

Bloom development and transport of toxic *Alexandrium fundyense* populations within a coastal plume in the Gulf of Maine

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Abstract

Toxic *Alexandrium fundyense* blooms in the western Gulf of Maine (GOM) are a common occurrence, causing paralytic shellfish poisoning (PSP) each spring. In contrast, high *A. fundyense* abundances and PSP toxicity commonly occur later in the summer in the eastern GOM and the Bay of Fundy. The objective of this study was to determine if the bloom dynamics of the two areas are linked early in the bloom season when initial outbreaks of toxicity are reported. *A. fundyense* cell abundance and hydrographic data were acquired during three cruises in May and June, 2001 spanning areas of the western and eastern GOM. Surface drifters also were released into the nearshore coastal flow of the eastern GOM. These data provide a coherent view of the springtime evolution of toxic *A. fundyense* blooms in the GOM and the influence of both small- and large-scale circulation. Early in the bloom season (May), the bulk of the *A. fundyense* population was consistently observed in an alongshore band of cells in the eastern GOM associated with relatively low-salinity water (<32) that likely originated from inputs further upstream in the coastal flow, predominantly the St. John River in the Bay of Fundy. At that time, the western GOM was virtually devoid of cells. In June, the population was bifurcated, with one branch extending alongshore into the western GOM and the other into the offshore waters of the interior GOM. This pattern was consistent with circulation models of the coastal GOM that unambiguously revealed a bifurcated flow with the branch nearest the coast directed alongshore to the western GOM. The most significant finding of this study is that *A. fundyense* populations along the eastern Maine coast were delivered along an “inside track” relative to the core of the eastern segment of the Maine Coastal Current. The transport pathway carried cells across the mouth of Penobscot Bay and into the western GOM coincident with outbreaks of nearshore PSP toxicity. The transport is influenced by wind. In particular, some of the cells within the nearshore flow may be lost to the interior GOM when upwelling-favorable winds transport them offshore and into the large-scale circulation dominated by the cyclonic flow of the Jordan Basin Gyre. Downwelling-favorable winds keep the cells close to the coast and rapidly transport them into the western GOM. This study unequivocally demonstrates the linkage between early season *A. fundyense* bloom formation in the eastern GOM and blooms in the western GOM. It also indicates that the lack of toxicity along the mid-Maine coast commonly referred to as the “PSP sandwich” may be an artifact of the lack of shellfish sampling along the outer remote islands of Penobscot Bay, as populations sufficient to cause toxicity can be found adjacent to the coastline. The association of the *A. fundyense*

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populations with low-salinity water near the coast requires a refinement of the terminology for the eastern Maine Coastal Current to distinguish this nearshore water mass from the adjacent, more saline offshore waters. We name this feature the Gulf of Maine Coastal Plume (GOMCP) to reflect the freshwater inputs into the GOM that are critically important in the long-distance transport and growth of *A. fundyense* populations along the New England coast. The GOMCP is likely to be important for other organisms as well.

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1. Introduction

Toxic blooms of the dinoflagellate *Alexandrium fundyense*¹ affect large coastal areas of the northeastern United States and Canada each year (Anderson, 1997; Martin and White, 1988). These blooms pose a serious human health threat, principally due to the accumulation of potent neurotoxins in shellfish that feed on the algal cells, resulting in a potentially fatal illness commonly known as paralytic shellfish poisoning (PSP) in consumers. Historically, toxic *A. fundyense* blooms in the Gulf of Maine (GOM) were thought to be limited to the Bay of Fundy and eastern Maine, but a massive bloom occurred in 1972 (Mulligan, 1973) that affected all the bordering coastal states and required the establishment of extensive shellfish monitoring programs throughout the region (Shumway et al., 1988). Since that time, repeated closures of shellfish resources have occurred along the New England coastline, usually during the spring and summer months. The harmful effects of *A. fundyense* extend to other components of the marine food web as well. These include zooplankton (Turner et al., 2000; Teegarden et al., 2003), larval and juvenile fish (White et al., 1989), and other organisms that may serve as toxin vectors responsible for the deaths of marine mammals (Geraci et al., 1989; Doucette et al., 2002).

Several studies have demonstrated that populations of *A. fundyense* within the GOM are associated with the major elements of the region's circulation, notably the coastal currents along the

coastlines of Maine, New Hampshire, and Massachusetts in the northeastern United States (reviewed in Anderson, 1997; Townsend et al., 2001; Anderson et al., 2005a). The general large-scale surface circulation is characterized by an influx of Scotian Shelf water, which enters the GOM around the southern tip of Nova Scotia (Canada) and merges with the complex currents of the Maine Coastal Current (MCC) system (Fig. 1). The general flow

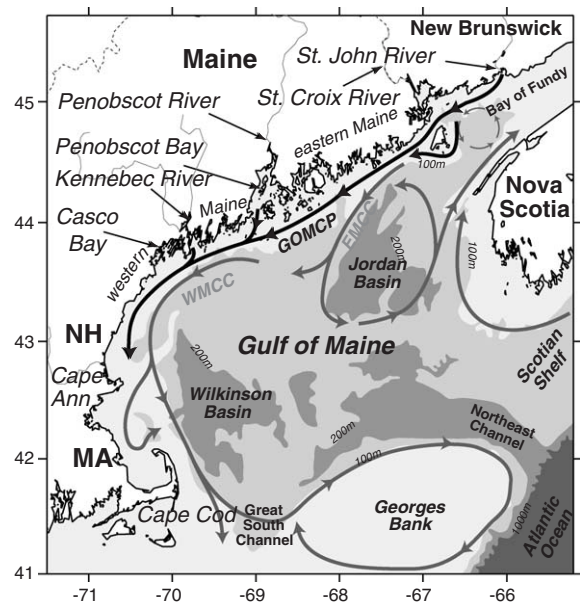


Fig. 1. General near-surface circulation of the Gulf of Maine (GOM). The gray arrows designate the principal features of the general circulation. Of pertinence to our study are several segments of the Maine Coastal Current; the Eastern Maine Coastal Current (EMCC), the Western Maine Coastal Current (WMCC), and the counterclockwise circulation around Jordan Basin (Jordan Basin Gyre). The EMCC is freshened principally through input from Scotian Shelf water and the St. John River. Primary freshwater inputs to the western GOM are from the Penobscot and Kennebec Rivers. Bathymetry is indicated by grayscale levels where dark shading represents the deep basins >200 m (adapted from Brooks, 1985; Beardsley et al., 1997; Lynch et al., 1997). A hypothesized nearshore element in the circulation, the Gulf of Maine Coastal Plume (GOMCP), is shown as dark arrows.

¹Both *A. tamarensis* and *A. fundyense* occur in the Gulf of Maine (Anderson et al., 1994). 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.

continues in a counterclockwise manner along the coastline, some of which exists the GOM through the Great South Channel, while another branch turns offshore and circulates around Georges Bank in a clockwise direction (Bigelow, 1927; Brooks, 1985; Beardsley et al., 1997).

The MCC system has several segments and multiple branch points (Lynch et al., 1997). Along the Maine shoreline, the MCC is divided into eastern and western segments, hereafter termed the Eastern Maine Coastal Current (EMCC) and the Western Maine Coastal Current (WMCC), respectively (Fig. 1). The EMCC extends from the Bay of Fundy in Canada to the Penobscot Bay mouth and often veers offshore to form a cyclonic flow near Jordan Basin. It receives inputs of low-salinity water from local rivers, principally from the St. John, and through the influx of Scotian Shelf water. Subject to vigorous tidal mixing, waters of the EMCC tend to be weakly stratified, or unstratified, in the vertical and often contain high concentrations of nutrients (Townsend et al., 1987; Brooks and Townsend, 1989; Pettigrew et al., 1998). The WMCC extends further south from Penobscot Bay along the western Maine, New Hampshire, and Massachusetts coastlines. In contrast to the EMCC, waters of the WMCC tend to have greater vertical stratification (due to major river inputs from the Penobscot and Kennebec Rivers) and weaker tidal mixing. The extent to which these two MCC segments are connected is the focus of active research (see Pettigrew et al., 2005) and is particularly noteworthy since that connection has important implications with respect to the *A. fundyense* blooms observed within those features. Lynch et al. (1997) proposed the concept of a branch point at the terminus of the EMCC, with some of the EMCC flow continuing alongshore and feeding the WMCC and the remainder being deflected offshore along the western margin of Jordan Basin (Fig. 1). Note also that Fig. 1 contains a feature we call the Gulf of Maine Coastal Plume (GOMCP), a hypothesized nearshore element of the circulation that is described herein.

Shellfish toxicity due to *A. fundyense* blooms occurs annually along the Maine coastline with significant temporal and spatial variability (see Bean et al., 2005). In the western Maine region, outbreaks typically occur from April to June; to the east of Penobscot Bay, outbreaks often occur later in the summer (Anderson, 1997). A notable anomaly occurs in the Penobscot Bay region where shellfish

toxicity is rare. This interrupted pattern of toxicity is commonly referred to as the PSP sandwich (Hurst and Yentsch, 1981; Shumway et al., 1988). Anderson (1997) and Townsend et al. (2001) hypothesized that the lack of toxicity in the Penobscot Bay area is due to the offshore deflection of the EMCC south of Penobscot Bay (Fig. 1), which presumably carries *A. fundyense* cells away from the coast.

Large-scale distributions of *A. fundyense* in the GOM, derived from survey samples in the summer of 1998, have recently been described by Townsend et al. (2001). The highest cell concentrations were observed within two broad areas: one in the Bay of Fundy and the other in coastal and offshore waters of the eastern and central GOM. The latter region appeared to be coincident with the EMCC and its offshore extension. Townsend et al. (2001) interpreted the spatial distribution based on a light-nutrient parameter and found that high densities were located in areas where relatively high nutrient concentrations ($>4\mu\text{M NO}_3$) and light were available ($>10\%$ surface irradiance).

In the western GOM, the evolution of *A. fundyense* blooms is strongly influenced by advection (Franks and Anderson, 1992a). This concept was advanced based on the observation of high *A. fundyense* abundances in the low-salinity, buoyant plumes of the western gulf. Those authors offered the “plume-advection hypothesis” suggesting that the blooms could be traced upstream to a source near the mouths of the Penobscot and the Kennebec Rivers. They further postulated that the transport of those blooms is greatly influenced by large-scale GOM circulation, river runoff, and wind stress. Recently, Anderson et al. (2005a) corroborated many of the elements of the plume-advection hypothesis and refined it to recognize the potential contribution of low-density *A. fundyense* populations entering the western GOM from eastern waters.

Previous studies have not fully resolved key issues related to *A. fundyense* source populations, bloom dynamics, and shellfish toxicity in the western GOM in the spring. Anderson et al. (2005a) suggested that a local source region was located near the Casco Bay region adjacent to Kennebec River mouth. In a companion paper that focused on *A. fundyense* populations in that region during the spring of 1998 and 2000, it became evident that populations in the upstream waters of the nearshore coastal flow are extremely important for bloom development and toxicity in Casco Bay (Keafer et al., 2005).

However, the nearshore flow field in the GOM and its impact on the evolution and transport of the early season (May) *A. fundyense* populations has not been addressed. For example, little is currently known about *A. fundyense* population dynamics in cold, eastern Maine waters early in the bloom season, or the extent to which those populations might supply cells to the western GOM, or how wind-driven and geostrophic flows combine to control the paths ultimately followed by *A. fundyense* populations.

Here we examine how the evolution of *A. fundyense* populations observed along the Maine coast in the spring 2001 is related to the flow field details. We approach this using data from three large-scale hydrographic surveys combined with drifter tracks and wind measurements. Among the issues considered are the relationship of the *A. fundyense* populations with the MCC system, the division of flow at the terminus of the EMCC, the potential impact of wind on the path followed by individual *A. fundyense* patches, and mechanisms by which *A. fundyense* populations delivered from eastern Maine waters may be entrained into the river plumes of the western GOM.

