambigua*), *A. islandica*, *Asterionella formosa*, and *Oscillatoria redekei* (= *Limnothrix redekei*), correspond to functional groups C, P, and S1 proposed by Reynolds (2002) (Table 6). 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 *Limnothrix redekei*, 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 *Oscillatoria redekei* (= *Limnothrix redekei*). The P group, defined as common to eutrophic epilimnia, composed of species tolerant of light deficiency, and characterized by diatoms including *Fragilaria crotonensis* and *Aulacoseira spp.* and the C group, defined as common to mixed, small to mid-sized eutrophic lakes, also tolerant of light deficiencies and characterized by diatoms including *Asterionella Formosa* and *Aulocoseira spp.*, were similar to the mid and outer bay Saginaw Bay phytoplankton communities of 1980 and 1990 through 1991

Peak zebra mussel densities on hard substrates occurred throughout Saginaw Bay in 1992, though densities were highly variable at small spatial scales (Nalepa et al. 2003). This was a period of low phosphorus loads as well (Bierman et al. 2005). In 1992, phytoplankton 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 1992-1993 in response to the changing ecological conditions.

Table 6: Annual mean cells/ml of common diatom species from samples used in the analysis.

Diatom Species	1990	1991	1992	1993	1994	1995	1996
<i>Asterionella formosa</i>	23.3	37.4	6.0	3.5	4.0	2.3	2.6
<i>Aulacoseira ambigua</i>	242.6	26.3	53.8	44.9	19.7	96.3	969.5
<i>Aulacoseira granulata</i>	7.7	4.0	1.6	0.9	0.2	1.4	136.5
<i>Aulacoseira islandica</i>	6.9	273.8	5.3	7.3	18.0	2.2	212.3
<i>Coscinodiscus spp.</i>	1.5	5.5	3.6	1.3	4.5	2.4	1.0
<i>Cyclotella atomus</i>	0.0	0.0	0.0	0.0	26.1	192.3	1,952.8
<i>Cyclotella comensis</i>	1,031.3	2,666.0	1,065.6	2,806.0	267.6	550.0	147.1
<i>Cyclotella ocellata</i>	15.1	169.2	24.1	14.6	1,522.6	1,300.0	59.2
<i>Diatoma spp.</i>	85.7	3.6	4.2	1.6	2.6	1.0	2.4
<i>Navicula spp.</i>	2.6	0.4	2.4	0.2	0.1	0.4	0.3
<i>Nitzschia spp.</i>	9.0	20.2	2.6	3.0	3.1	2.5	1.1
Other diatoms	20.0	22.7	6.9	4.8	7.8	2.8	3.6
<i>Stephanodiscus spp.</i>	13.6	33.4	1.2	1.9	37.8	56.8	32.5
<i>Synedra spp.</i>	50.7	84.5	11.6	11.2	7.0	7.9	9.3
<i>Tabellaria spp.</i>	36.8	47.4	15.4	6.6	3.1	2.9	2.1

A second set of changes did not become apparent until 1994. A shift in species within *Cyclotella* occurred in 1994, when *C. ocellata* replaced *C. comensis* (

Table 6). *C. ocellata* was reported as common in the outer bay and characteristic of the nutrient poor open Lake Huron waters during 1980 by 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* was prevalent and *C. comensis* was absent, *C. ocellata* cells were extremely abundant and appeared to vary greatly in cell length. The reason for this abrupt change in the composition and or morphology of the *Cyclotella* genus is unclear. It may be attributable to the increased light penetration caused by removal of particles from the water column by zebra mussels, although this is not a totally satisfactory explanation because of the three year delay between the initial colonization and the subsequent species composition shift. The association of *Cyclotella* and *Anacystis* (= *Aphanocapsa*) has been described as an indigenous assemblage common in the oligotrophic waters of the Great Lakes (Stoermer 1978). Overall, while diatom biovolume decreased after the typical 1980-1990 community disappeared, *Cyclotella* spp. biovolume did not change, making it seem resistant to the effects of the zebra mussel invasion (Figure 11). Another possibility is that the *Cyclotella* spp. that dominated the assemblage in the inner and outer bay are indicative of the influence of Lake Huron waters. Thus, the prevalence could be indicative of cells being transported into the bay and finding ample available nutrients and little competition or zooplankton grazing pressures. Further changes are hinted at in 1996 as the proportion of biovolume represented by *Cyclotella* spp. falls (Figure 11); however, the monitoring program ceased that summer.

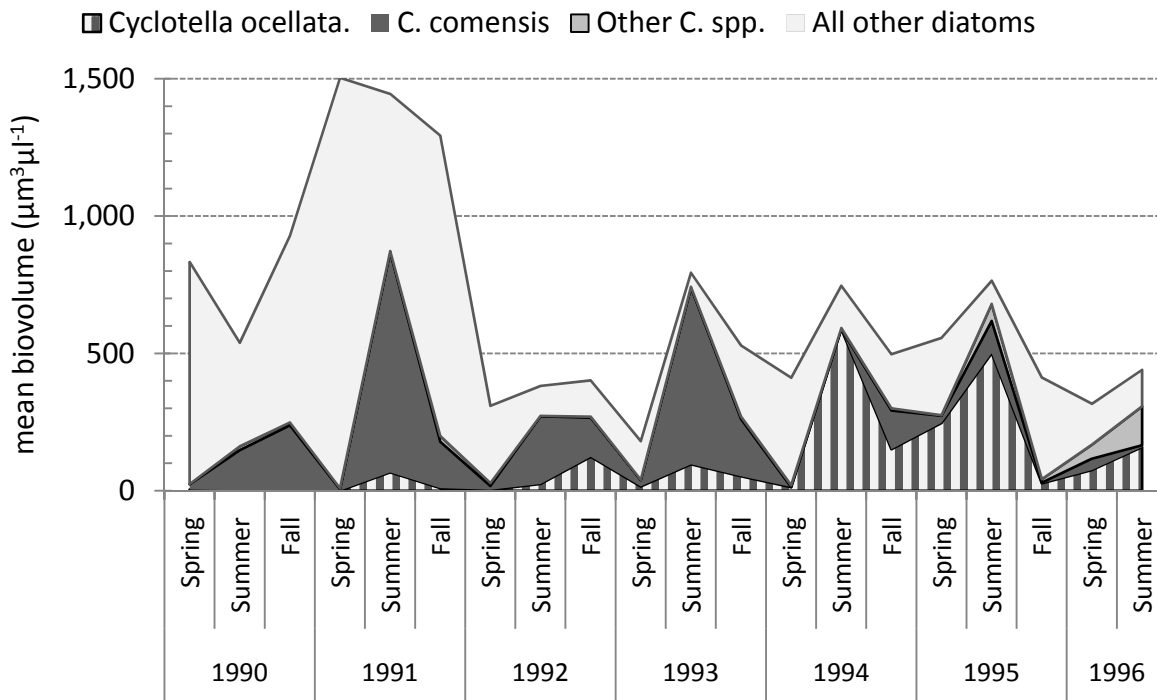


Figure 11: Saginaw Bay diatom mean biovolume ($\mu\text{m}^3\mu\text{l}^{-1}$) from 1990 -1996.

Changes in the cyanobacteria community question the move towards oligotrophy. Shifts were 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 sp.* dominated community, there were three intervening years when cyanobacteria were only represented by the *Aphanocapsa* cluster and overall abundances and biomass was low (Figure 12). However, in 1994 cyanobacteria biovolume increased due to the 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 (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 possible mechanism is that zebra mussels 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). 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 composed of a single species, may actually be composed of a heterogeneous 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). This both offers an explanation to the incongruity in laboratory versus *in situ* feeding experiments and suggests that if zebra mussels were to selectively reject unpalatable strains of *Microcystis* and return them to the water column as viable cells, a potent selective force would be operating that could promote shifting

dominance within a heterogeneous mix of species. *Microcystis* phenotypes also vary greatly, as evidenced by the variable propensity to produce toxins or form gelatinous colonies (Wilson et al. 2005). Evidence for selective pressure operating on *Microcystis* populations might be represented by a shift in composition towards a different phenotype or genotype. While the preservation and identification technique used with the Saginaw Bay survey program did not note colonial forms, nor were any genetic analyses undertaken, cell sizes were recorded. A shift in phenotype is noted in 1993, when two dominant forms of *Microcystis* were found: *Microcystis aeruginosa*, present from 1990-1993, was $50 \mu\text{m}^3 \text{ cell}^{-1}$ while *Microcystis sp.*, present from 1993-1996, was $34 \mu\text{m}^3 \text{ cell}^{-1}$. While it is unknown what characteristics such as colonial structure, toxicity, or ecological affinity may be associated with each species, a smaller individual cell size may be indicative of a colony forming phenotype. This shift from *M. aeruginosa* to *M. sp.* in 1993 is followed by blooms composed entirely of the smaller *Microcystis sp.* in 1994, 1995, and 1996 (Figure 12).

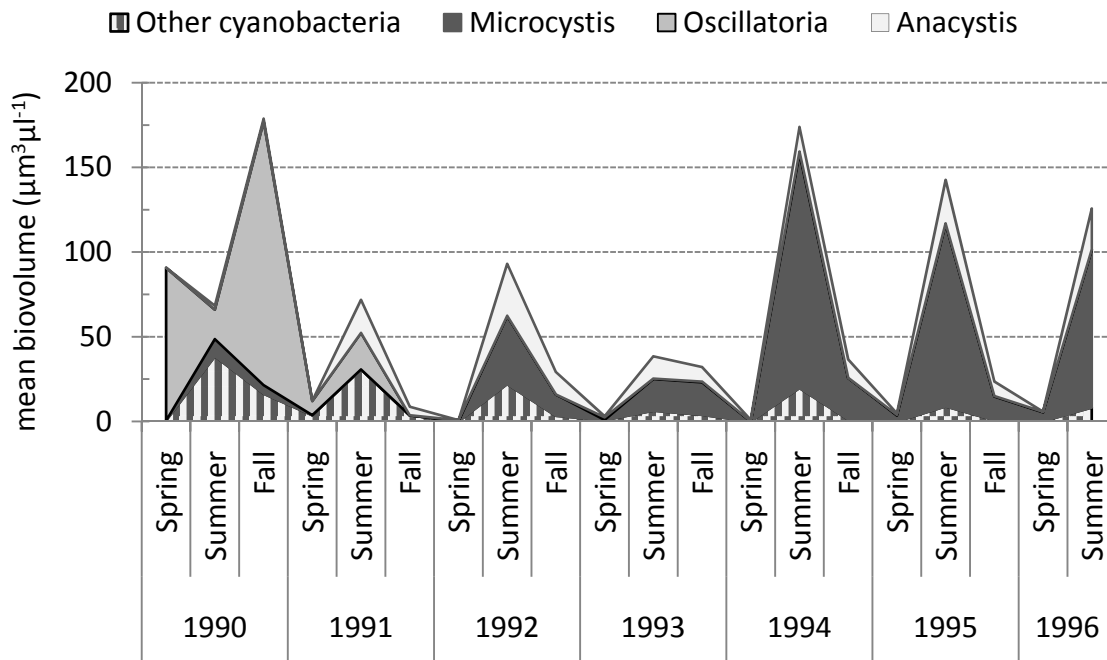


Figure 12: Saginaw Bay cyanobacteria mean biovolume ($\mu\text{m}^3\mu\text{l}^{-1}$) 1990 -1996.

In summary, the zebra mussel invasion of Saginaw Bay introduced several possible drivers of change in the phytoplankton community. The grazing effect of the dense colonization of the bay is a significant, direct pressure on phytoplankton populations. However, other forces, such as altered light regimes (Lowe and Pillsbury 1995, Skubinna et al. 1995) and altered nutrient cycling (Johengen et al. 1995) associated with the indirect physical effects of zebra mussel colonies have changed the balance of primary production between the benthic and pelagic zones and are likely significant drivers of changes in phytoplankton community composition.

Future research in Saginaw Bay should examine the continued role of zebra mussels in altering the ecology of the lower trophic levels. In Saginaw Bay, a significant piece of missing information in characterizing the impact to the lower food web is the lack of comprehensive analysis of the changes in the zooplankton community; preliminary results suggested large reductions in biomass and filtration rates (Bridgeman et al. 1995). With a clearer understanding of both the long and short term effects of the zebra mussel invasion on the Saginaw Bay phytoplankton community, focus in Chapter 2 turns towards characterizing the causal relationships driving the observed changes. Identifying the mechanisms that promoted significant changes in phytoplankton community composition could shed light on the lasting impact of zebra mussels and the magnitude of management actions necessary to address summer algal blooms. This work will be relevant not only to the Great Lakes community as management options are considered to address the impacts of zebra mussels, but also to communities recently affected or predicted to be affected by the continued spread of the zebra mussel.

Chapter 2: Development of an Ecosystem Model with Applications to 1991-1995

*The colonization of the Laurentian Great Lakes by the invasive mussel *Dreissena polymorpha* was a significant disturbance to the aquatic ecosystem of Saginaw Bay, Lake Huron. Zebra mussels became established during the late summer and fall of 1991, causing environmental changes and economic losses. Initially, clearer waters and lower algal biomass were associated with the establishment of zebra mussels in Saginaw Bay. An unexpected result three years after the initial invasion was the return of nuisance causing summer blooms of cyanobacteria, a problem that had been successfully addressed with phosphorus controls in the late 1970s. This problem has now been widely reported throughout many ecosystems affected by zebra mussels. The description of the phytoplankton community composition before, during, and after the zebra mussel invasion of Saginaw Bay in Chapter 1 was used to develop a multi-class phytoplankton model for Saginaw Bay. This model was based on a series of Saginaw Bay water quality models developed to establish links between phosphorus loads and summer algal blooms. Significant changes were undertaken to simplify the models. After successful calibration of the model to 1991 conditions, the application of the model to phytoplankton and water quality field data collected from 1991-1995 suggested that the changes seen in the phytoplankton community composition can be linked to three zebra mussel mediated effects: 1) the removal of particles resulting in a clearer water column; 2) the increased recycle of available phosphorus throughout the summer; and 3) the selective rejection of certain types of *Microcystis* spp. Light inhibition of certain phytoplankton assemblages altering competitive dynamics is a novel result of this model. These results confirm the significant role of zebra mussels in altering the lower trophic levels of Saginaw Bay and suggest that the physical re-engineering of the aquatic environment by zebra mussels was the major force driving changes in the phytoplankton community composition.*

Introduction

Ecosystem Models of Saginaw Bay, Lake Huron

Saginaw Bay, Lake Huron is an ideal location to study the impact of zebra mussels at the ecosystem scale (Nalepa and Fahnenstiel 1995). There is a long history of water quality modeling of Saginaw Bay and a reasonable set of water quality data collected 1991-1996 with the intention of supporting mathematical modeling efforts (Johengen et al. 2000). Two modern modeling efforts have begun to describe the role of zebra mussels in the Saginaw Bay ecosystem (Bierman et al. 2005, Millie et al. 2006). However, due to the complexity in applying models to long time scales and the lack of detailed analysis of the supporting field data, these modeling efforts either did not consider the long term impact of the zebra mussel invasion or did not consider changes in the phytoplankton community composition. With a detailed description of the phytoplankton community only recently available (Chapter 1), a more complete modeling investigation into the role of zebra mussels in altering the phytoplankton community and the ecology of Saginaw Bay is possible.

The mathematical model developed here is based on the Saginaw Bay multi-class phytoplankton model developed as a University of Notre Dame Ph.D. thesis by V. Bierman in 1974, applied in the establishment of phosphorus point source controls for the Great Lakes (Bierman and Dolan 1981, Scavia et al. 1981a), and documented in detail for the EPA (Bierman and McIlroy 1986). An updated model, “A Coupled Primary Productivity-Exotic Species Model for Saginaw Bay, Lake Huron,” was completed by Limnotech Inc. for the EPA in 1997 with

several important revisions to model process mechanisms undertaken since the 1986 documentation. The major revision was coupling the phytoplankton model to a zebra mussel bioenergetics model, though other significant process modifications included differentiation between wind and non-wind induced sediment resuspension rates and the division of particulate and dissolved unavailable nutrient forms (Limno-Tech 1997). This model, plus a benthic algae component, was used by Bierman et al (2005) with Saginaw Bay field data from 1991 to explore the role of zebra mussels and phosphorus loads in promoting summer cyanobacteria blooms.

Chapter 1 described the phytoplankton community throughout Saginaw Bay from 1990 – 1996 by using a multivariate statistical analysis and identified five characteristic community assemblages. Using phytoplankton samples collected at eight stations in the inner and outer bay, three main changes in the temporal distribution of these assemblages were identified over the course of the seven-year study period: 1) the disappearance of light sensitive phytoplankton; 2) the rise in dominance of *Cyclotella* spp. diatoms; and 3) summer blooms of *Microcystis* spp. cyanobacteria from 1994-1996. The five community assemblages were either characterized by one or two specific phytoplankton genera or, in one case, a mix of taxa indicative of turbid, eutrophic waters. The changes in community composition were most apparent among the centric diatoms, pennate diatoms, filamentous cyanobacteria, and chroococcoid cyanobacteria. In contrast to temporal transitions, there was little change in the spatial distribution of the phytoplankton community of Saginaw Bay (Chapter 1). The phytoplankton community of Saginaw Bay varied spatially along a eutrophication gradient from inner Saginaw Bay, which is

influenced by enriched Saginaw River flows, to outer Saginaw Bay, which mixes with oligotrophic Lake Huron (Stoermer & Theriot, 1985).

Objectives

Objectives of this modeling effort were to: 1) assemble the necessary environmental, water quality, and biological field data needed to implement and validate the model; 2) investigate the role of the zebra mussel invasion in altering the phytoplankton community composition of Saginaw Bay from 1991-1995 in conjunction with variable nutrient loadings from nonpoint source runoff; and 3) examine the water quality impacts of the reported 1991-1995 zebra mussel populations by considering the filtration and excretion effects of the colonies in inner Saginaw Bay. This investigation is critical for organizing a complete conceptual model of the long term implications of zebra mussel invasions, to identify areas for further research, and to comment on possible ecosystem management options for controlling nuisance summer blooms of cyanobacteria.

