

## Toxic *Alexandrium* blooms in the western Gulf of Maine: The plume advection hypothesis revisited

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### Abstract

The plume advection hypothesis links blooms of the toxic dinoflagellate *Alexandrium fundyense* in the western Gulf of Maine (GOM) to a buoyant plume derived from river outflows. This hypothesis was examined with cruise and moored-instrument observations in 1993 when levels of paralytic shellfish poisoning (PSP) toxins were high, and in 1994 when toxicity was low. A coupled physical–biological model simulated hydrography and *A. fundyense* distributions. Initial *A. fundyense* populations were restricted to low-salinity nearshore waters near Casco Bay, but also occurred in higher salinity waters along the plume boundary. This suggests two sources of cells—those from shallow-water cyst populations and those transported to shore from offshore blooms in the eastern segment of the Maine coastal current (EMCC). Observations confirm the role of the plume in *A. fundyense* transport and growth. Downwelling-favorable winds in 1993 transported the plume and its cells rapidly alongshore, enhancing toxicity and propagating PSP to the south. In 1994, sustained upwelling moved the plume offshore, resulting in low toxicity in intertidal shellfish. *A. fundyense* blooms were likely nutrient limited, leading to low growth rates and moderate cell abundances. These observations and mechanisms were reproduced by coupled physical–biological model simulations. The plume advection hypothesis provides a viable explanation for outbreaks of PSP in the western GOM, but should be refined to include two sources for cells that populate the plume and two major pathways for transport: one within the low-salinity plume and another where *A. fundyense* cells originating in the EMCC are transported along the outer boundary of the plume front with the western segment of the Maine coastal current.

Toxic dinoflagellate blooms are a serious economic and

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public health threat to coastal New England states. The most serious problem in this context is paralytic shellfish poisoning (PSP), a potentially fatal neurological disorder caused by human ingestion of shellfish that accumulate toxins as they feed on two species of dinoflagellates within the genus *Alexandrium*. These organisms are responsible for human illnesses, repeated closures of shellfish beds in nearshore and offshore waters (Shumway et al. 1988), the mortality of larval and juvenile stages of fish and other marine animals (White et al. 1989), and even the death of marine mammals such as humpback whales (Geraci et al. 1989). Thirty years ago, PSP was virtually unknown in New England, yet now, significant portions of the region's intertidal shellfish resources are closed annually because of toxicity. A further expansion of the problem occurred in 1989 when the offshore shellfish resources of Georges Bank and Nantucket Shoals were shown to contain dangerous levels of toxin (White et al. 1993).

Until recently, very little was known about the factors regulating the abundance and distribution of *A. tamarensis* and *Alexandrium fundyense*, the two closely related species

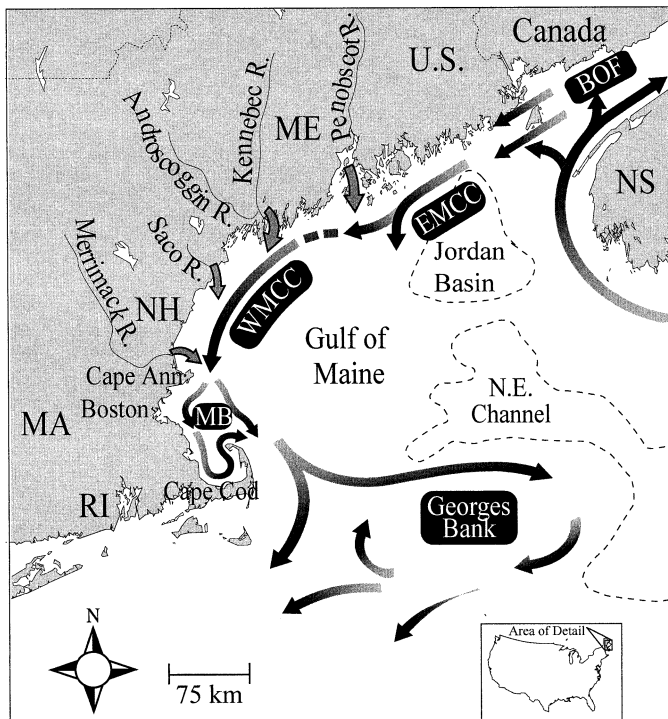


Fig. 1. Map illustrating the general counterclockwise circulation pattern in the Gulf of Maine associated with major *A. fundyense* habitats (adapted from Anderson 1997). The GOM is bordered by Canada—Bay of Fundy (BOF) and Nova Scotia (NS)—to the north and east and the United States—Maine (ME), New Hampshire (NH), Massachusetts (MA), and Massachusetts Bay (MB)—to the west. The major segments of the Maine coastal current (MCC) are highlighted as the western segment (WMCC) and the eastern segment (EMCC). Outflow from the Penobscot, Kennebec and Androscoggin, Saco, and Merrimack Rivers are indicated with arrows. This freshwater outflow produces a buoyant plume that is associated with the WMCC.

responsible for PSP in the Gulf of Maine (GOM) region (Anderson et al. 1994; Anderson 1997). 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.

Several transport pathways are involved in *A. fundyense* dynamics that are related to the regional circulation in the GOM (Fig. 1). Circulation tends to be counterclockwise (Bigelow 1927; Brooks 1985), with southwestward flow along the coast of Maine toward Massachusetts Bay driven by freshwater inflows from the Scotian Shelf overlying salty slope water input through the Northeast Channel and filling Jordan Basin. This region is also influenced by several rivers emptying into the western GOM that overlie the general circulation and extend southwestward along the coast and sometimes into Massachusetts Bay (Butman 1975; Franks and Anderson 1992a; Geyer et al. 1992).

A key feature of GOM circulation is the Maine coastal

current system (MCC), described by Lynch et al. (1997) as a composite of seven legs or segments with multiple branch points (Fig. 1). The upstream, eastern segment (EMCC) extends from Grand Manan basin in the Bay of Fundy to Penobscot Bay. This current derives from inflow from the Scotian Shelf and freshwater from the St. John's River (Bisagni et al. 1996). The EMCC often turns 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 (WMCC), which is then augmented by freshwater outflow from the Penobscot, Kennebec and Androscoggin (hereafter Kennebec), Saco, and Merrimack Rivers. This low-salinity water is hereafter termed the "plume." (In this study, the distinction will occasionally be made between the plume associated with these western Maine rivers and the portion of the WMCC that originates from the EMCC. Together, these two water masses compose the WMCC.) 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 which travels to and around Georges Bank.

The study reported here focuses on toxic blooms of *A. fundyense* that occur in the western Maine region and in Massachusetts Bay; thus, the plume and its interactions with the WMCC are of central interest. In the western GOM, *A. fundyense* was found to be associated with the warm, low-salinity buoyant plume originating from western Maine rivers (Franks and Anderson 1992a). Large-scale cruises in the offshore waters of the eastern GOM have shown that *A. fundyense* is also associated with the cold, nutrient-rich waters of the EMCC (Townsend et al. 2001). Thus, there are at least two "habitats" in the GOM in which populations of *A. fundyense* reside, curiously separated by an area near Penobscot Bay known as the "PSP sandwich" where shellfish toxicity is generally absent but occurs to both the immediate east and west (Shumway et al. 1988).

In the western GOM, the link between the toxic cells and the buoyant coastal plume led to the formulation of a conceptual model for PSP dynamics in the region termed the "plume advection hypothesis" (Franks and Anderson 1992a). Critical features of this model include (1) a source population of *A. fundyense* cells located near the Kennebec River mouth; (2) retention, transport, and growth of those cells in the coastally trapped, buoyant plume formed by outflow from these and other western Maine rivers; and (3) PSP toxicity in nearshore shellfish that relates directly to the alongshore and cross-shore location of the plume and its associated *A. fundyense* cells.

The plume hypothesized to be responsible for the southerly transport of *A. fundyense* into Massachusetts' coastal waters and possibly farther offshore onto Georges Bank (Anderson and Keafer 1992) is regulated by river runoff, Coriolis acceleration, wind stress, and advection. Of these factors, wind stress appears to be particularly important in determining transport variability in surface waters (Franks and Anderson 1992a; Fong et al. 1997). Downwelling-favorable wind (from the north or northeast) compresses the

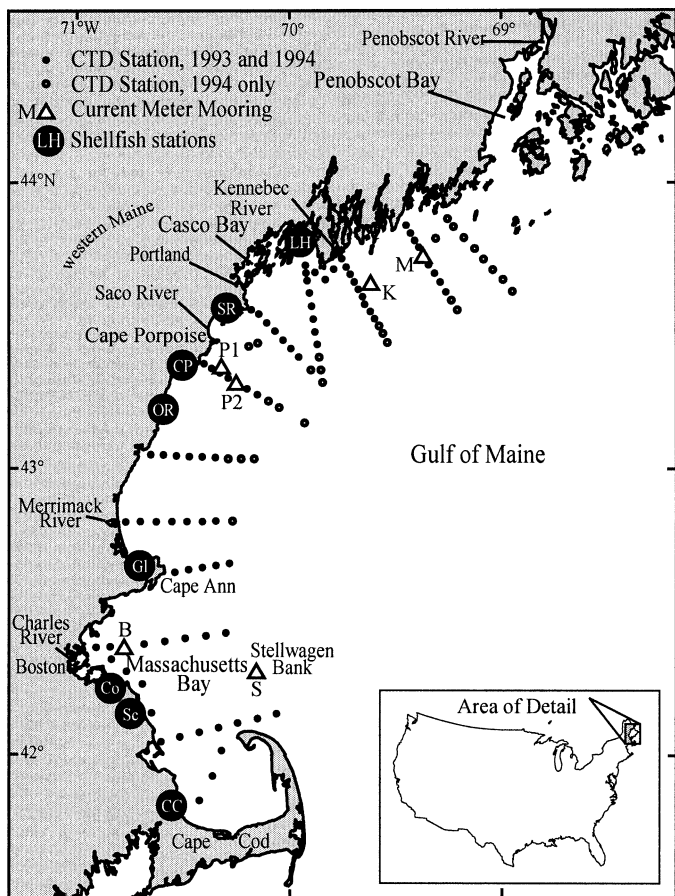


Fig. 2. Map of the western Gulf of Maine study area. Stations and mooring locations are shown for both study years 1993 and 1994. Selected shellfish monitoring stations in Maine and Massachusetts are indicated as follows: LH, Lumbo's Hole; SR, Spurwink River; CP, Cape Porpoise; OR, Ogunquit River; GI, Gloucester-Annisquam; Co, Cohasset; Sc, Scituate; CC, Cape Cod Canal.

plume against the coast and accelerates it alongshore, while an upwelling-favorable wind (from the south) flattens the pycnocline slope and thins the low-salinity surface plume as it is moved offshore. This would also retard the southward progression of the plume and its associated cells. In the downwelling case, PSP would spread rapidly along the coast, whereas with upwelling, toxicity would progress more slowly down the coast, remain constant, or decrease as the toxic cells are transported offshore.

Franks and Anderson (1992b) used 11 yr of PSP records and meteorological data to test the validity of these mechanisms. Direct field verification, however, was limited to hydrographic data from a series of cruises in the immediate vicinity of Portsmouth, New Hampshire, many along a single transect extending 35 km from shore (Franks and Anderson 1992a). Clearly, this limited geographic coverage left many issues unresolved, most notably the question of the source population responsible for the outbreaks and the distribution of the *A. fundyense* population within or near the plume. A more extensive study was therefore initiated, focusing on the large region between Penobscot Bay (Maine) in the north and Massachusetts Bay in the south (Fig. 2).

The structure, variability, and mechanics of this coastal current and its associated *A. fundyense* cells were investigated with a combination of shipboard hydrographic and biological measurements, moored current measurements, drifters, and satellite imagery. Field observations were also used to constrain and refine a hydrodynamic model of the study area, with biological features incorporated to simulate the *A. fundyense* transport and bloom dynamics.

Here, we report on the bloom dynamics of *A. fundyense* in the western GOM during 2 successive years, one in which PSP toxicity reached high levels and extended farther into Massachusetts and Cape Cod Bays than ever before (1993), and another with no toxicity in those bays with very little in western Maine as well (1994). The differences between the 2 yr provide valuable insights into the mechanisms underlying PSP toxicity in the region. Other publications from this study present the detailed physics (Fong et al. 1997; Geyer et al. 2004) and nutrient dynamics (Martarano and Loder 1997) of the coastal current. Additional field observations will also be provided by forthcoming publications from the ECOHAB-Gulf of Maine program. The latter cover sampling domains that are either focused on the eastern end of the WMCC in the Kennebec River and Casco Bay region or on a larger domain lying well to the east of the study area described here (e.g., Townsend et al. 2001).

