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Modeling the effect of invasive quagga mussels on the spring phytoplankton bloom in Lake Michigan

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ABSTRACT

The disappearance of the spring phytoplankton bloom in Lake Michigan has been attributed in some studies to the direct effect of quagga mussel filter-feeding. We applied a biophysical model to test whether the observed reduction in the spring bloom can be explained by direct effects of quagga mussel grazing. We developed a 1-D column biological model that simulated light and temperature limitation on phytoplankton growth, vertical mixing, and grazing by zooplankton and quagga mussels. We applied the 3-D finite volume coastal ocean model (FVCOM) to provide vertical mixing, with two scenarios of atmospheric forcing: (a) North American Regional Reanalysis (NARR) and (b) station interpolation using the Natural Neighbor Method. Simulated development of the spring bloom and formation of the deep chlorophyll layer in the early summer stratified period were consistent with observations. Increased strength of winter stratification (surface < 4 °C) in 1997 (cold spring) increased chlorophyll concentrations during March and April, compared to 1998, by reducing light limitation (reduced mixed-layer depth). Simulations with NARR forcing produced high-biased chlorophyll, resulting from low-biased wind speed and spring mixed layer depth. Simulated mussel filter feeding strongly reduced phytoplankton abundance when the water column was mixed to the bottom, but had little effect during periods of summer and winter stratification. These model simulations highlight the sensitivity of both phytoplankton growth and the impact of profundal quagga mussel filter-feeding to vertical mixing and stratification, which in turn is controlled by meteorological conditions.

Introduction

The population of non-indigenous quagga mussels (*Dreissena rostriformis bugensis*) expanded rapidly in Lake Michigan over the period 2000–2005 (Nalepa et al., 2009). Over the same period, the spring phytoplankton bloom was greatly reduced (Yousef et al., 2014). Earlier studies (Fahnenstiel et al., 2010; Vanderploeg et al., 2010) attributed the disappearance of the spring bloom to the direct effect of quagga mussel filter-feeding on phytoplankton, arguing that observed mussel abundance and clearance rates could outpace phytoplankton growth, under the assumption of a well-mixed water column during the spring isothermal period. Later studies observed reduced chlorophyll in the deep chlorophyll layer (DCL) during summer stratification, in addition to reduced spring chlorophyll, and discussed the influence of quagga mussels on phosphorus cycling and distribution (Pothoven and Fahnenstiel, 2013).

Stratification and vertical mixing have a strong influence on phytoplankton growth and on the coupling of benthic filter feeders to the euphotic zone. Lake Michigan is thermally stratified during the summer, approximately May through October, and vertically well-mixed when the surface temperature reaches 4 °C in fall and spring. The summer surface mixed layer (SML) depth may reach the bottom in nearshore areas with depth < ~20–30 m, resulting in intermittent periods of stratification and mixing in the nearshore. Ice cover and winter stratification (surface temperature < 4 °C) develop to some extent each year, but the spatial extent and duration are highly variable among years (Wang et al., 2012).

The spring phytoplankton bloom occurs under conditions of deep mixing in which light limitation plays an important role, as the SML depth is large relative to the euphotic zone depth for much of the lake (Fahnenstiel et al., 2000; Vanderploeg et al., 2007). The mean light exposure to phytoplankton cells depends on the euphotic zone depth as a fraction of the SML depth (Fahnenstiel et al., 2000). The SML is limited by bathymetric depth during the unstratified period, and by the balance between static stability and mechanical mixing during the stratified period. The direct effect of mussel filter feeding on phytoplankton is mainly limited to the unstratified period (Vanderploeg et al., 2010), when turbulent mixing effectively transports phytoplankton between the euphotic zone and the benthos.

During the stratified period, mussels may depend on lateral transport of food particles. It has been hypothesized that interception of cross-isobath transport of organic particles by dreissenid mussels

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(*mid-depth sink*, (Vanderploeg et al., 2010)) has altered nutrient cycles. In 2008, the maximum biomass of quagga mussels occurred in the 30–50 m depth range (Nalepa et al., 2010); prior to the quagga mussel invasion, a pronounced benthic nepheloid layer (BNL) existed during the stratified period in the same depth range. The BNL was believed to be caused by oscillating currents at a near-inertial period associated with internal waves in the stratified water column, although the exact mechanism of particle resuspension was unclear (Hawley, 2004). In biophysical models, simulation of the near-inertial period oscillating currents is of interest in order to characterize the physical environment where quagga mussels currently reside, and which formerly supported the BNL.

Hydrodynamic modeling studies in Lake Michigan have often focused on general circulation patterns and thermal structure during the summer stratified period. For example, an application of Princeton Ocean Model (POM) on a 2-km grid simulated circulation patterns with greater skill than a 5-km grid model, but problems with shallow mixed layer depth and diffuse thermocline persisted (Beletsky et al., 2006). Bai et al. (2013) applied the Finite-Volume Coastal Ocean Model (FVCOM) to simulate climatological-mean circulation patterns and thermal structure in all five Great Lakes. Relatively few studies have focused on the unstratified period, and few studies have tested the sensitivity of vertical mixing to alternate sources of forcing conditions. In one example, a POM simulation of a March 1998 storm event revealed that forcing by the MM5 meteorological model, versus interpolated observed winds, resulted in improved simulation of currents (Beletsky et al., 2003). Both types of forcing resulted in overestimated vertical gradients in simulated currents (their Fig. 8), suggesting low-biased vertical mixing during the unstratified period.

