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## Alexandrium fundyense cysts in the Gulf of Maine: Long-term time series of abundance and distribution, and linkages to past and future blooms



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## ABSTRACT

Here we document *Alexandrium fundyense* cyst abundance and distribution patterns over nine years (1997 and 2004–2011) in the coastal waters of the Gulf of Maine (GOM) and identify linkages between those patterns and several metrics of the severity or magnitude of blooms occurring before and after each autumn cyst survey. We also explore the relative utility of two measures of cyst abundance and demonstrate that GOM cyst counts can be normalized to sediment volume, revealing meaningful patterns equivalent to those determined with dry weight normalization.

Cyst concentrations were highly variable spatially. Two distinct seedbeds (defined here as accumulation zones with  $> 300$  cysts  $\text{cm}^{-3}$ ) are evident, one in the Bay of Fundy (BOF) and one in mid-coast Maine. Overall, seedbed locations remained relatively constant through time, but their area varied 3–4 fold, and total cyst abundance more than 10 fold among years. A major expansion of the mid-coast Maine seedbed occurred in 2009 following an unusually intense *A. fundyense* bloom with visible red-water conditions, but that feature disappeared by late 2010. The regional system thus has only two seedbeds with the bathymetry, sediment characteristics, currents, biology, and environmental conditions necessary to persist for decades or longer. Strong positive correlations were confirmed between the abundance of cysts in both the 0–1 and the 0–3 cm layers of sediments in autumn and geographic measures of the extent of the bloom that occurred the next year (i.e., *cysts*→*blooms*), such as the length of coastline closed due to shellfish toxicity or the southernmost latitude of shellfish closures. In general, these metrics of bloom geographic extent did not correlate with the number of cysts in sediments following the blooms (*blooms*→*cysts*). There are, however, significant positive correlations between 0–3 cm cyst abundances and metrics of the preceding bloom that are indicative of bloom intensity or vegetative cell abundance (e.g., cumulative shellfish toxicity, duration of detectable toxicity in shellfish, and bloom termination date). These data suggest that it may be possible to use cyst abundance to empirically forecast the geographic extent of the forthcoming bloom and, conversely, to use other metrics from bloom and toxicity events to forecast the size of the subsequent cyst population as the inoculum for the next year's bloom. This is an important step towards understanding the excystment/encystment cycle in *A. fundyense* bloom dynamics while also augmenting our predictive capability for this HAB-forming species in the GOM.

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### 1. Introduction

Many harmful algal bloom (HAB) species produce dormant cysts or resting spores during their life histories. The resulting

alternation between a dormant, benthic stage and a motile, vegetative existence is critically important in many aspects of bloom dynamics. Cyst germination provides an inoculum for blooms, and cyst formation can remove substantial numbers of cells from blooms as they terminate. Cysts also have other important ecological roles such as species dispersal, survival through adverse conditions, and genetic recombination when sexuality is involved in their formation (Wall, 1971).

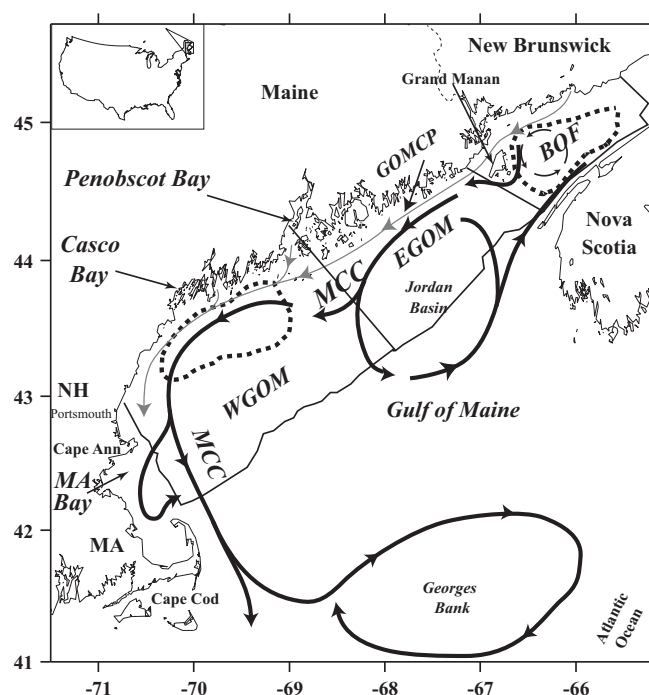
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Dinoflagellate resting cysts accumulate in bottom sediments (e.g., Anderson et al., 1982) or near-bottom nepheloid layers (Kirn et al., 2005; Piaskaln et al., 2014b); the amount of time spent in dormant or quiescent states (Pfiester and Anderson, 1987) is determined by both internal and external factors. Internal regulation includes a mandatory maturation period after cysts are formed that can prevent germination for days to months depending on the species (e.g., Anderson, 1980; Bravo and Anderson, 1994) and, for some species, an endogenous annual clock as observed in *Alexandrium fundyense* (Anderson and Keafer, 1987; Matrai et al., 2005). External regulation includes temperatures that inhibit germination above and below a “window” or permissive range (Dale, 1983; Anderson, 1998), and light, which is required by some species for germination or which speeds up the germination process compared to its rate in darkness (Anderson et al., 1987, 2005c). Most dinoflagellate species have an absolute requirement for oxygen during germination (Anderson et al., 1987; Rengefors and Anderson, 1998; Kremp and Anderson, 2000). Cysts buried deep in the sediment can thus remain quiescent for many years (decades to as long as a century (Ribeiro et al., 2011; Miyazono et al., 2012)), their fate being either eventual death if anoxia persists, or germination should they be transported to oxic conditions in the sediment surface or overlying water via physical processes or bioturbation.

