



Contents lists available at ScienceDirect

Journal of Great Lakes Research

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

Causes of phytoplankton changes in Saginaw Bay, Lake Huron, during the zebra mussel invasion

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ARTICLE INFO

Article history:

Received 22 July 2008

Accepted 20 April 2009

Index words:

Saginaw Bay

Phytoplankton

Zebra mussels

Dynamic modeling

Community composition

Invasive species

Microcystis

Phosphorus loads

ABSTRACT

Colonization of the Laurentian Great Lakes by the invasive mussel *Dreissena polymorpha* was a significant ecological disturbance. The invasion reached Saginaw Bay, Lake Huron, in 1991 and initially cleared the waters and lowered algal biomass. However, an unexpected result occurred 3 years after the initial invasion with the return of nuisance summer blooms of cyanobacteria, a problem that had been successfully addressed with the implementation of phosphorus controls in the late 1970s. A multi-class phytoplankton model was developed and tested against field observations and then used to explore the causes of these temporal changes. Model scenarios suggest that changes in the phytoplankton community can be linked to three zebra mussel-mediated effects: (1) removal of particles resulting in clearer water, (2) increased recycle of available phosphorus throughout the summer, and (3) selective rejection of certain *Microcystis* strains. Light inhibition of certain phytoplankton assemblages and the subsequent alteration of competitive dynamics is a novel result of this model. These results enhance our understanding of the significant role of zebra mussels in altering lower trophic level dynamics of Saginaw Bay and suggest that their physical re-engineering of the aquatic environment was the major force driving changes in the phytoplankton community composition.

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Introduction

The freshwater bivalve *Dreissena polymorpha* Pallas (the zebra mussel) became established in Lake St. Clair in 1986 and spread rapidly throughout the Laurentian watershed (Griffiths et al., 1991). The presence of zebra mussels indirectly alters a number of ecological functions in aquatic ecosystems (e.g., Heath et al., 1995; Vanderploeg et al., 2002; Miller and Watzin, 2007). Physical alterations of surrounding habitat include removing particulates from the water column, selectively consuming phytoplankton, and delivering previously suspended material to the benthos (Strayer et al., 1999; Vanderploeg et al., 2002). Removing particulates from the water column increases light availability (Holland, 1993). In Saginaw Bay, the 1992 zebra mussel populations were dense enough to theoretically clear the water of the inner bay in 2.6 day^{-1} (Fahnenstiel et al., 1995b), effectively overcoming phytoplankton growth. Mussels can directly alter nutrient recycling and nutrient availability, particularly the limiting nutrient P, through sequestering P in their body tissues and shells and release of nutrients in soluble

(Heath et al., 1995; James et al., 1997) and particulate (feces and pseudofeces) forms (Vanderploeg et al., 2002). Mussels may be regarded as homeostatic nutrient (P) excretors in that more soluble P will be released when feeding rate is high and P:C ratios in seston are high (Vanderploeg et al., 2002). In addition to direct effects on P recycling, P not only is shunted into the mussel body tissue but into the mussel associated benthic community, particularly benthic plants, making P less available to the pelagic community (Hecky et al., 2004; Vanderploeg et al., 2009). Altered nutrient cycling can also occur as the mussels release nutrients back to the water column. Zebra mussel colonies are also 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) as well as a deterioration of conditions for macroinvertebrates such as *Diporeia* (Nalepa et al., 2003). Collectively, these effects imply a capacity to significantly alter the ecology of the Saginaw Bay.

Nuisance summer blooms of *Microcystis* diminished following reduced phosphorus loads (Bierman et al., 1984) but are once again a problem throughout the Great Lakes following the widespread establishment of zebra mussels (Sarnelle et al., 2005). Multi-year analyses from the eastern basin of Lake Erie; the Bay of Quinte, Lake Ontario; Oneida Lake, New York; and the Hudson River suggest that significant changes in 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). A common occurrence in

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Great Lakes waters after zebra mussel invasions has been an increase in chroococcoid cyanobacteria (e.g., Makarewicz et al., 1999; Nicholls et al., 2002), some of which can form nuisance blooms that are potentially toxic to humans and other organisms. Renewed blooms in Saginaw Bay were first noted in 1994 by Lavrentyev et al. (1995) 3 years after the invasion by zebra mussels. Interestingly, *Microcystis* was a summer dominant in 1992 but did not occur at bloom levels (Vanderploeg et al., 2001). In Saginaw Bay, short-term experiments 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). Selective feeding behavior may explain these effects, although experimental results on selective feeding offer conflicting conclusions. Vanderploeg et al. (2001) demonstrated that mussels selectively rejected (toxic) colonies of *Microcystis* from Saginaw Bay and Lake Erie as loosely consolidated pseudofeces. The rejection process depended on the *Microcystis* occurring as colonies, which could be sorted out from other phytoplankton. Moreover, they demonstrated in experiments with laboratory cultures that only certain *Microcystis* strains were selectively rejected. Rejected strains included natural colonies from Saginaw Bay and Lake Erie and the LE-3 strain isolated from Lake Erie, whereas long-established laboratory strains from culture collections, including a strain known to be lethal to zooplankton, were readily ingested (e.g., Vanderploeg et al., 2001; Pires and Van Donk, 2002). The ready ingestion of naturally occurring *Microcystis* in some systems and of certain laboratory strains has led to the recognition of the importance of strain to the selective rejection process and controversy regarding the universality of the mechanism (Vanderploeg et al., 2001).

An analysis of the 1990–1996 Saginaw Bay phytoplankton community identified five assemblages in the period before, during, and after the zebra mussel invasion and suggested phytoplankton community stability from 1980 to 1990 but major changes followed the 1991 invasion (Fishman, 2008; Fishman et al., Submitted for publication). Three main changes were identified over the 7 years: (1) disappearance of light sensitive phytoplankton (filamentous cyanobacterium, *Limnothrix*) in the fall of 1991, (2) rise in dominance of centric diatoms (*Cyclotella* spp.) starting in 1992, and (3) return of summer blooms of *Microcystis* spp. and other colonial chroococcoid cyanobacteria such as *Aphanocapsa incerta* from 1994 to 1996. The changes in community composition were most apparent among the centric diatoms, pennate diatoms, filamentous cyanobacteria, and chroococcoid cyanobacteria. The phytoplankton community varied spatially along a eutrophication gradient from the inner to outer bay in a similar distribution as that described by Stoermer and Theriot (1985).

Our objectives were to adapt, modify, and apply a dynamic ecosystem model of the lower trophic levels of Saginaw Bay, Lake Huron, to explore the relative roles of zebra mussel filtration (both direct effects on algal mortality and indirect effects through alteration of light climate), selective feeding, and altered nutrient cycling in producing a novel phytoplankton community.

Model development

The model developed here is based on the Saginaw Bay multi-class phytoplankton model developed for the establishment of phosphorus point source controls for the Great Lakes (Bierman and Dolan, 1981; Scavia et al., 1981; Bierman and McIlroy, 1986). An updated model (Limno-Tech, 1995, 1997; Bierman et al., 2005) incorporated several important revisions, including coupling the phytoplankton model to a zebra mussel bioenergetics model and the addition of wind induced sediment resuspension rates and the division of nutrients into particulate and dissolved unavailable forms. The 1997 Limno-Tech model, plus a benthic algae component, was used by Bierman et al. (2005) to explore the role of zebra mussels and phosphorus loads in promoting Saginaw Bay summer cyanobacteria

blooms in 1991. This model and one other (Millie et al., 2006) have been used to explore the role of zebra mussels in Saginaw Bay. 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.

The original form of the Saginaw Bay multi-class model included three to five spatial segments within the inner bay (Bierman and Dolan, 1981). Our model was further simplified to reflect only the major physical, chemical, and biological changes observed in the inner and outer bays by considering a single horizontally and vertically mixed system for the inner Bay region using outer Bay data as boundary conditions. The conceptual model and external inputs are summarized in Fig. 1 and described in the following sections.

Field data in the outer bay, collected biweekly to monthly from multiple stations 1991–1995, were synthesized to monthly averages near the inner/outer bay boundary and used as boundary conditions for the inner bay model. While boundary exchange is important, generally the outer bay acts as a constituent sink. Water quality data were available from 1991 to 1996 and zebra mussel densities and phosphorus loads were available through 1995, so we limited our analysis to 1991–1995.