## Methods

**Shellfish toxicity**—Shellfish toxicity typically occurs in the spring each year in western Maine waters and progresses southward into Massachusetts Bay. In some years, the toxicity does not extend that far south. Both the Maine Department of Marine Resources and the Massachusetts Division of Marine Fisheries routinely test shellfish weekly along the western GOM coast using the standard mouse bioassay for PSP (AOAC 1980). The data presented here are based on the blue mussel, *Mytilus edulis*. Several key stations that generally represent the levels of toxicity in the study area (four in Maine and four in Massachusetts; Fig. 2) were selected from a list of primary sampling sites.

**Shipboard measurements**—During the spring (April–June) of 1993 and 1994, numerous hydrographic cruises were conducted in the region between Penobscot Bay and Cape Cod. Large areal surveys with more than 80 stations and covering more than 200 km of coast out to 50 km offshore were completed within a 3-d time frame aboard either the R/V *Argo Maine* or the OSV *Peter W. Anderson* (Fig. 2). In 1993, a total of five sampling cruises were completed with a frequency of every 2 weeks. In 1994, four hydrographic surveys were completed, but with a modified sampling design to address short-term variability in hydrography and the associated biology. At two different intervals (early and late May), the same transects and stations were sampled twice in immediate succession (i.e., less than 1 week apart) rather than at biweekly intervals as in 1993. Also in 1994, transects near the Kennebec River and near a moored transect off Cape Porpoise (Fig. 2) were sampled with small vessels at times when the larger vessels were not scheduled.

Water properties were measured with conductivity–tem-

perature–depth profilers (Neil Brown Mark III CTD/rosette on the R/V *Argo Maine*; Seabird 9/11 CTD/rosette on the R/V *Anderson*; Seabird Seacat 19 Profiler on the small vessels). The CTD data were pressure-averaged in 0.5-m bins ranging from about 2 m to the bottom. Data from less than 2 m depth were considered to be unstable because of wave action on the sensors. With the use of rosetted Niskin bottles, water samples were collected at the surface for *A. fundyense* cell counts and nutrients at every station. Because of the large number of samples collected, deeper samples from 10 m (cell counts and nutrients) and 20 m (nutrients only) were collected at every other station.

**Alexandrium fundyense analysis**—For each *A. fundyense* sample, 2 liters of raw seawater were drawn into sample-rinsed plastic bottles directly from the Niskin bottles, immediately sieved onto 20- $\mu$ m mesh, backwashed to a final volume of 15 ml of filtered seawater, and preserved in 5% formalin (final concentration). In the laboratory, these samples were further concentrated by settling and removing the overlying supernatant by aspiration. A 1-ml concentrate equivalent to 1 liter of seawater was then counted in a Sedgwick-Rafter counting chamber with a standard Zeiss light microscope at  $\times 100$ .

**Nutrient analysis**—Nutrient samples were collected in acid-washed, sample-rinsed vials and then frozen. In the laboratory, each sample was analyzed for inorganic nitrate plus nitrite, ammonium, silicate, and phosphate. A three-channel Technicon autoanalyzer was used according to the methods described by Technicon and summarized by Glibert and Lodder (1977).

**Drifters**—To determine the potential transport pathways of *A. fundyense* populations entrained into the freshwater outflow, several Davis-type satellite-tracked surface drifters (Brightwaters), cross-vented to track the top 2 m of water, were released near the mouth of the Kennebec River. Fixes were obtained by ARGOS satellite six to eight times per day with accuracies of  $\pm 300$  m.

**Stream flow data**—Stream flow data were provided by the U.S. Geological Survey regional district offices in Marlboro, Massachusetts, and Augusta, Maine, for the major rivers entering into the study area. The following stream gauges were used: Androscoggin River at Auburn, Maine; Kennebec River at North Sydney, Maine; Penobscot River at Eddington, Maine; Saco River at Cornish, Maine; and Merrimack River at Lowell, Massachusetts. The measurements were corrected for drainage areas downstream of the gauging stations by a multiplier derived by dividing the total drainage area by the upstream discharge area.

**Wind data**—Meteorological data were obtained from the National Oceanographic and Atmospheric Administration (NOAA) from the NOAA buoy (#44007) offshore of Portland, Maine. Wind stress was calculated by Large and Pond's (1981) quadratic drag formulation. Alongshore and cross-shore winds were calculated by rotating the wind stress vector into a coordinate system aligned parallel and perpendicular to the coastline.

**Moored instrumentation**—Several moorings were deployed in the study region (Fig. 2) to provide continuous hydrographic measurements: one near Monhegan Island (site M) and another near Cape Porpoise (site P2). The M mooring provided data upstream (relative to the ambient, along-coast flow) of the mouth of the Kennebec River. The P2 mooring was intended to provide data within and beneath the Kennebec plume. The mooring locations were slightly different in 1994. The Monhegan Island mooring was relocated closer to the mouth of the Kennebec River to better document freshwater inputs into the coastal area (site K), and another mooring was added near Cape Porpoise (site P1; 50 m depth) to complement the P2 mooring and examine cross-shelf transport in that region. These moorings had vector-measuring current meters (VMCMs) at 5-m depths and vector-averaging current meters (VACMs) at 27- and 50-m depths. Temperature and salinity were measured at the same depths as the velocities with Seabird sensors.

All current-meter data were filtered to remove tides and inertial motions and were rotated into alongshore and cross-shore components on the basis of the local bathymetry. The near-surface current measurements obtained from the VMCMs during both 1993 and 1994 showed a persistent offshore component of flow that is believed to be a consequence of a systematic error in the compasses caused by interference from the battery packs of the Seabird sensors. A correction of 25° clockwise rotation was performed on all of the near-surface current data (Geyer et al. 2004). The correction was consistent with Ekman and geostrophic forcing and with the observations at the same locations. However, because of the uncertainty of the corrections, the estimates of the offshore component of the flow should be treated with caution.

**Satellite imagery**—Sea surface temperature imagery of the GOM was obtained through NOAA CoastWatch. The images were derived from the advanced very high resolution radiometer (AVHRR) sensors aboard the NOAA-11 and NOAA-12 satellites. Each NOAA-series satellite passed over the study region twice per day, yielding four images per day during favorable weather. Near real-time images were obtained from the northeast node of the NOAA CoastWatch program at Narragansett, Rhode Island, whereas archived CoastWatch images were obtained through the NOAA Coastal Archive and Access System. Data were displayed and features enhanced with the Interactive Digital Image Display and Analysis System (NOAA) and Windows Image Manager (©Mati Kahru).

**Modeling**—A coupled physical–biological model of the regional circulation was developed for the study area between Massachusetts Bay and Penobscot Bay (Franks and Signell 1997; McGillicuddy et al. 2003). The hydrodynamic model was a derivative of the Blumberg and Mellor (1987), fully nonlinear three-dimensional primitive equation model. It solved the primitive equations by finite differencing on a curvilinear orthogonal grid in the horizontal plane and discrete levels in the vertical. A level 2.5 turbulence closure scheme was used to represent vertical mixing (Mellor and Yamada 1982). This version of the model, called ECOM-si

(Estuarine, Coastal and Ocean Model, semi-implicit), was modified to eliminate the need for separate internal and external mode time steps by solving the external mode implicitly (Blumberg 1991). In these runs, a 310.5-s time step was used. Model output was averaged over 1 d to remove tidal and diurnal fluctuations. The model grid was developed to be slightly larger than the region covered by the observational program and to provide high horizontal and vertical resolution along the coast, especially in the vicinity of the presumed source regions for *A. fundyense*. The horizontal plane comprised  $70 \times 130$  grid elements, with a resolution of approximately 1.5 km near the coast and 3 km offshore. Because this is close to the scale of some of the observed plume structures, it was recognized that the model would not capture all of the complex frontal dynamics of the plumes. The goal was to represent the essential behavior of the plumes as they evolve away from the source regions. The vertical dimension comprised 12 nonuniformly spaced layers, with the top 3 layers spanning 1%, 3%, and 6% of the water depth for increased near-surface resolution. The lower nine layers each spanned 10% of the water depth.

A variety of boundary conditions and source terms were specified to drive the model: elevation, temperature, and salinity on the open boundaries; heat fluxes and wind stress at the sea surface; and discharge characteristics at the rivers. Elevation on the open boundaries was specified by a radiation condition with a restorative term (Blumberg and Kantha 1985). A small relaxation time was chosen along the eastern boundary, resulting in essentially a "clamped" condition. The elevation was specified along this boundary as a combination of tides, obtained from a GOM tidal model (Lynch and Naimie 1993), and mean elevation specified by interpolating the March–April and May–June solutions of Lynch et al. (1997). Along the southern open boundary off Cape Cod, a gravity wave radiation condition was applied to allow wave energy to exit the domain. Salinity and temperature on the open boundary were specified by advecting interior values out on outflow and exponentially approaching specified data on inflow with a 2-d time scale. The data values specified on inflow were determined by extrapolation and interpolation of salinity and temperature data from moored instruments, CTD surveys, and, for depths greater than 150 m, climatology. Discharges from the Kennebec, Merrimack, Saco, and Charles Rivers were determined from daily U.S. Geological Survey runoff data and were specified by introducing 0-salinity water into the upper half of the water column at the location of the river mouths. The concentration of *A. fundyense* was specified in the discharge. Wind stress was based on wind speed and direction from the Portland offshore buoy (#44007); heat fluxes were determined from observations at the Portland buoy, and insolation was measured in Woods Hole. The sensible and latent heat fluxes were derived by the Large and Pond (1981) bulk formulae.

The biological model included only the irradiance-, temperature-, and salinity-dependent growth of *A. fundyense*. Functional forms for the temperature and salinity dependence were fit to the data of Watras et al. (1982) and Prakash (1967). Growth rate was assumed to depend linearly on ambient irradiance levels, with a simple exponential decay with depth. The diffuse attenuation coefficient for subsurface ir-

radiance was set at  $0.7 \text{ m}^{-1}$ . Irradiance fluctuated over a day in relation to the surface heat flux. The maximum irradiance was scaled to 1, and the minimum was 0. This irradiance scaling factor was then multiplied by the temperature- and salinity-dependent growth rate to yield the final growth rate. *A. fundyense* transport was treated as if the cells were passive particles.

*A. fundyense* cells were initialized into the model domain at specific locations and rates to test different bloom initiation scenarios, all with cells initialized on April 1. For one scenario, *A. fundyense* cells were input uniformly throughout the water column across the entire model domain. For the second scenario, cells were continuously fed into all the river mouths, whereas the third scenario had cells input at only the mouth of the Kennebec River, near the presumed "source" region in the plume advection hypothesis.

## Results

**Shellfish toxicity**—Shellfish toxicity was detected within the study area during the spring 1993 and 1994 in both Maine and Massachusetts nearshore waters (Fig. 3; see Fig. 2 for shellfish sampling station locations). Differences between years, however, were significant: 1993 was a year with high toxicity in both states, and 1994 had limited toxicity in Maine and virtually no toxicity in Massachusetts. In 1993, a small increase in toxicity was recorded in early May, followed by a much larger peak in early mid-June. Initial detection on 3 May was localized in the extreme western Maine area (Ogunquit River; Fig. 3) and northern Massachusetts (Gloucester; Fig. 3). This outbreak occurred after the onset of the spring freshet into the coastal waters (Fig. 4A) and immediately following a downwelling-favorable period that is evident in the wind and current records (Fig. 4) and in AVHRR imagery. The latter shows warm, surface plume waters close to shore, with cold waters from eastern Maine along the plume edge (Fig. 5A). The second increase in toxicity began during late May and early June and included both Maine and Massachusetts stations (Fig. 3). The highest toxicity ( $>2,000 \mu\text{g} [100 \text{ g}]^{-1}$ ) occurred along the western Maine coast during mid-June, also following a strong downwelling event. Although hydrographic sampling had ended by that time, this event was captured by AVHRR imagery that shows cold water from the WMCC extending as far south as Cape Ann (similar to Fig. 5C, but data not shown).

