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Initial observations of the 2005 *Alexandrium fundyense* bloom in southern New England: General patterns and mechanisms

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Abstract

From May to July, 2005, an extensive bloom of *Alexandrium fundyense* occurred along the coast of southern New England. The outbreak eventually closed shellfish beds from central Maine to Massachusetts, including Nantucket Island and portions of Martha's Vineyard, and resulted in the closure of 40,000 km^2 of offshore federal waters as well. The coastal *Alexandrium* bloom was exceptional in several ways: high toxin levels were measured farther south than ever before in New England; levels of toxicity in many locations were higher than previously observed at those stations; for the first time toxicity at some locations was above quarantine levels; cell concentrations far exceeded those observed in the coastal waters of southern New England in the past; and for the first time in the region the governors of Maine and Massachusetts officially declared the red tide to be a disaster, clearing the way for federal assistance.

Initial observations suggest that several factors contributed to this bloom. Abundant rainfall and heavy snowmelt substantially increased the amount of fresh water entering the Gulf of Maine. Combined with other freshwater inputs, we hypothesize that this provided macro- and micro-nutrients, a stratified water column, and a transport mechanism that led to high cell abundances and broad, region-wide dispersal of the organism. Warm temperatures in western waters also would have favored *A. fundyense* growth. In addition, several storms with strong winds out of the northeast occurred at times when cells were abundant and in locations where the winds could advect them into Massachusetts and Cape Cod Bays and keep them there, leading to high cell concentrations and toxicity. Another contributing factor may have been the high abundance of newly deposited cysts in western Gulf of Maine sediments, as documented in a fall 2004 survey. Here, we evaluate this bloom and the patterns of toxicity in light of the conceptual models for *A. fundyense* dynamics developed during the Ecology and Oceanography of Harmful Algal Blooms (ECOHAB)–Gulf of Maine (GOM) program. Several features of the 2005 bloom conform to the mechanisms proposed in those models, including the alongshore transport of cells in major water masses and episodic intrusions of cells toward shore due to downwelling-favorable wind forcings. The

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models need to be refined and expanded, however, based on new data and observations. For example, it is now clear that cells and bloom patches can reach the outer side of Cape Cod and even Nantucket and Martha's Vineyard. Transport to the coastal waters of Rhode Island and even Connecticut/Long Island is also possible. A critical modification also may be necessary in terms of mechanisms through which *A. fundyense* cells occur in Massachusetts Bay. In the past, toxicity only developed when blooms were transported from the north and into the bay via the western segment of the Maine Coastal Current. Now, it is possible that the bay might serve as a source of cells through the germination of cysts deposited in those waters during the 2005 bloom. If proven in subsequent surveys, this potential for in situ bloom development could have major implications on the timing and extent of toxicity within Massachusetts Bay and southern New England waters in future years.

Keywords: *Alexandrium fundyense*; Cysts; Gulf of Maine; PSP; Harmful algal blooms; Red tides

1. Introduction

Paralytic shellfish poisoning (PSP) is a recurrent and serious problem caused by blooms of several toxic dinoflagellate species in the genus *Alexandrium*. Potent neurotoxins produced by these organisms are accumulated by filter-feeding shellfish and other grazers and are passed on to humans and animals at higher trophic levels, leading to illness, incapacitation, and even death. PSP is a relatively new phenomenon within the northeastern United States, but is now recurrent and widespread, affecting vast expanses of the Gulf of Maine coastline (Anderson, 1997). Toxicity was historically restricted to the far eastern sections of Maine near the Canadian border, with the first documented PSP in 1958 (Hurst, 1975; Shumway et al., 1988), but in 1972, a massive, visible red tide of *Alexandrium fundyense*[1] stretched from southern Maine through New Hampshire and into Massachusetts, causing toxicity in southern areas for the first time. Virtually every year since the 1972 outbreak, western Maine has experienced PSP outbreaks, and on a less-frequent basis, New Hampshire and Massachusetts have as well. This pattern has been viewed as a direct result of *Alexandrium* cysts being retained in western Gulf of Maine waters once introduced there by the 1972 bloom (Anderson and Wall, 1978).

For approximately three months in mid-2005, another extensive bloom of *A. fundyense* occurred in southern New England coastal waters. This outbreak was the largest since the 1972 event, and ultimately resulted in shellfish harvesting closures due to the threat of PSP that extended from the central Maine coast through Massachusetts to its offshore islands of Martha's Vineyard and Nantucket. Additionally, a 40,000 km^2 area of offshore (federal) shellfish resources was closed. Press reports estimated the economic loss from this outbreak to exceed $15 million in Massachusetts alone, with unwarranted fears about seafood safety (e.g. the "halo" effect) and other factors potentially doubling this estimate. Maine and New Hampshire also experienced significant losses.

A. fundyense blooms in the Gulf of Maine have been the subject of an intense five-year investigation through the Ecology and Oceanography of Harmful Algal Blooms (ECOHAB)–Gulf of Maine (GOM) program. A series of large-scale field surveys provided data that were combined with mooring observations and numerical model simulations to document the complex dynamics of *A. fundyense* blooms within this region (Anderson et al., 2005d). A synthesis of the results of many of those studies was provided by Anderson et al. (2005c) and McGillicuddy et al. (2005) in the form of conceptual models of *A. fundyense* bloom dynamics. Townsend et al. (2001) also formulated a conceptual model for *A. fundyense* blooms that develop in eastern Maine waters. Derived from different approaches, these models have many features in common, and some differences as well.

Central to these formulations are the major hydrodynamic transport pathways along the coast of the GOM. One key feature is the Maine Coastal Current (MCC) system, described by Lynch et al. (1997) as a composite of seven legs or segments with multiple branch points (Fig. 1). This system also has been termed the GOM Coastal Current by

[1]Both *A. tamarense* and *A. fundyense* occur in the Gulf of Maine. We consider these to be varieties of the same species (Anderson et al., 1994; Scholin et al., 1995). Neither antibody nor oligonucleotide probes can distinguish between them, and only detailed analysis of the thecal plates on individual cells can provide this resolution. This 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.

Fig. 1. Gulf of Maine surface circulation and the major *A. fundyense* transport pathways via the Maine Coastal Current (MCC) system. The pathways are the eastern segment (EMCC) and the western segment (WMCC) as well as a nearshore feature, the Gulf of Maine Coastal Plume (GOMCP), that is formed from the major river inputs to the GOM in the spring. Further downstream in the coastal flow, *A. fundyense* cells are delivered along Stellwagen Bank and outer Cape Cod with a branch point to Georges Bank and Nantucket Shoals (ME—Maine; MA—Massachusetts; BOF—Bay of Fundy; NS—Nova Scotia; EMCC—eastern Maine Coastal Current; WMCC—western Maine coastal current). Base map modified from Pettigrew et al. (2005).

Pettigrew et al. (2005). The upstream, eastern segment of the MCC extends from Grand Manan basin in the Bay of Fundy to Penobscot Bay. This current, hereafter termed the EMCC, derives from inflow from the Scotian Shelf and freshwater from the Saint John River (Bisagni et al., 1996). The EMCC often veers offshore south of Penobscot Bay, which defines a branch point. Some EMCC water continues offshore (Fig. 1), and some returns shoreward to form the western segment or WMCC, which is then augmented by freshwater outflow from the Penobscot, Kennebec/Androscoggin, Saco, and Merrimack Rivers. Near Cape Ann, Massachusetts, another branch point is found, with

some WMCC water entering Massachusetts Bay, and some traveling along the eastern flank of Stellwagen Bank. Downstream, the Stellwagen segment undergoes another bifurcation into a Nantucket segment, exiting the GOM at the Great South Channel, and a Georges Bank segment that travels to and around Georges Bank.

A related hydrographic feature that figures prominently in *A. fundyense* blooms has been termed the Gulf of Maine Coastal Plume (Fig. 1; Keafer et al., 2005b). This transport pathway is shoreward of the EMCC and carries low salinity water from the Bay of Fundy and eastern Maine across the mouth of Penobscot Bay and into the western GOM where it merges with western river plumes. This (''inside track'') transport is density-driven and influenced by wind as well as the large-scale GOM circulation.

Massachusetts Bay (which includes Cape Cod Bay) is a semi-enclosed basin bounded on the east by the relatively shallow waters of Stellwagen Bank, which rises to within 20 m of the surface (Fig. 1). The dominant circulation regime in the bay is a counterclockwise flow that enters the bay just south of Cape Ann, travels south through most of Massachusetts Bay, and exits through a deep channel between the southern end of Stellwagen Bank and Provincetown at the tip of Cape Cod, heading offshore toward Georges Bank and southern waters via the Great South Channel (Geyer et al., 1992). Superimposed on this pattern are episodic intrusions of low-salinity water from the WMCC, which enter Massachusetts Bay around Cape Ann (Butman, 1975; Franks and Anderson, 1992a). This area represents another fork or bifurcation point in the MCC system. Depending on the local wind stress, water from the coastal current can either enter the bay or bypass it entirely, traveling instead along the eastern flank of Stellwagen Bank toward Georges Bank. Within Massachusetts Bay, the mesoscale circulation and the location of the plume can be modified by southwest or northeast winds that cause significant upwelling or downwelling, respectively.