Equations describing physical transport (advective and diffusive), phytoplankton growth, biological recycling of nutrients, and grazing were adapted from Chapra (1997). The impacts of zebra mussels were explored by adding zebra mussel filtration and excretion effects estimated with a zebra mussel bioenergetics model outlined by Schneider (1992). To couple this bioenergetics model to the phytoplankton model, we used the set of equations describing the filtration of the water column outlined by Bierman et al. (2005) and represented zebra mussel populations as three individual cohorts with specified initial wet weights. The initial condition for an individual zebra mussel young-of-the-year was set to 6×10^{-6} g wet weight for each year in 1991–1995 (Bierman et al., 2005). For 1st and 2nd year cohorts, the simulated wet weight from the preceding year's simulation was used as an initial value. Reproductive losses, as a percentage of biomass, were assigned to the 1st and 2nd year mussel cohorts to calibrate to observed seasonal trends in biomass (Nalepa et al., 1995).

The model structure, based on the Limno-Tech (1997) model, is shown in Fig. 2. The structure was modified by eliminating nitrogen as a potential limiting nutrient, replacing equations to describe zooplankton dynamics, eliminating variable algal internal nutrient pools, and simplifying the physical transport equations (Fig. 2). All modifications were adapted from (Chapra, 1997) and the significant modifications are discussed below.

The basic model form is:

$$V \frac{dc}{dt} = -Qc + E'(c_{\text{Boundary}} - c_{\text{InnerBay}}) \pm Sc \quad (1)$$

where

c = constituent concentration

V = volume of the inner bay

Q = sum of flows into inner bay (tributary + outer bay)

E' = bulk diffusion coefficient

S = sources and sinks of constituent in the inner bay

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

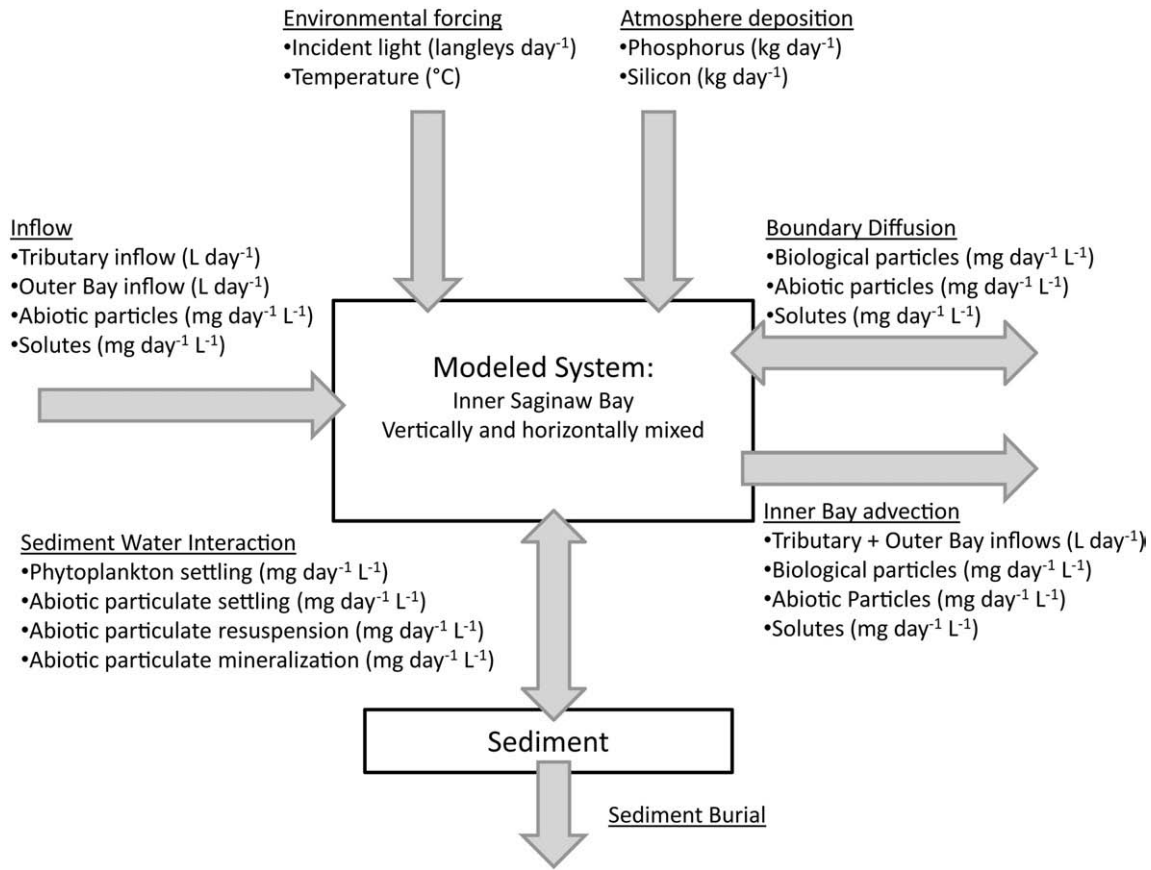


Fig. 1. Model system definition modified from Bierman et al. (2005). Arrows into and out of the modeled system box represent flows of mass entering or leaving the inner Saginaw Bay water column. Some flows, such as tributary inflow, are one-way interactions (single direction arrows), while the sediment water interaction and boundary diffusion (two sided arrows) can be positive or negative depending on the concentration gradients.

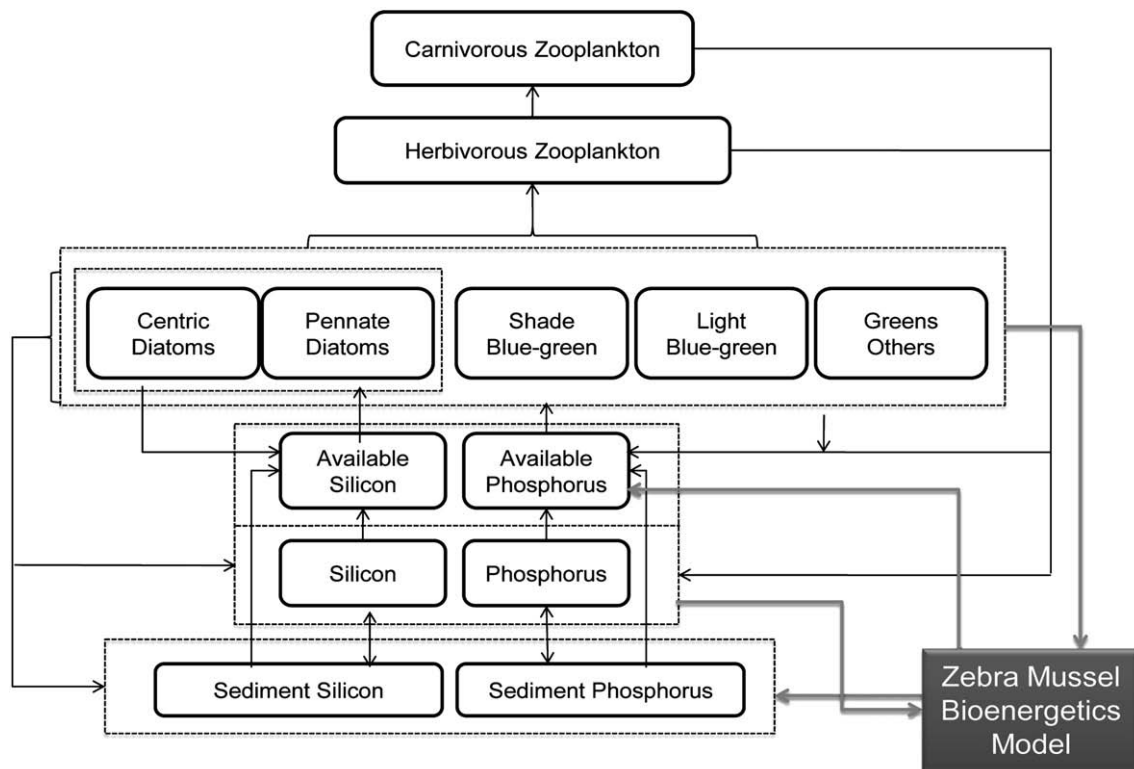


Fig. 2. Saginaw Bay multi-class phytoplankton model modified from Bierman et al. (2005). Boxes represent state variables, in mg L⁻¹. Arrows represent the connections between state variables, i.e., all phytoplankton variables both take up available phosphorus and excrete available phosphorus.

