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Blooms of the toxic dinoflagellate, *Alexandrium fundyense* in the Casco Bay region of the western Gulf of Maine: Advection from offshore source populations and interactions with the Kennebec River plume

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Abstract

The Casco Bay region, an embayment adjacent to the Kennebec River, has been suggested as a source region for *Alexandrium fundyense* bloom development in the western Gulf of Maine (GOM). In this study, shipboard observations were acquired within Casco Bay and the nearby coastal waters during the spring of 1998 and 2000. In the early bloom season, low *A. fundyense* abundances (<100 cells l^{-1}) were observed within the bay, sometimes isolated from *A. fundyense* populations observed in adjacent coastal waters. When high abundances of *A. fundyense* (>500 cells l^{-1}) were observed within Casco Bay, they were contiguous with coastal populations observed within the Kennebec/Penobscot river plume and within offshore waters of the western segment of the Maine Coastal Current (WMCC). This general distributional pattern occurred during both study years. Wind directly affected the pathway of the incoming coastal populations. Downwelling-favorable winds generally facilitated bloom formation (and outbreaks of shellfish toxicity) within Casco Bay by enhancing the connection with offshore populations via alongshore and onshore transport of cells from the upstream coastal waters. In contrast, persistent upwelling-favorable winds were associated with low *A. fundyense* cell abundances (and shellfish toxicity) in Casco Bay by slowing the advance of the coastal population and shifting it offshore with the Kennebec plume front. The striking difference between late season (June) population abundances of the two study years can be explained by a combination of the wind pre-history and interannual differences in large-scale (Gulf-wide) circulation patterns, as evidenced by higher salinities in the coastal waters in 2000 vs. 1998. Advection of *A. fundyense* cells into Casco Bay and retention, not local growth within the Bay, are likely the dominant processes that typically result in the accumulation of high populations and shellfish toxicity in the Bay. A variety of mechanisms (e.g., circulation underneath or steerage around the Kennebec plume) promote the transfer of cells across the Kennebec/Penobscot plume barrier and into the Bay. These dynamics are complex given the variability of the wind, river inputs, and the Maine Coastal Current structure. Nonetheless, general distributional patterns of *A. fundyense* and the associated hydrography clearly demonstrate that populations within Casco Bay are not isolated, but instead are part of the large-scale coastal populations that inhabit the western GOM, likely originating from further upstream in the coastal flow. With that knowledge, the ultimate goal of

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predicting outbreaks of shellfish toxicity in the western GOM based on meteorological and hydrographic conditions may become a reality.

Keywords: Harmful algal bloom; *Alexandrium fundyense*; Kennebec River; Coastal current; Paralytic shellfish poisoning; Casco Bay

1. Introduction

Toxic *Alexandrium fundyense*[1] blooms affect large coastal areas of the northeastern United States and Canada each year (Anderson, 1997; Martin and White, 1988). Serious human health concerns accompany each bloom event due to paralytic shellfish poisoning (PSP), a potentially fatal illness caused by consumption of shellfish that have accumulated potent neurotoxins as they filter-feed on the algal cells. To protect the public health, shellfish monitoring programs were established in each affected New England coastal state. Maine's program has operated nearly 50 years, but other states began monitoring in response to a massive, visible "red tide" bloom that occurred in the Gulf of Maine (GOM) in 1972 (Mulligan, 1973). The shellfish resources along the extensive Maine coastline have been particularly difficult to manage given the prevalence of toxicity associated with annually recurrent blooms (Shumway et al., 1988). The toxins produced during the blooms also have been transferred through the food web to higher trophic levels including marine mammals (Geraci et al., 1989; Doucette et al., 2002; Turner et al., 2000; Campbell et al., 2005; Doucette et al., 2005; Turner et al., 2005).

The coastline of the western GOM from Penobscot Bay, Maine to Massachusetts Bay often experiences seasonal shellfish closures from about April through June, preceding outbreaks in eastern Maine or the Bay of Fundy that peak later in summer (Anderson, 1997). The first detection of shellfish toxicity along the Maine coast (in the sentinel organism, the blue mussel, *Mytilus edulis*) commonly occurs in the Casco Bay region every year within or downstream of the Bay, usually reaching higher levels and often persisting longer than other areas along the western GOM coastline (Franks and Anderson, 1992b; Anderson et al., 2005c; Bean et al., 2005). However, the direct link between shellfish toxicity and *A. fundyense* bloom dynamics in the region is not well understood.

Several studies have demonstrated that populations of *A. fundyense* are associated with the major coastal currents that are part of the general circulation of the GOM (reviewed in Anderson, 1997; Townsend et al., 2001; Anderson et al., 2005c). In particular, the Maine Coastal Current (MCC) has been implicated in the transport of the populations. The MCC has several branches or segments, and multiple branch points (Fig. 1). Terminology pertaining to these elements varies in the literature (e.g., Brooks, 1985; Lynch et al., 1997; Pettigrew et al., 1998). A common theme is a coastal current that generally flows along the Maine coastline from east to west along isobaths, with a branch point offshore of the mid-Maine coast. At that branch point, the eastern segment turns offshore near Jordan Basin and the western segment continues along the coast. The eastern segment of the MCC is referred to hereafter as the EMCC and includes the offshore extension of that flow. The western segment, which continues alongshore, is referred to hereafter as the WMCC. Fluctuations in these various circulation elements and their interconnections continue to be an active area of research (Churchill et al., 2005; Keafer et al., 2005; Pettigrew et al., 2005) and are extremely important with respect to the growth and transport of *A. fundyense* populations in the GOM.

In the western GOM, high *A. fundyense* abundances have been observed in spring, associated within a warm, low-salinity, buoyant plume (Franks and Anderson, 1992a). These observations led to the "plume-advection hypothesis", a conceptual model that states that the blooms likely originate near the mouths of the major rivers entering the western GOM—the Penobscot and the Kennebec Rivers. Furthermore, the transport of those blooms is greatly influenced by the larger GOM circulation, river runoff, and wind stress. Anderson et al.

[1]Two saxitoxin-producing species of *Alexandrium* occur in the Gulf of Maine: *A. fundyense* and *A. tamarense*. We consider these to be varieties of the same species (Anderson et al., 1994). Neither antibody nor oligonucleotide probes can distinguish between *A. fundyense* and *A. tamarense* from this region; only detailed analysis of the thecal plates on individual cells can provide this resolution. Since this is not practical for large numbers of field samples, for the purpose of this and other field studies, we use the name *A. fundyense* to refer to both forms.

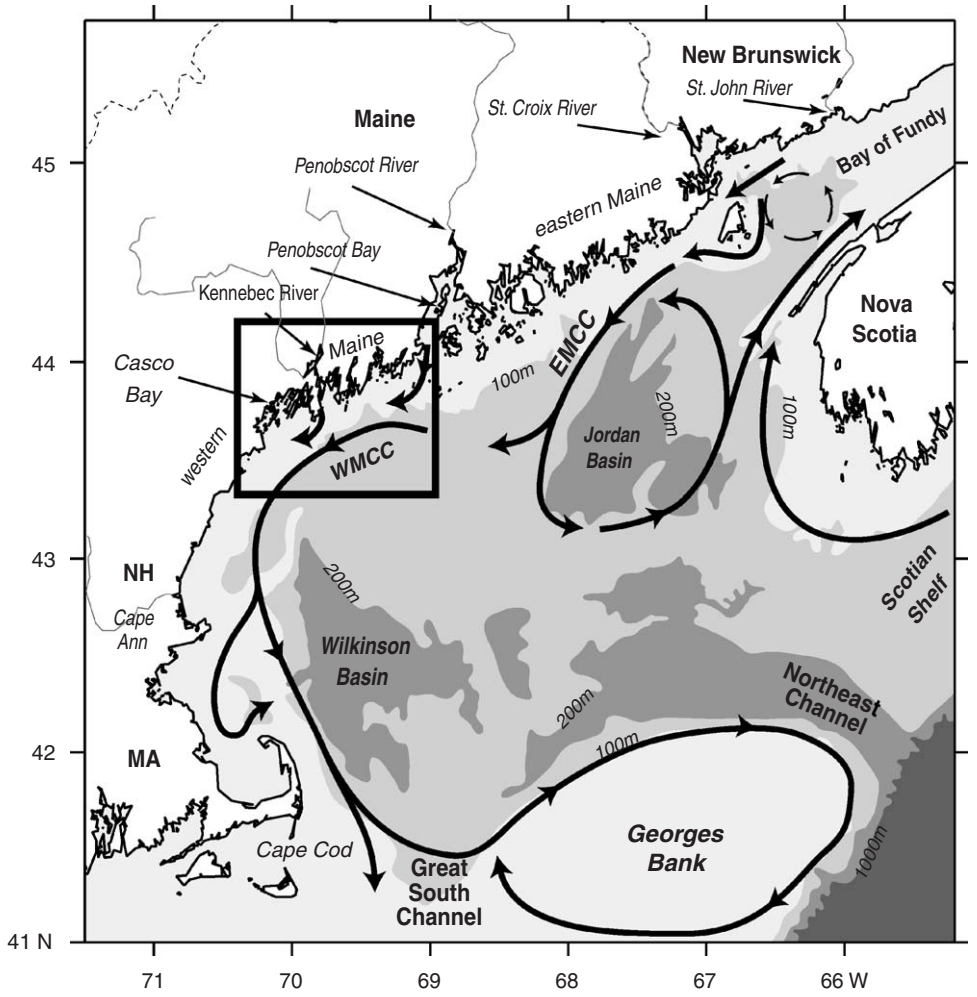

Fig. 1. General near-surface circulation of the Gulf of Maine. The circulation pattern is generally counterclockwise around the periphery of the Gulf and clockwise around Georges Bank. Along the Maine coast, two segments of the Maine Coastal Current are shown that potentially feed in to the study area near Casco Bay, the eastern Maine coastal current (EMCC) and the western Maine coastal current (WMCC). Major freshwater inputs in the region are Scotian Shelf water, the St. John River entering into the Bay of Fundy and the Penobscot and Kennebec Rivers entering the western GOM. Bathymetry is indicated by greyscale levels where dark shading represents the deep basins >200 m (adapted from Brooks, 1985; Beardsley et al., 1997; Lynch et al., 1997).

(2005c) confirmed that *A. fundyense* populations were associated with the Kennebec River plume, often near the frontal boundary with the WMCC as it branches from the EMCC. Their results corroborated key elements of the plume advection hypothesis, but the source populations for the blooms in the western GOM and in particular for the Casco Bay region were not well defined. Two possible sources were hypothesized, one from locally germinated benthic cyst populations and one from advection of established populations in the upstream waters of the MCC where *A. fundyense* populations have been observed associated with the edges of the cold, well-mixed and nutrient-rich waters of the EMCC (Townsend et al., 2001). Thus, *A. fundyense* appears to reside in at least two different habitats along the Maine coast—the EMCC and the WMCC (Anderson, 1997). The focus of this study was in the Casco Bay region, located near the intersection of these two habitats in a complex environment of coastal currents and river inputs (Fig. 1).

The outflow from the Kennebec River has a significant influence on the hydrography of the

region (Fong et al., 1997; Geyer et al., 2004; Janzen et al., 2005). Although *A. fundyense* populations have not been documented within the river itself, several studies have reported cells within the plume waters (Franks and Anderson, 1992a; Anderson and Keafer, 1992; Anderson et al., 2005c), suggesting that an entrainment mechanism must be operative to transfer cells originating in the coastal ocean to the low salinity plume waters. Furthermore, simulations using coupled biological/physical numerical models indicated that one scenario capable of reproducing the observed pattern of field populations in the western GOM was when cells were released into the Kennebec River plume near the mouth of the river (Anderson et al., 2005c). These observations suggest that the Casco Bay/Kennebec River mouth area may be a site for development of local blooms or an area favorable for accumulation and growth of advected populations.

Several components of the ECOHAB-GOM (Ecology and Oceanography of Harmful Algal Blooms in the GOM) program examined *A. fundyense* dynamics in the Casco Bay region. Since toxicity has been commonly reported early in the bloom season within Casco Bay (April) and the blooms have been reported in the Kennebec River plume, that area was identified as a likely region to focus the search for source populations for larger scale blooms that occur in the western GOM (Anderson et al., 2005c). The objective of the study reported here was to use cruise observations and moored measurements during a 2-year period to identify *A. fundyense* populations early in the bloom development processes that can explain seasonal shellfish toxicity outbreaks that occur along that key area of the western Maine coastline. We hypothesized that blooms in Casco Bay can be initiated locally within the Bay and contribute to blooms along the western Maine coastline. Alternatively, blooms within Casco Bay may be initiated offshore either within the Kennebec plume waters or the adjacent coastal waters. Additionally, our goal was to establish linkages, if any, between the western GOM populations located within Casco Bay and the Kennebec plume with populations observed upstream and offshore in the EMCC or WMCC. Results addressing the latter objective are presented in a companion paper that extended the sampling domain further upstream in the coastal flow along the mid- and eastern Maine coastlines (Keafer et al., 2005).