A key feature in the ECOHAB–GOM conceptual models are two large *A. fundyense* cyst ''seed beds''—one located in the Bay of Fundy, and the other offshore of Penobscot and Casco Bays (Anderson et al., 2005c). Cells are presumed to germinate from these benthic deposits, swimming to surface waters where they divide and initiate the blooms. (Note that other workers have suggested that benthic seedbeds are not important in this bloom process, and that resuspended cysts in the water column serve as the appropriate inoculum instead; Kirn et al., 2005). The conceptual models begin with cysts that germinate within the Bay of Fundy seedbed, causing localized, recurrent blooms in that area that are self-seeding with respect to future outbreaks as well as ''propagatory'' in nature—i.e. some cells escape the retention zone and enter the EMCC. Some EMCC cells are entrained into the WMCC, while others eventually deposit cysts offshore of Penobscot and Casco Bays, creating a large, offshore cyst seedbed in that area (Anderson et al., 2005c; McGillicuddy et al., 2005). In subsequent years, these latter cysts serve as a seed population for the blooms that are transported to the south and west by the WMCC, causing toxicity along the coasts of western Maine, New Hampshire, and Massachusetts before the cells are either lost due to mortality or encystment, or are advected out of the region (Anderson et al., 2005a). These two conceptual models argue that *A. fundyense* blooms occur earlier in the western GOM than in eastern waters due to more favorable growth conditions at that time, such as warmer temperatures that support faster growth and more water-column stratification. Indeed, at this writing, the 2005 bloom in the western Gulf had ended, but toxicity is widespread in eastern Maine and the Bay of Fundy, consistent with the trend of early western blooms, and later eastern outbreaks. Townsend et al. (2001) also point out that growth conditions are not favorable for *A. fundyense* growth at the upstream (eastern) end of the EMCC due to turbulence and deep mixing and that cells begin to grow and accumulate at the western end of the EMCC only as those waters stratify and light no longer limits uptake of the abundant nutrients.

Episodes of PSP within Massachusetts Bay are more sporadic than those in southwestern Maine, occurring every few years rather than annually during the 1970s, 1980s, and early 1990s (Franks and Anderson, 1992b). There was little or no toxicity in the Massachusetts Bay region from 1994 to 2004. Toxin was detected at low levels in nearby Gloucester in 1994, 1995, and again in 2000, and 2003, but this occurred in an estuary (the Annisquam River) that cuts across Cape Ann and that is thus subject to cells that enter from the north. There were no harvesting closures due to PSP at stations directly within the bay over this long interval.

The conceptual models described above were derived from ECOHAB–GOM observations from 1998 to 2002. During that time, there was little or no PSP toxicity in Massachusetts Bay or coastal waters to the south, so the concepts that were highlighted in the models are those that addressed blooms and toxicity in eastern and western Maine, New Hampshire, and northern Massachusetts. The extensive 2005 bloom covered much of this region, but also included waters farther to the south and west. It was a significant event in many regards, and provides a timely opportunity to test recent observations against the conceptual models and to suggest refinements or changes to the models. Here, we present initial field observations of the 2005 *A. fundyense* outbreak, and discuss these in the context of the ECOHAB–GOM program's conceptual models. We emphasize that there are numerous field samples yet to be analyzed and that considerable work remains to be done to complete data reduction and synthesis. Future publications will provide greater detail on the bloom and its underlying mechanisms.

2. Methods

2.1. Cruises

Multiple vessels were used to survey the areas affected by the *A. fundyense* bloom. Surveys were run by personnel from the Woods Hole Oceanographic Institution (on the R/V *Oceanus* (Cruise OC412), R/V *Tioga*, and R/V *Gulf Challenger*), the Provincetown Center for Coastal Studies at Provincetown (vessels: *Ibis* and *Shearwater*), and the Massachusetts Water Resources Authority (MWRA) and Battelle (R/V *Aquamonitor* and *Nauset*). On one occasion, during routine surveys of Buzzards Bay conducted by the University of Massachusetts Dartmouth, WHOI personnel sampled from the R/V *Lucky Lady* to collect and process samples of those waters. Samples also were collected on numerous occasions when a vessel of opportunity was working in the region's waters on other projects.

2.2. Sampling

On most of the cruises, CTD casts provided vertical profiles of hydrographic properties (temperature, salinity, in situ fluorescence, and light transmission). Water samples were collected on the upcast for cell counts and nutrients at 1, 10 and 20 m depths. Acoustic Doppler current profiler (ADCP) measurements were made during most of the WHOI and Battelle cruises. Meteorological and hydrographic data were obtained from moorings maintained by NOAA, USGS, and the Gulf of Maine Ocean Observing System (GoMOOS). During a two-month period, 29 satellite-tracked drifters were deployed.

2.3. Cell counts

Throughout the bloom event, estimates of cell abundance were provided in two ways. On some cruises, weather permitting, counts of live *Alexandrium* sp. cells were made by examining two transects across a Sedgewick-Rafter counting slide using an on-board light microscope at $200\times$. The slide was loaded with 1 ml of concentrated material sieved (20 μm) from a surface sample (10 l) and resuspended to 14 ml. This provided a lower limit of detection (LLD) of 14 cells l^{-1}. These are hereafter referred to as "live counts". These abundance estimates were immediately communicated to coastal managers and other interested parties, and proved very useful in decision-making. In the laboratory at WHOI, more accurate counts with a LLD $\sim$1 cell l^{-1} were conducted using preserved material and whole-cell molecular probe technology that allows positive identification of *A. fundyense* and rapid turn-around of samples (Anderson et al., 2005b). Linear regression of the two methods, live vs. preserved whole cell, on the same samples yielded an r^2 value of 0.77 and a slope of 1.3 ($n = 131$). The slight deviation from a slope of 1 was likely due to the co-occurrence of a similar species, *A. ostenfeldii*, that is not easily distinguished from *A. fundyense* in the live samples (Anderson et al., 2005b).

2.4. Nutrients

Samples for nutrient analysis were collected from the Niskin bottles on the CTD rosette. These were syringe filtered (0.2 μm Sterivex filters) into acid cleaned (10% HCl) scintillation vials, and stored frozen until analysis. Nutrient analyses (nitrate, nitrite, phosphate, ammonium, silicate) were performed using standard colorimetric methods (Grasshoff, 1983) on a Lachat QuickChem 8000 Flow Injection Analyzer.

2.5. Shellfish toxicity measurements

Shellfish were collected and assayed for their content of the saxitoxins as part of the routine Maine, Massachusetts, and New Hampshire PSP monitoring programs. The content of saxitoxins was determined using the standard AOAC mouse bioassay (Association of Official Analytical Chemists, 1980).

2.6. Drifters

Several drifters were deployed during R/V *Oceanus* cruise OC412. These were standard surface drifters (Davis, 1985) consisting of four $\sim 1\,m^2$, subsurface, cloth sails mounted orthogonally around a 1.2-m length of 5-cm PVC pipe, supported by fiberglass rods, floated by four pairs of fish net buoys, and ballasted by a 3.2-kg window sash weight. A low-cost GPS transmitter was mounted topside that sends near-hourly fixes to the GLOBALSTAR satellite.

2.7. Model simulations

Circulation during the early phases of the bloom was simulated using the Dartmouth data assimilative modeling system. This consists of both forward and inverse modeling components. The forward ocean model is a finite-element circulation model (Quoddy) described in detail in Lynch et al. (1996). It is three-dimensional, hydrostatic, free-surface, and fully nonlinear. Vertical mixing is represented by Mellor-Yamada 2.5 turbulence closure scheme (Mellor and Yamada, 1982). Horizontal viscosity is represented by a mesh- and shear-dependent Smagorinsky (1963) scheme. A general terrain-following coordinate system with 21 sigma layers is used, with non-uniform vertical discretization that allows proper resolution of surface and bottom boundary layers. The system assimilates both moored and ship-board ADCP current measurements via the inversion for the unknown sea-level open boundary (OB) conditions. This is done by two linear inverse sub-models of Quoddy: Truxton (Lynch et al., 1998) and Casco (Lynch and Hannah, 2001), respectively. Truxton is a linear, frequency-domain inverse model that improves the accuracy of tidal amplitude and phase specifications along the OB. Casco, on the other hand, is the time domain inverse model that refines the time-dependent boundary elevations at subtidal scales.

The model simulation was set up as in He et al. (2005), for real-time assimilation aboard R/V *Oceanus* cruise OC412. An objective mapping method (Smith, 2004) was used to generate the model initial condition by merging CTD measurements with the GOM temperature and salinity climatology (Lynch et al., 1996). The forward model was forced by surface winds observed by GoMOOS buoys. Observations of surface heat fluxes were not available and thus neglected with the assumption that they played a secondary role (compared with surface wind and offshore boundary forcing) in affecting the coastal circulation dynamics during the two-week field survey. The spatial and temporal scales of the simulation are those of OC412.

3. Results

3.1. Chronology of PSP toxicity during the 2005 A. fundyense bloom

The following narrative summarizes the events of the 2005 *A. fundyense* bloom. The timing and geographic extent of shellfish harvesting closures is given in Fig. 2, and the trends in PSP toxicity scores in Fig. 3, broken down by region.

The first detectable PSP toxicity of 2005 was recorded along the western Maine coast by the Maine Department of Marine Resources (DMR). Toxicity was detected unusually early in April, unusually far west along the Maine coast, and was unusually widespread among western Maine stations (D. Couture, pers. comm.). DMR closed the Maine coast south of Portland on May 4 as the levels rose near the $80\,\mu g\,STX\,100\,g^{-1}$ regulatory limit (Fig. 2).

The first high level of toxicity of 2005 ($567\,\mu g\,STX\,100\,g^{-1}$) was measured one day later (May 5) 8 km offshore at Star Island (part of Appledore Island) by the New Hampshire Department of Environmental Services (DES), prompting immediate closure of offshore NH islands on that day (Fig. 2; C. Nash, pers. comm.). This was the first measurement of the season at Star Island because earlier sampling is operationally difficult. Lacking earlier data, the toxicity measured at Star Island was a surprise to many observers because coastal NH had no toxicity, and coastal Maine had only low toxicity at that time.