Biophysical modeling studies in Lake Michigan have not focused on simulation of the vertical distribution of chlorophyll, nor on the impact of quagga mussel grazing on chlorophyll concentration. An application of FVCOM to Lake Michigan with coupled nutrient–phytoplankton–zooplankton–detritus model (NPZD), focused on simulation of the spatial distribution of surface chlorophyll prior to the quagga mussel invasion; they attributed formation of the ‘doughnut’ shaped spring phytoplankton bloom observed in satellite imagery primarily to physical processes, including constrained nearshore–offshore transport by the thermal bar (Luo et al., 2012). An application of POM with a coupled lower food web model focused on the impacts of sediment resuspension events on the lower food web in March during the pre-mussel period, but did not extend simulations into the summer stratified period (Chen et al., 2004). Pauer et al. (2008) applied a linked lower food web model forced by a 5-km grid POM simulation for 1994–95 to evaluate the impacts of phosphorus loading on chlorophyll and phosphorus concentration in the pre-mussel period. Most Great Lakes biophysical models have neglected photoacclimation of phytoplankton and applied a fixed chlorophyll to carbon ratio, although White et al. (2012) recently applied the photoacclimation model of Geider et al. (1997) in Lake Superior.

We applied a biophysical model to test whether the observed reduction in the spring phytoplankton bloom after ~2004 can be explained by direct, local effects of quagga mussel grazing. We developed a 1-D column phytoplankton model based on the Great Lakes Primary Production model, and extended the model to simulate phytoplankton growth rate, chlorophyll concentration, and variable chlorophyll to carbon ratio (photoacclimation). The biophysical model simulated light limitation, vertical mixing, and grazing by zooplankton and quagga mussels. We used photosynthesis-irradiance parameters that were measured in Lake Michigan at ambient nutrient concentrations, representative of nutrient-limited values during the 1980s, but we did not simulate spatial and temporal variation in nutrient limitation. Dreissenid mussels remove particulate phosphorus from the water column, and excrete soluble phosphorus along with particulate feces and pseudofeces; the net effect on phosphorus cycling may be either to enhance or retard phytoplankton growth (Bocaniov et al., 2014; Zhang et al., 2011). By not simulating dynamic nutrient limitation, we isolate the direct impact of mussel grazing on phytoplankton from feedback effects on phosphorus cycling. We applied the 3-D finite volume coastal ocean model (FVCOM) to provide realistic vertical mixing. We selected 1997 and 1998 to represent pre-mussel years that were colder than normal and warmer than normal, respectively (Vanderploeg et al., 2012) to show the effect of varying meteorological conditions on phytoplankton growth and mussel grazing impacts. A secondary objective of this study was to assess the model sensitivity to atmospheric forcing and evaluate the ability of the hydrodynamic model to simulate physical features that would be important not only for the 1-D biological model applied here, but also in future applications of more complex 3D biogeochemical models; these features included currents and vertical mixing during the unstratified season, spatial extent and duration of stratification, surface mixed layer depth, and near-inertial period oscillating currents during the stratified season.

Methods

Hydrodynamic model

FVCOM (v. 3.1.6) is an unstructured grid, finite-volume, free surface, three-dimensional primitive equation ocean model that solves the momentum, continuity, temperature, salinity, and density equations (Chen et al., 2003). Turbulence closure is implemented through the MY-2.5 scheme for vertical mixing (Galperin et al., 1988) and the Smagorinsky scheme for horizontal mixing. We applied the model to Lake Michigan with 20 sigma layers of uniform thickness. The unstructured grid consisted of 5795 nodes and 10,678 elements, with element side lengths of 0.6 to 2.6 km near the coast and 4.5 to 6.8 km near the center of the lake (median 3.1 km). The lateral boundaries were closed, including the Straits of Mackinac (Fig. 1). Bathymetry was interpolated from the NOAA National Geophysical Data Center (www.ngdc.noaa.gov/mgg/greatlakes/greatlakes.html). The model was initialized on January 1, 1997 or 1998, with uniform temperature of 4 °C (obtained from NOAA CoastWatch Great Lakes Surface Environmental Analysis (GLSEA), see Observational data), and salinity and current velocities set to zero. Surface fluxes of momentum, sensible heat, and latent heat were calculated by the NOAA COARE bulk algorithm (v. 2.6) (Fairall et al., 1996). External and internal time steps were 10 s. The coefficient used in the Smagorinsky scheme for horizontal mixing was set to 0.1, and the minimum bathymetric depth was 0.1 m. Light penetration length scales were set to 5.0 m (equivalent to a diffuse attenuation coefficient of 0.2 m^{-1}), based on analysis of light penetration profiles collected in Lake Michigan during the 1990s.

Atmospheric forcing

We evaluated two sources of atmospheric forcing data in order to determine which one would provide the most accurate simulations of temperature fields, currents, and stratification for use in the biological model: one scenario with atmospheric forcing interpolated from land-based and buoy meteorological stations using the Natural Neighbor Method (NNM) (referred to here as “Interpolated forcing” or “interp”) and the other with atmospheric forcing from the North American Regional Reanalysis (NARR). Atmospheric forcing variables were U and V components of 10-m wind velocity, air temperature, relative humidity, downward shortwave, and downward longwave radiation. Upward longwave radiation was calculated in FVCOM using the simulated water surface temperature.

The interpolated forcing scenario was generated using computer codes developed for use in the NOAA Great Lakes Coastal Forecasting System, which were described in detail elsewhere (Beletsky et al., 2003; Schwab and Beletsky, 1998). Hourly atmospheric forcing variables of wind speed, wind direction, air temperature, dewpoint temperature, and cloud cover were interpolated over Lake Michigan from 18 land-based meteorological stations. In addition, wind speed, direction,

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