There were two major tasks undertaken to implement this model. First, a mathematical model was programmed to reflect the significant changes to the conceptual framework of the multi-class phytoplankton model upon which this modeling effort was based (Bierman and Dolan 1981, Scavia et al. 1981b, Bierman et al. 2005). Second, it was necessary to assemble the environmental conditions affecting Saginaw Bay and create a detailed set of environmental

forcing functions and validation data. This was accomplished through the analysis and interpretation of both previously published data and original analysis of unpublished data.

Model System Definition

The model was simplified to a single horizontally and vertically mixed system representing five classes of phytoplankton in inner Saginaw Bay because of the limited spatial coverage from the field collections and the lack of available field data to describe the outer bay/ Lake Huron boundary. The original form of the Saginaw Bay multi-class model upon which this effort is based included three to five spatial segments within the inner bay (Bierman and Dolan 1981). However, no contemporary field data exist to characterize the transport of water among spatial segments in the inner bay. Furthermore, field collections, with one sample per month per segment, were insufficient to adequately support such a spatially detailed analysis in the model. Additionally, results of the phytoplankton community analysis suggested no significant differences in community composition within the inner bay beyond those predicted by the eutrophication gradient (Chapter 1). While there is finer scale spatial variability in water quality within the inner bay, most of Saginaw Bay can be described by considering the inner and outer bay separately (Millie et al. 2006).

The model system and external inputs are summarized in Figure 13 and described in the following sections. The outer bay was not modeled; field data from the outer bay were used as boundary conditions for the inner bay model. While boundary exchange is important, generally

the outer bay acts as a constituent sink. In previous Saginaw Bay models, boundary exchange did not drive the model (Bierman and Dolan 1981). All of the changes in the phytoplankton community composition described in Chapter 1 affected inner Saginaw Bay, so this simplified system is an appropriate scale to capture the important mechanisms driving the temporal changes reported in the phytoplankton community composition. Water quality data were only available from 1991-1996 and zebra mussel densities and phosphorus loads were only available through 1995, so despite the available description of the phytoplankton community from 1990 – 1996, this model was limited to 1991-1995.

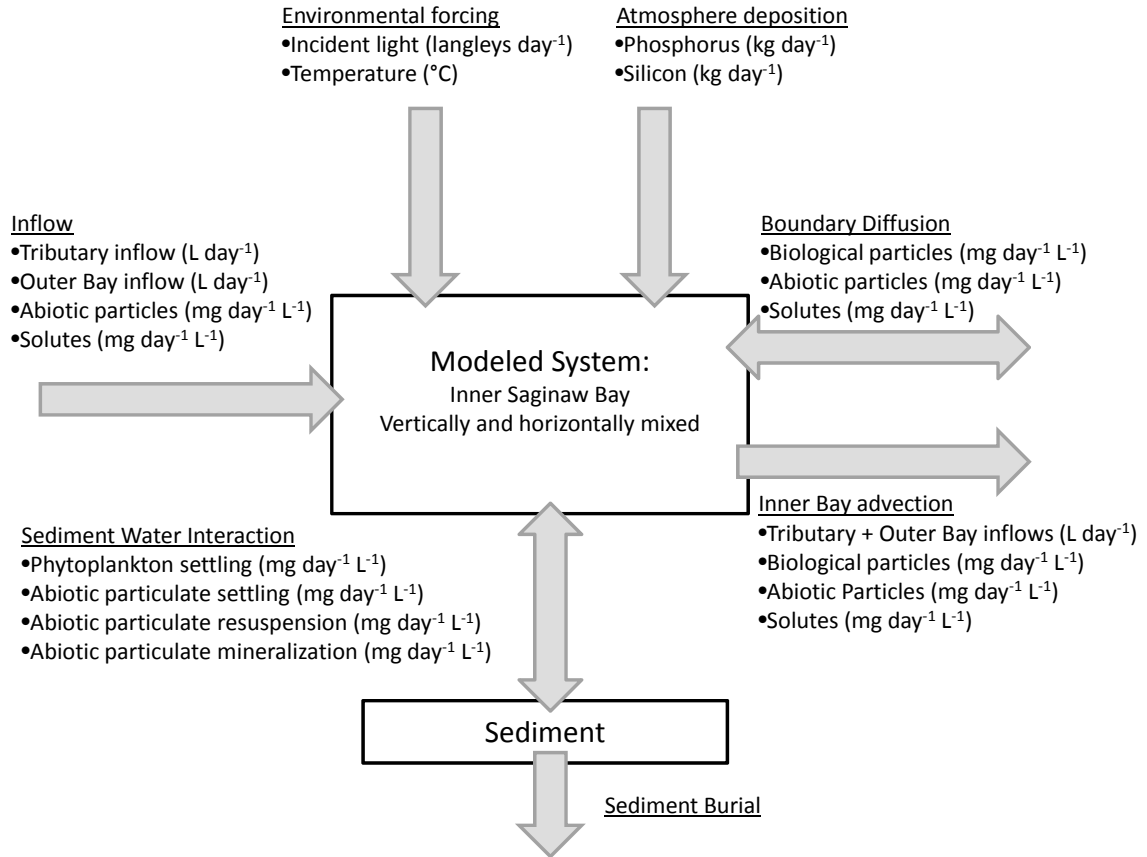


Figure 13: Model system definition modified from (Bierman et al. 2005). Arrows into and out of the modeled system box represent flows of mass entering or leaving the inner Saginaw Bay water column. Some flows, such as tributary inflow, are one-way interactions (single direction arrows) while the sediment water interaction and boundary diffusion (two sided arrows) can be positive or negative, depending on the concentration gradients.

Model Structure

Using STELLA modeling software, a nutrient-phytoplankton-zooplankton (NPZ) water quality model was developed for inner Saginaw Bay (Figure 13). Equations describing physical transport (advective and diffusive), phytoplankton growth, biological recycling of nutrients, and grazing were adapted from Chapra (1997). The impact of zebra mussels in Saginaw Bay were

explored by adding output from a zebra mussel bioenergetics model as outlined by Schneider (1992). To couple this bioenergetics model to the NPZ model and characterize the water quality impacts of zebra mussel populations, I used the set of equations describing the filtration of the water column outlined by Bierman et al. (2005). In the model, the zebra mussel population is represented by externally specified cohorts with externally specified initial wet weights. The 1991-1995 fixed value for the initial zebra mussel young of year wet weight was 6×10^{-6} g. For the other cohorts, the predicted wet weight from the preceding year's simulation was used. To ensure reasonable tissue weights, the first order reproductive losses forced on first and second year mussels were calibrated based on seasonal trends in biomass calculated by Nalepa et al. (1995).

Using the 1997 version of the Limnotech Inc. model as a starting point, fundamental changes in the conceptual model structure were undertaken to both simplify the application of the model and to direct it towards the research questions at hand (Figure 14). Significant alterations include the elimination of nitrogen as a potential limiting nutrient, new equations to describe zooplankton dynamics, and the elimination of variable algal internal nutrient pool nutrient kinetics. Additionally, physical transport equations were simplified. All modifications were adapted from (Chapra 1997) and the significant modifications are discussed in detail below.

The conceptual model presented in **Error! Reference source not found.** shows the interaction of the zebra mussel bioenergetics model with the multi-class phytoplankton model.

The zebra mussel model simulates the growth and respiration of a single zebra mussel in a particular age cohort. However, the model does not predict zebra mussel population dynamics or densities; these are supplied external to the model (see Table 11). In combination with these externally specified zebra mussel densities, the model was used to examine the effect of zebra mussel filtration on suspended particles as well as the effect of zebra mussel excretion of available phosphorus on water quality. Except for 1) a modification of the pathway for the recycle of available phosphorus to the water column necessitated by the elimination of the variable internal algal nutrient pool and 2) calibration of reproductive losses to 1992 and 1993 field data, the zebra mussel model is adapted without modification from Bierman et al. (2005).

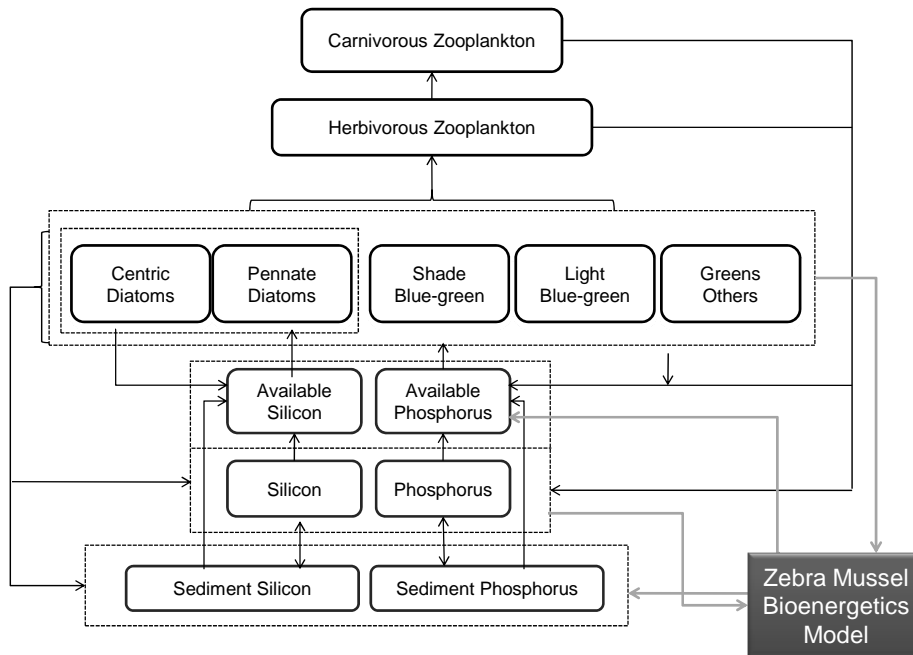


Figure 14: Saginaw Bay multi-class phytoplankton model modified from Bierman et al. (2005). Boxes represent state variables, in mg L^{-1} . Arrows represent the connections between state variables, i.e. all phytoplankton variables both take up available phosphorus and excrete available phosphorus.

Model Implementation

Model process rates were compared to phytoplankton productivity rates (Fahnenstiel et al. 1995a) and zooplankton grazing (Bridgeman et al. 1995) in Saginaw Bay. Model state variables (nutrient, phytoplankton, and zooplankton concentrations) were compared to field data collected by NOAA GLERL. In each of the five 365 day simulations (representing January 1, 1991 – December 31, 1995), the model produces daily changes in concentrations of 15 state variables (chloride and abiotic suspended solids are not shown in Figure 14). The fourth order Runge-Kutta method was used to solve the equations:

$$V \frac{dc}{dt} = -Qc + E'(c_{Boundary} - c_{Inner Bay}) \pm Sc$$

(1)

Where:

c = Constituent concentration $\left(\frac{\text{mass}}{\text{volume}}\right)$

V = Volume of the inner bay

Q = Sum of flows into inner bay (tributary + outer bay) $\left(\frac{\text{volume}}{\text{time}}\right)$

E' = Bulk diffusion coefficient $\left(\frac{\text{volume}}{\text{time}}\right)$

S = Sources and sinks of constituent in the inner bay

Allochthonous sources of solutes and particles are flow-dependant external loadings, constant atmospheric deposition, wind dependant particulate resuspension, and the mineralization of settled particulates from the sediment. Autochthonous sources include biological excretion, respiration and “bacterially” mediated (see Bierman & McIlroy 1986) decomposition of particulates into solutes. Sinks are biological uptake of non-conservative solutes, settling and decomposition of particulates, and particulate filtration by zebra mussels.

Autochthonous sources of biomass depend on phytoplankton primary production. Primary production is described as a maximum growth rate modified by considering the ambient concentrations of nutrients, the amount of light available for photosynthesis, and the water

temperature. Primary production of a specific phytoplankton group A_i is described numerically as:

$$A_i \text{Production} = GMAX_i * \phi T_i * \min(\phi I_i, \phi N_i) * A_i$$

(2)

Where:

$$GMAX_i = \text{maximum growth rate } \left(\frac{1}{\text{day}}\right)$$

$$\phi T_i = \text{temperature effect on growth, } \theta_i^{(°C-20)}$$

$$\theta_i = \text{rate coefficient for temperature}$$

$$\phi I_i = \text{light effect on growth, } \frac{2.078f}{k_e Z} (e^{-\alpha_{1i}} - e^{-\alpha_{0i}})$$

$$k_e = \text{extinction coefficient}$$

$$f = \text{photoperiod}$$

$$z = \text{water column depth}$$

$$\alpha_{0i} = \frac{I_a}{I_{s_i}}$$

$$I_a = \text{Available light}$$

$$I_{s_i} = \text{Saturation light}$$

$$\alpha_{1i} = \alpha_{0i} e^{-k_e Z}$$

$$\phi N_i = \text{nutrient effect on growth, } \text{Min} \left(\frac{Si}{k_{Si_i} + Si}, \frac{AVP}{k_{AVP_i} + AVP} \right)$$

$$K_{Si}, k_{AVP} = \text{half saturation constants on silicon and phosphorus uptake}$$

$$A_i = \text{Phytoplankton of type } i$$

Light extinction is an important term in the limiting factors controlling modeled phytoplankton growth, so rather than use field data based light extinction coefficients (K_{par}) as a forcing function, a regression submodel was used to predict underwater light extinction based on model state variables. This was necessary to examine the impact of zebra mussel filtration of suspended particles to the light environment. After the model was calibrated to the 1991 field conditions using externally specified K_{par} values, model output was used to develop a regression submodel to internally predict K_{par} . This submodel was then used when generating model results for 1991-1995. The submodel was:

$$K_{par} = [0.2 * TSS + 0.310] (r^2 = 0.84),$$

Where:

$$TSS = \text{Abiotic solids} + \text{phytoplankton dry weight.}$$

Biological uptake of available phosphorus by all types of phytoplankton and of available silicon by the two types of diatoms was calculated with fixed stoichiometric conversions. For phosphorus, this was based on the normalized mass ratios for plant tissues of 1% P : 40% C, or 0.025 mg P/mg C (Chapra 1997). For the two types of diatoms, different silicon to carbon ratios were used to represent variability in silicon requirements. Silicon to carbon ratios in the modeling literature vary from 0.03-2.5 mg Si/mg C (Bowie et al. 1985, Reynolds 2006); values of 1.0 for centric diatoms and 1.5 for pennate diatoms were used.

Two types of zooplankton were modeled: herbivorous zooplankton (generalized cladoceran/calanoïd grazer) and carnivorous zooplankton (generalized cyclopoid predator). In both cases, the numerical representation of growth was the same: a maximum filtration rate reduced by assimilation efficiency, temperature, and available food:

$$Z_i \text{ Growth} = \epsilon_{Z_i} * \left[FMAX_{Z_i} * \phi T_{Z_i} * \phi F_{Z_i} * food \frac{mg}{l} \right] * Z_i$$

(3)

Where (for herbivorous zooplankton):

ϵ_{Z_H} = Assimilation efficiency

$FMAX_{Z_H}$ = Maximum filtration rate $\left(\frac{L}{mg \text{ day}} \right)$

$$\phi F_{Z_H} = \left[\frac{\sum_i \alpha_i A_i}{k_A + \sum_i \alpha_i A_i} \right]$$

α_i = Electivity of zooplankton for phytoplankton A_i

$food$ = total phytoplankton concentration

Z_i = Zooplankton of type i

For carnivorous zooplankton:

$$\phi F_{Z_C} = \left[\frac{Z_H}{k_{Z_H} + Z_H} \right]$$

$food$ = herbivorous zooplankton concentration

Grazing is given by the growth term without the reduction for assimilation efficiency. For example: herbivory ($\text{mg L}^{-1} \text{ day}^{-1}$) on phytoplankton type A_i :

$$\text{Grazed} = FMAX_{Z_H} * \phi T_{Z_H} * \phi F_{Z_H} * (\alpha_i A_i) * Z_H$$

Biological recycle of available phosphorus to the water column is an important source of nutrients throughout the summer, when tributary inputs are low. All biological variables excreted available phosphorus at a rate proportional to respiration and, for phytoplankton, cell death. Additionally, to maintain stoichiometry, the two diatom variables also release available silicon in the same manner. In the model, the numerical expression for the total biological recycle is given by summing the products of equations (4), (5), and (6):

$$A_i \text{AVP recycle} = \left[A_i \text{RESP} * \frac{\text{mg P}}{\text{mg C}_i} \right] + \left[A_i \text{DEATH} * \frac{\text{mg P}}{\text{mg C}_i} \right] * A_i \quad (4)$$

Where:

$A_i \text{RESP}, A_i \text{DEATH}$ = Phytoplankton respiration and decomposition losses ($\frac{\text{mg}}{\text{L}}$)

$$Z_i \text{AVP recycle} = Z_i \text{RESP} * \frac{\text{mg P}}{\text{mg C}_{Z_i}} * Z_i \quad (5)$$

Where:

Z_iRESP = Zooplankton respiration losses ($\frac{mg}{l}$)

$$ZM_YAVP \text{ recycle} = ZMRESP_Y * \frac{200 \text{ mg C dwt}}{1 \text{ g wwt}} * \frac{\text{mg P}}{\text{mg C}_{Z_M}} * \frac{S.A.* \#_Y}{V_{water}}$$

(6)

Where:

$ZMRESP_Y$ = Zebra mussel respiration in g wet weight

Y = Age cohort

$\#$ = Zebra mussels per m^2

S.A. = Surface area of inner Saginaw Bay substrate (m^2).

V_{water} = Volume of inner Saginaw Bay (m^3).

Saginaw Bay Environmental Conditions

Variable environmental conditions and external forces drove the differences in model output from year to year. To run the model, daily values were necessary for each of the external components to the modeled system described in Figure 13 (daily time series were needed to describe each component under the inflow; environmental forcing; atmosphere deposition; boundary diffusion, inner bay advection, and sediment water interaction headings). These external forcing data were calculated from NOAA GLERL field collections (for tributary flows gage data from the USGS were used) or adapted from previous modeling applications. In cases where daily values could not be calculated, linear interpolations between data points were used. The following sections describe the methods used to compile and calculate the necessary external data.