A "northeaster" (an extratropical cyclone with strong winds out of the northeast) struck the next weekend (May 7–8). Massachusetts Department of

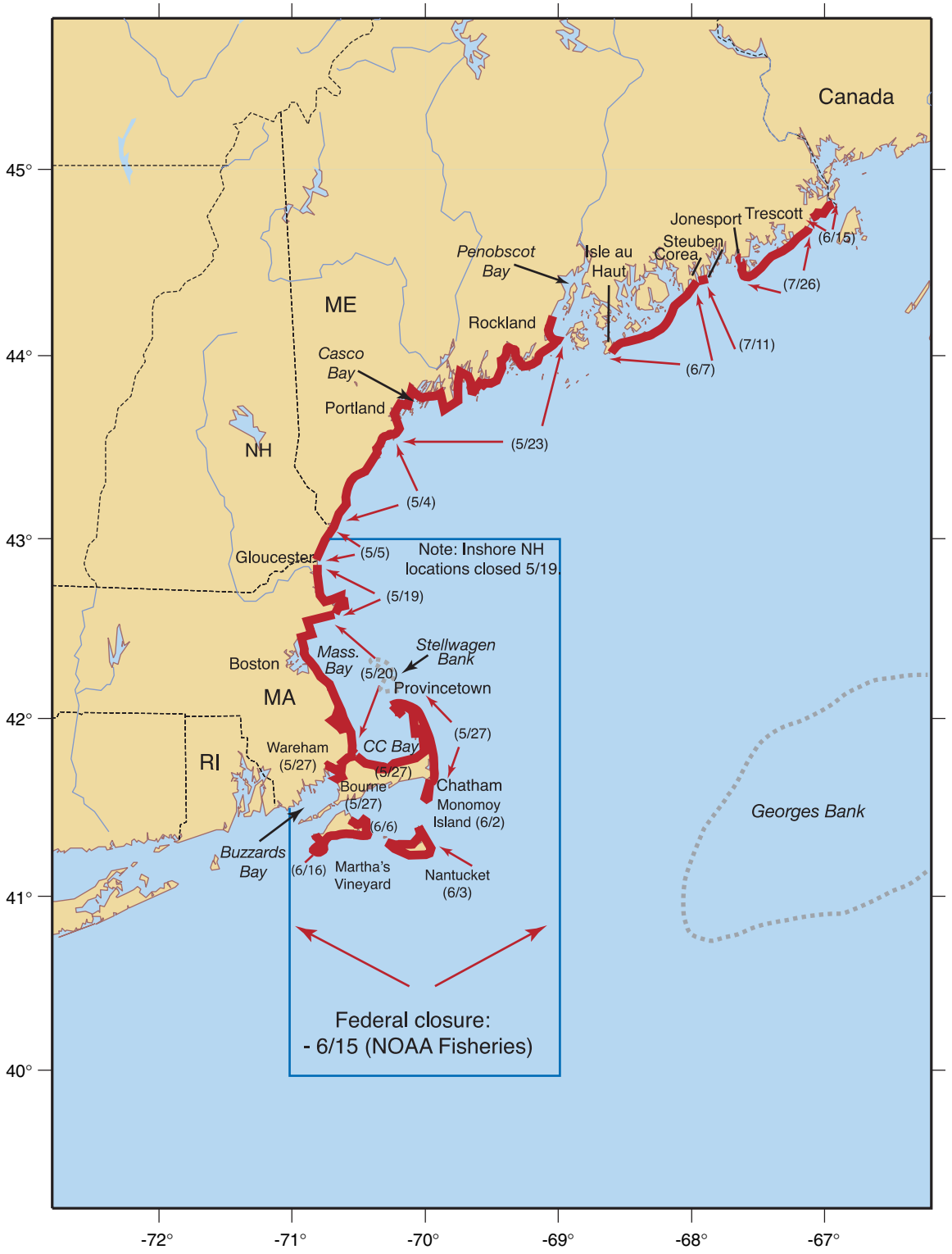

Fig. 2. Shellfish closures along the coastlines of Maine, New Hampshire, Massachusetts, and the adjacent offshore waters due to detection of PSP toxins during the 2005 *A. fundyense* bloom. Issuance dates of these closures are indicated. (Compiled from information provided by the Massachusetts Division of Marine Fisheries, the New Hampshire Department of Environmental Services, and the Maine Department of Marine Resources.)

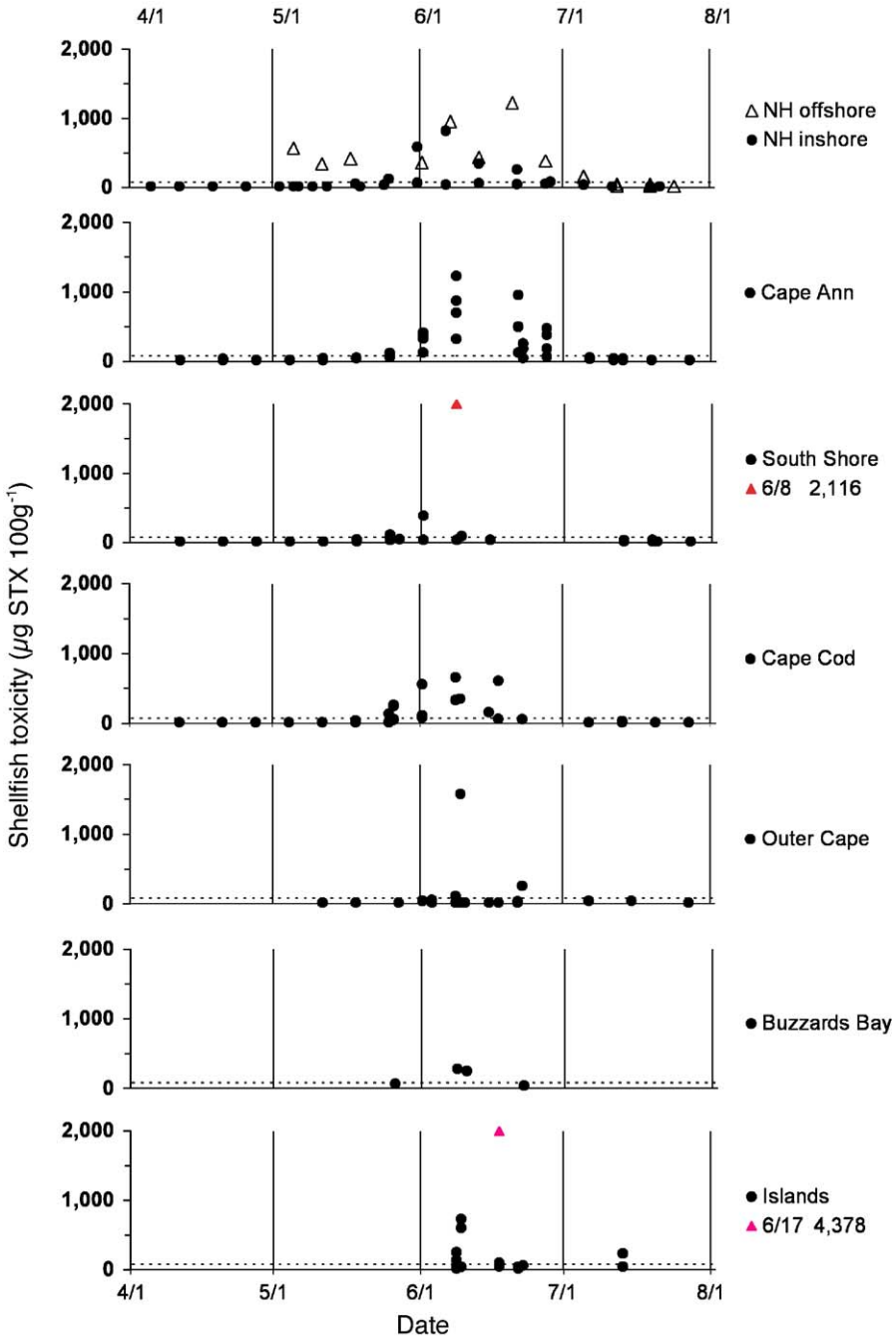

Fig. 3. Time series of PSP toxicity (μg STX equivalents $100\,g^{-1}$ shellfish meat) in mussels from Massachusetts and New Hampshire, grouped into seven regions. (Non-detects $<40\,\mu g\,100\,g^{-1}$ are plotted as 20. Closure level of 80 is indicated by the dotted line.) Levels that are off scale are noted by triangles, with toxin scores given numerically in the right column. (South Shore—stations between Boston and the Cape Cod Canal; Cape Cod—stations from the Canal to the inner side of Provincetown; Outer Cape—Provincetown to Monomoy; and Islands—Nantucket and Martha's Vineyard.)

Marine Fisheries (DMF) began sampling their northern stations on May 11 and detected toxicity north of Cape Ann. A week later, toxicity was detectable inside Massachusetts Bay at four of five stations on the western shore as far south as Sandwich (at the eastern entrance to the Cape

Cod Canal). On the basis of these results plus additional information on cell abundance and winds, DMF closed the Massachusetts coast north of Cape Ann, and a day later the coast north of the Cape Cod Canal (Fig. 2).

While toxicity remained high offshore at Star Island, inshore NH toxicity was undetectable until May 18. DES then extended the offshore closure to the remainder of the NH coast.

