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journal homepage: www.elsevier.com/locate/dsr2Georges Bank: A leaky incubator of *Alexandrium fundyense* bloomsD.J. McGillicuddy Jr.^{a,*}, D.W. Townsend^b, B.A. Keafer^c, M.A. Thomas^b, D.M. Anderson^c^a Department of Applied Ocean Physics and Engineering, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA^b School of Marine Sciences, University of Maine, Orono, ME 04469, USA^c Biology Department, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA

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ABSTRACT

A series of oceanographic surveys on Georges Bank document variability of populations of the toxic dinoflagellate *Alexandrium fundyense* on time scales ranging from synoptic to seasonal to interannual. Blooms of *A. fundyense* on Georges Bank can reach concentrations on the order of 10^4 cells l^{-1} , and are generally bank-wide in extent. Georges Bank populations of *A. fundyense* appear to be quasi-independent of those in the adjacent coastal Gulf of Maine, insofar as they occupy a hydrographic niche that is colder and saltier than their coastal counterparts. In contrast to coastal populations that rely on abundant resting cysts for bloom initiation, very few cysts are present in the sediments on Georges Bank. Bloom dynamics must therefore be largely controlled by the balance between growth and mortality processes, which are at present largely unknown for this population. Based on correlations between cell abundance and nutrient distributions, ammonium appears to be an important source of nitrogen for *A. fundyense* blooms on Georges Bank.

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1. Introduction

Whereas the ecology and oceanography of the toxic dinoflagellate *Alexandrium fundyense* are relatively well characterized in the coastal Gulf of Maine (Anderson et al., 2005b; Franks and Anderson, 1992), comparatively less is known about blooms of this organism in offshore waters of that region. Evidence of its presence offshore was documented more than fifty years ago, when small amounts of Paralytic Shellfish Toxins (PSTs) were detected in the viscera of sea scallops (*Placopecten magellanicus*) harvested on Georges Bank (Bourne, 1965). This finding was later confirmed by measurements in 1977–1981 (Jamieson and Chandler, 1983). It was not until the late 1980s that elevated levels of PSTs were found in the digestive glands of Georges Bank scallops in a monitoring program associated with an emergent roe-on scallop fishery in the Canadian sector of the bank (White et al., 1993). Toxicity assays on surfclams (*Spisula solidissima*) harvested from southern Georges Bank in August 1989 yielded PST levels far in excess of the regulatory standard for safe human consumption, prompting an emergency closure. The fishery was re-opened the following year, only to be closed again in May 1990 when surfclam toxicities were again above the threshold. Two incidents involving eight cases of paralytic shellfish poisoning (PSP) occurred in May–June 1990 when fishermen became ill after eating blue mussels (*Mytilus edulis*) from bycatch on Georges

Bank. Recognition of the long-term persistence of PSTs in surfclams on Georges Bank (White et al., 1993) and the difficulties of monitoring this offshore resource led to the closure being extended indefinitely, and it was expanded to include ocean quahogs, mussels, and all parts of sea scallops except for the adductor muscle. Only recently has the Georges Bank surfclam fishery become accessible on a limited basis under an onboard screening and dockside testing protocol (DeGrasse et al., this issue), in concert with a research program (GOMTOX¹) focused on understanding the heretofore uncharacterized blooms of *A. fundyense* on Georges Bank.

Study of these offshore blooms is facilitated by a substantial body of knowledge concerning the physical, biological, chemical, and geological aspects of Georges Bank, which is home to prodigious natural resources, both living and mineral (Backus, 1987). Mean circulation on the bank (Fig. 1) is clockwise (Bigelow, 1927), fed by adjacent waters emanating from coastal currents of the Gulf of Maine. The around-bank current results from a combination of tidal rectification (Loder, 1980) and buoyancy-driven flow (Flagg, 1987), the latter varying seasonally (Butman and Beardsley, 1987). Residence times on Georges Bank inferred from drifter observations range from 40 days in winter to 90 days in summer (Brink et al., 2003), reflecting higher retention of water on the bank when the around-bank flow is stronger. The mean circulation is subject to episodic intrusions from the western Gulf

* Corresponding author. Tel.: +1 508 289 2683; fax: +1 508 457 2194.
E-mail address: dmcgillicuddy@whoi.edu (D.J. McGillicuddy Jr.).

¹ Gulf of Maine TOXicity (GOMTOX) <http://www.whoi.edu/gomtox/>.

