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Biophysical modeling assessment of the drivers for plankton dynamics in dreissenid-colonized western Lake Erie

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ABSTRACT

Given that phytoplankton and zooplankton communities have served as key ecological indicators of anthropogenic and other perturbations, a high-resolution Finite Volume Coastal Ocean Model (FVCOM) based Integrated Compartment Model (FVCOM-ICM) was implemented to investigate plankton dynamics with the inclusion of dreissenid invasion in Lake Erie, particularly in the most productive western basin. After identifying suitable horizontal and vertical resolutions that allowed for accurate depiction of in-lake nutrient concentrations and plankton biomass, we explored how variation in nutrient (phosphorus, nitrogen) loading and dreissenid mussel density could influence plankton dynamics. Our scenario-testing showed that western Lake Erie's phytoplankton community appeared more limited by phosphorus than nitrogen on both seasonal and interannual scales with light limitation occurring in the nearshore and Maumee River plume areas. Dreissenid mussel impacts varied temporally, with phytoplankton communities being highly influenced by dreissenid nutrient excretion at times (under low nutrient availability) and dreissenid grazing at other times (under bloom conditions). It was concluded that the effect of zooplankton predation on phytoplankton was stronger than that of dreissenid mussels, and that multiple algal groups could promote the efficiency of nutrient assimilation and the overall plankton production. Additionally, river inputs and wind-driven water circulation were important by causing heterogeneity in habitat conditions through nutrient advection and vertical mixing, and wind-induced surface waves could result in non-negligible down-wind redistribution of plankton biomass, which increased with wind/wave magnitude.

1. Introduction

Ability to describe the distribution and dynamics of plankton (phytoplankton and zooplankton) communities can benefit the understanding of estuarine and coastal ecosystem in numerous ways. For example, shifts in plankton community composition has been used to track environmental changes in lake and ocean ecosystems, as well as assess ecosystem health (Allinger and Reavie, 2013). Phytoplankton is often distributed in non-random patterns, potentially due to the influences of nutrient concentration, physical gradients and grazing pressure, which, in turn, affects zooplankton and ichthyoplankton dynamics (Stockwell et al., 2002). Additionally, knowledge of plankton dynamics and spatial heterogeneity has been applied to predict the behavior, performance and dynamics of fish consumers and the fisheries that they support (Beaugrand et al., 2003; Castonguay et al., 2008). For this reason, much research has been devoted to understanding the mechanisms that drive spatial and temporal variation in plankton dynamics.

Lake Erie has undergone tremendous ecological changes throughout the past fifty years of trophic history (Ludsin et al., 2001; Makarewicz and Bertram, 1991; Makarewicz et al., 1999), and it is critical to use a model to track temporal changes of plankton communities. In particular, the plankton communities in its western basin are extremely sensitive and susceptible to the ecological shifts, due to its shallow bathymetry (mean depth 7.4 m), rare stratification and high riverine runoff. For instance, plankton abundance has been substantially reduced because of the phosphorus abatement plan in the 1970s (Conroy et al., 2005a), and the

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invasion of exotic zebra (*Dreissena polymorpha*) and quagga mussels (*Dreissena bugensis*) since the late 1980s sequestered zooplankton production by reducing algal biomass especially in the well mixed western basin (Makarewicz et al., 1999). Since the 1990s, harmful *Microcystis* blooms reappeared in Lake Erie and plankton growth has been enhanced in response to the increasing total phosphorus loading and weather-driven changes (Michalak et al., 2013). Herein, we sought to improve our ability to understand the plankton dynamics in Lake Erie, particularly western Lake Erie, which has been complicated and remains largely unresolved in recent decades with the interaction of the establishment of filter-feeding *Dreissena* spp. (MacIsaac et al., 1999), increases in soluble reactive phosphorus and nitrogen (Baker et al., 2014; Daloğlu et al., 2012), and weather-driven changes in water circulation and river inflows (Michalak et al., 2013). Given that knowledge of the mechanisms that drive plankton dynamics would improve understanding and forecasting fisheries recruitment and promote interpreting the ecological status, biophysical assessment of the plankton standing stocks could benefit Lake Erie fisheries and water quality managers.