A second northeaster storm occurred on May 24–25. On May 26, toxicity in southern Massachusetts Bay surpassed levels measured at Massachusetts stations north of Cape Ann (Fig. 3). Furthermore, for the first time ever, mussels at the western end of the Cape Cod Canal (which links Cape Cod Bay to Buzzards Bay) became toxic ($70\,\mu g\,STX\,100\,g^{-1}$), presumably from cells introduced from one bay to the other via tidal exchange through the canal. DMF subsequently extended the closure to portions of Buzzards Bay (Bourne and Wareham), eastern Cape Cod Bay, and the outer Cape nearly as far south as Chatham (Fig. 2).

On June 1, toxicity was detected at Chatham. That result plus cell abundance data prompted the decision to close Monomoy Island (at the "elbow" of Cape Cod), a major shellfish resource and wildlife refuge. Toxin scores continued to increase throughout the region (i.e. New Hampshire's Star Island reached $1224\,\mu g\,STX\,100\,g^{-1}$ on June 20), and reached closure levels on Nantucket and the eastern and southern shores of Martha's Vineyard as well. Cell concentrations were clearly very high near these offshore islands, with toxin scores as high as $4378\,\mu g\,STX\,100\,g^{-1}$ in mussels on Martha's Vineyard on June 17.

On June 16, the widespread cell distribution, as well as wind and drifter tracks showing the transport pathways of water and cells (see below) led federal officials to close 40,000 km^2 of offshore shellfish resources that lie outside state jurisdictions (Fig. 2).

In late June and early July, toxicity began to drop region-wide, and state agencies began re-opening the closed areas, with the first Massachusetts re-opening occurring on July 1. As of this writing (late August 2005), the federal offshore closure remains in effect, but much of the southern New England coastline is now open for harvesting. There is ongoing toxicity in eastern Maine and the Bay of Fundy, as is often observed in mid to late summer in that region (Shumway et al., 1988; Anderson, 1997).

3.2. Cruise observations

A region-wide cruise was conducted on the R/V *Oceanus* during the early stages of the *A. fundyense* bloom from May 9 to 18, 2005 (Cruise OC412). Cells were already present at moderate concentrations in Massachusetts Bay ($\sim$1000 cells l^{-1}), and were distributed to the north as well in lower concentrations that extended to the Bay of Fundy (Fig. 4A). The cells were predominantly associated with low-salinity water close to the coast (Fig. 4C), with the exception of the outer reaches of Massachusetts Bay. Temperatures were warmer in the immediate nearshore waters and within Massachusetts Bay than they were further out in the Gulf, or to the east in the EMCC and Bay of Fundy regions. The cold core of the EMCC is also evident in these data, extending alongshore and offshore from the eastern Maine coastline (Fig. 4B). The salinity distribution (Fig. 4C) shows a continuous, alongshore band of low-salinity water (<32) extending from the Bay of Fundy to Massachusetts Bay. This feature resembles the GOMCP described by Keafer et al. (2005b). Fig. 4D shows the concentration of nitrate plus nitrite over the cruise domain. The highest concentrations are in the eastern Maine region, associated with the EMCC and the outflow from the Bay of Fundy, with concentrations in excess of 8 μM. Some additional structure is seen in the western region, with a band of moderately high concentrations (2.5–6.6 μM) extending from Casco Bay to northern Massachusetts Bay.

The second intense storm with winds from the northeast on May 24 and 25 was associated with an increase in the intensity of the bloom and further dispersal. Exceptionally high cell concentrations for the southern New England region ($\sim$40,000 cells l^{-1}) were detected in samples collected in Cape Cod Bay on May 28–29 (Fig. 5A). Planozygotes, the precursors to *A. fundyense* resting cysts, were observed in these samples. The population extended well beyond the sampling domain. Subsequent expanded cruises in early June (Fig. 5B) indicated that the bloom extended to the Atlantic-facing areas of outer Cape Cod and eastern portions of Nantucket Sound. At that time, notably, high cell concentrations were detected near Monomoy Island. Tern mortalities reported at that time on Monomoy have subsequently been shown to be caused by saxitoxins (T. Leighfield, pers. comm.). Cells were observed in moderate concentrations (2400 cells l^{-1}) in the Cape Cod Canal and the northeast end of Buzzards Bay,

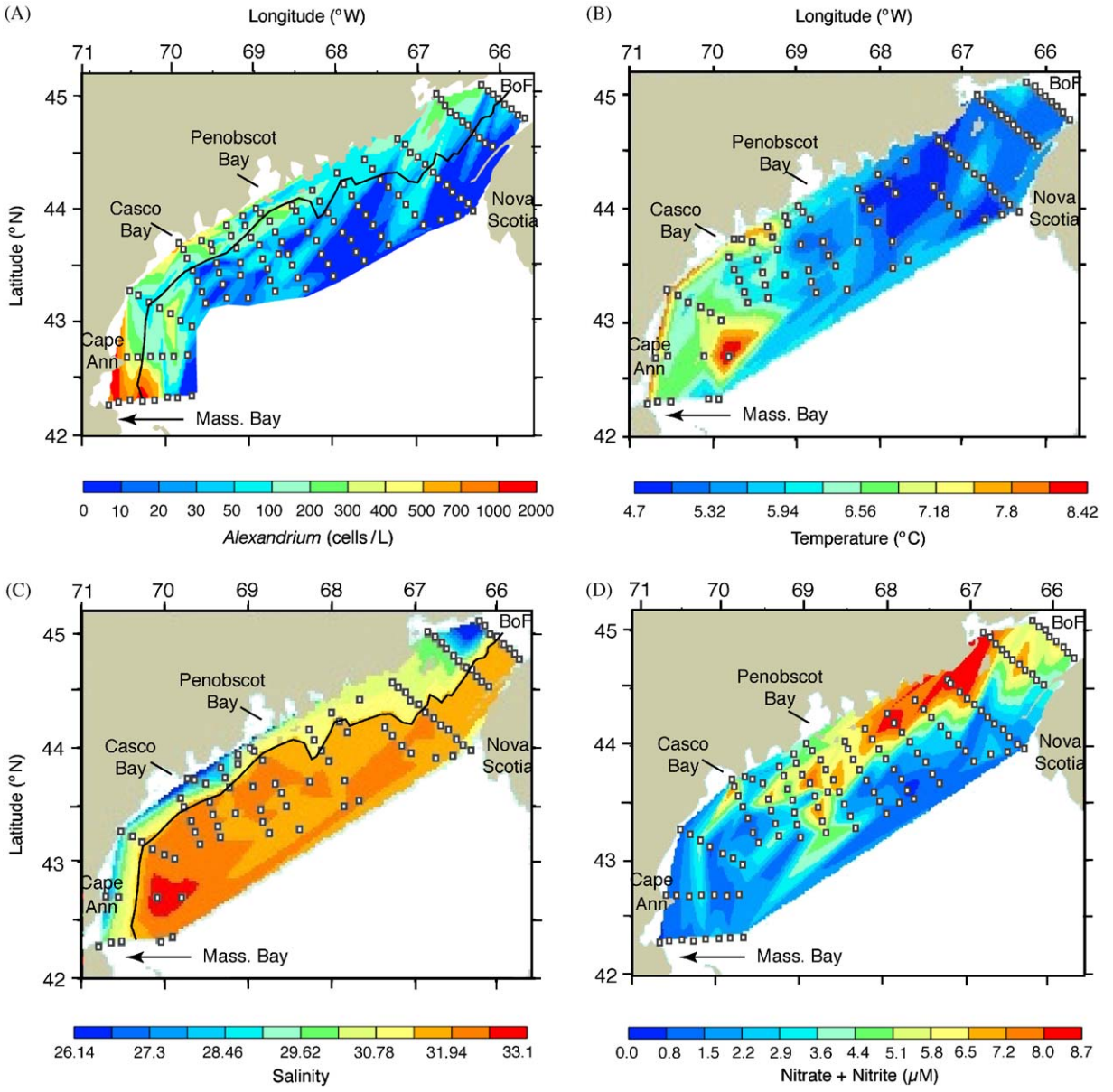

Fig. 4. Near-surface distribution of *A. fundyense* abundance, hydrographic properties, and nutrients during initial bloom detection on R/V *Oceanus* cruise OC412, Leg I, May 10–14, 2005, Gulf of Maine. (A) "Live count" estimates of *A. fundyense* abundance (cells l^{-1}); (B) temperature (°C); (C) salinity; (D) nitrate and nitrite (μM). The dark line in panels A and C depicts the 31.4 psu salinity contour, indicative of the Gulf of Maine Coastal Plume. Stations are indicated by small open squares.

consistent with the harvesting closure there. Cell concentrations remained well below 1000 cells l^{-1} and shellfish areas remained open in other areas of that bay (Fig. 5B).