2. Measurements and methods

2.1. Shipboard measurements

The data used in our study included measurements from three shipboard surveys of the Maine coastal region. Two were conducted from the R/V *Cape Hatteras* during May 6–14, 2001 and the third was carried out from the R/V *Oceanus* during June 6–10, 2001. The stations for each survey were arranged along cross-shore lines, designated by letters A–J, oriented roughly perpendicular to the coastline (Fig. 2). At each station, vertical profiles of temperature and salinity were obtained from the downcast data using the ships' CTD (Sea-bird 9/11 plus for all cruises). Water samples were collected during the upcast from Niskin bottles (10 l) attached to the CTD frame, at depths of 1, 5, 10, 20, 30, and 40 m. These were later analyzed for *A. fundyense* cell abundance (see below). Often, the deeper samples (from 30 to 40 m) were not analyzed due to an overwhelming number of samples collected and the general lack of *A. fundyense* cells at depth.

The temporal and spatial coverage of the stations varied somewhat from survey to survey. During the survey of May 6–11 all lines were occupied. The second survey in May (May 11–14) was designed to

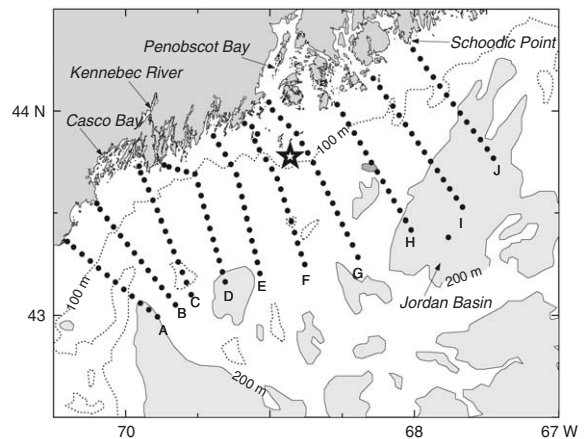


Fig. 2. Station locations of the 2001 hydrographic surveys with cross-shore line designations indicated. The star between the F and G lines marks the location of the Matinicus Rock meteorological station.

examine short-term changes in the population distribution and immediately followed the first cruise. It was confined to the nearshore portion of lines C–I with the distance between stations reduced by half on some lines to resolve the cross-shore patch size. Additionally, the C line was occupied multiple times on May 14–15 (data not shown). Within 3 weeks, the June survey was initiated and occupied all but the easternmost J line.

2.2. Laboratory analysis of *A. fundyense* abundance

A. fundyense abundance was quantified using a whole cell format with an oligonucleotide probe (NA-1) that targets the North American ribotype *Alexandrium catenella/tamarense/fundyense* LSU rRNA (Scholin et al., 1994; Anderson et al., 2005b). A dual-label approach was used to simultaneously target the co-occurring species, *Alexandrium ostenfeldii* using another oligonucleotide probe (AOST01; developed by U. John, Alfred Wegener Institute). These probes unambiguously discriminated between the two *Alexandrium* species present in the samples (see Anderson et al., 2005b). Only the *A. fundyense* (aka *A. tamarense* as noted above) distribution and dynamics are presented here since that species is most relevant to shellfish toxicity due to PSP. The reader is referred to Gribble et al. (2005) for a description of the *A. ostenfeldii* cell and spirolide toxin distribution.

In the field, 2 l of seawater were collected directly from Niskin bottles into sample-rinsed plastic bottles, concentrated by sieving onto 20- μ m Nitex

mesh, backwashed to a final volume of 14 ml with filtered seawater, and preserved with 0.75 ml formalin (5% final). Samples were immediately centrifuged ($1700 \times g$ for 5 min), the formalin removed by aspiration, the remaining cell pellet resuspended to 15 ml in cold methanol, and stored at -20°C . The formalin must be replaced within ca. 24 h with cold methanol to stabilize the target rRNA molecules for long-term storage (>1 yr).

In the lab, a 7.5-ml aliquot of the sample material was filtered onto a 25-mm Cyclopore membrane (Whatman Inc., $5\ \mu\text{m}$ pore size) using custom filter holders attached to a 20-position filtration manifold to control the flow of reagents (described by Scholin et al., 1997; Promega Corp., #A7231). The probing procedure was performed directly on the filters. Before adding the probes, 1.0 ml of pre-hybridization buffer [$5 \times \text{SET}$ (750 mM NaCl, 5 mM EDTA, 100 mM Tris-HCl [pH 7.8]), $0.1\ \mu\text{g ml}^{-1}$ polyadenylic acid, 0.1% Tergitol NP-40 (Sigma Chemical Co. #T-7631), and 10% ultrapure formamide] was added onto each filter and allowed to incubate (5 min at RT). This solution was removed by filtration and replaced with 1.0 ml hybridization buffer (pre-hybridization buffer plus the two probes; final probe concentration for each probe was $4.8\ \mu\text{g ml}^{-1}$). For the dual-labeling approach, the NA-1 probe (NA-1 Cy3; 5' Cy3-AGT GCA ACA CTC CCA CCA-3') was conjugated on the 5' end with a Cy3TM fluorochrome, while the AOST01 probe (AOST01 FITC; 5' FITC-ATT CCA ATG CCC ACA GGC-3') was conjugated with fluorescein. The filter tubes were capped to minimize evaporation and placed (along with the manifold) in a dark bag to minimize degradation of the fluorochromes during hybridization (1 h at 50°C). Following hybridization, the sample was incubated (10 min at RT) with 1.0 ml, 50°C , $0.2 \times \text{SET}$ as a final wash to remove excess probe and the wash solution was removed by filtration. The filter was semi-permanently mounted on a microscope slide, using component A of SlowFade Lite (Molecular probes #S7461) as a mounting medium to prevent fluorochrome degradation. Samples were stored cold (4°C) and dark until microscopic analysis (within 1 day). Control samples containing cultured cells of both *A. fundyense* and *A. ostentfeldii* were processed simultaneously to confirm the consistency of the staining procedure.

The entire filter (equivalent to 1 l of whole water) was enumerated for *A. fundyense* cells by epifluorescence using a Zeiss Axioskop equipped with a

$10 \times$ Zeiss fluar objective ($100 \times$ total magnification) coupled with a high-quality Cy3 filter set (Chroma #41032) that yielded bright orangish *A. fundyense* target cells that could be easily discriminated from other similar autofluorescent particles (e.g., phycoerythrin-containing cells). *A. ostentfeldii* cells were not visualized unless an FITC filter set (Zeiss #09/Chroma #HQ510LP) was in place to enumerate the green-fluorescent, vacuole-containing cells.

2.3. Drifters

To sample nearshore flow during our study period, seven satellite-tracked surface drifters were deployed in the coastal region east of the Penobscot Bay mouth. A lobsterman set out five drifters off of Schoodic Point, near the most inshore station along the J line (Fig. 2). He released a single drifter roughly once per week over the period of April 6–May 7. The other two drifters were set out as part of the shipboard operations of the May and June surveys. All were Davis-style surface followers (Davis, 1985), manufactured by MetOcean Inc., and designed to track the upper 1 m. Each consisted of a cylinder housing an electronics package and vanes that radiated from the cylinder and provided drag. Tracking was accomplished using system ARGOS, which provided $6\text{--}8$ fixes day^{-1} with accuracies of ± 300 m.

2.4. Winds

The wind data used in our study were obtained from the NOAA meteorological station at Matinicus Rock (Fig. 2). The vector winds were rotated into a local alongshore and across-shore coordinate system with the alongshore axis orientated at 65°T (degrees clockwise of true north). This approximately coincides with the orientation of the Maine coastline and is roughly equivalent to the wind direction of maximum coherence with the sea-surface elevation recorded near Portland Maine (Churchill et al., 2005; Janzen et al., 2005). The wind direction was defined according to the oceanographic convention, i.e., the direction to which the wind is blowing.

2.5. Sea-surface temperature (SST) imagery from satellites

In the spring, runoff from the western GOM rivers is warmer than the cold, receiving waters of

the GOM and can be distinguished in advanced very high-resolution radiometer (AVHRR) imagery (Keafer and Anderson, 1993). Although the warm water is not a perfect tracer of the plume, the feature behaves in a manner that is consistent with upwelling- and downwelling-favorable conditions providing an indication of the response of the plume waters to the wind. Relatively cold water along the eastern Maine coast, which is deflected offshore and alongshore as part of the EMCC and the WMCC, is visible as well (Townsend et al., 2001; Anderson et al., 2005a; Luerksen et al., 2005). Data were acquired and processed through a SeaSpace Terascan HRPT (ca. 1-km resolution) ground station located at the Satellite Oceanography Data Laboratory at the University of Maine. This tracking dish provided direct real-time downlink of NOAA's AVHRR data, from which SST was derived. The AVHRR sensors onboard the NOAA-12 and NOAA-14 satellites passed over the study region twice per day yielding four images per day. The absolute temperature measurements from these two satellites are accurate to less than 1 °C. However, various factors (e.g., atmospheric aerosols, skin-layer effects) can influence those measurements. For example, the temperature even from a single satellite can vary with a 1–2 °C range between night and day as the “skin” heats up. Despite these temperature variations, important oceanographic features were identifiable from the relative SSTs observed in the imagery during clear atmospheric conditions.

3. Results

3.1. *A. fundyense* distributions of May and June 2001—general characteristics

The distributions of *A. fundyense* during May and June 2001 show development of the population along the Maine coast, with bloom initiation in eastern Maine waters during early May, and further development that extended both alongshore and offshore in June (Figs. 3–6). The “early season” populations during bloom initiation in the spring were consistently above detection limits of the counting method (lower limit of detection = 1 cell l⁻¹) with maximum abundances (ca. 150 cell l⁻¹) observed at a few stations generally just below concentrations that typically result in detectable levels of shellfish toxicity. Based on field surveys performed prior to and coincident with toxicity outbreaks, *A. fundyense* abundances of

approximately 200 cell l⁻¹ are present when toxicity is first reported (in the sentinel blue mussel, *Mytilus edulis*) along the western Maine coast (Anderson et al., 2005a; Keafer et al., 2005).

Shellfish toxicity had not been reported anywhere along the Maine coast during early May, 2001 (see Bean et al., 2005) when generally low cell abundances (20–150 cell l⁻¹) were largely confined to the coastal region of eastern Maine, to the east of 69°W (Figs. 3 and 4). Although the population was low, it was higher than other areas within the sampling domain, identifying that area as a possible source region for the early season emergence of *A. fundyense* populations that may ultimately affect downstream shellfish resources in the western GOM, commonly the first area along the coast to be affected by the blooms. It is noteworthy, however, that a similar low abundance (ca. 20 cell l⁻¹) also was detected within Casco Bay, isolated from the upstream, coastal population. The population was predominantly observed near the surface. For example, 83% of the total cell abundance was from samples collected in the upper 10 m. Those cells were located in an alongshore band associated with relatively freshwater (<32 psu), with the highest concentrations (50–150 cell l⁻¹) roughly coincident with the 31.7 psu isohaline (Fig. 3A and B). Generally, cell abundance declined with depth. While the abundance at 10 m was lower than at 1 m, the cells were still distributed in an alongshore band revealing the narrow core of the population (Fig. 3C and D). Occasionally, cells were observed at modest abundances (5 cell l⁻¹) in deeper water, >30 m. For those deeper samples that were counted in the two May surveys, 5.5% of the population was observed between 30 and 40 m, indicating that their contribution to the overall population is relatively small early in the bloom season.