2. Measurements and methods

2.1. Description of the study area

The western GOM near the Casco Bay region receives freshwater inputs primarily from three major rivers; the Penobscot, Androscoggin and Kennebec Rivers (Fig. 1). The Penobscot River empties into the western GOM just upstream of the sampling domain (Fig. 2), while the Androscoggin and Kennebec Rivers share a common mouth (referred to hereafter as the Kennebec River) adjacent to Casco Bay. The discharges from these rivers coalesce into a low salinity coastal plume that is maximal during the spring runoff period (Geyer et al., 2004). The input of freshwater directly into Casco Bay is relatively small since its watershed is only 1/10 the size of the adjacent Androscoggin/Kennebec watershed (Pait and Pacheco, 1994).

The sampling domain of this study (ca. 2500 km^2) included stations located both within Casco Bay and near the Kennebec River plume (Fig. 2). The inshore stations were specifically located close to shellfish monitoring sites near the New Meadows River and Lumbo's Hole, two "hotspots" in northeastern Casco Bay that generally report high shellfish toxicity each spring.

The study area was repeatedly sampled during the spring of 1998 and 2000 aboard the R/V Gulf Challenger, a 16 m coastal vessel with a cruising speed of 27 $km\,h^{-1}$ that allowed each survey to be completed within two successive days. In 1998, six biweekly surveys sampled four cross-shore transects that extended from northeastern Casco Bay and the mouth of the Kennebec River into the adjacent coastal waters (42 stations/survey; Fig. 2). In the intervening weeks, the two transects within Casco Bay were sampled to provide a weekly time series of *A. fundyense* data consistent with weekly shellfish monitoring performed by the Maine Department of Marine Resources (see Bean et al., 2005) for a total of 11 surveys spanning the period from April through June. In year 2000, a total of eight weekly surveys (28 stations/survey) were completed from mid-April to mid-June sampling along two transects; one that extended from Casco Bay into the adjacent coastal waters within the influence of the Kennebec River and one further upstream in the coastal flow, presumably out of the influence of the Kennebec River (Fig. 2). In response to observations of offshore toxicity and offshore populations of toxic cells in 1998 (see results below)

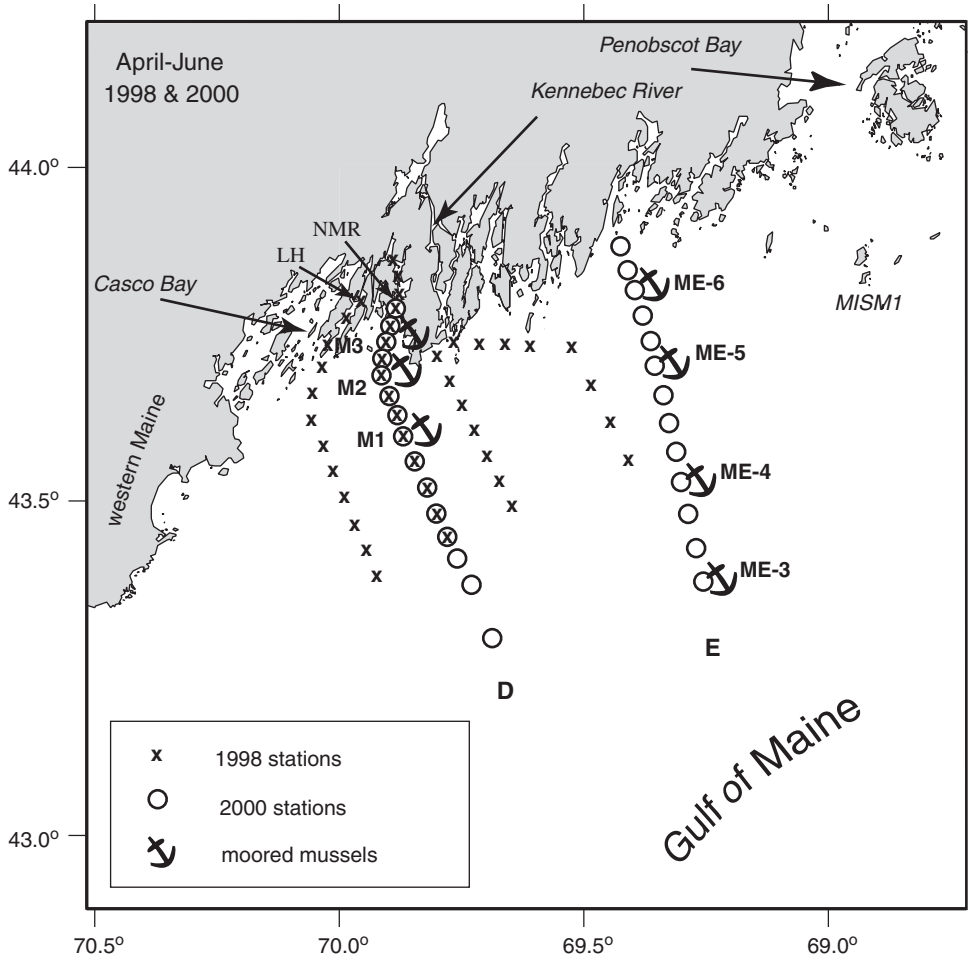

Fig. 2. Hydrographic and *A. fundyense* station locations for the ECOHAB spring field study in the western Gulf of Maine near Casco Bay and the Kennebec River mouth. In 1998 (X), four transects were sampled biweekly, while the two transects extending into Casco Bay were sampled on a weekly frequency. In 2000 (O), weekly stations were relocated further east and offshore along two transects, the D line and the E line. Mussels were deployed at hydrographic moorings M1, M2 and M3 sites in 1998 and M1, M2, and the ME sites in year 2000. Wind measurements were acquired from Matinicus Rock (MISM1). Two "hotspots" of shellfish toxicity in Casco Bay are labeled: NMR = New Meadows River; LH = Lumbo's Hole.

and to the report of populations in the offshore waters of the eastern GOM (Townsend et al., 2001), the two transects sampled in 2000 were extended further offshore than those sampled in 1998.

2.2. Shipboard measurements

At each station, vertical profiles of temperature, salinity, PAR, fluorescence and beam attenuation were acquired using a Falmouth Scientifics iCTD. All hydrographic data were pressure-averaged in 0.5-m bins ranging roughly from 2 m below the surface to within 2 m above the bottom. Data at less than 2 m depth were considered to be unstable because of wave action on the sensors. In the first year of the study (1998), near-surface water samples were collected at 1, 3.5 and 7 m using 10-l Niskin bottles attached to the CTD frame. These samples were combined in equal volumes to provide one near-surface sample for *A. fundyense* cell counts and nutrients at every station (a total of 42 depth-averaged samples/survey; for nutrient description see Love et al., 2005). Of those 42 stations, six were selected for discrete vertical sampling to 20 m (1, 3.5, 7, 10 and 20 m) during each survey. The locations of those stations were along the two transects that extended into Casco Bay covering the offshore, mid-transect, and inshore areas. In 2000, all stations were sampled discretely at 1, 3.5, 7, 10 and 20 m without combining the near-surface

samples (a total of 28 stations/survey × 5 depths = 140 samples/survey).

2.3. Laboratory analysis of *A. fundyense* abundance

An immunofluorescent method utilizing a mouse monoclonal antibody (M8751-1; Adachi et al., 1993; Sako et al., 1993) was routinely used for all counts since it yielded a relatively bright signal (Anderson et al., 1999) and had performed well in a previous field study in the GOM (Turner et al., 2000). However, during the course of the 1998 study, large *Alexandrium* cells, now known to be *A. ostenfeldii* (see Gribble et al., 2005; Anderson et al., 2005a), were occasionally noted that cross-reacted with the M8751-1 antibody (see Anderson et al., 2005a). It is difficult to assess the degree to which the presence of *A. ostenfeldii* interfered with the *A. fundyense* estimates in 1998. The large *Alexandrium* cells were first noted, but not quantified, during cruise 2 (late April) of the 1998 surveys. Anecdotally, the large cells contributed perhaps as much as 30–50% of the population at some stations at that time. However, the contribution was significantly reduced in the subsequent surveys, perhaps contributing $<10\%$ to the overall *Alexandrium* population.

In year 2000, an adjustment was made in the counting process to discriminate *A. fundyense* from *A. ostenfeldii*. This modification was based on a concurrent study using a species-specific nucleic acid probe (NA-1) that did discriminate *A. fundyense* from *A. ostenfeldii* (Anderson et al., 2005a). These authors demonstrated that excluding large cells that contain food vacuoles from the antibody count improved the correlation between antibody-based and nucleic acid-based estimates of the population. Therefore in year 2000, co-occurring *A. ostenfeldii* cells with a size $>50\,\mu m$ and with the presence of food vacuoles were excluded from enumeration of *A. fundyense* to obtain better estimates of the *A. fundyense* populations. Using this method, the data indicated that the overestimate due to the contribution from *A. ostenfeldii* cells varied widely, ranging from approximately 0–60% with a mean of 30% of the population, on the same order as noted anecdotally in the 1998 observations above. Thus, the 1998 *A. fundyense* data may at times be overestimates of the population and should be interpreted with some caution, especially during survey 2 (late April).

In the field, 2 l of seawater were collected directly from Niskin bottles into sample-rinsed plastic bottles. The target *A. fundyense* cells were immediately concentrated by sieving onto 20-μm Nitex mesh, backwashed to a final volume of 14 ml with filtered seawater, preserved with 0.75 ml formalin (5% final), and stored at 4 °C in the dark. In the lab, a 7.5-ml aliquot was filtered onto a 25-mm Cyclopore membrane (Whatman Inc., 5 μm 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 sample was incubated (RT for 30 min) directly on the filter with 1 ml 5% normal goat serum in 0.02-M phosphate buffered saline [NGS/PBS; (NGS; Sigma Chemical Co. #9023) (PBS; 0.02 M PO_4, 0.15 M NaCl, pH 7.45)] to block non-specific binding. NGS/PBS was removed by filtration and the filter re-incubated (30 min at RT) with 315 μl primary antibody (M8751-1; 1:50 v/v in 5% NGS/PBS). After washing 3 × with 5 ml 0.5% NGS/PBS, the sample was incubated again with 300 μl goat anti-mouse secondary antibody conjugated to fluorescein [(GAM-FITC, 1:300 v/v in 5% NGS/PBS) Molecular Probes Inc., #F-2761]. The sample was finally washed 3 × with 5 ml volumes of 0.5% NGS/PBS. The filter was semi-permanently mounted on a glass microscope slide using 25 μl of 80% glycerol/PBS with a cover glass for protection and stored at 4 °C in the dark until microscopic counting (stable for at least 1 week or longer, but counted within days). Control samples containing cultured cells of *A. fundyense* were processed simultaneously to confirm the consistency of the staining procedure.

The whole filter (equivalent to 1 l of seawater) was enumerated for *A. fundyense* cells by epifluorescence using a Zeiss Axioskop at 100 × magnification equipped with Zeiss filter set # 487709 (excitation = BP 450–490 nm, emission = LP 520 nm). Only those cells labeled with a bright green FITC-label around the periphery of the cell and red chlorophyll *a* autofluorescence within the cytoplasm were included in the count.

2.4. Shellfish toxicity measurements at hydrographic moorings

A mooring program was implemented as part of the 1998 and 2000 field seasons to provide continuous hydrographic and water velocity measurements. During both field seasons, offshore shellfish toxicity measurements were acquired at the mooring sites by attaching mussel bags to the

surface buoys (Fig. 2). In 1998, mussels were deployed at the three hydrographic mooring sites off of Casco Bay (M1, M2 and M3 in Fig. 2). In 2000, only two mussel moorings were set near Casco Bay (M1 and M2), while an additional four mussel moorings were established along transect E (ME-3, ME-4, ME-5, and ME-6) out of the influence of the Kennebec River plume and perpendicular to the incoming coastal flow of the Penobscot plume and the WMCC.