In 1994, initial low-level toxicity was recorded at Gloucester as early as 9 May (Fig. 3), after the onset of the spring runoff (Fig. 4A) and following a strong downwelling event evident in the wind and current records (Fig. 4E,F), similar to our 1993 observations. However, toxicity was not recorded within Massachusetts Bay, in contrast to the high toxicities recorded there in 1993. Furthermore, along the western Maine coast, toxicity started later in the season (26 May 1994 vs. 3 May 1993), was much lower (maximum toxicity  $<500$  vs.  $>2,000 \mu\text{g} [100 \text{ g}]^{-1}$ ), and ended earlier (27 June 1994 vs. 12 July 1993) than during the 1993 bloom season.

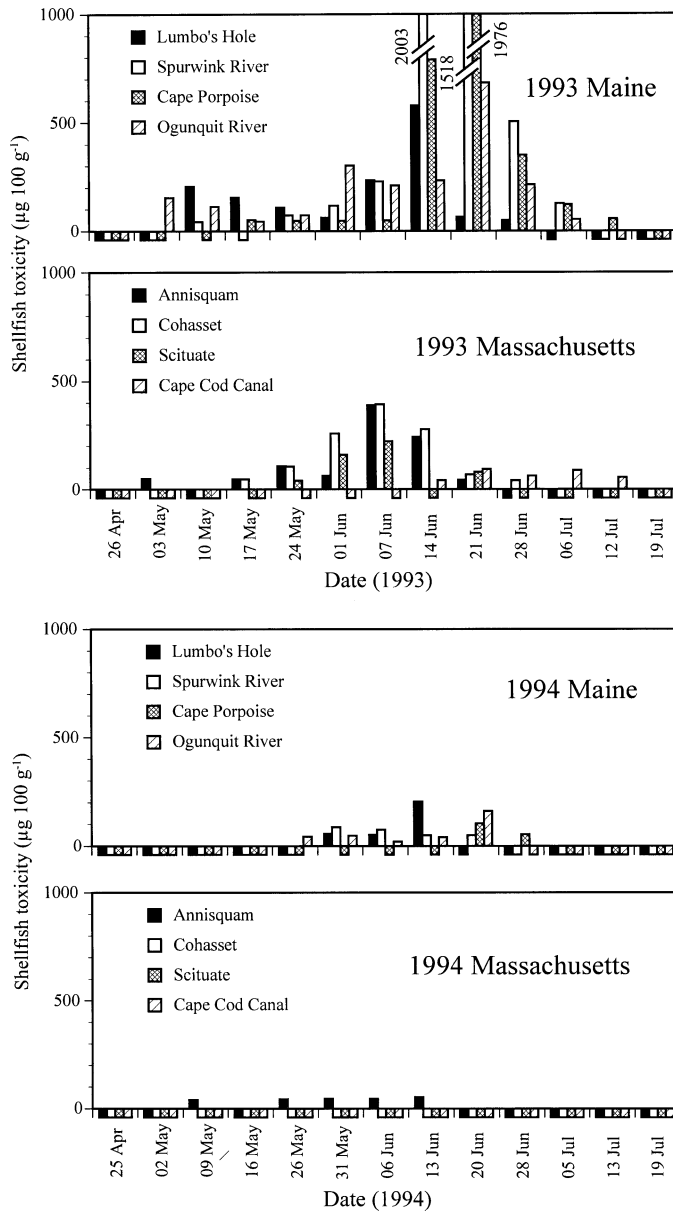


Fig. 3. Weekly time series of shellfish toxicity ( $\mu\text{g}$  of saxitoxin equivalents  $[100 \text{ g}]^{-1}$  of shellfish meat) in the blue mussel (*Mytilus edulis*) reported for Maine and Massachusetts during the *A. fundyense* bloom seasons of 1993 and 1994.

**Wind data**—For both years, the wind stress in the region exhibited large fluctuations at time scales of 1–3 d and amplitudes of 0.1–0.2 Pa (Geyer et al. 2004; Fig. 4B,E). Although the long-term mean was small, wind stress during April 1994 was generally upwelling-favorable during the time of peak river discharge (Fig. 4D,F), whereas 1993 had predominantly downwelling-favorable winds during the comparable period (Fig. 6). In both years, there were short-term effects of the wind on the behavior of the coastal plume (Fong et al. 1997). Generally, during upwelling-favorable winds, the plume was spread farther offshore, at times widening it to over 50 km in offshore extent (Fig. 7A), whereas downwelling-favorable winds narrowed the plume width to

as little as 10 km (Fig. 7C). The *A. fundyense* populations associated with the plume were spread farther offshore during upwelling-favorable conditions (Fig. 7B) and were compressed against the coast during downwelling-favorable conditions (Fig. 7D). Toxicity generally increased following periods of downwelling-favorable conditions, (e.g., late April to early May 1993, Fig. 3; early June 1993, Fig. 3; early May 1994, Fig. 3) and was not detected, did not rise, or sometimes declined following upwelling (e.g., 11–17 May 1993, Fig. 3; early June 1994; Fig. 3). Specifically, during the mid-May 1993 upwelling event, toxicity was not detected in Massachusetts Bay, declined or remained the same at Gloucester, and declined at the Ogunquit River. Although it initially increased at Lumbo's Hole and Spurwink River, it remained low or declined in the following 2 weeks. Likewise, toxicity rose at Lumbo's Hole in Casco Bay during an upwelling period in early June 1994. However, other stations to the south did not rise, and even Lumbo's Hole did not reach the levels observed during the comparable downwelling-favorable period in late May and early June 1993. The variability of the wind, infrequent measurements of toxicity (weekly), and retention of accumulated toxins in the shellfish obscure the relationship between upwelling and the stabilization or decrease of toxicity that is being highlighted here. Despite these limitations, the overall patterns are inescapable—1993 was a year with more downwelling and 1994 a year with more upwelling conditions during the critical early portion of the PSP season (Fig. 6).

**Satellite imagery of sea surface temperature**—In the spring, a warm feature ( $8\text{--}12^\circ\text{C}$  and  $1\text{--}2^\circ\text{C}$  warmer than the receiving waters of the GOM) could be identified in sea surface temperature (SST) imagery that corresponds to the low-salinity surface plume waters from the rivers in the western GOM (Fig. 5). Along the northernmost section of the study area, an SST feature identified as the cold ( $6\text{--}7^\circ\text{C}$ ) waters of the EMCC was commonly present, with part of the EMCC turning offshore and the other part continuing alongshore to form the WMCC that is subsequently supplemented by river outflow.

Several key SST images highlight downwelling–upwelling dynamics in the study area during the early bloom season of 1993 (Fig. 5A,B) and the later bloom season of 1994 (Fig. 5C,D). During the initial outbreak of shellfish toxicity in 1993 at Gloucester and Ogunquit River (May 3; Fig. 3), warmer water was compressed along the coast, indicative of downwelling conditions, while fingers of offshore colder water penetrated close to the western Maine coastline (Fig. 5A). During a subsequent strong upwelling event, SST images showed that the warmer surface waters were spread to the east and offshore, and as a result, the colder surface extension of the WMCC did not penetrate as far south and was deflected offshore of the Kennebec River mouth (Fig. 5B). As noted before, toxicity declined at both Gloucester and Ogunquit River the following week.

As the bloom season progressed, the plume waters became more difficult to distinguish from the warming coastal waters with SST. However, during a downwelling event in mid-June 1993, colder water from the EMCC ( $9\text{--}11.5^\circ\text{C}$ ) penetrated into the warmer waters of the western GOM ( $>12^\circ\text{C}$ ; data

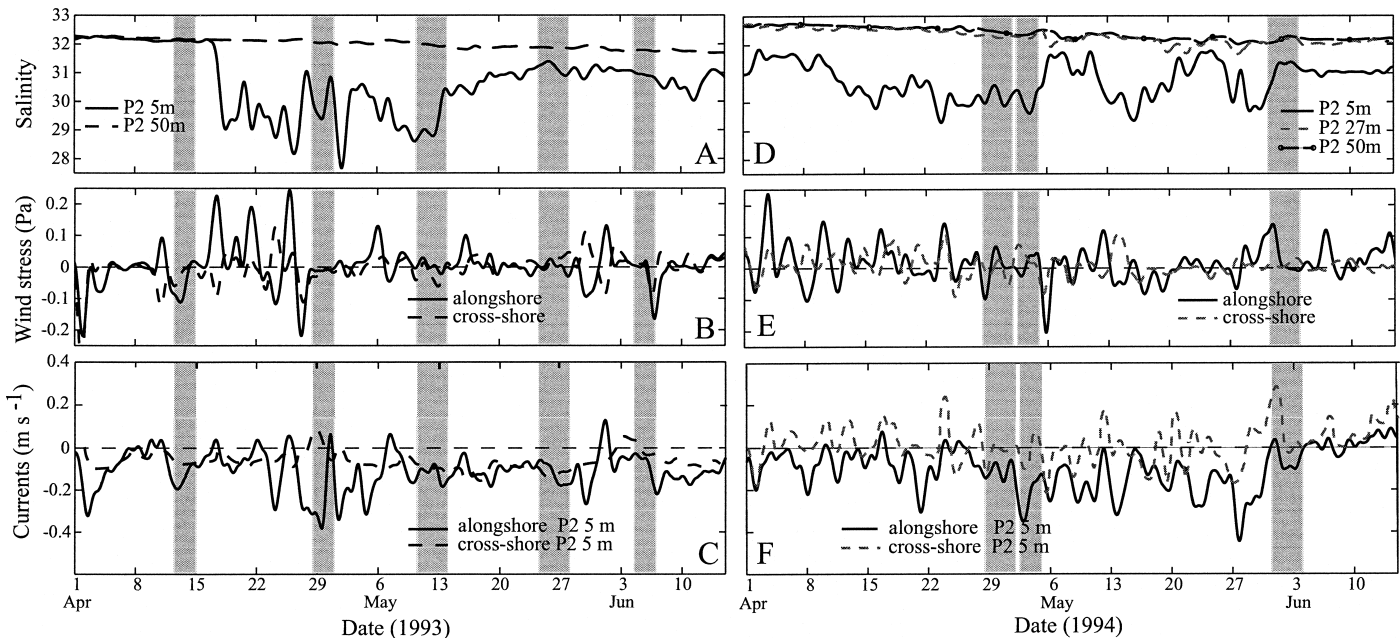


Fig. 4. Time series of moored observations at the P2 mooring in 1993 and 1994. (A) Salinity at 5 and 50 m; (B) alongshore and cross-shore components of the wind stress at the nearby Portland buoy; (C) alongshore and cross-shore components of the currents at 5 m; (D) salinity at 5, 27, and 50 m; (E) alongshore and cross-shore components of the wind stress at the nearby Portland buoy; (F) alongshore and cross-shore components of the currents at 5 m. For the alongshore winds and currents, positive values indicate upcoast flow and negative values indicate downcoast flow. For the cross-shore winds and currents, positive values indicate offshore flow and negative values indicate onshore flow. Shaded bars show the time period of the cruises.

not shown) coincident with the highest measurements of shellfish toxicity along the western Maine coastline during this study (Fig. 3—1993). Similarly, when toxicity increased in late May 1994 (Fig. 3), cold waters from the EMCC (8–9°C) penetrated well into the western Gulf adjacent to the warmer waters of the river plume (10–12°C) that was compressed tightly against the coast during the downwelling (Fig. 5C). When upwelling-favorable conditions prevailed, the warm plume waters were pushed offshore, replaced by colder, newly upwelled water adjacent to the western Maine coast (Fig. 5D). Thus, in each of 2 yr during critical times for PSP toxicity along the western Maine coastline, plume waters were compressed against the coast by downwelling-favorable winds, while the adjacent colder waters of the WMCC (originating from the EMCC) were extended alongshore. In contrast, during upwelling-favorable conditions, the plume and the WMCC were spread offshore, limiting their intrusion into the nearshore waters of the western GOM. During upwelling conditions, toxicity remained unchanged or declined, most notably in the westernmost portions of the Gulf.

**Stream flow**—The Kennebec and Penobscot River accounted for more than 70% of the flow into the western GOM during 1993 and 1994 (Geyer et al. 2004). In both years, the volume of the stream flow was similar with the combined peak discharge from all the major rivers entering the western GOM, exceeding  $7,000 \text{ m}^3 \text{ s}^{-1}$  in mid-April. The peak discharge occurred when the annual *A. fundyense* bloom was just beginning and the concentration of toxic cells in the western GOM was low. When toxicity in the

region was detected during May and June, discharge was much lower ( $\sim 1,000\text{--}2,000 \text{ m}^3 \text{ s}^{-1}$ ), with a few minor freshets recorded (Geyer et al. 2004).