The distribution of the *A. fundyense* population during survey 2 was similar to the first survey since it followed directly afterward (Fig. 4). When surveys 1 and 2 were compared along common transects, the mean surface abundance was nearly the same, 10 cell l⁻¹ vs. 8 cell l⁻¹, respectively. The highest abundances remained along the easternmost transect, while the leading edge of the population at 20 cell l⁻¹ remained nearly stationary. SST imagery (e.g., May 8, 2001; Fig. 5A) indicated that the westward extension of the population ended at the frontal boundary between the cold, eastern Maine coastal waters (5–6 °C) and the warm waters of the

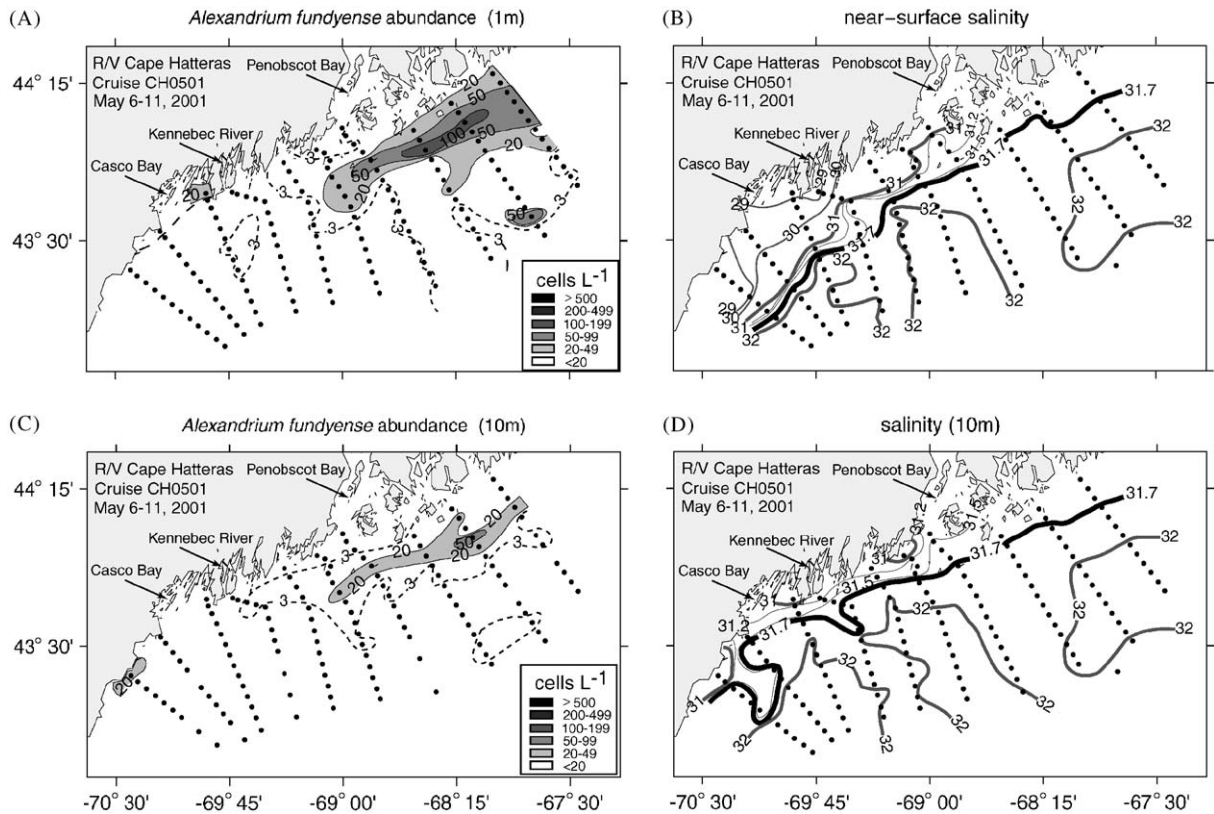


Fig. 3. Early season bloom distributions of *A. fundyense* abundance and salinity at 1 and 10 m as measured during survey 1 of the May 2001 cruise (May 6–11): (A) *A. fundyense* abundance near the surface (1 m); (B) near-surface salinity distribution; (C) *A. fundyense* abundance at 10 m; and (D) salinity distribution at 10 m. Dotted line indicates cell detection at extremely low densities of 3 cell L⁻¹, otherwise shaded contours levels of *A. fundyense* abundance are as shown. The 31.7 isohaline is bold to indicate the general association of the core population with that salinity.

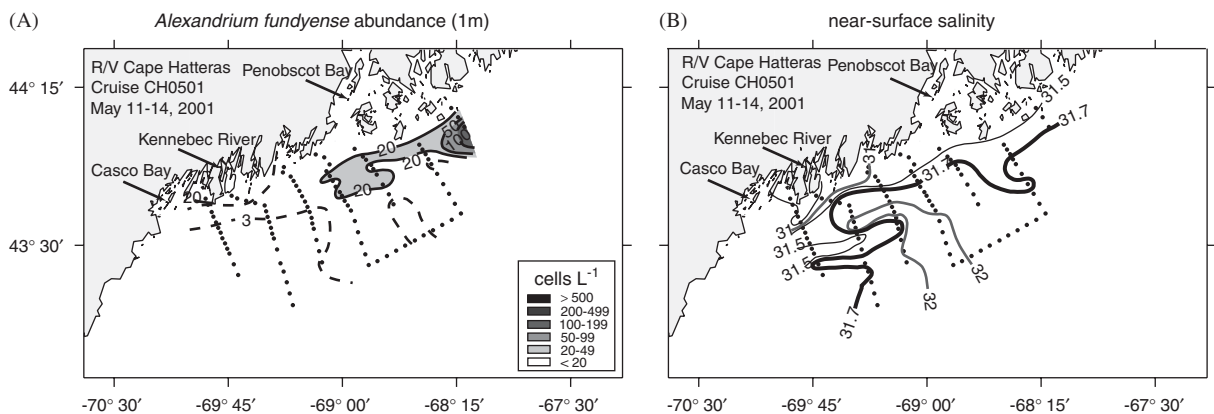


Fig. 4. Early season distributions of *A. fundyense* abundance and salinity during survey 2 of the May 2001 cruise (May 11–14). Many of the same stations shown in Fig. 3 (initially sampled on May 6–11) were resampled during survey 2. (A) *A. fundyense* abundance near the surface (1 m) and (B) near-surface salinity distribution. As in Fig. 3, the 31.7 isohaline is bold. Data from 10 m are not shown.

western Gulf (7–10 °C). The warm feature in the western GOM, generally devoid of cells, consisted of warm plume waters (< 31) spread offshore during

upwelling-favorable conditions as well as warm offshore waters (> 32; Fig. 3B). No significant penetration of cold water and cells into the warm

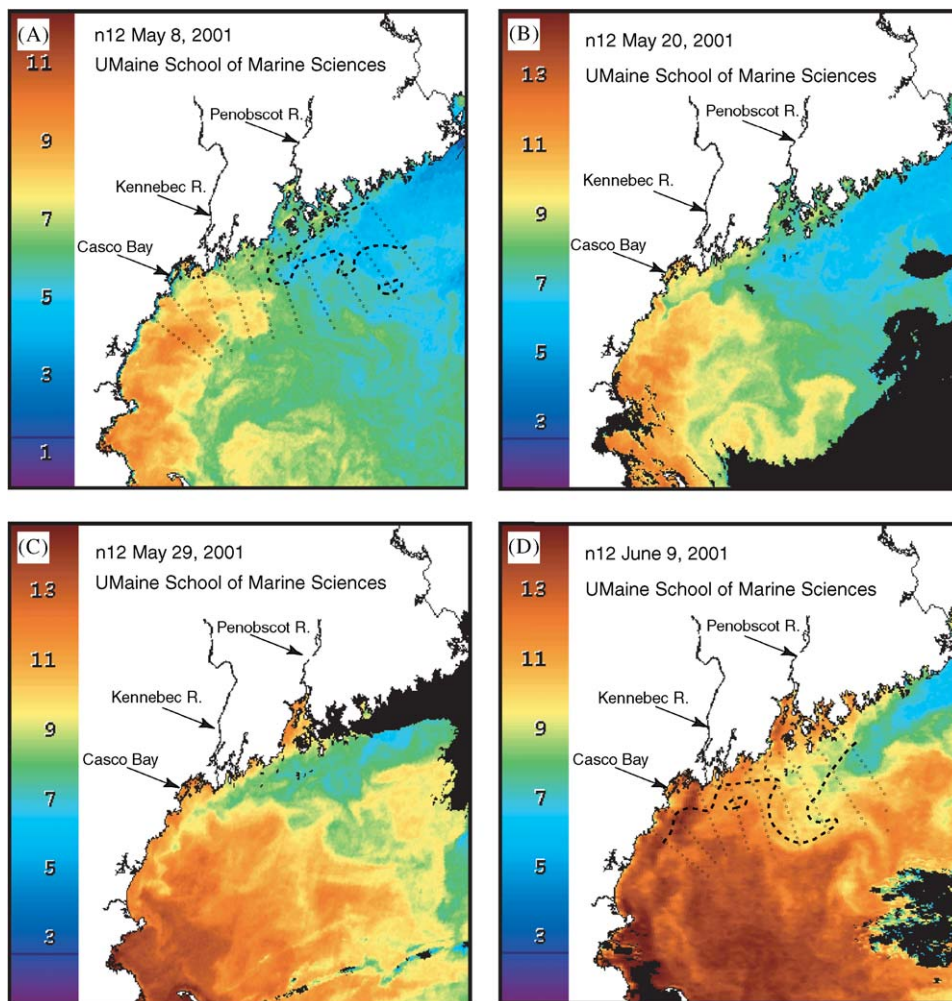


Fig. 5. Sequence of SST imagery (NOAA-12) during *A. fundyense* bloom development in spring 2001. Generally, the coldest waters (blue) represent the core of the EMCC, while the warmest waters (orange-red) represent either western river plume waters or warm, salty offshore waters in the western GOM. Dotted lines in panels A and D represent the 20 cell l^{-1} boundary of the *A. fundyense* surface population from the May and June surveys. (A) The connection of the eastern *A. fundyense* population with the western GOM was minimized during upwelling-favorable conditions, as the warm western river plume waters were offshore on May 8. (B) Intrusion of intermediate temperature water (blue-green) adjacent to the western river plumes during downwelling-favorable conditions. Note circulation around the Kennebec plume. (C) Extension of the intermediate temperature (green-yellow) water further into the western GOM with continued downwelling. (D) Transition back to upwelling-favorable conditions. Note that the eastern nearshore population was located in intermediate temperature water shoreward of the cold core of the EMCC and wrapped around that cold feature, while the western extension of that population was observed in progressively warmer waters along the western Maine coast.

waters of the western GOM was apparent at this time.