Prior to the bloom season, wild mussels (*M. edulis*) free of PSP toxins were harvested, placed in nylon-mesh bait bags (ca. 25 mussels/bag), and maintained in a toxin-free area out of the survey region. Each week, a snorkeler placed one of these uncontaminated mussel bags at each site and harvested a bag attached there during the previous week. A control bag that was never deployed in the study area was also collected each week. All shellfish samples were analyzed using the standard mouse bioassay for PSP (AOAC, 1984) along with samples collected as part of the weekly shellfish monitoring program. Only selected toxicity data from the mussel sites are presented here accompanied by the near-surface current velocities derived from a moored electromagnetic (S4) current meter at mooring M1.

The current meter data shown here were filtered with a 33-h half power point filter to remove most of the signal due to tides and near-inertial motions. The velocities were rotated into a local along-shore and across-shore coordinate system with the along-shore axis orientated at 65 °T (degrees clockwise of true north). This approximately coincides with the orientation of the western Maine coastline. For detailed analysis of the 1998 and 2000 moored measurements, the reader is referred to Churchill et al. (2005) and Janzen et al. (2005).

2.5. Drifters

To determine the potential transport pathways of *A. fundyense* populations, several Davis-type (Davis, 1985) satellite-tracked surface drifters (Met-Ocean, Inc.) were released in the study area. Each drifter was designed to follow the surface current at 1 m. The principal drag elements of each drifter consisted of four vanes radiating from a central cylinder housing the electronics. In 1998 and 2000, two drifters were released every 1–2 weeks during the surveys in the Casco Bay/Kennebec area, while several others were set out from UNOLS vessels working further to the northeast. Fixes were obtained by ARGOS satellite, 6–8 times per day, with accuracies of ± 300 m. Here we focus on drifter tracks from the 2000 field effort. Analysis of the drifter tracks from the 1998 field season is provided by Janzen et al. (2005).

2.6. Wind data

Meteorological data were obtained from the National Oceanographic and Atmospheric Administration recording station at Matinicus Rock (Fig. 2). The vector winds from this site were rotated into a local along-shore and across-shore coordinate system with the alongshore axis orientated at 65 °T. As noted above, this approximately coincides with the orientation of the Maine coastline. It is also 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).

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

In spring, runoff from the western GOM rivers warms more rapidly than the cold, receiving waters of the GOM and can be distinguished in AVHRR (Advanced Very High Resolution Radiometer) imagery (Keafer and Anderson, 1993). Relatively cold water along the eastern Maine coast that is deflected offshore and alongshore as part of the EMCC and the WMCC is visible as well (Townsend et al., 2001; Anderson et al., 2005c; Luerssen et al., 2005). Data were acquired 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 sea-surface temperature 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 during favorable weather.

3. Results

Populations of *A. fundyense* and associated outbreaks of shellfish toxicity were widespread along the western Maine coast during both study years. In particular, both showed strong mid-May peaks, but there were also differences in the timing of the

events and the distributional patterns that are important for unraveling the complex dynamics detailed below.

3.1. Moored mussel bag observations

Shellfish toxicity was detected during the spring of both study years at the offshore and inshore mooring sites and along the western Maine coastline, including Casco Bay. While the wind and currents were quite variable during the spring bloom period, trends were apparent in the weekly toxicity data and the *A. fundyense* abundance coincident with meteorological and hydrographic events (Figs. 3 and 4). In general, shellfish toxicity rose following and during times of strong downwelling-favorable winds (directed to the SW) and declined following and during times of strong upwelling-favorable winds (directed to the NE).

The alongshore surface currents at the M1 mooring (located in the coastal region offshore of Casco Bay) were predominately directed to the SW,

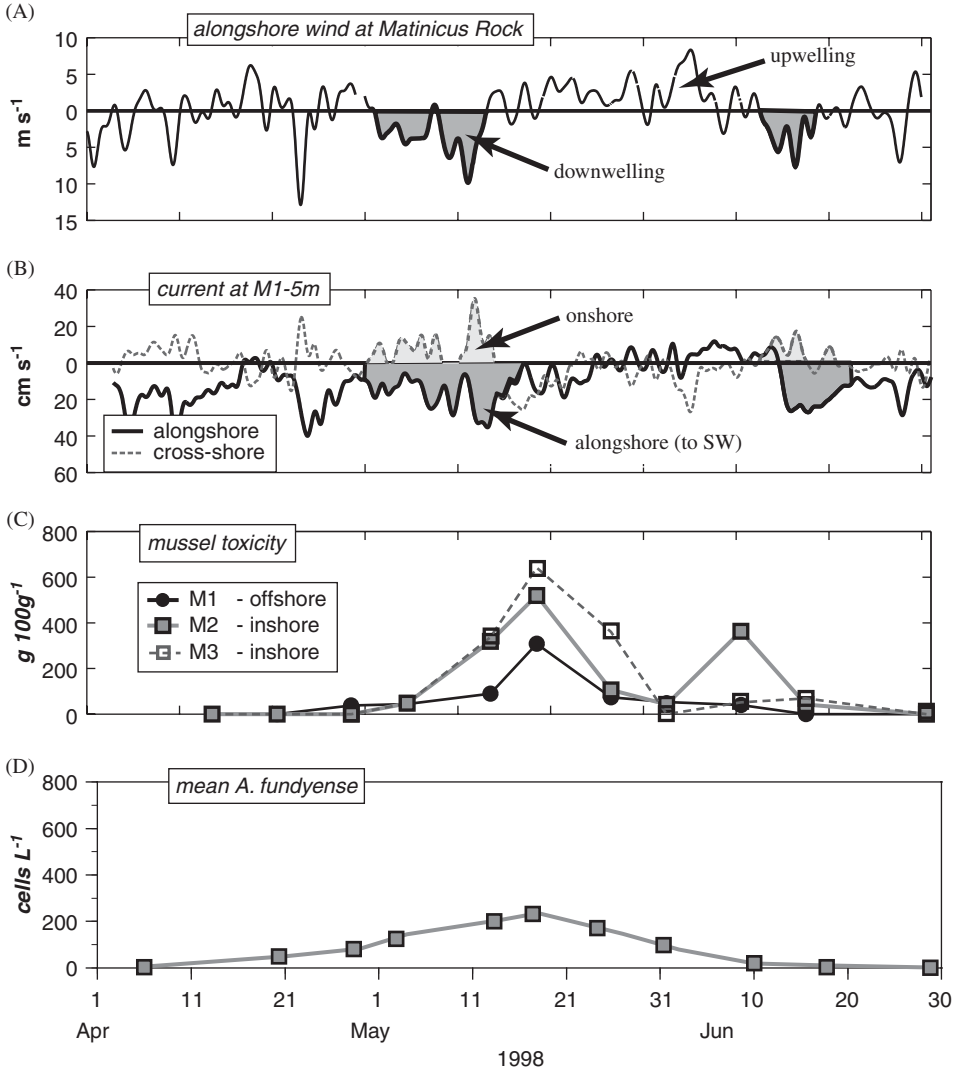

Fig. 3. Time series of winds, currents, shellfish toxicity, and mean *A. fundyense* abundance during 1998. (A) Alongshore wind at Matinicus Rock (MISM1). Negative values indicate downwelling-favorable conditions and positive values indicate upwelling-favorable conditions. Two prominent downwelling periods are highlighted during the bloom season. (B) Near-surface currents at M1 (5 m). The bold line indicates the alongshore component of the current; positive indicates to the southwest and negative indicates to the northeast. The dotted line indicates the cross-shore component; positive indicates onshore flow and negative indicates offshore flow. (C) near-surface shellfish toxicity at the three moorings near Casco Bay. (D) Mean *A. fundyense* abundance of the "pooled" near surface samples.

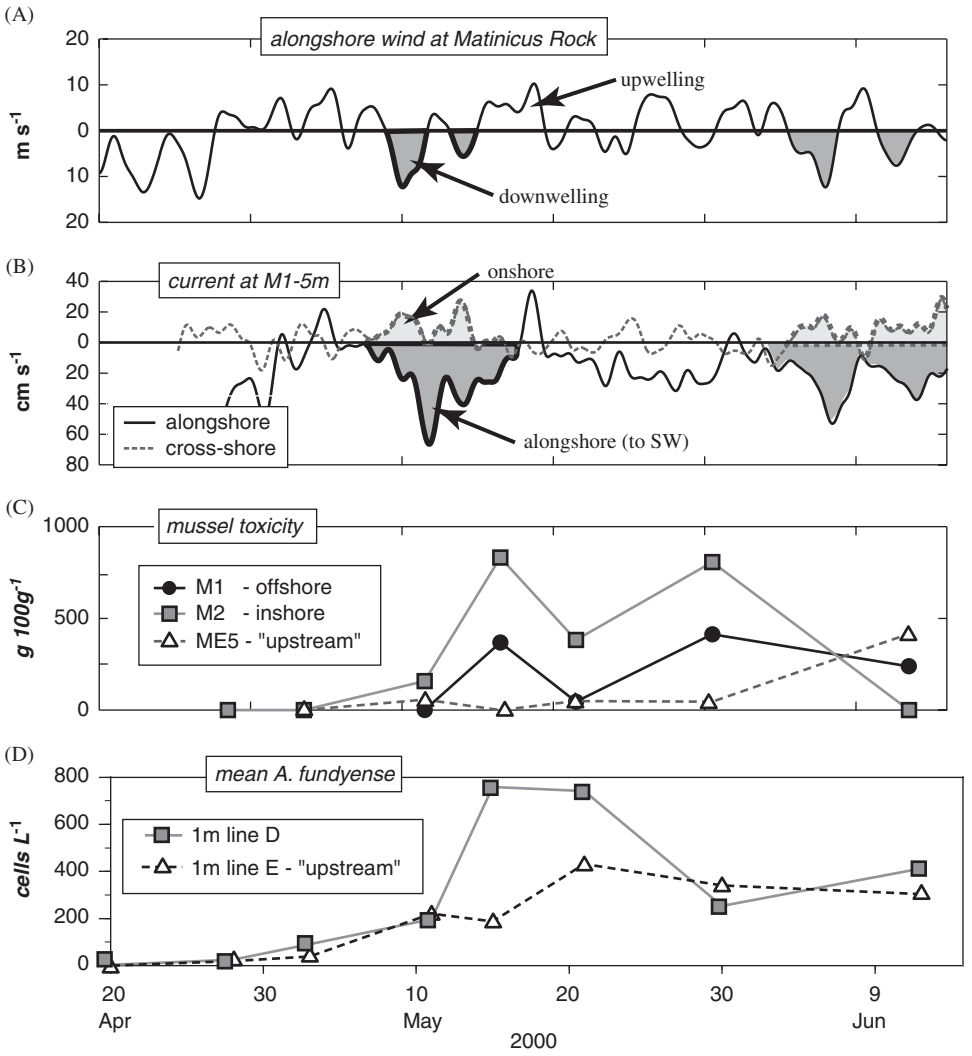

Fig. 4. Time series of winds, currents, shellfish toxicity, and mean *A. fundyense* abundance during 2000. (A) Alongshore wind at Matinicus Rock (MISM1). (B) Near-surface currents at M1 (5 m). (C) Near-surface shellfish toxicity deployed at two moorings near Casco Bay and one mooring upstream. (D) Mean *A. fundyense* abundance of the "discrete" surface samples (1 m) along Line D (across Casco Bay and the Kennebec River plume) and Line E, upstream and out of the influence of the Kennebec plume. Convention for winds and currents are as in Fig. 3 above. Two prominent periods of downwelling-favorable conditions are highlighted in the wind and current record.

accelerating to $>20\,\mathrm{cm\,s^{-1}}$ during strong downwelling-favorable periods, while decelerating and even reversing during periods of strong upwelling-favorable conditions (Figs. 3A, B and 4A, B; see also Churchill et al., 2005).

In 1998, shellfish toxicity was first detected during late April at the most offshore mooring, M1, followed 1 week later by detection at M2 and M3 within Casco Bay (Fig. 3C). The inter-tidal shellfish monitoring sites within Casco Bay (e.g., Bear Island near the New Meadows River) and along the western Maine coast lagged detection at the moorings by yet another week with some stations within Casco Bay reaching high levels (ca. $700\,\mu\mathrm{g\,100\,g^{-1}}$; Bean et al., 2005), higher than the levels observed at M1 further offshore. The progression of toxicity from offshore to inshore was associated with downwelling-favorable wind conditions that transported water (and presumably toxic cells) into Casco Bay and along the western Maine coast as indicated by the alongshore and onshore components of the current velocity at M1 (Fig. 3A–C). Coincident with the peak in toxicity and following the extended downwelling-favorable period, mean cell abundances reached ca. $200\,\mathrm{cells\,l^{-1}}$ averaged over the entire domain, while maximum

concentrations within Casco Bay were near 1000 cells l^{-1} (Fig. 3C and D). The decline in toxicity and cell abundance was coincident with a 3-week period of strong upwelling-favorable conditions when the currents slowed, reversed, and were directed offshore. However, following a second downwelling event in late spring, there was no apparent relationship between the wind and toxicity since few toxic cells were observed in the region.