Inflow

Tributary drainage into Saginaw Bay is a major source of allochthonous nutrients. Daily mean river flows were estimated from gage data published on the United States Geological Survey website². River inflow to the inner bay from tributaries is mostly due to the Saginaw River. A daily tributary inflow time series was developed for the inner bay using the Saginaw River flows plus 25% additional flow to represent the other tributaries that drain into the inner bay (such as the Kawkawlin, Au Gres, and Rifle River) (Figure 15). Because flow data for the Saginaw River were not available for the entire time period in question, those flows were estimated with flow from its tributaries. The four major tributaries to the Saginaw River are the

² <http://waterdata.usgs.gov/nwis/sw>

Cass, Flint, Shiawasse and the Tittabawassee River; however, daily mean flow data throughout the entire period were available only for the Cass and Tittabawassee Rivers. Gage data for the Flint River was not available after September 30th, 1992, while gage data on the Shiawasse was not available after September 30th, 1994. I assumed that since the tributaries are in reasonable proximity to each other and drain similar types of terrain, regressions could be developed to estimate periods of missing flows. Flint River flows from October 1992 onwards were predicted using the relationship between the Flint and Cass River flows from 1990-1992 ($r^2=.67$). Flows for the Shiawasse River from October 1994 onwards were predicted using the relationship between the Shiawasse and Tittabawassee and the Shiawasse and Cass Rivers ($r^2=.54$ and $r^2=.49$) from 1990-1994. Because the fit of these regressions were not as good, the average of the two predicted flows was used. To estimate the Saginaw River flow rate, these four tributary flows were summed and then multiplied by 1.3 to represent the ungaged downstream reach of the Saginaw River (Bierman et al. 2005) (Table 7).

Advective inflow to the inner bay from the outer bay is significant. In previous modeling applications of Saginaw Bay, detailed measurements to characterize this flow were taken. These inflow estimates, in cubic meters per second, were calculated on a monthly basis (Bierman and Dolan 1981). Detailed data were not collected in 1990-1996, so I assumed little change across years and used the previously calculated flows.

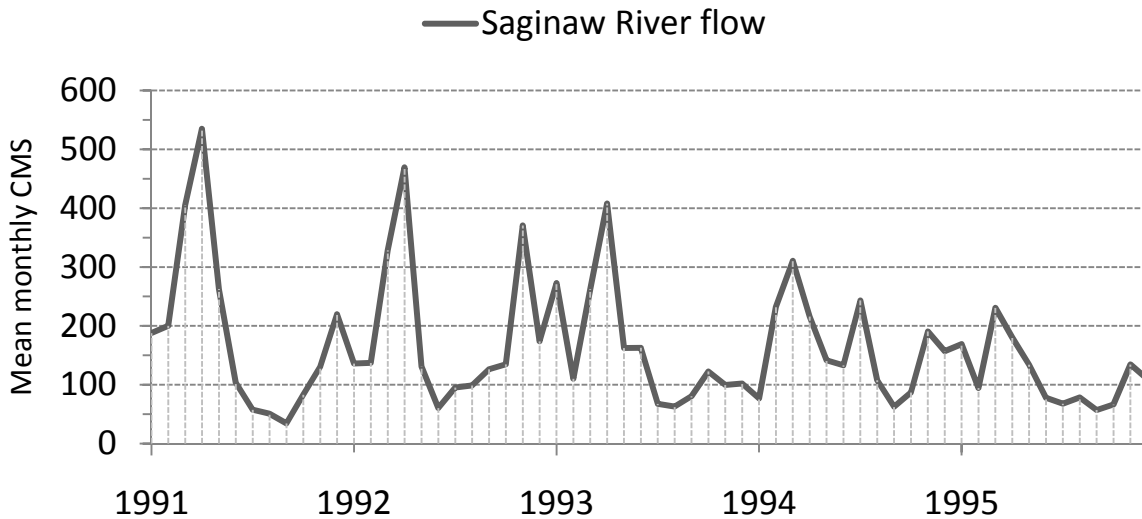


Figure 15: River inflow to inner Saginaw Bay. Daily mean flows are summarized as monthly mean flow in cubic meters per second (CMS).

Table 7: Saginaw River tributaries annual mean daily flow, in cubic meter per second (CMS) from USGS gage data. Starred entries were calculated using the regression models. Saginaw flows are the sum of the tributaries * 1.3.

Year	Cass	Flint	Shiawasse	Tittabawassee	Saginaw
1991	21	27	15	81	189
1992	19	31	19*	75	188
1993	17	26	20*	59	160
1994	21	28	21*	55*	163
1995	12	23	15*	40*	117

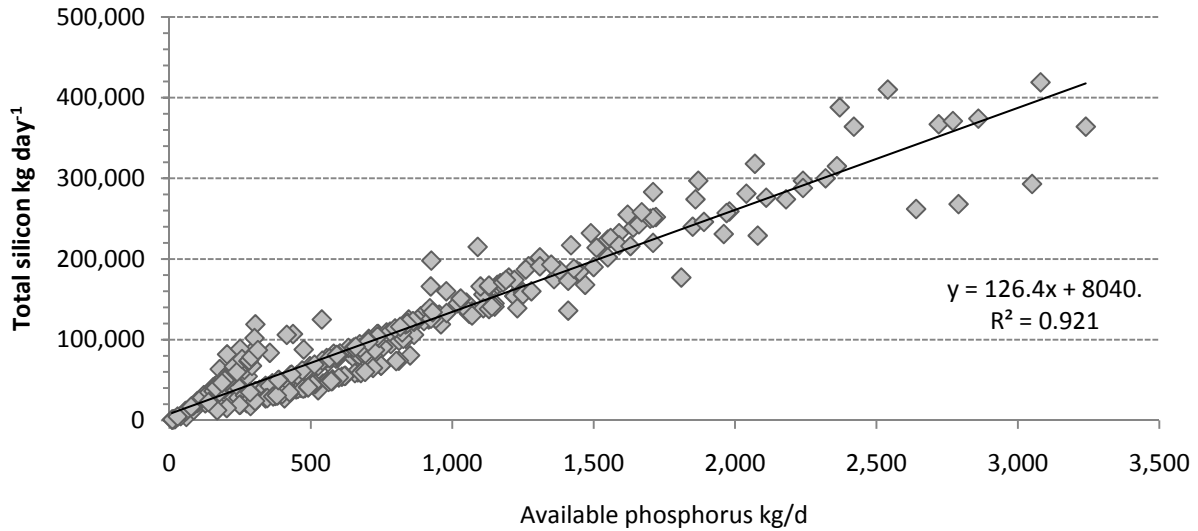
External Loads

Tributary inflow transports suspended particles and dissolved solutes into Saginaw Bay.

Yearly total phosphorus loads (both available and total phosphorus) for the Saginaw River were calculated through 1995 (Bierman et al. 2005). I used these data, in metric tons year⁻¹, with the

daily flow rates to prorate the loads to daily values in kg day^{-1} . Using the daily loads for available phosphorus calculated by the above method for 1991 and daily loads for total silicon, chloride, and abiotic suspended solids used in the previous model of Saginaw Bay in 1991, regressions using available phosphorus daily loads to predict the other water quality parameters as response variables were used. The resulting predicted loads for 1991 were compared to the previously estimated loads using simple ANOVAs and time series plots. The results were satisfactory with no significant differences and peak and base loads well represented. For example, the implementation of these methods for 1991 silicon loads is shown in Figure 16. The 1991 regression equations were assumed to be applicable throughout the remaining years and were used to calculate the daily loads of silicon, chloride, and abiotic particles for the entire time period. Available silicon loads were assumed to be $\frac{1}{2}$ of the total silicon loads. The annual mean loads used in the model for total phosphorus (TP), available phosphorus (dissolved phosphate phosphorus, AVP), total silicon (TS), and available silicon (dissolved silicate silicon, AVS) are shown in Table 8. Because phosphorus is the major limiting nutrient for phytoplankton growth in Saginaw Bay (Heath et al. 1995), nitrogen dynamics were not modeled.

a)



b)

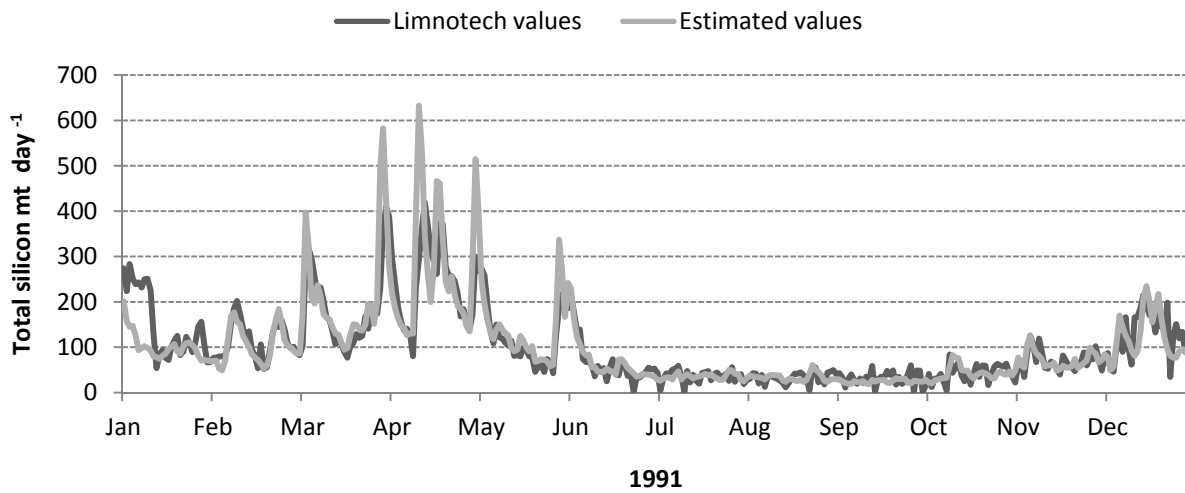


Figure 16: Daily loads for total silicon were estimated by a) using a regression between the 1991 daily loads from the previous model and the newly calculated available phosphorus daily loads and b) comparing these predicted loads to the previously calculated loads. This method was also used to estimate chloride and abiotic solids.

Table 8: Annual mean daily loads in kg day⁻¹ of phosphorus and silicon from Saginaw River inflow to Saginaw Bay calculated using yearly phosphorus loads in Bierman 2005. AVP = dissolved phosphate phosphorus, TP = total dissolved and particulate, AVS = dissolved silicate silicon, TS = total particulate and dissolved silicon.

Nutrient	1990	1991	1992	1993	1994	1995
AVP	548	734	423	370	649	357
TP	1,386	3,140	1,669	1,984	2,578	1,588
AVS	38,650	50,424	30,785	27,395	45,057	26,591
TS	77,300	100,849	61,570	54,791	90,113	53,183

Advective and Diffusive Transport

Advective and diffusive exchanges across the inner/outer bay boundary were calculated for all state variables in the model. Boundary conditions determine the transport of constituents across the open boundary between inner and outer Saginaw Bay. Field water quality and phytoplankton data were used to calculate constituent concentrations in the outer bay. Advective outflow was modeled as the concentration of the Inner Bay variable times the sum of the tributary and advective inflow from the outer bay (see Figure 13). To describe diffusive transport, the bulk diffusion coefficient E' was calculated by using the conservative substance chloride as a natural tracer. Measured chloride concentrations were used to calculate average monthly values for the inner and outer bay stations. Following Chapra (1997), estimated chloride loadings were used with the measured concentrations data to calculate monthly diffusion coefficients as:

$$E' \left(\frac{m^3}{sec} \right) = \frac{W_I - Q_I S_I}{S_I - S_O}$$

Where W is the external load to the inner bay, Q is the outflow from the inner bay, and S_I and S_O

are the chloride concentrations in the inner and outer bay. Diffusive transport was then calculated as E' times the difference in the constituent concentration between the outer and inner bay.

Boundary Conditions

Phytoplankton boundary conditions and inner bay validation points were calculated using the biovolume ($\mu\text{m}^3 \mu\text{l}^{-1}$) for each group. Assuming a specific density of 1.27 and dry weight as 10% of wet weight (Chapra 1997), biovolume was converted to biomass in dry weight mg liter^{-1} . Boundary conditions and validation points for the other water quality parameters were calculated using NOAA GLERL field data from the selected inner and outer bay stations (see Figure 17). Zooplankton boundary conditions were used from the 1991 model and inner bay validation points were used from Bridgeman et al. (1995).

Saginaw Bay Field Data Collections

The spread of zebra mussels to Saginaw Bay was anticipated after the discovery of the heavy colonization of Lake St. Claire in 1988. Zebra mussels colonized Saginaw Bay in the fall of 1991. In anticipation of this ecosystem perturbation, two major survey efforts were undertaken by the Great Lakes Environmental Research Laboratory of the National Oceanic Atmospheric Agency (NOAA GLERL) in order to characterize the impacts of the zebra mussel invasion to the lower trophic levels of the pelagic and benthic ecosystems. A biological sampling program collected monthly samples from April-October, 1990-1996 and a water quality sampling program collected monthly samples from April – October, 1991-1996 (Figure 17). Phytoplankton samples were collected roughly monthly from April - October at eight

locations throughout the duration of the survey program. Phytoplankton data were provided by Henry Vanderploeg from NOAA GLERL (per. comm.), see Fahnenstiel et al. (1998) for a general description of the sampling methodology. A description and analysis of changes in the phytoplankton community composition can be found in Chapter 1.

The water quality data used herein were originally published within NOAA technical reports TM-091 and TM-115, which included measurements of nutrient and chlorophyll concentrations as well as water clarity (Nalepa et al. 1996, Johengen et al. 2000). These data were most recently summarized by Millie et al. (2006). Additional data summaries and interpretations were drawn from the 1995 special issue to *Journal of Great Lakes Research* (Nalepa and Fahnenstiel 1995) and from (Bierman et al. 2005). Zebra mussel data are from Nalepa et al. (1995).

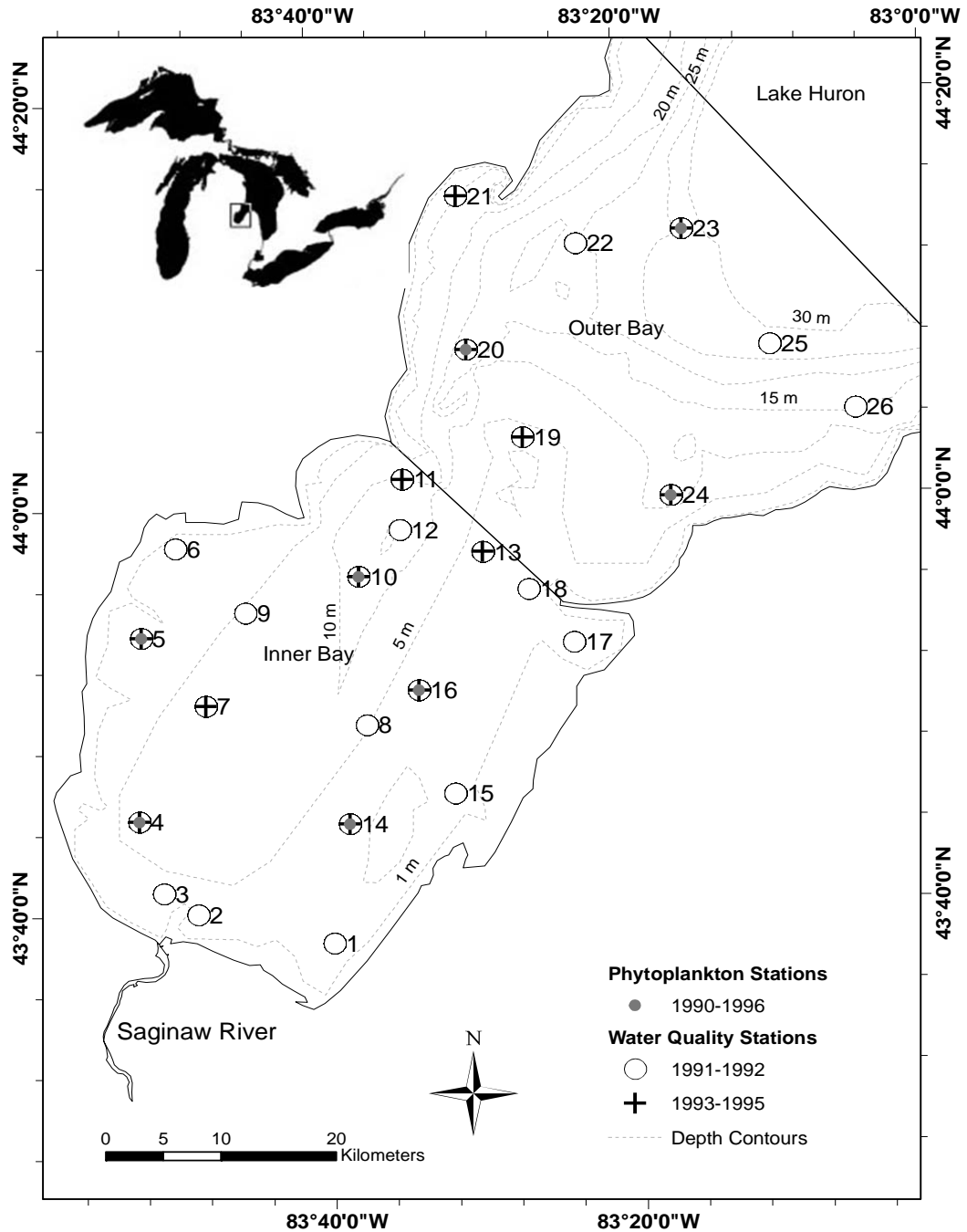


Figure 17: Location of selected phytoplankton and water quality sampling sites in Saginaw Bay, Lake Huron from NOAA GLERL monitoring 1990 – 1996.

Temperature and Light

Average monthly inner bay water temperature from April – October, 1991-1995 was calculated using data from the NOAA GLERL water quality survey of the inner bay (Johengen et al. 2000; Nalepa et al. 1996). While relative patterns were similar, with temperature warming to 21-23 degrees in the summer, temperatures were variable year to year (Table 9).

Table 9: Average temperature of inner Saginaw Bay in °C calculated from the NOAA GLERL water quality survey. Months without samples are denoted with *.