Observations during the June survey show the complex development of the population alongshore and offshore as the total abundance increased nearly eight-fold from May (Fig. 6). In a general sense, the June cell distribution can be divided into three connected branches that are apparent at both 1 and 10 m depths. One is a band of relatively high cell concentrations (>200 cell l^{-1}) in the eastern

Maine coastal region. This band is spatially consistent with the alongshore band of relatively low abundance seen in the earlier May surveys (Figs. 3 and 4). The highest abundance (>500 cell l^{-1}) within this band was found at the most inshore station, coincident with reports of shellfish toxicity at Duck Cove (just shoreward of the easternmost transect). Another branch also was composed of relatively high cell concentrations (>200 cell l^{-1}) and extended offshore along the

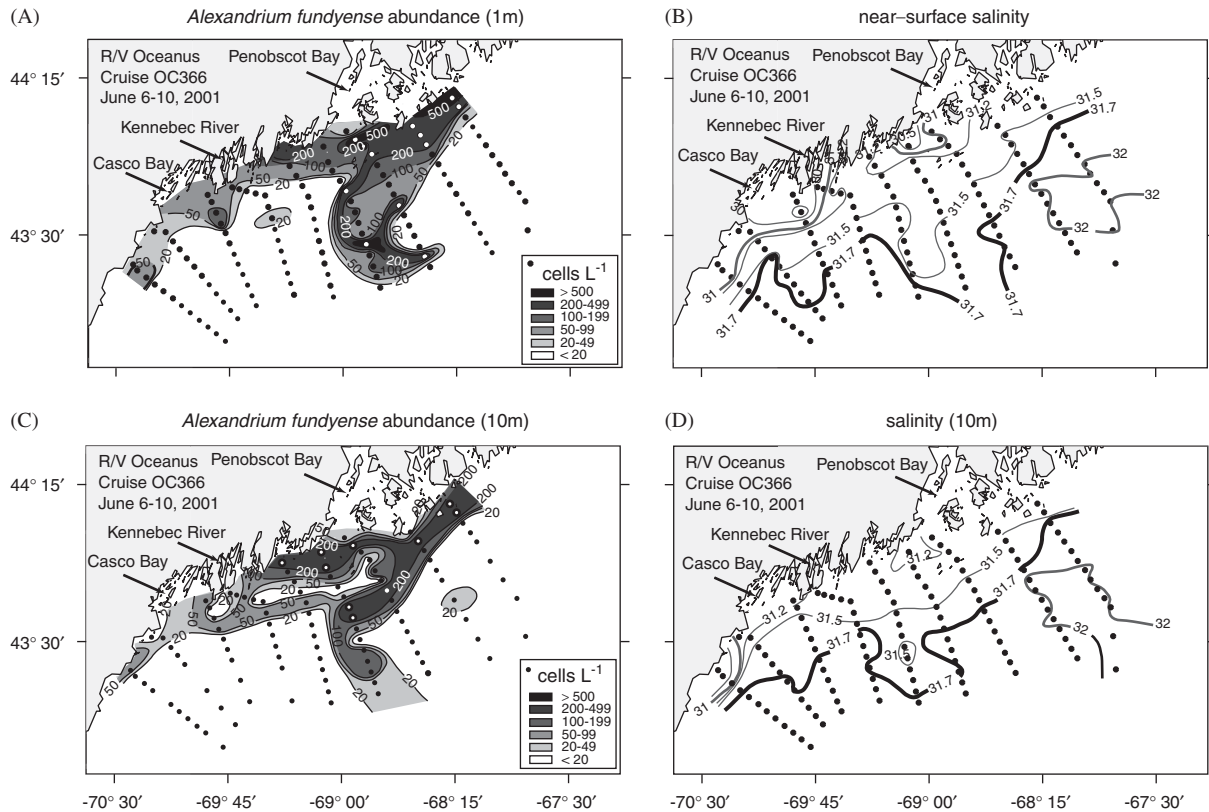


Fig. 6. Distribution of *A. fundyense* abundance and salinity sampled at 1 and 10 m during survey 3 of the June 2001 cruise (June 6–10): (A) *A. fundyense* abundance near the surface (1 m); (B) near-surface salinity distribution; (C) *A. fundyense* abundance at 10 m; and (D) salinity distribution at 10 m. The 31.5 isohaline is bold to indicate the general association of the core population with salinities <31.5 that were transported to the western GOM. Note that populations between Casco Bay and Penobscot Bay exceeded 200 cell l⁻¹ coincident with detection of shellfish toxicity along that section of the coast.

western boundary of Jordan Basin (between 69° and 69°15'W). The third branch was a continuation and extension of the highest (>500 cell l⁻¹) and most shoreward eastern population into the western GOM. Although abundances generally declined to <100 cell l⁻¹ as the population extended westward, the highest concentrations (>200 cell l⁻¹) were found between Penobscot and Casco Bays coincident with reports of shellfish toxicity along that part of the coast. As with the *A. fundyense* populations observed during the May surveys, the June populations were predominantly located near the surface (82% at <10 m) with less than 5% observed in the deeper waters >30 m.

Similar to the May surveys, the population in June was also contained mostly in low-salinity water. Significantly, the bulk of the near-surface (<10 m) *A. fundyense* population sampled in June was confined by the 31.7 psu isohaline (Fig. 6) and was always present in the stratified water column. In

particular, the core of high cell concentrations was embedded in density gradients of roughly 0.01 kg m⁻⁴. Consistent with the survey measurements, SST imagery during the June survey (June 9, 2001) indicated that the highest cell concentrations in eastern Maine (>500 cell l⁻¹) were contained in cool, nearshore waters (>9 °C), clearly shoreward of the coldest waters commonly recognized as the core of the EMCC (6–7 °C; Fig. 5D). The population (as defined by the >20 cell l⁻¹ boundary) extended both alongshore and offshore as noted above associated with temperatures of ca. 8–10 °C. An implication is that the branch extending offshore may have originated within the nearshore, warm, and low-salinity coastal water drawn seaward into the Jordan Basin Gyre, a possibility that will be explored further in ensuing sections. Furthermore, the branch that extended the population alongshore into the western GOM was associated with progressively warmer (12–13 °C) and lower-salinity

(<31) water as the population met the western river plumes. At its westernmost extent, the surface population was clearly associated with the low-salinity Kennebec plume waters (Fig. 6), indicating that the cells had either crossed the salinity barrier to reside within the buoyant western river plumes and/or grown locally within the plume waters. That dynamic also will be examined further in sections below.

3.2. *A. fundyense* distributions in relation to water masses and regional currents

To examine the relationship of the observed *A. fundyense* populations with the GOM circulation, profiles of geostrophic velocity were computed along each survey line. The calculations were carried out using densities derived from the CTD data. With these densities, vertical geostrophic velocity profiles were determined between adjacent CTD stations, assuming a level of no motion at the deepest common observation of the two stations. This procedure, also used by Brooks and Townsend (1989) in studying the MCC, essentially gave the flow relative to the bottom. Each velocity profile was assigned a location midway between the bracketing CTD stations. Contouring the distribution of geostrophic velocity through a particular line was accomplished by combining the line's individual geostrophic velocity profiles. There are a number of concerns with this approach. It does not account for the effects of friction or the interaction of density stratification with a sloping bottom (e.g., Holland, 1973; Rattray, 1982). Nonetheless, the results give a quantitative view of the flow field associated with density gradients in the survey region.

In the eastern Maine coastal region, the computed geostrophic velocities show a strong westward flow, with maximum values exceeding 20 cm s^{-1} , during both the May and June surveys (Figs. 7A and 8A). Although this may be designated as the EMCC, it appears to be comprised of at least two components, each with distinct characteristics. One has the signature of a buoyancy-driven coastal current. It is confined to within 30 km of the coast and is contained within relatively fresh (<32 psu) coastal water. The geostrophic velocities of this current component are highly sheared in the upper 50 m and are due to the density contrast between the coastal water and the more saline water directly offshore. The other flow component is seen further offshore and has relatively little vertical shear in the

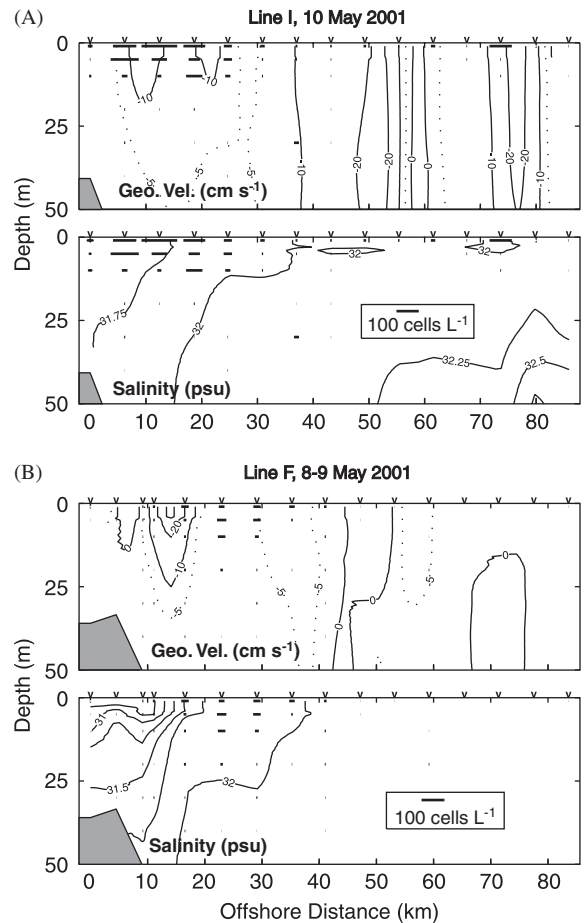


Fig. 7. Vertical distributions of geostrophic velocity and salinity across survey lines I and F as determined from measurement from survey I of the May cruise. Superimposed on the distributions are *A. fundyense* abundances represented by bar length (see scale bar for 100 cells L^{-1}).

upper 50 m. In the May survey geostrophic velocity distribution along line I, this flow component appears at 40–60 km from the shoreward end of the line (Fig. 7A). In the June survey geostrophic velocity distribution, it appears at 30–50 km from the shoreward end of line I (Fig. 8A). In both surveys, this current is principally the result of horizontal density gradients between 50 and 150 m depth.

The overwhelming bulk of the *A. fundyense* populations seen in the eastern Maine coastal region during May and June surveys were found within the nearshore current component described above, i.e., in the buoyancy-driven coastal current (Figs. 7A and 8A). According to our velocity calculations,

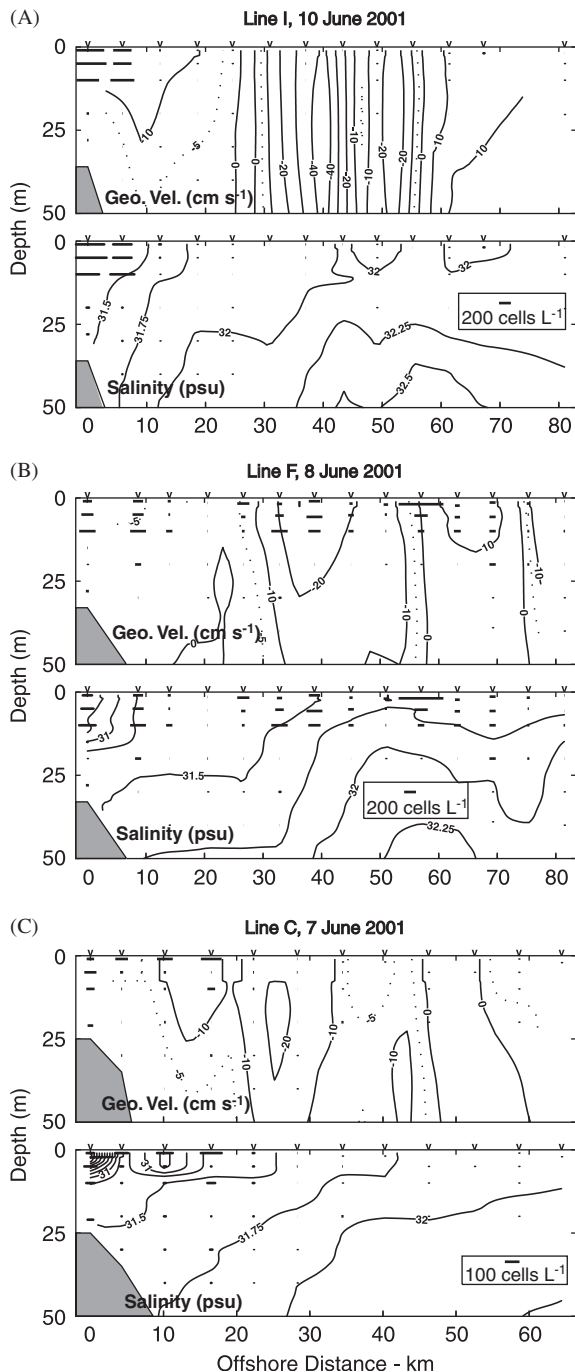


Fig. 8. Vertical distributions of geostrophic velocity, salinity, and *A. fundyense* abundance across survey lines I, F, and C as determined from measurement from survey 3 of the June cruise. As in Fig. 7 above, *A. fundyense* abundances are represented by bar length, but note scale bar change to 200 cell L^{-1} .

these cells were contained within a flow with an alongshore, geostrophic component directed to the southwest and with a strength of 5–10 $cm s^{-1}$.

