Deep-Sea Research II ∎ (∎∎∎∎) ∎∎∎–∎∎∎

Contents lists available at ScienceDirect

Deep-Sea Research II

journal homepage: www.elsevier.com/locate/dsr2

Nutrients and water masses in the Gulf of Maine–Georges Bank region: Variability and importance to blooms of the toxic dinoflagellate *Alexandrium fundyense*

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ARTICLE INFO

Keywords:
Nutrients
Water masses
Alexandrium fundyense
Gulf of Maine
Georges Bank
T–S diagrams
Slope waters
Shelf waters
Phosphate limitation
Ammonium

ABSTRACT

We report here the results of ten oceanographic survey cruises carried out in the Gulf of Maine–Georges Bank region of the Northwest Atlantic during the late spring to summer period in 2007, 2008 and 2010, for which we examine and characterize relationships among dissolved inorganic nutrient fields, water mass dynamics and cell densities of the toxic dinoflagellate *Alexandrium fundyense*. Nutrients are supplied to continental shelf waters of the Gulf of Maine–Georges Bank region by inflows of deep offshore water masses; once in the Gulf they are transported with the residual circulation and mix with surface waters, both in the Gulf and on the Bank. Those fluxes of offshore water masses and their nutrient loads are the major source of nutrients for phytoplankton production in the region, including annual blooms of *A. fundyense* in the Gulf and on Georges Bank. This much is already known. We suggest here that the locations and magnitude of *A. fundyense* blooms are controlled in part by variable nutrient fluxes to the interior Gulf of Maine from offshore, and, those interior Gulf of Maine waters are, in turn, the main nutrient source to Georges Bank, which are brought onto the Bank by tidal pumping on the Northern Flank. We present evidence that nitrate is the initial form of nitrogenous nutrient for *A. fundyense* blooms, but it is quickly depleted to limiting concentrations of less than 0.5 μM, at which time continued growth and maintenance of the population is likely fueled by recycled ammonium. We also show that phosphate may be the limiting nutrient over much of Georges Bank in summer, allowing recycled ammonium concentrations to increase. Our temperature–salinity analyses reveal spatial and temporal (seasonal and interannual) variability in the relative proportions of two deep source waters that enter the Gulf of Maine at depth through the Northeast Channel: Warm Slope Water (WSW) and Labrador Slope Water (LSW). Those two source waters are known to vary in their nutrient loads, with nitrate concentrations about 50% higher in WSW than LSW, for example, and as such the proportions of these two water masses to one another are important determinants of the overall nutrient loads in the interior Gulf. In addition to these deep slope water fluxes, we show evidence here of episodic fluxes of relatively fresh and low-nutrient shelf waters from the Nova Scotian Shelf, which enter the Gulf in pulses at depths between the surface and approximately 150 m, displacing deep slope waters, and consequently they significantly dilute the Gulf's interior waters, reducing nutrient concentrations and, in turn, affect the magnitude of *A. fundyense* blooms.

1. Introduction

1.1. *Alexandrium fundyense* blooms

Studies of the oceanography and population dynamics of the toxic dinoflagellate *A. fundyense*, blooms of which are responsible for outbreaks of Paralytic Shellfish Poisoning in the Gulf of Maine region (Fig. 1) and shelf waters throughout much of the world ocean (Wyatt and Jenkinson, 1997), have intensified in recent years (e.g., see Anderson, 1997; Anderson et al., 2005a; and papers in this issue). Those studies have led to a number of important refinements in our understanding of the basic physical and biological factors that control bloom dynamics, and have begun to highlight the importance of variable water mass dynamics in the Gulf region and the resulting variability in dissolved inorganic nutrient fluxes.

Blooms of *A. fundyense* occur annually in the Gulf of Maine and on Georges Bank but they vary among years in their cell densities and areal coverage (McGillicuddy et al., 2005a, this issue; Anderson et al., this issue-a). Seasonal blooms in the coastal Gulf of Maine commence

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http://dx.doi.org/10.1016/j.dsr2.2013.08.003

