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Relationships between satellite-measured thermal features and *Alexandrium*-imposed toxicity in the Gulf of Maine

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Abstract

Relationships between satellite-derived sea-surface temperature (SST) patterns and the occurrence of paralytic shellfish poisoning (PSP) toxicity events caused by *Alexandrium fundyense* in the western Gulf of Maine are examined. Comparisons between surface *A. fundyense* cell distribution patterns and SST images indicate that highest cell concentrations are associated with colder waters of the eastern segment of the Gulf of Maine coastal current (EMCC) and that frontal zones at the edges of the EMCC often act as boundaries to surface distributions. Surface thermal patterns coincident with a May 2000 PSP toxic event and shellfish harvesting closure on the western Maine coast show enhanced connectivity between the EMCC and the western Gulf of Maine, suggesting transport linking *A. fundyense* cells in the EMCC to inshore areas of the western Gulf of Maine. Surface drifter data support such transport. Thirteen years (1990–2002) of toxicity data from eight monitoring sites along the coast of Maine and concurrent SST data show that in years of either large or very reduced toxicity, a consistent relationship exists between the timing and strength of fronts, taken as an indicator of alongshore connectivity, and the occurrence and strength of toxic events. Years with weak fronts and/or fronts that become established relatively late in the summer growing season are years of the strongest toxicity events in western Gulf of Maine. Years of early and strong fronts are years with few and/or weak toxicity events. Our results suggest that advective connections exist between cells present in the EMCC and toxicity along the western Gulf of Maine coast and that large-scale hydrographic processes, characterized here as surface thermal patterns, influence *A. fundyense* populations in the western Gulf of Maine, either through delivery of actual cells or advection of advantageous conditions into the region. These data point to the utility of satellite and other coastal observing system data for the monitoring and prediction of conditions linked to toxic events in coastal waters.
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Keywords: Harmful algal blooms; Gulf of Maine; Satellite data; Sea-surface temperature; Frontal zones; PSP

1. Introduction

The saxitoxin associated with the dinoflagellate *Alexandrium fundyense*[2] causes paralytic shellfish

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[2]At least two saxitoxin-producing species of *Alexandrium* occur in the Gulf of Maine, *A. fundyense* and *A. tamarense*, separable

poisoning (PSP) in the Gulf of Maine (Fig. 1), with direct health and therefore economic implications (Blaxter and Southward, 1997). The toxin can be fatal to humans in doses as small as $500 \, \mu g / 100 \, g$ ingested tissue (Hallegraeff, 1995). Shellfish toxicity events in the Gulf of Maine have been recorded annually since 1972. To ensure public safety, the Maine Department of Marine Resources (DMR) monitors toxin levels in shellfish at an extensive series of coastal sites using a mouse bioassay. If toxin levels approach or exceed $80 \, \mu g \, toxin / 100 \, g$ tissue, shellfish beds in the local vicinity are closed to further harvesting. Economic losses resulting from shellfish closures are difficult to quantify over the entire Gulf of Maine; however, the cost of closures in 1994 in Casco Bay alone was estimated at \$1.6–\$1.7 million (Maine Environmental Properties Project (MEPP), 1996).

In 1997, a multi-institution, multi-investigator program to study the oceanographic ecology of *A. fundyense* in the region was initiated (ECOHAB, Gulf of Maine). Here, we use results from this program and the historical record of toxicity events along the Maine coast to examine the relationship between satellite-measured sea-surface temperature (SST) patterns, *A. fundyense* distribution, and the occurrence of toxicity events in the western Gulf of Maine.

Previous work using data from broad-scale ECOHAB ship surveys in 1998 and 2000 established that large *A. fundyense* cell densities can occur in offshore waters in the Gulf of Maine during summer months (Townsend et al., 2001), spatially continuous with elevated concentrations in the Bay of Fundy reported by Martin and White (1988). Townsend et al. (2001) note that the locations of highest cell concentrations (ca. $5.5 \times 10^3 \, cells \, l^{-1}$) are coincident with the cold, nutrient-rich eastern segment of the Gulf of Maine coastal current (EMCC) (Pettigrew et al., 2005), possibly due to increased light penetration and elevated nutrient concentrations in surface waters. These cells are hypothesized to originate from a seed population in the Bay of Fundy, with highest cell densities found in the southeastern part of the Bay near the coast of Nova Scotia (Martin and White, 1988). White and Lewis (1982) also found the highest concentration

of *A. fundyense* cysts in the winter in offshore waters north and east of Grand Manan Island. High vegetative cell concentrations in the Bay of Fundy suggest that these cysts could be a major source for summer bloom initiation (Martin and White, 1988).