**Moored observations**—Continuous observations of salinity from a mooring along the Cape Porpoise transect (P2, Fig. 2) clearly show the presence of the buoyant plume waters in the surface layer of the WMCC during both years (Fig. 4A,D). In April of both years, surface salinity was 2–3 levels below ambient. The plume appeared about 1 week after the peak freshet at the Kennebec. In 1993, the onset was abrupt, likely because of the location of the compressed plume inside the mooring location at P2, followed by the rapid transition from downwelling to strong upwelling-favorable conditions, which transported the plume across the mooring and offshore. In contrast, the onset of low-salinity waters at the P2 mooring was earlier and more gradual in 1994, perhaps because plume waters were continuously pushed across the offshore mooring site by persistent upwelling-favorable conditions coincident with the early and mid-April discharge.

Currents were directed generally downcoast (southwestward), both within and beneath the plume (Fig. 4C,F; Geyer et al. 2004). The combination of low surface salinity and strong downwelling-favorable winds produced the highest alongcoast velocities of  $>0.40 \text{ m s}^{-1}$ . Frequent reversals of the surface current were driven by upwelling-favorable winds, but these tended to be short-lived and weak, even during strong wind events. Beneath the low-salinity surface layer, the flow was persistently southwestward, with veloc-

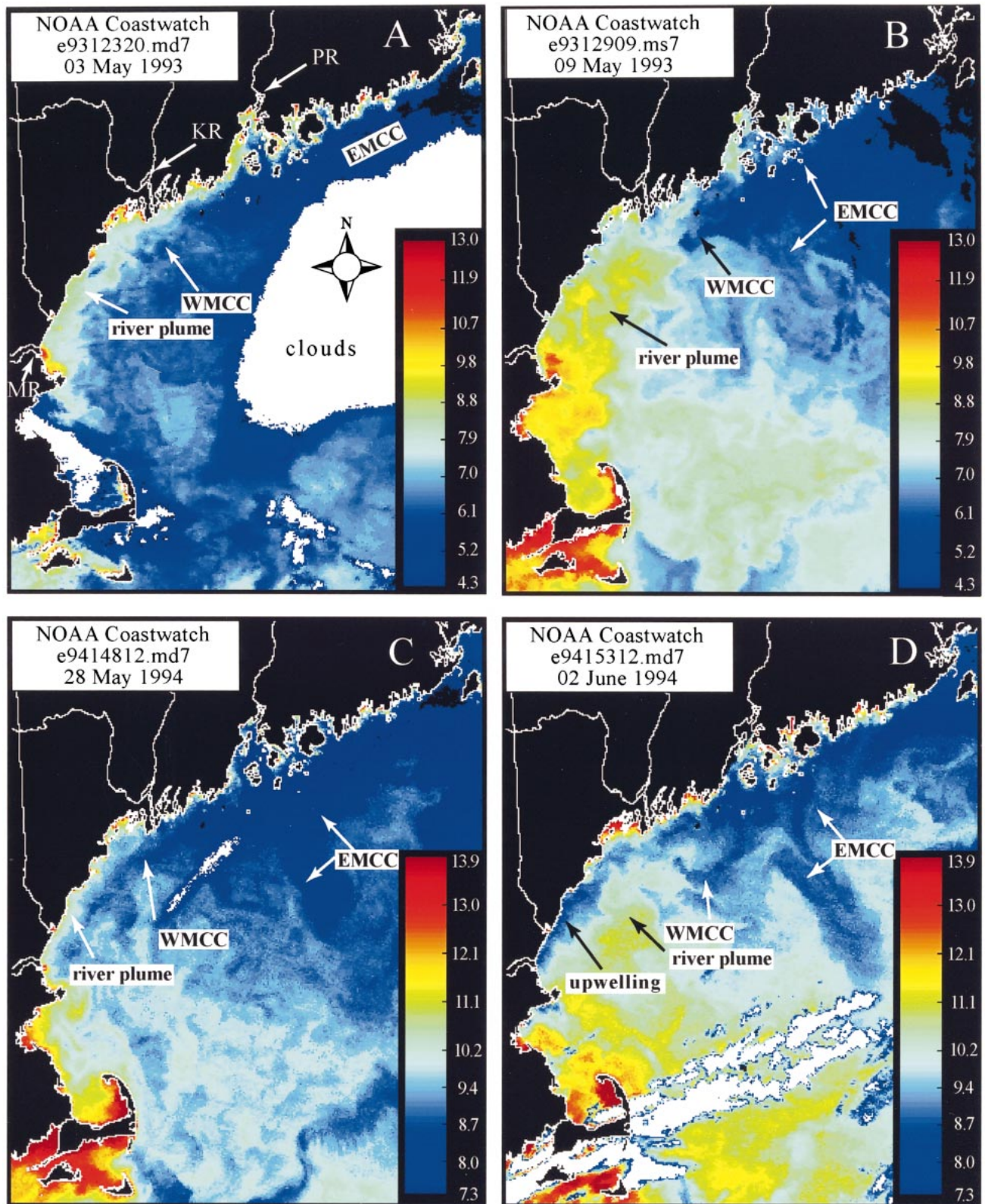


Fig. 5. Satellite-derived sea surface temperatures (SSTs) in the western Gulf of Maine on (A) 3 May 1993, (B) 9 May 1993, (C) 28 May 1994, and (D) 2 June 1994. SST images (A, C) show conditions when shellfish toxicity increased following downwelling. Toxicity decreased during subsequent upwelling-favorable conditions (B, D). When toxicity increased (A, C), warm surface plume waters were observed close to the coastline (9.5–12°C; light blue–light green–yellow), while a cold feature from the WMCC (8–9°C; dark blue) extended well into the western GOM, sometimes all the way to Cape Ann as in panel C. During upwelling-favorable periods when toxicity declined (B, D), the warm plume waters were spread offshore. As upwelling continued, deeper cold water was observed adjacent to the coast (D).

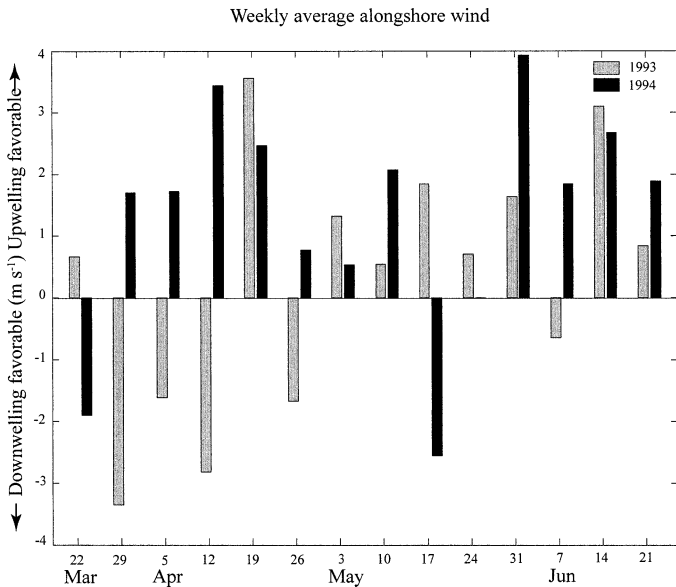


Fig. 6. Weekly averaged winds for 1993 and 1994. Wind speeds ( $\text{m s}^{-1}$ ) at 5 m height at the NOAA Portland ME Buoy (#44007) were rotated into alongshore and cross-shore components with the use of  $35^\circ$  to the east of true north as the alongshore direction. Positive values denote periods of persistent upwelling, and negative values denote downwelling.

ities of approximately  $0.1 \text{ m s}^{-1}$  (data not shown; Geyer et al. 2004).

Cross-shore velocities in the surface waters were generally positive (i.e., directed offshore) during upwelling-favorable winds and negative (directed onshore) during downwelling-favorable winds, consistent with Ekman drift theory (Fig. 4C,F; Fong et al. 1997; Geyer et al. 2004). Comparison of

the 1993 and 1994 cross-shore 5-m velocities show clear differences. During 1993, the cross-shore currents were directed onshore during most of the study period (Fig. 4C). In contrast, currents were predominantly directed offshore early in the 1994 bloom season (April) and later as well (early June; Fig. 4F), with notable exceptions. During the toxicity outbreak in late May 1994, cross-shore velocities were directed onshore, associated with downwelling-favorable conditions. Cross-shore velocities below the pycnocline (27 m) were weak ( $<0.1 \text{ m s}^{-1}$ ) and usually directed onshore with the highest velocities noted following downwelling conditions during both years (data not shown; Geyer et al. 2004).

**Drifters**—Surface drifter trajectories were persistently downcoast in 1993, interrupted by reversals and offshore excursions during upwelling-favorable periods. Transit from the Kennebec to Cape Cod took 18–20 d, with a maximum downcoast velocity of  $\sim 0.50 \text{ m s}^{-1}$  and average velocity of  $0.14\text{--}0.15 \text{ m s}^{-1}$  (Fig. 8; Geyer et al. 2004). Drifters deployed early in 1994 were similar to those in 1993, generally advecting downcoast. Drifters deployed later in 1994 had no mean alongshore motion (Fig. 8), reflecting the predominance of upwelling-favorable winds in early June.

**Shipboard observations**—Five hydrographic surveys were completed in the spring of 1993 during the evolution of a low-salinity coastal plume (Figs. 9A,C, 10A,C; cruise 5 not shown), *A. fundyense* bloom development (Figs. 9B,D, 10B,D), and concurrent outbreaks of shellfish toxicity along the southern Maine, New Hampshire, and Massachusetts coastlines (Fig. 3). The surveys were initiated in mid-April during maximum spring discharge, with the bulk of the freshwater outflow localized near the mouths of the Kennebec and Merrimack Rivers (Fig. 9A). Within 2 weeks the

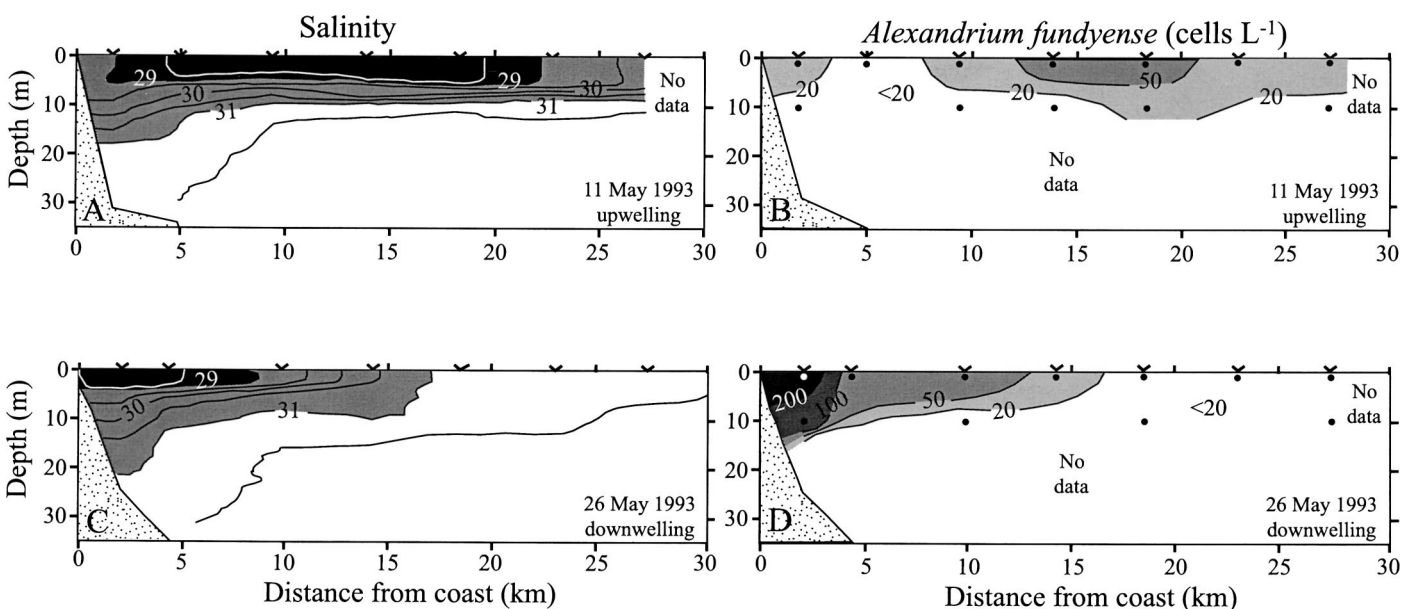


Fig. 7. Cross-shelf distribution of salinity and *A. fundyense* from the Cape Elizabeth transect during upwelling on 11 May 1993 and downwelling on 26 May 1993. Surface plume waters (A, C; delimited by the 31 salinity isohaline) and the associated *A. fundyense* population (B, D) were offshore during upwelling and compressed against the coast during downwelling.

