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Special Issue: Quagga Mussels in the Western United States

Research Article

Dreissenids in Lake Erie: an algal filter or a fertilizer?

Hongyan Zhang[1*], David A. Culver[2] and Leon Boegman[3]

[1] *Cooperative Institute for Limnology and Ecosystems Research, University of Michigan, Ann Arbor, MI 48108, USA*
[2] *Department of Evolution, Ecology, and Organismal Biology, The Ohio State University, Columbus, OH 43212, USA*
[3] *Department of Civil Engineering, Queen's University, Kingston, Ontario, K7L 3N6, Canada*
E-mail: *zhanghy@umich.edu* *(HZ),* *culver.3@osu.edu* *(DAC),* *Leon.Boegman@civil.queensu.ca* *(LB)*

[*] *Corresponding author*

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Editor's note:
This paper was prepared by participants attending the workshop entitled "Quagga Mussels in the Western United States – Monitoring and Management" held in San Diego, California, USA on 1-5 March 2010. The workshop was organized within the framework of the National Shellfisheries Association, American Fisheries Society (Fish Culture Section) and World Aquaculture Society's Triennial Conference. The main objective of this workshop was to exchange and share information on invasive quagga mussels among agencies. The data presented in this special issue provide critical baseline information on quagga mussel monitoring and management at the early stages of introduction in the western United States.

Abstract

After successfully occupying the benthos of all the Laurentian Great Lakes and connecting channels, quagga mussels [*Dreissena rostriformis bugensis* (Andrusov, 1897)] have been colonizing the western United States at a much faster rate. Study findings and management experience in the Great Lakes will benefit the water resource managers in the western United States and help them be better prepared to act quickly and effectively to mitigate mussel impacts. We investigated the impacts of dreissenid mussels on nutrients and plankton using a two-dimensional Ecological model of Lake Erie (EcoLE), and compared their impacts with those of mesozooplankters. Model results showed that in the shallow western basin, mussel daily grazing impact was less than 10% of the combined Non-Diatom Edible Algae (NDEA) and diatom biomass, although they cleared a volume equivalent to 20% of the water column daily. Moreover, in the deep central and eastern basins, dreissenids grazed only 1-2% of the NDEA and diatom biomass per day. The relative importance of dreissenids' grazing impact on diatoms and NDEA to those of zooplankton's varied among years and basins in Lake Erie. In general, zooplankton had slightly higher grazing impacts than did the mussels on NDEA and diatoms in the western basin but much higher grazing impacts in the central basin. Dreissenid mussels excreted a big portion of phosphorus in the bottom water, especially in the western basin, while zooplankton kept a big portion of algal phosphorus in the water column, especially in the central and eastern basins. Non-Diatom Inedible Algae (NDIA) abundance increased with more phosphorus available and was less responsive to mussel selective grazing. Dreissenid mussels affected crustacean zooplankton mainly through their impacts on NDEA. Our results thus indicate that dreissenid mussels have weak direct grazing impacts on algal biomass due to a concentration boundary layer above the mussel bed, while their indirect effects through nutrient excretion have much greater and profound negative impacts on the system. EcoLE is a modification of CE-QUAL-W2, which is frequently applied to western aquatic systems, and we suggest that with this modification, the models can be used to predict dreissenid impacts in western lakes, reservoirs, and rivers in which they may become established.

Key words: Quagga mussels, Zebra mussels, *Microcystis*, zooplankton, Lake Erie, non-native species, water quality modeling

Introduction

Understanding the effects of invasive species is important to biodiversity conservation and ecosystem sustainability and being able to predict subsequent effects is crucial. Non-native species often pose a serious threat to the invaded environment and our ability to manage invaded ecosystems (Parker et al. 1999).

Two non-native dreissenid mussels (zebra mussels [*Dreissena polymorpha* (Pallas, 1771)] and quagga mussels [*D. rostriformis bugensis* (Andrusov, 1897)] have been a focus of research for over two decades in eastern (and more recently, western) North America. Remarkably, these thumbnail-sized animals can greatly impact their environment, but it is difficult to understand and accurately predict the magnitude and types of their impacts on ecosystems.

Zebra mussels, originated in the Ponto-Caspian Sea and dispersed through ships' ballast water, are well known successful invaders. Within several years after they were first seen in Lake St. Clair in 1988 (Hebert et al. 1989), zebra mussels were found in the benthos of all the Laurentian Great Lakes and connecting channels (Vanderploeg et al. 2002). They can survive low dissolved oxygen and desiccation for several days (McMahon 1996). They have high fecundity, with 24-mm females producing one million oocytes each year (Neumann et al. 1993), and they spawn at temperatures as low as 12°C (Sprung 1989). Their larvae are briefly planktonic and settlers reach sexual maturity within 1 year (Garton and Haag 1993). These traits help zebra mussels rapidly colonize an empty niche and develop dense populations. For example, MacIsaac et al. (1991) described 10-fold increases in settled mussel densities in reefs in western Lake Erie from a maximum mean density of 3.2×10^4 individuals$\cdot$m^{-2} in May 1989 to 34.2×10^4 individuals$\cdot$m^{-2} in October 1990. Quagga mussels have attracted increasing attention because they are competitively replacing zebra mussels in many waters. Compared with zebra mussels, quagga mussels have a lower respiration rate and devote a greater proportion of their energy input to body mass growth and less to reproduction (Stoeckmann 2003). Quagga mussels also have a lower egg maturation temperature, 4.8°C (Roe and MacIsaac 1997), and a higher tolerance of starvation (Baldwin et al. 2002). All these traits make quagga mussels competitive even in an established mussel bed, and they have become the dominant invasive bivalve in the Great Lakes (Nalepa et al. 2009). Despite programs (e.g., the 100th Meridian Initiative) designed to prevent dreissenid movement further into western North America, quagga mussels were discovered in Lake Mead near Las Vegas, Nevada, in 2007 and subsequently in other reservoirs within the lower Colorado River Basin, at a much faster spreading rate (Bossenbroek et al. 2009). Quagga mussels have also been discovered in a series of sites in California, Arizona, Utah, and Colorado. Zebra mussels have so far been found in fewer spots in the far western United States (USGS 2010).

While monitoring and transport prevention activities are critical in managing invasive species, studies on mussels' ecological and economic impacts are important in educating people and making adaptive management plans. One of the initial concerns about the impacts of dreissenid invasions was that mussels would clear the water of algae and, together with phosphorus loading reduction programs, result in productivity too low to support fisheries in the systems (Charlton 1994). This concern was supported by estimations of high grazing rates on phytoplankton (MacIsaac et al. 1992; Bunt et al. 1993), the increased clarity of nearshore waters, and decreases in phytoplankton biomass in water bodies in which zebra mussels became established (MacIsaac et al. 1992; Holland 1993; Leach 1993). Subsequent field experiments by Ackerman et al. (2001) and Edwards et al. (2005) took hydrodynamics into account and showed that the mussels' direct grazing influence was limited to a ~1 m thick boundary layer adjacent to the mussels. Mussel impacts on waters in the upper, productive layers thus depend on the rate of delivery of algae to the bottom boundary layer (i.e., the vertical turbulent diffusivity). The realization that hydrodynamic conditions were a critical factor in accurately estimating the impacts of dreissenid mussels in an ecosystem led to the application of coupled hydrodynamic and biogeochemical computational models with high temporal-spatial resolution. These models show that the ability of dreissenid mussels to graze from the entire ~10 m water column in western Lake Erie is limited when diurnal stratification suppresses vertical turbulent mixing (~60% of the time, Ackerman et al. 2001) and a concentration boundary layer develops above the mussel bed. Refiltration (the water being taken in by a feeding mussel has already been cleared of algae) will occur if the rate of delivery of phytoplankton to the benthic dreissenids through vertical turbulent mixing is less than the mussel grazing rate. Refiltration within the concentration boundary layer has been frequently documented (O'Riordan et al. 1995; Yu and Culver 1999; Edwards et al. 2005; Boegman et al. 2008a). This illustrates the importance of spatial-dynamic gradients in algae relative to the mussel location on the bed.

Arnott and Vanni (1996), Conroy et al. (2005), and Mellina et al. (1995) all demonstrated that dreissenid mussels also play an important role in lacustrine nutrient dynamics, particularly for phosphate-P, through phosphate excretion into the water and P sequestration into their body tissue and shells. For example, Conroy et al. (2005) showed that mussels excreted phosphorus at a rate as high as 2.8 mg m^{-2} day^{-1} in western Lake Erie, sufficient to replace the pool of soluble reactive phosphorus (SRP) in the water column in less than 10 days, raising the question of whether phytoplankton growth due to mussel excretion's contribution to the P supply can offset the loss of phytoplankton to mussel grazing. The estimates of phosphate excretion in these studies are based on a fully-mixed-water column situation, and are insufficient, because dreissenids release phosphate at the lake bottom and excreted nutrients must be in the euphotic zone to be made available to the phytoplankton. Approaches with higher spatial resolution are warranted.