In the eastern Gulf of Maine, the westward-flowing EMCC (Fig. 1) is considered the dominant hydrographic feature (Brooks and Townsend, 1989). Extensive tidal mixing keeps surface waters relatively cold and nutrient-rich throughout the year. In the vicinity of Penobscot Bay, the EMCC turns cyclonically offshore. At this point, portions of the EMCC contribute either to the cyclonic gyre over Jordan Basin or feed into the western segment of the Gulf of Maine coastal current (WMCC) continuing down the coast (Fig. 1). The amount of EMCC water that contributes to either branch is seasonally dependant and is related to vertical density structure over Jordan Basin (Brooks and Townsend, 1989). As summer approaches, more water contributes to the gyre over Jordan Basin than continues into the WMCC. At this divergence point of the EMCC from the coast (the Penobscot Bay region), Shumway et al. (1988) identified a toxin-free portion of the coast with sites both east and west of this region exhibiting reoccurring toxicity events.

Warming and the increase in stratification over both offshore and western Gulf of Maine waters in spring/summer makes the (at least surface) offshore deflection of the relatively cold EMCC easily visible in satellite infrared images. At this time, two surface frontal zones become prominent. In the vicinity of Penobscot Bay where offshore-flowing cold EMCC surface waters lie adjacent to the warmer, more stratified waters of the western Gulf of Maine, a strong surface thermal gradient and frontal zone oriented in the cross-shore direction results (Xue et al., 2000). Additionally, upstream of this position within the eastern Gulf of Maine, an alongshore-oriented surface thermal front forms along the offshore margin of the EMCC, where it lies next to more stratified Jordan Basin waters (Fig. 2B).

Anderson (1997) hypothesized that the cyclonic offshore branching of the EMCC in the vicinity of Penobscot Bay makes it unlikely that cells present in the western Gulf of Maine result from transport from an eastern Gulf of Maine source. This scenario necessitates an independent population of *A. fundyense* in the western Gulf of Maine having its own source and transport pathways (Anderson, 1997). Townsend et al. (2001), however, suggest that

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(*footnote continued*)
morphologically with an electron microscope. As this was not practical for large numbers of field samples, for this study we use the name *A. fundyense* to refer to all forms.
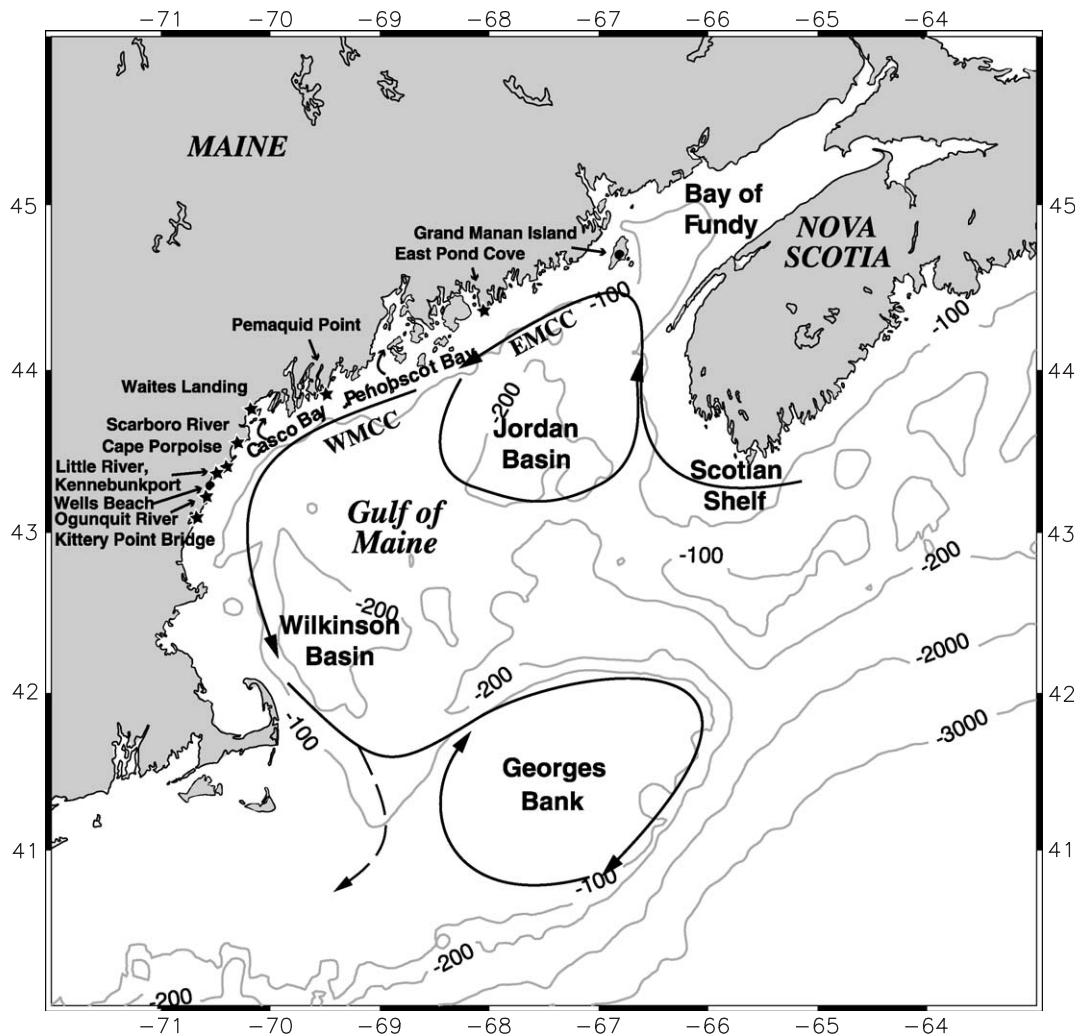
Fig. 1. The Gulf of Maine study area showing major bathymetric contours, geographic features, the location of eight shellfish toxicity monitoring stations (stars), and other locations mentioned in the text (dots). Arrows show the general residual circulation of the Gulf of Maine including the WMCC, the EMCC and its divergent path off Penobscot Bay, which contributes to the cyclonic circulation around Jordan Basin.