The time series in toxicity during the spring of 2000 demonstrated both similarities and differences from the 1998 observations. Similar to 1998, the rapid rise in toxicity at the offshore M1 mooring and the Casco Bay mooring at M2 followed strong downwelling-favorable conditions and transport of near-surface waters onshore and alongshore, as shown by current velocities at the M1 mooring (Fig. 4A–C). However, the initial detection of toxicity at the offshore moorings lagged the rise at Lumbo's Hole within Casco Bay by about 1–2 weeks (Bean et al., 2005). The inshore levels remained near detection limits until May 12 (after the downwelling event) when toxicity rose rapidly both at M1 and M2, coincident with a rapid rise within Casco Bay. Concurrent with that rise, the upstream ME-4 and ME-5 moorings signaled that cells were entering the study domain along the upstream boundary with the WMCC, although the levels remained low. The mean cell abundance along the D line (Casco Bay transect) also increased sharply during this period, from 200 to nearly 800 cells l^{-1} with maximum concentrations within Casco Bay exceeding 2500 cells l^{-1}. The mean cell concentration along the upstream E line rose more gradually (Fig. 4D).

Unlike 1998, high cell abundances and shellfish toxicity generally persisted in the region in 2000. This observation was consistent with the current velocities at M1, which remained directed alongshore and onshore, albeit at low velocities during the oscillating period of upwelling- and downwelling-favorable conditions in late May. When persistent and strong downwelling-favorable conditions returned late in the bloom season, toxicity increased at the ME-5 site, persisted at the M1 site, but was not observed within Casco Bay. The persistent toxicity at the offshore mooring sites was consistent with the mean cell abundance >200 cells l^{-1} along both the D line and the upstream E line located near the outer boundary of the Kennebec plume and not within Casco Bay (see Fig. 8C below). Shellfish toxicity also persisted further downstream at several inshore monitoring sites along the western Maine coastline (Bean et al., 2005) indicating that the offshore population bypassed Casco Bay during the second major downwelling-favorable event.

3.2. Cruise observations

The *A. fundyense* abundance and associated hydrographic data from two field seasons in the spring of 1998 and 2000 show the development of the bloom in the Casco Bay region and the influence from Kennebec River plume (Figs. 5–8). In the early spring period (April) of both years, *A. fundyense* cells were present within Casco Bay and in a narrow alongshore band of >50 cells l^{-1} located in the adjacent offshore waters (Fig. 5). Few cells (<20 cells l^{-1}) were located at the mouth of the Kennebec River, generally a common feature throughout the study. In 1998, the offshore *A. fundyense* population was continuous across a salinity range from >31 psu at the offshore and upstream boundary to 28 downcoast of the Kennebec plume and within Casco Bay (Fig. 5A and B). The continuity of the population from the offshore waters into Casco Bay (>20 cell l^{-1}) is suggestive of a pathway that circulates around the Kennebec plume. Similarly in 2000, the early season offshore population (>50 cells l^{-1}) converged with the frontal boundary of the Kennebec plume, but unlike 1998, the station resolution in Casco Bay was inadequate to determine if the population was primarily directed alongshore or into Casco Bay (Fig. 5C and D). However, it is noteworthy that the Kennebec plume structure was also different at this time. In early 1998, the 31 psu isohaline was located at the most offshore and upstream boundary and the gradient of the plume structure was directed offshore, generally indicative of upwelling, while in early 2000, the 31 and the 32 isohaline were present across both transects and the gradient of the plume was directed alongshore, indicative of downwelling.

During the peak bloom season of both years, when shellfish toxicity rose rapidly in Casco Bay, the *A. fundyense* abundance was >200 cells l^{-1} both within the Bay and in the adjacent offshore waters (Figs. 6 and 7). Sampling immediately following persistent and strong downwelling-favorable conditions during early May 1998 revealed the highest population within the low-salinity (<30 psu) waters of the Kennebec plume that wrapped continuously into Casco Bay within the 30 isohaline (Fig. 6A and B).

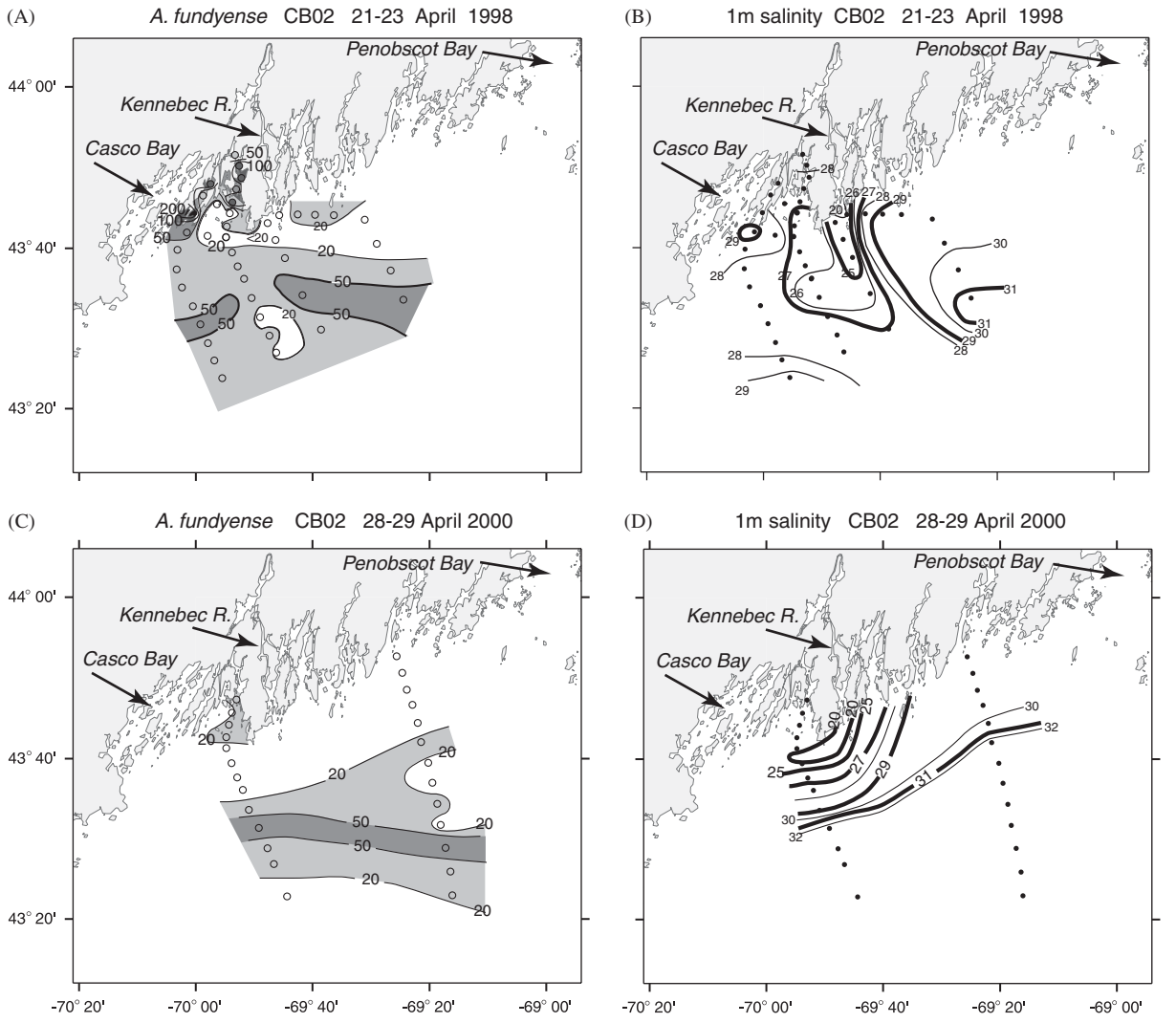

Fig. 5. Early season April distribution of *A. fundyense* and salinity within Casco Bay and the adjacent coastal waters during 1998 and 2000 prior to detection of shellfish toxicity. (A) *A. fundyense* distribution on April 21–23, 1998. (B) Salinity distribution on April 21–23, 1998. (C) *A. fundyense* distribution on April 28–29, 2000. (D) Salinity distribution on April 28–29, 2000. Contour levels below 20 cells l^{-1} are not shown.

During a subsequent upwelling-favorable event less than 1 week later, that continuity began to break-up, leaving the highest inshore Casco Bay population disconnected from the highest offshore population as some of the coastal population diverged offshore with the 29–31 psu isohalines (Fig. 6C and D). Similarly, in May 2000, a population of 50–200 cells l^{-1} was located near the Kennebec plume front (30–31 psu) and was clearly disconnected from the inshore Casco Bay population in early May as general upwelling-favorable conditions prevailed (Fig. 7A and B). By the next week following a downwelling-favorable event, a high *A. fundyense* population (>200 cells l^{-1}) was shifted closer to shore and concentrated near the boundary of the Penobscot and Kennebec plumes (30–32 isohaline; Fig. 7C and D). As in 1998, some of that population merged with the low salinity Kennebec plume waters and wrapped into Casco Bay.

During the latter part of the spring season (mid-June), a time when shellfish toxicity in the western GOM commonly declines, the *A. fundyense* abundances were drastically different between the 2 years (Fig. 8). By mid-June 1998, there were few cells within the Bay and virtually none within the less-saline Kennebec plume waters or even further

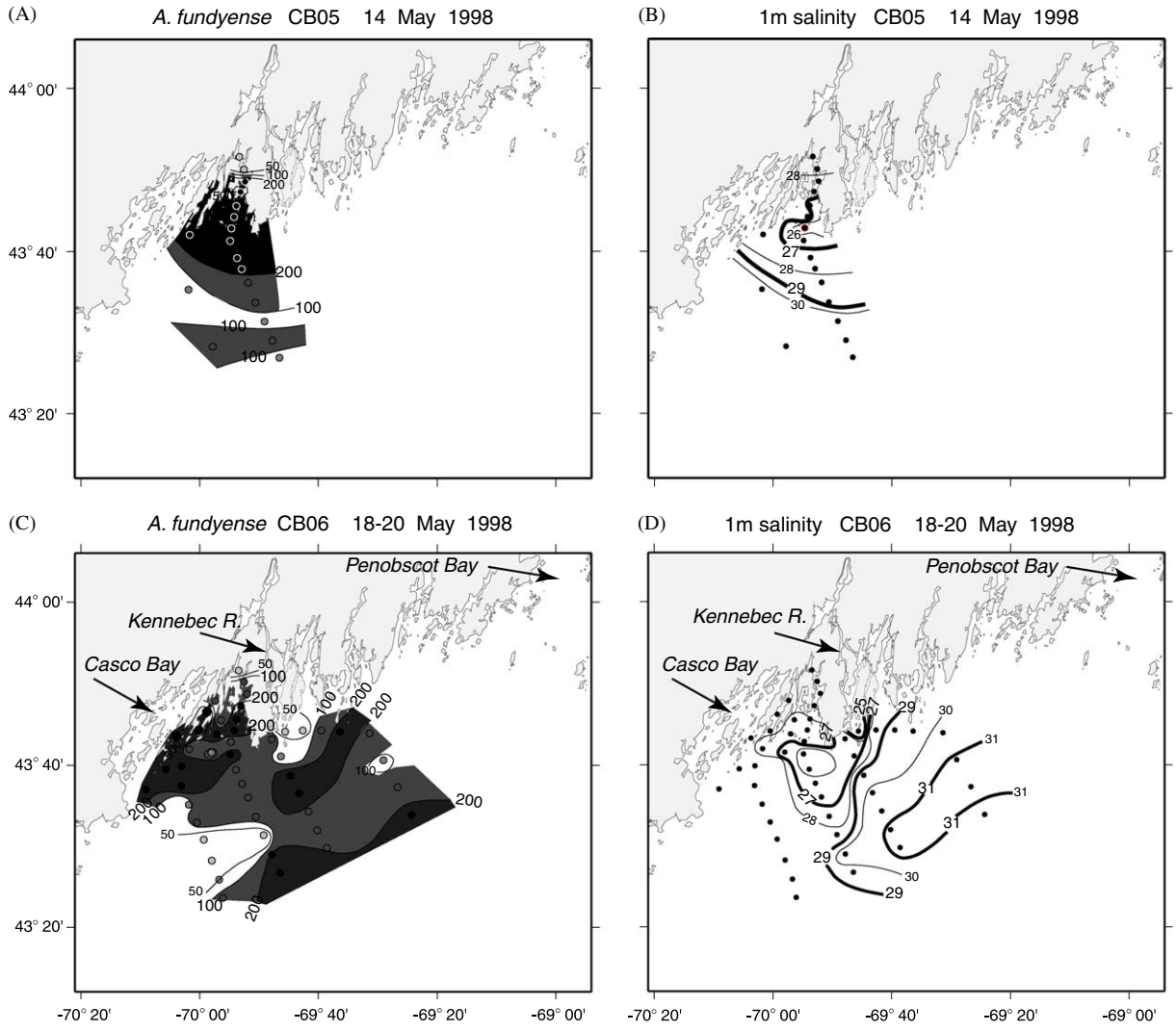

Fig. 6. Distribution of *A. fundyense* and salinity near Casco Bay and the adjacent coastal waters coincident with a rapid rise in shellfish toxicity in mid-May, 1998. (A) *A. fundyense* distribution with high abundances within northeast Casco Bay on May 14, 1998 immediately following downwelling-favorable conditions. (B) Salinity distribution showing 29–30 psu isohalines directed into Casco Bay on May 14, 1998. (C) Distribution of *A. fundyense* showing strong cross-shore variability on May 18–20, 1998 at the onset of 3 weeks of upwelling-favorable conditions. (D) Salinity distribution on May 18–20, 2000 showing 29–30 isohalines directed offshore. Only *A. fundyense* contours >100 cells l^{-1} are filled.

