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Nutrient input and the competition between *Phaeocystis pouchetii* and diatoms in Massachusetts Bay spring bloom

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ABSTRACT

The phytoplankton community in Massachusetts Bay has displayed significant inter-annual variability and possible trends over the last two decades, with increasing frequency and magnitude of strong *Phaeocystis pouchetii* blooms and generally opposite fluctuations in diatom abundances. An analysis of historical data suggests that changes in winter nitrate and silicate concentrations (both their absolute and relative values) may play a critical role in the competition between diatoms and *P. pouchetii*. We developed a new ecosystem model to simulate *Phaeocystis* dynamics and to test the significance of variable winter nutrient levels. Idealized simulations for the years 1992–2009 generally reproduced the observed inter-annual variability of *P. pouchetii* and diatoms during the spring blooms, with modeled peaks in biomass of diatoms and *P. pouchetii* significantly being correlated with their observed mean abundances. Moreover, modeled peak biomass ratio and observed mean abundance ratio between diatoms and *P. pouchetii* during the spring blooms were similarly depending on both the winter nitrate and residual nitrate (nitrate minus silicate) concentrations. These results are consistent with resource competition theory in which relatively low winter nutrient concentrations would favor species with faster growth rate (diatoms, in this case). With sufficiently high winter nutrient concentrations, however, *P. pouchetii* was able to grow before nitrate being depleted by diatoms, even though winter Si > N. Our observations further indicate that inter-annual nutrient variability and consequently spring bloom phytoplankton variability in Massachusetts Bay are likely driven by changes in winter nutrient fluxes from Gulf of Maine rivers and winter convective mixing. These fluxes may have been modulated by large-scale processes such as the North Atlantic Oscillations and Arctic melting through the river discharges, winter-storm activities (and hence winter mixing and nutrient supply), and the deep waters inflow into the Gulf of Maine.

1. Introduction

Massachusetts Bay (MB) is a coastal embayment in the western Gulf of Maine (GOM) (Fig. 1). Recent studies indicated that the phytoplankton community in the bay displayed strong inter-annual variability and possible trends over the last two decades (Hunt et al., 2010). In particular, both the frequency and magnitude of *Phaeocystis pouchetii* blooms have increased with diatom and *P. pouchetii* abundances largely fluctuating in opposite phase. Yet, the dynamic mechanisms leading to such changes remain unclear. Given the different nutrient requirements of diatoms and *P. pouchetii*, one potential mechanism is the nutrient competition between these two species (e.g. Egge and Aksnes, 1992; Lancelot and Rousseau, 1994; Officer and Ryther, 1980; Wilson et al., 2007).

Circulation in MB is driven by local forcing (winds and runoff) and the GOM intruding current around Cape Ann (Fig. 1), which is a branch of the western Maine Coastal Current (WMCC), a buoyancy- and wind–driven current that extends from the eastern Maine Coastal Current (EMCC) (Bigelow, 1927; Brooks, 1985; Geyer et al., 1992, 2004; Lynch et al., 1997; Pettigrew et al., 2005). The WMCC also includes contributions from a coastal freshwater plume driven by river discharges. In spring, strong river runoff and downwelling favorable winds produce a narrower and stronger coastal jet and an enhanced intruding flow (Churchill et al., 2005; Geyer et al., 2004). The jet may separate from the coastline to form meso-scale eddies in the North Passage (Jiang et al., 2011). During winter and spring, the intruding current from the GOM tends to extend southward along the MB coast, and sometimes can penetrate deeply into Cape Cod Bay. Thus, MB is a semi-enclosed system with strong input from the GOM through the North Passage.