A. fundyense in the EMCC can be transported into the western Gulf of Maine, meaning that a single *A. fundyense* population, possibly originating in the Bay of Fundy, could influence the entire study region. The degree of connection between eastern and western Gulf of Maine appears highly variable (Pettigrew et al., 1998) making generalizations about connections between observed high offshore cell densities and toxicity within inshore shellfish beds difficult based on sparse or episodic data.

Here, we first use coincident ship and satellite SST data to show the relationship between cell surface spatial patterns and surface thermal features

linked to circulation in the Gulf of Maine. Using satellite and surface drifter data, we then document a direct connection between surface EMCC water and the western Gulf of Maine coast that was coincident with a toxic event and shellfish harvesting closure. We then use a 13-year timeseries of toxicity measurements from Maine coastal sites and coincident satellite SST imagery to examine the relationship between toxicity events along the western Gulf of Maine coast and the apparent connectivity between the EMCC and the western Gulf of Maine. We hypothesize that interannual differences in the occurrence and magnitude of
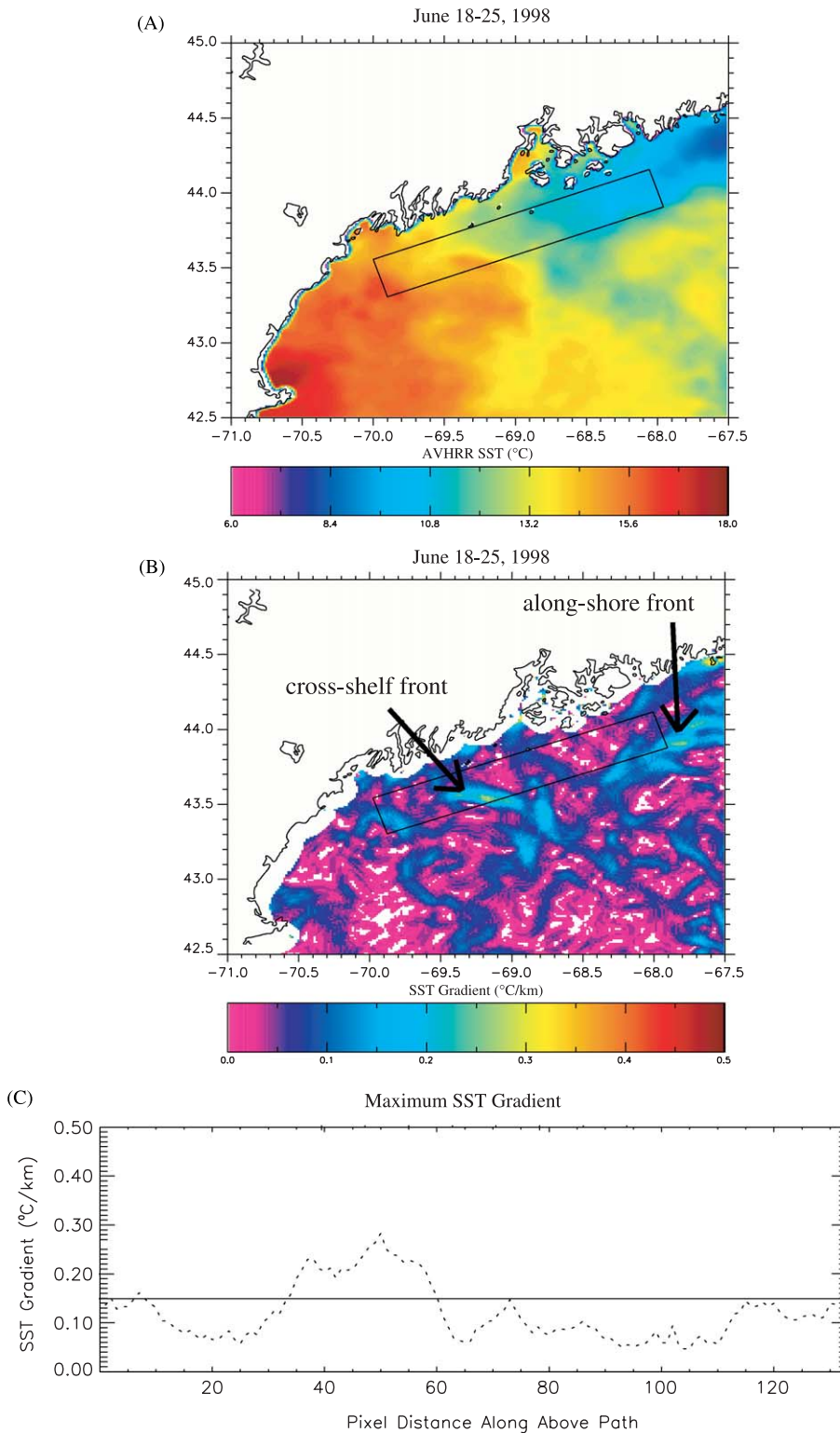
Fig. 2. An example 8-day composite SST image (A) and the SST gradient magnitudes calculated from this image (B), both showing the location of the box from which maximum SST gradients are extracted. These are shown in (C). Evident in (A) is the cold EMCC water and the frontal zone formed where these waters diverge south of Penobscot Bay. Major frontal zones are labeled with arrows in (B). The dashed line in (C) shows the 0.15 °C/km threshold used to define intensified frontal strength.