Month	1991	1992	1993	1994	1995
April	8.5	4.2	7.5	6.7	*
May	13.5	12.0	13.3	*	11.2
June	22.7	18.8	19.0	17.3	18.9
July	23.5	20.8	21.6	22.2	23.4
August	22.3	21.7	20.7	20.4	24.1
September	21.8	18.9	19.7	19.3	19.7
October	12.0	4.2	12.0	14.1	10.1

Incident photosynthetically active radiation was assumed to not vary significantly among years. The values used were based on the time series used in the original multi-class phytoplankton model of Saginaw Bay from Bierman & Stoermer (1980). Secchi depth was measured monthly by NOAA GLERL (Table 10). Underwater light extinction (KPAR) was measured monthly in 1991, 1992, and 1995, but not in 1993 or 1994, so secchi depth was used in a regression to predict KPAR (Figure 18). The equation $K_{par} = \exp((\ln \text{secchi} * -0.922) + 0.215)$, $R^2 = .90$ was used to estimate values for 1991-1995.

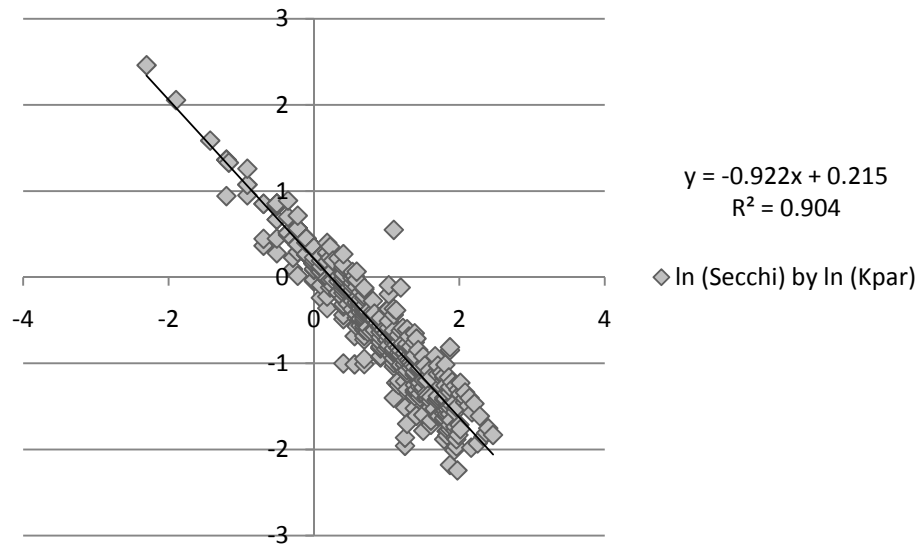


Figure 18: Regression between $\ln(\text{secchi depth})$ (X) and $\ln(\text{kpar})$ (Y) calculated using the NOAA GLERL field data from 1991-1992, and 1995.

Table 10: Mean monthly Secchi depths for inner Saginaw Bay calculated from the NOAA GLERL field data. Starred entries represent months when no samples were taken.

Secchi (m)	1991	1992	1993	1994	1995
April	0.75	1.97	1.75	2.43	*
May	0.87	2.08	2.40	*	3.09
June	1.71	2.15	4.48	3.14	3.00
July	1.63	2.33	3.32	1.76	1.50
August	1.11	1.71	2.61	1.74	1.44
September	1.62	1.51	2.33	1.49	1.28
October	1.86	1.51	1.85	1.88	1.25

Phytoplankton Biomass

Phytoplankton field data for the outer bay were used to calculate boundary exchange between inner and outer bays and to both calibrate and validate the model results. Phytoplankton were grouped into five groups: centric diatoms (i.e. *Cyclotella comensis* and *Aulacoseira ambigua* (=italica)), pennate diatoms (i.e. *Fragilariaria crotonensis* and *Asterionella formosa*), shade tolerant filament cyanobacteria (i.e. *Oscillatoria redekei* (=Limnothris redekei) and *Gomphosphaeria lacustris*), light tolerant chroococcoid cyanobacteria (i.e. *Microcystis aeruginosa* and *Aphanocapsa incerta*), and all others (including chlorophytes, cryptophytes, chrysophytes, pyrophytes and protozoan flagellates). These groups are an adaptation of the 5 phytoplankton groups used in the original multi-class phytoplankton model of Saginaw Bay. However, to utilize the Chapter 1 identification of 5 community assemblages, there are important differences and the resulting groups are a hybrid of the previous model groups and the assemblages identified in Chapter 1. Additionally, nitrogen fixing cyanobacteria such as *Aphanizomenon flos-aquae* were not common in Saginaw Bay from 1991-1995, so they were not included in the model.

Zebra Mussel Density

Zebra mussel population structure and density data were adapted from Nalepa et al. (1995) (Table 11). Population structure was calculated by separating the zebra mussel population into three cohorts based on shell length frequencies. To calculate population density per square meter through the bay, weighted averages were used to balance differential zebra mussel densities on

hard and soft substrate. The distribution of hard and soft substrate throughout Saginaw Bay was calculated for the 1997 Limnotech model, used by Bierman et al. (2005), and provided by V. Bierman (per. comm.).

Table 11: Yearly zebra mussel densities (# m⁻² of inner bay bottom surface area). The zebra mussel population is broken into three cohorts: Young of year (YOY), first year (1st), and second year and older (2nd) on the basis of shell lengths.

	1991	1992	1993	1994	1995
YOY	1,184	1434	205	1843	309
1st	0	1925	429	1688	684
2nd	0	0	455	432	158

Results

Model Calibration

The model was calibrated to observed values from 1991 using coefficients in Table 12 and Table 13. Phytoplankton nutrient uptake half saturation constants, respiration rates, and sinking rates as well as zooplankton feeding half saturation constants and assimilation efficiencies were adjusted to better match field nutrient and biomass data, primary production, and zooplankton filtering rates. Comparisons of model results to field data are limited because field data were not collected in early spring or late fall. In general, the model over predicts estimated 1991 biomass. The estimated springtime bloom of diatoms ($0.25 \text{ mg dry weight L}^{-1}$) and the June minimum ($0.05 \text{ mg dry weight L}^{-1}$) are particularly overrepresented, but given the uncertainty in interpreting the field data, the overall predicted biomass is within reasonable ranges (Figure 19).

Daily algal primary production in $\text{mg C L}^{-1} \text{ day}^{-1}$ is calculated in the model as algal growth (day^{-1})* algal concentration (mg L^{-1}). Seasonal algal areal primary production in $\text{mg C m}^{-2} \text{ day}^{-1}$ was estimated in Saginaw Bay for 1991 and 1992 by Fahnenstiel (1995a). Daily model output was converted to areal production for comparison (Figure 20). In general, the estimated daily primary production corresponds roughly to the ranges suggested by the field calculations. Peak production was predicted to reach $600 \text{ mg C m}^{-2} \text{ day}^{-1}$ from July to August (Figure 20).

Table 12: Phytoplankton parameters.

Coefficients	Definition	Units	Phytoplankton parameters					Source
			<u>Centric</u>	<u>Pennate</u>	<u>Others</u>	<u>Shade</u>	<u>Light</u>	
APC	Stoichiometric conversion	mg P/mg C	0.025	0.025	0.025	0.025	0.025	Bowie et al. 1985
ASiC	Stoichiometric conversion	mg Si/mg C	1.0	1.5	0	0	0	Bowie et al. 1985
ASINK	Sinking velocity	m/day	0.2	0.2	0.15	0.05	0.05	Bowie et al. 1985
GMAX	Maximum growth	1/day	2.5	2.3	1.5	1.5	1.5	Bierman and McIlroy 1986
kPCell	Half saturation for phosphorus uptake	mg/l	0.0075	0.0075	0.0075	0.01	0.01	Bowie et al. 1985
kSiCell	Half saturation for silicon uptake	mg/l	0.02	0.05	0	0	0	Bowie et al. 1985
RADSAT	Saturation light	ly/day	150	50	100	75	200	Bierman and McIlroy 1986
RDCMP	Decomposition rate	1/day	0.35	0.35	0.35	0.5	0.5	Bierman and McIlroy 1986
kDCMP	Rate coefficient of decomposition	unitless	90	90	90	90	90	Bierman and McIlroy 1986
RRESP	Respiration rate	1/day	0.27	0.25	0.25	0.3	0.3	Bierman and McIlroy 1986
Adwt	mg C per mg dry weight	mg dwt/mg C	0.32	0.5	0.41	0.39	0.39	Bierman and Stoermer 1980
TBASE	Rate coefficient for temperature	unitless	1.07	1.06	1.08	1.08	1.08	Bierman and Stoermer 1980
ZELECT	Zooplankton electivity	unitless	1.0	1.0	1.0	0.2	0.2	Bierman and Stoermer 1980

Table 13: Zooplankton parameters.

Coefficients	Definition	units	Zooplankton Parameters		Source
			<u>Herbivore</u>	<u>Carnivore</u>	
EffG	Efficiency of assimilation	unitless	0.8	0.7	Chapra 1997
ZMAX	Maximum optimal growth	L/mg day	6.0	5.0	Chapra 1997
ZkSAT	Half saturation constant for feeding	mg/l	0.25	0.5	Chapra 1997
ZRESP	Respiration rate	1/day	0.1	0.08	Chapra 1997
PISCO	Piscovory rate	1/day	0	.02	Bowie et al. 1985
ZTBASE	Rate coefficient for temperature	unitless	1.08	1.08	Chapra 1997
ZPC	Stoichiometric conversion	mg P/mg C	0.025	0.025	?

The model calculates phytoplankton community composition in five groups (see Table 12). Each group was assigned a different carbon to dry weight ratio and converted to dry weight to compare the predicted community composition to the selected NOAA GLERL field samples. Model results generally hit peak field values but were overall much smoother than the validation data. In 1991, predicted phytoplankton biomass was mostly centric diatoms (annual mean = 0.24 mg L^{-1}). Predicted pennate diatom biomass was higher in the spring and fall (annual mean = $0.04 \text{ mg mg L}^{-1}$). Predicted biomass for the “others” group did not contribute a large fraction of the biomass. Cyanobacteria biomass was generally minor because of the small cell sizes (Figure 21, Figure 22). In the spring, model results tended to under predict phytoplankton biomass and over predict nutrient concentrations (Figure 21, Figure 23).

There are six main water quality variables in the model. Concentrations were compared to 1991 monthly mean calculated from the NOAA GLERL field data (Figure 23). To examine the impact of zebra mussel water column filtration, the model does not use an externally specified KPAR but calculates the underwater light extinction coefficient based on a submodel that uses the total suspended solids (phytoplankton dry weight + abiotic suspended solids) concentration in a regression to calculate KPAR. The extinction coefficient KPAR was measured monthly by NOAA GLERL at 18 locations throughout the inner bay in 1991. While there was considerable spatial variation throughout inner Saginaw Bay in this measurement, the model estimate of KPAR was a reasonable representation of the mean value. Predicted 1991 extinction was highest in the spring ($\sim 2.4 \text{ m}^{-1}$) and lowest in the summer ($\sim 0.65 \text{ m}^{-1}$) (Figure 24)

Zooplankton biomass (mg L^{-1}) is calculated in the model for two types: herbivore biomass (cladoceran and calanoid zooplankton) and carnivore biomass (cyclopoid zooplankton). Zooplankton grazing is calculated as herbivore filtration rate ($\text{L mg}^{-1} \text{ day}^{-1}$) * zooplankton concentration * algal concentration. Calibration data were used from Bridgeman et al. (1995), who reported mean May-August zooplankton biomass by division, seasonal total biomass, and June herbivory ($\text{mg algal C grazed m}^{-3}$). While the utility of comparing model output to these field data is limited in scope by the narrow time periods reported, in general model output compares reasonably to the calculated field data. Mean predicted June biomass (194.6 mg m^{-3}) is lower than biomass estimated from the field samples collected at 8 locations throughout inner Saginaw Bay (Table 14, Table 15). Mean predicted June herbivory (48 mg C m^{-3}) is higher than what was measured, however field measurements were only collected at two sample stations (Table 16, Table 17).

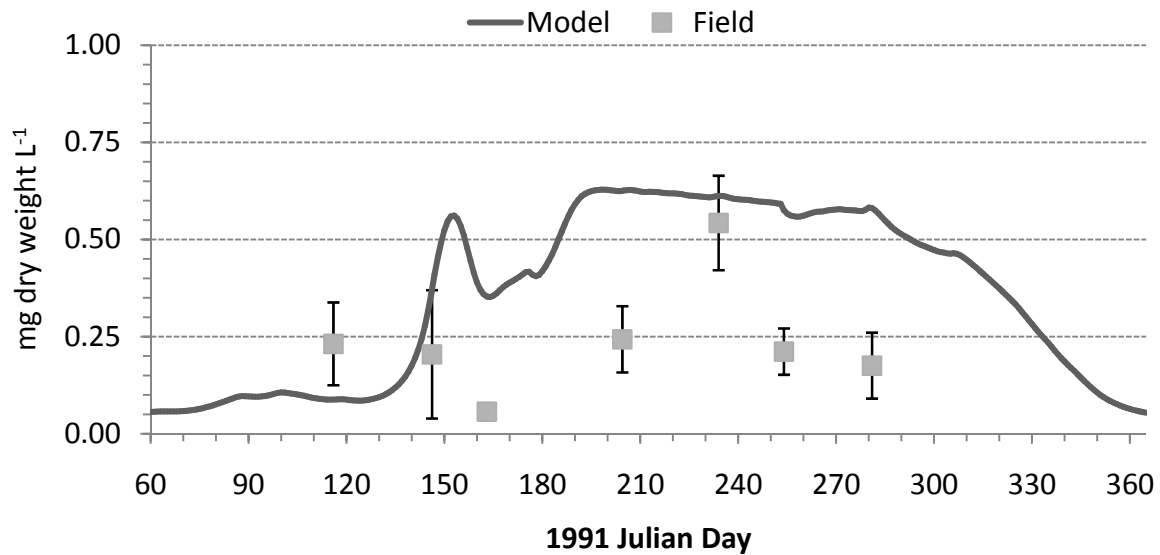


Figure 19: Total phytoplankton biomass from the selected NOAA GLERL collections from the inner bay in 1991 compared to the model output. Error bars on field points represent the standard error of the mean.

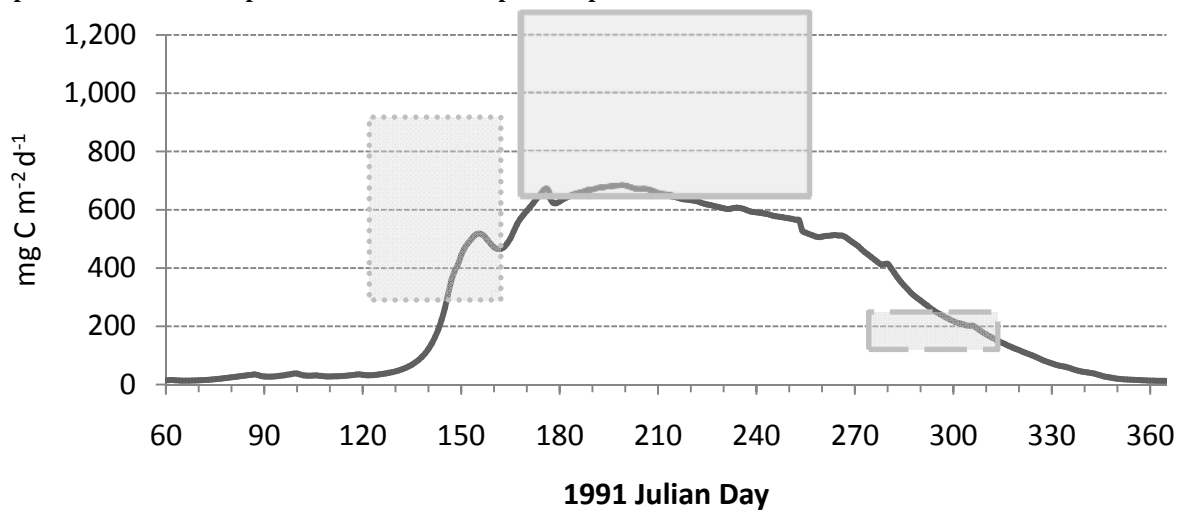


Figure 20: Comparison of primary production rates estimated by the model to calculated Saginaw Bay primary production for 1991. The grey boxes represent from primary production redrawn from Fahnenstiel 1995, where the middle represents the mean production rate, the upper and lower bounds represent \pm S.E. of the mean, and the left and right bounds represent the spring (dotted border), summer (solid border), and fall (dashed border) time periods.

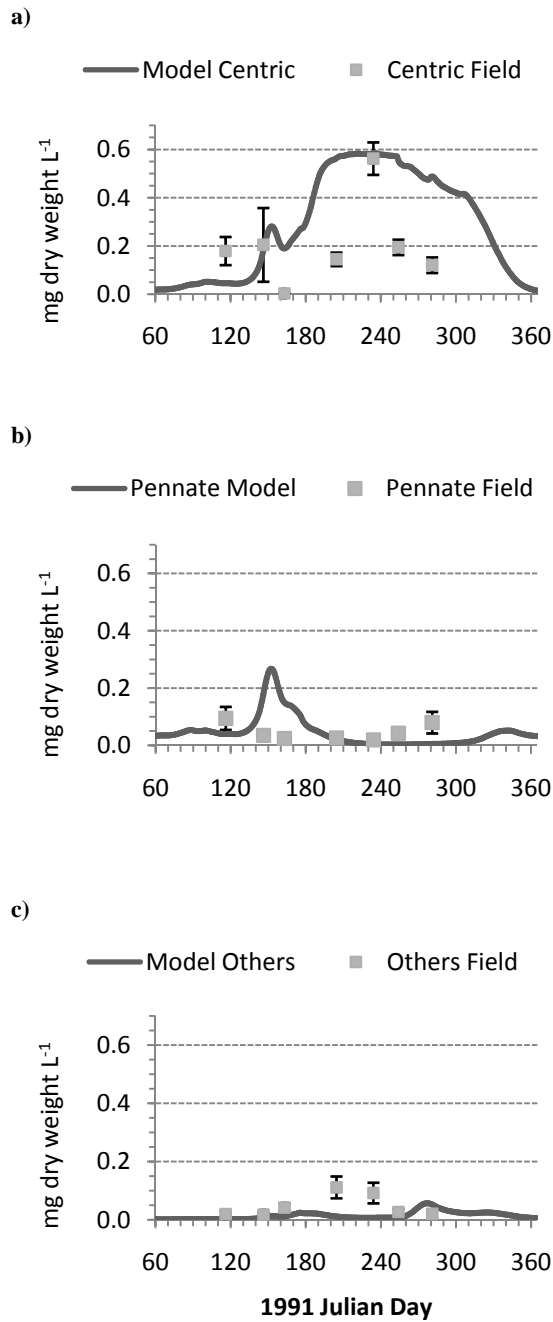


Figure 21: 1991 predicted a) centric diatoms, b), pennate diatoms, and c) “others” biomass (mg dry weight L⁻¹) compared to the selected NOAA GLERL samples.