Further downstream along survey line F, off the eastern Penobscot Bay mouth, the *A. fundyense* relationship with geostrophic flow is somewhat more complicated. As noted above, the coastal band of *A. fundyense* appears to terminate between the F and E survey lines during the May surveys (Figs. 3 and 4). The geostrophic velocities determined along the F line using the May survey data show a strong westward flow of 10–30 $cm s^{-1}$ associated with the Penobscot River plume, in water of salinity <31.5 (Fig. 7A). A small number of *A. fundyense* cells are found within this plume water. However, the bulk of the *A. fundyense* population observed along the F line is located further offshore in water with salinities of 31.75–32.0 and with weak westward geostrophic flow. The coastal band of *A. fundyense* observed during May thus appears to be embedded in a westward geostrophic flow that tends to weaken toward the band's terminus.

The geostrophic velocities determined along the F line with the June survey data show evidence of strong flows offshore of the coastal zone that are not apparent in the May geostrophic velocities (Fig. 8B). The velocities determined along lines further to the east also show a May–June intensification of the flow seaward of the coastal zone (e.g., Figs. 7A and 8A). Along the F line, the pattern of geostrophic flow conforms to the circulation pattern that may be deduced from the June *A. fundyense* distribution (Fig. 6). Over the portion of the line where the *A. fundyense* distribution exhibits a westward bulge, the geostrophic velocities are directed to the west. Further offshore, eastward geostrophic velocities coincide with the portion of the line where the *A. fundyense* distribution appears to hook toward the east. The highest offshore abundance was observed when the velocity is zero, i.e., between the westward and eastward velocities. A reasonable conclusion is that the offshore *A. fundyense* distribution seen in the June survey (at >30 km from the coast) is primarily the result of large-scale circulation that includes a cyclonic flow in the eastern GOM.

Like the surface contours, the cross-shore *A. fundyense* distribution in June along the F line also shows a significant number cells within and at the frontal boundary of the Penobscot River plume, which according to the geostrophic calculations has a westward density-related flow of order 5 $cm s^{-1}$ (Fig. 8B). Samples collected along the E line, directly to the west, also show cells embedded in

the Penobscot plume (data not shown). Still farther to the west, samples and CTD data acquired along the C lines clearly show cells associated with the westward geostrophic velocities of the combined Kennebec–Penobscot River plumes (Fig. 8C).

3.3. Bifurcation of the *A. fundyense* distribution

The progression of cell distributions from May to June (Figs. 3 and 6) suggests that the *A. fundyense* population originating along the eastern Maine coast may split into two branches, with one branch extending offshore along the western margin of Jordan Basin and the other continuing alongshore into the western Maine coastal region. Certainly, germination and growth contribute to the development of these populations during transport. However, because the evolution of the *A. fundyense* population in the GOM must be influenced by circulation, it is of interest to determine if the Gulf's circulation pattern at that time is consistent with the bifurcation of the population.

To this end, distributions of dynamic height were computed from the May and June CTD data.

Because the geostrophic velocities of the coastal and offshore regions arise from density gradients in

different depth bands, as noted above, dynamic height distributions for two reference levels are presented (Fig. 9). One, with dynamic height referenced to 50 m, indicates the nearshore geostrophic circulation; while the other, referenced to 130 m, reveals the pattern of geostrophic circulation further offshore. Referencing dynamic heights to a fixed level has been used in previous studies of GOM circulation by Brooks (1985) and Pettigrew et al. (1998). This approach was justified based on its ease of implementation and its straightforward interpretation of the differences between the nearshore and offshore region. We recognize that there are more sophisticated methods for determining dynamic height in coastal waters (e.g., Csanady, 1979; Sheng and Thompson, 1996).

Taken together, the collection of dynamic height distributions show two potential pathways of geostrophic flow leading from the eastern Maine coast. One is indicated by contours of the dynamic heights referenced to 50 m, which extends across the coastal region in most of the survey area. This may be regarded as an “inside track” of nearshore geostrophic flow extending across the eastern and western Maine coastal regions. The other pathway is indicated by the contours of dynamic height

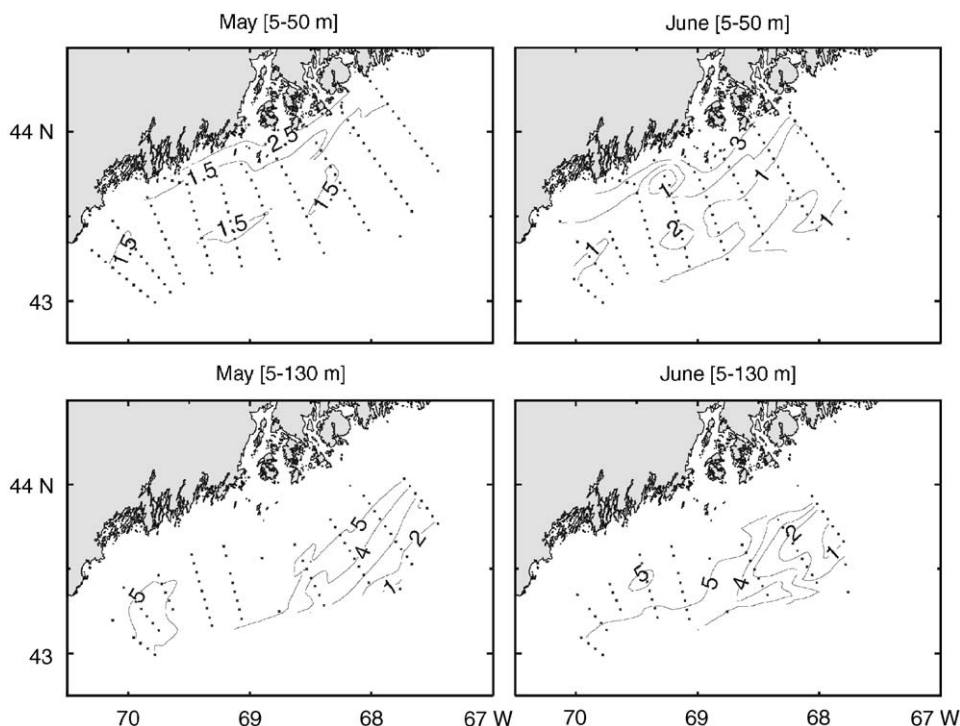


Fig. 9. Contours of dynamic height (in dynamic cm) at 5 m relative to 50 m (top panels) and at 5 m relative to 130 m (bottom panels) as determined from data of survey 1 of the May cruise (left panels) and from the June cruise data (right panels).

referenced to 130 m. These indicate that in the more offshore sections of the transects, the pathway tends to be directed offshore. A cyclonic circulation along the margin of Jordan Basin is apparent in the dynamic height distributions of the June survey, referenced to 130 m. This circulation pattern roughly matches the offshore distribution of *A. fundyense* seen in the June survey (Fig. 6). An implication of these circulation patterns is that material (or cells) entering the nearshore portion of the EMCC would tend to be carried by the geostrophic flow alongshore and that material entering the offshore portion of the EMCC would tend to be deflected offshore.

The division of the westward coastal current in the eastern GOM into two branches also is indicated by the tracks of the drifters set out in 2001. Of the seven drifters released during April–June 2001, four have tracks that were deflected

offshore along the western margin of Jordan Basin (between survey lines G and H), while the tracks of two extended along the coast from the eastern to the western Maine coastal regions (Fig. 10A and C). One of the latter tracks is of a drifter released during the first May survey into a relatively high concentration of *A. fundyense* cells ($>100 \text{ cell l}^{-1}$ at 1 m) to the east of the Penobscot River mouth. The extension of this track westward of the Penobscot River mouth is strong evidence of cell transport from the eastern to the western Maine coastal region.

The flow fields implied by these drifter tracks and the dynamic height fields discussed above are remarkably similar to the circulation determined by recent numerical modeling of the GOM coastal region. Here, we show the tracks of drifters released into modeled flow fields to simulate the transport of near-surface *A. fundyense* populations within the coastal GOM circulation during the climatological

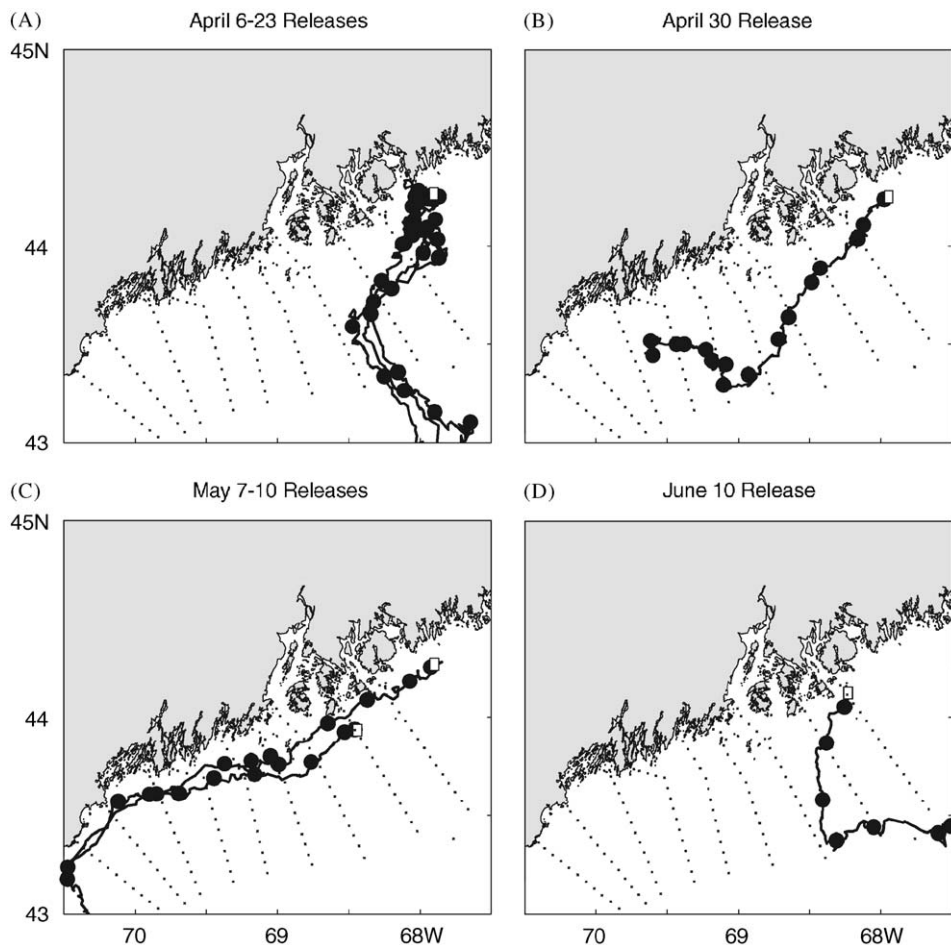


Fig. 10. Trajectories of drifters released in the eastern Gulf of Maine in spring of 2001. Release dates are indicated as separate panels A–D and release points are indicated by open squares. Dots are placed on the tracks at 2-day intervals.

periods of March–April and May–June (Fig. 11). These simulated drifters were released across a transect where *A. fundyense* populations were present in both May and June (Figs. 3 and 6).

