Research papers

# Importance of the bacterial dynamics in model simulations of seasonal hypoxia

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ABSTRACT

The occurrence and spread of hypoxia in coastal waters is known to depend strongly on nutrients, primary production, water column structure, wind and tidal mixing. Accurate prediction of the onset, intensity and areal extent of hypoxia remains a challenge. Previous modeling efforts have needed to "tune" vertical mixing or phytoplankton respiration in order to obtain results that agree with field observations of dissolved oxygen (DO). In this study, we use a one-dimensional physical model coupled with a biogeochemical model to establish mechanistic links between factors involved in the evolution of seasonal hypoxia in western Long Island Sound. The coupled model includes bacterial dynamics, which allows accurate prediction of the onset of late summer hypoxia and subsequent recovery. Model results indicate that a hyperbolic temperature response function represents temperature control on bacterial community growth rate better than the traditional $Q_{10}$ function. We also find that onset of hypoxia's late summer relaxation is sensitive to factors beyond wind mixing alone. Wind mixing contributes at most 30% to the late summer DO variability. The cost of not including the bacterial dynamics in the model is an overestimation of bottom DO by as much as 700% in summer. By including bacterial dynamics, we eliminate the need to distort vertical mixing or phytoplankton respiration rate to simulate observed seasonal variability in DO. In order to accurately model DO dynamics under normal wind forcing, therefore, coastal ecosystem models need to explicitly include terms for major components of the microbial loop.

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## 1. Introduction

Eutrophication is a process that brings excessive nutrients into coastal estuaries, fuels phytoplankton production and increases organic carbon transport to the seabed (Welsh and Eller, 1991). As a consequence, seasonal hypoxia can occur when DO concentration in the water column falls below 3 mg/l (Diaz and Rosenberg, 1995; Ritter et al., 1999). The seasonal evolution of DO depletion in coastal embayments and estuaries is shaped by interactions among physical and biogeochemical processes. These processes include air–sea exchange, nutrient input, vertical mixing, horizontal advection, primary productivity, sedimentation and organic matter decomposition, as well as sediment DO demand ( Welsh and Eller, 1991; Jensen et al., 1990; Lee and Lwiza, 2008; Officer et al., 1984; Pokryfkil and Randall, 1987; Rabalais et al., 1991; Ritter et al., 1999). Hypoxia affects a wide range of coastal areas globally, and notably the Gulf of Mexico, Chesapeake Bay, Neuse Estuary, Narragansett Bay and Long Island Sound (LIS) in the U.S.

The traditional understanding of hypoxia is that bottom DO becomes under-saturated when density stratification in the overlying water is maximum, wind speeds decline to their minimum, and organic matter decomposition fuels biological oxygen demand (BOD) consuming DO, while recovery of DO from minimum levels is primarily driven by increased mixing (McCardell and O'Donnell, 2009; O'Donnell et al., 2008; Welsh and Eller, 1991). Lee and Lwiza (2008), however, noted that further depletion of DO after the onset may not be a response to further intensification of stratification. They also found that DO recovery is not associated with increased wind mixing alone, and proposed that it may be induced by horizontal exchange or reduced microbial activity.

Observational analysis of the interplay of processes responsible for eutrophication and hypoxia has always been confounded by logistical difficulties presented by conducting systematic and comprehensive field measurements with sufficient temporal resolution. However, with the piece-meal information gathered from field experiments, responses of seminal processes can be evaluated using a modeling approach. For many coastal eutrophied areas, hydrodynamic and eutrophication models have been developed to understand nutrient dynamics, biogeochemical responses and to facilitate hypoxia management. The Army Corps of Engineers Integrated Compartment Water Quality Model (CE-QUAL-ICM), for example, is one of the

models applied in Chesapeake Bay (Cerco and Cole, 1993). ChesROMS is another hydrodynamic model based on the Regional Ocean Modeling System, i.e., ROMS, (Haidvogel et al., 2008, http://www.myroms.org/) and adapted to predict harmful algal blooms and hypoxia in Chesapeake Bay. ROMS has also been adapted to study eutrophication in the Northern Gulf of Mexico (Fennel et al., 2011). In LIS, several generations of water quality models have been developed since 1987 to examine the mechanisms leading to seasonal hypoxia. The first two generations (LIS1.0 and LIS2.0) were steady-state 2-D models. The third generation model LIS3.0 is 3-D and time-varying (LISS, 2003; Science and Technical Advisory Committee, 2003). In 2001, a system-wide eutrophication model called SWEM was developed for LIS with the eutrophication module of Row Column Aesop (RCA) (HydroQual, 2001; LISS, 2003; Science and Technical Advisory Committee, 2003).

Early results from the SWEM model applied to LIS showed that DO depletion is linearly dependent on increases in dissolved nitrogen concentrations in the Sound (Science and Technical Advisory Committee, 2003). As a result, the states of Connecticut and New York and the Environmental Protection Agency (EPA) developed a Total Maximum Daily Load (TMDL) limit for LIS to enforce nitrogen reduction targets and meet standards for DO (US Environmental Protection Agency, 1998). Despite these efforts however, hypoxic conditions in LIS, 25 years later have not improved significantly and some locations have become even worse in terms of the frequency, spatial and temporal extent of hypoxia (Lee and Lwiza, 2008; O'Shea and Brosnan, 2000; Suter et al., 2014). These results suggest that nitrogen loadings may not be the single most important mechanism promoting hypoxia and that alternative hydro-dynamical and biological processes warrant closer examination.