offshore and upstream (Fig. 8A and B). Although there were few cells and little shellfish toxicity within Casco Bay in June 2000, a broad, offshore band of cells (>500 cells l^{-1}) was present within the 31–32 psu isohalines upstream of Casco Bay and the Kennebec River mouth (Fig. 8C and D), in stark contrast to the lack of cells in that region in late spring, 1998.

A key difference between the 2 years in mid-June is apparent in both the hydrography and the wind patterns. The absence of the 31 isohaline (and the 32 isohaline) in the offshore waters in mid-June, 1998 is striking (Fig. 8B), indicating that the freshwater transport into the western GOM was limited in June, 1998 relative to June, 2000. While both the June 1998 and 2000 sampling times followed periods of downwelling-favorable winds, strong and persistent upwelling-favorable conditions occurred in late-May and June prior to the moderate downwelling event in mid-June 1998. In contrast, persistence of upwelling-favorable conditions did not occur prior to the strong downwelling event in

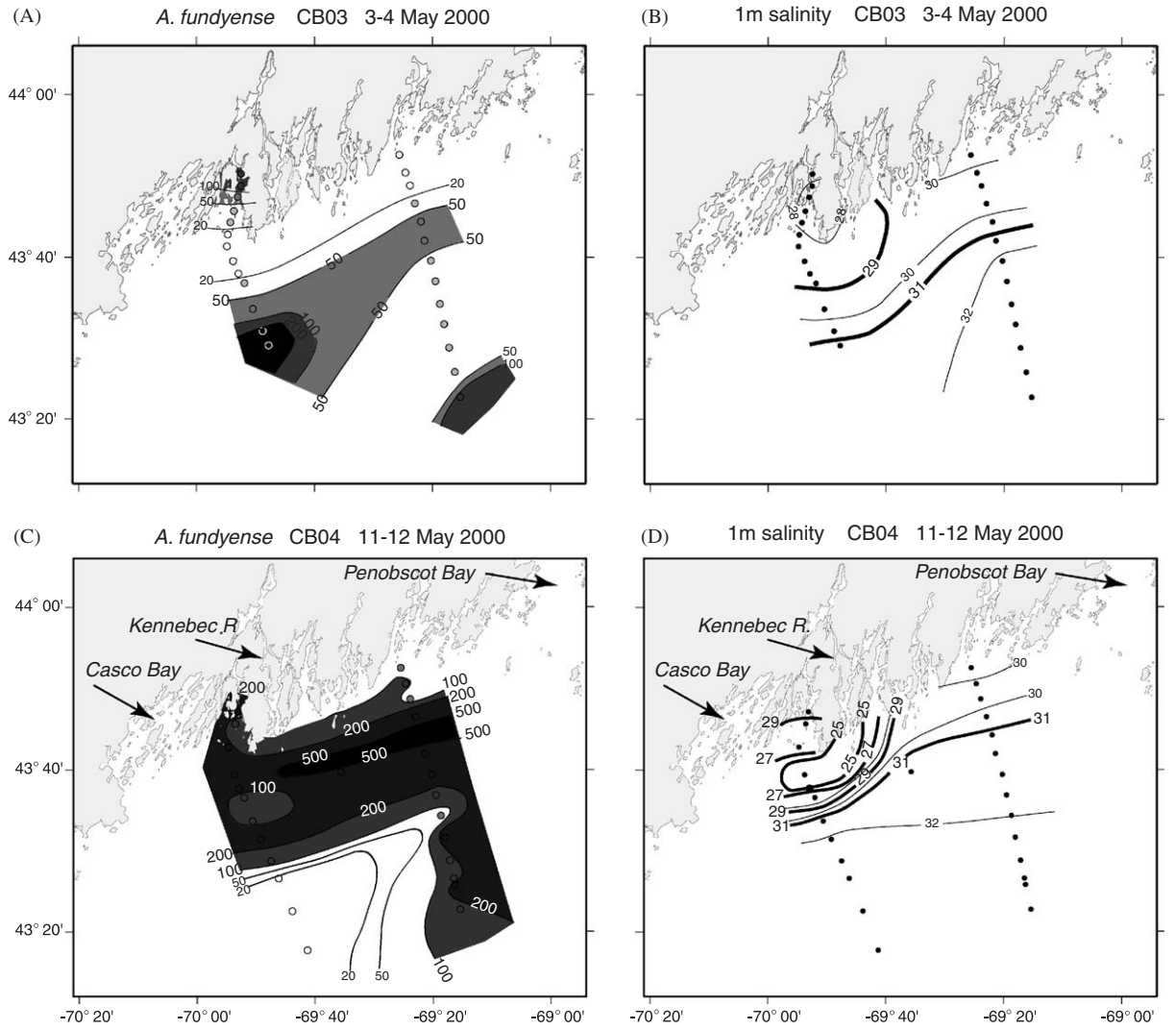

Fig. 7. Distribution of *A. fundyense* and salinity near Casco Bay and the adjacent coastal waters coincident with a rapid rise in shellfish toxicity in mid-May, 2000. (A) *A. fundyense* distribution on May 3–4, 2000 showing cells within Casco Bay and along the Penobscot/Kennebec plume front during upwelling-favorable conditions. (B) Salinity distribution on May 3–4, 2000 showing 31–32 psu isohalines directed offshore of the Kennebec plume. (C) *A. fundyense* distribution on May 11–12, 2000 with high abundances in Casco Bay and along the Penobscot/Kennebec plume front following downwelling favorable-conditions. (D) Salinity distribution on May 11–12, 2000 showing the 31–32 isohalines directed alongshore. Only *A. fundyense* contours >100 cells l^{-1} are filled.

mid-June 2000. These results suggest that interactions of large-scale processes in the adjacent upstream coastal waters in combination with the wind likely transported low-salinity coastal waters away from the Casco Bay region during persistent upwelling-favorable conditions in 1998. A single downwelling event was insufficient to bring that freshwater water back into the western GOM.

The highest *A. fundyense* concentrations were at times clearly observed within the low-salinity waters of the Kennebec and/or Penobscot plumes (<31) as well as within Casco Bay (e.g., Fig. 6A and B), while at other times the population was concentrated offshore near the frontal boundary (31 isohaline) with few cells within the Bay (e.g., Fig. 8C and D). This result is also strikingly evident in the vertical cross-shore transects (Line D) that extended seaward from Casco Bay into the adjacent coastal waters during two successive weeks in May, 2000 (Fig. 9; see Fig. 7 for the horizontal distribution). On May 4, 2000, prior to any significant toxicity

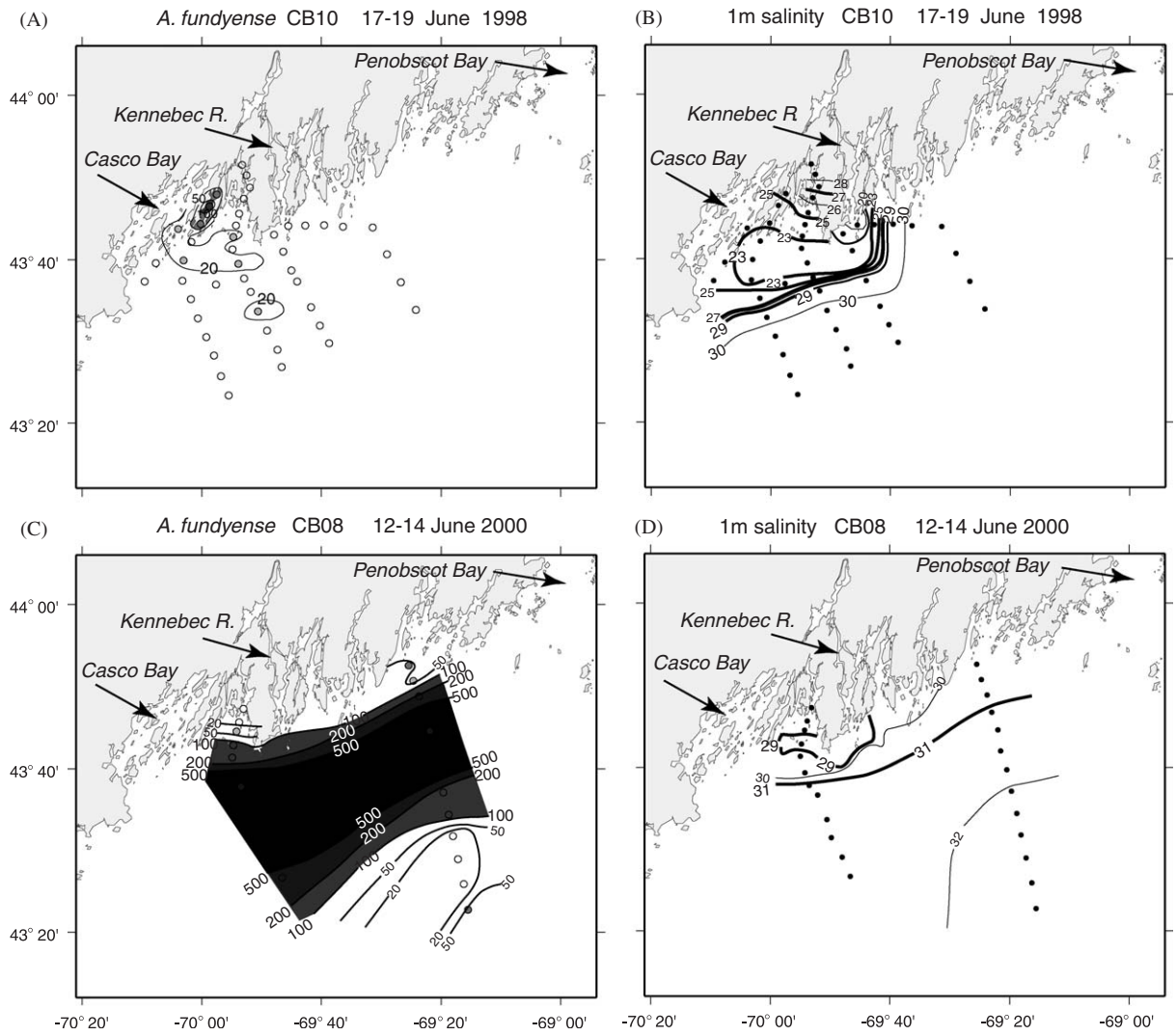

Fig. 8. Late season June distribution of *A. fundyense* and salinity near Casco Bay and the adjacent coastal waters during the 1998 and 2000. (A) "Remnant" population of *A. fundyense* in Casco Bay distribution during June 17–19, 1998 following a second downwelling event in the spring of 2000 when few source cells were in the adjacent coastal waters. (B) Salinity distribution during June 17–19, 1998. Note the low-salinity water from a runoff event from the Kennebec River, but the lack of a 31 psu isohaline in the sampling domain, presumably located well offshore. (C) *A. fundyense* distribution during June 12–14, 2000 during the second major downwelling event in the spring of 2000 when the population was high in the upstream coastal waters. (D) Salinity distribution during June 12–14, 2000. Note the presence of both the 31 and 32 isohalines within the domain, unlike panel B. Only *A. fundyense* contours $>100\,\text{cells}\,\text{l}^{-1}$ are filled.

within Casco Bay, the highest abundance of *A. fundyense* cells was $>500\,\text{cells}\,\text{l}^{-1}$ near the outer frontal boundary of the Kennebec plume near the 31 psu isohaline, while only ca. $100\,\text{cells}\,\text{l}^{-1}$ were within the Bay (Fig. 9A). Very few cells were observed within the low-salinity Kennebec plume waters just offshore of Casco Bay that separated the offshore population from the inshore population within the Bay. In the subsequent week (May 11, 2000), that scenario changed dramatically following a strong downwelling-favorable event as the edge of the plume (denoted by the 30–31 psu isohalines) was compressed closer to the coast and the highest cell abundances were observed within the lowest salinity waters of the Kennebec plume (<26) just offshore of Casco Bay (Fig. 9B; see Fig. 4A for winds). Of particular note was the presence of a deep *A. fundyense* population (10–20 m) at salinities of 31–32, directly below the highest cell concentrations within the surface plume.