Primary production is modeled as a maximum growth rate modified by nutrient concentrations, available light, and temperature. Primary production of a specific phytoplankton group is described as:

$$P_i = \text{GMAX}_i * \phi T_i * \min(\phi I_i, \phi N_i) * A_i \quad (2)$$

where

- GMAX_i = maximum growth rate ($\frac{1}{\text{day}}$)
- ϕT_i = temperature effect on growth, $\theta_1^{(T_i - 20)}$
- θ_1 = rate coefficient for temperature
- ϕI_i = light effect on growth, $\frac{2.078f}{k_e Z} (e^{-\alpha_0 I_i} - e^{-\alpha_0 I_s})$
- k_e = underwater light extinction coefficient
- f = photoperiod
- Z = water column depth
- $\alpha_0 = \frac{I_a}{I_s}$
- I_a = available light
- I_s = saturation light
- $\alpha_0 I_i = \alpha_0 e^{-k_e Z}$
- θN_i = nutrient effect on growth, $\text{MIN} \left(\frac{S_i}{k_{Si} + S_i}, \frac{AVP}{k_{AVP} + AVP} \right)$
- K_{Si}, k_{AVP} = half saturation constant on silicon and phosphorus uptake
- A_i = phytoplankton of type i

To investigate the effects of zebra mussel clearance rates on the light climate, light extinction coefficients must be internally calculated by the model. A regression model was developed to predict underwater light extinction, k_e^* , based on modeled suspended particle concentrations. Field observations of 1991 light extinction coefficients, k_e , were used in the model calibration phase to generate suspended particle concentrations for 1991. The best model ($R^2 = 0.84$) to predict light extinction in 1991 was:

$$k_e^* = [0.2 * SS + 0.310]$$

where

SS = abiotic solids + phytoplankton (mg/L)

This regression was then used to generate light extinction parameters for the 1991–1995 model runs investigating zebra mussel impacts. Predicted light extinction in the default scenarios (with zebra mussel filtration) was compared to measured light extinction using ANOVA and no significant differences were found.

Biological uptake of available phosphorus by all phytoplankton groups and of available silicon by 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). Diatom silicon to carbon ratios vary from 0.03 to 2.5 mg Si/mg C (Bowie et al., 1985; Reynolds, 2006); we used 1.0 for centric diatoms and 1.5 for pennate diatoms.

We included herbivorous (generalized cladoceran/calanoïd grazer) and carnivorous (generalized cyclopoid predator) zooplankton in the model and growth rate was modeled as a maximum filtration rate reduced by assimilation efficiency, temperature, and available food:

$$Z_i Gr = \epsilon_{Z_i} * [FMAX_{Z_i} * \phi T_{Z_i} * \phi F_{Z_i} * C \frac{\text{mg}}{L}] * Z_i \quad (3)$$

where for herbivorous zooplankton:

- ϵ_{Z_H} = Assimilation efficiency
- $FMAX_{Z_H}$ = Maximum filtration rate ($\frac{L}{\text{mg day}}$)
- $\phi F_{Z_H} = \left[\frac{\sum_i a_i A_i}{k_A + \sum_i a_i A_i} \right]$
- α_i = electivity of zooplankton for phytoplankton A_i
- k_A = half saturation constant for feeding on phytoplankton ($\frac{\text{mg}}{L}$)
- C = total phytoplankton concentration
- Z_i = zooplankton of type i

for carnivorous zooplankton:

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

k_{Z_H} = half saturation constant for feeding on zooplankton
 C = herbivorous zooplankton concentration

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

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

Phytoplankton and zooplankton release available phosphorus to the water column at rates proportional to respiration and, for phytoplankton, cell death. Additionally, to maintain stoichiometry, diatoms also release available silicon in the same manner. In the model, the numerical expression for the total biological recycle is given by summing Eqs. (4), (5), and (6):

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

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

$$ZM_Y \text{ recycle} = ZMR_Y * \frac{200 \text{ mg C dwt}}{1 \text{ g ww}} * \frac{\text{mg P}}{\text{mg C}_{Z_M}} * \frac{\text{S.A.} * N_Y}{V_{\text{water}}} \quad (6)$$

where

- R_i, D_i = phytoplankton respiration and decomposition
- $\frac{\text{mg P}}{\text{mg C}_i}$ = specific phosphorus to carbon ratio phytoplankton type i
- ZR_i = zooplankton respiration
- ZMR_Y = zebra mussel respiration in g wet weight
- Y = age cohort
- N = zebra mussels per m^2
- S.A. = surface area of inner Saginaw Bay substrate
- V_{water} = volume of inner Saginaw Bay

The conceptual model (Fig. 2) shows the interaction of the zebra mussel bioenergetics model with the multi-class phytoplankton model. The zebra mussel model simulates growth and respiration of a single zebra mussel in a particular age cohort. While model results were used with field observations from Nalepa et al. (1995) to set initial cohort wet weights for the 1992–1995 scenarios, the model does not predict changes in zebra mussel densities (mussels per m^2); these are supplied external to the model (see Table 4).

The model was programmed in STELLA, and for each of the five 365-day simulations (January 1, 1991 to December 31, 1995), the model produces daily changes in concentrations of 15 state variables (chloride and abiotic suspended solids are not shown). The fourth order Runge–Kutta method was used to solve the equations.

Saginaw Bay environmental conditions

Daily values for each of the external drivers described in Fig. 1 were calculated from field data collections from 1991 to 1995 or adapted from previous modeling applications. In cases where daily values could not be calculated, linear interpolations between data points were used, as described below.

Inflow

Daily mean river flows were estimated from gage data published on the U.S. Geological Survey website <http://waterdata.usgs.gov/nwis/sw>. River inflow to the inner bay from tributaries is primarily from the Saginaw River, so a daily tributary inflow time series was

developed using the Saginaw River flows (Fig. 3). Because data for the Saginaw River were not available for the entire period, those flows were estimated with flow from its tributaries. The four major tributaries to the Saginaw River are the Cass, Flint, Shiawassee, and the Tittabawassee rivers (Table 1).

USGS gage data for daily mean flow were not recorded in the Flint and Cass rivers for the entirety of 1991–1995, so to replace missing values, daily flows were modeled where necessary using flow data from adjacent tributaries. After the confluence of these four major tributaries, the Saginaw River continues for several miles before reaching Saginaw Bay; to represent this unengaged reach, the summed flows of the tributaries were increased by 30%, following the methodology of Bierman et al. (2005). The Saginaw River represents about 75% of the average mean tributary inflow to Saginaw Bay in most years. To represent the tributary inflow of numerous smaller rivers, streams, and drains, the estimated Saginaw River daily mean flows were increased by 25%.

Advective inflow from the outer bay was characterized on a monthly basis for previous modeling applications by Bierman and Dolan (1981). We assumed that there was little change in the hydrodynamics of the bay and used these estimates.

Temperature and light

Temperature data from NOAA inner bay samples were used to establish monthly averages (Table 2). We assumed that incident photosynthetically active radiation did not vary year to year and used a time series developed for earlier modeling applications by Bierman and Stoermer (1980). Underwater light extinction, k_e , was not measured every year; however, the tight relationship between Secchi depth and extinction in Saginaw Bay was used to estimate it in years when it was not measured. It is important to recall at this point that externally specified observations of k_e did not drive the model; rather, they were used to develop a submodel to predict k_e based on internally predicted suspended particle concentrations.

External loads

Annual total phosphorus loads (both available and total phosphorus) were calculated through 1995 by Bierman et al. (2005). We used daily flow rates to prorate the loads to daily values. Using those daily loads for available phosphorus for 1991 and daily loads for total silicon, chloride, and abiotic suspended solids from Limno-Tech (1997), relationships between available phosphorus daily loads and other water quality parameters were established through regression analysis. For 1991 loads, loads predicted using the regression analysis results were compared to those calculated by Limno-Tech using both ANOVA tests and qualitative time series comparisons. There were no significant differences between the loads, and the peak and base values were comparable (Fishman, 2008). The regression equations were used to calculate daily loads of silicon, chloride, and abiotic particles from 1991 to 1995. Available silicon loads were assumed to be half the total silicon loads. The annual mean loads used in the model for total phosphorus (TP), dissolved phosphate phosphorus

Table 1
Saginaw River tributaries annual mean daily flow, in cubic meter per second (CMS) from USGS gage data.

Year	Cass	Flint	Shiawassee	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

Saginaw flows are the sum of the tributaries * 1.3.

* Calculated using the regression models.

Table 2
Average temperature and Secchi disk depth of inner Saginaw Bay in °C calculated from the NOAA GLERL water quality survey.

	Temperature (°C)					Secchi depth (m)				
	1991	1992	1993	1994	1995	1991	1992	1993	1994	1995
April	8.5	4.2	7.5	6.7	*	0.75	1.97	1.75	2.43	*
May	13.5	12.0	13.3	*	11.2	0.87	2.08	2.40	*	3.09
June	22.7	18.8	19.0	17.3	18.9	1.71	2.15	4.48	3.14	3.00
July	23.5	20.8	21.6	22.2	23.4	1.63	2.33	3.32	1.76	1.50
August	22.3	21.7	20.7	20.4	24.1	1.11	1.71	2.61	1.74	1.44
September	21.8	18.9	19.7	19.3	19.7	1.62	1.51	2.33	1.49	1.28
October	12.0	14.2	12.0	14.1	10.1	1.86	1.51	1.85	1.88	1.25

* Months without samples.