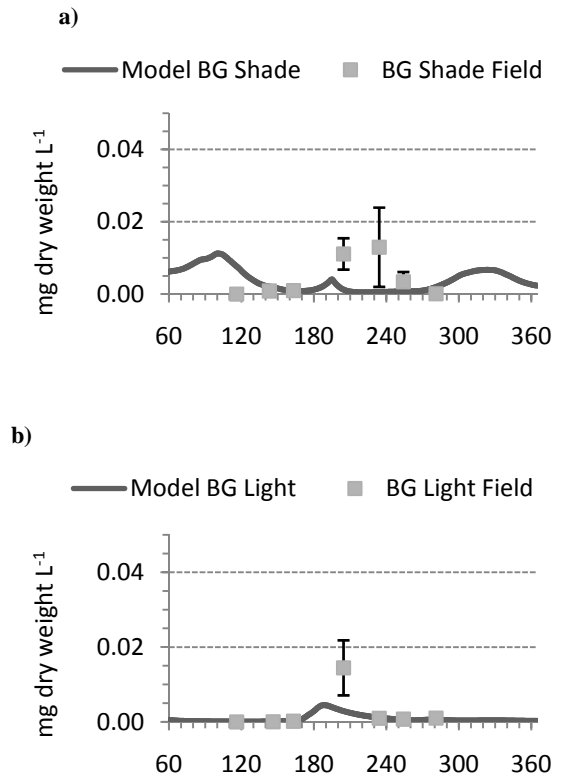


Figure 22: 1991 predicted a) cyanobacteria (BG) shade tolerant (ie *Oscillatoria* spp.) and b) light tolerant (ie *Microcystis* spp.) biomass (mg dry weight L⁻¹) compared to the selected NOAA GLERL samples.

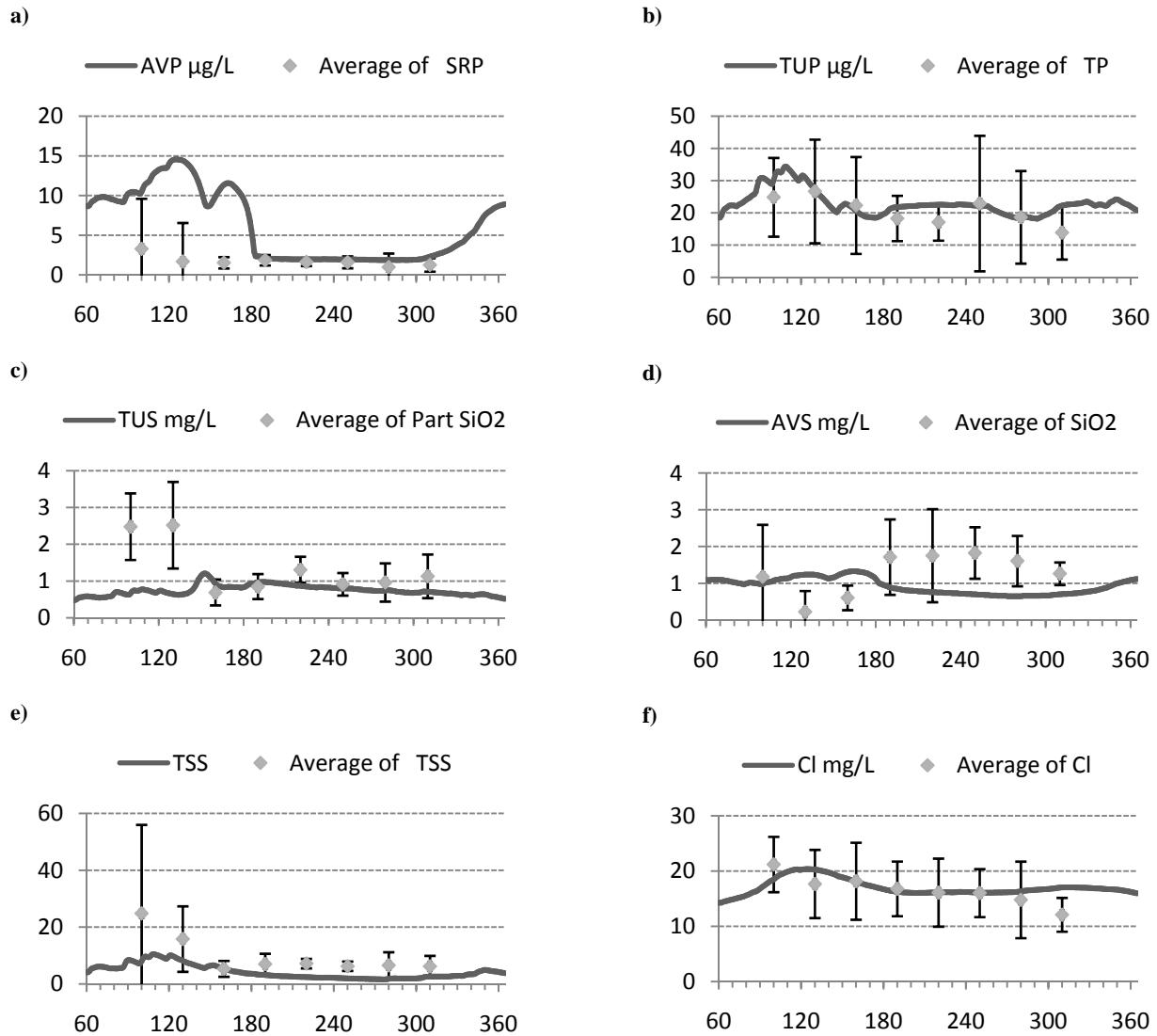


Figure 23: 1991 model predicted and solute concentrations in inner Saginaw Bay compared with monthly mean field data from the NOAA GLERL samples. Brackets represent the standard error of the mean. a) is dissolved available phosphorus $\mu\text{g L}^{-1}$, b) total unavailable phosphorus $\mu\text{g L}^{-1}$, c) dissolved available silicon mg L^{-1} , d) total particulate silicon mg L^{-1} , e) total suspended solids mg L^{-1} , and f) chloride mg L^{-1} .

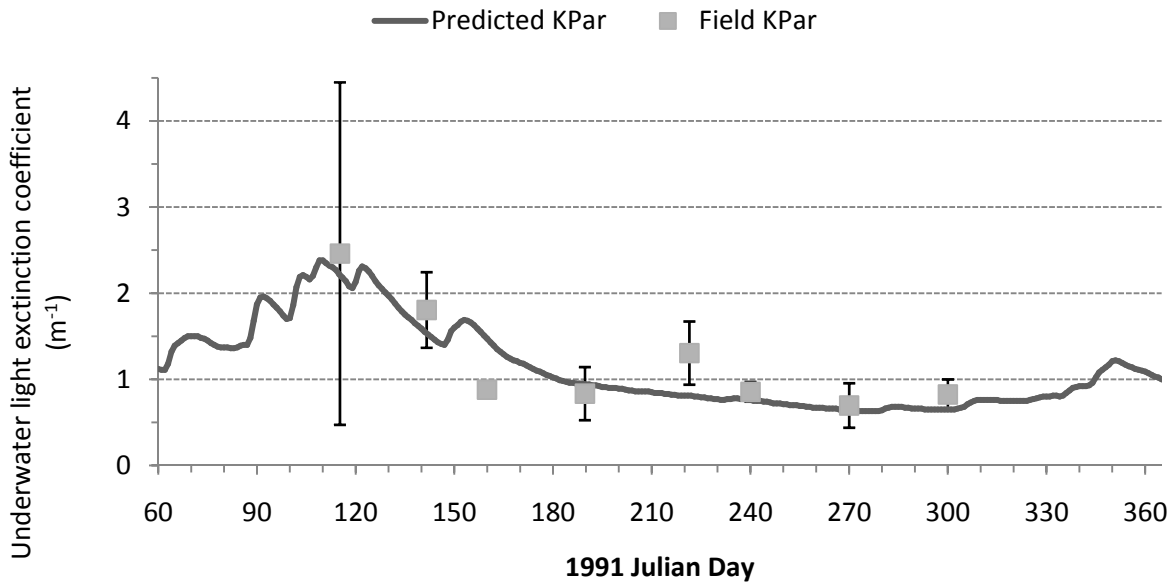


Figure 24: Monthly mean underwater light extinction from the 1991 NOAA GLERL inner Saginaw Bay sample sites compared to submodel predicted extinction.

Table 14: Amount of phytoplankton carbon grazed in June calculated from community filtering rate in Bridgeman et al. 1995. Assumes 50 mg C/mg Chl A.

June	Sample Station	Grazed (mg C m ⁻³ d ⁻¹)
1991	4	14
	14	22
	Mean	18

Table 15: Amount of phytoplankton carbon grazed by herbivorous zooplankton based on 1991 model calibration.

1991	Grazed (mg C m ⁻³ d ⁻¹)
April	0
May	1.0
June	48
July	51
Aug	46
Sept	37
Oct	19
Mean	29

Table 16: 1991 monthly mean total zooplankton biomass (mg per cubic meter) in inner Saginaw Bay reproduced from Bridgeman et al. 1995.

1991	Total Zooplankton mg m ⁻³
May	240
June	220
July	20
Aug	60
Mean	130

Table 17: Monthly mean biomass of herbivorous and carnivorous zooplankton based on 1991 model calibration.

1991	Herbivore mg m ⁻³	Carnivore mg m ⁻³
April	13	0.26
May	16	0.07
June	193	1.59
July	145	116.62
Aug	118	119.81
Sept	111	99.10
Oct	101	57.94
Mean	100	56.43

1992-1995 Simulations

On the basis of the results for 1991, when the most detailed field data and previous modeling results were available, the model was assumed to be sufficiently calibrated to examine the role of zebra mussels in altering the lower trophic levels of inner Saginaw Bay from 1992 to 1995. Model runs were conducted using the same coefficients from the 1991 calibration with loads, boundary conditions, temperatures, and zebra mussel densities from the 1992-1995 field data. Predicted total phytoplankton biomass is shown for 1992 -1995 (Figure 25). The predicted phytoplankton biomass in 1992 corresponded closely to the field data (Figure 25 a). In 1993, the model tended to over predict spring biomass, though summer biomass compared well to the field data (Figure 25b). In 1994 and 1995, the model tended to over predict biomass by 0.05-0.1 mg dry weight L⁻¹ (Figure 25 c&d).

The results from the phytoplankton community composition analysis, described in Chapter 1, suggested three important time periods when changes occurred in the phytoplankton community: 1991, 1992, and 1994. For comparison to the model test scenarios in 1992 and 1994, the community composition from the selected NOAA GLERL samples for 1992 and 1994 is shown in Figure 26. For each year, the model was driven by external forcing data (zebra mussel densities, boundary conditions, water temperature, advective and diffusive flows, and nutrient loadings) to examine the role of zebra mussels in promoting changes in the phytoplankton community. For these years the model was also run with zebra mussels “switched on” and

“switched off” to analyze their effects on the seasonal composition of the phytoplankton community (Figure 27-29).

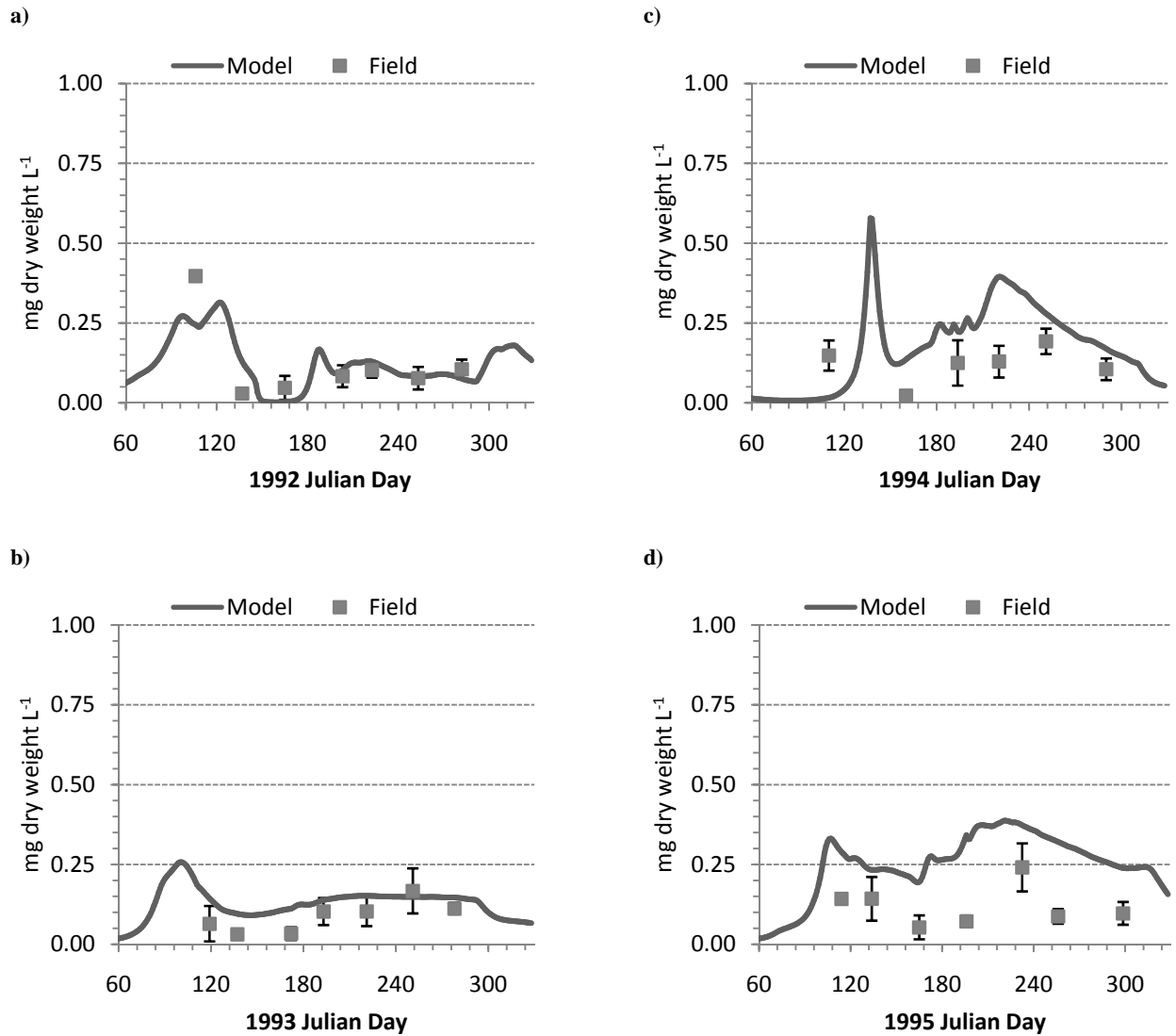


Figure 25: Total phytoplankton biomass from the selected NOAA GLERL collections from inner Saginaw Bay compared to the model output for A0 1992, b) 1993, c) 1994, and d) 1995. Brackets represent standard error of the mean

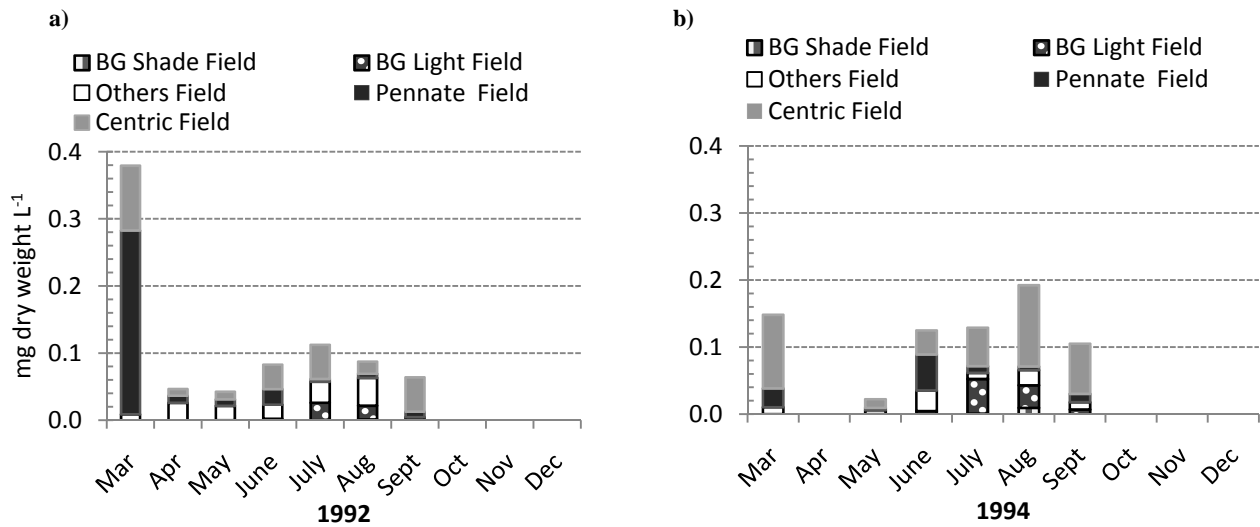


Figure 26: Phytoplankton community composition (mg dry weight L^{-1}) in a) 1992 and b) 1994 calculated from the selected NOAA GLERL collections from inner Saginaw Bay. BG Shade are filamentous cyanobacteria (i.e. *Oscillatoria*) and BG Light are chroococcoid cyanobacteria (i.e. *Microcystis*).