The modeled flows were computed on a high-resolution coastal grid described by Lynch et al. (1997) and using temporally averaged wind and temperature–salinity fields as described by Lynch et al. (1996, 1997). Clearly seen in the drifter tracks determined from these flow fields is a bifurcation of the coastal flow south of Penobscot Bay that bears a close resemblance to the separation of the flow implied by our drifter tracks, the dynamic height fields of May and June 2001, and the *A. fundyense* population distribution, particularly in June. In both simulations, only those drifters deployed close to the coast were transported into the western

GOM. Furthermore, of those drifters, only the few released closest to the coast were transported very close to or made landfall along the western Maine shoreline, supporting the view of an “inside track” that can bring populations from eastern Maine coastal waters to the western Maine shoreline via nearshore, density-driven flow.

3.4. Influence of alongshore wind on *A. fundyense* transport

Comparing the drifter tracks with the wind record from Matinicus Rock reveals how the transport of near-surface material may be influenced by the combination of wind-driven flow and density-related large-scale circulation (Fig. 12). All of the drifters that were deflected offshore have release times during a period of upwelling-favorable alongshore wind (directed to the northeast; note the oceanographic convention of wind direction). For example, the tracks of all four drifters set out in April exhibit offshore deflection, and three of these turn southward and exit the GOM coastal region. Their release times were embedded in a 30-day period when the mean alongshore wind was directed to the northeast and of 2.1 m s^{-1} in magnitude (Fig. 12). Similarly, the release time of the drifter set out in June, which also exited the coastal region to the south, was within a period of very strong upwelling-favorable winds (Fig. 12).

The tracks of the drifters that exit the coastal region to the south (between survey lines G and H) exhibit common behavior before turning southward from the coastal region. It is characterized by a migration offshore and to the west during a period of upwelling-favorable winds. The offshore migration is sometimes superimposed on meandering without much net motion. These drifters eventually make their turn southward in the region where the computed dynamic height distributions show offshore geostrophic flow near the surface (Fig. 9). A simple, but reasonable, explanation for this behavior is that it reflects an offshore deflection of the drifters, due to Ekman drift associated with upwelling-favorable winds, into a region where they are swept southward by the large-scale geostrophic flow of the eastern GOM.

The tracks of the two drifters that extend across the coastal Maine region rapidly traverse (at $13\text{--}30 \text{ cm s}^{-1}$) the Penobscot Bay mouth, and thus pass from the eastern to the western Maine coastal region, during a period of strong

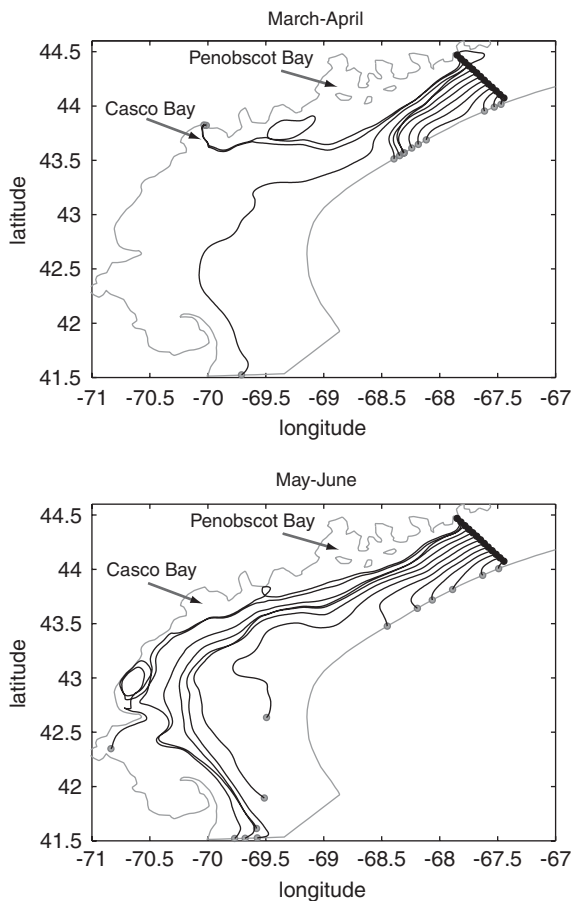


Fig. 11. The tracks of simulated drifters released into model flow fields representing the coastal Gulf of Maine circulation during March–April (top panel) and May–June (bottom panel) climatological conditions. In generating both panels, drifters were released at 5 m to the east of the Penobscot Bay mouth (near line J) and followed for 60 days.

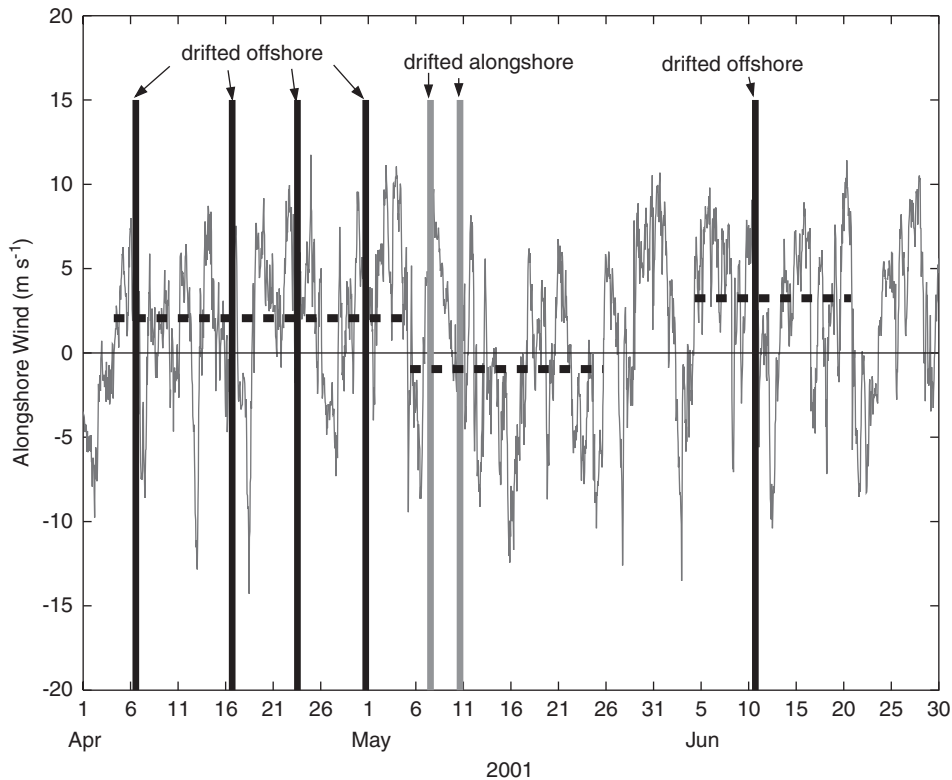


Fig. 12. Alongshore wind velocity during spring and early summer 2001 with times of drifter release indicated by vertical lines. The horizontal dashed lines indicate averaged alongshore wind for periods of alongshore drifter motions and of offshore drifter motion. In the oceanographic wind convention used, positive winds are directed to the northeast and are upwelling-favorable and negative winds are directed to the southwest and are downwelling favorable.

downwelling-favorable alongshore winds, May 13–17 (Fig. 10C). This is consistent with the notion that downwelling-favorable wind tends to strengthen the nearshore coastal current (as demonstrated using moored current meter data by Churchill et al., 2005) and tends to retain near-surface material within this coastal current.

Further evidence of lengthy southwestward transport of surface water along the Maine coast during periods of downwelling-favorable winds was observed in the satellite-derived SST imagery of the study period (Fig. 5). Two SST images from the later portion of May characterized by nearly persistent downwelling-favorable winds (Fig. 12) show a filament of cool water penetrating into the western Maine region (Fig. 5B and C). The image on May 20, 2001 shows a branch that is suggestive of circulation around the Kennebec plume front, while the image on May 27, 2001 shows further penetration into the western GOM. In each image, the filament appears to originate in the nearshore band of cold water marking the eastern Maine

coastal waters. During our study period, cool-water filaments of this type were not apparent in images from times of upwelling-favorable winds (e.g., Fig. 5A and D).

The influence of downwelling-favorable winds in transporting near-surface material from the eastern to western GOM regions may extend further offshore. This is suggested by the track of the drifter released on April 30 (Fig. 10B). Although this track shows an initial offshore migration during a 10-day period of upwelling-favorable alongshore winds, it also exhibits westward motion across a region offshore of the Penobscot Bay mouth during the subsequent period of downwelling-favorable alongshore wind (Fig. 12).

The impact of alongshore winds on near-surface currents may also account for the lack of alongshore progress of the coastal *A. fundyense* distribution between the first and second surveys in early May as noted earlier (Figs. 3 and 4). The time between the occupation of the E line across the leading edge of the population during these surveys (May 8–12) was

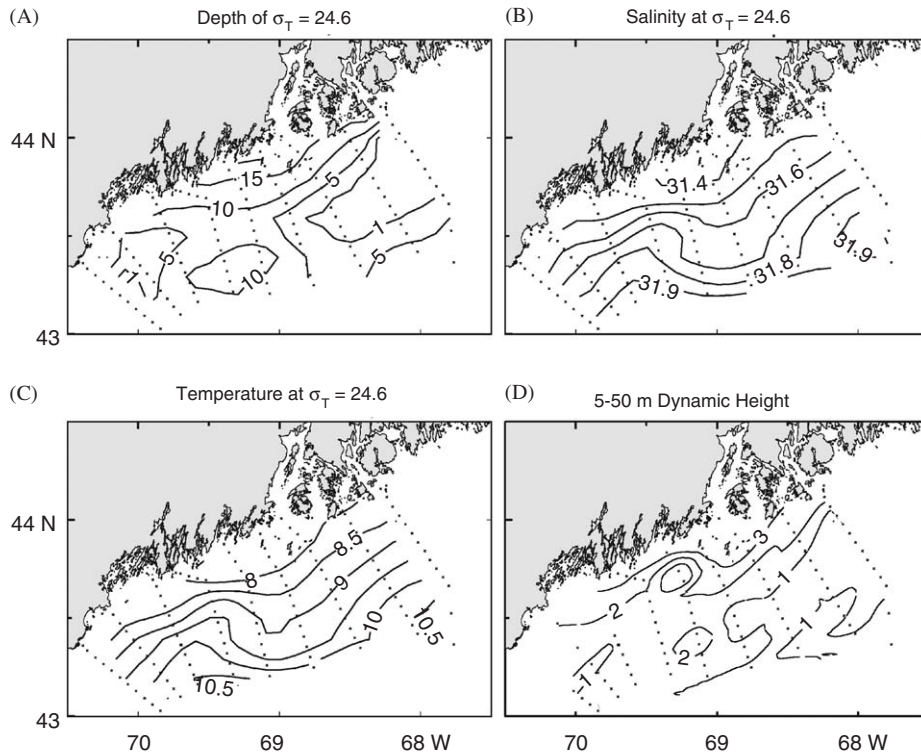


Fig. 13. Properties of depth (m), salinity, and temperature ($^{\circ}\text{C}$) on the $24.6\sigma_T$ surface as determined using the June 2001 survey data (panels A–C). Panel D shows the dynamic height distribution between the 5 and 50 m as determined from the same survey data (reproduced from Fig. 9 for easy comparison with panels A–C).

a period of strong upwelling-favorable alongshore wind in the Matinicus Rock wind record, averaging 2.4 m s^{-1} to the northeast (Fig. 12). In light of the observations discussed above and the analysis of Churchill et al. (2005), it is reasonable to suggest that the western edge of the coastal band of high *A. fundyense* concentrations did not progress between the first and second May surveys because the northeastward (upwelling-favorable) wind slowed (or perhaps even reversed) the southwestward geostrophic coastal flow of the May period.