(AVP), total silicon (TS), and dissolved silicate silicon (AVS) are shown in Table 3.

Advective and diffusive transport

Advective and diffusive exchanges across the inner/outer bay boundary were calculated for all state variables in the model based on observed water quality and phytoplankton data. Advective outflow was modeled as the inner bay concentration times the sum of the tributary and advective inflow from the outer bay (see Fig. 1). To describe diffusive transport, the bulk diffusion coefficient E' was calculated by using measurements of the conservative substance chloride. Following the methods for calculating diffusive transport described by Chapra (1997), diffusive transport was calculated using Saginaw Bay chloride loads and concentrations. 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 the diffusion coefficient times the difference in the constituent concentration between the outer and inner bay.

Boundary conditions and validation points for the other water quality parameters were calculated using NOAA field data from the selected inner and outer bay stations (see Fig. 4). Zooplankton boundary conditions were used from Limno-Tech (1997) and inner bay validation points were used from Bridgeman et al. (1995). Water quality data are from Nalepa et al. (1996) and Johengen et al. (2000). These data were most recently summarized by Millie et al. (2006). Additional data summaries and interpretations of zebra mussel biomass and reproductive timing were drawn from Nalepa and Fahnenstiel (1995) and Bierman et al. (2005). Zebra mussel data are from Nalepa et al. (1995).

Phytoplankton data are from Vanderploeg (unpublished). See Fahnenstiel et al. (1998) for a general description of the sampling

Table 3
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 et al. (2005).

Nutrient	1990	1991	1992	1993	1994	1995
AVP	548	734	423	370	649	357
TP	1386	3140	1669	1984	2578	1588
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

Abbreviations: AVP, dissolved phosphate phosphorus; TP, total dissolved and particulate; AVS, dissolved silicate silicon; TS, total particulate and dissolved silicon.

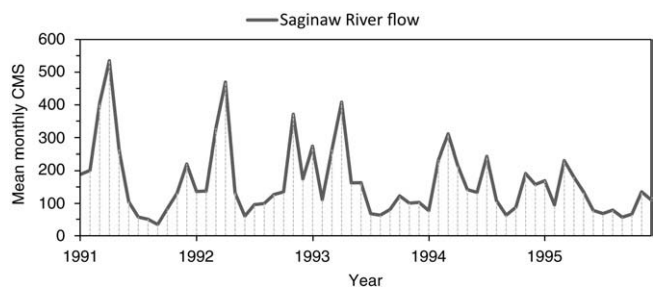


Fig. 3. River inflow to inner Saginaw Bay. Daily mean flows are summarized as monthly mean flow in cubic meters per second (CMS).

methodology. Phytoplankton boundary conditions and inner bay validation points were calculated as biovolume for each group (Fishman, 2008; Fishman et al., Submitted for publication). Assuming a specific density of 1.27 and dry weight as 10% of wet weight

(Chapra, 1997), biovolume was converted to dry weight 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 was grouped into five groups: centric diatoms (e.g., *Cyclotella comensis* and *Aulacoseira ambigua* (=italica)), pennate diatoms (e.g., *Fragilaria crotonensis* and *Asterionella formosa*), filamentous cyanobacteria (e.g., *Oscillatoria redekei* (=Limnothrix redekei)), colonial chroococcoid cyanobacteria (e.g., *Microcystis aeruginosa* and *A. incerta* and *Gomphosphaeria lacustris*), and all others (including chlorophytes, cryptophytes, chrysophytes, pyrrophytes, and protozoan flagellates). These groups are an adaptation of the five phytoplankton groups used in the original multi-class phytoplankton model of Saginaw Bay (Fig. 2). However, to use the description of the five community assemblages from 1990 to 1996, there are important differences and the resulting groups are a hybrid of the previous model groups and the newly identified assemblages. Ecological affinities for each group were parameterized using values from the previous modeling

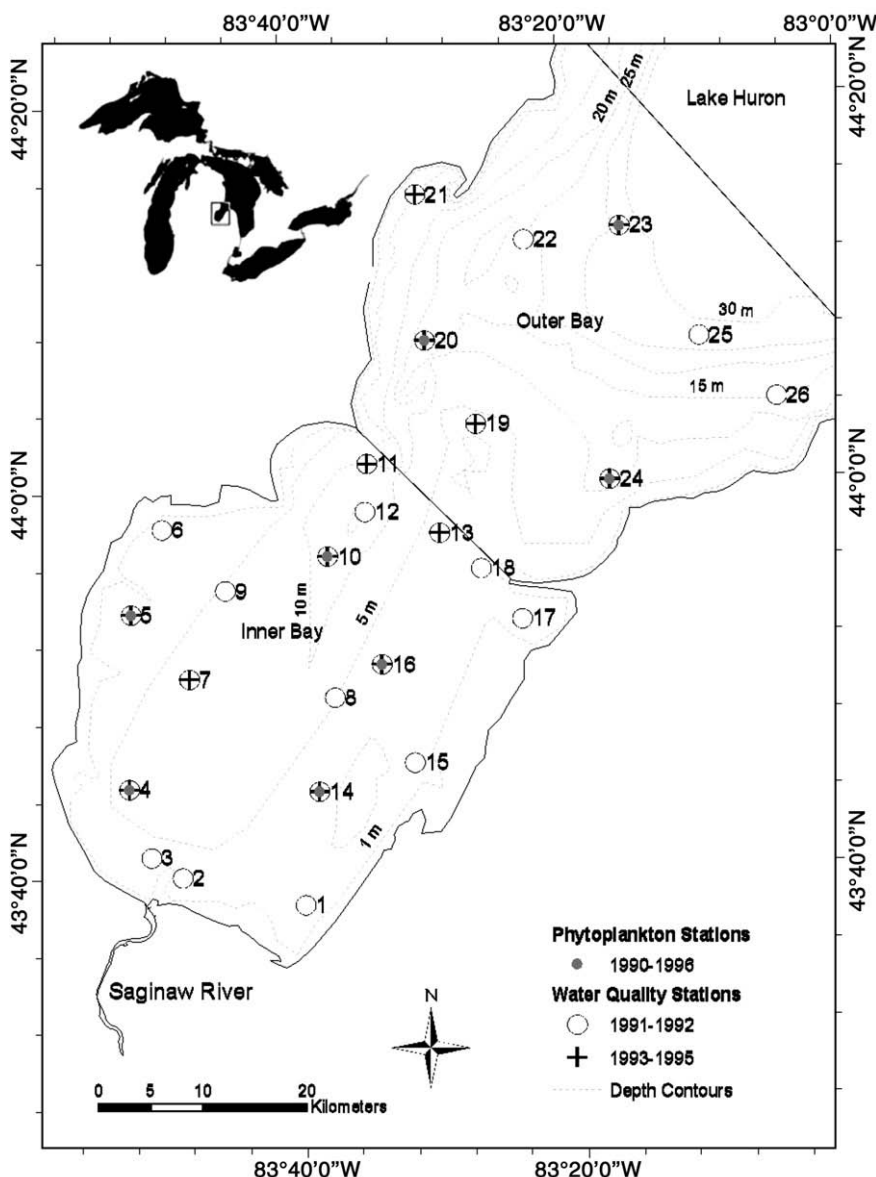


Fig. 4. Location of selected phytoplankton and water quality sampling sites in Saginaw Bay, Lake Huron, from NOAA GLERL monitoring 1990–1996. In 1991 and 1992, water quality data were collected approximately monthly, April–October, at 18 inner bay stations. In subsequent years, data were collected at eight inner bay stations. Phytoplankton data were collected approximately monthly at five inner bay stations, 1990–1996. For both water quality and phytoplankton, not all stations were visited in a given month due to weather. See Nalepa et al. (1996) and Johengen et al., 2000 for complete sampling details.

Table 4
Yearly zebra mussel densities (# m⁻² of inner bay bottom surface area).

	1991	1992	1993	1994	1995
YOY	1184	1434	205	1843	309
1st	0	1925	429	1688	684
2nd	0	0	455	432	158

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.

applications and interpretations drawn from literature on cyanobacteria (Komarek and Anagnostidis, 1999; Komarek et al., 2003) and diatoms (Reynolds et al., 2002; Reynolds, 2006), taxonomy, and environmental associations. Additionally, nitrogen fixing cyanobacteria such as *Aphanizomenon flos-aquae* were not common in Saginaw Bay from 1991 to 1995, so they were not included in the model (Fig. 2).

Zebra mussel population structure and density data were adapted from Nalepa et al. (1995) (Table 4). Population structure was calculated by separating the zebra mussel population into three cohorts based on shell lengths. To calculate bay-wide population density, weighted averages were used to balance differential zebra mussel densities on hard and soft substrate (Bierman et al., 2005) and were provided by V. Bierman (personal communication).