Zooplankton is a critical link between the primary production and pelagic fish production, but its responses to the dreissenid mussel invasion remain largely unclear. Some studies showed that in the western basin of Lake Erie there was no significant change in zooplankton density after dreissenids invaded (Wu and Culver 1991; Idrisi et al. 2001), while others suggested that zooplankton was negatively affected by dreissenid mussels (Nicholls and Hopkins 1993; Johannsson et al. 2000). Results from Noonburg et al.'s (2003) two-compartment model showed that zooplankton density was insensitive to the dreissenid invasion, and they also demonstrated that hydrodynamic mixing factors were important in estimating competition between dreissenid mussels and zooplankton for algae. However, given the importance of boundary layers to the impact of dreissenids, and the distribution of zooplankton throughout the water column, the relative importance of zooplankton and dreissenid grazing and nutrient excretion on phytoplankton temporal and spatial dynamics remains unstudied. Therefore, we used a two-dimensional (2D) mathematical computational modeling approach to estimate the basin-wide impacts of dreissenid mussels on phytoplankton and nutrient dynamics relative to those of the zooplankton, and to analyze how the zooplankton community responds to the dreissenid invasion in Lake Erie (Figure 1). We constructed the model with a spatially explicit implementation of the US-Army Corps of Engineers' CE-QUAL-W2 2D model system (Cole and Buchak 1995). CE-QUAL-W2 has been implemented in hundreds of reservoirs and rivers throughout the world, including many in the western United States. For example, CE-QUAL-W2 has been implemented for Lakes Mead, Mohave, and Powell (e.g., Jain et al. 2003). Our expansions of CE-QUAL-W2 illustrate means by which the relative ecological impacts of dreissenids and zooplankton on phytoplankton may be modeled for western lakes, reservoirs, and rivers.

Our model has high temporal-spatial resolution, and explicitly includes chemical, biological, hydrodynamic and hydrologic components. It includes three algal groups, two zooplankton groups as state variables, and dreissenid mussels as external forcing functions (Figure 2). These modifications of CE-QUAL-W2 enable our model to be used for investigating ecosystem processes regarding algal succession, competition between mussels and zooplankton for food, the relative importance of internal and external phosphorus loading, etc. Using the model calibrated and verified for Lake Erie, we test whether: 1) zooplankters graze more algae than do the dreissenids; 2) phosphorus excreted by zooplankton is more important to primary production than that released by dreissenids due to their respective spatial locations; and 3) competition between zooplankton and dreissenids for phytoplankton is indeed strong.

Methods

Study site

Lake Erie is the smallest, southernmost and the most productive lake of the Laurentian Great Lakes. It constitutes a very dynamic system, given its many changes in water quality and fish populations and the invasions of exotic species. With the growth of the human population in its drainage basin, especially along its southern shoreline, Lake Erie underwent cultural eutrophication in the 1970s, which was particularly severe in the shallow western basin. With a greater than 50% reduction in point-source phosphorus (P) loading by 1985 (primarily through the adoption of tertiary treatment in wastewater treatment plants to decrease phosphorus in their effluents), Lake Erie became clearer. However, the invasion of dreissenids into Lake Erie continues to complicate evaluation of the effect of changes in external P loading on the lake.

Lake Erie is centered at 42°15'N and 81° 15'W, with its long axis oriented at about N 70° E. The lake is approximately 386 km (240 mi) long and more than 80 km (50 mi) wide near the midpoint of its long axis, so wind stress has an ample opportunity to affect the distribution of heat, solutes, and suspended matter in the lake. Lake Erie has three distinct geographic basins,

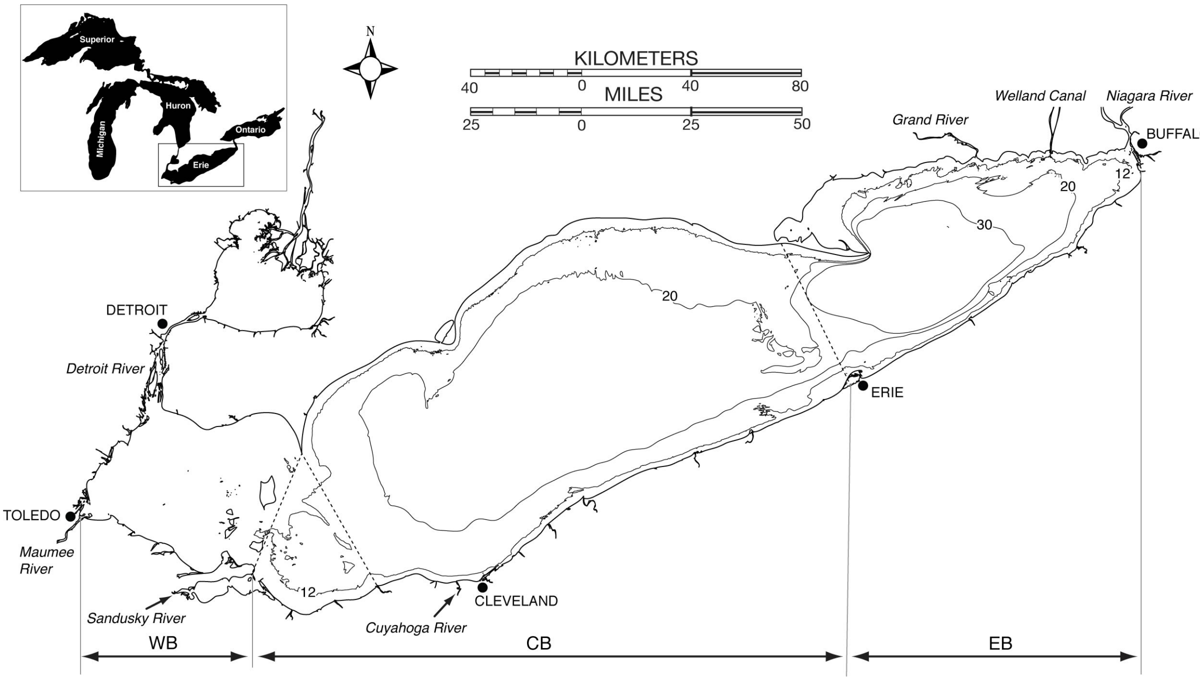


Figure 1. Lake Erie and its western (WB), central (CB) and eastern (EB) basins. The 5 m depth contour may be seen most clearly in the WB, whereas the 12, 20, and 30 m depth contours may be seen in the CB and EB.

the western, central and eastern basins. The western basin is the shallowest, with an average depth of 8 m; the central basin is relatively flat with an average depth of 18 m; and the eastern basin is the deepest with an average depth of 25 m (Bolsenga and Herdendorf 1993). During late May, or the beginning of June, water starts to stratify, and by mid July, seasonal stratification is firmly established in the central and eastern basins. At this time, the western basin is comprised entirely of epilimnetic water. By early October, convective cooling erodes the stratification, and fall turnover occurs (Schertzer et al. 1987), so seasonal thermal stratification lasts throughout the growing season in all but the western basin. The density gradient through the metalimnion in the stratified central and eastern basins reduces the rate of vertical mixing, impeding the exchange of nutrients between the epilimnion and the hypolimnion, and traps particles settling from the epilimnion. Thus, stratification cannot be ignored when evaluating the effects of *Dreissena* on the ecosystem. Even in the western basin, diurnal stratification restricts mussel effects to the bottom boundary layer (Ackerman et al. 2001; Edwards et al. 2005; Boegman et al. 2008a).

Model description

The 2D Ecological model of Lake Erie, EcoLE (Figure 2) is described in detail in Zhang et al. (2008) and a simpler version in Boegman et al. (2008a, b). Here, we provide a brief description. EcoLE is based on a 2D hydrodynamic and water quality model (CE-QUAL-W2). It divides Lake Erie into 222 longitudinal segments from west to east and up to 65 1-m thick vertical layers from the surface to the bottom. The orientations and widths of the segments are varied. Segments 65–222 (central and eastern basins) are spaced at 2000-m intervals and are oriented along the longitudinal axis of the NOAA grid (27.33° counterclockwise from the chart central meridian); to account for the "angled" nature of the western basin to this axis, segments 1–52, spaced at 1414-m intervals, are oriented 162.33° counterclockwise from the chart central