toxicity events along the coast of western Gulf of Maine are associated with interannual variability in the strength and timing of the seasonally modulated EMCC contribution to the WMCC.

2. Data and methods

Toxicity, determined by mouse bioassay, is measured at up to 300 possible stations along the coast of Maine each year by the Maine DMR. If the toxin level at a station is at, or approaching, $80\,\mu g/100\,g$ tissue, the DMR closes the area to the harvesting of that species of shellfish. Toxicity is measured in a varying range of shellfish species at each site. Here, we use toxicity from *Mytilus edulis* (blue mussel) from the years 1990–2002 as this species was extensively and most consistently sampled by Maine DMR in both time and space and because *M. edulis* is widely regarded in environmental and toxicity literature as an excellent indicator species.

Eight stations (Fig. 1) were subjectively chosen from the 300 available sites based on the frequency/consistency of *M. edulis* sampling, the temporal continuity of sampling at that station over the 13-year period and to their local geographic location with respect to general Gulf of Maine circulation. Five stations (Pemaquid Point, Cape Porpoise, Little River Kennebunkport, Ogunquit River, and East Pond Cove) are located in areas well exposed to the general circulation of the Gulf of Maine. Within these five stations, East Pond Cove is located "upstream" of the region where the EMCC diverges from the coast. This station remains influenced by cold EMCC water throughout the season. Pemaquid Point is at the mouth of Penobscot Bay, an area known for its lack of toxicity events (Shumway et al., 1988) and the other three stations are in the western Gulf of Maine. The remaining three stations (Waites Landing, Scarboro River and Kittery Point Bridge), also located in the western Gulf of Maine, are located inside rivers and in bays where they are less directly influenced by Gulf of Maine circulation. Toxicity levels at these stations may be less related to Gulf circulation and the connectivity between EMCC and the WMCC than the other five stations and more likely driven by local processes. Timeseries of toxicity were created for each of the eight stations for each study year using the approximately weekly sampling available over the spring, summer, and fall in each year.

Thirteen years (1990–2002) of Advanced Very High Resolution Radiometer (AVHRR) SST satellite images were remapped to a standard grid covering the study area. The 4–5 images available per day were composited into sequential 8-day periods (Fig. 2A) beginning January 1 in each year to reduce the data volume and partially fill gaps in time/space created by clouds. The satellite data are from two sources with different processing protocols. Data from 1990 to 1997 are from the Graduate School of Oceanography at the University of Rhode Island, processed to SST using the Pathfinder protocol (Ullman and Cornillon, 1999) and the cloud-masking approach of Cayula and Cornillon (1996). Data from 1998 to 2002 were processed to SST from the direct satellite telemetry stream in real time at the University of Maine using standard NOAA coefficients and a modified Cayula and Cornillon (1996) cloud-masking scheme. Correlations (not shown) between SST from the two series in the period of overlap (1997–1998) were >0.9 with slopes not significantly different from 1. As SST data are used in this study to compare relative thermal pattern rather than absolute SST, the slight differences in processing should have minimal effect on our results.

