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Investigating the importance of sediment resuspension in *Alexandrium fundyense* cyst population dynamics in the Gulf of Maine

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ABSTRACT

Cysts of *Alexandrium fundyense*, a dinoflagellate that causes toxic algal blooms in the Gulf of Maine, spend the winter as dormant cells in the upper layer of bottom sediment or the bottom nepheloid layer and germinate in spring to initiate new blooms. Erosion measurements were made on sediment cores collected at seven stations in the Gulf of Maine in the autumn of 2011 to explore if resuspension (by waves and currents) could change the distribution of over-wintering cysts from patterns observed in the previous autumn; or if resuspension could contribute cysts to the water column during spring when cysts are viable. The mass of sediment eroded from the core surface at 0.4 Pa ranged from 0.05 kg m^{-2} near Grand Manan Island, to 0.35 kg m^{-2} in northern Wilkinson Basin. The depth of sediment eroded ranged from about 0.05 mm at a station with sandy sediment at 70 m water depth on the western Maine shelf, to about 1.2 mm in clayey–silt sediment at 250 m water depth in northern Wilkinson Basin. The sediment erodibility measurements were used in a sediment-transport model forced with modeled waves and currents for the period October 1, 2010 to May 31, 2011 to predict resuspension and bed erosion. The simulated spatial distribution and variation of bottom shear stress was controlled by the strength of the semi-diurnal tidal currents, which decrease from east to west along the Maine coast, and oscillatory wave-induced currents, which are strongest in shallow water. Simulations showed occasional sediment resuspension along the central and western Maine coast associated with storms, steady resuspension on the eastern Maine shelf and in the Bay of Fundy associated with tidal currents, no resuspension in northern Wilkinson Basin, and very small resuspension in western Jordan Basin. The sediment response in the model depended primarily on the profile of sediment erodibility, strength and time history of bottom stress, consolidation time scale, and the current in the water column. Based on analysis of wave data from offshore buoys from 1996 to 2012, the number of wave events inducing a bottom shear stress large enough to resuspend sediment at 80 m ranged from 0 to 2 in spring (April and May) and 0 to 10 in winter (October through March). Wave-induced resuspension is unlikely in water greater than about 100 m deep. The observations and model results suggest that a millimeter or so of sediment and associated cysts may be mobilized in both winter and spring, and that the frequency of resuspension will vary interannually. Depending on cyst concentration in the sediment and the vertical distribution in the water column, these events could result in a concentration in the water column of at least 10^{4} cysts m^{-3}. In some years, resuspension events could episodically introduce cysts into the water column in spring, where germination is likely to be facilitated at the time of bloom formation. An assessment of the quantitative effects of cyst resuspension on bloom dynamics in any particular year requires more detailed investigation.

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1. Introduction

Several types of harmful algal blooms (HABs) occur in the Gulf of Maine. The most significant of these are caused by the toxic dinoflagellate *Alexandrium fundyense*,[1] an organism that produces potent neurotoxins that accumulate in shellfish, causing paralytic shellfish poisoning (PSP) in human consumers. The life-history of *A. fundyense* has been described by Anderson and Wall (1978), Anderson (1998), and Anderson et al. (2005c). In brief, blooms

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[1] In this study, we have focused on the harmful algal species *Alexandrium tamarense* Group I, which we refer to as *A. fundyense*, the renaming proposed by Lilly et al. (2007).

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begin in spring (April and May) when dormant cysts in the bottom sediments or near-bottom waters (Kirn et al., 2005; Pilskaln et al., this issue-b) transition to motile, vegetative cells (germlings) when an internal, annual clock allows them to germinate (Anderson and Keafer, 1987). That germination is further regulated by oxygen, temperature, and light (Anderson, 1980; Anderson et al., 1987). As long as oxygen is present, germination is possible and the rate of germination increases with higher temperature and more light. For example, laboratory studies of germination of cysts from the Gulf of Maine in light increased from 1.6% day^{-1} at 6 °C to 8.7% day^{-1} at 15 °C; at 15 °C in dark conditions, germination was 4.2% day^{-1} (Anderson et al., 2005c). The mechanism(s) by which cysts exit the upper centimeter or so of the bottom sediment has not yet been elucidated. Germination may occur only in a thin, oxygenated veneer at the sediment surface. Cysts buried below that level have insufficient oxygen to germinate and thus will eventually die unless they are moved back to the sediment surface by bioturbation or some other mixing process (Anderson et al., this issue-b). *Alexandrium* cysts are thought to remain viable in the sediment for at least a few decades (Keafer et al., 1992).

Once in the water column and depending on conditions such as temperature, light, nutrient availability, and currents, the single-cell germlings can divide and produce vegetative cells that continue to divide asexually to produce blooms, commonly called ‘red tides.’ Shellfish that ingest sufficient numbers of these cells can become toxic to humans, and their presence requires that the shellfisheries be closed. As blooms subside, the *A. fundyense* cells form cysts that sink to the sea floor and are sequestered in bottom sediment or the benthic nepheloid layer (Kirn et al., 2005; Pilskaln et al., this issue-a) over the winter where they remain dormant until the following spring.