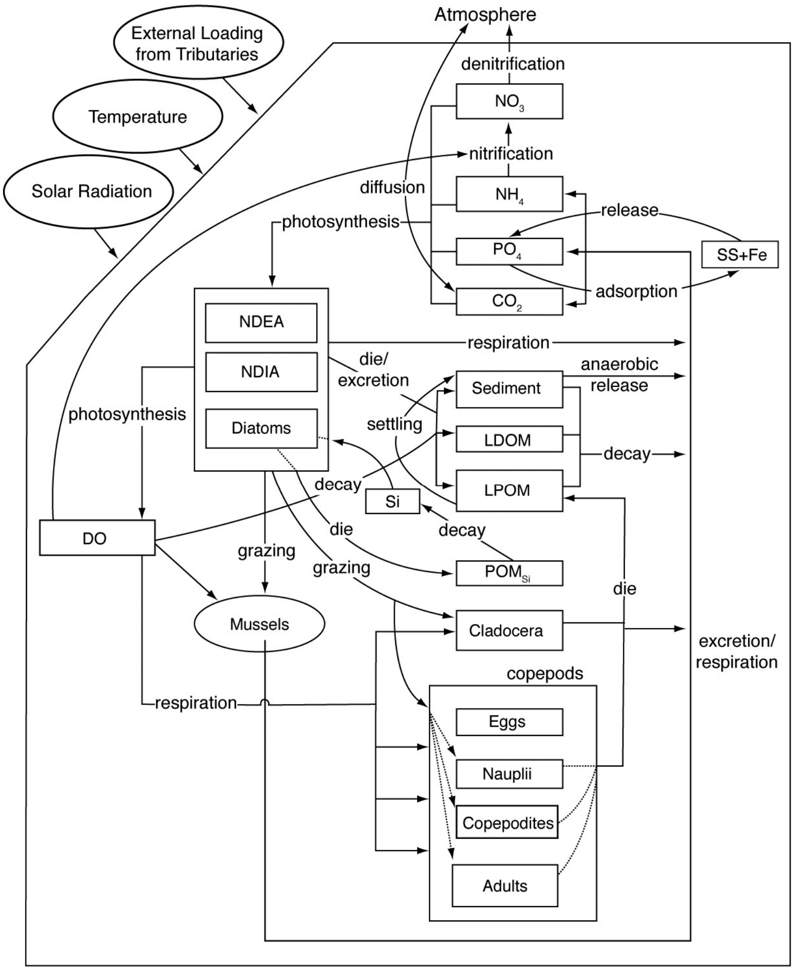


Figure 2. Model structure of the chemical and biological components of EcoLE.

meridian; segments 53–64 (triangle from Sandusky, Ohio, to Point Pelee, Ontario, to Lorain, Ohio) are spaced at 1779-m intervals and are transitionally oriented between western- and central-basin segments (Boegman et al. 2001).

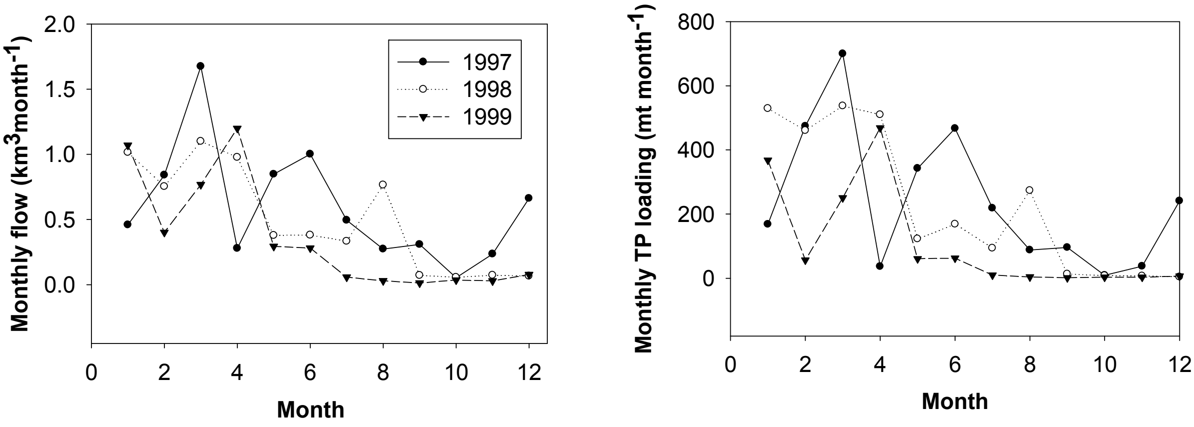
Using sub-daily (every three hours) meteorological input data, the model calculates physical conditions (water level, current velocities and temperature) using a variable timestep, to maintain hydrodynamic stability, of approximately 10 minutes. The chemical and biological variables are calculated every three physical-calculation timesteps. The biological state variables include diatoms, Non-Diatom Edible Algae (NDEA, dominated by chlorophytes and chrysophytes), Non-Diatom Inedible Algae (NDIA, dominated by *Microcystis*; we parameterized the NDIA submodule with *Microcystis* parameter values if available or other blue-green algal parameter values), cladocerans and copepods, while chemical state variables include ammonium, nitrate+nitrite, soluble reactive phosphorus, labile organic matter, particulate organic matter, silicon, silicon particulate organic matter, and oxygen. *Dreissena* biomass is not a state variable in the model, in part because dreissenids have a complicated life history. For example, the dispersal and settlement of their planktonic veligers are especially hard to simulate, so predicting the population dynamics of dreissenids is not a goal of this study. Instead, dreissenids are treated as external forces to the model, and mussel abundances and size distribution are assumed to remain constant over time. That is, their grazing impacts and nutrient remineralization impacts were calculated with a pre-determined population density. Since zebra mussels and quagga mussels have different physiology, they were treated as two separate groups.

The model has been calibrated and verified in the simulation of thermal structure and biogeochemistry for the years 1997-1999 (Zhang et al. 2008). The growing season is simulated from May 10 to September 30 of 1997, from June 10 to October 30 of 1998, and from May 20 to September 29 of 1999, reflecting the availability of field data (from the Ohio State University's LEPAS database) for water temperature, chemistry, and phytoplankton and zooplankton abundance and biomass variables for model initialization, calibration and verification. Plankton data are based on samples collected every two weeks from a series of 32 to 46 stations throughout the lake. The model reasonably simulated the state variables of water temperature (e.g., mean absolute error < 2°C; Boegman et al. 2001), total dissolved phosphorus, ammonium, NDEA, diatoms, cladocerans and copepods over the growing season of both the calibration year (1997) and the verification years (1998 and 1999). The median relative errors between the observations and model predictions of the above chemical and biological state variables were between 12 – 48%. Moreover, the model has also been shown in other studies to reproduce the main hydrodynamic processes that govern the generation of currents (e.g., seiches; Boegman et al. 2001) and turbulent mixing (e.g., storm events; Boegman et al. 2008a). Year 1997 was a wet year with high inflows and high external phosphorus loading, year 1999 was a dry year with low inflows and low external phosphorus loading, while year 1998 with intermediate level of inflows and external phosphorus loading (Figure 3). External phosphorus loading was highly correlated with the inflows. Averaged daily inflows during simulation periods from the Maumee River were 150, 102, and 42 $m^3 s^{-1}$ for 1997, 1998 and 1999, respectively, and averaged daily total phosphorus loading from the Maumee River during simulation periods were 8.6, 4.1, and 0.9 mt d^{-1}, respectively. Another difference among simulation years was that there was a *Microcystis* bloom in 1998, but not in the other two years.

Jarvis et al. (2000) found that in 1998, 84.4 % of mussels in the eastern basin were quagga mussels, 99.7% in the central basin, but only 36.9% in the western basin. For simplicity, we assume that for 1997, 1998, and 1999, all western basin dreissenids are zebra mussels, while all are quagga mussels in the central and eastern basins. Generally, zebra mussels prefer hard surfaces, while quagga mussels can attach to soft surfaces as well as hard surfaces. However, their distribution is also affected by oxygen conditions, food conditions, and their predators, etc. Thus, zebra and quagga mussel distributions vary greatly in time and space, and there are no accurate estimations of the two populations. Nevertheless, the depth-dependent estimations by Jarvis et al. (2000) are used in this model, and the mussel abundance in each model cell is the product of the depth-dependent density (ind. m^{-2}) and the sedimental area (m^2) of each model cell. We assume that mussels are uniform in size (10 mm). Our simplified mussel populations have similar population biomass to those populations observed by Jarvis et al. (Zhang et al. 2008).

This two-dimensional approximation causes difficulties in representing the spatial distribution of dreissenid mussels with depth across the lateral dimension (and hence the offshore region). To address this issue, which is particularly significant in the shallow, flat-bottomed western basin (Segments 2-56), the bathymetry of each western basin segment is modeled as a rectangular box of equivalent surface width and total volume. The model source and sink terms are then only applied in the bottom layer of water. In this approach, mussels are represented, within the constraints of the laterally averaged model, as true benthic organisms, and their activities first affect the layer at maximum depth for that segment. For the deeper central and eastern basins, all benthic boundary conditions are applied to the model layers based upon the sediment area associated with that depth. This adjustment has been thoroughly discussed and justified in Boegman et al. (2008a, b) and Zhang et al. (2008).

The two-dimensional geometry hinders the spatial representation of the dreissenid mussel beds and loading dynamics — in particular differences between nearshore and offshore regions are not simulated (e.g., Hecky et al. 2004). However, no high-resolution three-dimensional coupled hydrodynamic and biogeochemical model with zooplankton and dreissenid mussel components has yet been successfully implemented for the Great Lakes. At present, such models are capable of only reproducing phytoplankton dynamics (e.g., Leon et al., manuscript submitted to *J. Great Lakes Res.*). Compared to a 3D model, a 2D model has some distinct advantages. For example, 2D models are very time efficient (seasonal runs take hours of CPU time as opposed to weeks for 3D), while there are obvious disadvantages as well, all of which have been discussed in detail in Zhang et al. (2008). This 2D EcoLE, to the authors' knowledge, is the first model with fine temporal-spatial resolution and components of zooplankton and dreissenid mussel that has been calibrated, verified, and implemented



A) B)

Figure 3. Monthly water discharge (a) and total external phosphorus loading (b) from the Maumee River into Lake Erie, 1997-1999.