3.5. Potential mechanism of cell transport to waters beneath the western Maine river plumes

The continuity of the *A. fundyense* populations extending from the eastern Maine coastal region to the relatively warm, low-salinity waters of the Kennebec and the Penobscot plumes suggests that these populations can cross the density barrier(s) of the western Maine river plumes. In Section 4, we consider various mechanisms by which this may occur. Here, we offer evidence of a transport pathway by which cells originating in the eastern

Maine coastal region may be transported to locations directly beneath the western Maine river plumes, where some may enter the plumes through upward swimming behavior.

An indication of this transport pathway is found through examination of temperature–salinity properties along constant-density surfaces as determined from the June survey data. Of particular interest are properties along the $24.6\sigma_T$ surface. In the near-shore region, this density surface extends from the area of high *Alexandrium* concentrations in the eastern GOM to points directly underneath the Penobscot and Kennebec River plumes in the western gulf (Fig. 13). Within the nearshore region, the lines of constant elevation of this density surface roughly parallel the lines of constant dynamic height that mark the flow pathway termed the “inside track” (Fig. 13A and D). In addition, the temperature and salinity properties found along the $24.6\sigma_T$ surface are nearly uniform in the alongshore direction, a condition that would be expected if this density surface were a conduit for alongshore transport of a coastal water mass (Fig. 13B and C). That such a transport could carry

cells from the eastern Maine coastal region to locations beneath the Kennebec River plume is suggested by the *Alexandrium* distribution seen at 10 m in the June survey. This shows a band of cells that follows the 31.5 isohaline from the eastern GOM to the region offshore of Casco Bay and directly underneath the Kennebec River plume (Fig. 6C and D).

4. Discussion

The hydrographic and biological data from 2001 provide a coherent view of the springtime evolution of toxic *A. fundyense* blooms in the GOM and the important role of nearshore circulation in the development of shellfish toxicity. Low abundance ($50\text{--}150\text{ cell l}^{-1}$) populations of *A. fundyense* were observed in the eastern GOM coastal region in May that subsequently developed during June, expanding alongshore into the western GOM and into the offshore, interior waters of the GOM. Based on the alongshore continuity of the populations, drifter tracks, dynamic height fields, satellite imagery, and modeling runs, this study provides evidence that unequivocally demonstrates for the first time the linkage between early season blooms in the eastern GOM and those observed in the western GOM. The most significant finding of this study is that populations along the eastern Maine coast can be delivered along an “inside track” across the mouth of Penobscot Bay and into the western GOM where they are entrained into the western river plumes. The transport is density driven and influenced by wind as well as the large-scale GOM circulation.

In the following discussion, we describe the initiation of source populations in low-salinity coastal waters of eastern Maine, emphasize the manner in which they are transported to the western GOM, and offer one of many possible mechanisms for entrainment into the western GOM river plumes linking the association of the blooms with freshwater sources of the two regions. Taken together, these elements explain the long-distance transport of *A. fundyense* blooms along the Maine coast in a continuous hydrographic feature, which we term the GOMCP.

4.1. Source populations and bloom initiation

Upstream from our survey domain, the Bay of Fundy is well known for recurrent *A. fundyense* blooms that could serve as source populations for blooms along the Maine coast (Martin and White,

1988). Generally, these blooms do not peak until water temperatures warm in the summer when extremely high population ($>10^4\text{ cell l}^{-1}$) were shown to extend into the eastern GOM near the easternmost transects of our surveys. Townsend et al. (2001) also documented high populations of *Alexandrium* sp. in the Bay of Fundy and the eastern Maine region later in the bloom season (June–August). Those populations were primarily transported offshore at the edges of nutrient-rich water from the EMCC. Cysts are produced near the end of the bloom as part of the *A. fundyense* life cycle, accumulating in the deep basin of the Bay where they serve as an inoculum for blooms in subsequent years (Anderson et al., 2005c; McGillicuddy et al., 2005). This large cyst reservoir in the Bay of Fundy, supplemented by a continuous cyst population in the deep sediments ($>100\text{ m}$) along the Maine coast, is the probable source for the eastern Maine motile cell populations observed in this study.

Nutrients required for growth are generally abundant along the tidally mixed eastern Maine coast and would not be considered limiting early in the season (Townsend et al., 1987; Townsend et al., 2001). However, very little growth of the emergent population occurred in early May since temperatures were cold ($5\text{--}6^\circ\text{C}$), evidenced by no change in the population abundance over 1 week in the successive cruises. As temperatures warmed to $7\text{--}10^\circ\text{C}$ in June, the population increased nearly eight-fold (net growth of 0.1 div day^{-1} assuming no advection), while nutrients declined (Townsend et al., 2005). This is consistent with field observations (Love et al., 2005) and modeled studies (McGillicuddy et al., 2005) that determined temperature was a limiting factor early in the bloom season and nutrients later. Surface nutrients may become limiting as the bloom season progresses in June, especially in the western GOM where the prior dominance of diatom blooms and/or other phytoplankton (e.g., spring *Phaeocystis* blooms) reduces the surface nutrient pools without replenishment from below in those vertically stratified waters (Anderson et al., 2005a; Love et al., 2005). The moderate abundances of *A. fundyense* observed in the western GOM often accumulated at frontal boundaries of the western river plumes or within embayments (e.g., Fig. 6) is evidence of transport to the western GOM as low surface nutrients there would not generally support rapid local growth (Anderson et al., 2005a; Keafer et al., 2005; Love

et al., 2005). This supports the view that the highest *A. fundyense* production occurs primarily in the eastern GOM, while the blooms in the western GOM are a westward extension of that production, due primarily to transport, as described below.

A factor influencing bloom initiation is the development of vertical stratification since the highest abundances were clearly located in the cool, low-salinity water shoreward from the coldest, well-mixed water of the EMCC core (e.g., Figs. 5 and 8A). While the well-mixed, core waters may provide nutrients at the surface, intense tidal mixing and the breakdown or absence of stratification can cause light limitation in *A. fundyense* populations in the EMCC (Townsend et al., 2001). Similarly, intense mixing has been linked to the termination of *A. tamarensis* blooms in Hiroshima Bay, Japan (Yamamoto et al., 2002). In spite of intense tidal mixing in eastern Maine, the results show that at least some of that stratification is preserved as a nearshore, buoyant plume. The low-salinity waters associated with the *A. fundyense* population provide sufficient water-column stability and nutrients to support dinoflagellate growth, since the vertical structure maintains the population in relatively high light and nutrient conditions (Jones and Gowen, 1990; Townsend et al., 2001).

4.2. Transport pathways

In 2001, the *A. fundyense* populations that originated in eastern GOM coastal waters appeared to be directed along two pathways. One we refer to as an inside track that carries nearshore cells along the coast into the western GOM. The other, an outside track, carries cells, originally in water more than roughly 20 km from the coast, into the GOM interior, near the western margin of Jordan Basin. In support of these inferences, simulated drifters released close to the coastline of the model domain remained alongshore, consistent with the observed cell distributions. These observations are also consistent with previous field studies that recognized the influence of populations coming into the western GOM near the outer boundary of the Penobscot and Kennebec river plumes (Anderson et al., 2005a; Keafer et al., 2005). Brooks and Townsend (1989) also noted an inshore branch of the MCC evidenced in cross-sections of geostrophic velocity and in satellite imagery as a cool plume moving west toward Penobscot Bay that escaped the offshore turn of the main branch of the cold

EMCC. The outside track observed here is consistent with the offshore veering of *A. fundyense* populations at the edges of the core of the EMCC (Townsend et al., 2001). The numerical model flow fields generated using climatological temperature and salinity distributions reproduce this flow bifurcation, suggesting that it is a robust feature of the mean springtime circulation in the GOM.

Recent studies by Churchill et al. (2005) and Pettigrew et al. (2005) have revealed significant year-to-year variation in circulation in the GOM during spring, 1998 and 2000. According to their analyses, the circulation field of 1998 was characterized by an offshore deflection of a large portion of the EMCC south of the Penobscot Bay mouth and a relatively weak coastal current to the west of Penobscot Bay. By contrast, the dynamic height fields of 2000 show a southwestward flow extending across the Maine coastal region with no evidence of offshore geostrophic flow south of the Penobscot Bay (i.e., no offshore veering of the EMCC). The impact of these interannual differences in circulation on the delivery of *A. fundyense* populations to the western Maine coastal region was manifest as low cell abundance and shellfish toxicity in 1998 and high abundance and toxicity in 2000, with some of that variability also related to wind events (Keafer et al., 2005).

A combination of wind-driven currents and the geostrophic flow field may largely control the path of an individual patch of *A. fundyense* cells, evidenced by the 2001 drifter track data. In the most idealized sense, the impact of wind on the transport of a nearshore and near-surface *A. fundyense* patch can be explained by alongshore wind direction. A downwelling-favorable alongshore wind (directed to the southwest) would tend to accelerate the nearshore southwestward flow (of the inside track) and generate an onshore near-surface current. In contrast, an upwelling-favorable alongshore wind (directed to the northeast) would have the effect of retarding, or in some cases reversing, the southwestward near-surface geostrophic flow and would generate offshore flow. While this dynamic and its effects on *A. fundyense* populations is well documented in the western GOM river plumes (Franks and Anderson, 1992a; Fong et al., 1997; Anderson et al., 2005a), the manner in which it acts on the *A. fundyense* populations in the weakly stratified, nearshore buoyant plume of the eastern Maine region has not been considered.

The wind effects on the drifters suggest that downwelling-favorable conditions would favor retention of near-surface cells in the domain of the nearshore flow, enhancing the inside track and its connection with the western GOM. An upwelling-favorable wind would carry near-surface cells in the eastern Maine coastal region offshore into the domain where the geostrophic flow is eventually deflected offshore (i.e., the outside track indicated by the 2001 dynamic height distributions). If upwelling is not persistent, the population may not be lost to the interior GOM as some of the cells may return nearshore and penetrate into the western GOM, particularly during subsequent downwelling events (e.g., Fig. 10B). Indeed, an increase in *A. fundyense* abundance was detected in Casco Bay by an automated, in situ moored sensor (Scholin et al., in press) in the interim between the May and June cruises when winds were downwelling favorable (Fig. 12). During this time, two drifters tracked into the western GOM (Fig. 10C), while the satellite imagery (Fig. 5B and C) showed cool filaments penetrating into the western GOM. Shellfish toxicity was detected shortly thereafter both in eastern Maine (Duck Cove) and western Maine (Lumbo's Hole and Boothbay Harbor; Bean et al., 2005), i.e., both sides of the "PSP sandwich" (Shumway et al., 1988) following this period. These observations are consistent with previous studies that have shown a positive correlation between shellfish toxicity along the western Maine coast and downwelling-favorable alongshore winds (Franks and Anderson, 1992b; Anderson et al., 2005a). In a companion paper, Keafer et al. (2005) offer further evidence that downwelling-favorable alongshore winds tend to generate a circulation favoring the alongshore and onshore transport of offshore populations in the upstream coastal flow into Casco Bay. Therefore, one key to expanding our understanding beyond the original plume-advection hypothesis is the recognition that *A. fundyense* populations located in the upstream eastern Maine coastal waters also can be influenced by the wind effects on the density-driven flows.