Efforts are underway to predict the intensity and extent of *A. fundyense* blooms in the Gulf of Maine, which vary from year to year (McGillicuddy et al., 2005; Anderson et al., this issue-b), using coupled physical and biological models (Stock et al., 2005; McGillicuddy et al. 2005, 2011; He et al., 2008; Li et al., 2009). The seasonal prediction strategy uses the distribution of *A. fundyense* cysts in the upper 1 cm of bottom sediment mapped during autumn (a ‘cyst map’ of the potential seed population) and hydrodynamic model predictions driven by hydrodynamic and atmospheric conditions from past years to form an ensemble of predictions for the current year. During the bloom season, results from an experimental weekly nowcast/forecast system are also available (http://omglnx3.meas.ncsu.edu/GOMTOX/2013forecast/). Results show that the cyst abundance is a first-order predictor of overall modeled bloom severity (He et al., 2008; McGillicuddy et al., 2011). Metrics for characterizing the intensity of blooms include the concentration of the bloom (He et al., 2008; Li et al., 2009), geographic extent of coastline impacted (Kleindinst et al., this issue; Anderson et al., this issue-b), and the southernmost extent of coastline closed due to toxicity (McGillicuddy et al., 2011). The model does not include cyst resuspension by currents or waves.

The magnitude of bottom shear stress (tangential force per unit area; hereafter simply stress) caused by the combined action of steady currents and oscillatory wave flow determines sediment (and hence cyst) resuspension. Kirn et al. (2005) observed *A. fundyense* cysts in the water column in the Gulf of Maine and Bay of Fundy in winter and spring, attributed them to resuspension by waves and currents, and proposed that such cysts from resuspension are important in inoculating the spring bloom. This paper extends these ideas by investigating the importance of resuspension and transport in two phases of the *A. fundyense* life history. Two questions are addressed: (1) Are stress events in spring (April and May), when cysts are viable, sufficient to resuspend them from the bottom sediment and mix them into the water column; and (2) can wave- and current-induced resuspension and transport redistribute the dormant cyst population during the winter (October–March), thus altering the distribution of cysts mapped the previous autumn? The answers to both these questions have significant implications for forecasting HABs. For example, if mixing of cysts into bottom water is influenced by stress events, germination might occur episodically rather than at a more constant, gradual rate. Resuspended cysts will germinate more easily in the water column due to the presence of oxygen and possibly light, compared to those in the sediments. If redistribution of the cysts by resuspension occurs after the autumn cyst map data are collected, forecasts might be improved by including this redistribution.

The relationship between the physical forcing (stress) and the sediment response (erodibility) is a key to understanding the mobilization potential of *A. fundyense* cysts. This paper presents estimates of bottom stress in the winter of 2010–2011 and spring of 2011 computed from wave and current models, and field measurements of sediment eroded as a function of stress magnitude at selected locations in the Gulf of Maine. The sediment erodibility observations and stress estimates are used to assess the extent of sediment resuspension and its possible effect on the abundance and germination of *A. fundyense* cysts. Estimates of wave-induced stress for the period 2004–2010 provide an assessment of the inter-annual variability of large stress events.

2. Methods

2.1. Sampling

Sampling of the bottom sediment in the western Gulf of Maine was carried out on two autumn cyst surveys: R.V. *Endeavor* cruise 486 (EN486) from October 10 to 23, 2010 and R.V. *Oceanus* cruise 477 (OC477) from October 23 to November 4, 2011 (Fig. 1). Stations are referenced by letters that refer to their geographic location: Grand Manan (GM), eastern Maine shelf (EMS), central Maine shelf (CMS), western Maine shelf (WMS), central Maine seed bed (CMSB), western Jordan Basin (WJB), and northern Wilkinson Basin (NWB). Although stations are referenced by geographic area for simplicity, they are observations at a single location. The primary objective of these cruises was to map the concentration and distribution of *A. fundyense* cysts in the surficial sediment in autumn to use as the basis for model predictions of blooms the following spring. Samples to determine cyst concentrations and sediment texture were obtained at 101 stations on EN486 and 109 stations on OC477 using a Craib corer with a 0.06-m diameter core barrel that reliably collects cores with undisturbed surface layers (Craib, 1965). Six replicate Craib cores were obtained at stations 43, CMSB, and GM to assess local variability. For cyst analysis, 5 cm^3 of sediment were obtained from the 0 to 1 cm interval of the core and 5 cm^3 from the underlying 1 to 3 cm interval. After sampling for cyst enumeration, there was insufficient sediment left from the 0 to 1 cm sample for texture analysis, so 5 cm^3 of sediment from the 0 to 1 cm interval and 10 cm^3 from the 1 to 3 cm interval were combined, providing a 15 cm^3 sample for texture analysis that characterizes the average texture in the upper 3 cm.

Two 10.7-cm diameter cores were obtained for analysis of sediment erodibility at six locations on EN486 (4, 15, CMS, CMSB, EMS, and GM) and at 10 locations on OC477 (4, 9, WMS, NWB, CMS, CMSB, EMS, 52, WJB, and GM) (Fig. 1) with a U.S. Geological Survey (USGS) hydraulically damped gravity corer designed to collect undisturbed samples of the surficial sediment (Bothner et al., 1997; Law et al., 2008). On OC477, video imagery of the core barrel entering the sediment was obtained at stations in water depths less than 200 m (the pressure limit of the video housing). A qualitative assessment of core quality was based on the video of

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