The bloom continued to spread further south toward Nantucket and Martha's Vineyard, which were closed in early June. Once again, surveys documented high cell concentrations (>10,000 cells l^{-1}) in these offshore waters (data not shown). With those closures, more than 3/4 of the productive shellfish beds (~2400 km^2) in the state of Massachusetts were closed due to PSP. All of the New Hampshire coast, and more than half of the Maine coastline was closed as well (Fig. 2). Cell counts for a transect along the border between Massachusetts and Rhode Island (data not shown) revealed that *A. fundyense* cells were present at

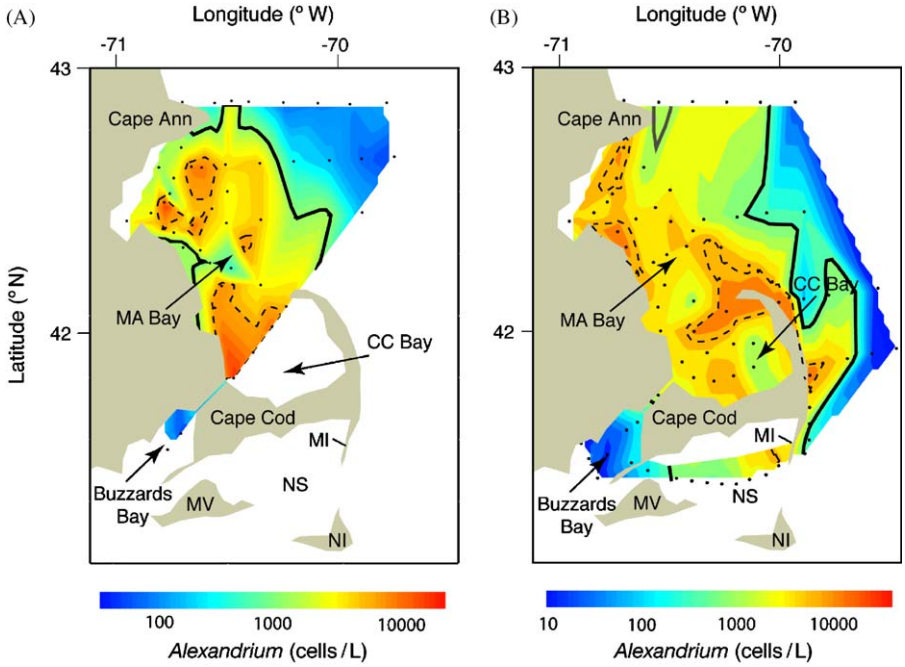

Fig. 5. Surface (1 m) distributions of *A. fundyense* abundance in the Massachusetts Bay (MA Bay), Cape Cod Bay (CC Bay), Buzzards Bay, and outer Cape Cod regions in late May and early June, 2005. (A) Estimates of *A. fundyense* abundance (cells l^{-1}) during two concurrent cruises; "live counts" from R/V *Tioga* cruise 96, May 27–29, 2005 and "whole-cell" hybridization counts from Aquamonitor cruise, May 28, 2005. (B) "Whole-cell" counts of *A. fundyense*, June 2–4, 2005, from four concurrent survey cruises; Tioga 98, Aquamonitor, Shearwater, and Lucky Lady. In each panel, the solid line depicts the 1000 cells l^{-1} contour, and the dashed line the 10,000 cells l^{-1} contour. (MV—Martha's Vineyard; NI -Nantucket Island; MI—Monomoy Island; NS—Nantucket Sound.)

low concentrations nearshore (~100 cells l^{-1}), and slightly less abundant offshore (~10 cells l^{-1}) in mid-June. One week later, the distribution changed, as offshore cell concentrations along the border were in the 300–400 cells l^{-1} range, while nearshore concentrations fell to 10 cells l^{-1} or below. This was likely due to the advection of the Martha's Vineyard offshore population (>10,000 cells l^{-1} in mid-June) into the offshore waters of Rhode Island.

By mid-June, concentrations of *Alexandrium* began to decrease in the surface waters of Massachusetts Bay, coincident with an increase in counts in the 10-m depth samples, which peaked at 32,094 cells l^{-1} in central Cape Cod Bay. Elevated abundances of 10,000–20,000 cells l^{-1} were found in subsurface samples throughout much of the bay. High counts also were observed to the south of both Nantucket and Martha's Vineyard islands, and very low abundances to the west, south of Narragansett Bay (~10–100 cells l^{-1}). *A. fundyense* abundances declined rapidly over the course of the next several weeks and by the end of June were <10 cells l^{-1} in both surface and subsurface waters throughout most of Massachusetts and Cape Cod Bays. Surface water values of >10 cells l^{-1} were only found at the stations in northeastern Massachusetts Bay and were even higher (1000 cells l^{-1}) further offshore east of Stellwagen Bank in the Gulf of Maine. High abundances (10–20,000 cells l^{-1}) were observed at several stations at 20 m depths at offshore stations east of Cape Ann and Stellwagen Bank. By mid-July, *Alexandrium* abundances within Massachusetts Bay were all <10 cells l^{-1}, while only 300 cells l^{-1} were detected at 20 m at the outermost stations offshore of Cape Ann and Stellwagen. The bloom was effectively over in southern New England.

3.3. Drifters

The southerly transport pathway of the cells causing this bloom, as well as the chaotic nature of the flow field can be inferred from the track of surface drifters released from cruise OC412 near Cape Ann on May 9 (Fig. 6). This release was coincident with the initial detection of high concentrations of *A. fundyense* in Massachusetts Bay and just after the first northeaster storm. While the

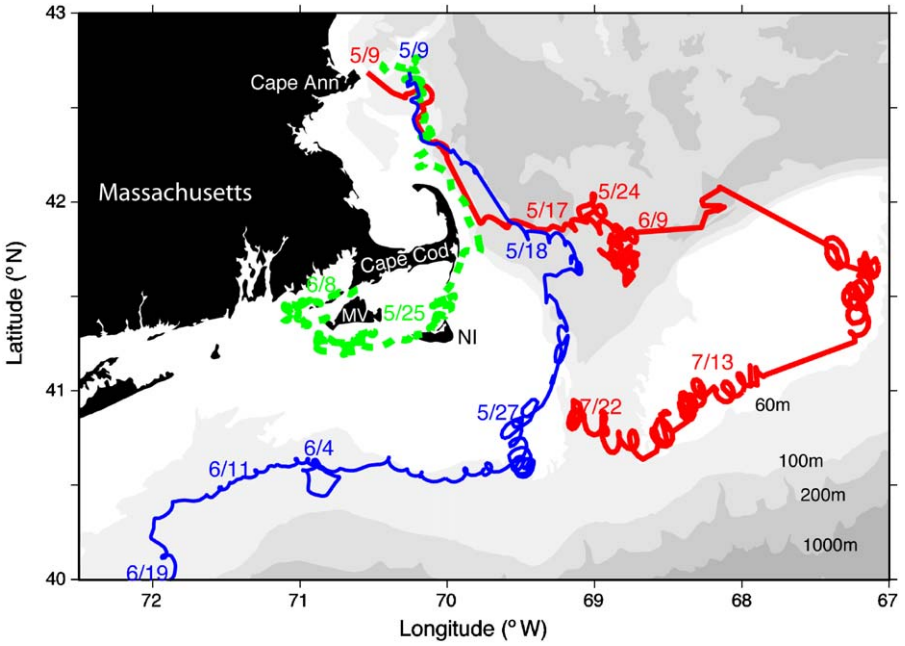

Fig. 6. Trajectories of three surface drifters released during cruise OC412 near Cape Ann on May 9, 2005. For general reference to time, several dates are labeled along each drifter track. Bathymetry is shown as different shades of gray (white is shallow and dark is deep). (MV—Martha's Vineyard; NI—Nantucket Island.)

three units were deployed within a few hours of each other and were separated by less than 10 km, their pathways were significantly different. One traveled along the eastern flank of Stellwagen Bank, down the outer Cape and entered Nantucket Sound, carving a pathway between Nantucket and Martha's Vineyard. This matches the pattern and timing of nearshore toxicity extremely well. Other drifters followed an offshore trajectory, with both traveling east of Stellwagen Bank, after which one was transported down the Great South Channel, while the other headed east toward Georges Bank.

It is notable that none of these drifters entered Massachusetts Bay, where very high *A. fundyense* cell concentrations were found. However, this drifter release occurred subsequent to the first northeaster storm, after the period of transport conditions favorable for entry into the bay. By the time of the second storm with winds from the northeast, the drifters had already passed by the potential entry point to the bay.

3.4. Pre-bloom cyst surveys

Table 1 shows *A. fundyense* cyst abundance in the top cm of sediment in several GOM domains, calculated from a cyst survey conducted in 1997 (Anderson et al., 2005c), and another in 2004 (D. M. Anderson, unpubl. data). Each domain represents a different region of the coast and includes two adjacent offshore transects from the cyst surveys. Domain D1 extends from Portsmouth NH to Cape Porpoise, D2 from Casco Bay to the Kennebec River, D3 spans Penobscot Bay, D4 extends from Mt. Desert Island to Jonesport, and D5 is the Bay of Fundy east of Grand Manan

Table 1
Cyst abundance in the top cm of sediment in selected Gulf of Maine domains in 1997 and 2004

Domain	Geographical description	Cyst abundance (cysts cm^{-3})	
		Mean	
		1997	2004
D1	Western Maine	76 ($n = 8$)	83 ($n = 14$)
D2	Casco/Kennebec	169 ($n = 15$)	1172 ($n = 15$)
D3	Penobscot	117 ($n = 22$)	371 ($n = 10$)
D4	Eastern Maine	51 ($n = 14$)	201 ($n = 10$)
D5	Bay of Fundy	163 ($n = 6$)	568 ($n = 18$)
D1–D5	Entire region	105 ($n = 65$)	456 ($n = 67$)

Domain descriptions are given in the text. n = number of sediment samples per domain.

Island. Table 1 shows that in most domains, the mean cyst abundance was at least two-fold higher in 2004 compared to 1997, while the mean cyst abundance over all domains was about 4 × higher in 2004 than in 1997. That difference is highly significant (t-test; $p<0.001$).