Results

1991 calibration

A more robust calibration is obtained from not only comparing model and observed state variables but also comparing modeled and observed process rates (Scavia, 1980). The model was calibrated to phytoplankton biomass, productivity, and zooplankton grazing in 1991 using coefficients in Tables 5 and 6. The estimated diatom spring bloom (0.25 mg L⁻¹) and June minimum (0.05 mg L⁻¹) are overestimated, but given the uncertainty in interpreting field data and model simplifications, the overall predicted biomass is within reasonable ranges (Fig. 5a).

Modeled daily algal production, calculated as algal growth times algal concentration divided by water column depth, was compared to observed estimates (Fahnenstiel et al., 1995a). Our estimated daily primary production corresponds roughly to the ranges in field estimates, with modeled peak production reaching 600 mg C m⁻² day⁻¹ between July and August (Fig. 5b).

For phytoplankton, model results generally matched peak field values but were overall smoother than the field data. In 1991, simulated phytoplankton biomass was mostly centric diatoms (annual mean = 0.24 mg L⁻¹). Simulated pennate diatom biomass was higher

in the spring and fall (annual mean = 0.04 mg L⁻¹). Simulated biomass for the “others” group did not contribute a large fraction of the biomass. In spring, model results tended to underestimate phytoplankton biomass (Figs. 6 and 7) and overestimate nutrient concentrations (Fig. 8). Cyanobacteria biomass was generally minor because of the small cell sizes. Additionally, calculated light extinction values compare favorably with 1991 observations (Fig. 9), with simulated values highest in spring (~2.4 m⁻¹) and lowest in summer (~0.65 m⁻¹).

Zooplankton data from Bridgeman et al. (1995) include mean May–August biomass by division, seasonal total biomass, and June herbivory (mg algal C grazed m⁻³ day⁻¹). Herbivorous zooplankton grazing is calculated as herbivore filtration rate multiplied by zooplankton concentration and algal concentration, and while comparing model output to these field data is limited in scope by the narrow time periods for observations, the model compares reasonably to the calculated field data. Mean simulated June biomass (194.6 mg m⁻³) is lower than biomass estimated from field samples collected at eight locations throughout inner Saginaw Bay (Table 7). Mean simulated June herbivory (48 mg C m⁻³ day⁻¹) is higher than observed; however, field measurements were only collected at two sample stations (Table 7).

1992–1995 simulations

We used the calibrated model to explore the influence zebra mussels on lower trophic level dynamics from 1992 to 1995. Using the same coefficients from the 1991 calibration and loads, boundary conditions, temperatures, and zebra mussel densities from 1992 to 1995 field data, we simulated total phytoplankton biomass for 1992–1995 (Fig. 10). Simulations corresponded closely to the field data for 1992 (Fig. 10a) and tended to overestimate spring and coincide with summer biomass in 1993 (Fig. 10b) and overestimate values in 1994 and 1995 (Fig. 10c and d). For expediency, detailed reporting of phytoplankton group-specific comparisons of model output to field observations for 1992–1995 is not shown; however, a summary of observed community composition in 1992 and 1994 as biomass of the five phytoplankton groups is shown in Fig. 11. Process field data were not available at the same level of detail in the later years, but where possible, these were also considered and found to be within similar ranges as those reported for the calibration results. Therefore, we judged the model sufficiently tested to explore additional scenarios.

To analyze the potential effects of zebra mussels on seasonal phytoplankton community composition, the model was run with zebra mussels “switched on” and “switched off”. The change in biomass of each phytoplankton group without zebra mussels present in the system was calculated and displayed as the predicted difference in monthly average dry weight (Fig. 12). There was little

Table 5
Phytoplankton parameters.

Coefficients	Definition	Units	Phytoplankton parameters					Source
			Centric	Pennate	Others	Shade	Light	
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 C/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
ZSELECT	Zooplankton electivity	unitless	1.0	1.0	1.0	0.2	0.2	Bierman and Stoermer, 1980

Table 6
Zooplankton parameters.

Coefficients	Definition	Units	Zooplankton parameters		Source
			Herbivore	Carnivore	
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	?

effect with and without zebra mussels in 1991 mean phytoplankton biomass (0.5 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 (Fig. 12a).

In 1992, mean phytoplankton biomass was 0.30 mg L^{-1} higher without zebra mussels (Fig. 12b). Higher pennate diatom was predicted in spring and summer and higher centric diatom biomass was predicted throughout summer and fall. Lower *Microcystis* (i.e., the chroococoid type cyanobacteria group) biomass was predicted in summer. Mean primary production in 1992 with zebra mussels was $92 \text{ mg C m}^{-2} \text{ day}^{-1}$; without zebra mussels it was $275 \text{ mg C m}^{-2} \text{ day}^{-1}$, compared to measured values of $30\text{--}300 \text{ mg C m}^{-2} \text{ day}^{-1}$ (Fahnenstiel et al., 1995a,b).

With zebra mussels, 1994 predicted mean biomass of total phytoplankton was 0.1 mg L^{-1} higher without zebra mussels (Fig. 12c). Similar to 1992, more pennate diatom biomass was predicted in spring and summer and more centric diatom biomass was predicted in summer and fall. Summer *Microcystis* spp. blooms in inner Saginaw Bay were noted in 1994 by Lavrentyev et al. (1995) and simulated in model runs with zebra mussels. In August, *Microcystis* (i.e., the chroococoid type cyanobacteria group) biomass was sharply lower without zebra mussels. Simulated 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.

In both 1992 and 1994, modeled zebra mussels had a strong impact on phytoplankton community composition. With zebra

mussels, pennate diatoms diminished earlier in spring and chroococoid cyanobacteria (i.e., *Microcystis* spp.) were important in summer. Without zebra mussels, pennate diatoms persisted through August and *Microcystis* was not present (Fig. 12b and c).

Effects of selective rejection of Microcystis

In the model, zebra mussels were assumed to selectively reject the chroococoid type cyanobacteria group (i.e., *Microcystis* spp.) and eject viable cells back to the water column in pseudofeces. The 1992 peak predicted cyanobacteria biomass was 0.04 mg L^{-1} , estimated peak field biomass was 0.026 mg L^{-1} , and community composition was of 45% cyanobacteria through parts of the summer. In 1994, peak predicted biomass was 0.085 mg L^{-1} compared to peak field biomass of 0.052 mg L^{-1} , and the community was composed of 50% cyanobacteria biomass. In 1992 and 1994, the selective rejection assumption was tested by running the model with zebra mussels present but with selective rejection of the chroococoid type cyanobacteria group eliminated. In that scenario, peak *Microcystis* (the chroococoid type cyanobacteria group) biomass decreased by 0.03 mg in 1992 (Fig. 13a) and by 0.07 mg in 1994 (Fig. 13b).

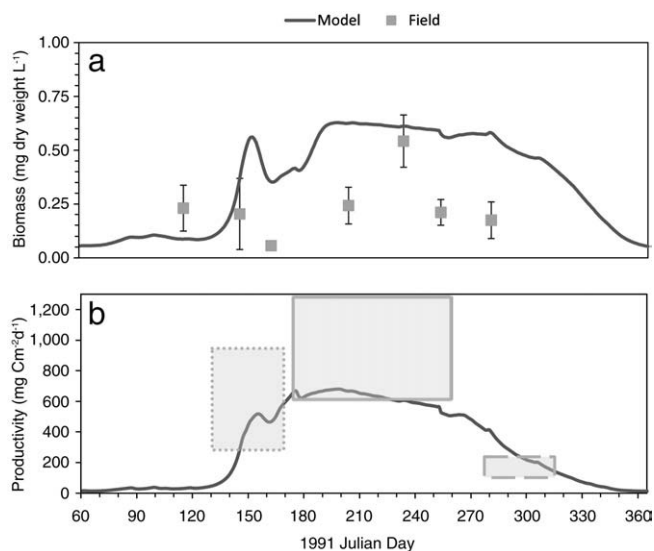


Fig. 5. Total (a) phytoplankton biomass and (b) primary productivity. Comparisons are of the selected NOAA GLERL field samples from the inner bay in 1991 to the model output. For (a), error bars on biomass data represent the standard error of the mean. For (b), the grey boxes represented for primary production are redrawn from Fahnenstiel (1995a), 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.