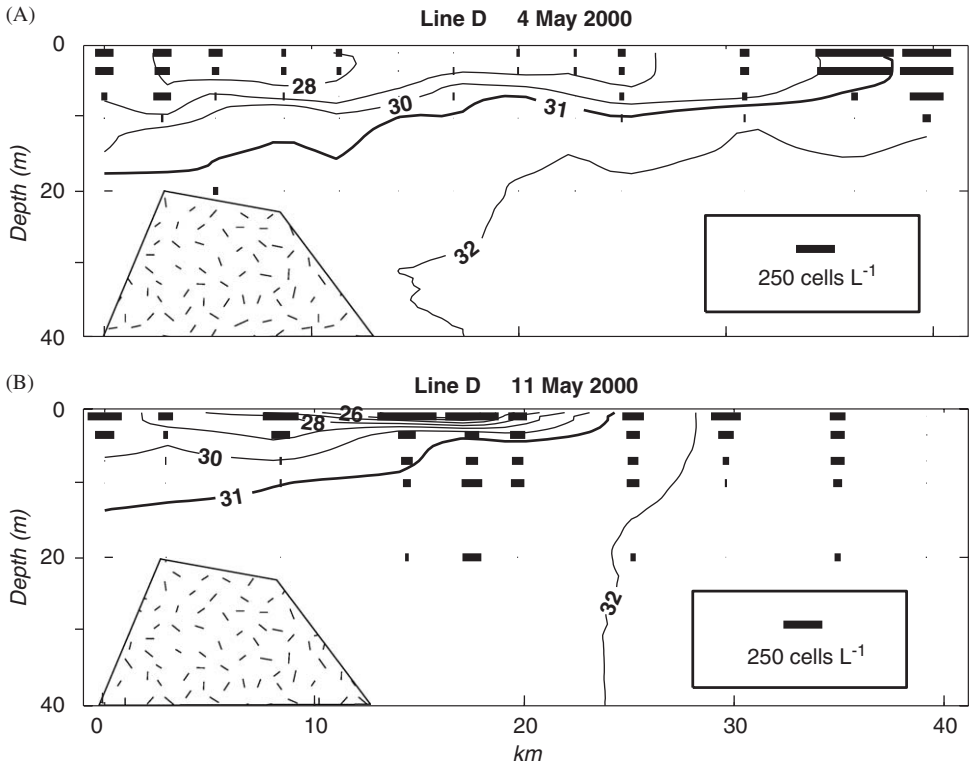

Fig. 9. Cross-shore distribution of *A. fundyense* and salinity from northeast Casco Bay into the adjacent coastal waters. *A. fundyense* abundances are indicated by the length of the horizontal bars that are linearly scaled to the 250 cell l^{-1} bar in the legend. (A) High abundances of *A. fundyense* at the outer edge of the Kennebec plume and within Casco Bay on May 4, 2000 during upwelling-favorable conditions. (B) High abundance of *A. fundyense* within the low-salinity plume waters during the subsequent cruise on May 11, 2000 following downwelling favorable conditions. Note the shoreward and downward shift of the offshore population with the 31 and 32 psu isohaline during downwelling.

Since the deep population underneath the plume might provide cells for the overlying plume through light-seeking swimming behavior, the significance of the deep population was explored by a comparison of the water mass characteristics of that deep population directly below the plume along the D Line (temperature >6.35 and $<7.00\,^{\circ}C$ and salinity >31.4 and <31.7) with those same characteristics along the adjacent, upstream transect, the E Line (Fig. 10). The analysis indicated that the water properties associated with the deep population beneath the Kennebec plume matched the same properties of a near surface population located "upstream" at the outer boundary of the Penobscot plume.

3.3. Drifter trajectories

The tracks of the drifters released during our 2000 field season revealed the manner in which winds influence the transport of near-surface material along the coast of Maine. This is demonstrated here by a sequence of 4-day drifter tracks divided into periods of persistent upwelling- and downwelling-favorable winds (Fig. 11). Early in this period, during a time of downwelling favorable wind, two drifters deployed along the E-line moved rapidly to the southwest (at $>20\,cm\,s^{-1}$) while remaining close to shore and traversing the mouth of Casco Bay (Fig. 11A). Drifters set out 10 days later, after the wind had shifted to an upwelling-favorable direction, also initially moved to the southwest. However, their tracks revealed the wind's influence on the coastal flow in that they exhibited an offshore deflection and a relatively steady deceleration (Fig. 11B). As the upwelling wind persisted, the drifter tracks indicated a reversal of the very near-shore flow to a northeastward direction, and a virtual stalling of the alongshore flow further offshore (Fig. 11C). A return to

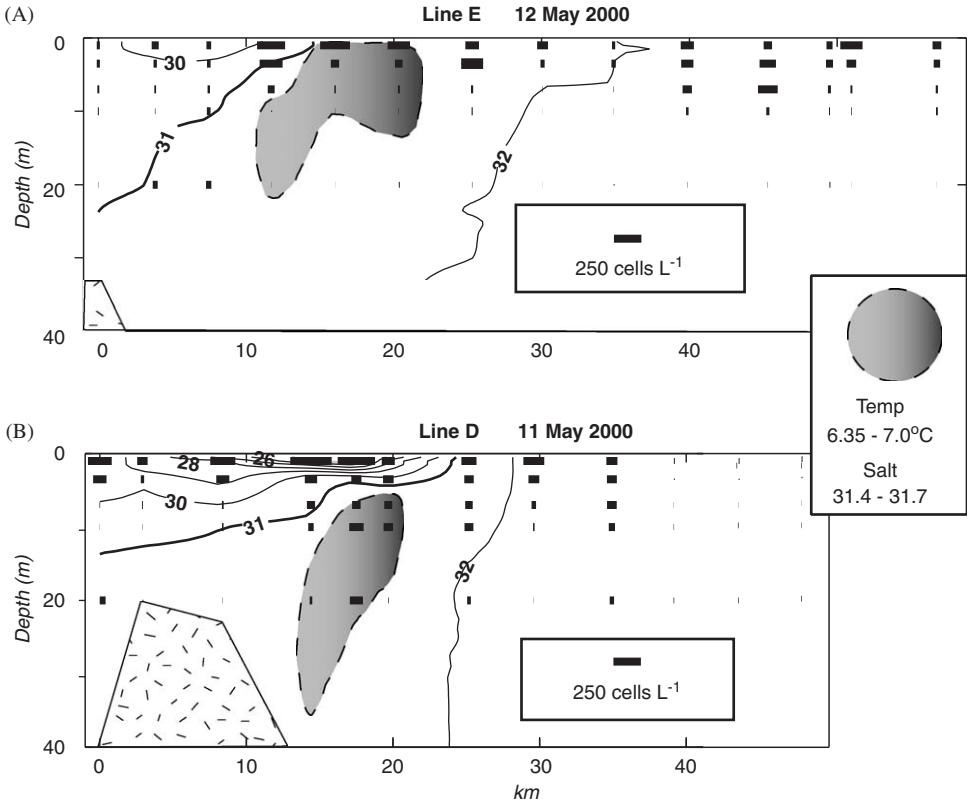

Fig. 10. Subduction of upstream *A. fundyense* populations underneath the Kennebec plume diagnosed using temperature and salinity analysis across two adjacent transects in the coastal flow. *A. fundyense* abundances are indicated by the length of the horizontal bars that are linearly scaled to the 250 cell l^{-1} bar in the legend. Shaded region in panel A indicated an area that contained a near-surface population with identical temperature and salinity properties as the shaded region in panel B that contained a population underneath the Kennebec plume.

downwelling-favorable winds brought about an abrupt reversal of the near-shore flow to a southwestward direction. This flow carried two drifters rapidly (at $>40\,cm\,s^{-1}$) across the Casco Bay mouth (Fig. 11D). One of these drifters subsequently grounded to the west of Casco Bay during a period coincident with a rapid rise in cell abundance and toxicity along the western Maine coastline as indicated by the increase in toxicity at M1 and M2 and the spike in cell abundance along the D Line (Fig. 4C and D). It is noteworthy that the surface current during this period of strong downwelling-favorable wind also carried a drifter, released in the eastern Maine coastal region, rapidly westward across the Penobscot Bay mouth towards Casco Bay (Fig. 11D). This drifter was later carried offshore during a subsequent period of upwelling favorable wind.

The full collection of drifter tracks from 1998 and 2000 revealed a relationship between the wind and near-shore flow that mirrors that described above. In essence, near-shore drifter tracks acquired during times of downwelling-favorable winds tended to move rapidly alongshore to the southwest. Such drifters often approached the coast and occasionally grounded. By contrast, drifter tracks acquired during periods of upwelling-favorable wind tended to exhibit acceleration to the northeast, and often revealed a reversal of the predominant southwestward flow near the Maine coast. These tracks were often deflected offshore. No near-shore drifters grounded during periods of upwelling-favorable winds.

3.4. Sea surface temperature (SST) imagery from satellites

A series of sea surface temperature (SST) images acquired during the rapid increase in shellfish toxicity in mid-May 1998 indicated that cold waters

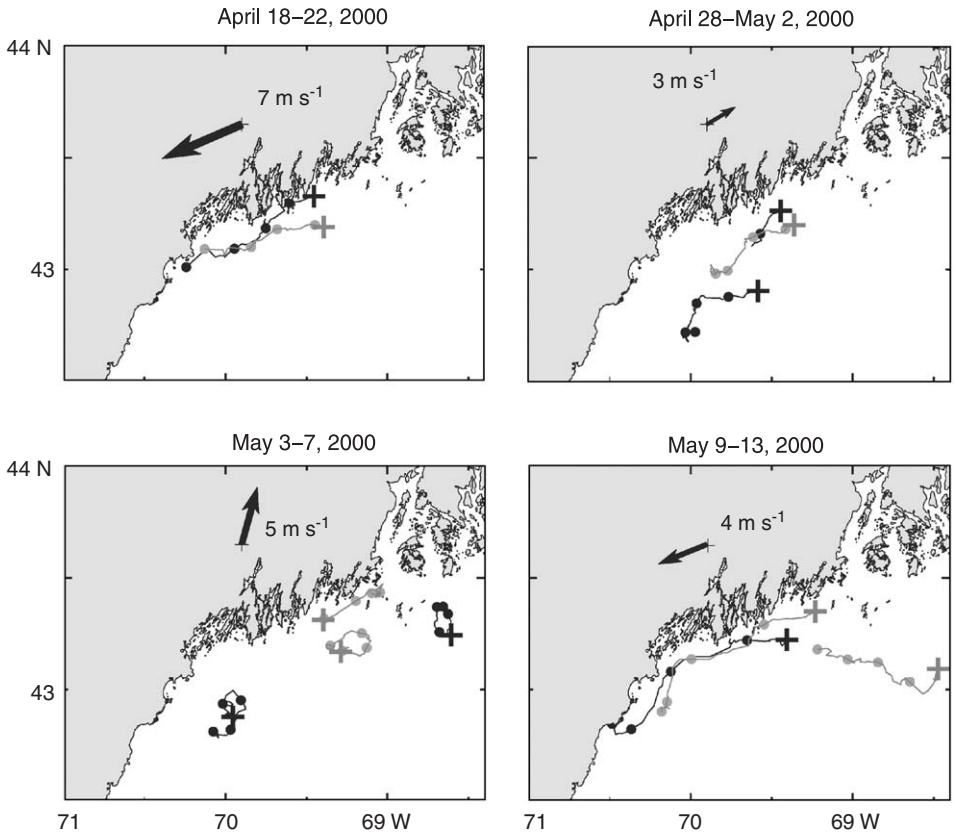

Fig. 11. Trajectories from surface drifters released in the western Maine coastal waters leading up to shellfish toxicity outbreaks in the spring of 2000. In each panel, tracks of drifter for the indicated period are shown, starting with a (+). Also displayed is the mean wind vector for each period computed from the wind record from Matinicus Rock (Fig. 2). The dots on each drifter track mark the drifter position at the start of each day (GMT) of the indicated period. Both black and grey tracks are shown to distinguish the different tracks when they cross paths.

