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

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

[a] University of Michigan School of Natural Resources and Environment, 440 Church Street, Ann Arbor, MI 48109-1041, USA
[b] NOAA GLERL, 4840 South State Road, Ann Arbor, MI 48109, USA

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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.

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) excreters 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

* Corresponding author.
E-mail addresses: dbfish@umich.edu (D.B. Fishman), adlerste@umich.edu (S.A. Adlerstein), henry.vanderploeg@noaa.gov (H.A. Vanderploeg), gary.fahnenstiel@noaa.gov (G.L. Fahnenstiel), scavia@umich.edu (D. Scavia).

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Great Lakes waters after zebra mussel invasions has been an increase in chrococcoid 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 chrococcoid 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 chrococcoid 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:

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

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.