3.5. Mooring observations

The effects of the storm on May 7 and 8 were evident at several instrumented mooring sites in Massachusetts Bay (Fig. 7). Persistent winds from the north and large waves were measured from May 7 to May 9 at the NOAA meteorological buoy in the bay (Fig. 7A, B). These winds established a flow toward the south typical of the counterclockwise circulation pattern that occurs in Massachusetts Bay under these forcing conditions (Geyer et al., 1992). These storm-driven flows were measured at the surface (5 m) and subsurface (20 m) at the USGS-MWRA LT-A mooring, located well within Massachusetts Bay.

3.6. River discharge

The abundant snowfall and heavy rains of the winter and spring led to heavy river runoff into the GOM in early 2005. The major western gulf rivers (the Merrimack, Kennebec, and Penobscot) all showed the same basic pattern for April and May 2005 (Fig. 8)—three large pulses of runoff that were at or near flood level, and overall discharge about 50% higher than the 76-year average (R. Signell, pers. comm.).

3.7. Model simulations

A snapshot of model-simulated GOM coastal circulation at 1500 h, May 7, 2005 is shown in Fig. 9A, tidally averaged to represent the wind-driven response. Strong (downwelling-favorable) winds from the northeast during the storm caused an intensive downwelling response in the coastal circulation. Surface currents traveled with velocities up to 0.5 m s^{-1}, causing significant onshore transport and sea-level rise along the entire coast. The underlying westward (alongshore) flow tendency nearshore was preserved and enhanced; the surface flow at key branch points (Penobscot, Cape Ann) was dominated by this effect. At Penobscot Bay, the flow favored the alongshore option, with resultant transport from the eastern to the western Gulf. At Cape Ann, the surface flow entered Massachusetts Bay, rather than following the alternative pathway east of Stellwagen Bank.

Lagrangian trajectories of surface water parcels are shown in Fig. 9B, C and D for the same simulation. These are all initiated at the beginning of the northeaster, May 7, and cover the duration of OC412, May 9–18 plus a three-day forecast to May 21. They illuminate the pathways for *A. fundyense* between the WMCC offshore and Massachusetts Bay. Individual trajectories show the detailed effect of the wind forcing on the nonlinear Lagrangian outcomes. Fig. 9B shows trajectories for particles or cells originating near Cape Ann. Nearshore trajectories are recruited heavily into Massachusetts Bay due to the northeast storm; those originating further offshore, while still affected by the wind event, are less likely to be recruited and an effective divide is visible. Fig. 9C shows trajectories initiating further "upstream" that arrived at Cape Ann after the northeast wind event, and thus largely bypassed Massachusetts Bay in favor of the pathway seaward of Stellwagen Bank toward Provincetown, consistent with the drifter trajectories (Fig. 6). Together, the two panels of Fig. 9B and C illustrate the space–time variability of the Cape Ann branch point.

Fig. 9D shows trajectories for simulated particles originating within Massachusetts Bay. These were heavily retained within the bay by the initial shoreward transport in the May 7 and 8 northeast storm, followed by the return of more quiescent partial recirculation in the bay. Also evident in Fig. 9D is the exit lane from the bay at Race Point, (the northern tip of Cape Cod), potentially seeding outer Cape Cod and Nantucket areas with exported cells from Massachusetts and Cape Cod Bays. All of these pathways are for inert particles fixed at near-surface; transport pathways occurring at depth are not depicted. Downwelling zones appear as convergence zones for surface trajectories.

4. Discussion

Initial observations from the 2005 *A. fundyense* bloom in southern New England allow us to evaluate the extent to which the patterns of toxicity and cell abundance agree with several conceptual models for *A. fundyense* bloom dynamics developed during the ECOHAB–GOM program. These models were formulated on the basis of field observations during years in which toxicity was limited in

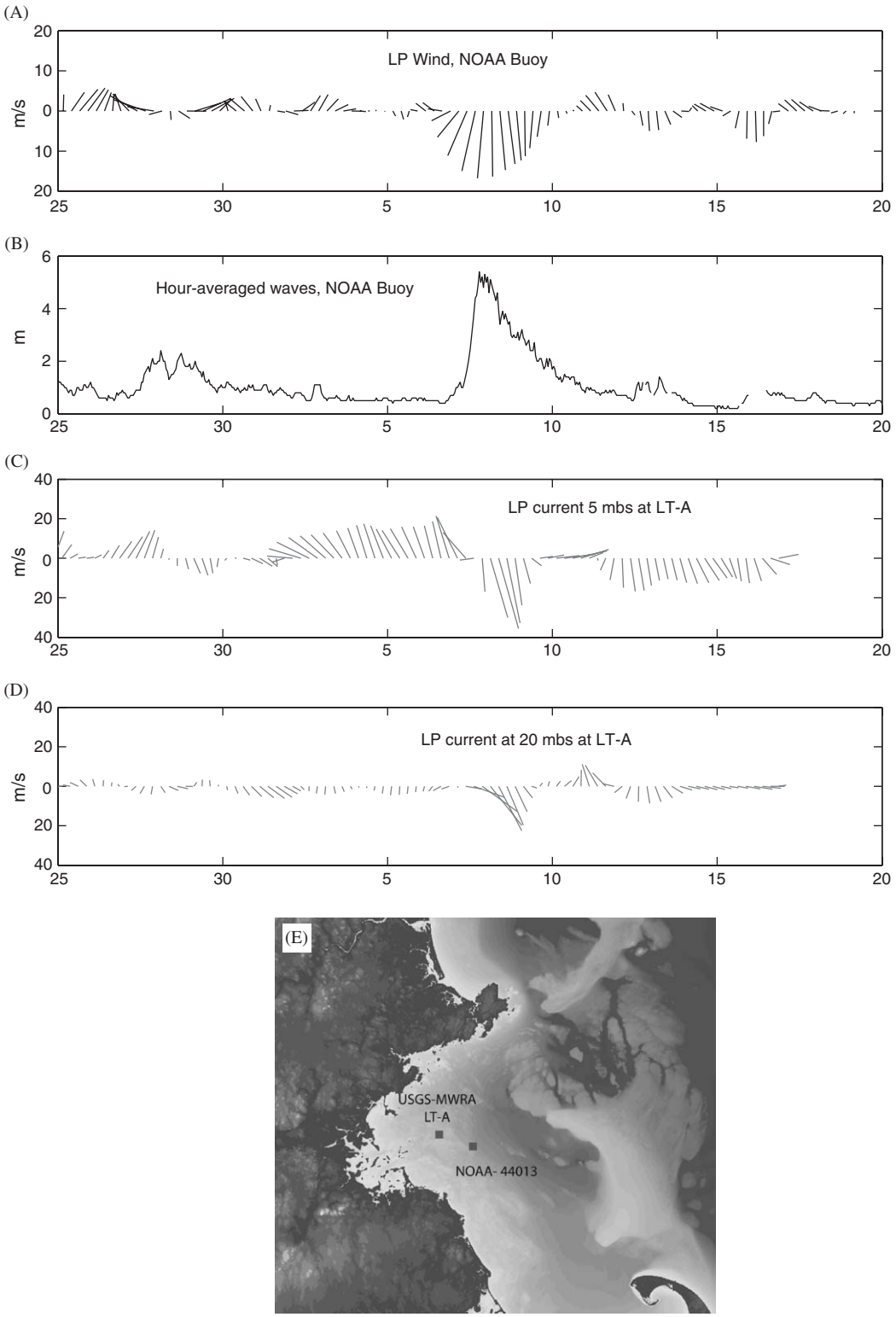

Fig. 7. Time series plots of winds, waves, and currents from data acquired at instrumented moorings located in Massachusetts Bay for the period April 25–May 20, 2005. (A) Wind at NOAA Buoy 44013; (B) hourly averaged surface wave height at NOAA Buoy 44013; (C, D) low-passed current at 5 and 20 mbs (meters below surface) at USGS-MWRA LT-A; (E) location of moorings. Data courtesy of B. Butman, United States Geological Survey (USGS).

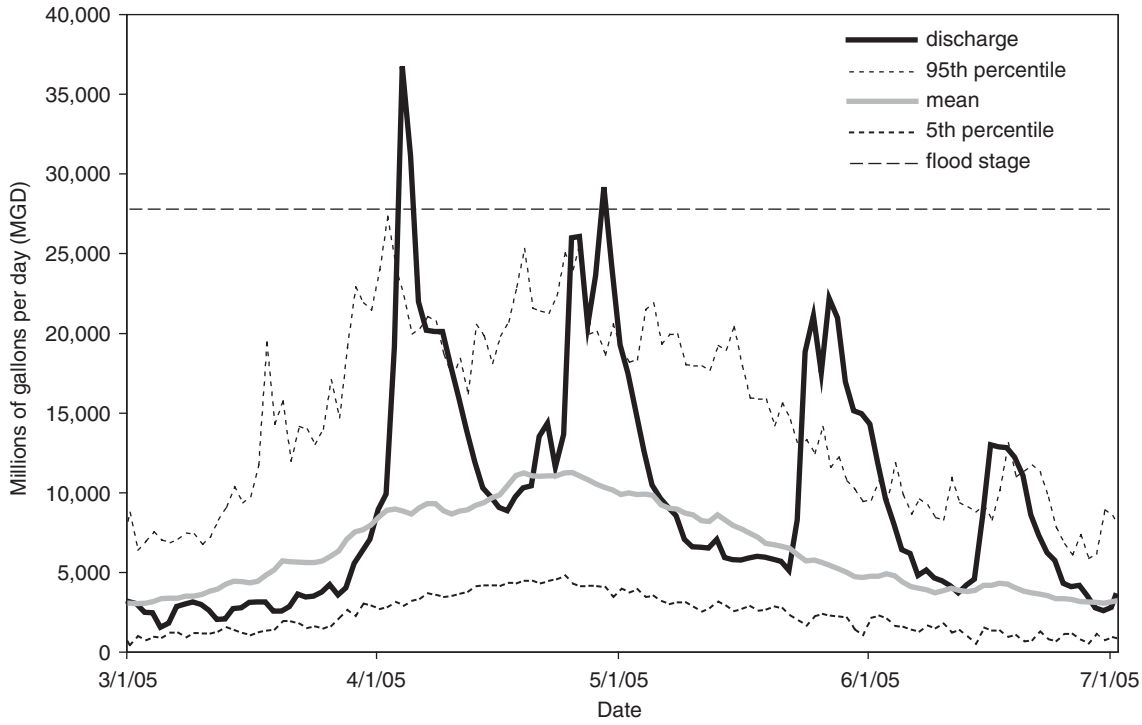

Fig. 8. Discharge data for the Androscoggin River in March–June, 2005. (Mean—76-year mean of daily average flow.) Source: R. Signell, USGS.

southern New England, and thus it is a useful exercise to see if the proposed mechanisms apply to the 2005 event, which extended well into southern waters. The primary focus is on several key features of the conceptual models, including: (1) sources and transport pathways for bloom initiation in southwestern GOM waters; (2) conditions for cell growth in western vs. eastern GOM waters during the early stages of the bloom season; and (3) wind-driven, episodic events that directly affect alongshore transport of cells and shellfish toxicity.