SST gradient magnitudes (Fig. 2B) were extracted from the 8-day composite image sequence using a two-dimensional gradient operator with a distance metric of seven-pixels (~ 8 km). The formula used, adopted from Van Woert (1982), is

$$T(x,y) = 1/(2\Delta h)\big\{[T(x-\Delta h, y) - T(x+\Delta h, y)]^2$$
$$+ [T(x, y-\Delta h) - T(x, y+\Delta h)]^2\big\}^{1/2}, \quad (1)$$

where T is the SST, x and y represent the pixel location, and Δh is the number of pixels in either direction to use for calculating the gradient (set to three here, resulting in the seven pixel distance metric mentioned above). The equation computes an unweighted central difference, or a two-dimensional gradient, (units $= {}^{\circ}C/km$) that highlights areas of extreme thermal change, such as the frontal systems that form along the edges of the EMCC (Fig. 2B). Brooks and Townsend (1989) showed that the offshore-turning point of the EMCC can move tens of kilometers over a few weeks. To capture this variability, a box (Fig. 2A and B) was defined that extends from eastern to western Gulf of Maine, covering the area where the EMCC is observed to turn offshore (Fig. 1) resulting in strong frontal zones. SST gradients were extracted from this box

and the maximum gradient observed across the width of the box at each along-shore location (from west to east) was isolated, resulting in a single alongshore-oriented transect quantifying maximum observed gradients for each time period. These maximum SST gradients are plotted as a function of location along the transect (west to east) to illustrate the location and strength of the cross-shelf front separating cold EMCC from western Gulf of Maine water (Fig. 2C). An overview of the 13-year timeseries suggested that stronger gradients could be characterized as those $> 0.15\,^{\circ}\text{C/km}$.

3. Results

3.1. Broad-scale spatial patterns and evidence of east–west connections

Relationships between satellite-derived SST and the distribution of *A. fundyense* in surface waters of the Gulf of Maine collected during three broad-scale surveys in 1998 are shown in Fig. 3. These data suggest, especially early in the summer (June and July, Fig. 3A and B), that highest cell concentrations are located within the colder waters of the EMCC and that surface cell distributions are modulated by circulation patterns (Fig. 1). These results are consistent with the comparisons of cell distribution and hydrography for the same data reported by Townsend et al. (2001). Surface SST gradients for the same periods (Fig. 3D–F) show the location of major frontal zones in the Gulf of Maine. Especially relevant here are those cross-shelf oriented fronts immediately south of Penobscot Bay separating colder EMCC water from more stratified and warmer western Gulf of Maine surface water and the alongshore-oriented front separating EMCC water from more stratified conditions over Jordan Basin. Comparisons of cell surface patterns to surface SST patterns and gradients suggest frontal zones play a role in the distributional ecology of *A. fundyense*, acting as boundaries to surface distributions in the Gulf of Maine. These data show that cell delivery and the potential for toxicity in western Gulf of Maine coastal areas might be related to EMCC flow along the coast, one metric of which is the strength of the frontal zone offshore of Penobscot Bay (Figs. 1and 3). Additionally, Anderson et al. (2005) and Keafer et al. (2005a) saw patterns in their hydrologic and cell count data that suggest cells from the EMCC may

have been delivered to the western Gulf of Maine in 1993/1994 and 2001, respectively.

In mid-May 2000, toxin concentrations greater than $80\,\mu\text{g}$ toxin/100 g tissue in shellfish samples caused the Maine DMR to issue a closure for shellfish beds along the western Maine coast beginning at the New Hampshire border. Individual daily satellite SST images were examined for this (unfortunately quite cloudy) period. Imagery from May 12, 2000 shows a coldwater plume, extending from the east and just offshore of the Kennebec River outflow, meandering inshore in close proximity of the western Maine coast (Fig. 4A). Such an SST pattern is consistent with a surface advective mechanism capable of transporting populations of *A. fundyense* within the EMCC along the coast and delivering cells to coastal areas of the western Gulf of Maine. Townsend et al. (2001) also observed a filament of cold water at the end of the EMCC connecting to the coast in 1998. Further evidence of direct connections between EMCC water and western Maine coastal regions comes from drifter data. A surface-drogued drifter, released into the EMCC on June 8, 2000 (J. Churchill, personal communication, July 2000) washed ashore at Wells Beach (Fig. 4B). SST patterns at this time (Fig. 4B) are consistent with direct connections between eastern Gulf of Maine surface water and western coastal regions. Additionally, wind vectors calculated from satellite scatterometer data from the May closure period (May 10, 2000; not shown) show winds from the east (downwelling favorable) that would result in the alongshore and onshore transport observed in the SST image and the drifter data. Wind-driven onshore surface advection (and/or increased alongshore transport), consistent with the processes described by Franks and Anderson (1992), therefore could have resulted in *A. fundyense* cells being transported from upstream and offshore locations to the western Gulf of Maine coast. Keafer et al. (2005b) showed similar findings in 1998 and 2000, suggesting a similar mechanism for delivery of cells in the EMCC to regions in the offshore waters of the western Gulf of Maine as well as a similar mechanism to get the offshore populations onshore.