Previous research has laid the foundation in elucidating the spatiotemporal dynamics of phytoplankton and zooplankton in western Lake Erie. For example, it was found that external phosphorus loading is not the sole driver of the phytoplankton biomass variability of Lake Erie in the long term (Conroy et al., 2005a). The introduced dreissenid mussels could either inhibit the plankton population by direct filtration (Barbiero et al., 2006; Higgins and Vanderzanden, 2010) or stimulate it through remineralization (Hecky et al., 2004); the strong filtration of *Dressena* spp. has decoupled lake production from phosphorus input (Meilina et al., 1995), reconfigured the phytoplankton community (Barbiero et al., 2006) and shunted the energy flux between nearshore and offshore areas in Lake Erie (Hecky et al., 2004). While such questions have been explored with two-dimensional (2D) physical-biological models (Boegman et al., 2008a,b; Zhang et al., 2008), controversy on inhibition or stimulation of plankton production by *Dreissena* mussels still exists, and these models neither included nearshore/offshore gradients nor calculated the mass balance of suspension feeder species. Similarly, understanding of the relative roles of zooplankton versus dreissenid mussel grazing as a determinant of phytoplankton composition and abundance remains limited. On small time scales, other high-frequency processes such as underwater light climate (Porta et al., 2005), wind (Guildford et al., 2005) and stratification (Boegman et al., 2008b) could modify the plankton standing crop to some extent. However, the field investigations are limited by using a multiple stressor approach (Fitzpatrick et al., 2007). More recently, a three-dimensional (3D) model ELCOM-CAEDYM simulated phytoplankton biomass associated with the zonation of physical, chemical, and biological properties in Lake Erie (Leon et al., 2011). However, it was limited in inability to follow the complex nearshore coastlines with high resolution (e.g., Sandusky Bay was missing in the domain), which is believed to strongly affect the littoral transport (Rao and Schwab, 2007). Furthermore, Leon et al.'s (2011) 3D model did not simulate zooplankton, *Dreissena* spp., and waves, the latter of which are critical in nearshore and coastal processes (Niu et al., 2015) and likely influence plankton dynamics.

Given these information gaps (and many others), a 3D high-resolution and unstructured-grid based eutrophication model (Khangaonkar et al., 2012; Kim and Khangaonkar, 2012) was applied to Lake Erie. Our decision to use a linked physical-biological model to better resolve the drivers of Lake Erie's plankton communities emanated from the success that such approaches had in other ecosystems, both freshwater and marine (Khangaonkar et al., 2012; Leon et al., 2011; Xia et al., 2010, 2011). Moreover, biophysical models offered a means to account for potentially important biological processes (e.g., zooplankton and dreissend mussel predation, interspecies competition), as well as variation in physicochemical phenomena, including riverine loading, wind and gravity waves, which cannot be easily explored using field investigations. Overall, this study aimed to: (1) examine the interannual variability of plankton production responding to multiple environmental stressors, (2) assess the ecological implications of external nutrients loading to the onset of re-eutrophication, (3) quantify the relative importance of predation pressure of zooplankton and *Dreissena* spp. to phytoplankton proliferation, and (4) shed light on the role of physical forcing (wind, riverine forcing and surface gravity waves) in regulating plankton dynamics in western Lake Erie. In Section 2, the model configuration and settings are briefly described, and calibration and validation results are presented in Section 3. Major impacts of chemical, biological and physical factors on planktonic lake production are discussed in Section 4, and Section 5 delineates major conclusions.

2. Methods

2.1. Study site

Being the shallowest (7.4 m average depth) and smallest of Lake Erie's three basins (Fig. 1), the western basin has typically been the most biologically productive across all trophic levels (Bolsenga and Herdendorf, 1993; Ludsin et al., 2001). Western Lake Erie is also a highly dynamic, spatially heterogeneous basin, owing to inflows of the Detroit and Maumee River, which respectively contribute ∼80% and ∼5% of the total annual water to the lake (Bolsenga and Herdendorf, 1993), as well as the vast majority of nutrients (nitrogen, phosphorus) and total suspended solids (TSS) that enter the lake (Baker and Richards, 2002; Baker et al., 2014). While inflows from the Detroit River depend heavily on snowmelt in the upper Great Lakes, precipitation is the major driver of the Maumee River's flow regime (Baker and Richards, 2002), with river discharge and wind being major drivers of the extent and spatial location of the resultant open-lake Maumee River plume (Reichert et al., 2010).

2.2. Model description

We used the offline linked FVCOM-ICM (Kim and Khangaonkar, 2012) to simulate the biogeochemical kinetics in western Lake Erie, driven by the hydrodynamics model FVCOM. The configuration and verification of FVCOM (Chen et al., 2003) applied in Lake Erie is described in detail by Niu et al. (2015). The triangular unstructured grid (8721 nodes and 15,578 elements) of Lake Erie (Fig. 1a) presents a high resolution in nearshore areas of western basin and a coarser resolution in central and eastern basins with grid size ranging from 17 m to 7800 m. A transect near the Maumee River plume was taken to gain insight into the vertical distribution of phytoplankton and zooplankton (Fig. 1b and c). Two sets of grids in western Lake Erie were generated and tested for the optimal resolution, and the minimum grid size of the fine (Fig. 1b) and coarse mesh (Fig. 1c) was 17 m and 246 m, respectively. The model was also run with six, 11 and 21 sigma levels to assess the effects of vertical resolution on plankton dynamics.

The eutrophication/water quality model was built based on CE-QUAL-ICM (Cerco and Cole, 1995) with extensive adaption to accommodate triangular meshes and the advection-diffusion transport scheme in FVCOM. In each time step, the eutrophication model used hydrodynamics information from FVCOM including current velocity, temperature, water elevation, eddy viscosity and boundary flux (Kim and Khangaonkar, 2012). The mass-balance