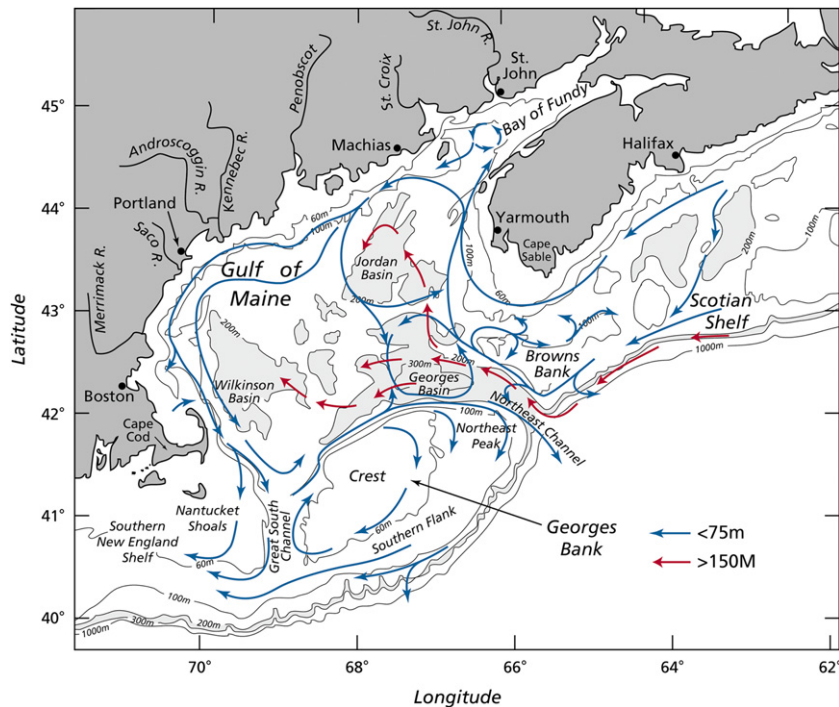


Fig. 1. General circulation in the Gulf of Maine/Georges Bank region during stratified conditions (May to September). Adapted from Beardsley et al. (1997).

of Maine, the Scotian Shelf, and warm-core Gulf Stream Rings (Brink et al., 2009; Smith et al., 2001).

The energetic hydrodynamic setting of Georges Bank fuels one of the most productive ecosystems in the world (Cohen and Grosslein, 1987; Steele et al., 2007). Tidal pumping provides a persistent source of nutrients from the adjacent deep basins (Franks and Chen, 2001; Horne et al., 1989; Hu et al., 2008; Ji et al., 2008). Phytoplankton chlorophyll is typically highest on the crest and decreases in the deeper areas along the periphery of the bank, with high rates of primary production throughout the year (O'Reilly et al., 1987). Winter/spring blooms dominated by diatoms can begin as early as January, with dinoflagellates becoming more abundant in the post-bloom period (Cura, 1987; Townsend and Thomas, 2002).

This classical paradigm of plankton species succession, together with the observed seasonal characteristics of *A. fundyense* blooms in the Gulf of Maine (Anderson, 1997; Anderson et al., 2005b; Franks and Anderson, 1992; McGillicuddy et al., 2005a; Townsend et al., 2001), framed the temporal parameters for this investigation of blooms of this species on Georges Bank. Detailed surveys, similar in spatial extent to the U.S. GLOBEC Georges Bank Broad-scale sampling pattern (Wiebe et al., 2006), were conducted in the April–August time frame in each of three years. These observations document the abundance and distribution of *A. fundyense* vegetative cells along with relevant environmental parameters such as hydrography, nutrients, and total chlorophyll—providing information on bloom dynamics for time-scales ranging from synoptic to seasonal to interannual. In light of the importance of resting cysts for initiation of blooms in the coastal Gulf of Maine (Anderson et al., 2005c), cyst distributions on Georges Bank were also measured on a single survey in fall 2007.

2. Methods

Hydrographic profiles and water samples were collected with a standard CTD-rosette system with Niskin bottles on a series of eleven cruises (Table 1; see Fig. 2 for station positions). Nutrient

Table 1

Research voyages during which *A. fundyense* populations were sampled on Georges Bank.

| Year | Dates | Vessel/Voyage number |
|------|------------------|-----------------------------|
| 2007 | May 17–31 | R/V <i>Endeavor</i> , EN435 |
| 2007 | June 21–July 5 | R/V <i>Endeavor</i> , EN437 |
| 2007 | October 8–18 | R/V <i>Oceanus</i> , OC440 |
| 2008 | April 28–May 5 | R/V <i>Oceanus</i> , OC445 |
| 2008 | May 27–June 4 | R/V <i>Oceanus</i> , OC447 |
| 2008 | June 27–July 3 | R/V <i>Endeavor</i> , EN448 |
| 2008 | July 29–30 | R/V <i>Tioga</i> , TI326 |
| 2010 | May 1–10 | R/V <i>Oceanus</i> , OC460 |
| 2010 | May 26–June 4 | R/V <i>Endeavor</i> , EN476 |
| 2010 | June 30–July 8 | R/V <i>Oceanus</i> , OC465 |
| 2010 | July 26–August 6 | R/V <i>Oceanus</i> , OC467 |

samples were filtered through Millipore HA filters, placed immediately in a seawater–ice bath for 5–10 min, and frozen at -18°C . Concentrations of NO_3+NO_2 , NH_4 , $\text{Si}(\text{OH})_4$ and PO_4 were measured on shore following each cruise with a Bran Luebbe AA3 AutoAnalyzer using standard techniques.

A. fundyense cells were enumerated from water samples using a species-specific oligonucleotide probe and methods described in Anderson et al. (2005a). Both *A. tamarensis* and *A. fundyense* occur in the Gulf of Maine, and these are considered to be varieties of the same species (Anderson et al., 1994; Scholin et al., 1995). Available molecular probes cannot distinguish between them, and only detailed analysis of the thecal plates on individual cells can provide this resolution—which is not practical for large numbers of field samples. Accordingly, for the purpose of this study, the name *A. fundyense* is used to refer to both forms.

Cysts of *A. fundyense* were collected and enumerated from sediment samples using methods described in Anderson et al. (2005c). Samples were obtained with a Craib corer in a dedicated survey in fall 2007. The sampling pattern consisted of 14 cross-shore transects in the coastal Gulf of Maine and three transects across Georges Bank, for a total of approximately 120 stations.

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