Table 1. Comparisons of grazing pressure and nutrient excretion between the mussel population in this study and the varied mussel populations in Zhang et al. (2008) in the western basin.

	Varied mussel populations	This study
Grazing on NDEA (% d^{-1})	0.29 - 7.5	6.2
Grazing on diatoms (% d^{-1})	0.47 - 13.67	6.66
SRP excretion (mt P d^{-1})	0.03 – 728	6.57
NH_4 excretion (mt N d^{-1})	0.66 – 7765	89

Table 2. Mussel shell length (mm) - soft-tissue dry mass (mg) regression and clearance rates (m^3 day^{-1}).

	Length-mass regression	Clearance rates
Western Basin	$DW=0.0057L^{2.732}$ (1)	$CR=0.046DW(g)^{0.88}$ (3)
Central Basin	$DW=0.0046L^{2.848}$ (1)	$CR=0.005DW^{0.5419}$ (4)
Eastern Basin	$DW=0.004L^{2.96}$ (2)	$CR=0.005DW^{0.5419}$ (4)

(1) Conroy et al. (2005); (2) Roe and MacIsaac (1997); (3) Pontius (2000) (we assume particle removal is 100%); (4) Baldwind et al. (2002)

to study basin-scale ecological problems in Lake Erie. When 3D models have been successfully implemented, it will be instructive to apply them to investigate 3D processes and compare those results to ours.

Zhang et al. (2008) discuss the effects of varying mussel population density and size distributions on simulation of dreissenid impacts on phytoplankton grazing and nutrient release. The population in this study has medium to high levels of grazing capacity and low nutrient excretion rates when compared to the ranges for different mussel populations of varying density from 0.1 to 20x and mean size from 5 mm to 20 mm (Table 1). Copepods and cladocerans are the two major crustacean zooplankton taxa in the lake, and are simulated using Fennel and Neumann's (2003) stage-structured population model for copepods and a generic bioenergetic model for cladocerans (Zhang et al. 2008).

Grazing on phytoplankton

The filtering rate is defined as the volume of water that an individual organism filters per day (ml ind^{-1} d^{-1}) and the clearance rate is the volume of water that an individual organism clears of particles per day (ml ind^{-1} d^{-1}) (Wu and Culver 1991). Only if the organism can clear all food particles in the water as it filters (100% removal) and avoids refiltering water it has already processed, does the filtering rate equal the clearance rate. For dreissenids, these rates are a function of soft-tissue body mass (Table 2). The grazing rate of a population (mg d^{-1}) is a product of the clearance rate and the food particle concentration in the water (mg l^{-1}) and the number of individuals in the population. Use of filtering rates instead of clearance rates thus overestimates grazing rates because near-bed water can be refiltered within the concentration boundary layer (e.g., Boegman et al. 2008a).

We estimate the dreissenids' grazing impacts, defined as the percentage of algal biomass of the whole basin, or lake that is grazed by dreissenid populations in a given period of time. Thus, the daily grazing impacts of dreissenids (I) on algae are computed as the percentage of algal biomass (B) that is grazed by dreissenids (G) during one day in each basin. The instantaneous basin-wide grazing rate (g, mt DW s^{-1}) is the sum of the products of mussel clearance rates ($c_{(i,j)}$) and the algal concentrations ($b_{(i,j)}$) and the numbers ($n_{(i,j)}$) of mussels in the model cells at layers i and segments j of the basin. That is, we assume only algae in the same model cell with dreissenids are instantaneously available to the mussels. Algae in other model cells will be available to dreissenids only when they are transported or settle into the model cell where dreissenids are located. Then the mean g over the simulation period was converted into daily grazing rate G.

$$g = \sum_i \sum_j c_{(i,j)} b_{(i,j)} n_{(i,j)}$$

$$I = \frac{G \times 100}{B} \%$$

We then compare the grazing impacts of mussels with the grazing impacts of crustacean zooplankton, which are calculated in the same manner as for dreissenids, using different grazing rates, g. For cladoceran zooplankters, they are a function of the maximal weight-specific ingestion rate (g_{max}, a constant), algal concentration (F), and cladoceran biomass density (w_{clad}, g m^{-3}). For cladocerans,

$$g = \sum_i \sum_j ((g_{\max} \frac{F_{(i,j)}}{K + F_{(i,j)}}) w_{clad\,(i,j)} v_{(i,j)})$$

where K is the half-saturation constant, and F is the weighted combination of algal biomass and detritus mass (i.e., weights are 1 for NDEA, 0.5 for Diatoms, 0 for NDIA, and 0.2 for detritus), and $v_{(i,j)}$ is the volume of model cell at layer i and segment j. For copepods, we use an equation from Fennel and Neumann (2003) to calculate the ingestion rate for different stages

$$g = \sum_k \sum_i \sum_j (\beta_0 e^{(\alpha T_{(i,j)})} (1 - e^{(-I_k{}^2 F_{(i,j)}{}^2)}) f(m_{k,(i,j)}, X_{k,(i,j)}) n_{k,(i,j)} v_{(i,j)})$$

where k is the stage of nauplii, copepodites, or adults; β_0, α, and I are constants; m_k is the individual weight of stage k; X_k is the critical individual weight of stage k; and $n_{k,(i,j)}$ is the copepod density of stage k in model cell (i, j). Crustacean zooplankters are evenly distributed in the water column at the beginning of simulations, which is near the spring turnover. Their vertical and horizontal distributions are then determined by physical mixing and biological processes (such as growth, death, maintenance cost, etc). Their active mobility, such as diel vertical migration, is not considered in the model.

Phosphorus excretion

Zooplankton and dreissenid mussels excrete both phosphate and ammonia, which are bioavailable nutrients to phytoplankton. Recently, studies speculate that nitrogen nutrients may play an important role in *Microcystis* bloom occurrence in the western basin and the hypoxia formation in the central basin of Lake Erie (Zhang 2006; Bruesewitz et al. 2008). However, since phosphorus is the primary limiting nutrient for algal growth in Lake Erie (Guildford et al. 2005), and has been the target nutrient for water quality management for the past several decades (Dolan and McGunagle 2005), we focus on phosphorus in this study.

Dreissenid excretion

Zebra mussels and quagga mussels have different weight-specific daily phosphorus excretion rates, ZMP and QMP (µg P mg^{-1} DW d^{-1}) (Conroy et al. 2005).

$$\log_{10}(ZMP) = 0.506[\log_{10}(W_{zm})] - 1.172$$

$$\log_{10}(QMP) = 0.297[\log_{10}(W_{qm})] - 1.195$$

Where W_{zm} and W_{qm} are the soft-tissue dry masses (mg) of individual 10-mm mussels. Thus, the phosphorus excretion of a mussel population (f_{zmP} for zebra mussels; f_{qmP} for quagga mussels) in a model cell over the growing season (g P m^{-3}) was calculated as the sum of the products of individual excretion rates and the numbers of mussels over the simulation periods.

$$f_{zmP} = \sum^{T} (N_{zm}(W_{zm} ZMP)) / V$$

$$f_{qmP} = \sum^{T} (N_{qm}(W_{qm} QMP)) / V$$

Where V is the volume of the corresponding model cell, m^3.

To determine the availability of excreta to phytoplankton, we calculated the soluble reactive phosphorus (SRP) mass in the upper mixed layer (< 12 m under water surface, which was the top depth of the metalimnion during early stratified period in our simulations; for locations where water depth was less than 12 m, the whole water column excluding the bottom meter was included). Phosphorus in the bottom meter water, where dreissenid mussels were located, was not included in shallow water (<12m deep) in this analysis because 1) during the weakly stratified periods phosphorus in the bottom layer was more available to benthic algae than to phytoplankton; or 2) during the well-mixed periods SRP distributed evenly throughout the water column, so modeling with and without the bottom 1 meter will not affect our conclusions. For each simulation day, the SRP mass is a sum of products of SRP concentration of each model cell and the cell volume in the upper mixed layer. The averaged SRP mass over each simulation period was reported in the RESULTS section.

Crustacean zooplankton excretion

We used a ratio of phosphorus to dry weight (δ_{P-cop} for copepods, δ_{P-clad} for cladocerans) to convert maintenance costs to phosphorus excretion (Andersen and Hessen 1991). Therefore, the total crustacean P excretion (f_{CP}) during the growing season (g P m^{-3}) was calculated as:

$$f_{CP} = \sum^{T} (\delta_{P-clad} r_{clad,t} m_{cladoceran,t} + \sum_{k}^{copepod} (\delta_{P-cop} r_{cop,t} m_{k,t}))$$

Where r was respiration rate (g g^{-1} s^{-1}); t was model time step; T was the duration of a growing season; m was biomass (g m^{-3}).