3.2. Interannual variability in coastal toxicity and frontal development

The toxicity timeseries for the eight stations over the 13 years of this study reveal strong interannual
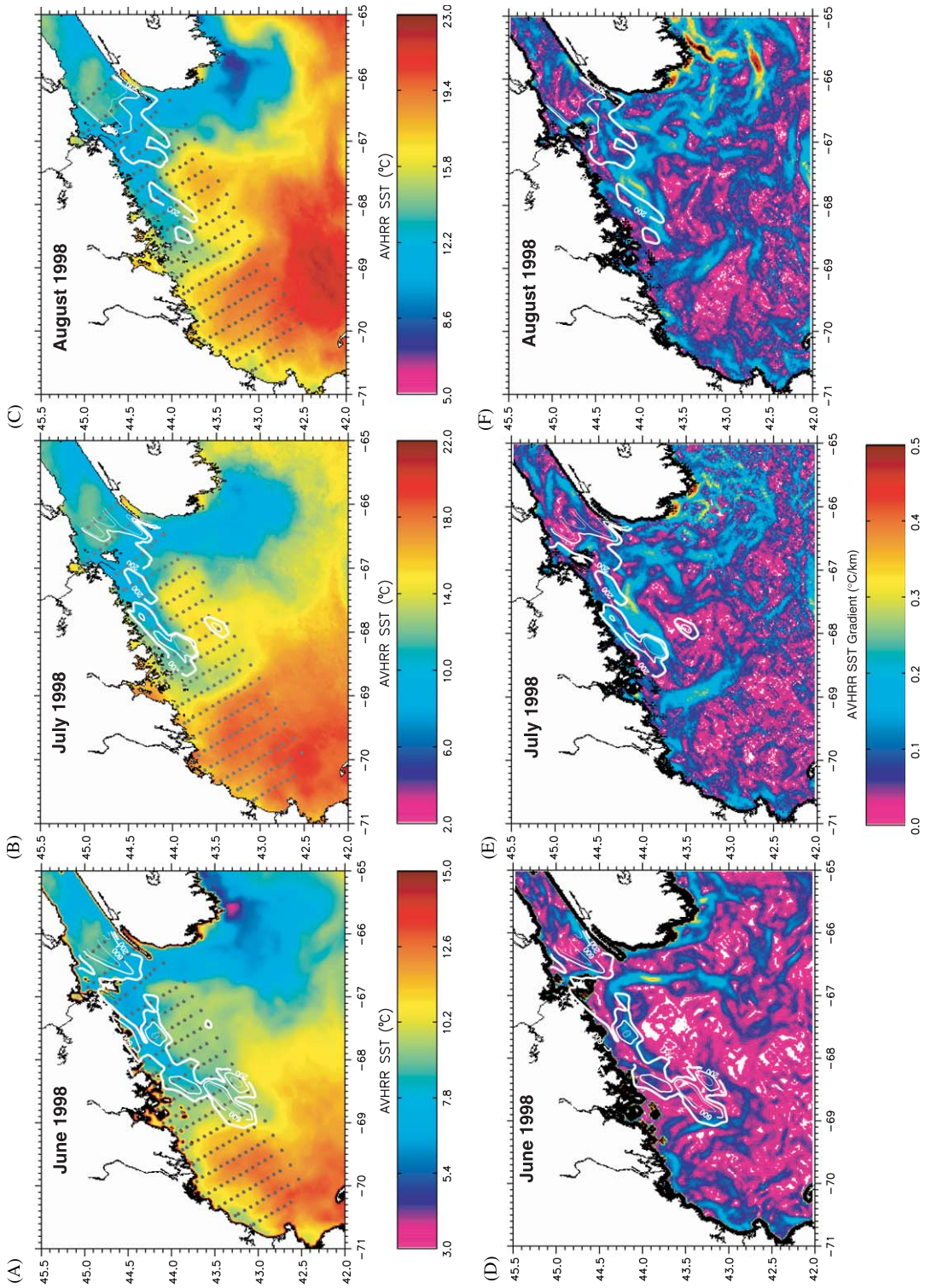
Fig. 3. Satellite-measured SST patterns during field sampling periods in 1998, showing the relationship of colder regions to concurrent surface *A. fundyense* concentrations (cells/L) in (A) June, (B) July and (C) August. Each image is a temporal composite over the cruise period (~12 days) with cruise station locations plotted (A). SST gradient magnitudes calculated from these images show their relationship to surface *A. fundyense* concentrations (cells/L) in each month (D), (E), and (F).
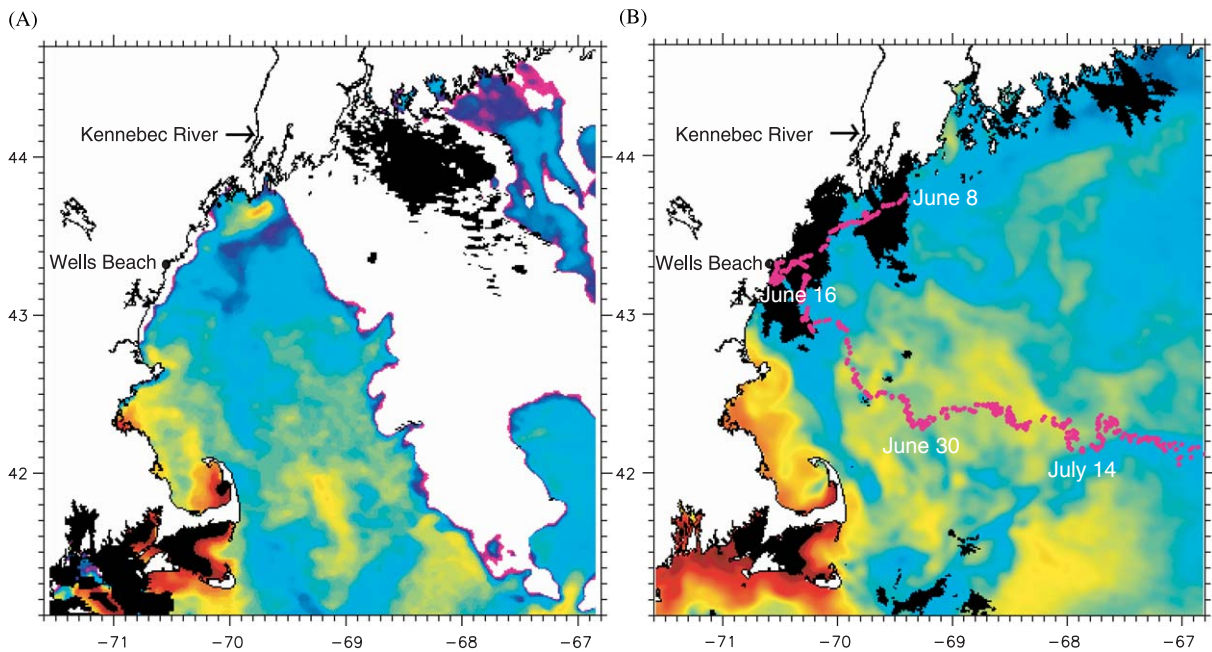
(A)   (B)