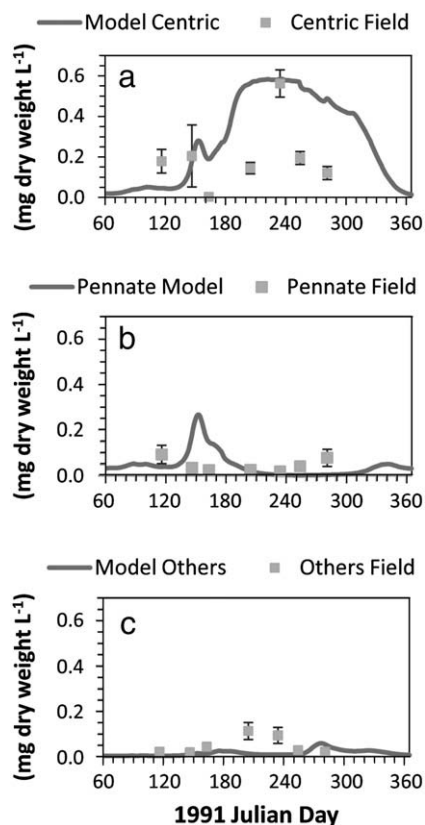


Fig. 6. 1991 predicted (a) centric diatoms, (b) pennate diatoms, and (c) "others" biomass ($\text{mg dry weight L}^{-1}$) compared to the selected NOAA GLERL samples.

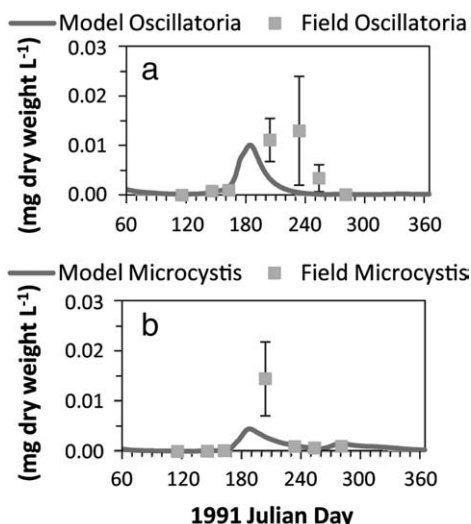


Fig. 7. 1991 predicted (a) *Oscillatoria* (i.e., filamentous cyanobacteria) and (b) *Microcystis* (i.e., chroococcoid cyanobacteria) biomass (mg dry weight L⁻¹) compared to the selected NOAA GLERL samples.

Effects of altered light

We explored the potential role of increased water clarity by examining the effects of zebra mussel filtering on the underwater light regime. Zebra mussels have the potential to filter the entire water column of Saginaw Bay daily (Fanslow et al., 1995), and the model predicted that this filtration would significantly reduce total suspended solid (abiotic solids+phytoplankton dry weight) concentration. In both 1992 and 1994, this effect was similar: from May to October, zebra mussels were responsible for a greater than 50% decrease in total suspended solid concentration.

Increasing water clarity through this substantial increase in filtration should affect competition among phytoplankton groups. Filamentous cyanobacteria, such as the shade tolerant *O. redekei*,

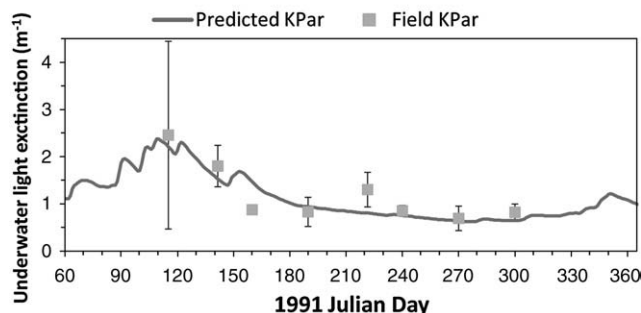


Fig. 9. Monthly mean underwater light extinction from the 1991 NOAA GLERL inner Saginaw Bay sample sites compared to submodel predicted extinction.

were important components of the phytoplankton community in 1980 through the spring of 1991 but were absent in fall 1991 through 1996 (Stoermer and Theriot, 1985; Fishman et al., Submitted for publication). In 1992, as in 1980, 1990, and 1991, the pennate diatoms (i.e., *A. formosa* or *Fragilaria crotonensis*) were an important component of the modeled early spring community. However, in a significant change from 1991, this low-light tolerant group disappeared from modeled community midway through May of 1992. In the model, phytoplankton growth is a function of both light and nutrients, calculated using Eq. (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 5).

The growth limiting factors were examined for pennate diatoms in 1992 with and without zebra mussels. Because total suspended solid concentration is strongly related to light extinction, zebra mussel filtration lowered the light extinction coefficient (Fig. 14), and the resulting high-light environment inhibited growth of pennate

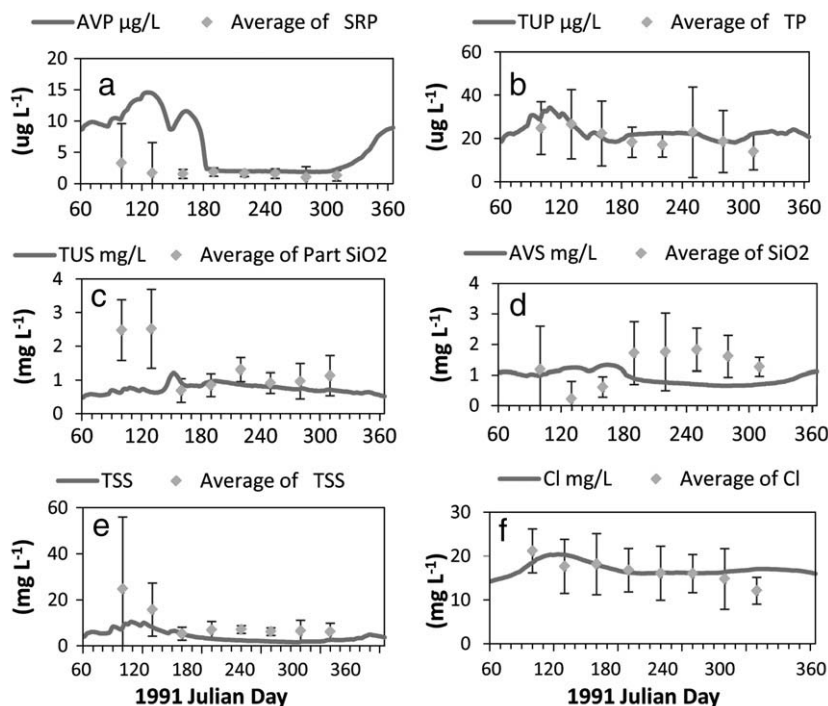


Fig. 8. 1991 model predicted and solute concentrations in inner Saginaw Bay compared with monthly mean field data from the NOAA GLERL samples. Brackets represent the standard error of the mean. (a) Dissolved available phosphorus (μg L⁻¹). (b) Total unavailable phosphorus (μg L⁻¹). (c) Dissolved available silicon (mg L⁻¹). (d) Total particulate silicon (mg L⁻¹). (e) Total suspended solids (mg L⁻¹). (f) Chloride (mg L⁻¹).

Table 7

Inner Saginaw Bay monthly mean total zooplankton biomass (mg m^{-3}) and phytoplankton carbon grazed ($\text{mg C m}^{-3} \text{ day}^{-1}$) by herbivorous zooplankton in 1991.

	Field data		Model results		
	Total zooplankton (mg m^{-3})	Grazing rate ($\text{mg C m}^{-3} \text{ day}^{-1}$)	Herbivore (mg m^{-3})	Carnivore (mg m^{-3})	Grazing rate ($\text{mg C m}^{-3} \text{ day}^{-1}$)
April	n/a	n/a	13	0.26	0
May	240	n/a	16	0.07	1
June	220	18	193	1.59	48
July	20	n/a	145	116.62	51
Aug	60	n/a	118	119.81	46
Sept	n/a	n/a	111	99.1	37
Oct	n/a	n/a	101	57.94	19
Mean	130	18	100	56.43	29

Field data are reproduced from Bridgeman et al. (1995) and assumes 50 mg C/mg Chl A.

diatoms from May to August (Fig. 15). In the scenario without zebra mussels (resulting in more turbid waters), both groups were phosphorus (as opposed to light) limited and, because pennate and centric diatoms had the same phosphorus limitation factor, this gave less competitive advantage to the centric diatom group and forestalled seasonal succession.

Effects on phosphorus cycling

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 were lower in 1993. Zebra mussels excrete high levels of available phosphorus (Johengen et al., 1995; James et al., 1997) depending on feeding rates and P:C ratios in seston (Vanderploeg et al., 2002) and this 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).