Sensitivity analysis

To evaluate the importance of grazing and nutrient excretion by dreissenids and zooplankton, we took advantage of the numerical model's ability to isolate individual processes, using the following seven scenarios: (1) the base scenario runs the full model as described above (FULL), (2) the joint impact of dreissenid grazing and excretion is obtained by inactivating the dreissenid functions from the full model (NO_ZM), (3) the full model with dreissenid grazing inactivated is designated as (NO_ZMG), (4) the full model with dreissenid P excretion inactivated is designated as (NO_ZME), (5) the full model with the zooplankton submodule inactivated is designated as (NO_ZP), (6) the full model with decoupled link between zooplankton grazing and algae is designated as (NO_ZPG), that is the growth of zooplankton is still based on its grazing, but this grazing did not result in a loss in algal biomass, and (7) the full model with decoupled link between zooplankton P excretion and P dynamics is designated as (NO_ZPE). The simulation results from these scenarios show how algae respond to changes in the functions of dreissenids and zooplankton, and how the zooplankton community responds to changes in the functions of dreissenids

Results

Impacts of dreissenid and zooplankton grazing on phytoplankton

Full model results (Table 3) show that in all years in the western basin, dreissenids processed (filtered) a volume equivalent to approximately 20% of the water daily. The grazing impacts on NDEA were 6, 4 and 10% for 1997, 1998 and 1999, respectively, and on diatoms were 7-8% for all years. In the central and the eastern basins, dreissenids processed a volume equivalent to 3% of the water daily, while the grazing impacts on NDEA and diatoms were approximately 1-2%.

The comparisons of the grazing impact of zooplankton and dreissenids on NDEA and diatoms show that their relative importance varies among basins and years (Table 3). Zooplankton has a higher impact than dreissenids on NDEA in all three basins for 1997 and 1998, while they have a lower impact in the western basin in the dry year, 1999. Overall, the grazing impacts on NDEA for zooplankton and mussels are of a similar magnitude. The impact of zooplankton grazing on diatoms was even closer to that of dreissenids in the western basin for all three years. Zooplankters had a consistently higher grazing impact on NDEA and diatoms in the central basin than did dreissenids

Table 3. Basin-wide grazing impacts on NDEA and diatom dry-weight biomass by dreissenid mussels and crustacean zooplankton during 1997, 1998 and 1999. Interannual changes in basin volume result from annual changes in water depth.

		1997			1998			1999		
	Unit	WB	CB	EB	WB	CB	EB	WB	CB	EB
Basin Volume	km^3	24	316	161	24	316	161	23	309	159
Water processed by mussels	km^{3}d^{-1}	5	10	5	5	10	5	5	10	5
	%	21	3	3	21	3	3	22	3	3
Basin-wide NDEA	mt DW	6,712	26,320	7,982	6,903	43,849	17,561	4,595	47,862	28,119
NDEA grazed by mussels	mt DW d^{-1}	414	173	99	282	346	245	443	445	465
	%	6	1	1	4	1	1	10	1	2
NDEA grazed by zooplankton	mt DW d^{-1}	521	1,944	426	746	3,340	618	291	3,557	604
	%	8	7	5	11	8	4	6	7	2
Basin-wide diatoms	mt DW	1,625	27,429	4,576	4,766	32,416	5,522	4,175	31,162	14,006
Diatoms grazed by mussels	mt DW d^{-1}	108	294	60	345	405	73	344	367	219
	%	7	1	1	7	1	1	8	1	2
Diatoms grazed by zooplankton	mt DW d^{-1}	101	1,172	118	385	1,816	128	278	1,834	196
	%	6	4	3	8	6	2	7	6	1

Table 4. The relative importance of nutrients excreted by dreissenid mussels and zooplankton to the basin-wide nutrient phosphorus mass.

		1997			1998			1999		
	Unit	WB	CB	EB	WB	CB	EB	WB	CB	EB
Basin-wide SRP	mt	28.6	837.0	515.4	34.2	1203.4	824.8	11.9	809.6	825.1
SRP excretion by dreissenids	mt d^{-1}	6.6	13.6	6.4	6.6	13.6	6.4	6.6	13.6	6.4
	%	23.2	1.6	1.2	19.4	1.1	0.8	55.5	1.7	0.8
Turnover times	d	4.3	62.5	83.3	5.2	90.9	125.0	1.8	58.8	125.0
SRP excretion by zooplankton	mt d^{-1}	3.8	18.4	5.0	4.7	16.2	2.0	2.7	18.4	3.8
	%	13.3	2.2	1.0	13.7	1.3	0.2	22.7	2.3	0.5
Turnover times	d	7.5	45.5	100.0	7.3	76.9	500.0	4.4	43.5	200

Table 5. Comparisons of the effects of different model scenarios on SRP (metric tons) in the upper mixed layer. Means are averages of basin-wide SRP (metric tons) over the simulation periods. Fractions are the means of the ratios of SRP concentration in the upper mixed layer found for each simulation relative to those of the FULL model. * indicates special discussion occurs in the following text.

Scenarios	WB		CB		EB	
	Means	Fractions	Means	Fractions	Means	Fractions
1997						
FULL	62	1.00	904	1.00	201	1.00
NO_ZMs	42	0.68	902	1.00	185	0.92
NO_ZMG	64	1.03	995	1.10	209	1.04
NO_ZME	46	0.74	816	0.90	177	0.88
NO_ZP	45	0.73	551	0.61	145	0.72
NO_ZPG*	82	1.32	7947	8.79	1855	9.23
NO_ZPE	56	0.90	592	0.65	160	0.80
1998						
FULL	91	1.00	734	1.00	162	1.00
NO_ZMs	50	0.55	710	0.97	161	0.99
NO_ZMG	77	0.85	847	1.15	195	1.20
NO_ZME	64	0.70	632	0.86	132	0.81
NO_ZP	52	0.57	366	0.50	113	0.70
NO_ZPG*	200	2.20	25941	35.34	7179	44.31
NO_ZPE	75	0.82	370	0.50	119	0.73

Table 5 (continued).

Scenarios	WB		CB		EB	
	Means	Fractions	Means	Fractions	Means	Fractions
1999						
FULL	32	1.00	754	1.00	158	1.00
NO_ZMs	23	0.72	821	1.09	188	1.19
NO_ZMG	35	1.09	934	1.24	223	1.41
NO_ZME	25	0.78	649	0.86	133	0.84
NO_ZP	22	0.69	317	0.42	123	0.78
NO_ZPG*	115	3.59	19775	26.23	5495	34.78
NO_ZPE	29	0.91	344	0.46	130	0.82

in all years. In the eastern basin, the impact of zooplankton grazing on NDEA and diatoms was one to two times higher than that of dreissenids in 1997 and 1998, while slightly lower in 1999. It appears that in the flat, shallow western basin and, especially, in the gradually deepened eastern basin, the mussels' grazing impacts are sensitive to weather conditions. During a dry weather year (e.g., 1999), mussel grazing impact becomes strong, and is even greater than that of the zooplankton. NDIA are selectively rejected by dreissenids and zooplankton. Therefore, there is no direct grazing impact by dreissenids or zooplankton on NDIA.

Impacts of dreissenid and zooplankton excretion on phosphorus

Dreissenid mussels excreted each day an amount of SRP equivalent to a high proportion of the water column SRP in the western basin: 23%, 19% and 56% in 1997, 1998 and 1999, respectively. The proportions decreased to about 1% in the central and the eastern basins in all years (Table 4), due to the large water volume of the basins and the lower mass-specific phosphorus excretion rates of quagga mussels. Zooplankton excreted similar amounts of SRP as dreissenid mussels for each basin in all years (Table 4). Sensitivity analysis showed that NO_ZME decreased phosphorus in the western basin to 74, 70, and 78% of that in the full model (FULL), while NO_ZPE only decreased to 90, 82, and 91% of that in FULL (Table 5). In the central basin, zooplankton excretion provided a much higher contribution to the epilimnion phosphorus than did dreissenid mussels, while in the deep eastern basin, zooplankton contributed slightly more than did the mussels. One reason is that zooplankton had a lower density in the oligotrophic eastern basin than in the mesotrophic central basin. So zooplankton impacts decreased due to their low abundance. However, the impacts of mussel excretion in the eastern basin increased slightly compared to those in the central basin (Table 5). The differences in hydrodynamics and morphometry, between the central and the eastern basins, may also play an important role. Large scale internal Kelvin waves occur only in the eastern basin (Bartish 1987; Boegman 1999); they are believed to be topographically damped in the central basin. These waves drive ~20 cm s^{-1} near-bed currents above the thermocline in the littoral zone (Csanady 1975), which lead to much stronger mixing in this portion of the water column, relative to the central basin. Thus although mussel populations in the central basin excreted a larger proportion of phosphorus than those in the eastern basin (Table 4), their nutrient excretion had less impacts on the upper mixed layer.