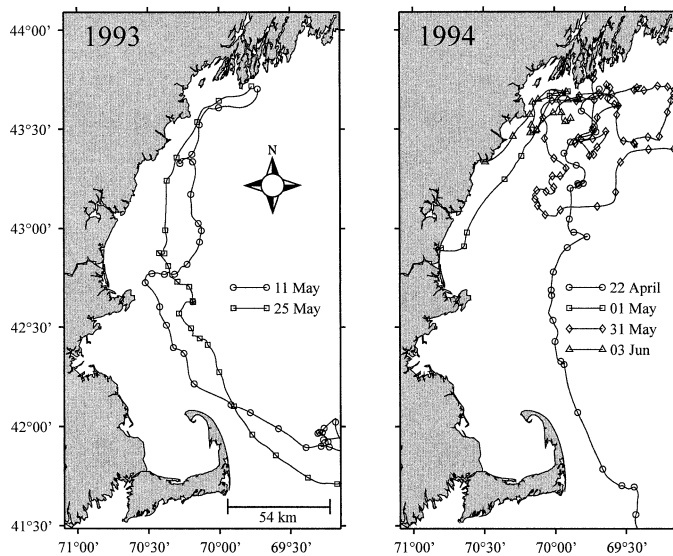


Fig. 8. Trajectories of ARGOS-tracked surface drifters released near the mouth of the Kennebec River in 1993 and 1994. Drifters traveled offshore and tended to loop during upwelling-favorable conditions. With downwelling-favorable winds, they traveled rapidly alongshore, sometimes making “landfall.” Each point represents 1 d.

freshwater input had coalesced into a distinctive coastal plume (Fig. 9C). The plume was compressed against the coast and progressed southward from its major initiation site near the Kennebec River mouth, but an upwelling event between cruises 2 (Fig. 9C) and 3 (Fig. 10A) spread the low-salinity waters offshore. Despite this offshore excursion, the plume was detected in Massachusetts Bay during cruises 3 and 4 (Fig. 10A, C). As river discharge declined to typical late spring and early summer levels, the low-salinity water was again localized near the mouths of the rivers at the time of cruise 5 (data not shown).

The short-term repetitive surveys of 1994 indicated that the extension and retraction of the Kennebec plume can occur on time scales of  $<1$  week, evidenced by the rapid downcoast change in the location of the 29 and 30 isohalines that occurred between the survey legs following downwelling-favorable conditions (Fig. 11A,C). Surveys suggest less freshwater in Massachusetts Bay in 1994 (Fig. 12A) than in 1993, even though total runoff volumes were similar for the 2 yr (Fig. 10 C; Geyer et al. 2004). Much of the freshwater plume was not transported downcoast in 1994, but was offshore and out of the study domain because of persistent upwelling-favorable conditions.

In 1993, the *A. fundyense* distributions generally progressed southward from initial populations observed predominantly near the northern edge of the study domain near Casco Bay and the Kennebec River mouth (Fig. 9B). In subsequent cruises (Figs. 9D, 10B,D), the population extended farther south into Massachusetts and Cape Cod Bays while increasing in abundance, although maximum cell densities were only 200–500 cells  $L^{-1}$ . These levels however, coincided with the detection of shellfish toxicity along the western Maine and Massachusetts coasts (Fig. 3).

This type of southward progression was also observed

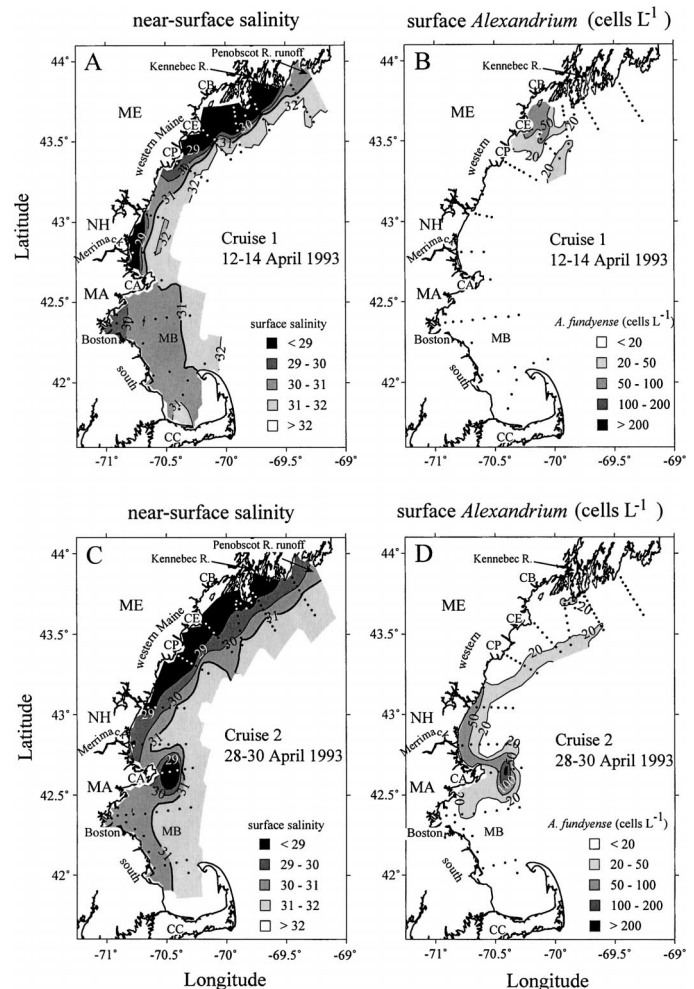


Fig. 9. “Early-season” distribution of near-surface salinity and *A. fundyense* in the western Gulf of Maine during cruise 1 (A, B) and cruise 2 (C, D) in April 1993. Cruise 1 shows the initial population within the Kennebec River plume, whereas cruise 2 shows the downcoast development at the intersection of an offshore population and the distal end of the nearshore plume waters. Black represents the lowest salinities of the river plume(s) for panels A and C, whereas the offshore boundary of the plume waters is represented by the bolded 31 isohaline. For *A. fundyense* concentrations (B, D), background low abundances of  $<20$  cells  $L^{-1}$  are not contoured, whereas contours indicating the highest abundances ( $>200$  cells  $L^{-1}$ ) are filled with black.

during the repetitive surveys of 1994 that permitted tracking of the same population over a short interval of time (Fig. 11B,D). In less than 1 week, the surface population nearly doubled (from a maximum of 100 to 200 cells  $L^{-1}$ ), and the leading edge of the bloom progressed about one to two transects ( $\sim 50$  km) farther down the western Maine coastline, consistent with estimated advection velocities of 0.20–0.40  $m s^{-1}$  determined from moored current meters (Fig. 4F). These observations were also consistent with toxicity recorded just downstream near Cape Ann at Gloucester the following week (Fig. 3). In less than a month, the population had progressed into the waters of Massachusetts Bay (Fig. 12B) but was located offshore because of upwelling-favor-

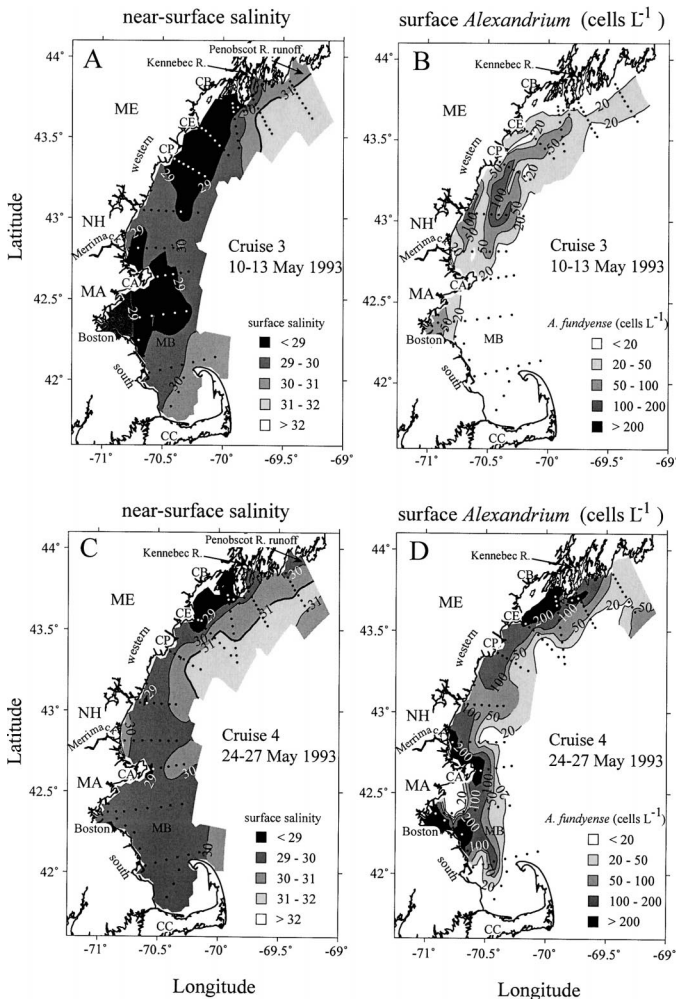


Fig. 10. Development of the *A. fundyense* bloom along the western Gulf of Maine coastline during cruise 3 (A, B), and cruise 4 (C, D) in May 1993. Cruise 3 represents an upwelling-favorable period as the plume waters (A) and *A. fundyense* populations (B) are spread offshore, whereas cruise 4 shows downcoast bloom development associated with less saline waters along the whole western GOM coastline, including Massachusetts Bay. Legends as in Fig. 8.

able conditions (Fig. 4B), in stark contrast to 1993 when the population was highest near the shoreline (Fig. 10D).

During the southward progression, *A. fundyense* populations were commonly observed both inside and outside the plume waters (defined as the 31 isohaline), but during both years, the highest abundances ( $>50$  cells  $L^{-1}$ ) were usually within the low-salinity plume waters. The best example was during the shellfish outbreak of late May to June 1993, when the *A. fundyense* population extended along the entire coast in close association with the plume waters (Fig. 10D). At other times, higher abundances were observed near the outer plume edge than within the core of the WMCC (e.g., Fig. 11D). Commonly, relatively low abundances ( $<50$  cells  $L^{-1}$ ) were observed offshore, upstream of the plume, or in both places (e.g., Figs. 9, 10), implicating the EMCC in population dynamics in the western Gulf. For example, the pattern

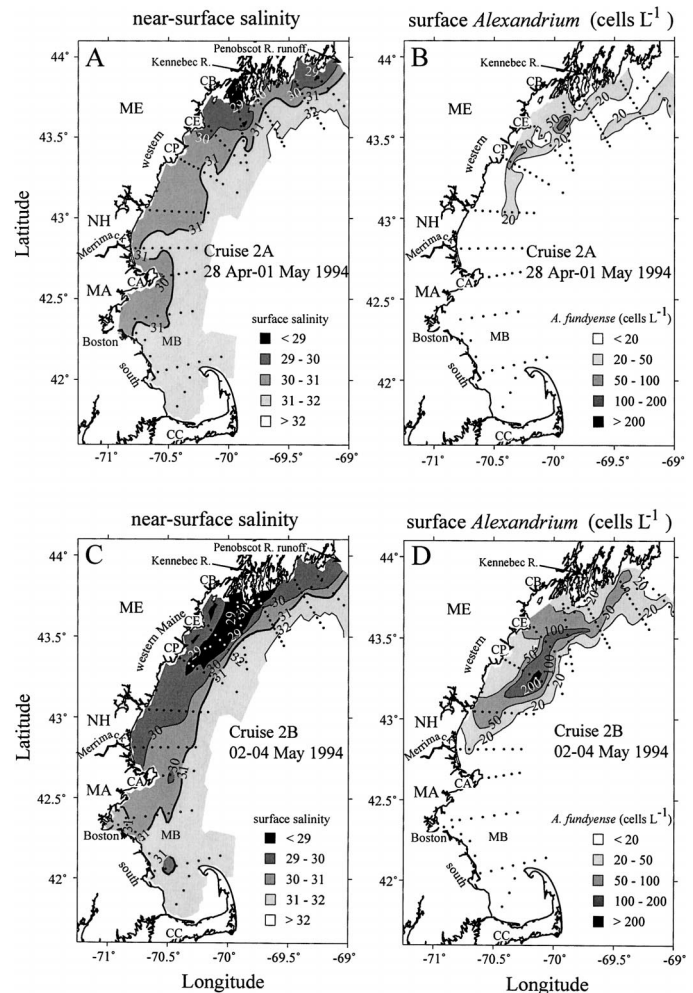


Fig. 11. "Early-season" distributions of near-surface salinity (A, C) and *A. fundyense* (B, D) during repetitive surveys in April and May 1994. Cruise 2A (A, B) shows the initial *A. fundyense* population located offshore of Casco Bay near the Kennebec plume front, whereas the second leg, cruise 2B (C, D), was resampled just a few days later and shows the rapid extension of the plume and the population.

of cold and warm water in SST imagery from 9 May 1993 (Fig. 5B) is strikingly similar to the distribution of *A. fundyense*, with the offshore population located in more saline (cold) waters, whereas the more abundant western population was located in the less saline (warm) plume (Fig. 10A,B). Sometimes, an offshore WMCC population was distinct from that within the plume (e.g., Figs. 9B, 11B), whereas more commonly, these populations coalesced into a continuous distribution along the coast (e.g., Figs. 10B,D, 12B).