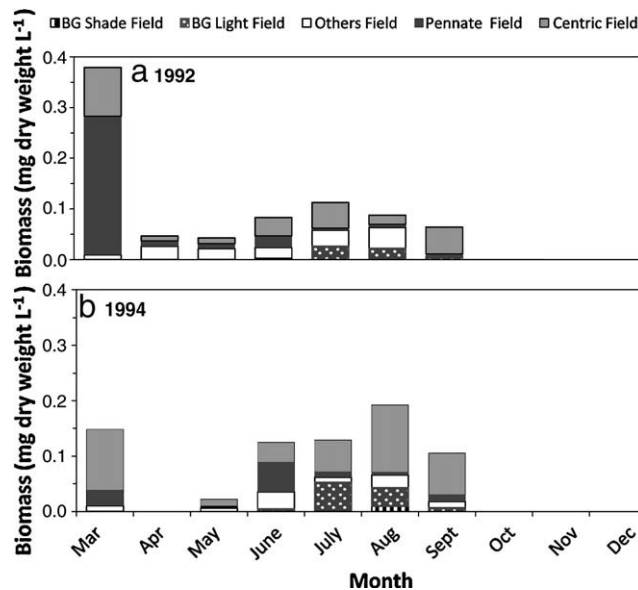


Fig. 11. Phytoplankton community composition ($\text{mg dry weight L}^{-1}$) in (a) 1992 and (b) 1994 calculated from the selected NOAA GLERL collections from inner Saginaw Bay. BG Shade are filamentous cyanobacteria (i.e., *Oscillatoria*) and BG Light are chroococcoid cyanobacteria (i.e., *Microcystis*).

Using the model results from the 1991 calibration (zebra mussels present and selectively rejecting the chroococcoid group), simulated daily phosphorus excretion was examined for 1992, 1993, and 1994 (Fig. 16). Recycle rates were highest in 1994 and lowest in 1993. In 1992 and 1994, zebra mussel recycling was on average 24% of the recycled daily total available phosphorus. In 1993 this average was 2%. Older, larger mussels in 1994 contributed a disproportionate amount to the phosphorus recycle compared to 1992 and 1993 (Table 8). Available phosphorus tributary loads would have to be reduced by 75% to overcome the increased

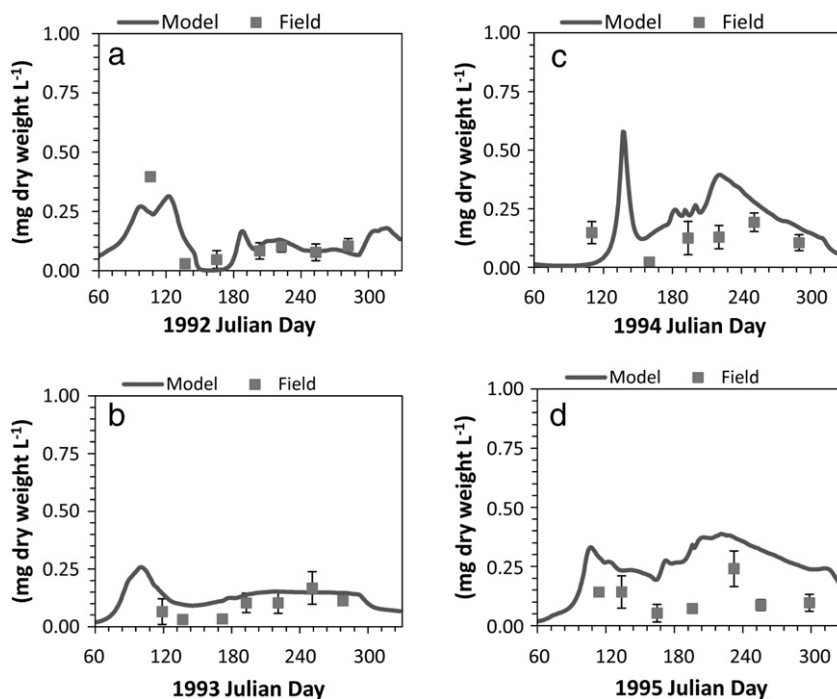


Fig. 10. Total phytoplankton biomass from the selected NOAA GLERL collections from inner Saginaw Bay compared to the model output for (a) 1992, (b) 1993, (c) 1994, and (d) 1995. Brackets represent standard error of the mean.

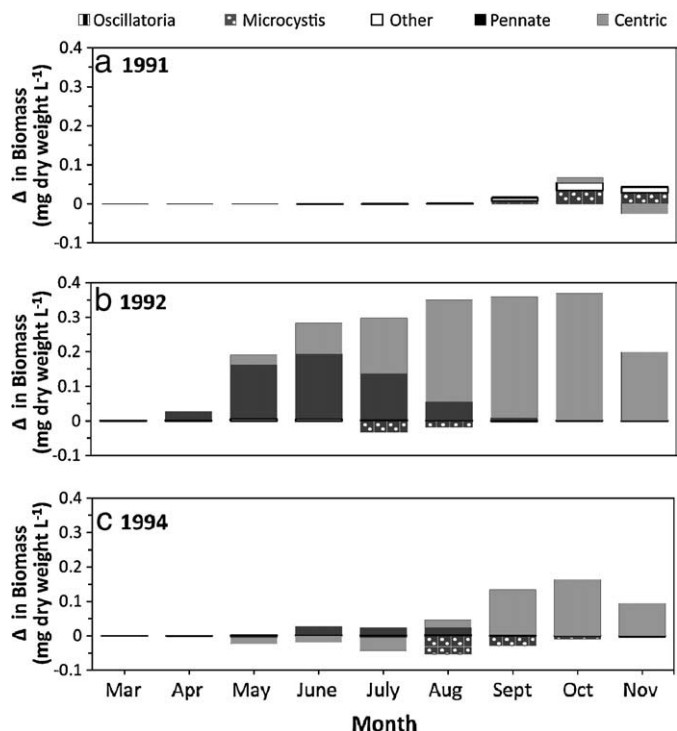


Fig. 12. The change in phytoplankton biomass by community group without zebra mussels present is shown (switched “off”). Model scenarios were run with zebra mussels turned “on” and “off” and the average monthly difference in biomass by phytoplankton group was calculated for (a) 1991, (b) 1992, and (c) 1994.

available phosphorus provided by zebra mussel recycle and prevent summer cyanobacteria blooms in 1994 (Fig. 17).

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., increased water clarity) were examined with a model of nutrient, phytoplankton, and zooplankton coupled with output from a zebra mussel bioenergetics model. Using environmental forcing data from 1991 to 1995, the model predicted significant changes in the ecosystem structure of inner Saginaw Bay consistent

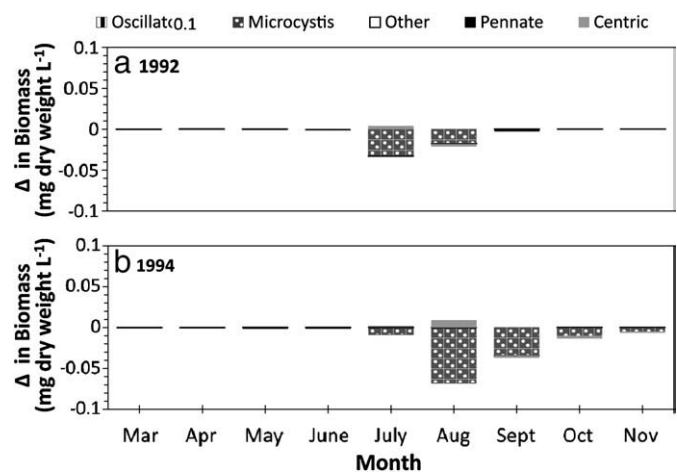


Fig. 13. The change in phytoplankton biomass by group without selective rejection of *Microcystis* by zebra mussels shown. Model scenarios were run with selective rejection “on” and “off” and the average monthly difference in biomass by phytoplankton group was calculated for 1992 and 1994.

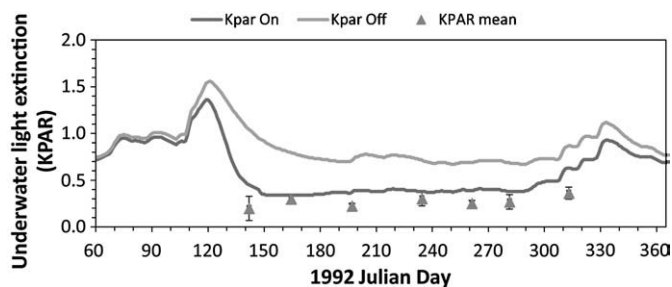


Fig. 14. Predicted underwater light extinction coefficient k_e^* or Kpar (m^{-1}) with zebra mussels “on” and “off” compared to the monthly mean estimated values from NOAA GLERL field k_e or KPAR samples in 1992 (after zebra mussel colonization).

with previously reported observations of increased water clarity (Fahnenstiel et al., 1995b), altered nutrient levels (Johengen et al., 1995; Raikow et al., 2004), and the onset of summer algal blooms after several years (Vanderploeg et al., 2001). The model simulations also support conclusions of previous experimental and modeling efforts that selective rejection could promote intense summer blooms of cyanobacteria (Bierman et al., 2005).