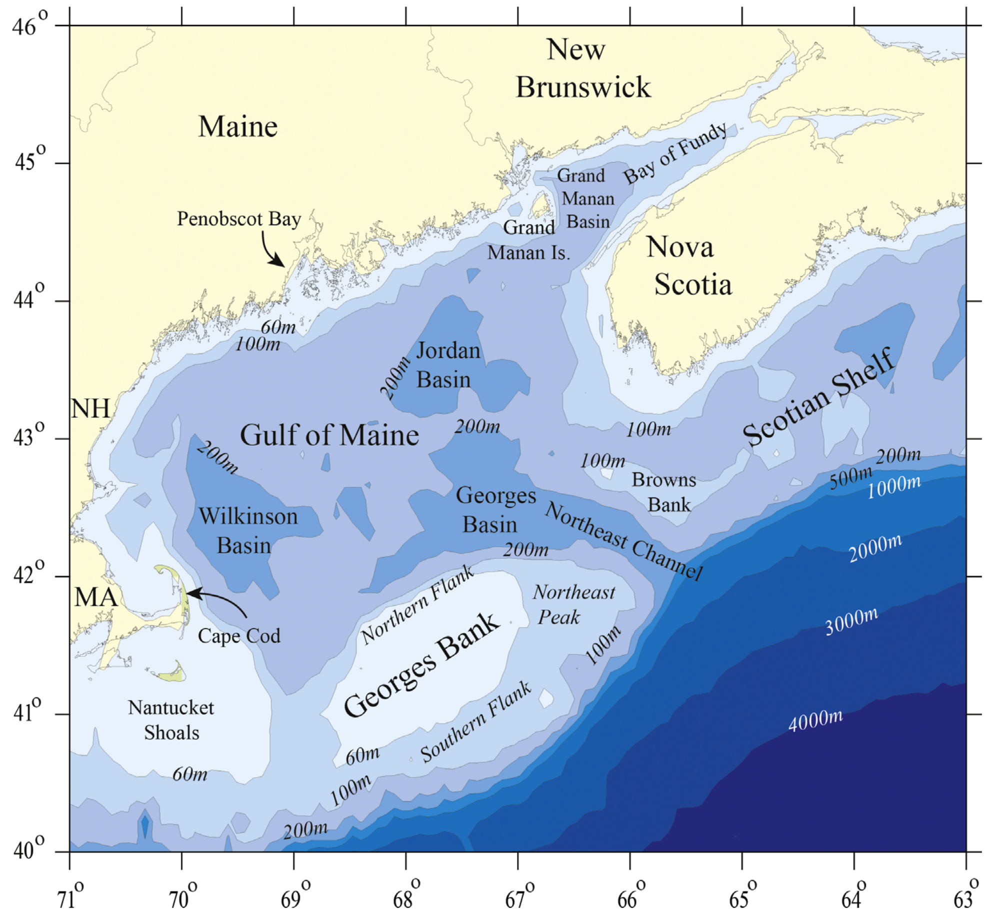

Fig. 1. Map of the Gulf of Maine and Georges Bank with key bathymetric features identified, and specific geographic areas identified. Bottom depths are given in meters.

when overwintering benthic resting cysts germinate in the spring and inoculate surface waters with vegetative cells (Anderson et al., 2005b; Matrai et al., 2005), although suspended cysts may also play a role (Kirn et al., 2005; Pilskaln et al., this issue). The initial appearance of these *A. fundyense* cells generally follows the annual spring phytoplankton bloom, which is dominated by diatoms (Bigelow, 1926; Bigelow et al., 1940). The *A. fundyense* growth season may begin as early as March in near shore waters, and in some years it can last into October, especially in offshore waters on Georges Bank and in the Bay of Fundy (e.g., Anderson et al., this issue-a; McGillicuddy et al., this issue). As the *A. fundyense* cells multiply they are transported throughout the region in the residual near-surface circulation. Of course, being autotrophic phytoplankton, their rates of photosynthesis and population growth are potentially limited by a number of factors, including light and nutrients (Townsend et al., 2001; McGillicuddy et al., 2005b), zooplankton grazing (Turner and Borkman, 2005), and possibly by competitive interactions with other phytoplankton taxa, particularly diatoms (Townsend et al., 2005; Gettings, 2010; Gettings et al., this issue).

In addition to bloom dependence on the initial stock size of benthic resting cysts each year (Anderson et al., this issue-b; McGillicuddy et al., 2011), interannual variability in the distributions and cell densities of *A. fundyense* blooms may be controlled by the availability of dissolved inorganic nutrients (Townsend et al., 2001, 2005), concentrations and proportions of which (e.g., proportions of nitrate and silicate) may in turn be undergoing climate change-related alterations in the Gulf of Maine region (Townsend et al., 2010; Rebuck, 2011).

Dependence of *A. fundyense* bloom initiation and population maintenance on the availability of dissolved inorganic nitrogen, in the form of nitrate, explains the occurrence of three fairly distinct population centers in the region where cells reach their highest densities; those population centers are the western Bay of Fundy, the northern Gulf of Maine, and Georges Bank (Anderson, 1997; Townsend et al., 2005; McGillicuddy et al., this issue). Each of these areas is characterized by vigorous vertical mixing by tides and associated tidal pumping of deep water nutrients into surface waters, which are subsequently entrained in the residual surface circulation; those areas of energetic tidal mixing are easily seen as cooler surface waters in satellite images of sea surface temperature (e.g., Townsend et al., 2006; Fig. 2). The first of these three *A. fundyense* population centers, the western Bay of Fundy, is believed to be a site of significant retention of plankton populations in the Minas Basin cyclonic gyre, in warmer, vertically stratified surface waters surrounded by tidally well mixed waters where new nutrients are injected which stimulate and sustain the blooms. The gyre itself is leaky (e.g., see Aretxabaleta et al., 2008, 2009) and as a result, some cells escape the Bay of Fundy and seed the northern Gulf of Maine population where cells continue to grow in the Eastern Maine Coastal Current (EMCC), waters that are also enriched with nutrients as a result of tidal mixing (Townsend et al., 1987; Brooks and Townsend, 1989). Perhaps more important than cells leaking from the Bay of Fundy in seeding the Gulf of Maine population is the additional input of cells into the EMCC from an extensive benthic cyst bed off the Maine coast (Anderson et al., 2005b). The trajectory and volume transport of the EMCC that carries cells and nutrients to the west is variable, with a branch turning offshore in the eastern Gulf of Maine (Pettigrew et al., 2005), and an inner coastal limb (the Western Maine Coastal Current) that can at times extend much farther to the west along

Please cite this article as: Townsend, D.W., et al., Nutrients and water masses in the Gulf of Maine–Georges Bank region: Variability and importance to blooms of the toxic dinoflagellate *Alexandrium*.... Deep-Sea Res. II (2013), http://dx.doi.org/10.1016/j.dsr2.2013.08.003