The coalescence of the upstream and offshore population and the plume population appeared to be associated with the behavior of the Kennebec plume. When the plume was substantial and extended well along the coast (e.g., Fig. 9C,D), a narrow band of offshore cells ( $20\text{--}50$  cells  $L^{-1}$ ) was observed in more saline waters ( $>31$ ) that ultimately intersected with the coast at the westward end of the plume. In areas downstream of this landfall and within less saline waters ( $<31$ ), the *A. fundyense* abundances were highest. The

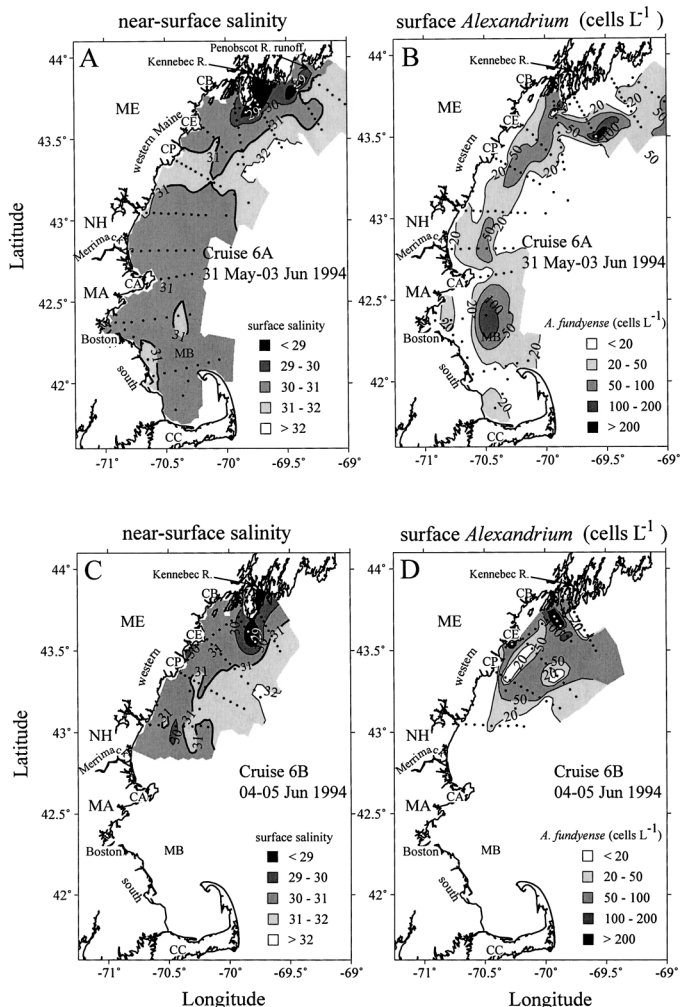


Fig. 12. "Late-season" distribution of near-surface salinity and *A. fundyense* during repetitive surveys in May and June 1994. Cruise 6A (A, B) shows the *A. fundyense* population located offshore along the coast, whereas the second leg, cruise 6B (C, D), was resampled just a few days later and shows that the offshore population circulated around the Kennebec plume and into Casco Bay.

presence of *A. fundyense* cells in these nearshore, low-salinity waters is consistent with the onset of toxicity a few days after this cruise (3 May 1993) at the western Maine border (Ogunquit) and in northern Massachusetts (Gloucester; Fig. 3). Similarly, when the Kennebec plume was weak and localized nearer its river mouth and close to Casco Bay (e.g., Fig. 12A,B), the offshore population in higher salinity waters remained outside the plume but ultimately intersected the coast at its distal end near Casco Bay. The subsequent repeat survey showed that portions of that population continued around the plume edge and into Casco Bay (Fig. 12C,D). These distributions were consistent with observed toxicity patterns (Fig. 3), which showed highest toxicity at Lumbo's Hole within Casco Bay (6 June 1994) immediately after the repeat survey. This population reached nearshore waters, but other cells within the plume of the downstream low-salinity waters near Massachusetts Bay remained offshore and pre-

sumably exited the domain near the tip of Cape Cod with no effect and no recorded toxicity within Massachusetts Bay (Fig. 3).

Cross-shore variability of *A. fundyense* abundance was greater when the population was spread offshore during upwelling- compared with downwelling-favorable conditions. This pattern was evidenced as nearshore patches, separated from the bulk of the offshore population by areas of low abundance. For example, patches are notable close to shore in extreme western Maine and New Hampshire (Fig. 10B) and within Massachusetts Bay (Fig. 12B), as well as in cross-section (e.g., Fig. 7B).

**Nutrient data**—Nutrient analyses are summarized in Martorano and Loder (1997). The major sources of nutrients to the surface waters of the western coastal GOM are the Kennebec plume, the eastern Maine coastal current, wind-induced upwelling, tidally driven wave-sill interaction on Stellwagen Bank, local river inputs (such as the Merrimack), and sewage effluent from Boston Harbor. Generally, nutrient levels were higher earlier in the bloom season and higher inside the coastal plume than outside, but there were exceptions. For example, early in the bloom season (cruise 93-1), higher nutrients were observed outside of the plume and offshore in the WMCC, presumably associated with inputs from eastern Maine via the shoreward transport of EMCC waters. By the end of May, surface nutrient concentrations were near detection limits both inside and outside the coastal plume and were only elevated near the mouths of the rivers.

*Alexandrium fundyense* populations were generally observed in low-nutrient waters with low N:P ratios (<10:1). Approximately 90% of cell densities >100 cells L<sup>-1</sup> were associated with nitrate and ammonium concentrations of <1.0  $\mu\text{mol L}^{-1}$ , dissolved inorganic nitrogen (DIN) concentrations of <2.0  $\mu\text{mol L}^{-1}$ , and phosphate levels of <0.4  $\mu\text{mol L}^{-1}$ . In particular, the highest *Alexandrium* cell concentrations observed during the 1993 and 1994 sampling seasons were measured in waters that contained DIN levels of 0.30 and 0.73  $\mu\text{mol L}^{-1}$ , respectively.

**Modeling**—A series of numerical models were used to interpret the field data for 1993 and 1994. The most extensive of these was a three-dimensional coupled physical-biological model of the regional circulation from Cape Cod to Penobscot Bay. Initial model runs examined possible bloom initiation scenarios (Franks and Signell 1997). When a uniform distribution of *A. fundyense* cells was input throughout the domain, the model run yielded unrealistic results compared with the cruise observations and shellfish toxicity patterns. In particular, this formulation showed *A. fundyense* populations growing first in the south near Massachusetts Bay (because of warmer temperatures), and then spreading toward the north—the opposite of the spatial and temporal trends seen in our observations and earlier reports (Figs. 9–12; Franks and Anderson 1992b). Likewise, when cells were input only in the vicinity of the major river and estuarine systems in the western Maine region, unrealistic results were again obtained. However, continuous cell input at the mouth of the Kennebec River near Casco Bay gave results in qualitative agreement with cruise and shellfish toxicity obser-

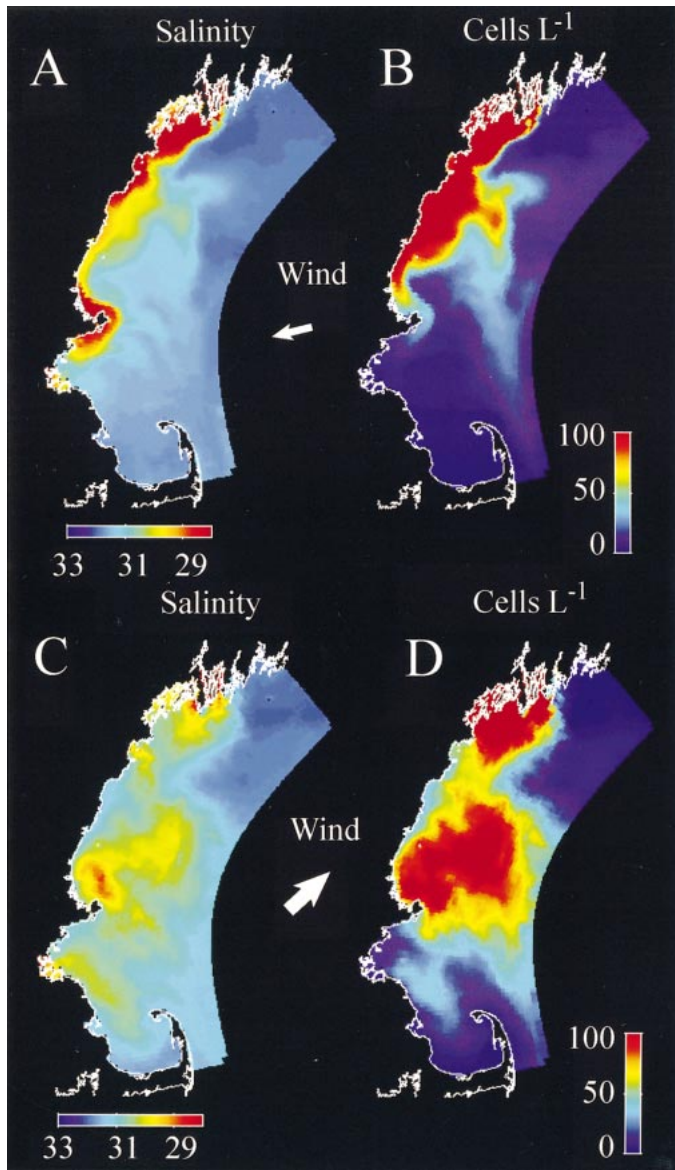


Fig. 13. Modeled simulation of the surface plume and associated *A. fundyense* population. This scenario used actual winds and runoff from April 1993, with cells released into the model domain at the mouth of the Kennebec River. (A, B) The simulated effects of downwelling-favorable winds on 30 April 1993, which compressed low-salinity waters of the buoyant plume and its *Alexandrium* cells close to shore, with rapid propagation of toxicity along-shore. (C, D) The simulated upwelling-favorable conditions on 9 May 1993, which transported the plume and *A. fundyense* cells offshore, leaving reduced cell concentrations at the immediate shoreline. Wind vectors are shown between each set of panels.

ventions for 1993, when extensive PSP toxicity was detected throughout the region. The simulation showed many of the observed elements of the WMCC behavior, including along-shore transport of the population with trapping of cells along the coast during downwelling and offshore spreading during upwelling (Fig. 13).