Filtration effects had a clear impact on phytoplankton community composition. Predicted suspended solid concentrations were 50% lower with zebra mussels and, in zebra mussel scenarios for 1992 and 1994, total phytoplankton biomass was lower with zebra mussels than without. In addition to lower total biomass, our results show three major changes in phytoplankton community composition following the initial zebra mussel invasion in fall 1991: (1) disappearance of shade tolerant filamentous cyanobacteria in the same year as the invasion, (2) transition in 1992 away from a May–June pennate diatom dominated community and towards a centric diatom dominated community, and (3) onset of summer blooms of the colonial cyanobacterium *Microcystis*.

Three key mussel-mediated changes were identified: (1) increased water column clarity via removal of suspended solids, (2) increased dissolved available phosphorus recycling, and (3) promotion of certain types of algal groups via selective feeding. By running test scenarios as the zebra mussel invasion progressed and the population structure stabilized, a more complete picture of the causes of observed changes in the phytoplankton community emerged. These results agree with suggestions from previous modeling work that altered nutrient cycling and selective rejection of cyanobacteria were important factors. Modeled selective rejection (Vanderploeg et al., 2001) predicted that this behavior was necessary in promoting blooms of cyanobacteria in 1992, 1994 (Fig. 12), and 1995 (results not shown). In addition, modeled zebra mussel phosphorus excretion is weight dependant (Schneider 1992), and thus, the presence of older, larger mussels in 1994 (see Table 4) enhanced phosphorus recycling (Table 8). To fully diminish the cyanobacteria blooms, our model suggests that a 75% reduction in 1994 phosphorus tributary loads would be needed to compensate for the increased recycling by zebra

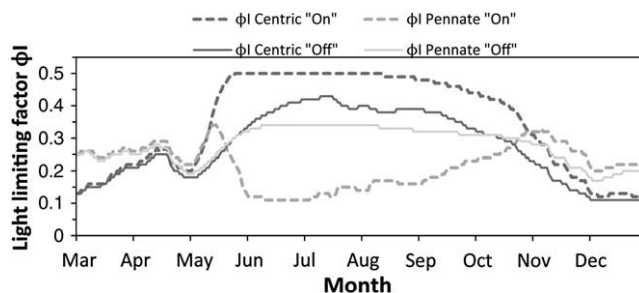


Fig. 15. 1992 predicted light limitation of growth (ϕ) of the centric and pennate diatom groups with and without zebra mussels (“on” and “off”).

Table 8
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%

mussels. 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 8). An important advancement by this effort is the simulation of the 5-year transition in phytoplankton community composition captured in the field data.

A novel result from our model is that zebra mussel filtration influenced the competitive balance among diatom groups by altering the light environment. Bierman and 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 vary among diatom taxa. 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 and 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 (Nicholls et al., 2002; 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 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 (Fishman, 2008; Fishman et al., Submitted for publication), the driving forces appear to be different. Mean silicon concentrations from April to June were variable in inner Saginaw Bay from 1991 to 1995. However, spring light extinction sustained a 40% decrease from 1991 to 1992–1995. Following the zebra mussel invasion, successively greater light adapted centric diatom species (first *C. comensis* 1992–1993 then *C. ocellata* 1994–1996) typical of Lake Huron waters became more

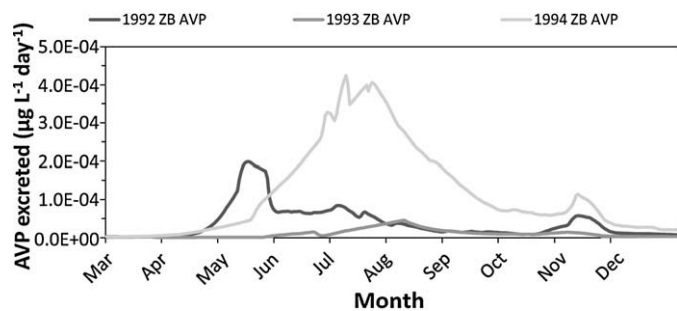


Fig. 16. Predicted available phosphorus recycle ($\mu\text{g L}^{-1} \text{day}^{-1}$) from zebra mussel excretion in 1992, 1993, and 1994.

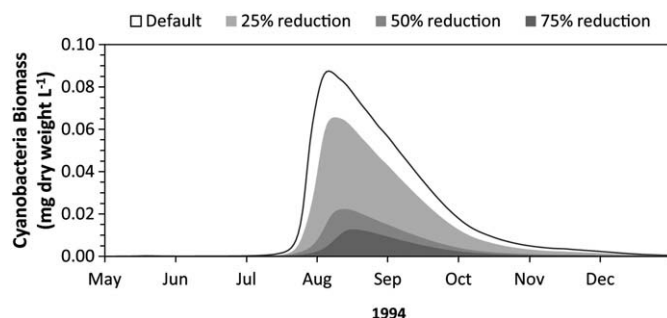


Fig. 17. The effect of successive phosphorus load reductions scenarios on 1994 predicted cyanobacteria biomass.

prevalent in inner Saginaw Bay in combination with chroococcoid cyanobacteria, while the spring dominance of pennate diatoms such as *F. crotonensis* diminished (Fishman, 2008; Fishman et al., Submitted for publication). These results suggest that the diatom community, which was likely stable from 1980 to 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. The model identified both abiotic (increased light penetration) and biotic (nutrient cycling and selective feeding behavior) factors as important in driving 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. Impacts on water clarity are system and substrate dependant. Water clarity did not increase in the western basin of Lake Erie after the invasion of the zebra mussel (Makarewicz et al., 1999) likely because of high concentrations of easily resuspended, silty substrate that are unaffected by mussel feeding (Vanderploeg et al., 2002).

The overall response to the zebra mussel invasion suggests that complex interactions between top-down pressures such as grazing and bottom-up controls such as limits to growth on the phytoplankton community produced a novel community in Saginaw Bay. At first, with the ramp up of mussel biomass, there was an extreme drop in chlorophyll throughout the year, which ultimately changed to an extended clear water phase during the spring and nuisance blooms of *Microcystis* during summer (Vanderploeg et al., 2001, 2002). In addition to showing that selective rejection is an important mechanism in driving development of *Microcystis* blooms in the bay as advocated by experimental work of Vanderploeg et al. (2001, 2002) and the model of Bierman et al. (2005), we demonstrated that changes in light climate and nutrient recycling are important drivers of changes in species composition. Interestingly, *Microcystis* was an important dominant during 1992 but did not attain bloom concentration (Vanderploeg et al., 2001) until 1994. Was this because mussel grazing was so intense that even if most *Microcystis* was rejected, the population was knocked down? Also, given the importance of *Microcystis* strain to the selective rejection mechanism, there may have been a selection process that took time for the *Microcystis* strains (genetic diversity and phenotypic expression) to develop.

Mussel nutrient excretion is driven by feeding intensity, C:P ratios of the seston, and assimilation efficiency, which likely decreases with increasing seston C:P ratio (e.g., Vanderploeg et al., 2002, 2009). The low *Microcystis* biomass in 1992 could be a result of P being tied up in mussel biomass with low recycling rate. Changes in phytoplankton communities 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).

Zebra mussels may have also 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 altered the ecology in a complex manner by providing clearer water in spring, increasing phosphorus recycling in some systems, and promoting nuisance blooms of toxic *Microcystis* during summer (Vanderploeg et al., 2001, 2002). Increased light penetration can also lead to increased benthic vegetation, which can be a sink for nutrients, thereby decreasing P availability to phytoplankton in the pelagic system (Reeders and Bij de Vaate, 1990; Vanderploeg et al., 2002, Hecky et al., 2004) as benthic vegetation increases over time. With a renewed field sampling program, it will be interesting to see if the changes observed in Saginaw Bay from 1990 to 1996 resulted in a new, stable configuration of the phytoplankton community. While we cannot suggest new phosphorus targets, our work does confirm the notion that current loading strategies should be re-examined in the context of a newly restructured ecosystem. This may be a complex task, as changes in the bay may be still emerging.

Acknowledgments

The authors thank Tom Nalepa at NOAA GLERL for providing the zooplankton and water quality data, Mark Edlund at the Science Museum of Minnesota for his help with diatom taxonomy, and Vic Bierman and Joe DePinto at Limno-Tech, Inc. for providing access to model files and data. Gene Stoermer and Richard Barbiero provided much appreciated help with interpreting diatom data. The excellent graduate student support of the University of Michigan's School of Natural Resources and Environment was instrumental in the completion of this manuscript. We would also like to acknowledge the time and care of the three anonymous reviewers who provided insightful comments on improving the manuscript. This is GLERL Contribution No. 1530.

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