of the WMCC were adjacent to the warm waters of the Penobscot and Kennebec River plumes (Fig. 12). Although cloud-free images are difficult to obtain during downwelling-favorable conditions, an image on May 12 revealed that the river plumes were compressed along the coast and the WMCC was impinging on the mouth of Casco Bay (Fig. 12A). When the winds shifted to upwelling-favorable, an image 3 days later on May 15 indicated that the Kennebec plume was located further offshore, while the cold waters from the WMCC wrapped into the mouth of Casco Bay and around the bulge of the Kennebec plume, suggesting anticyclonic motion that created a break in the alongshore plume structure (Fig. 12B). For comparison with the cell abundances near the time of the imagery, the reader is referred to Fig. 6 where the warm, low-salinity waters of the river plume (<30) observed in Casco Bay contained the highest *A. fundyense* abundances (>200 cells l^{-1}) wrapping into Casco Bay, while populations (100–200 cells l^{-1}) also were observed in the colder, more-saline offshore waters of the WMCC (>30) suggesting a possibility of two transport pathways for cells into the Bay.

4. Discussion

Observations on the *A. fundyense* distributions and associated hydrographic data were collected in Casco Bay and the adjacent coastal waters near the Kennebec River mouth, an area recognized for annually recurrent shellfish toxicity outbreaks during the spring in the western GOM. The distributional patterns of both *A. fundyense* and salinity demonstrate that populations within Casco Bay are not isolated, local blooms that originate within the embayment. Both field years (1998 and 2000) showed that when high populations occur within

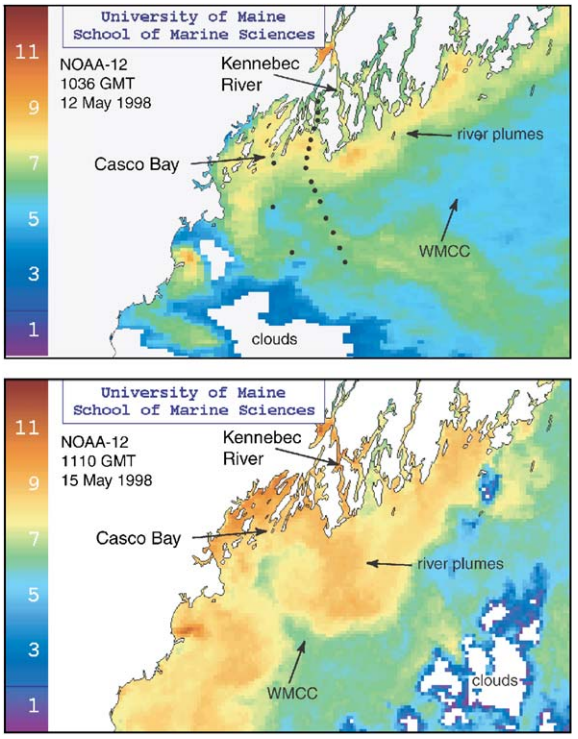

Fig. 12. Sequence of SST imagery (NOAA-12) observed during the outbreak in shellfish toxicity in mid-May, 1998. Generally, the coldest waters (blue) represent upstream waters of the WMCC, while the warm coastal waters (yellow-orange) represent coalesced river plume waters from the Penobscot/Kennebec. (A) SST image on May 12, 1998 during a strong downwelling-favorable period; (B) SST image on May 15, 1998 at the onset of upwelling-favorable conditions. Note the wrapping of cold WMCC water with warm plume water at the entrance to Casco Bay.

Casco Bay, they are likely derived from populations that originated from the adjacent less-saline coastal flow. These populations are likely a western extension of a large-scale population that inhabits the eastern GOM (Anderson, 1997; Townsend et al., 2001; Anderson et al., 2005c; McGillicuddy et al., 2005). Often, the *A. fundyense* populations were most abundant near the outer edge of the Kennebec River plume front, blocked from further entry into the inshore zone. At other times, the highest *A. fundyense* abundances were clearly within Casco Bay, contiguous with the low salinity waters of the river plumes and suggestive of an entrainment mechanism. The observations show important similarities as well as differences between cruises and between the study years (e.g., the lack of cells in the mid-June 1998 vs. mid-June 2000 surveys) that help to unravel the complexity of the dynamics such as the influence of downwelling- and upwelling-favorable winds coupled with the large scale circulation. The relationships of the populations within Casco Bay to the meteorological and hydrographic conditions and ultimately to the timing of shellfish toxicity outbreaks in the Casco Bay region are emerging for the first time.

4.1. Casco Bay *A. fundyense* populations: local growth vs. advection

The Casco Bay/Kennebec River region has been suggested as a source region for *A. fundyense* bloom development in the western GOM, because populations are often observed within the low-salinity waters of the western GOM and the Kennebec River is one of the major sources of that freshwater (Franks and Anderson, 1992a; Anderson et al., 2005c; Geyer et al., 2004). Observations from the 1998 and 2000 surveys consistently showed that high *A. fundyense* populations occurred both within Casco Bay and in the adjacent coastal waters. At times, it appeared that the two populations were isolated from one another, suggesting that in situ or local growth might be responsible for the populations and shellfish toxicity within Casco Bay (Figs. 5C and 7A). However, at other times the populations within Casco Bay were clearly contiguous with the coastal populations, indicating that advection from the adjacent coastal waters is an important factor in bloom development (Figs. 6 and 7C). These processes (growth vs. advection) are difficult to separate in a field study, especially when species-specific growth rates are not obtainable. However, a close examination of the spatial and temporal similarities and differences between the surveys and the years provide evidence for only one major source population responsible for outbreaks of high levels of toxicity within Casco Bay—that derived from cells that originate outside the Bay and are advected in.

High cell populations observed within Casco Bay could result from local germination of benthic cysts and subsequent local growth, giving rise to high shellfish toxicities. However, concentrations of *A. fundyense* cysts were generally 5–10 × lower than in the adjacent offshore basin (Anderson et al., 2005b). Furthermore, model simulations indicate that the contribution to the overlying plankton from germination in the inshore areas was relatively weak compared to the offshore areas (Stock et al., 2005). To account for the high abundances observed within the Bay (e.g., $>500\,\text{cells}\,l^{-1}$), either the local

Bay population must grow very rapidly or coastal populations (i.e. those originating outside of Casco Bay in the nearshore or offshore waters) must be advected alongshore and cross-shore where they can accumulate within Casco Bay. Given a typical *A. fundyense* growth rate at the expected temperatures of 8–10 °C in mid-May ($0.3\,day^{-1}$), the population might double in less than 1 week. However, the observations show a rapid rise in both toxicity (from barely detectable to $>300\,\mu g\,100\,g^{-1}$) and mean cell abundance ($4\times$) following general downwelling-favorable conditions in mid-May of both years in about a week (e.g., Fig. 4). In fact, the cell abundance along the upstream E-line actually decreased slightly when the abundance along the D-line increased rapidly suggesting a westward transport of the upstream population along the coast and into the Bay. Furthermore, low abundances of *A. fundyense* observed within Casco Bay early in the bloom season (e.g., Fig. 5) did not reach high abundances and cause significant shellfish toxicity within the Bay until those populations were contiguous within the adjacent coastal waters (e.g., Figs. 6A, C and 7C). While the Bay's population is undoubtedly increasing as the bloom season progresses, the observations do not generally support the local growth hypothesis within Casco Bay since the appearance of high cell densities and high shellfish toxicity are closely linked with downwelling-favorable conditions.

The generally low surface-nutrient concentrations observed within the Casco Bay region also do not support the notion of rapid local growth. Nutrients were low when *A. fundyense* abundance was high, suggesting that the cells were nutrient-limited and likely out-competed by the prior occurrence of diatom blooms (Love et al., 2005). Love et al. report one case when a runoff event in June, 1998 (see Fig. 8B) was responsible for an infusion of new nutrients into Casco Bay. That event was coincident with the general decline in the *A. fundyense* abundance and toxicity in the Bay, not an increase (Figs. 3A and 8A), suggesting that local nutrient inputs did not control the blooms conditions near Casco Bay. Further evidence of nutrient limitation is provided by the toxin characteristics of *A. fundyense* populations that are sensitive to changes in their relative toxin derivatives with nitrogen limitation (Poulton et al., 2005). Local predation may be a factor as well since toxins were accumulated in zooplankton (Turner et al., 2005; Doucette et al., 2005; Campbell et al., 2005), indicating net growth was not high within Casco Bay at that time. The more likely explanation is that local bloom control is related to advection of populations from the nutrient-rich areas further upstream in the MCC system. This supposition is consistent with moderate nutrients levels observed along the E-Line in early in 2000 (Love et al., 2005). Low nutrients in the western GOM in 1998 relative to 2000 may even have contributed to the relatively low *A. fundyense* abundances in the western GOM that year. Thus, the observation of a rapid rise in the populations in Casco Bay is inconsistent with the lack of high surface nutrient concentrations to fuel that local growth, unless the species can survive these conditions using abundant dissolved organic nitrogen such as urea (Dyhrman and Anderson, 2003; Love et al., 2005). The lack of nutrients in the western GOM may explain the low cell abundances typically observed in the western GOM compared to other nutrient-rich regions (e.g., the Bay of Fundy) in the eastern GOM as suggested by Anderson et al. (2005c), Love et al. (2005), and McGillicuddy et al. (2005).

Our observations also do not support the view of transport of motile cells or benthic cysts directly out of the Kennebec River into the adjacent coastal waters and Casco Bay. Although *A. fundyense* cells were often present at the station nearest the river mouth, the abundances were generally low relative to surrounding stations located both offshore and within the Bay (Fig. 5A), in agreement with the observations of Anderson et al. (2005c). Furthermore, Kennebec runoff near the northeast entrance to Casco Bay often contained very few cells and tended to separate the inshore populations within Casco Bay from the populations further offshore (Figs. 7A and 9A). These observations are consistent with previous studies that searched, but did not find, *A. fundyense* cells or benthic cysts within the Kennebec River itself (Anderson and Keafer, 1992; Keller and Phinney, 2001). Therefore, the Kennebec River is not a likely source of *A. fundyense* cells to the adjacent coastal waters or to Casco Bay.

A strong case can be made for advection of populations into Casco Bay from the adjacent coastal waters. During development of the bloom in both years, *A. fundyense* cells were always present within near-surface coastal waters outside of Casco Bay. Furthermore, when shellfish toxicity was rising rapidly, it was detected at the offshore mussel bag sites either prior to or concurrently with the inshore sites, particularly in 1998 (Figs. 3 and 4). This was

consistent with the observation that *A. fundyense* populations were often higher in the adjacent coastal waters compared to Casco Bay (Fig. 5C). When concentrations were higher within the Bay than the coastal waters, evidence of a spatially continuous population was apparent between the inshore and adjacent coastal waters (Fig. 5A). That connection was most notable during mid-May of both study years (Figs. 6 and 7C), when *A. fundyense* populations within Casco Bay were high and clearly contiguous with *A. fundyense* populations located in the alongshore coastal flow during the rapid rise in toxicity within the Bay. In particular, the highest populations outside the Bay during that time were located in the low-salinity waters of the adjacent river plumes (<31 psu isohaline) supporting the original observations of the plume advection hypothesis (Franks and Anderson, 1992a). At other times, the cells were located along the plume front (>31 isohaline), in agreement with the recent amendment to the plume advection hypothesis that accounts for incoming populations from the upstream waters of the WMCC (Anderson et al., 2005c).