In Maine, and farther south in Massachusetts, there was very little toxicity in 1994 (Fig. 3). When the 1994 year was

simulated by the model, *A. fundyense* populations were initially transported away from shore by persistent west and southwest winds that caused upwelling. Many of these cells were lost across the eastern edge of the model domain because of this offshore transport. However, as the model run continued, the new cells that were being continuously input near the Kennebec river mouth were eventually entrained in the coastal current and carried to, and into, Massachusetts Bay to the southwest. The model therefore predicted late-season shellfish toxicity within Massachusetts Bay, where actual measurements showed no toxin above detection limits at all stations sampled within the Bay that year (Fig. 3).

## Discussion

Cruise and moored-instrument observations were conducted during two large-scale blooms of *A. fundyense* in the western GOM. A coupled physical-biological model was also formulated to simulate hydrography and *A. fundyense* population distributions for those bloom intervals. Two years were studied: one (1993) with extensive toxicity from Maine to Massachusetts and another (1994) with little or no toxicity over that same region. These observations, and in particular the between-year toxicity that differed dramatically, provide new insights into the dynamics of *A. fundyense* in the region and allow a re-examination of the conceptual model of those blooms developed more than a decade ago—the plume advection hypothesis (Franks and Anderson 1992a). Elements of that conceptual model that were confirmed include the development of initial bloom populations near Casco Bay and the common mouth of the Kennebec Rivers; the association of those populations with a buoyant river plume that composes part of the WMCC; the rapid alongshore advection and coastal trapping of that population during downwelling-favorable conditions; and the retardation, offshore dispersal, and possible reversal of the waters of the WMCC and the associated *A. fundyense* cells during upwelling. The plume advection hypothesis can now be refined to better define the origin of *A. fundyense* cells that populate the WMCC because there are at least two potential sources: (1) populations that originate in the nearshore waters within or adjacent to Kennebec River and (2) populations that are introduced from offshore populations, farther upstream, or both. Other new features that emerge from cruise observations are (1) the association of *A. fundyense* populations in the WMCC with low-nutrient waters, consistent with the very low cell densities generally observed in the region, and (2) the manner in which *A. fundyense* cells achieve “land-fall” near the distal ends of the river plume, at locations where the cross-shore salinity gradients are weak and thus where transport of offshore water and cells around the plume edges and toward shore is facilitated. These and other observations are discussed in more detail below.

**Source populations**—The first element of the plume advection hypothesis relates to the initiation of the *A. fundyense* blooms that occur within the western GOM. The origin was hypothesized to be near the mouth of the Kennebec River (Franks and Anderson 1992a). This somewhat vague inference was made on the basis of a limited series of tran-

sects and cruise observations. In a follow-up study, Anderson and Keafer (1992) reported that *A. fundyense* cells were observed near the outer Kennebec plume front early in the bloom season. They did not observe this species within the Kennebec or the Merrimack Rivers, concluding that the rivers entering the western GOM were not the source of *A. fundyense* cells. Our more comprehensive observations at the outset of the 1993 and 1994 bloom seasons do not show high *A. fundyense* concentrations at the station closest to the river mouth. Instead, they were initially restricted to the Kennebec plume area, including the waters near Casco Bay, with a few cells elsewhere in the sampling domain (Figs. 9B, 11B). Most cells were located in low-salinity coastal waters, but some were observed in the colder, higher salinity ( $>31$ ) waters just offshore and upstream of the Kennebec plume, indicative of incoming waters from the EMCC (Fig. 11B). In the absence of continuous or more frequent observations, we are unable to conclude that the initial nearshore populations originated from germinated cysts in shallow, local sediments within or near Casco Bay, although this is one possibility. Alternatively, or in addition, nearshore populations might derive from established motile cells in offshore waters that were transported toward shore by downwelling winds or other physical forcings. Observations from nearly every cruise consistently document the existence of low-concentration *A. fundyense* populations in the offshore, higher salinity waters (e.g., Figs. 8—1994, 9B, 11B), so this source scenario is clearly feasible and might be the most likely.

There are two possible origins for these offshore cells: the germinated cysts that lie in deep-water accumulation zones to the north and east of Casco Bay (McGillicuddy et al. 2003; Anderson et al. unpubl. data) or from the EMCC, which has been shown to contain *A. fundyense* populations (Townsend et al. 2001). Indeed, SST imagery from 9 May 1993 (Fig. 5B) shows a filament of cold water extending alongshore from eastern Maine into the western GOM in the same area the offshore population of *A. fundyense* was observed several days later during the cruise of 10–13 May (Fig. 10B). Likewise, the cold filament originating in eastern Maine shown in Fig. 5C extended all the way to Cape Ann during downwelling-favorable conditions, coincident with toxicity along the western Maine and northern Massachusetts coastlines (Fig. 3). Thus, conditions that lead to the along-shore or onshore transport of cold waters of the EMCC could introduce *A. fundyense* cells to the western GOM. These features are the subject of detailed study in the ongoing ECOHAB–Gulf of Maine program and will be described in more detail in subsequent publications.

Possible sources for the *A. fundyense* cells in the plume waters were also investigated with the physical–biological model. In the simulations, cells were continuously introduced into the region at fixed concentrations, giving realistic results for some scenarios but not for others. Of the three scenarios used (cells uniformly distributed throughout the region, cells input only in the vicinity of river mouths, and cells input only at the mouth of the Kennebec River), only the last was moderately successful in reproducing the qualitative spatial and temporal patterns of the 1993 and 1994 cruise observations (Franks and Signell 1997), supporting the view that the Kennebec River plume–Casco Bay region

is a critical area with respect to the dynamics of the *A. fundyense* population in the western GOM.

*Growth and transport in the coastal plume*—The second element of the plume advection hypothesis highlights the role of a buoyant plume in the transport and growth of *A. fundyense*. Our observations confirm this important pathway and add additional features or refinements to the concept.

The principle observation on which the plume advection hypothesis was founded is that *A. fundyense* cells were predominantly observed within the low-salinity coastal waters emanating from major rivers in western Maine (Franks and Anderson 1992a). Our data confirm that the highest concentrations of *A. fundyense* cells were most commonly, but not always, observed in surface waters with salinities  $<31$  (our definition of the boundary of the plume, as in Fig. 7A,C). For all samples for which *A. fundyense* cell abundance was  $>100$  cells  $L^{-1}$ , mean surface salinity was 29.52 in 1993 and 30.09 in 1994. Overall, the conditions were slightly less saline in 1993 compared with 1994, with mean salinities of all surface samples of 29.81 and 30.44, respectively. Thus, *A. fundyense* cells were associated with relatively low salinity plume waters in both years, but in 1994, more were observed at higher salinities on the outer plume boundaries, presumably because of persistent upwelling-favorable wind conditions (Fig. 11B,D), as discussed below.

Anderson and Keafer (1992) also reported that *A. fundyense* cells in the western GOM were predominantly observed in the low-salinity surface waters of the WMCC. The mechanisms by which the cells enter the plume along its transport pathway need to be resolved. McGillicuddy et al. (2003) offer one possible mechanism involving the offshore dispersal of the plume by upwelling-favorable winds, allowing cells that had germinated from cysts in deeper offshore waters to swim into the plume as it extends offshore and then be transported back to shore when winds reverse and become downwelling favorable. Hetland et al. (2003) offer a related explanation for the entrainment of offshore cells at the frontal boundary that involves upwelling conditions and critical *A. fundyense* vertical swimming speeds as the plume overrides the offshore waters.

The moderate increases in surface cell concentration between cruises (Figs. 9–12) indicate that growth could also be an important factor in bloom dynamics. The coastal plume has characteristics that provide a better environment for growth of this dinoflagellate compared with offshore waters such as slightly warmer temperatures, lower salinities that provide a stable water column, and humic substances and other growth factors from land (Prakash and Rashid 1968). Thus, differential growth might lead to higher abundances within the plume relative to the offshore waters. However, major nutrient concentrations, especially nitrogen, were typically low in the plume during the *A. fundyense* blooms (Martorano and Loder 1997), consistent with our observations of cell concentrations that rarely exceeded 1,000 cells  $L^{-1}$ . Populations were generally observed in waters with low N:P ratios and low nitrate, ammonium, and phosphate concentrations. Nutrients had been “stripped” from the surface waters by early spring diatom blooms by the time *A. fundyense* began to bloom. Overall, *A. fundyense*

blooms were likely nutrient limited within the plume, leading to low growth rates and only moderate cell abundance. This is in contrast to eastern Maine (Townsend et al. 2001) and Bay of Fundy *A. fundyense* populations (White 1987), in which strong tidal mixing provides relatively high nutrients throughout the spring and summer, leading to much higher *A. fundyense* cell concentrations (30,000–60,000 cells  $L^{-1}$ ).

Although surface nutrient conditions might have influenced the abundance of the *A. fundyense* populations in the WMCC, the physical environment nevertheless appears to be the dominant factor regulating cell distributions. Our physical observations support the view that transport of *A. fundyense* cells in the western GOM waters were forced by three major components: the underlying barotropic flow, the baroclinic motion caused by freshwater runoff, and the effects of local wind stress (Geyer et al. 2004). The barotropic current was the largest contributor to plume transport, evident as a persistent alongshore flow of waters of nearly uniform salinity beneath the plume and directed slightly onshore (Fig. 4A,D; deeper current data not shown). Essentially, this flow is due to the large-scale cyclonic circulation of the GOM (Bigelow 1927; Brooks 1985) and provides the underlying “conveyor belt” on which the plume travels. Although the bulk of the *A. fundyense* population was observed in the surface plume waters, the distributions at 10-m depths were sometimes directed more shoreward and farther downcoast than the overlying population, suggesting that these deeper populations and waters were isolated from surface processes.

The flow of the MCC (Fig. 1) at the northeastern section of the sampling domain is complex, with a branch point near Penobscot Bay where the EMCC is commonly deflected offshore because of the influence of the Jordan Basin gyre (Brooks and Townsend 1989; Bisagni et al. 1996; Pettigrew et al. 1998). However, portions of the EMCC flow can continue alongshore into the western GOM to form the WMCC (Lynch et al. 1997), augmented by the river outflow. This mechanism was apparently responsible for the transport of low-density *A. fundyense* populations into the WMCC domain in both 1993 and 1994 (Figs. 10B, 11B, 12B).

**Plume behavior**—The final element of the plume advection hypothesis states that the volume of freshwater outflow, local wind stress, and underlying GOM circulation all combine to regulate the along- and cross-shore location of the plume and its associated *A. fundyense* cells.

The *A. fundyense* distributions were clearly influenced by river flow. Geyer et al. (2004) observed a relatively weak ( $0.06 \text{ m s}^{-1}$ ) southwestward motion of nearshore waters that was attributed to the baroclinic flow from the freshwater runoff. They also observed localized peak velocities near strong density gradients (mostly due to salinity) that exceeded  $0.40 \text{ m s}^{-1}$ . *A. fundyense* populations near the plume edge can thus be advected downcoast from Casco Bay to Cape Ann, a distance of  $\sim 100 \text{ km}$  in  $< 1$  week. The baroclinic motion is extremely important because the populations observed within the plume and especially at the plume front are also strongly influenced by the wind and the motion around the plume edges as discussed below.

There were important responses of the plume structure to short-term, episodic wind forcing in both 1993 and 1994 (Geyer et al. 2004). Near-surface plume velocities were generally correlated with both alongshore wind stress and cross-shore wind stress, consistent with Ekman dynamics (Fong et al. 1997; Geyer et al. 2004). In particular, the moored measurements (Fig. 4) and the drifters (Fig. 8) both indicated that the surface plume accelerated downcoast during downwelling-favorable conditions. *A. fundyense* cells within the fresher plume waters were generally compressed against the coast (Fig. 7C,D) and extended in a uniform, narrow band alongshore (e.g., Fig. 10D), in agreement with the plume behavior. Offshore populations were commonly adjacent to the plume front and potentially were affected by the wind as well (e.g., Fig. 11C,D). This view is also supported by the SST imagery, which consistently revealed colder waters from the EMCC intruding into the western GOM alongside the plume during downwelling (Fig. 5A,C) while the warmer waters of the plume were compressed against the coast. These water masses combine to form the WMCC. Keafer and Anderson (1993) also observed the compression of warmer water against the coast in SST imagery, but the significance of the colder incoming EMCC waters that contain *A. fundyense* populations was unrecognized at the time. Thus, the present data consistently show that downwelling-favorable conditions are extremely important to rapid delivery of *A. fundyense* cells along the coast within the WMCC as well as to the delivery of offshore cells from the EMCC into the western GOM.