Dreissenid and zooplankton impacts on NDEA

The trends in NDEA biomass for different simulations in the sensitivity analysis were similar for all three years (Figure 4). Compared to the FULL model, the NO_ZM, NO_ZMG, NO_ZP, and NO_ZPG simulations showed increased NDEA biomass. The NO_ZM and NO_ZP simulations had substantially higher NDEA biomass than the FULL scenario, which indicated that grazing losses of NDEA to dreissenids and/or zooplankton were greater than the gain of NDEA stimulated by phosphorus excreted by dreissenids or zooplankton. Compared to NDEA biomass achieved in the FULL model, NO_ZME or NO_ZPE decreased NDEA biomass consistently for all three basins and all three years.

Although trends of increases and decreases in NDEA biomass in mussel sensitivity analysis (NO_ZM, NO_ZMG, NO_ZME) were similar to those in zooplankton sensitivity analysis (NO_ZP, NO_ZPG, NO_ZPE), the importance of

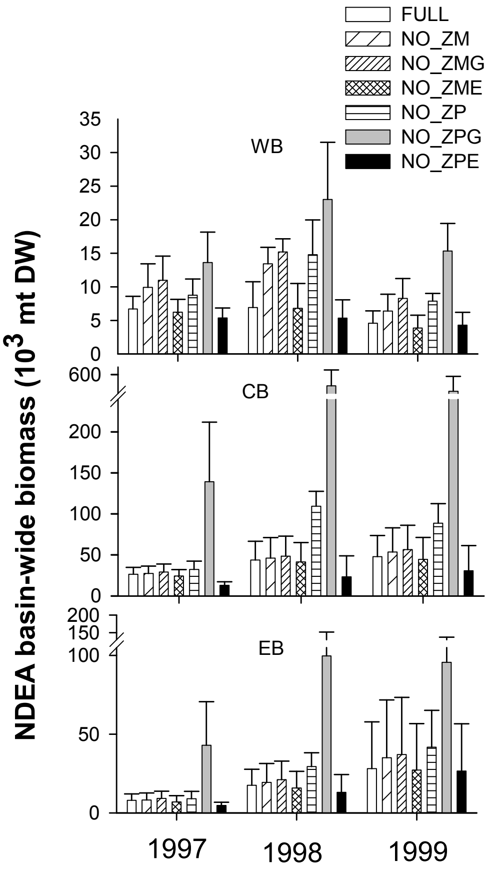


Figure 4. Comparisons of seasonal means of basin-wide Non-Diatom Edible Algae (NDEA) biomass for the sensitivity analysis. The error bar represents one standard deviation of the mean. Note the different scales and breaks on the vertical axes.

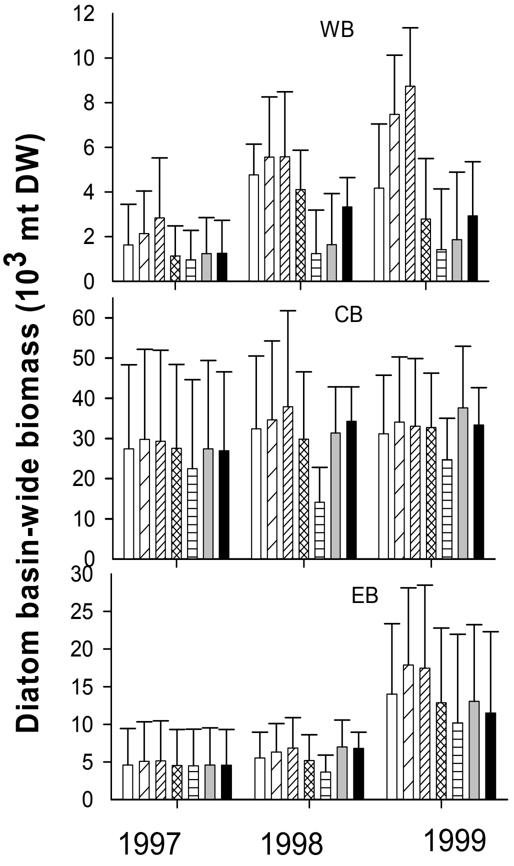


Figure 5. Comparisons of seasonal means of basin-wide diatom biomass for the sensitivity analysis model scenarios. The error bar represents one standard deviation of the mean. Note the different scales on the vertical axes. See Figure 4 for legends.

impacts of mussels and zooplankton to NDEA biomass was different among basins and years. Mussels (NO_ZM) and mussel excretion (NO_ZME) showed stronger influence on NDEA biomass in 1997 than their zooplankton-absent counterparts (NO_ZP and NO_ZPE), weaker in 1998 and 1999. In the central and eastern basins, zooplankton consistently showed stronger impacts than mussels, especially in the deep and flat central basin. For example, in the central basin, NDEA biomass in the NO_ZP simulation increased by +23 to +149% more than in the NO_ZM (+4 to +12%) compared to the FULL model, while NDEA biomass decreased in the NO_ZPE by 36 to 51% less than in the NO_ZME scenario (5 - 8%).

NO_ZPG resulted in the most abundant NDEA in the sensitivity analysis, and the high NDEA biomass supported a large zooplankton population. The large zooplankton population excreted more phosphorus (Table 5) which, in turn, relieved NDEA from phosphorus limitation and further enhanced NDEA growth. While this scenario is a numerical experiment and is not realistic, it helps explain some mechanisms relating to algal community succession (discussed below). The NO_ZMG simulation did not show this positive feedback, because dreissenid populations did not grow over time in the model and dreissenid excretion is sequestered in the benthos where it is isolated from the euphotic upper mixed layer (Boegman et al. 2008b, Figure 8 therein).

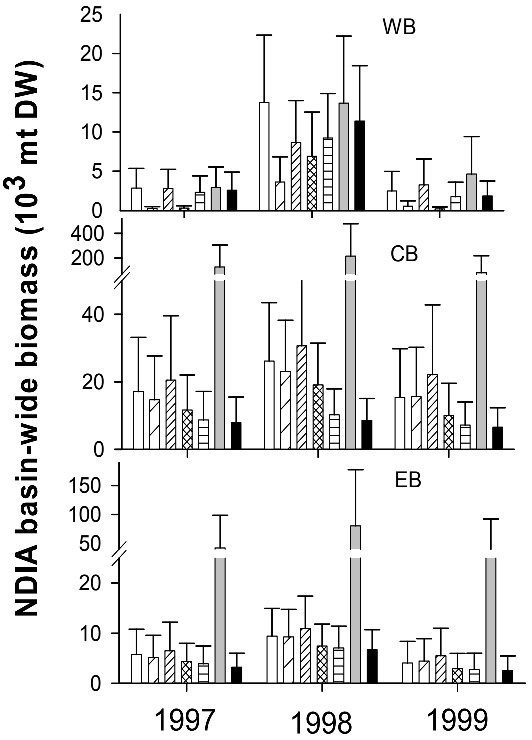


Figure 6. Comparisons of seasonal means of basin-wide Non-Diatom Inedible Algae (NDIA) biomass for the sensitivity analysis. The error bar represents one standard deviation of the mean. Note the different scales and breaks on the vertical axes. See Figure 4 for legends.

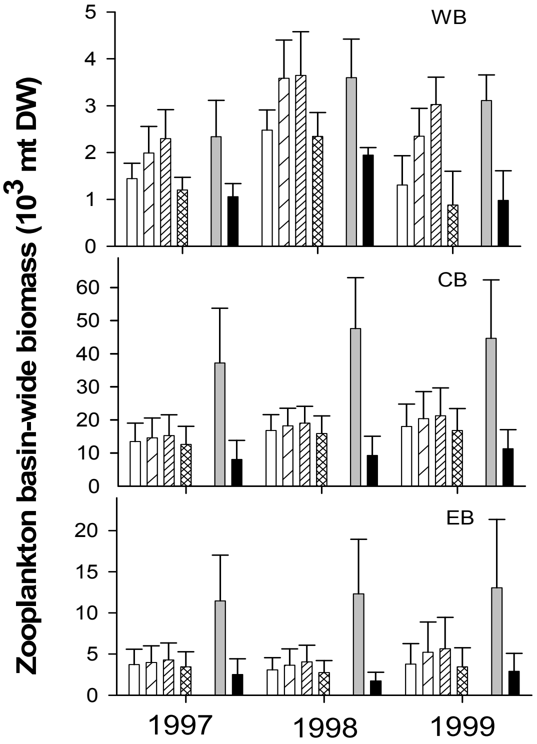


Figure 7. Comparisons of seasonal means of basin-wide zooplankton biomass for the sensitivity analysis. The error bar represents one standard deviation of the mean. Note the different scales on the vertical axes. See Figure 4 for legends.