Although the effect of alongshore wind on the nearshore transport of *A. fundyense* cells is well documented, it is critical to realize that the nearshore circulation in the GOM is not a simple superposition of geostrophic and wind-driven flows. From analysis of moored current meter data sets acquired in different decades, Churchill et al. (2005) and Vermersch et al., (1979) separately conclude

that only a fraction of the nearshore current variance (order 50%) in the western GOM can be statistically related to wind forcing. Churchill et al. offer evidence that large variations of flow in the western GOM may be due to eddies embedded within the coastal current, and presumably generated by instability of the current. As part of a related study, Janzen et al. (2005) relate the circular path of a drifter released in the western Maine coastal region to the presence of an eddy as deduced by satellite radiometer-derived SST imagery. It follows that the transport of nearshore *A. fundyense* cells may at times be strongly influenced by nearshore eddies that may have to be considered when predicting *A. fundyense* transport.

The complexity is especially apparent where the *A. fundyense* populations along the inside track meet the strong river inputs in the western GOM. Modeling studies in the GOM have revealed the steering influence of the river plumes on the coastal flow and that influence can extend offshore (50 km) and as deep (20 m) as the populations observed here. (Brooks, 1994; Lynch et al., 1997; Geyer et al., 2004). For example, if the Penobscot and/or the Kennebec plumes extend well offshore during persistent upwelling, then blockage may limit the intrusion of eastern populations into the western GOM. Evidence of that blockage is revealed by the slowing of the geostrophic velocity near the front (Fig. 7B), and the lack of penetration of the population (Fig. 3) and cool water (Fig. 5) into the western GOM during early May, resulting in a delay of onset and relatively low toxicity for that year. The blockage is also evident in the distribution of co-occurring *A. ostentifeldii* populations (Gribble et al., 2005). This is consistent with the reports from Anderson et al., for 1994, a year of low toxicity and strong/upwelling-favorable conditions early in the bloom season and in general agreement with the analysis of Luerksen et al. (2005), who showed that relatively low toxicity years were associated with the lack of cool water penetrating into the western GOM. The blockage may not be due just to the deceleration of the alongshore flow, but also to the salinity and temperature barrier created by the offshore flow of the western river plumes meeting the warm offshore waters of the western GOM. Populations that are not entirely blocked from the western GOM, may be blocked from the inshore waters and accumulate at the outer edges of the plume front or they can be entrained in the river plumes (Franks, 1992; Anderson et al., 2005a;

Keafer et al., 2005). For toxicity to occur in the western GOM, those cells must cross the salinity barrier to affect the intertidal shellfish resources.

4.3. Cell entrainment in the western GOM river plumes

The sources of the *A. fundyense* cells observed within the western river plumes are open to question. The rivers themselves are unlikely contributors to these populations as there are no documented observations of *A. fundyense* cells, at least in the Kennebec River (Anderson and Keafer, 1992; Keller and Phinney, 2001). Certainly, local germination of cysts within the western Maine coastal region would contribute to these plume cells, especially during upwelling when the plume is displaced over deep-water cyst reservoirs (McGillcuddy et al., 2003). However, given the clear evidence for alongshore transport from the eastern to the western Maine coastal regions, it is likely that cells from the *A. fundyense* populations off the eastern coast of Maine would be transported to the vicinity of the Penobscot and Kennebec River plumes. What is required is a mechanism for entraining these cells into the river plumes from adjacent waters.

Multiple mechanisms are possible. The analysis of density surfaces presented here suggests that cells that find themselves near the bottom of the surface mixed layer (e.g., >10 m) can be transported westward directly underneath the thin plume structure and seed the overlying plume via vertical, light-seeking swimming behavior (Fig. 13). As an alternative to the direct throughput of deep populations along density surfaces, Keafer et al. (2005) infer from analysis of temperature and salinity properties that surface populations at the outer edge of the Penobscot plume can be subducted underneath the lower-salinity Kennebec plume, giving rise to high abundances within the plume, presumably as a result of vertical swimming behavior. Recently, Hetland et al. (2002) proposed a mechanism by which cells may be entrained into a river plume undergoing onshore and offshore excursions as a result of alternating upwelling- and downwelling-favorable winds. Termed “the frog-tongue” mechanism, it relies on critical velocities of upward swimming, light-seeking behavior of cells that allows them to be entrained in a river plume that has advanced seaward through upwelling circulation. As in all the proposed mechanisms,

the cells that make their way into the plume are later carried onshore during periods of downwelling circulation where they can affect intertidal shellfish resources along the entire western Maine coastline. Clearly, both short-term observations and modeling studies are needed to resolve the complexity of cell entrainment into river plumes.

4.4. The Gulf of Maine Coastal Plume

The association of the *A. fundyense* population with low-salinity water in the nearshore waters of eastern Maine and its importance as a pathway to the western GOM coastal waters raises an important question concerning the ultimate source of that water and those populations. That association is consistent with a major source of freshwater from the St. John River in the Bay of Fundy that flows above a benthic cyst reservoir in the Bay (Anderson et al., 2005c; McGillcuddy et al., 2005) and enters the eastern GOM during the spring (Brooks, 1994; Bisagni et al., 1996; Lynch et al., 1997). As noted earlier, Brooks and Townsend (1989) consistently observed an inshore branch of the EMCC that was attributed to a nearshore band of slightly fresher coastal water. Bisagni et al. (1996) argued that the St. John was largely responsible for the salinity minimum and nutrient maximum observed inshore along a west to east cross-Gulf transect that was different from the characteristics of the western and eastern branches of the MCC. Lynch et al. (1997) specifically state that there is an approximate division centered near the 100 m isobath between the local and remote dynamical regimes in the GOM, consistent with the bifurcation of the observed and simulated drifter trajectories reported here. Furthermore, Geyer et al. (2004) concluded that 30% of the freshwater in the western GOM in 1994 originated from sources upstream of the Penobscot and strongly suggested the St. John as its major source, while Scotian Shelf water (32–32.5) coming around the southern tip of Nova Scotia may contribute to the deeper waters. This implies that a low-salinity, coastally trapped plume originating from the upstream freshwater sources may be responsible for the long-distance transport of *A. fundyense* populations along the eastern Maine coast (i.e., along the “inside track”) that are ultimately transported to the western Gulf in the spring.

Recognizing this important transport pathway, it has become necessary to refine the terminology for

the MCC to distinguish the nearshore water mass characteristics from the adjacent offshore waters. The adjacent offshore waters are characteristic of what has been consistently termed the cold waters of the eastern segment of the MCC or EMCC that tend to veer offshore near Penobscot Bay in the vicinity of Jordan Basin (Townsend et al., 1987; Brooks and Townsend, 1989; Lynch et al., 1997; Pettigrew et al., 1998). We did not observe abundant *A. fundyense* populations (or *A. ostenfeldii*, Gribble et al., 2005) in those offshore waters, but instead found nearshore populations that were closely associated with a coastal plume aligned alongshore and drawn offshore around the edges of that EMCC cold feature (e.g., Fig. 5D). These same hydrographic characteristics are evident in the data of Townsend et al. (2001). Therefore, we propose to name the nearshore feature the GOMCP, recognizing the freshwater inputs into eastern Maine coastal waters that apparently remain intact during transit down the coast and are distinct from the adjacent waters commonly referred to as the EMCC.

The GOMCP can span the length of the GOM's eastern and western shore with the connection most apparent as cool water penetrates into the western GOM following downwelling-favorable conditions (e.g., Fig. 5B and C; Anderson et al., 2005a). In the west, it should also be distinguished from the WMCC, at least at its origin. The GOMCP is a continuum of the freshwater along the coast, while the WMCC is generally defined as the western branch of the EMCC. When the WMCC and its intermittent connection with its EMCC parent are evident, the *A. fundyense* populations were predominantly located in low-salinity water shoreward of the maximum geostrophic velocities characteristic of the core of the WMCC (Fig. 8C), not unlike the juxtaposition in eastern Maine. This is also apparent in other studies that show that *A. fundyense* populations were most abundant within the western river plumes or at their outer edge (Anderson et al., 2005a; Keafer et al., 2005) and indicates that during transit westward, populations are maintained in a continuous nearshore feature within low-salinity waters as those waters are freshened from the western GOM rivers. Therefore, we conclude that the GOMCP is a part of the MCC linking the major freshwater sources of the eastern and western GOM (as shown in Fig. 1). It is located shoreward of the core of the major coastal current segments, usually within the 100 m isobath unless drawn offshore by a combination of the effects of the wind and the

Jordan Basin Gyre. A conceptual diagram is provided distinguishing the short-term effects of the wind on the *A. fundyense* distributions within the GOMCP during persistent downwelling and

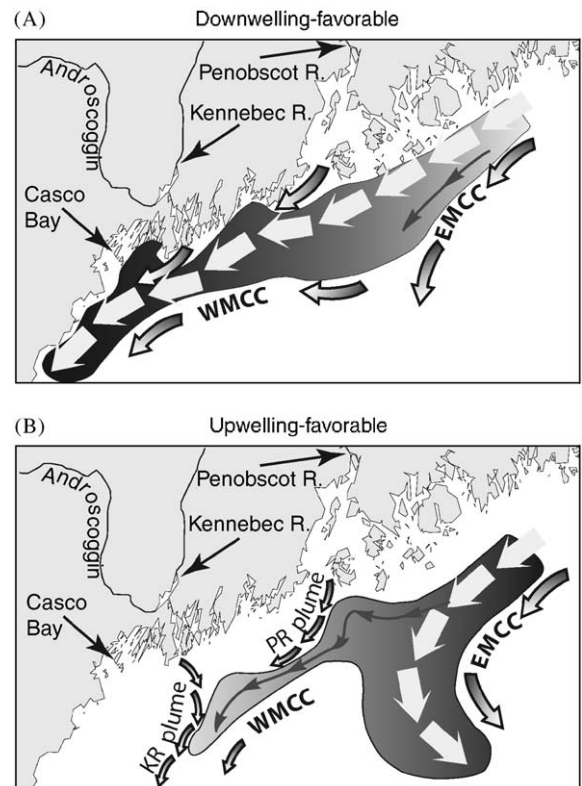


Fig. 14. Conceptual diagram of the delivery of *A. fundyense* populations from eastern Maine to the western Maine coastline. The shaded gradient represents *A. fundyense* populations within low-salinity waters (<32) of the Gulf of Maine Coastal Plume, presumed to originate upstream in the coastal flow as the St. John River plume flows over cyst beds in the Bay of Fundy and along the Maine coast (see Fig. 1). The large light arrows represent the dominant flow paths of the populations, while the small, dark arrows represent the pathway of the remainder of the total population transported along the coast. The outlined and shaded dark arrows represent the major coastal currents offshore or the Kennebec and Penobscot plume waters entering the western GOM. (A) Following periods of strong or persistent downwelling-favorable conditions, the eastern population is close to the coast and converges along an inside track to the western Maine coastline. (B) Following periods of strong or persistent upwelling-favorable conditions, the eastern population is further offshore and follows a more offshore track to the interior GOM, pulled by the effects of the Jordan Basin Gyre, while the inside track to the western GOM is reduced. Some of that offshore population may reconnect to the western GOM during a return to strong downwelling-favorable conditions. Eastern populations in the westward coastal flow can either merge with the freshwater inputs from the Penobscot and Kennebec River plumes (most common during downwelling) or be blocked and steered around those features (most common during upwelling).

persistent upwelling-favorable periods (Fig. 14), which are important in the transport of populations from eastern to the western GOM, but note that a number of scenarios are possible between these two extremes (Fig. 14).

The GOMCP is an important element in the growth and transport of early season *A. fundyense* populations along the Maine coast. Even though part of the population is directed offshore south of the Penobscot, there are sufficient cells present nearshore in May and June to cause toxicity, indicating that the “PSP sandwich” is most likely a phenomenon due primarily to the lack of shellfish sampling along the remote offshore islands of Penobscot Bay. The GOMPC is also sure to be important in the ecology and distribution of many other important species in GOM waters, and thus deserves special recognition as an integral part of the MCC system.

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