Field collections were not available in October 1992 and April 1994, so the following mean values are for May-September. With and without zebra mussels, there was little effect on 1991 mean biomass ($0.5 \text{ mg } L^{-1}$ in both scenarios), mean primary production ($500 \text{ mg C m}^{-2} \text{ day}^{-1}$ versus $498 \text{ mg C m}^{-2} \text{ day}^{-1}$), and seasonal community composition (Figure 27). The comparison between 1991 model and field community composition is discussed in detail in the model calibration section. In 1992 with zebra mussels, mean biomass was $0.10 \text{ mg dry weight } L^{-1}$ and without zebra mussels it was $0.40 \text{ mg dry weight } L^{-1}$ (Figure 28). Comparison between community composition estimated from the 1992 field data and 1992 model predictions showed an intense pennate diatom bloom in March while the model predicted diatom blooms in April and May (Figure 26a, Figure 28a). While the model accurately predicted the presence of cyanobacteria in July and August, it did not capture the presence of the “others” category of

phytoplankton. In the field data, this included colorless flagellates, which were not modeled. Mean primary production in 1992 with zebra mussels was $92 \text{ mg C m}^{-2} \text{ day}^{-1}$ and without zebra mussels it was $275 \text{ mg C m}^{-2} \text{ day}^{-1}$ (In 1992, Fahnenstiel et al. (1995) calculated a range of primary production from $30 - 300 \text{ mg C m}^{-2} \text{ day}^{-1}$ for the inner bay). In 1994, anecdotal reports of summer *Microcystis* blooms in inner Saginaw Bay were noted by Laurentyev et al. (1995) and *Microcystis* dominated the community assemblage (Chapter 1). With zebra mussels, 1994 predicted mean biomass was 0.21 mg L^{-1} and without zebra mussels it was 0.18 mg L^{-1} (Figure 29). 1994 mean primary production was $298 \text{ mg C m}^{-2} \text{ day}^{-1}$ with zebra mussels and $239 \text{ mg C m}^{-2} \text{ day}^{-1}$ without. Comparison between community composition estimated from the 1994 field data and 1994 model predictions showed that the model did not capture the March diatom bloom estimated from the field data (Figure 26b, Figure 29a). While overall biomass was over predicted in June, relative proportions of centric and pennate diatoms were accurate. The August of centric diatoms estimated by the field data was predicted in the model, but cyanobacteria blooms, estimated in the field data from July-August, were predicted for August-September.

In both 1992 and 1994, the presence of zebra mussels had a strong impact on the seasonal community composition. With zebra mussels, the pennate diatom group diminished earlier in the spring and the light adapted bluegreens group (i.e. *Microcystis* spp.) was an important component of the community in the summer (Figure 28a, 29a). Without zebra mussels, pennate diatoms persisted through August and the light adapted bluegreen group was not present (Figure 28b, 29b)

Selective Rejection of Microcystis

In the model, zebra mussels were assumed to selectively reject the light adapted bluegreens (i.e. *Microcystis* spp.), ejecting viable cells back to the water column in pseudofeces. The 1992 community composition was composed of 45% cyanobacteria in August (Figure 28a), the predicted cyanobacteria biomass was 0.04 mg L^{-1} and the estimated field biomass was 0.026 mg L^{-1} . In 1994 the September community composition was 50% cyanobacteria with predicted biomass of 0.085 mg L^{-1} and estimated field biomass of 0.052 mg L^{-1} . In 1992 and 1994, the selective rejection assumption was tested by turning off selective rejection. With zebra mussels present but with selective rejection off, the light adapted bluegreens group disappeared and the summer community composition was instead dominated by centric diatoms (Figure 30).

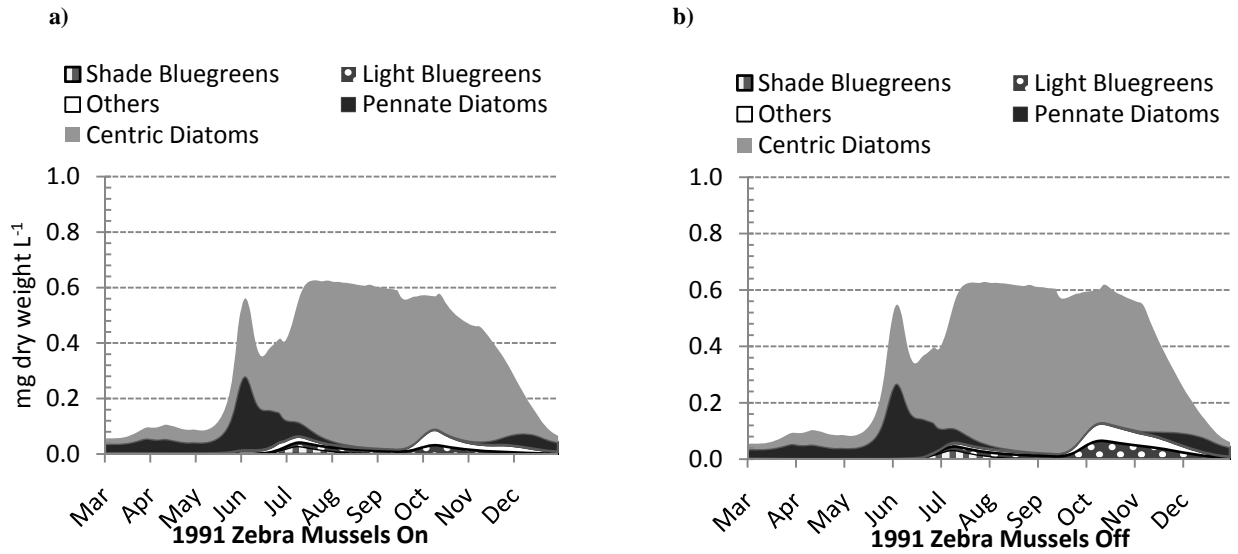


Figure 27: Differences in 1991 predicted seasonal phytoplankton community composition (mg dry weight L⁻¹) a) with zebra mussels present and b) no zebra mussels.

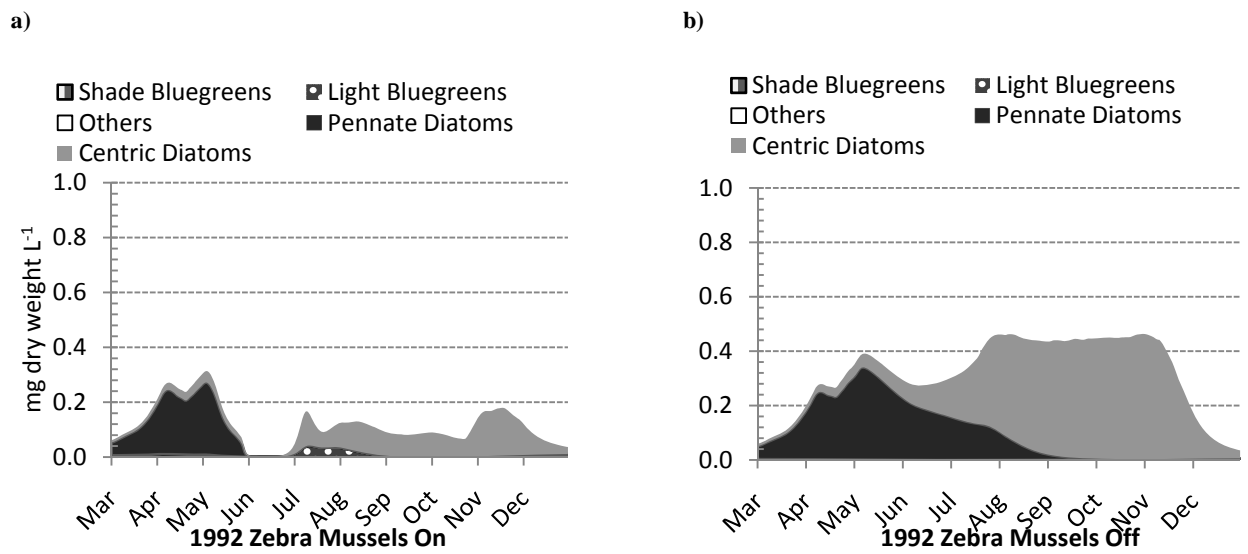


Figure 28: Differences in 1992 predicted seasonal phytoplankton community composition (mg dry weight L⁻¹) with a) zebra mussels present and b) no zebra mussels.

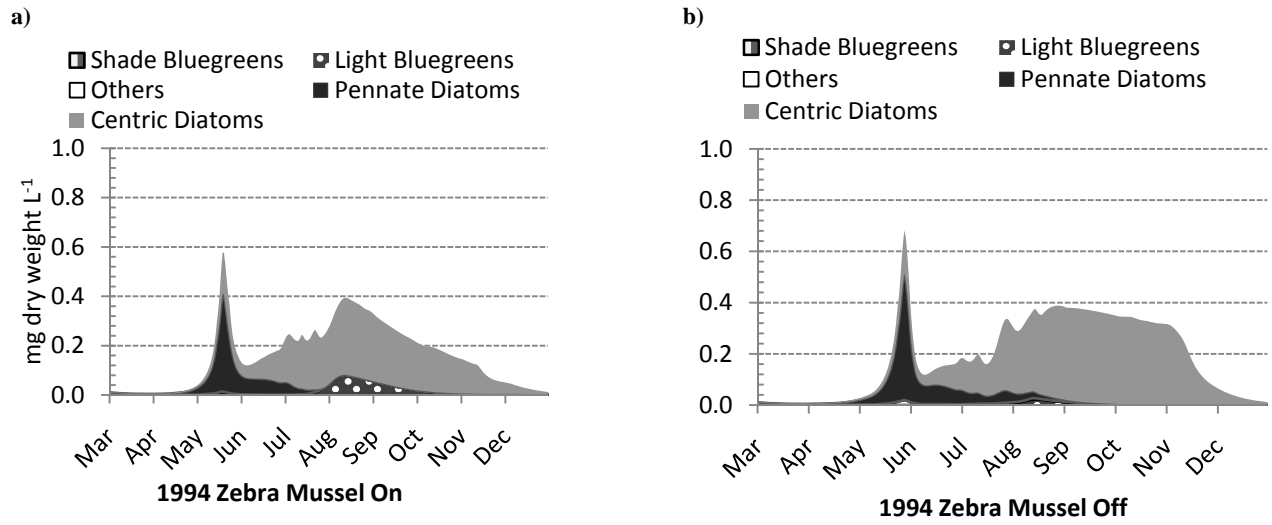


Figure 29: Differences in 1994 predicted seasonal phytoplankton community composition (mg dry weight L⁻¹) with a) zebra mussels present and b) no zebra mussels.

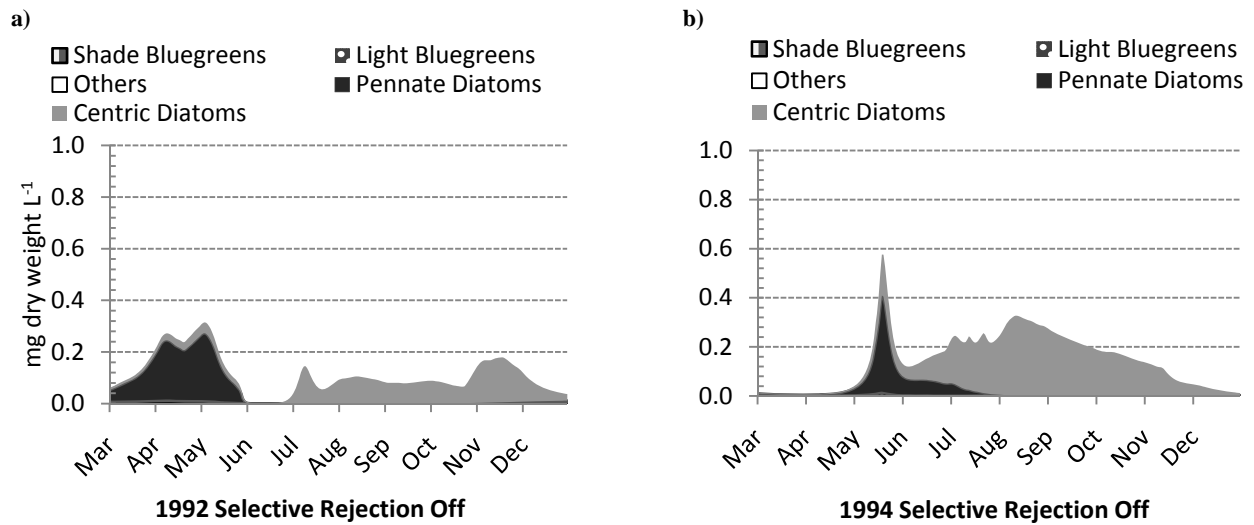


Figure 30: Predicted phytoplankton biomass and seasonal community composition (mg dry weight L⁻¹) with selective rejection of *Microcystis* (Light Bluegreens) turned off in a) 1992 and b) 1994.

Light Effects

The presence of zebra mussels indirectly alters a number of ecological functions in aquatic ecosystems (e.g. Heath et al. 1995, Miller and Watzin 2007). The other changes in community composition seen in 1992 and 1994 were explored by examining the role of two indirect effects associated with zebra mussel invasions: increased water clarity and altered nutrient cycling. Here the light effects are described. In the model, water clarity is calculated by the underwater light extinction coefficient, which is calculated via a sub-model based on total suspended solids concentration. Zebra mussel filtration rates were noted by Fanslow et al. (1995) to be high enough to filter the entire water column of Saginaw Bay daily. The model predicted that this filtration would produce a significant drop in total suspended solids (abiotic solids + phytoplankton dry weight) concentration. In both 1992 and 1994, this effect was similar: from May – October, zebra mussels were responsible for a >50% drop in total suspended solids concentration.

The clearing of the water column was predicted to have significant impacts on the competitive dynamics among the phytoplankton groups. Filamentous cyanobacteria, such as the shade tolerant *Oscillatoria redekei*, were important components of the phytoplankton community in 1980 through the spring of 1991, but were absent in fall 1991-1996 (Chapter 1, Figure 22a). In 1992, as in 1980-1991, the pennate diatoms (i.e. *Asterionella formosa* or *Fragilaria crotonensis*) were predicted to be an important component of the early spring community (Chapter 1, Figure 21 b). However, in a significant change from 1991, this low-light tolerant

group disappeared midway through May of 1992 (Chapter 1, Figure 26). In the model, phytoplankton growth is a function of the minimum of the light reduction factor and the nutrient reduction factor calculated using Equation (2). Based on ecological affinities suggested by Reynolds (2006), a major difference between the modeled centric and pennate diatom groups was the light saturation (tolerance) constant: pennate diatoms were assumed to be low light adapted by using a low light saturation constant and centric diatoms were assumed to be high light adapted by using a high constant (Table 12).

The growth limiting factors were examined for pennate diatoms in 1992 with and without zebra mussels. Since total suspended solids is strongly related to light extinction, the presence of zebra mussels meant clearer waters and thus a lower light extinction coefficient (Figure 31). This high light environment translated to inhibited growth for the pennate diatoms from May-August (Figure 32). In the scenario without zebra mussels, the more turbid waters meant both groups were phosphorus limited, influencing the competitive dynamics between the pennate and centric diatoms because the modeled phosphorus limitation factor for each group was the same. Without zebra mussels, this gave less competitive advantage to the centric diatom group and forestalled seasonal succession (Figure 28).

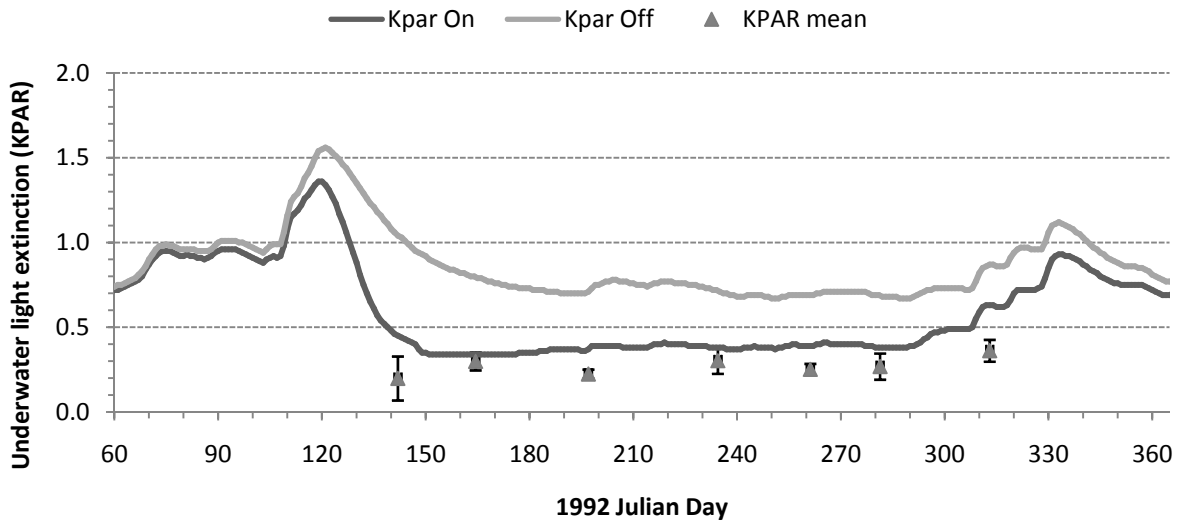


Figure 31: Predicted underwater light extinction coefficient (m^{-1}) with and without zebra mussels (“on” and “off”) compared to the monthly mean estimated values from NOAA GLERL field samples.

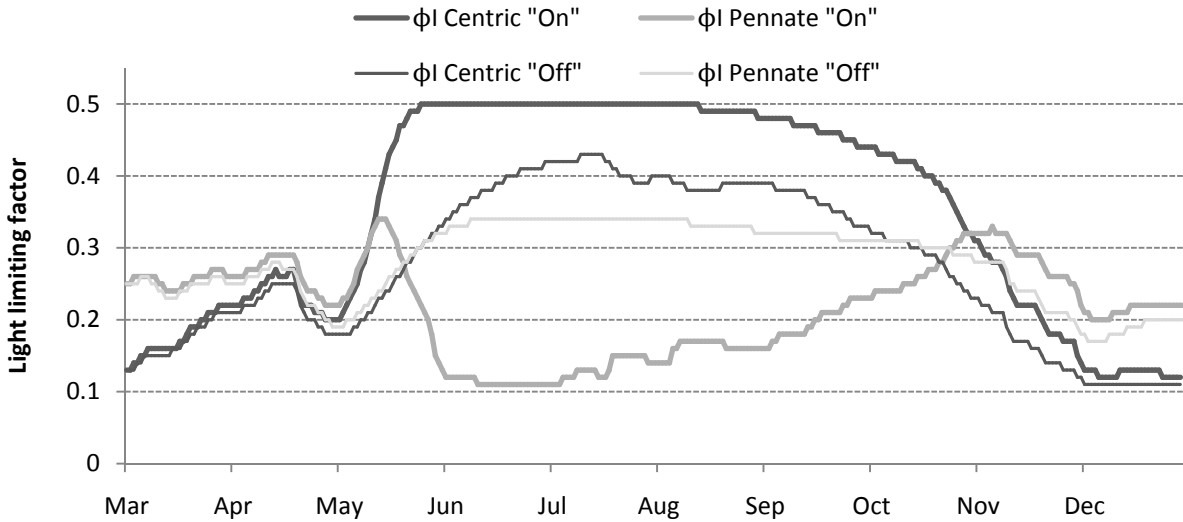


Figure 32: 1992 predicted growth limitation factors of the centric and pennate diatom groups with and without zebra mussels (“on” and “off”).