Dreissenid and zooplankton impacts on diatoms

Compared to the FULL simulation, the NO_ZM simulation increased diatom biomass in all three basins and all three years. The biomass increased by 17–79% in the western basin, 7–9% in the central basin, and 11 - 28% in the eastern basin. Conversely, NO_ZP decreased diatom biomass by 41–74%, 18–56%, 2–34% in the corresponding basins (Figure 5). Compared to the FULL simulation, NO_ZMG increased diatom biomass in all three basins and all three years by 6 – 109%, while NO_ZPG decreased diatom biomass in most of the cases. These indicate that diatom biomass gain due to no zooplankton grazing loss is weaker than biomass loss caused by other factors. Compared to the FULL simulation, the NO_ZME simulation decreased diatom biomass in the western basin by 14 – 33% over all three years, and decreased or increased diatom biomass slightly in the other two basins. Compared to the FULL simulation, NO_ZPE decreased diatom biomass by 23 – 30% in the western basin over the three years, while increased diatom biomass in the central and eastern basins except in the central basin in 1997. These results suggest that dreissenids impacted diatoms by direct grazing, while zooplankton affected diatoms by indirectly modifying competition between algal groups. For example, diatoms lost competition to NDEA in the NO_ZP scenarios, because NDEA populations grew more and suffered less loss without zooplankton (grazing weight factor is 1 for NDEA and 0.5 for diatoms) and became a strong nutrient competitor to diatoms. However, the responses of diatoms to changes in the system are not completely explained because more factors are involved, such as silica limitation (Schelske et al. 2006) and high sinking rates that make diatoms more susceptible to dreissenids.

Dreissenid and zooplankton impacts on NDIA

Compared to the FULL model, the NO_ZM simulation decreased NDIA biomass in the western basin, while it generated similar, if not lower, NDIA biomass in the central and eastern basins (Figure 6). NO_ZMG increased NDIA biomass in all basins and all years, except in the western basin of 1998 when the phosphorus concentration in NO_ZMG was lower than that in the FULL simulation (Table 5). NO_ZME, NO_ZP, and NO_ZPE simulations decreased NDIA biomass consistently in all cases, while NO_ZPG increased NDIA biomass in all cases. NDIA changes reflected (but not proportionally) the changes in availability of phosphorus, i.e., NDIA increased as more phosphorus was made available to them (Fraction > 1, Table 5), and vice versa. For example, compared with the FULL model, the NO_ZP simulation had higher NDEA, which implied lower phosphorus availability to NDIA as NDEA was a strong competitor (Table 5). Accordingly, NO_ZP had lower NDIA than the FULL model. This is also evident in comparison of the FULL model to NO_ZPG, which had much higher NDEA. However, instead of having lower NDIA (as NDIA was a weak phosphorus competitor) the treatment also had much higher NDIA than the FULL because of the positive feedback (as mentioned above) resulting in higher phosphorus availability to NDIA given abundant NDEA (Table 5).

Dreissenid impacts on crustacean zooplankton

The impacts of mussels on crustacean zooplankton (cladocerans and copepods) were very similar to those on NDEA, but the magnitudes were an order of magnitude lower (Figures 4 and 7). The NO_ZPG simulation showed that zooplankton biomass increased for all basins and all years. Interestingly, the increases in the western basin were much smaller than those in the other basins, which can be attributed to the much smaller increases in NDEA biomass in the western basin (Figure 4). The increases in phosphorus concentrations in the upper mixed layer were much lower in the western basin in terms of increasing rates (Fractions in Table 5), which indicated that nutrient circulation in the pelagic water was much more rapid in the central and eastern basins. Compared to the FULL model, zooplankton grazing rates increased in the scenarios of NO_ZM and NO_ZMG and decreased in the NO_ZME (Figure 8).

Discussion

Dreissenid impacts on phytoplankton

Dreissenid mussels have high filtering rates and have great potential to decrease the phytoplankton biomass in ecosystems (MacIsaac et al. 1992; Bunt et al. 1993; Holland et al. 1993; Leach 1993). Using the different filtering rates from Kryger and Riisgard (1988), Kondratev (1963), and Micheev (1966) and a mussel population density of 2.6×10^5 m^{-2} from Hen Island Reef, MacIsaac et al. calculated three filtering rates of 132 m^3 m^{-2} d^{-1}, 115 m^3 m^{-2} d^{-1}, and 25 m^3 m^{-2} d^{-1}. If the population density in their study is adjusted by using our more recent depth-dependent densities (2927 m^{-2} at depth of 0-5 m and 6419 m^{-2} at depth of 5-10 m), then their filtering rates would be 1.5-3.3 m^3 m^{-2} d^{-1}, 1.3-2.9 m^3 m^{-2} d^{-1}, and 0.3-0.6 m^3 m^{-2} d^{-1}. For a water column of 7 m, the updated population would filter a volume equivalent to 4%-47% of the water column per day. This may be compared to the estimate by MacIsaac et al. (1992) that the mussels could filter the entire water column 3.5–18 times daily. Our result of 20% per day (Table 5) is well within the MacIsaac et al. range when these lower densities are applied. A result of the lower densities is that the filtering capability of mussel populations is now far less striking than it was predicted during the first several years after they first successfully colonized western Lake Erie (Barbiero and Tuchman 2004; Boegman et al. 2008b).

Although mussels filtered a volume equivalent to more than 20% of the water column per day in the western basin, they only grazed less than 10% of the NDEA and diatom biomass per day. Because they are filtering from the boundary layer, they have a refiltration rate of 71, 81 and 55% for 1997, 1998 and 1999, respectively. Ackerman et al. (2001) and O'Riordan et al. (1995) reported lower refiltration rats of 42-48%. However, they both used an equation developed under flows of 8-40 cm s^{-1}, thus, seston was continuously brought to the mussels, not surprisingly resulting in lower refiltering rates.

While western Lake Erie is shallow and has no seasonal stratification, it certainly is not a well-mixed reactor. Ackerman et al. (2001) studied an isolated reef in western Lake Erie and found that 60% of the time, the water column was stratified

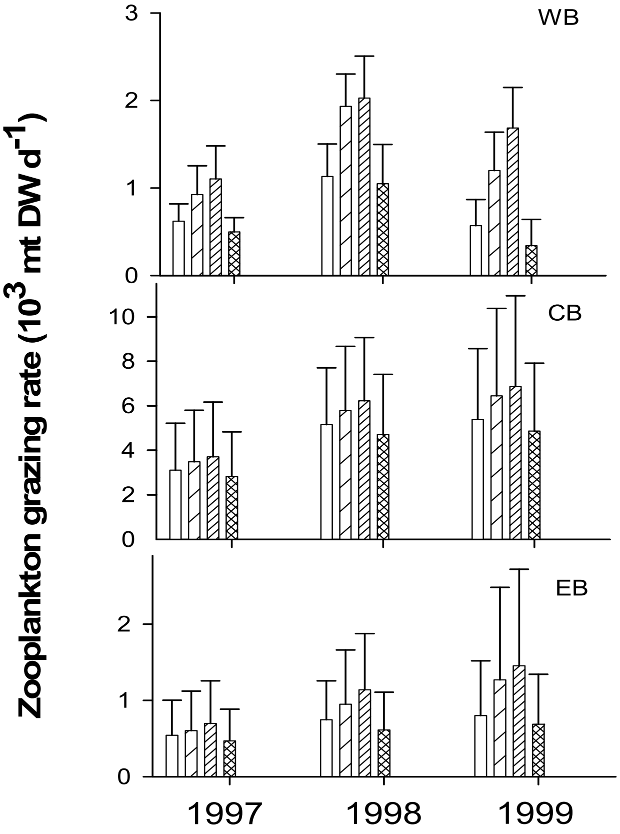


Figure 8. Comparisons of seasonal means of basin-wide grazing rates of zooplankton for the sensitivity analysis. The error bar represents one standard deviation of the mean. Note the different scales on the vertical axes. See Figure 4 for legends.

during the day due to solar heating (diel thermocline) and intrusions of cold central basin water. This stratification suppresses turbulent supply of algae toward the bed. MacIsaac et al. (1999) found a chlorophyll *a* depleted concentration boundary layer of 1.85 m above the lakebed at six locations in the western basin of Lake Erie. Their location-parameterized 2D hydrodynamic model predicted that mussel grazing caused as high as 90% of the reduction in chlorophyll *a* near the lake bottom. Their model also predicted much lower reductions in surface chlorophyll *a* concentration. Edwards et al. (2005) also reported a zone of depletion in algal biomass near the mussel bed, but they found little evidence of algal depletion in the upper water column. Boegman et al. (2008a), using a previous version of our model, demonstrated explicitly how a temporary calm water column resulted in the formation of a concentration boundary layer above mussel beds in the western basin. Vertical turbulent mixing was effectively suppressed by a ~1°C temperature gradient over the 7 m water column. The western basin was only fully mixed, thus allowing grazing mussels access to the entire water column, during storm events (occurring every ~ 10 days) during which the mean daily wind speed was in excess of 6 m s^{-1}.