Clearly, the location of cyst accumulations in bottom sediments (termed “seedbeds”) can be an important determinant of the location of resulting blooms, and the size of the cyst populations and the timing and extent of excystment and encystment can directly affect the magnitude of the blooms in some regions (Wall, 1971; Anderson, 1998; McGillicuddy et al., 2011). Surveys of the distribution and abundance of cysts can therefore be very useful in ecological and monitoring studies. Historically, such mapping studies have been used to define the geographic range of a particular HAB species (e.g., Anderson et al., 1982; Imai et al., 1991), to identify potential seedbeds for bloom initiation (e.g., Tyler et al., 1982) or sites for monitoring (Anderson et al., 1982; Hattenrath et al., 2010), to study the dispersal of an organism from one region to another (e.g., Imai et al., 1991; Anderson et al., 1982), or for use in numerical models of HAB population dynamics (McGillicuddy et al., 2003, 2005; Anderson et al., 2005c; Stock et al., 2005; He et al., 2008).

The concept of a discrete seedbed may not be appropriate in some locations due to the widespread, dispersed distribution of some cysts and the likelihood that germination will therefore occur over a large area. In many areas, however, there is evidence for localized cyst accumulations, both in estuarine systems and in deeper coastal waters. Within the shallow Nauset Marsh System on Cape Cod, for example, surveys revealed three highly localized *A. fundyense* cyst seedbeds at the extreme ends of the complex network of channels and salt ponds that comprise that system (Crespo et al., 2011). Surveys during bloom seasons document the tight link between these seedbeds and the areas of bloom initiation and retention within the system. A similar linkage between cyst seedbeds and localized blooms has been observed in lagoons, harbors, or other such sites in the Mediterranean, such as in Thau Lagoon, France (Genovesi et al., 2009), Cork Harbor, Ireland (Ni Rathaille and Raine, 2011) and Arenys de Mar harbor, Spain (Angeles et al., 2010, 2012).

Examples of cyst seedbeds in deeper coastal waters are less common (e.g., Anderson and Keafer, 1985; Turgeon et al., 1990; Anderson et al., 2005c), presumably due to the expense and difficulty of large-scale mapping. Here we describe the cyst accumulations documented during a nine-year series of large-scale, annual mapping surveys within the Gulf of Maine (GOM) coastal waters (USA and Canada) and examine relationships between those distributions and the magnitude and extent of



**Fig. 1.** Designation of the eastern Gulf of Maine (EGOM), western Gulf of Maine (WGOM), and Bay of Fundy (BOF) subregions of the study area. Note that the outer boundaries of these regions are defined by the cyst mapping survey areas. General locations of the mid-coast Maine cyst seedbed and the BOF seedbed are indicated by dotted lines. Portions of the WGOM (e.g., Massachusetts Bay) are not included in this definition, but are indeed part of the GOM. Likewise, the BOF subregion does not include the entire bay. Major current systems are shown (black = Maine Coastal Current (MCC); light grey = Gulf of Maine Coastal Plume (GOMCP; Keafer et al., 2005). (NH – New Hampshire; MA – Massachusetts).

*A. fundyense* blooms in the years preceding and following each survey. We also present data on the manner in which cysts can be enumerated in surface sediment samples for ecological studies, and on the variability inherent in cyst sampling and counting<sup>1</sup>.

These cyst distributions are best understood in the context of GOM hydrography (Fig. 1), of which a dominant feature is the Maine Coastal Current or MCC (Brooks and Townsend, 1989; Lynch et al., 1997; Pettigrew et al., 2005) – a composite of multiple segments and branch points. Conceptual models of *A. fundyense* bloom dynamics within the MCC have been provided by Anderson et al. (2005c) and McGillicuddy et al. (2005). Briefly, key features are two large cyst seedbeds – one in the Bay of Fundy (BOF) and the other offshore of mid-coast Maine (Anderson et al., 2005c). Cysts germinate from the BOF seedbed, causing recurrent blooms within the bay that are self-seeding with respect to future outbreaks in that area. In effect, the BOF is an incubator for localized populations in that area, but the incubator is leaky (Aretxabaleta et al., 2008, 2009), as cells can be transported into the MCC, where they bloom, particularly at the distal end of the eastern segment of that coastal current, where waters warm and stratify (Townsend et al., 2001). Some cells travel south and west with the MCC, while others deposit cysts in the mid-coast Maine seedbed. In subsequent years, these latter cysts (combined with vegetative cells from populations in the eastern segment of the MCC) initiate blooms that cause toxicity in western portions of the Gulf. Shellfish toxicity along the coast is regulated not only by bloom dynamics but also by coastal current transport, with northeasterly

<sup>1</sup> 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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