4.1. Bloom initiation

Given the seasonality of *A. fundyense* blooms, the ultimate source of cells for blooms in the GOM each year is presumably benthic or suspended cysts (Anderson et al., 2005c; Kirn et al., 2005). Both McGillicuddy et al. (2005) and Anderson et al. (2005c) highlight two large cyst seedbeds in their conceptual models. The Bay of Fundy seedbed is considered to be the source of germinated cells that populate a retentive gyre at the mouth of the bay, from which some vegetative cells escape and travel with the EMCC to the south and west. The seedbed offshore of Penobscot and Casco Bays is thought to provide inoculum cells to the WMCC region, supplemented by episodic intrusions of water and cells from eastern Maine. Townsend et al. (2001) also link blooms of *A. fundyense* in the EMCC region to cells that originate within the Bay of Fundy, and hypothesize episodic delivery of cells from the EMCC to the WMCC.

The only data that might be used to infer the relative importance of the major cyst seedbeds in bloom initiation is that of the large scale OC412 cruise in early May, which shows a moderate concentration of *A. fundyense* cells ($>1000\,\text{cells}\,\text{l}^{-1}$) inside Massachusetts Bay, grading to lower concentrations in the western Maine region between Cape Ann and Penobscot Bay, with even fewer cells in eastern Maine and the Bay of Fundy region (Fig. 4A). Without direct excystment flux measurements, however, it is not possible at this time to estimate the relative contribution of the two large regional seedbeds to the bloom that developed in southern New England.

We do note, however, that cyst abundance was significantly higher throughout the GOM in late

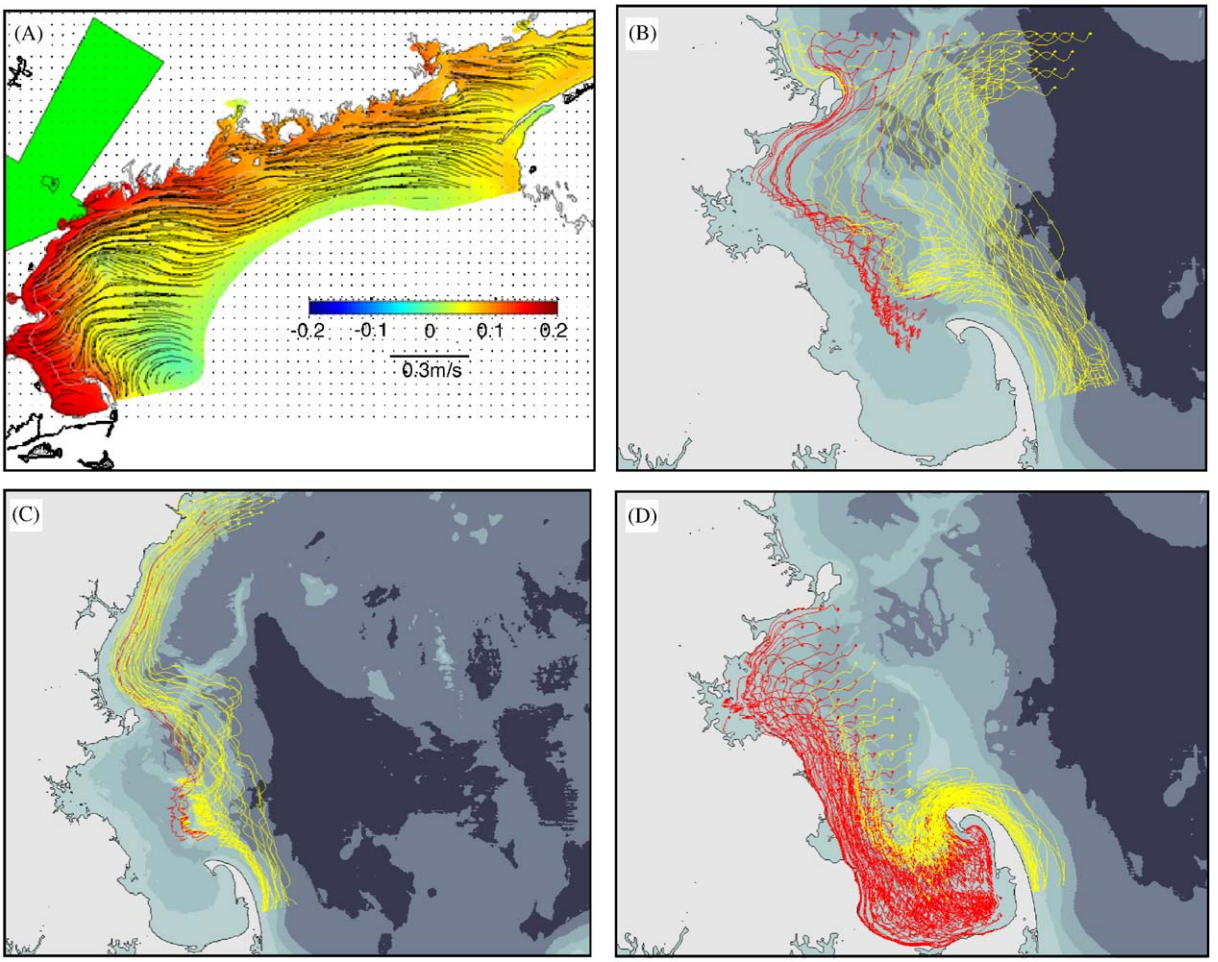

Fig. 9. Model simulations of hydrography and particle transport during the 2005 *A. fundyense* bloom. (A) A snapshot of model-simulated Gulf of Maine coastal circulation at 1500 h, May 7, 2005. The green arrow over land represents the direction and intensity of prevailing winds. The vector contours in the ocean depict the direction of flowing currents and their magnitude (in ms^{-1}). Colors represent sea-surface height in m. (B) Lagrangian near-surface trajectories for the period May 7–21, illustrating the Cape Ann branch point. Trajectories originating near Cape Ann generally recruit into Massachusetts Bay due to the northeaster storm. (C) Trajectories originating upstream. Particles generally bypass the bay, arriving at Cape Ann after the May 7–8 storm and heading instead for Provincetown and Nantucket Shoals. (D) Lagrangian trajectories originating within Massachusetts Bay. These trajectories are largely retained by the northeaster storm. The overwhelming exit path is visible at the tip of Cape Cod, connecting Massachusetts Bay with Nantucket Shoals. Here and in (B), (C), the trajectory color indicates final position: in (red) or out (yellow) of Massachusetts Bay.

2004 compared to a previous survey conducted in 1997 (Table 1). This increase may reflect a large fall bloom of *A. fundyense* that occurred in the western GOM in 2004 (D. Couture, C. Nash, pers. comm.), which appears to have deposited a large number of cysts that would then have been available for germination in the spring 2005. Model simulations that use the 2004 cyst distribution map as the source of *A. fundyense* cells will be useful in ascertaining if the apparent increase in cyst abundance in the region was responsible in part for the extent and magnitude of the 2005 bloom.

Presumably cells did enter the water column from cysts that germinated along the GOM coast, with some high levels of input from the major seedbeds. It is, however, the transport and growth of the cells along the transport pathways that determines the ultimate size and impact of the bloom. One such pathway is the WMCC, which transports the cells that affect western Maine and southern New England. This water mass can receive cells from germinated offshore cysts in the Penobscot/Casco Bay area (Anderson et al., 2005c), or from established vegetative populations in the EMCC

(Townsend et al., 2001; Luerssen et al., 2005; Keafer et al., 2005a) that in turn originated within the Bay of Fundy. The WMCC also can receive cells from the GOMCP—a low-salinity buoyant current inshore of the EMCC that bypasses Penobscot Bay and travels to the southwest (Fig. 1; Keafer et al., 2005b).

All of these transport pathways were potentially operative during the early stages of bloom development for the 2005 event in southern New England. Extensive analysis of field observations and model simulations will be needed, however, to resolve the relative contributions of these different sources and pathways to the 2005 event. A critical objective of those analyses will be the identification of a mechanism that can account for the association of the bulk of the early season *A. fundyense* population with a nearshore band of low-salinity water that stretches from the Bay of Fundy to Massachusetts Bay (Fig. 4A). This might simply reflect the long-distance transport and growth of cells within the GOMCP (Keafer et al., 2005b), or a more complex mechanism that entrains cells from other sources and traps them and low salinity water against the coast, leading to elevated cell concentrations. In the latter context, McGillicuddy et al. (2003) and Hetland et al. (2002) both describe processes by which the interaction between vertically swimming *A. fundyense* cells and alternating upwelling and downwelling-favorable winds can lead to enhanced cell abundance in a nearshore buoyant plume.