Dreissenid grazing not only decreases algal biomass, but also changes phytoplankton community structure (Vanderploeg et al. 2001; Bierman et al. 2005). NDIA is dominated by *Microcystis* in our model, hence *Microcystis* will be discussed below. Our simulations show that *Microcystis* is not a strong nutrient competitor with other algal groups. When phosphorus concentration is low, *Microcystis* biomass decreases due to competition with other algae. Selective grazing by dreissenids showed little impact on the development of *Microcystis*, because *Microcystis* biomass increased in most of the cases in the NO_ZMG scenario (Figure 6). The only case with a significant decrease in *Microcystis* biomass was in the western basin of 1998, when a *Microcystis* bloom occurred. The

NO_ZME simulation resulted in a consistently lower *Microcystis* biomass than did the NO_ZMG or FULL simulations. The decreases in *Microcystis* biomass were much larger in percentage (e.g., 50 – 90% in the western basin) than those for NDEA (1 – 16%) and diatoms (14 – 33%), and so in the western basin, *Microcystis* is less affected by the vertical distribution of P, but was more affected by the total amount of available P in the water column, because they do not require a high light intensity to grow (Hesse and Kohl 2001) and can grow in the lower water column adjacent to mussel bed. Our simulation (not showed) found that *Microcystis* in the lower water column (including the bottom layer) has much higher concentration than in the upper water column, while NDEA and diatoms have low concentrations in the bottom layer. Edwards et al. (2005, their Figure 5) reported a vertical algal distribution profile in the western basin of Lake Erie and showed that a high *Microcystis* concentration occurred within 1 m above the mussel bed. Thus, P excreted by a mussel population on the lake bed will benefit *Microcystis* more than other algal groups. Our results clearly show that mussels have much stronger impacts on *Microcystis* by P excretion than by grazing in Lake Erie. More studies are needed to investigate the importance of mussels' nutrient excretion to the formation of the *Microcystis* bloom.

Despite the presence of a concentration boundary layer, and the mussels grazing less than 10% of the NDEA and diatom biomass, they have a grazing pressure comparable to that of zooplankton in the shallow western basin of Lake Erie. Dreissenid mussels are a significant phytoplankton biomass sink in the western basin.

Dreissenid impacts on phosphorus cycling

Dreissenid mussels are important internal SRP sources (Gardner et al. 1995; Heath et al. 1995; Johengen et al. 1995; Arnott and Vanni 1996), which can be directly taken up by phytoplankton. Makarewicz et al. (2000) found that SRP increased by 180% in western Lake Erie from the pre-*Dreissena* period to the post-*Dreissena* period. They attributed this directly to input from dreissenid mussel excretion and lower uptake by phytoplankton due to their grazing loss to dreissenid mussels. Our model predicts that mussels excrete 20–56% of the SRP in the western basin and about 1% SRP in the other basins. The dreissenid populations in our model were much smaller (in density and mussel size) than populations studied by others (MacIsaac et al. 1991, Arnott and Vanni 1996). A sensitivity analysis by Zhang et al. (2008) on mussel density and body size showed that increasing dreissenid body size from 10 mm to 15 mm or even 20 mm, or increasing density by 10-fold increases the population's P excretion dramatically (Table 1). These higher population densities and larger size distributions may be quite realistic for those found on many hard substrates on the lake bottom, whereas we used abundances that are characteristic of average densities across all substrates. A high SRP concentration from excreta in the bottom waters of the weakly stratified western basin and central/eastern basin littoral zones, incubating *Microcystis* as discussed above, will be mixed to the surface waters during frontal storm systems every ~ 10 days (Ackerman et al. 2001; Boegman et al. 2008a). This internal phosphorus loading may boost the growth of phytoplankton temporarily, which weakens the efficiency of the external phosphorus loading reduction programs temporarily and superficially, especially if this upward flux of phosphorus occurs during a *Microcystis* bloom (e.g., in 1998). However, due to the relative efficiency of P cycling, for most lacustrine systems the productivity is ultimately regulated by external phosphorus loads.

Our results show that dreissenids grazed 522 mt DW d^{-1} of NDEA and diatoms in the western basin in 1997 (Table 3). Assuming that 1% of the dry weight is phosphorus (Cole and Buchak 1995), dreissenids consumed 5.22 mt P d^{-1}, but in our model, mussels excreted 6.6 mt P d^{-1} (Table 4). The differences show that the mussel excretion is not fully dependent on the ingested P from algal biomass. This difference is reasonable as we do not include the grazing of detritus (particulate organic matter, POM). There are large POM sources in our modeled system. For example, the daily mortality rates for both NDEA and diatoms were 7%, which entered the organic particle pool immediately in the simulation, and cladocerans egested 40% of their ingestion as unassimilated food into the POM pool.

The model does not simulate sediment resuspension and so settled POM remains at the sediment-water interface and is thus removed from the system, even though it is not directly grazed. Our model results (not shown) show that the POM had a similar mass (8273 mt DW) to the total mass of NDEA and diatoms (8337 mt

DW) in the western basin in 1997. Near Point Pelee, one-third of observed organic seston in western Lake Erie was estimated to be living algae; the remainder being mainly detritus (Leach 1975). Garton et al. (2005) found that seston comprised ~50% of the food sources for mussels in Lake Erie. Other studies showed that dissolved organic carbon (Roditi et al. 2000) and microzooplankton (Pace et al. 1998; Wong et al. 2003) were alternative dreissenid food sources. If mussels grazed POM at a similar rate (6-7% d^{-1}) of NDEA or diatoms, the mussels would gain 496 – 579 mt DW d^{-1}. We estimated that POM settled at a rate of 520 mt DW d^{-1} in the western basin in 1997, which is a sufficient supply to overcome the loss of ~1.4 mt P d^{-1} and allow mussel growth.

As discussed earlier, dreissenid mussels are a significant phytoplankton sink. Population growth also sequesters a considerable amount of nutrients into their body tissue and shells (Mellina et al. 1995). However, their excretion accelerates nutrient remineralization rates compared to nutrient release from degrading dead organic matter (Boegman et al. 2008b). The net phosphorus flux to a dreissenid-invaded water body may be from sediment into the bottom water. In the shallow waters, with frequent full-mixing events, phosphorus concentrated in the bottom water is mixed up into the upper water column, weakening the effects of external phosphorus reduction programs, and even worse, enhancing the harmful algal blooms. However, in deep invaded water, this nutrient remineralization of mussels potentially plays a major role in increasing water clarity, as opposed to direct grazing by mussels on algae. Deep water is usually seasonally thermally-stratified, so nutrients accumulated in the bottom water as particulate nutrients sink to the bottom water and are remineralized by dreissenid mussels causing the oligotrophic system to becoming even more oligotrophic (Vanderploeg et al. 2010). Furthermore, growth of macrophytes and benthic algae (e.g., *Cladophora*, which grows heavily in the northern shore of the eastern basin (Auer et al. 2010; Higgins et al. 2008)) increases the likelihood that phosphorus excreted by mussels will remain in the bottom waters (Hecky et al. 2004). Thus, even less phosphorus is available to the upper mixed layer, although a portion of the phosphorus could be released back into the water column through fish predation (Campbell et al. 2009; Madenjian et al. 2010).

Dreissenid impacts on zooplankton

The impacts of dreissenid mussels on zooplankton have been less well studied. Field observations indicated that rotifer abundance declined by 74% between before and after the establishment of *Dreissena* populations in western Lake Erie (Leach 1993; MacIsaac and Rocha 1995). Evidence was also provided that rotifers could be ingested directly by mussels (MacIsaac et al. 1991; Pace at al. 1998; Wong et al. 2003). There are far fewer studies on the impacts of dreissenid mussels on mesozooplankton. Pace et al. (1998) found lower abundances of copepods and cladocerans post-*Dreissena* than pre-*Dreissena* in the Hudson River, but the differences were not statistically significant. Idrisi et al. (2001) found no significant impacts of zebra mussels on cladoceran biomass in Oneida Lake, New York. Our simulations suggest that zooplankton biomass and grazing rates on NDEA are depressed substantially by zebra mussels or mussel grazing (Figures 7-8) in the western basin, which indicates food competition between zooplankters and mussels. However, the competition should not be strong, since mussel grazing is limited by boundary layers, and both mussels and zooplankters only grazed about 10% of algal biomass over the growing season. However, a clear-water phase occurs during early July, when food is sparse for zooplankton, and competition among zooplankters might be more severe than between zooplankton and mussels during this period.

In summary, the EcoLE model serves as a useful tool to integrate and extrapolate knowledge gained in the laboratory and field to the whole lake ecosystem. Our results showed that basin-wide dreissenid populations grazed only as much as ~10% of phytoplankton biomass day^{-1} but excreted as much as 55.5% of the SRP concentration day^{-1} in Lake Erie. Our model showed moderate food competition between zooplankton and dreissenid mussels in the western basin and minimal food competition in the central and eastern basins. Dreissenid mussel selective grazing played a role in *Microcystis* proliferation in the western basin. However, *Microcystis* is very sensitive to the changes in SRP in the water column. The zooplankton community showed clear and strong impacts on algal biomass, and their impacts are not masked by those of mussel populations. The relative impact of zooplankton and dreissenid grazing and excretion on phytoplankton (including *Microcystis*) is of great importance to the ecology of western water bodies, in many of which dreissenids have recently become established. Implementation of this model for these lakes, reservoirs, and rivers may provide useful predictions of ecological changes that may be expected as dreissenid populations increase. Moreover, studies on multilevel changes in parameters of our sensitivity analysis would provide better understanding of the non-linear responses of ecosystems.

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