The striking difference between the *A. fundyense* abundances in June 1998 and 2000 provide strong supporting evidence for the necessity of an upstream source population for bloom development in the western GOM, and in Casco Bay in particular. In mid-June, 1998, the abundance of *A. fundyense* was extremely low in the adjacent coastal waters off Casco Bay, with relatively low populations also observed within the Bay (20–50 cells l^{-1}), insufficient to sustain the earlier toxicity (Fig. 8A). In stark contrast, when the abundance of *A. fundyense* in the adjacent coastal waters was high in June 2000, shellfish toxicity extended along the western Maine coast, although it did not penetrate into Casco Bay. Concurrent large-scale surveys during both years documented abundant *A. fundyense* populations (>500 cells l^{-1}) associated with the EMCC (Townsend et al., 2001, 2005). In June 1998, the population in the EMCC veered offshore to the interior GOM. In June 2000, the western extension of the EMCC population generally coincided with our observations of high abundance along the outer boundary of the Penobscot and Kennebec plumes in the small-scale region. Thus, in 1 year when the upstream population veered offshore and was cut off from the western GOM during the late season (1998), cell abundance was low and little or no toxicity occurred in Casco Bay, while in the other year (2000) when the upstream source extended into the western GOM, cell abundance was high and shellfish toxicity persisted in the western GOM region. Furthermore, when the small-scale study domain was expanded in 2001 to include waters further upstream in the coastal flow, these same patterns held true for *A. fundyense* and the co-occuring species *A. ostenfeldii*; an upstream population was apparent and linked to bloom development within Casco Bay (Keafer et al., 2005; Gribble et al., 2005). Keafer et al. (2005) suggested that those incoming populations were associated with a low-salinity nearshore feature that extended along the entire Maine coastline, termed the GOM Coastal Plume. Clearly, the 1998 and 2000 differences coupled with the observations from upstream in the subsequent year illustrate that populations in the coastal currents are a necessary component for bloom development and associated shellfish toxicity within the embayments of the western GOM, including Casco Bay.

Variability in the strength of the baroclinic coastal current related to both Gulf-scale processes and local wind forcing can contribute to the differences observed between years. The 31 psu isohaline present within the small-scale domain earlier in the 1998 season was not apparent in June, unlike year 2000 when both the 31 and 32 isohalines were within the domain throughout the entire sampling period. The larger-scale interactions of the EMCC with the WMCC were responsible for directing incoming populations further offshore in June 1998 vs. alongshore in June 2000 as suggested by Churchill et al. (2005) and Pettigrew et al. (2005). Indeed, high *A. fundyense* populations veered offshore with the EMCC in June 1998 but traveled alongshore in June 2000 as noted above.

4.2. The effects of the wind and its relationship to cell abundance and toxicity in the region

The effects of wind-forcing on the behavior of the western Maine river plumes and the WMCC and its relationship to shellfish toxicity is particularly noteworthy in the small-scale data set. During both years, the strong connection between the Casco Bay population and the coastal populations outside the Bay in mid-May was evidenced by a rise in cell abundance and shellfish toxicity following periods of downwelling-favorable winds (Figs. 3 and 4). This strongly suggests that populations in the upstream coastal waters were driven alongshore

and onshore in response to the wind. This view is supported by the moored near-surface current data at M1 (Figs. 3B and 4B), the drifter trajectories that tracked very close to the mouth of Casco during downwelling-favorable conditions (Fig. 11A and D), and satellite imagery (Fig. 12A) that showed warm, river plume waters compressed very tightly against the coast with cold water from the WMCC located near the mouth of Casco Bay. These observations are also in close agreement with results from an earlier 2-year study along the western GOM coastline where outbreaks of shellfish toxicity generally followed downwelling-favorable periods and similar hydrographic characteristics (Anderson et al., 2005c). They are also consistent with the "inside track" hypothesis that transported upstream populations located in the GOM Coastal Plume, across the mouth of Penobscot Bay and into the western GOM following a downwelling-favorable period (Keafer et al., 2005). However, there are exceptions, since a second strong downwelling-favorable event during mid-June 1998 did not result in high cell abundances and toxicity within the western GOM or Casco Bay. This was due to the presence of few cells in the adjacent coastal waters.

The explanation for the lack of cells in the western GOM study area at that time appears to be related not only to the large-scale circulation but to the local wind history as well. In contrast to the downwelling-favorable periods, the abundance of *A. fundyense* and toxicity in June, 1998 declined during 3 weeks of persistent upwelling-favorable winds (Fig. 3). The initial decline was likely due to the offshore deflection of the coastal population located within the low-salinity waters of the western river plumes. During that time, the local surface currents slowed, reversed and were generally directed offshore, consistent with the general tendency of surface drifters to follow a path offshore of Casco Bay (Fig. 11B and C). These characteristics are in agreement with the general concepts of the plume-advection hypothesis (Franks and Anderson, 1992a, b) and Ekman dynamics of a buoyant plume (Fong et al., 1997), and are apparent in the *A. fundyense* distributions. The offshore deflection of the highest *A. fundyense* abundances within the 29–30 psu isohalines during the start of upwelling-favorable conditions (Fig. 6) and the offshore trajectory of the incoming population along the plume front were two examples (Fig. 7A).

Spreading of the Penobscot and the Kennebec River plumes offshore during persistent upwelling may actually limit the intrusion of upstream populations into the western GOM (Keafer et al., 2005). These observations are again consistent with those reported by Anderson et al. (2005c) which documented a delay in the onset and reduced intensity of shellfish toxicity associated with persistent upwelling-favorable conditions early in the bloom season of 1994 (relative to 1993). The hindcast modeling results from those years also indicates that differences in the winds were responsible for variability in the behavior of the WMCC, where an upwelling wind stress of $0.5 \times 10^{-4}\,m^2\,s^{-2}$ is sufficient to block downcoast transport of freshwater (Hetland and Signell, 2005). In modeling experiments of the MCC, Lynch et al. (1997) note an increase in shoreward transport near Casco Bay when the May/June climatological wind stress (to the northeast and upwelling-favorable) is turned off. Thus, the variability in the *A. fundyense* abundances and shellfish toxicity in the western GOM including Casco Bay are partially related to the large-scale circulation, but superimposed on that circulation are wind events that can either enhance the alongshore delivery of populations into the western GOM (and into Casco Bay) or enhance their deflection offshore; both off of Casco Bay and the Kennebec plume as observed here and in the adjacent upstream waters off Penobscot Bay and eastern Maine (Keafer et al., 2005).

Once populations are advected into Casco Bay they can be retained and persist for extended intervals. Although the residence time of water in Casco Bay has never been estimated, evidence for *A. fundyense* retention is based on hydrography, moored observations, and drifter releases near the Bay mouth (Janzen et al., 2005). These authors demonstrate that onshore winds (to the NW) would tend to retain cells within the Bay, while offshore winds (to the SE) would clear the population out of the Bay. This is consistent with the trajectories of surface drifter released near M2 that were transported into the upper reaches of the Bay during onshore winds (Janzen et al., 2005). Furthermore, freshwater runoff from the Kennebec may also play a role in cell retention. Of the drifters released near M2, those shoreward of the freshwater lens of the Kennebec remained with the Bay (Janzen et al., 2005). This suggests that once populations are advected into the Bay from the adjacent coastal waters (e.g., following downwelling), they can be retained by onshore winds and subsequent new runoff from the adjacent Kennebec River, leaving

the population bisected as in Fig. 7A. Thus, the unique location of the Casco Bay embayment, just downstream of the Kennebec plume, tends to capture and retain coastal populations as they are advected down the coast. The populations observed within the Bay are likely "remnants" from earlier intrusions, as suggested by Anderson et al. (2005c), not from rapid local or in situ growth.

4.3. Possible mechanisms of cell entrainment into the western river plumes

Observations near the Kennebec plume often show continuous surface populations across strong salinity gradients (e.g., Fig. 7C and D), but the mechanism(s) by which the upstream high-salinity populations enter the western river plumes remain elusive. Cells within the upstream coastal flow must cross that frontal barrier in some manner by either going under it, around it, or perhaps even through it if breaks exist in the plume structure. Perhaps all of these pathways are possible in the complex circulation patterns near the river plumes. T, S analysis suggests that upstream surface populations can be subducted underneath the Kennebec plume during transport to the west, supplying cells to the plume from below presumably via light-seeking swimming behavior (Fig. 10). Alternatively, using similar analysis, populations that reside slightly deeper (e.g., <10 m) in a weakly stratified current can be transported along density surfaces underneath the western river plumes without invoking subduction, but swimming behavior is also necessary to get the cells into the surface plume (Keafer et al., 2005). In addition, the distributions of *A. fundyense* also suggest that populations may circulate around the Kennebec plume front and penetrate directly into Casco Bay as a result of the presence of low-density plume water that creates a dome of high pressure and imparts a clockwise steerage effect as illustrated in the SST imagery (Fig. 12B). The steerage effect by river plumes in the GOM has been previously recognized in modeling studies (Lynch et al., 1997). Based on the observations of *A. fundyense* populations and hydrography near the river plumes, Anderson et al. (2005c) suggested that populations at the outside edges of the plume are carried onshore near the distal boundary of those plumes where the cross-shore gradient in salinity is weak, i.e., downstream of the leading edge of the plume. The relatively high *A. fundyense* and *A. ostenfeldii* populations often observed between the Penobscot and Kennebec plumes supports that view (Keafer et al., 2005; Gribble et al., 2005).

Several alternative hypotheses based on results from modeled experiments indicate that offshore *A. fundyense* populations predominantly enter the plume during upwelling-favorable conditions and are subsequently delivered to the coast during downwelling. Hetland et al. (2002) advanced the "frog tongue" hypothesis where the swimming velocity of cells located at the outer edge of the plume is critically important for entrainment into the plume as it spreads offshore during upwelling, and retracts during relaxation (i.e. inoculation of the plume at the tip of the tongue when the tongue is out and shoreward advection when it retracts). Similarly, McGillicuddy et al. (2003) invoked the presence of a reservoir of offshore benthic cysts (see also Anderson et al., 2005c; Stock et al., 2005) that inoculate the plume with newly germinated, upward-swimming cells as the plume was spread offshore over the cyst beds by upwelling (i.e. inoculation from the underside of the tongue). However, the modeled results do not fit the field observations here since the rise in toxicity and cell abundance within the plume usually followed downwelling events as the incoming population was transported alongshore and onshore converging with the river plume. What is certain is that there are likely multiple mechanisms that result in the cells becoming entrained within the river plumes and those have yet to be resolved. The dynamics are complex, and therefore synoptic measurements coupled with modeling efforts are needed to distinguish those dynamics on varying temporal and spatial scales.

5. Summary

Observations from small-scale weekly field surveys near Casco Bay and the Kennebec River mouth support a scenario of alongshore and onshore delivery of *A. fundyense* populations from a source located upstream from the Kennebec River plume. The data do not support the view that Casco Bay is a significant source for *A. fundyense* cells that populate the western GOM. Rather, Casco Bay is one destination for the populations that inhabit the nearshore and offshore waters of the western GOM as part of a complex coastal current system that interacts with the western river plumes. The wind plays a critical role that affects the behavior of the Kennebec plume and the pathway of the incoming

coastal populations. Downwelling-favorable conditions facilitated bloom formation via alongshore and onshore transport of cells. In contrast, persistent upwelling-favorable conditions generally limited intrusion of coastal populations into the Bay. A variety of mechanisms (e.g., circulation underneath or around the Kennebec plume front) promote cell transfer across or around the plume barrier and into Casco Bay. These dynamics are complex due to the variability of the wind, river inputs, and coastal current structure. Nonetheless, general patterns in the distribution of the *A. fundyense* population and the associated hydrography clearly demonstrate a linkage between the Casco Bay region and the upstream coastal populations, and that linkage was strong and persistent in 2000 but not in 1998. Synoptic observations and physical-biological models on temporal and spatial scales that match the fluctuations in the wind and the freshwater inputs from the rivers are now needed to resolve this complexity near the Maine coast where the upstream source populations meet the river inputs in the western GOM. As part of a follow-up MERHAB (Monitoring and Event Response of Harmful Algal Blooms) study, efforts are currently ongoing to refine bio-physical transport models for forecasting HAB events along this region of the coast. These products will require near real time data assimilation of winds, currents, and *A. fundyense* abundances. Given the mechanisms for bloom formation presented here and elsewhere in this volume, short term forecasts, i.e., <1 week time scales related to meteorological and hydrographic conditions, are possible for the Casco Bay region, but only if sensors for the in situ detection of *A. fundyense* become readily available for deployment in the adjacent upstream coastal waters. With that knowledge, the ultimate goal of accurately predicting outbreaks of shellfish toxicity along the entire western Maine coastline may become a reality.

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