One major problem associated with the SWEM model is that vertical mixing has to be artificially forced to go to near zero in order to obtain a reasonable representation of hypoxia (Hydroqual, 2003; O'Donnell et al., 2010). In addition, phytoplankton respiration rates have to be increased to force adequate DO consumption (O'Donnell et al., 2010). This, however, leads to a distorted simulation of the phytoplankton system, and implies that mechanisms other than vertical mixing and phytoplankton respiration are required in order to explain depletions in bottom DO. One of these mechanisms is most certainly respiration by bacteria and their predatory protists, which consume large amounts of DO when decomposing organic matter. We further note that field observations reveal large bacterial biomasses, nearly matching phytoplankton biomasses in western LIS when integrated throughout the water column (Suter, 2011). This means that in order to understand DO variability and the mechanisms leading to hypoxia, it is important to incorporate bacterial dynamics into coastal models (Fenchel, 2008; Jahnke and Craven, 1995; Lee and Lwiza, 2008), and carefully examine how the microbial loop controls remineralization processes, driving significant DO consumption in near-bottom waters. The microbial loop concept describes the flow of energy, organic matter and nutrients through unicellular organisms, including bacteria, predatory protists and parasitic viruses, to multicellular organisms and dissolved pools (Pomeroy et al., 2007). Conceptual models describing trophic carbon transfer and regeneration of inorganic N and P through bacterial degradation of organic matter and its subsequent remineralization through bacterial ammonification and predator's excretion are relatively common (e.g., Taylor, 1982; Thingstad and Giske, 2008). However, incorporation of microbial loop processes into numerical models with physical forcing is relatively rare.

In this study we simplify microbial loop participation by parameterizing bacterial dynamics which includes aerobic bacterial biomass growth, respiration, regeneration of inorganic N and P, and grazing by zooplankton. It also includes the relative contributions of bacterial remineralization and zooplankton excretion to inorganic nutrient regeneration. However, for simplicity's sake and lack of well-constrained response functions, we ignore bacterial diversity, zooplankton disaggregation and varying impact of viral lysis in the loop. The mechanisms leading to seasonal hypoxia and recovery of bottom DO were investigated by applying a fully coupled 1-D physical–biogeochemical model to a western LIS station (i.e., A4, Execution Rocks, Fig. 1). With a 1-D model it is easier to tease out different factors controlling seasonal DO variability than in a 3-D model (Miladinova and Stips, 2010). In addition, it is vertical mixing that dominates the circulation structure instead of horizontal advection in LIS. O'Donnell et al., (2008) reported that 9 out of 11 observed events associated with ventilation at the Execution Rocks station in LIS resulted from enhanced vertical mixing instead of horizontal advection. We chose this location to run our simulation because it is the single most intensively studied site in LIS and DO seasonal variability is mostly driven by vertical mixing.

In order to examine impacts of activity associated with bacteria on seasonal DO variability, the code of the 1-D coupled model was
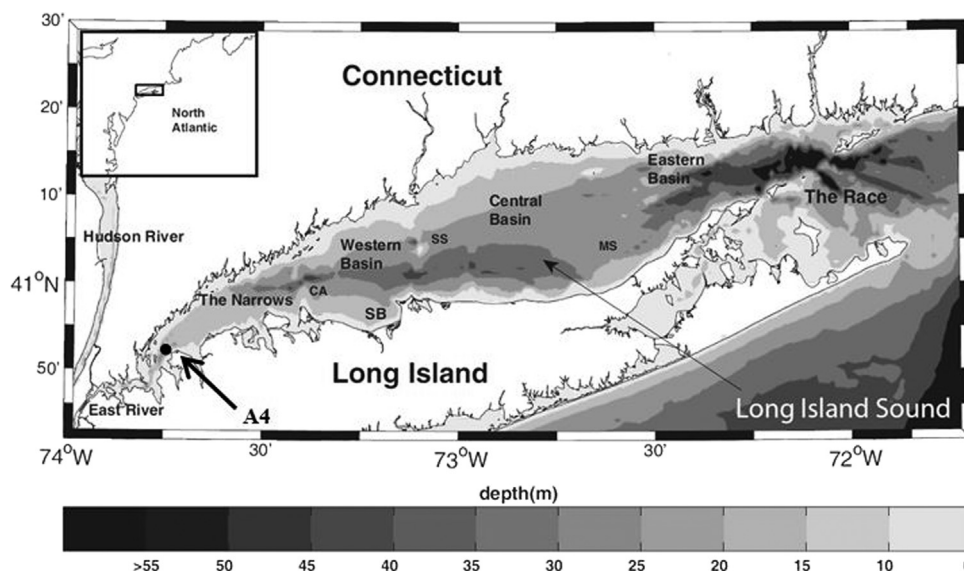


**Fig. 1.** Long Island Sound Bathymetry (Lee, 2009).