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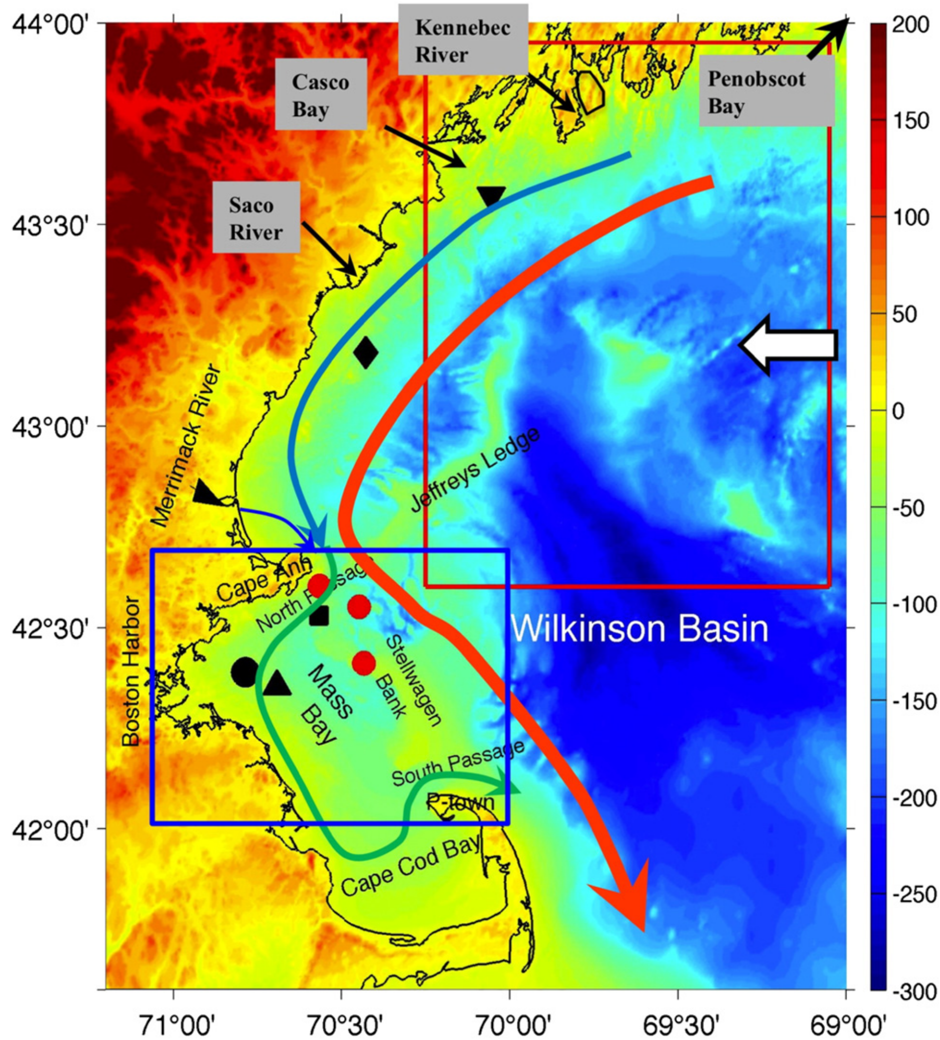

Fig. 1. Bathymetry (color) and circulation (broad arrows) in the western GOM and MB. Symbols: MWRA outfall (black dot), GoMOOS-buoy A, B, and C (square, diamond, and downward triangle), NDBC buoy 44013 (black triangle), and MWRA stations F26–28 (red dots) along the MB boundary (other stations not shown). Red box indicates the conceptual MB nutrient source area, and blue box indicates our western MB study area. Broad arrows highlight the general circulation pattern including GOM coastal plume (blue, high Si/N), WMCC (red, low Si/N), Merrimack River plume (deep blue, high Si/N), and MB coastal current including the GOM intruding current (green, median Si/N). Broad open arrow indicates input from the eastern Gulf of Maine including EMCC and transport of GOM deep waters.

The MB ecosystem is strongly influenced by the water, nutrients and zooplankton inputs from the GOM intruding current (Jiang et al., 2007a, b). In particular, nutrient input from the GOM constitutes the primary source for MB nutrients, with additional contribution from river discharges in Boston Harbor and the Boston sewage effluent (HydroQual and Normandeau, 1995). Therefore, we may expect a significant influence of the GOM nutrient input on the abundance and species composition in the MB phytoplankton community. Furthermore, the coastal current may propagate signals of large-scale processes into MB through transport of water, nutrients, and biota.

Phytoplankton in MB exhibit a strong seasonal cycle with typically strong spring and fall blooms. The spring bloom normally occurs in late March and early April while the fall bloom occurs in October and early November, both are dominated by diatoms species and both show strong inter-annual variations in magnitude (Hunt et al., 2010; Jiang et al., 2007a; Keller et al., 2001; Townsend et al., 1994). Surface nutrients, especially dissolved inorganic nitrogen (DIN), are nearly depleted following spring bloom and late spring and summer primary production is relatively low, with a phytoplankton assemblage dominated by small flagellates (e.g. Libby et al., 2007). *P. pouchetii* populations had been recorded during the spring bloom in 1990s, but the abundances had been relatively low. In recent years, however, *P. pouchetii* has become a more important component of the MB phytoplankton community during the spring bloom, with mean abundances in some years exceeding 2×10^6 cells L^{-1} (e.g., Hunt et al., 2010; Libby et al., 2007, 2008). These *P. pouchetii* blooms are more confined to western portion of MB, waters fed by the GOM intruding current.

Both diatoms and *Phaeocystis* are important to the global carbon cycle and production of dimethylsuflide (DMS; e.g. Arrigo et al., 1999; Smith et al., 1991; Stefels, 1997; Townsend and Keller, 1996). *Phaeocystis* blooms were typically viewed as a nuisance phenomenon, sometimes forming foam on beaches. Recent studies have suggested that *Phaeocystis* colonies have high hemolytic lipid content, which may be toxic to fish larvae (Eilertsen and Raa, 1995; Hansen et al., 2003; Stabell et al., 1999; van Rijssel et al., 2007). Intense *Phaeocystis* blooms may also affect benthic communities by depleting bottom dissolved oxygen following the demise of the blooms and the sinking of cells to the bottom (Rogers and Lockwood, 1990; Spilmont et al.,