Fig. 4. Evidence of surface hydrographic connections between the EMCC and the western Maine shoreline. (A) SST patterns on May 12, 2000 immediately preceding a PSP closure of western Maine coastal shellfish beds with a cold-water filament (offshore of mouth of the Kennebec River) originating in the vicinity of the EMCC extending to the coast near Wells Beach. (B) SST patterns on June 8, 2000 with a similar filament and the path of a surface drifter deployed in the EMCC in June, 2000, which subsequently grounded on the western Maine coast near Wells Beach.

variability in the overall strength and timing of toxicity events (Fig. 5). Toxicity events rarely begin earlier than May 1 (yearday 120) in the western Gulf of Maine. Toxicity events at the eastern Gulf of Maine station (East Pond Cove) consistently occur later in the season (June into early July) than those of the western Gulf of Maine stations (all other stations, late May to early June). This suggests a difference in the timing of toxicity events between the western and eastern Gulf of Maine. Only in 1990 does Pemaquid Point exhibit toxicity greater than 80 µg/100 g tissue (the level at which shellfish beds are closed to harvesting), confirming the Penobscot Bay region as one of reduced toxicity. The time-series also show that toxicity reaches higher levels at the western stations than the eastern station. Within the western stations, the timelines allow us to subjectively group years into three categories according to their overall annual toxicity level. In general, 1990, 1991, 1993 and 2000 were years of highest toxicity (greater than 400 µg/100 g tissue). Little or no toxicity (less than 100 µg/100 g tissue) occurred in the years 1992, 1996, 1999, 2001 and 2002. Other years (1994, 1995, 1997, 1998) had intermediate toxicity (100–400 µg/100 g tissue) (see also Bean et al., 2005).

Maximum SST gradient magnitudes extracted from the sampling box (Fig. 2) were contoured as a function of alongshore location (from west to east) and time over the toxicity sampling period (late March to early August) for each study year (Fig. 6). The toxicity timeseries at each of the eight stations is plotted adjacent to the contours of frontal strength/ position for each of the 13 years to compare similarities and differences between the timing and duration of frontal formation and that of toxicity events. Here, we do not distinguish between individual stations, treating all eight as a unit indicative of overall annual toxicity. Black bars plotted between the contour panels and the toxicity timelines indicate periods during which there was a maximum SST gradient of 0.15 °C/km or greater present in the general vicinity of the EMCC divergence point offshore of Penobscot Bay (50–75 km along the transect on the contour plot).