4.2. Growth conditions

PSP toxicity in the GOM typically occurs first in western sections and then in eastern waters, even though the predominant coastal flow direction is the opposite—from east to west (Anderson, 1997). As highlighted by McGillicuddy et al. (2005), growth of the vegetative cells is limited primarily by temperature from April through June throughout the Gulf, whereas nutrient limitation occurs in July and August in the western Gulf. Thus, the seasonal shift in the patterns of cells and toxicity from west to east can be explained by changing growth conditions: growth is more rapid in the western Gulf early in the season due to warmer temperatures and more rapid in eastern waters later in the season due to severe nutrient limitation in the western region during that time period.

Consistent with this conceptual model, at the beginning of the bloom in May and early June 2005, conditions were indeed favorable for *A. fundyense* growth in western GOM waters, including Massachusetts Bay. Temperatures were warmer in the west than in the east, with Massachusetts Bay ranging from 5.5 to 8.3 °C, western Maine from 5.8 to 7.5 °C, and eastern Maine and the Bay of Fundy from 4.9 to 6.1 °C during early May (Fig. 4B). Nutrients in western waters were also at reasonably high levels (i.e. 1.5 to 5.5 μM nitrate plus nitrite; Fig. 4D), presumably as a result of riverine inputs and interactions with the nutrient-rich EMCC waters.

The abundant runoff from GOM rivers and other freshwater sources also provided conditions that would have favored *A. fundyense* growth. The major western Gulf rivers all had discharge volumes 50% higher than the long-term average in early 2005 (Fig. 8). This input augmented a system that was already abnormally fresh, as coastal waters from the GOM to the Chesapeake Bay were 0.5 psu lower than normal as a result of a large-scale freshening event in the fall of 2004 (N. Pettigrew, pers. comm.). The scale of this combined freshwater influence was truly significant in 2005, as low-salinity water extended from the Bay of Fundy to Massachusetts Bay in early May (Fig. 4C). At the peak of the bloom in early June, low-salinity water (29–31 psu) was detected not only within Massachusetts Bay, but 15 km offshore of Stellwagen Bank and subsequently offshore of Martha's Vineyard and Nantucket on June 16 and 17, coincident with the discovery of high cell populations in those areas (data not shown).

Freshwater can enhance *A. fundyense* blooms in three ways. One is by providing macro- and micronutrients, including essential trace metals and organic materials that are known to be important growth factors for *A. fundyense* and related dinoflagellates (Prakash and Rashid, 1968; Wells et al., 1991; Gagnon et al., 2005). Freshwater also stratifies the water column, leading to a shallow mixed layer that is preferred by dinoflagellates (Cullen and Maclntyre, 1998). Furthermore, a freshwater plume is readily transported alongshore by downwelling-favorable winds (Franks and Anderson, 1992a; Fong and Geyer, 2001), concentrating the cells within it along the coastline, especially within Massachusetts Bay. We thus hypothesize that the large amounts of freshwater in the western Gulf in 2005 provided the nutrients, growth factors, and water-column stability that led to high cell abundance, as well as the transport mechanism that dispersed the extensive population over large areas.

4.3. Episodic, wind-driven transport of water and cells

The ECOHAB–GOM conceptual models for *A. fundyense* dynamics account for growth and alongshore transport of cells in water masses such as the EMCC, WMCC, and the GOMCP. They also include mechanisms whereby populations are displaced from, or delivered to, the coast as a result of upwelling and downwelling winds, respectively. Several examples of this type of episodic transport are apparent in the meteorological and hydrographic record from the 2005 bloom. The extensive toxicity and high cell abundance within Massachusetts and Cape Cod Bays clearly reflects strong downwelling-favorable winds associated with the two northeaster storms that hit the region on May 7, 8 and May 24, 25. Prior to the first storm, *A. fundyense* cells were abundant in the offshore waters just to the north of Cape Ann and Massachusetts Bay, evidenced by toxicity in western Maine and offshore New Hampshire shellfish. The effects of the storm's winds are evident in the records of several instrumented moorings that document a southward flow of surface and subsurface waters into the bay (Fig. 7C, D). The associated transport of *A. fundyense* cells into Massachusetts Bay is demonstrated by Lagrangian model simulations (Fig. 9B) of that same time interval.

The simulations also demonstrate the manner in which cells exited Massachusetts Bay near the tip of Cape Cod at Provincetown (Fig. 9D). Those cells can potentially augment the populations transported southward along the eastern edge of Stellwagen Bank in a pathway that bypasses the bay, as shown in model simulation (Fig. 9C). The relative contribution of these two sources of cells to the toxicity that subsequently occurred on outer Cape Cod and the islands of Martha's Vineyard and Nantucket is yet another important unknown that needs to be explored.

The toxicity that developed within Massachusetts Bay was therefore the result of several concurrent factors—the presence of cells in abundance in the offshore waters of western Maine and New Hampshire, just outside the bay, and the subsequent episodic forcing from strong, persistent winds from the northeast that pushed the buoyant WMCC waters and its associated cells into the bay. A subsequent storm several weeks later had a similar effect, and helped to retain the cells within the bay. As these forcings relaxed, cells were able to exit the bay, propagating the PSP outbreak further downstream to the outer Cape. Had those northeaster storms not occurred, many *A. fundyense* cells would presumably never have entered Massachusetts Bay, but instead would have traveled along Stellwagen Bank and eventually out to sea. That "bypass the bay" pathway is visible in the drifter tracks (Fig. 6) and in the Lagrangian model simulations (Fig. 9C). Episodic wind forcing and cell transport were clearly critical factors in *A. fundyense* bloom dynamics and in the patterns of toxicity in shellfish during the 2005 event.

5. Overview

A number of features of the 2005 *A. fundyense* bloom are consistent with the conceptual models formulated during the ECOHAB–GOM program. With respect to the source cells for bloom initiation, we cannot assign a specific source region or transport pathway for the cells or cysts that initiated the 2005 bloom, but it does seem probable that germinating cysts from one or both of the major regional seedbeds were involved. The fact that cysts were in high abundance in GOM waters in 2004 compared to levels measured in 1997 may have affected the timing and magnitude of the bloom.

The conceptual models invoke more favorable growth conditions in western waters relative to eastern waters in the early bloom season, in particular due to warmer water temperatures and favorable nutrient concentrations. Both of these conditions were observed in 2005 at the onset of the bloom in early May. Abundant freshwater inputs to the region also would have been favorable to *A. fundyense* growth and dispersal.

The *A. fundyense* conceptual models invoke long-distance transport of cells in the coastal plumes and currents that comprise the MCC. This was also apparent during the 2005 event, with cells distributed in a long band that stretched from the Bay of Fundy to Massachusetts Bay in early May (Fig. 4A). These cells could have originated within the GOMCP, or in the EMCC, and would have traveled southwestward along the coast with the downwelling-favorable wind forcing that was so prevalent during early May.

A key element of the conceptual models is episodic wind forcing that brings cells in the coastal currents to and from shore. Such events were evident throughout the 2005 bloom, and had much to do with the delivery and persistence of cells and

toxicity in Massachusetts Bay as well as the long-distance transport of the cells in lower-salinity waters all the way to Nantucket and Martha's Vineyard.

Overall, the 2005 *A. fundyense* bloom dynamics followed many of the patterns predicted by the ECOHAB–GOM conceptual models, though some specific details remain unconfirmed at this time (i.e. the sources of inoculum cells in the early stages of the bloom). Since this bloom extended well past Massachusetts Bay and impacted outer Cape Cod as well as Martha's Vineyard and Nantucket, the models need to be augmented with mechanistic explanations for those transport pathways. As the bloom traveled south, significant numbers of cells were present in waters well offshore, including those to the east of Stellwagen Bank and to the east of Nantucket toward the Great South Channel. The closure of 40,000 km^2 of offshore (federal) waters for shellfish harvesting reflects this offshore distribution and highlights a feature of the bloom dynamics that needs to be incorporated into updated conceptual models. Insufficient data are available to document the extent of that offshore toxicity, but flow patterns would suggest that outer Cape Cod, Georges Bank, as well as the Great South Channel and Nantucket Shoals areas should be incorporated into the region addressed by the models. The domain also should be extended to include the waters of Rhode Island and perhaps eastern Connecticut, as *A. fundyense* cells were observed in the former area, though in very low abundance.

A critical modification also may be necessary in terms of mechanisms through which *A. fundyense* cells occur in Massachusetts Bay. In the past, toxicity only developed when blooms were transported into the bay from the north via the WMCC. We hypothesize that the incursion of cells into southern New England waters in high abundance during the 2005 bloom, with the resulting deposition of resting cysts, may have established a third seedbed that can allow *A. fundyense* to colonize the region and propagate its blooms further to the south and west. In that instance, the bay could serve as a source of cells through the germination of cysts deposited in those waters during the 2005 bloom. This potential in situ bloom development could have major implications on the timing and extent of toxicity within Massachusetts Bay and southern New England waters in future years. In effect, the 2005 bloom may have been the "next step" in the southward expansion of the New England PSP problem. The first step in this progression was the 1972 New England red tide (Hartwell, 1975), which introduced the organism into western GOM waters, leading to recurrent outbreaks over the ensuing decades (Anderson, 1997).

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