Phosphorus Cycle

Cyanobacteria blooms were not seen in 1993, despite the presence of an established zebra mussel population. Nalepa et al. (1995) noted that compared to 1992, both the monthly standardized weight of mussels and the overall population density was lower in 1993. Zebra mussels excrete high levels of available phosphorus to the water column (Johengen et al. 1995, James et al. 1997). The role of zebra mussel excretion of available phosphorus has been suggested to play a role in promoting phytoplankton blooms in low ($<25 \mu\text{g L}^{-1}$) total phosphorus lakes (Raikow et al. 2004). Average total phosphorus in inner Saginaw Bay 1991-1996 was $18.6 \mu\text{g L}^{-1}$ (Millie et al. 2006). Using the model results from the default calibration (zebra mussels present and selectively rejecting the light bluegreens group), predicted daily phosphorus excretion ($\mu\text{g L}^{-1} \text{ day}^{-1}$) was examined for 1992, 1993 and 1994 (Figure 33). Recycle was highest in 1994 and lowest in 1993. In 1992 and 1994, zebra mussel recycling on average was 24% of the daily total available phosphorus recycle. In 1993 this average was 2%. The mussel population structure was a significant factor in the amount of phosphorus recycled when comparing the 1992 and 1993 populations to the 1994 population. The older, larger mussels in 1994 contributed a disproportionate amount to the phosphorus recycle (Table 18). The 1994 available phosphorus tributary loads to inner Saginaw Bay would have to be reduced by 75% to overcome the increased available phosphorus provided by zebra mussel recycle and prevent summer cyanobacteria blooms (Figure 34).

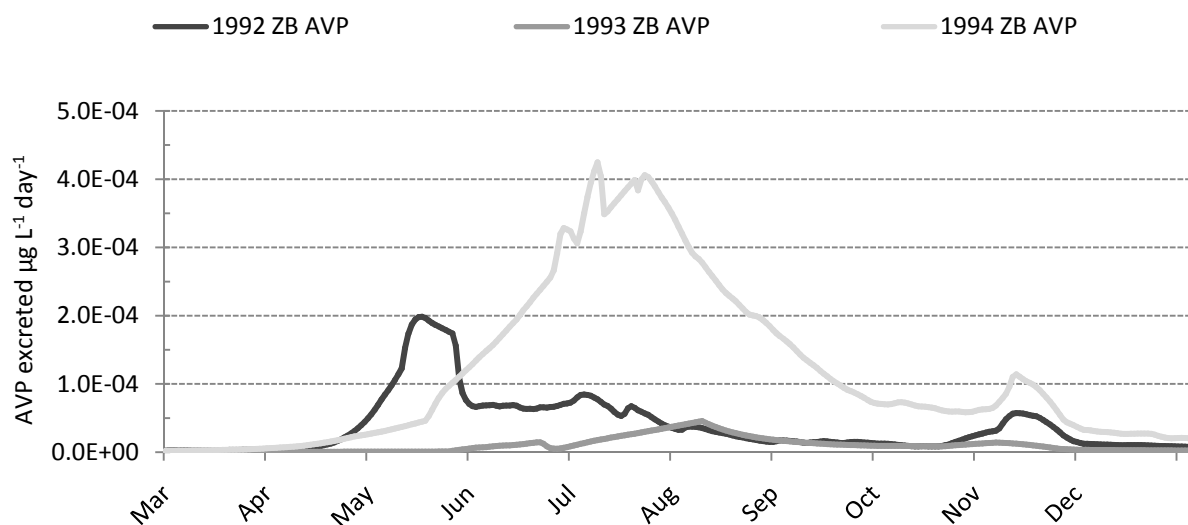


Figure 33: Predicted available phosphorus recycle ($\mu\text{g L}^{-1} \text{day}^{-1}$) from zebra mussel excretion in 1992, 1993, and 1994.

Table 18: Zebra mussel population density and available phosphorus recycle by age class cohort.

Year	Cohort	Proportion of Population	Proportion of AVP recycle
1992	YOY	42.7%	3.8%
	1st	57.3%	96.2%
	2nd	0.0%	0.0%
1993	YOY	18.8%	9.5%
	1st	39.4%	42.1%
	2nd	41.8%	48.5%
1994	YOY	46.5%	4.9%
	1st	42.6%	54.3%
	2nd	10.9%	40.8%

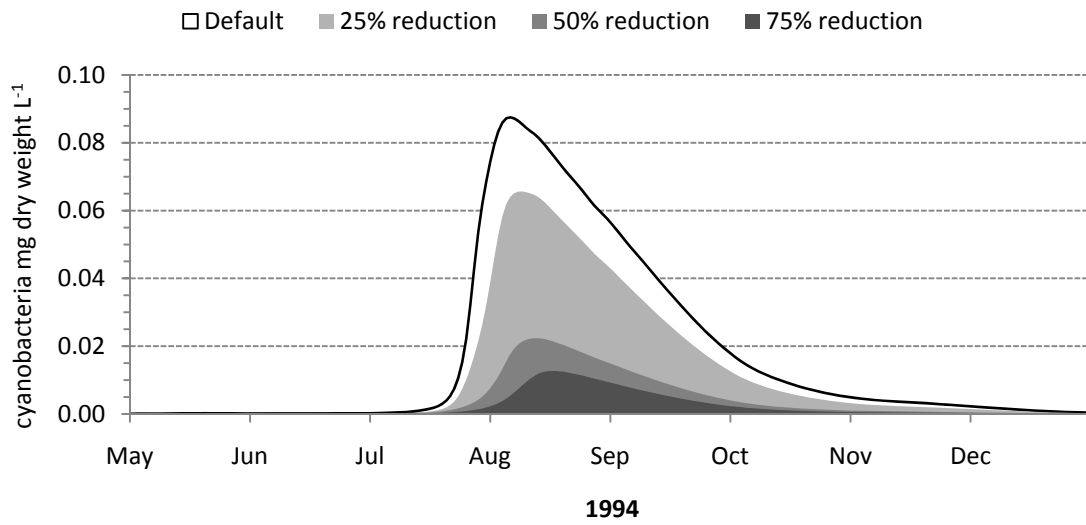


Figure 34: The effect of successive phosphorus load reductions scenarios on 1994 predicted cyanobacteria biomass.

Discussion

To analyze the role of an invasive mussel in altering the lower trophic levels of Saginaw Bay, direct effects (i.e. filtration) and indirect effects (i.e. altered nutrient cycling or increased water clarity) were examined with a mathematical model of nutrient, phytoplankton, and zooplankton (NPZ) dynamics coupled with output from a zebra mussel bioenergetics model. Using a detailed set of environmental forcing data from 1991-1995, the model predicted significant changes in the ecosystem structure of inner Saginaw Bay that were consistent with previously reported observations of increased water clarity (Fahnenstiel et al. 1995b), altered nutrient levels (Johengen et al. 1995, Raikow et al. 2004), and, after several years, the onset of summer algal blooms (Vanderploeg et al. 2001). The model predictions also support conclusions of the previous modeling efforts in Saginaw Bay that selective rejection could promote intense summer blooms of cyanobacteria (Bierman et al. 2005).

Filtration effects were highly significant. Predicted suspended solids concentrations were 50% lower with zebra mussels and, using scenarios in 1992 and 1994, total phytoplankton biomass was lower with zebra mussels than without. In addition to lower total biomass, results from this model show three major changes in the phytoplankton community composition of inner Saginaw Bay following the initial zebra mussel invasion in the fall of 1991. These changes operated on both short and long time scales. The model predicted 1) the disappearance of shade tolerant cyanobacteria in the same year as the invasion, 2) a transition in 1992 away from a May-

June pennate diatom dominated community and towards a centric diatom dominated community and 3) the eventual onset of summer blooms of the cyanobacteria *Microcystis*.

Three key mussel-mediated changes were identified in the modeled ecology of the system: 1) increased water column clarity via the removal of suspended solids; 2) increased dissolved available phosphorus recycle to the water column; and 3) promotion of certain types of algal groups via selective feeding behavior. By running test scenarios as the zebra mussel invasion progressed and the population structure stabilized, a more complete picture of the driving causes of the observed changes in the phytoplankton community described in Chapter 1 emerges. These results agree with suggestions from previous modeling work that altered nutrient cycling and selective rejection of cyanobacteria were important factors. The modeled zebra mussel filtration rate and thus available phosphorus excretion rate is weight dependant (Schneider 1992) and thus the presence of older, larger mussels in 1994 is predicted to enhance phosphorus recycle (Table 18). Modeling the observed *Microcystis spp.* selective rejection behavior reported by Vanderploeg et al. (2001) predicted that this behavior was necessary in promoting blooms of cyanobacteria in 1992, 1994, (Figure 30) and 1995 (results not shown). Variable tributary loads were not a significant factor in the 1994 summer blooms: 25% and 50% reductions in phosphorus loads made little difference in the community composition or biomass. To fully diminish the cyanobacteria blooms, a 75% reduction in 1994 phosphorus tributary loads was needed. The results of this analysis support the hypothesis in Bierman et al. (2005) that zebra mussel population structure is an important component in understanding the progression of

ecosystems affected by zebra mussels (Table 18). An important distinction between the previous work and this analysis is that these model results simulate the five year transition in field observations rather than using an extrapolation of Saginaw Bay conditions from a one year.

A novel result of the model is that filtration effects impacted the competitive balance among diatom groups by altering the light environment. Bierman & Stoermer (1980) concluded that in the original model, modeled phytoplankton growth was highly sensitive to variations in the light extinction coefficient. So, while this predicted result is not surprising, it is a significant factor in describing the possible mechanisms behind the shift seen in diatom species composition. Light saturation constants for diatoms differ. To reflect the historically turbid environment of inner Saginaw Bay, a deliberately low value was chosen for the traditional spring species assemblage (the pennate diatoms) to reflect the conceptual choice in modeled phytoplankton groups. Mur & Schreurs (1995) suggested that the cyanobacteria *Oscillatoria* is light sensitive and Nicholls et al. (2002) discuss the disappearance of this species following the zebra mussel invasion of the Bay of Quinte, Lake Ontario. In the two studies that discussed sustained shifts in diatom community composition following zebra mussel invasions of Great Lakes waters (by Nicholls et al. 2002 and Barbiero et al. 2006), water clarity was discussed but not identified as a driving cause of the observed changes. While Nicholls et al. (2002) did not suggest drivers for the changes seen in the Bay of Quinte, Barbiero et al. (2006) concluded that during the spring, silica dynamics were driving changes away from pennate diatoms and towards a light intolerant, high silicon requiring centric diatom, *Aulacoseira islandica*, in the Eastern Basin of Lake Erie.

While a similarly drastic shift in diatom community composition appears to have taken place in Saginaw Bay, the driving forces appear to be different. Mean silicon concentrations from April-June were variable in inner Saginaw Bay from 1991-1995. However, spring KPAR sustained a 40% decrease from 1991 to 1992 – 1995. Following the zebra mussel invasion, successively greater light adapted centric diatom species (first *Cyclotella comensis* 1992-1993 then *C. ocellata* 1994-1996) typical of Lake Huron waters became more prevalent in inner Saginaw Bay in combination with chroococcoid cyanobacteria while the spring dominance of pennate diatoms such as *Fragilaria crotonensis* diminished (Chapter 1). These model results suggest that the diatom community, which was likely stable from 1980 - 1990, underwent a sustained shift following the zebra mussel invasion due to altered light conditions. Diatom biomass in Saginaw Bay decreased immediately with the zebra mussel invasion and stabilized at approximately 50% of pre-invasion levels while community composition continued to change in the following years (Chapter 1). The model identified abiotic (increased light penetration) and biotic factors (nutrient cycling and selective feeding behavior) as important in driving both phytoplankton biomass and community composition. However, while the biotic factors varied in magnitude with the zebra mussel population structure, light penetration was consistently 40% greater than it would have been without zebra mussels following the invasion. Increased light penetration is a significant driver of the sustained shift in Saginaw Bay diatom community composition.

Further, detailed study of the role of mussel-mediated biological recycle of phosphorus is needed because the modeled phytoplankton community was highly sensitive to yearly initial zebra mussel weight as well as the timing and magnitude of mussel reproductive losses, which greatly reduces mussel weight from May – August . While the ecological implications of the shift in the diatom community are unclear, it seems likely that steep reductions in nonpoint phosphorus runoff will likely be necessary if summer algal blooms are to be addressed. A problem not addressed in this paper is the increased benthic primary production facilitated by increased light penetration to the benthos and the nutrient enrichment of the sediments. The combination of increased light and nutrient availability is likely significant in explaining the *Cladophora* blooms in Saginaw Bay (a benthic algae responsible for the “muck” fouling the shoreline), and due to the benthic phase of *Microcystis* colonies (Stahl-Delbanco et al. 2003), may be a significant factor in promoting *Microcystis* blooms as well.

Thesis Conclusions

In summary, results from this study in Saginaw Bay, Lake Huron showed that significant alterations in the phytoplankton community, which appeared stable from 1980-1990, followed the 1991 zebra mussel invasion. The changes seen in phytoplankton community composition, while fundamentally different in character, are on a scale analogous to the eutrophication of Saginaw Bay that resulted from anthropogenic phosphorus enrichment during the 1960s-1970s (Beeton 1965), even without any significant variability in 1990-1996 external nutrient loadings (Bierman et al. 2005).

These alterations, operating both on seasonal and multi-year time scales, resulted from the combination of direct and indirect ecosystem level effects associated with zebra mussel colonization of aquatic ecosystems. Despite the simplifications undertaken to represent a complex ecological system, the application of an ecosystem model of inner Saginaw Bay to five years of field data was an insightful way to analyze the mechanisms driving the observed changes in the phytoplankton community because it allowed a detailed examination of different causal mechanisms. By using different test scenarios, the analysis of the model output showed that the disturbance to the ecology of Saginaw Bay caused by the zebra mussel invasion was a complex combination of factors both directly related to grazing and indirectly related to ecosystem engineering.

The increased available phosphorus, mediated by zebra mussel excretion, is likely a major component acting in concert with selective rejection of unpalatable cells to promote blooms of *Microcystis*. However, due to the likely permanent alteration of the ecosystem function by the presence of zebra mussels, it is unclear what magnitude of reductions in phosphorus loads will be necessary to manage the water quality of Saginaw Bay to avoid harmful summer algal blooms. A complicating factor in this management objective is that although there were marked reductions in phytoplankton cell densities as well as chlorophyll concentrations following the zebra mussel invasion, the overall primary production in the bay remained unchanged as it appears that the clearer water column altered energy flows, allowing increased primary production in the benthos (Fahnenstiel et al. 1995a). This in turn allows for benthic algal blooms of *Cladophora*, a potentially more serious problem than summer *Microcystis* blooms (Bierman et al. 2005; Higgins et al. 2005).

The total response to the zebra mussel invasion by the lower trophic levels suggests that complex interactions between top-down pressures such as grazing and bottom-up controls such as limits to growth on the phytoplankton community are producing a novel community in Saginaw Bay. The longer-developing changes suggest that altered resource and light dynamics are driving fundamental changes in phytoplankton community composition. The changes described in Chapter 1 and modeled in Chapter 2 were mirrored in many other locations throughout the Great Lakes (Bailey et al. 1999, Idrisi et al. 2001, Nicholls et al. 2002, Ricciardi 2003, Barbiero et al. 2006, Higgins et al. 2006).

The universal impacts of zebra mussels in affected North American ecosystems are increased light penetration and decreased phytoplankton biomass (MacIsaac 1996). It is also clear that zebra mussels have altered the expected results of phosphorus abatement strategies in the Great Lakes. While nutrient enrichment from tributary runoff is still a driving factor in the eutrophication of aquatic ecosystems, the presence of zebra mussels alters the ecology in a complex manner by providing clearer water, increasing phosphorus recycle, and undertaking selective feeding behavior. This study cannot suggest new phosphorus targets though it confirms the important role water quality modeling can play in the management of aquatic ecosystems. A full sensitivity analysis was not done; however the modeled phytoplankton community results were sensitive to variations in the modeled upper trophic levels, including zooplankton grazing and zebra mussel filtration. This result reiterates the need for quality, long term ecological monitoring datasets if the role of novel disturbances in altering ecosystems is to be understood on a practical and predictive level.

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Appendix: Model Equations

Constituent concentration equations {Chapra, 1997}

$$V \frac{dc}{dt} = -Qc + E'(c_{Boundary} - c_{bay}) \pm Sc$$

Where:

c = Constituent concentration in Inner Bay $\left(\frac{\text{mass}}{\text{volume}}\right)$

V = Volume of the inner bay

Q = Sum of flows into inner bay (tributary + outer bay) $\left(\frac{\text{volume}}{\text{time}}\right)$

E' = Bulk diffusion coefficient $\left(\frac{\text{volume}}{\text{time}}\right)$

S = Sources and sinks of constituent in the inner bay

Water Column Physical State Variables {Bierman, 1986}

1. Available Phosphorus

$$\frac{dAVP}{dt} = \text{Boundary Contribution} + \text{Loadings} + \text{Biological recycle} - \text{Uptake}$$

$$1.1. AVPBC = \frac{Q_{lake \rightarrow bay}}{V_{bay}} (AVPBC) + \frac{E'}{V_{bay}} (AVPBC - AVP) - \frac{Q_{(trib)+(lake \rightarrow bay)}}{V_{bay}} (AVP)$$

$$1.2. WAVP = \text{Tributary} + \text{Atmosphere} + \text{Mineralization} + \text{Decomposition}$$

$$1.2.1. \text{Tributary (WAVPT)} = \frac{mg}{day l}. \text{ Externally specified using derived daily loadings.}$$

1.2.2. *Atmosphere (WAVPA)* = $\frac{mg}{day\ l}$. Externally specified using derived daily loadings.