Upwelling-favorable conditions had a markedly different effect on the plume and its *A. fundyense* populations. Moored measurements indicated that the surface velocity slowed or even reversed during upwelling (Fig. 4). A mean offshore veering was also noted in the mooring data that might be related to persistent upwelling-favorable conditions, especially in 1994 (Fig. 6; Fong et al. 1997; Geyer et al. 2004). Consistent with the moored data, surface drifters slowed, and their trajectories generally veered offshore, reversed during upwelling-favorable periods, or both (Fig. 8—1994). These conditions resulted in an *A. fundyense* population that was broader in the cross-shore direction, limited in the alongshore direction, and more variable than during downwelling-favorable conditions. SST imagery also indicated that the warmer waters of the plume were consistently spread to the east during upwelling, replaced by colder deep water nearshore (Fig. 5D). Finally, the colder water of the EMCC was generally directed farther offshore and was more limited in its excursions into the western GOM during upwelling. Model simulations of the coastal plume during persistent upwelling (as seen in early 1994) suggest that during the offshore transport, the plume thins and is therefore more susceptible to mixing (Fong and Geyer 2001). Thus, upwelling-favorable conditions generally do not favor bloom development or nearshore shellfish toxicity in the western GOM because the population within the plume waters becomes dispersed and dilute (e.g., Fig. 7B). In this respect, the plume advection hypothesis needs no revision except to account for the subsequent behavior of the offshore populations.

Although upwelling-favorable conditions limit the exten-

sion of the population farther downcoast, cells that are diverted offshore might not be lost completely. Recent modeling efforts suggest that offshore cells entrained within the plume during upwelling can participate in the alongcoast flow during subsequent downwelling events (Hetland et al. 2003). Upwelling-favorable conditions might also be responsible for “remnant” inshore *A. fundyense* populations that are common along the western Maine shoreline and in Massachusetts Bay (e.g., Figs. 10B, 12B). These populations are formed when the bulk of the population is displaced offshore, leaving behind residual populations near the coast that remain as evidence of an earlier downcoast intrusion (shown in cross-section in Fig. 7B). Areas disconnected from the coastal flow, such as those downstream of capes or headlands, might harbor these remnants because they offer protection from offshore Ekman transport during upwelling. Examples of “retentive areas” include Casco Bay (protected by Pemaquid Point—the western peninsula of the Kennebec River), the Spurwink River (protected by Cape Elizabeth), and Massachusetts Bay (protected by Cape Ann). Higher cell concentrations can persist in these areas because of the relatively long residence time of the water.

In addition to the transport of *A. fundyense* within the plume waters of the WMCC (e.g., Fig. 10), cells are also found adjacent to the plume’s outside edge and still within the WMCC (e.g., Fig. 9D). This suggests two major pathways for transport of *A. fundyense* cells in the western GOM: one within the core of the plume (i.e., the plume advection hypothesis) and another in which cells originating from the EMCC are transported into western waters along the outer boundary of the plume front. These offshore *A. fundyense* cells generally followed the isohalines defined by the plume boundary (Figs. 9D, 11D). Initially blocked from entry into the nearshore waters by the fresher waters of the plume, the offshore WMCC and plume populations coalesce where the isohalines (29–31) intersect with the coast farther “downstream,” resulting in the delivery of *A. fundyense* populations to nearshore, intertidal waters. In 1993 and 1994, that intersection happened at multiple locations—e.g., in western Maine and Massachusetts (Fig. 9D) or nearer the Penobscot and Kennebec Rivers, the latter bringing toxic cells into Casco Bay (Fig. 12B,D). Fig. 11D suggests that multiple intrusions along the coast can happen within the same time period.

A conceptual model is presented in Fig. 14 to illustrate the pathways the offshore *A. fundyense* populations can follow to reach the coast and the intertidal shellfish. Characteristics of the river flow have a significant influence on the transport velocities of *A. fundyense* populations within the WMCC and on the steering of offshore EMCC populations along the plume front; these populations ultimately can affect shellfish farther down the coastline as that plume structure weakens (Fig. 14A). Another scenario (Fig. 14B) is consistent with the modeled observations of Brooks (1994) whereby the residual coastal flow was initially deflected offshore by the river outflow near the Penobscot and Kennebec plume fronts. However, the flow reattached to the coast near Casco Bay with a “back-eddy” that can bring water toward Casco Bay from the south (Fig. 14B). Lynch et al. (1997) noted similar complex steering mechanisms nearshore.

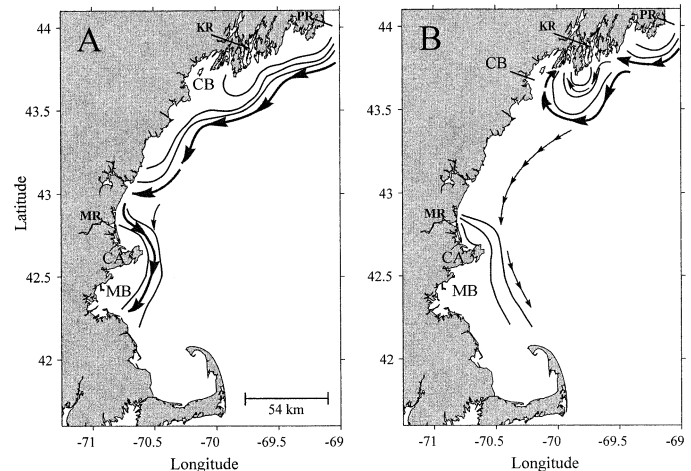


Fig. 14. Conceptual alongshore pathways of offshore *A. fundyense* “source” populations from eastern Maine waters into the western GOM. (A) An extended downcoast plume (shown as isohalines) during downwelling-favorable conditions. Offshore populations (shown as arrows to represent a band of cells) intrude westward along the Maine coastline but are blocked by the Kennebec and Penobscot River plumes. The population ultimately intersects the coast and merges with the Merrimack River (MR) plume, affecting intertidal shellfish resources as far south as Massachusetts Bay (MB). (B) A retracted plume during low river outflow conditions with upwelling-favorable winds and limited alongshore transport. Onshore transport is farther east along the Maine coast than in panel A, occurring just downstream of the Penobscot plume, merging into and around the Kennebec plume, and causing toxicity in Casco Bay (CB). In both cases, residual populations reaching Massachusetts waters are deflected offshore by the Merrimack plume and enter Massachusetts Bay if conditions favor inflow south of Cape Ann (CA).

**Shellfish toxicity**—The patterns of shellfish toxicity reflected the downcoast extension of the plume, the influence of the plume and EMCC populations, and the local wind stress. The initial outbreak of May 1993, as well as the second major peak in June 1993, followed downwelling-favorable conditions (Fig. 3). Likewise, the initial detection of toxicity at Gloucester in 1994 and the rise in toxicity in western Maine later in May and early June of that year followed downwelling (Fig. 3). Downwelling affects toxicity in several ways: (1) it brings MCC populations farther into the west; (2) it compresses the WMCC plume against the coast and accelerates the transport of cells down the coast, resulting in rapid propagation of toxicity; and (3) it extends the point of entry of eastern populations into western GOM waters farther downcoast as the coastal plume is extended. Examples of the latter were seen in both 1993 and 1994 when toxicity was detected first in the western waters and later in eastern waters (near Casco Bay—Lumbo’s Hole), contrary to what the plume advection hypothesis might suggest (Franks and Anderson 1992b). Shellfish data for 1993 and 1994 clearly show that toxicity can initially occur as far downstream as Gloucester (Fig. 3), opposite to the more commonly accepted progression pattern from western Maine to Massachusetts. Thus, progression of toxicity downcoast is due not only to cells entrained within the plume (which do

follow the plume advection hypothesis progression), but also to the intrusion of the populations traveling on the outside edge of the plume. The latter only affect nearshore shellfish when the cross-shore salinity structure weakens at the distal end of the plume and allows those cells to be transported onshore, as illustrated in Fig. 14. Thus initial toxicity can be first observed well to the west of the origin of the WMCC.

Later in the transition from spring to summer, when runoff is reduced and upwelling-favorable wind conditions prevail, areas upstream (east) from Casco Bay and the Kennebec can become toxic. These areas generally do not become toxic first because of the blocking effect of the Penobscot River outflow and perhaps from temperature limitation of growth in the cold upstream waters. However, when the plume structure is weak, eastern *A. fundyense* populations can intrude into those regions as well.

Thus, the patterns of PSP can be explained by refining the plume advection hypothesis to include the behavior of incoming EMCC populations adjacent to the river plumes and understanding the conditions that allow for their transport into nearshore waters. The offshore EMCC populations (or cells originating from germination of offshore cysts) are a critical element in PSP events in the western GOM, as hypothesized by Anderson (1997) and Townsend et al. (2001).

The relative lack of shellfish toxicity in 1994 versus 1993 relates to differences in upwelling and downwelling dynamics between the 2 yr. Figure 6 shows weekly averaged wind speeds rotated into the alongshore direction. During the critical interval of April and May 1993, the winds were dominantly downwelling-favorable, whereas during the same interval in 1994, upwelling winds dominated. Upwelling-favorable conditions would tend to keep populations within the plume and the EMCC confined to offshore waters and limit their downcoast, onshore influence. Persistent upwelling in 1994 thus resulted in a delay in the onset of toxicity and reduced intensity and duration at most western Maine stations compared with 1993 (Fig. 3).

**Model simulations of cell transport**—Model simulations for 1993 showed good agreement with the observed cell distributions (Fig. 13), as well as with the pattern of PSP toxicity in shellfish (Fig. 3). With cells input only near the mouth of the Kennebec River, the simulated bloom development proceeded in a downcoast direction, with *A. fundyense* cells reaching Massachusetts Bay at approximately the same time as toxicity was observed by state monitoring programs in 1993. In 1994, the simulations were consistent with the lack of shellfish toxicity in April and early May (Fig. 3), as persistent upwelling-favorable winds transported the plume and its associated *A. fundyense* cells offshore and away from the intertidal shellfish. The second half of the 1994 run was not realistic however, because it showed a new bloom population developing near Casco Bay in May and June, with these cells growing and being transported downcoast during a downwelling episode. Virtually no toxicity was observed in western waters during that interval (Fig. 3). We believe the discrepancy between the late-season blooms in the 1994 model and the lack of significant toxicity in western Maine or Massachusetts that year reflects our model assumption that *A. fundyense* cysts germinate continuously

(i.e., that there is no seasonal or temporal variability in the rate or location of cell input to the Kennebec River plume area). A more realistic simulation would be obtained if the cell input (presumed to be from cyst germination as well as episodic pulses from the EMCC) had slowed or ceased in mid-May or early June, because there would then have been insufficient cells to initiate a late-season bloom that then propagated to the south. Likewise, limitations because of low nutrients or mortality or encystment could reduce the late-season bloom magnitude. The model used here had no nutrient, mortality, or encystment functions.

Hindcasts of the 1993 and 1994 bloom season thus indicate that toxicity in the western GOM cannot be attributed solely to physical variability of wind and river discharge, but reflect biological variability as well. Model performance can be improved through better parameterization of the cell input function (i.e., where, when, and at what rate cysts are germinating) and the growth function that includes nutrient limitation and mortality. A new model is under development that is based on laboratory-derived germination rates and cyst distributions mapped during survey cruises (McGillicuddy et al. unpubl. data; Stock et al. unpubl. data).

The conceptual model called the plume advection hypothesis (Franks and Anderson 1992a) that was advanced to explain the patterns of PSP toxicity in western Maine and Massachusetts has stood the test of time and reanalysis well. Here, we present observation and modeling data that confirm the general elements of that model but that also augment and refine it. In the latter context, we confirmed the existence of a "source region" for *A. fundyense* cells near the mouth of the Kennebec River, but we now recognize two possible sources of cells: those emerging from benthic cyst populations from offshore sediments in that area and those brought to the region from established *A. fundyense* blooms in the EMCC. The critical importance of upwelling- and downwelling-favorable conditions was also highlighted, with the underlying bloom dynamics mechanisms refined to include a recognition of (1) the potential loss of cells because of mixing and dispersion after upwelling has spread the plume into a thin layer extending well offshore, (2) the occurrence of isolated inshore *A. fundyense* populations downstream of capes or headlands that are protected from offshore Ekman transport during upwelling, and (3) the delivery of offshore cells from the EMCC into the western GOM and into the nearshore shellfish areas influenced by downwelling-favorable conditions.

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