1.2.3. *Mineralization (WAVPS)* = $TPSED * k_{AVP} * f(^{\circ}C) * \frac{Z_{sediment}}{Z_{water\ column}}$

1.2.4.

Decomposition (WAVPD) = $\frac{dissolved\ TUP}{total\ TUP} * RTUP * f(^{\circ}C) * \frac{TUP}{k_{TUP+\Sigma phytoplankton}} * TUP$

1.3. $AVPR = \sum_i A_i AVP + Z_H AVP + Z_C AVP + Z_M AVP$

1.4. $AVPUP = \sum_i \left[A_i Prod * \frac{mg\ P}{mg\ C_i} \right]$

2. Total Unavailable Phosphorus

$\frac{dTUP}{dt} = Boundary\ Contribution + Loadings + Biological\ recycle - Decomposition$
 $- Settling - Filtration$

2.1. $TUPBC = \frac{Q_{lake \rightarrow bay}}{V_{bay}} (TUPBC) + \frac{E'}{V_{bay}} (TUPBC - AVP) - \frac{Q_{(trib+lake \rightarrow bay)}}{V_{bay}} (TUP)$

2.2. $WTUP = Tributary + Atmosphere + Resuspension$

2.2.1. *Tributary (WTUPT)* = $\frac{mg}{day\ l}$. Externally specified using derived daily loadings.

2.2.2. *Atmosphere (WTUPA)* = $\frac{mg}{day\ l}$. Externally specified using derived daily loadings.

2.2.3. *Resuspension (WTUPS)* = $\frac{TPSED * VUPP}{Z_{sed}} * WIND * \frac{V_{sediment}}{V_{water\ column}}$

2.3. $Recycle (TUPR) = Z_H TUP + Z_C TUP$

$$2.4. \text{ Decomposition (TUPD)} = \frac{\text{dissolved TUP}}{\text{total TUP}} * RTUP * f(^{\circ}\text{C}) * \frac{\text{TUP}}{k_{TUP+\Sigma \text{ phytoplankton}}} * TUP$$

$$2.5. \text{ Sinking (TUPS)} = \frac{\text{particulate TUP}}{\text{total TUP}} * \frac{\text{TUPSINK}}{Z_{\text{water column}}} * TUP$$

$$2.6. \text{ Filtration (Z}_{MP}) = \frac{\text{particulate TUP}}{\text{total TUP}} * TUP * V_{\text{filt}}$$

3. Available Silicon

$$\frac{dAVS}{dt} = \text{Boundary Contribution} + \text{Loadings} + \text{Biological recycle} - \text{Uptake}$$

$$3.1. AVSBC = \frac{Q_{\text{lake} \rightarrow \text{bay}}}{V_{\text{bay}}} (AVSBC) + \frac{E'}{V_{\text{bay}}} (AVSBC - AVP) - \frac{Q_{(\text{trib}+\text{lake} \rightarrow \text{bay})}}{V_{\text{bay}}} (AVS)$$

$$3.2. WAVS = \text{Tributary} + \text{Atmosphere} + \text{Mineralization} + \text{Decomposition}$$

$$3.2.1. \text{ Tributary (WAVST)} = \frac{\text{mg}}{\text{day l}}. \text{ Externally specified using derived daily loadings.}$$

$$3.2.2. \text{ Atmosphere (WAVSA)} = \frac{\text{mg}}{\text{day l}}. \text{ Externally specified using derived daily loadings.}$$

$$3.2.3. \text{ Mineralization (WAVSS)} = TSSSED * k_{AVS} * f(^{\circ}\text{C}) * \frac{Z_{\text{sediment}}}{Z_{\text{water column}}}$$

3.2.4.

$$\text{Decomposition (WAVSD)} = \frac{\text{dissolved TUS}}{\text{total TUS}} * RTUS * f(^{\circ}\text{C}) * \frac{\text{TUS}}{k_{TUS+\Sigma \text{ phytoplankton}}} * TUS$$

$$3.3. \text{ Recycle (AVSR)} = \Sigma A_i AVS$$

$$3.4. AVSUP = \Sigma \left[A_i \text{Prod} * \frac{\text{mg Si}}{\text{mg C}_i} \right]$$

4. Total Unavailable Silicon

$$\frac{dTUS}{dt} = \text{Boundary Contribution} + \text{Loadings} + \text{Biological recycle} - \text{Decomposition} \\ - \text{Settling} - \text{Filtration}$$

$$4.1. TUSBC = \frac{Q_{lake \rightarrow bay}}{V_{bay}} (TUSBC) + \frac{E'}{V_{bay}} (TUSBC - AVP) - \frac{Q_{(trib+lake \rightarrow bay)}}{V_{bay}} (TUS)$$

$$4.2. WTUS = \text{Tributary} + \text{Atmosphere} + \text{Resuspension}$$

$$4.2.1. \text{Tributary (WTUST)} = \frac{mg}{day \cdot l}. \text{ Externally specified using derived daily loadings.}$$

$$4.2.2. \text{Atmosphere (WTUSA)} = \frac{mg}{day \cdot l}. \text{ Externally specified using derived daily loadings.}$$

$$4.2.3. \text{Resuspension (WTUSS)} = TSSSED * VUPS * WIND * \frac{1}{Z_{sediment}} * \frac{Z_{sediment}}{Z_{water column}}$$

$$4.3. \text{Recycle (TUSR)} = Z_H TUS$$

$$4.4. \text{Decomposition (TUSD)} = \frac{\text{dissolved TUS}}{\text{total TUS}} * RTUS * f(^{\circ}C) * \frac{TUS}{k_{TUS + \Sigma \text{phytoplankton}}} * TUS$$

$$4.5. \text{Sinking (TUSS)} = \frac{\text{particulate TUS}}{\text{total TUS}} * \frac{TUSSINK}{Z_{water column}} * TUS$$

$$4.6. \text{Filtration (Z}_M\text{S)} = \frac{\text{particulate TUS}}{\text{total TUS}} * TUS * V_{filt}$$

Sediment Physical Variables {Bierman, 1986}

5. Total Sediment Phosphorus

$$\frac{dSEDP}{dt} = \text{Loading} - \text{Resuspension} - \text{Burial}$$

$$5.1. \text{Loading} = \left[(TUPS + Z_M P) * \frac{Z_{water column}}{Z_{sediment}} \right] + \left[V_{filt} * \sum_i \left(A_i * \frac{mg P}{mg C_i} \right) \right]$$

$$5.2. \text{Resuspension} = WTUPS$$

$$5.3. \text{Burial} = SEDP * \frac{VPLONG}{Z_{sediment}}$$

6. Total Sediment Silicon

$$\frac{dSEDS}{dt} = \text{Loading} - \text{Resuspension} - \text{Burial}$$

$$6.1. \text{Loading} = \left[(TUSS + Z_{MS}) * \frac{Z_{water\ column}}{Z_{sediment}} \right] + \left[\frac{V_{filt} * \sum_i \left(A_i * \frac{mg\ Si}{mg\ C_i} \right)}{V_{sediment}} \right]$$

$$6.2. \text{Resuspension} = WTUSS$$

$$6.3. \text{Burial} = SEDS * \frac{VSLONG}{Z_{sediment}}$$

7. Phytoplankton {Chapra, 1997}

$$\frac{dA_i}{dt} = \text{Boundary Contribution}_i + \text{Production}_i - \text{Nonpredatory losses}_i \\ - \text{Predation}_i$$

Where:

A_i = Phytoplankton type

$$7.1. A_i BC = \frac{Q_{lake \rightarrow bay}}{V_{bay}} (A_i BC) + \frac{E'}{V_{bay}} (A_i BC - A_i) - \frac{Q_{(trib)+(lake \rightarrow bay)}}{V_{bay}} (A_i)$$

$$7.2. A_i Prod = A_i Growth * A_i$$

$$7.2.1. A_i Growth = GMAX_i \phi T_i \phi I_i \phi N_i$$

Where:

$$GMAX_i = \frac{1}{day}$$

$$\phi T_i = \theta_i^{(°C-20)}$$

$$\phi I_i = \frac{2.078f}{k_e Z} (e^{-\alpha_{1i}} - e^{-\alpha_{0i}})$$

$f = \text{photoperiod}$

$$\alpha_{0i} = \frac{I_a}{I_{s_i}}$$

$$\alpha_{1i} = \alpha_{0i} e^{-k_e Z}$$

$$\phi N_i = \text{Min} \left(\frac{S_i}{k_{S_{i=diatoms}} + S_i}, \frac{AVP}{k_{AVP_i} + AVP} \right)$$

$$7.2.2. \quad A_i \text{Nonpred} = \text{Decomposition}_i + \text{Respiration}_i + \text{Settling}_i$$

$$7.2.3. \quad A_i \text{Decomp} = RDCMP_i * \phi T_i * \frac{\sum_i A_i}{\sum_i A_i + k_{DCMP} * GR_i} * A_i$$

$$7.2.4. \quad A_i \text{Resp} = RRESP_i * \phi T_i * A_i$$

$$7.2.5. \quad A_i \text{Settle} = \frac{ASINK_i \left(\frac{m}{day} \right)}{Z_{\text{water column}} (m)} * A_i$$

$$7.2.6. \quad A_i \text{Pred} = Z_H \text{Grzd}_i + Z_M \text{Fltr}_i$$

8. Phytoplankton Nutrient Uptake and Recycle {Chapra, 1997}

$$8.1. \quad A_i \text{AVP uptake} = A_i \text{Prod} * \frac{mg P}{mg C_i}$$

$$8.2. A_i AVS \text{ uptake} = A_i Prod * \frac{mg Si}{mg C_i}$$

$$8.3. A_i AVP \text{ recycle} = \left[A_i Resp * \frac{mg P}{mg C_i} \right] + \left[A_i Decomp * \frac{mg P}{mg C_i} \right]$$

$$8.4. A_i AVS \text{ recycle} = \left[A_i Resp * \frac{mg Si}{mg C_i} \right] + \left[A_i Decomp * \frac{mg Si}{mg C_i} \right]$$

$$8.5. A_i SEDP \text{ settling} = A_i Settle * \frac{mg P}{mg C} * \frac{Z_{water column}}{Z_{sediment}}$$

$$8.6. A_i SEDS \text{ settling} = A_i Settle * \frac{mg Si}{mg C} * \frac{Z_{water column}}{Z_{sediment}}$$

9. Herbivorous Zooplankton {Chapra, 1997 }

$$\frac{dZ_H}{dt} = \text{Boundary Contribution} + \text{Growth} - \text{Nonpredatory losses} - \text{Predation}$$

$$9.1. Z_H \text{ Growth} = \epsilon_{Z_H} * [GMAX_{Z_H} \phi T_{Z_H} \phi F_{Z_H} \sum_i A_i] * Z_H$$

$$\phi F_{Z_H} = \left[\frac{\sum_i \alpha_i A_i}{k_A + \sum_i \alpha_i A_i} \right]$$

$$9.2. Z_H \text{ Grzd}_i = GMAX_{Z_H} * \phi T_{Z_H} * \left[\frac{\alpha_i A_i}{k_A + \sum_i \alpha_i A_i} \right] * Z_H * A_i$$

Where:

$$\epsilon_{Z_H} = \text{Efficiency of assimilation}$$

$$GMAX_Z = \text{Filtration rate} \frac{l}{mg \text{ day}}$$

$$\alpha_i = \text{Electivity on phytoplankton}_i$$

$$k_A = \text{Half saturation constant for } Z_H \text{ feeding}$$

$$\alpha_Z = \text{Electivity on zooplankton}_H$$

$$9.3. Z_H \text{ Nonpred} = \phi T_{Z_H} * RLOSS_{Z_H} * Z_H$$

$$9.4. Z_H \text{ Pred} = Z_C \text{ Grzd}_{Z_H} + Z_M \text{ Fltr}_{Z_H}$$

10. Carnivorous Zooplankton{Chapra, 1997}

$$10.1. \frac{dZ_C}{dt} =$$

Boundary Contribution + Growth - [Nonpredatory + predatory] losses

$$10.2. Z_C \text{ Grwth} = \epsilon_{Z_C} * [GMAX_{Z_C} \phi T_{Z_C} \phi F_{Z_C} Z_H] * Z_C$$

$$\phi F_{Z_C} = \left[\frac{Z_H}{k_{Z_H} + Z_H} \right]$$

$$10.3. Z_C \text{ Grzd}_{Z_H} = GMAX_{Z_C} * \phi T_{Z_C} * \phi F_{Z_C} * Z_C * Z_H$$

$$10.4. Z_C \text{ Loss} = \phi T * RLOSS_{Z_C} * Z_C$$

11. Zooplankton Nutrient Recycle{Chapra, 1997 #164}

$$11.1. Z_H \text{ AVP recycle} = \phi T_{Z_H} * RLOSS_{Z_H} * Z_H * \frac{mg P}{mg C_{Z_H}}$$

$$11.2. Z_C \text{ AVP recycle} = \phi T_{Z_C} * RLOSS_{Z_C} * Z_C * \frac{mg P}{mg C_{Z_C}}$$

$$11.3. Z_H \text{ TUP recycle} = (1 - \epsilon) * GMAX_{Z_H} * \phi T_{Z_H} * \phi F_{Z_H} * Z_H * \left(\sum_i A_i \frac{mg P}{mg C_i} \right)$$

$$11.4. Z_H \text{ TUS recycle} = GMAX_{Z_H} * \phi T_{Z_H} * \left[\frac{\sum_i \alpha_i A_i}{K_A + \sum_i \alpha_i A_i} \right] * Z_H * \left(\sum_i A_i \frac{mg S_i}{mg C_i} \right)$$

$$11.5. Z_C \text{ TUP recycle} = (1 - \epsilon) * GMAX_{Z_C} * \phi T_{Z_C} * \phi F_{Z_C} * Z_C * Z_H * \frac{mg P}{mg C_{Z_H}}$$

12. Zebra Mussel Respiration {Schneider, 1992}

These equations represent respiration and are not a population model. Externally specified zebra mussel densities in $\frac{\#}{m^2}$ are required to implement this model.

Consumption and respiration are proportional to wet weight, so three age cohorts are specified. The change in average wet weight of a single zebra mussel in a cohort is given by:

$$\frac{dZ_{M\gamma}}{dt} = \omega_f \text{Consumption}_{\gamma} - \omega_r \text{Respiration}_{\gamma} - \omega_f \text{Egestion}_{\gamma} - \omega_f \text{Excretion}_{\gamma} \\ - \text{Reproduction}_{\gamma}$$

Where:

Z_M = wet weight (g)

γ = yearly cohort class

$$\omega_f = \text{efficiency of assimilation} \left(\frac{g_{TSS}}{g_{Z_M}} \right)$$

$$\omega_r = \text{respiration efficiency} \left(\frac{g_{Z_M}}{g_{O_2}} \right)$$

$$12.1. \quad \text{Consumption } (C_{\gamma}) = C_{MAX} * Z_{M\gamma}^{\beta_c} * \psi T * \psi F$$

Where:

β_c = exponent for weight dependence of C_{MAX}

$\psi T = 0 - 1$ multiplier for temperature effect on respiration

$\psi F =$

$0 - 1$ multiplier for suspended solids concentration effect on consumption

12.2. $Respiration\ in\ (R_Y) = R_{MAX} * Z_{M_Y}^{\beta_r} * \psi T_{Z_M}$

Where:

$\beta_r = 0 - 1$ multiplier for weight dependence of R_{MAX}

12.3. $Egestion\ (F_Y) = C_Y * \alpha_F e^{(\gamma_F * \psi F)}$

Where:

α_f = proportion egested versus proportion of C_{MAX} realized

γ_F = dependence of egestion on ψF

12.4. $Excretion\ (E_Y) = 0.064 (C_Y - F_Y)$

12.5. $Reproduction\ (G_Y) =$ first order loss based on timing of veliger appearance
{Bierman, 2005}

13. Zebra mussel water quality impacts {Bierman, 2005 }

The removal of total suspended particulates (TSS) from the water column depends

on the filtration rate (FR) in $\frac{l}{gZ_M\ day}$. $FR = \frac{C_Y}{TSS} * \alpha_f$, where α_f represents the

production of pseudofeces. For a single zebra mussel, the impact on TSS is then given by:

$$V \frac{dTSS}{dt} = FR * Z_M * TSS$$

13.1. By summing across cohorts, the total effect of a zebra mussel population on a particulate concentration [PP] in $\frac{mg}{l \text{ day}}$ is given by $Z_M Fltr_{[PP]}$:

$$V \frac{d[PP]}{dt} = \left[\sum_Y (n_Y * FR_Y * Z_{M_Y}) * S.A \right] * [PP]$$

Where:

n_Y = externally specified # of zebra mussels (m^{-2}) in cohort

$S.A.$ = surface area of bay bottom (m^2)

$[PP]$ = particulate concentration $\left(\frac{mg}{l}\right)$

$$\sum_Y (n_Y * FR_Y * Z_{M_Y}) * S.A = V_{\text{filt}} \left(\frac{l}{\text{day}}\right)$$

13.2. Zebra mussel respiration excretes available phosphorus to the water column by:

$$V_{\text{water column}} Z_M AVP = \sum_Y \left(\phi_{T_{Z_M}} * \omega_r R_Y * \frac{200 \text{ mg C dwt}}{1 \text{ g wwt}} \right) * \frac{\text{mg P}}{\text{mg C}_{Z_M}}$$

14. Zebra mussel sediment impacts (Bierman et al. 2005)

Zebra mussel P and S egestion (defecation) is represented as a function of the volume of particulate phosphorus filtered:

$$14.1. \quad Z_M \text{SEDP} = \left[\left(\sum_i \frac{mg P}{mg C_i} A_i + Z_H \frac{mg P}{mg C_{Z_H}} \right) \right] + \left[\frac{\text{particulate TUP}}{\text{total TUP}} * TUP \right] * \frac{V_{filt}}{V_{sediment}}$$

$$14.2. \quad Z_M \text{SEDS} = \left[\sum_i \frac{mg Si}{mg C_i} * A_i \right] + \left[\frac{\text{particulate TUS}}{\text{total TUS}} * TUS \right] * \frac{V_{filt}}{V_{sediment}}$$

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