Years with highest toxicity (1990, 1991, 1993 and 2000) show consistent patterns in frontal strength and timing (Fig. 6A,B,D,K) that are different from other years. In these years, gradients are weak, with strong (>0.15 °C/km) SST gradients present in the region of interest (between the dashed lines in Fig. 6) for relatively few (<6) 8-day periods. More

importantly, if strong gradients are present in these years, they occur late in the season (mid-June or later) or they occur for only short periods of time sporadically throughout the sampling period. The weak frontal structure suggests a prolonged period of surface connectivity between the EMCC and the western Gulf of Maine during these years.

Gradients during years that experienced little to no toxicity in the western Gulf of Maine (1992, 1996, 1997, 1999, 2001 and 2002) are markedly different from those described above. The SST data during years of weak toxicity (Fig. 6C,G,J,L,M) generally indicate strong thermal gradients present throughout most of the sampling season in the
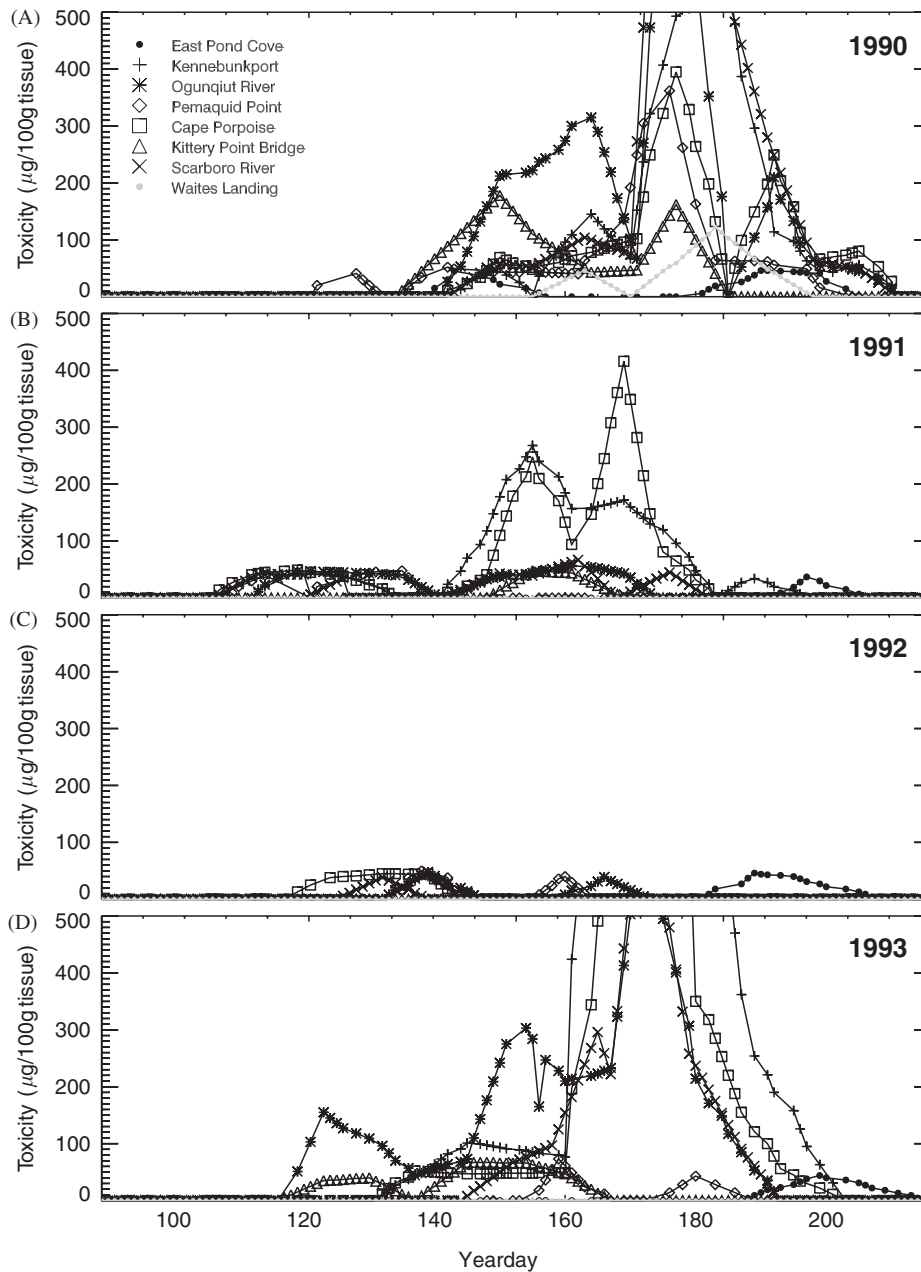
Fig. 5. (A)–(M) Timeseries of toxicity measured at each of the eight stations in each study year. Symbols indicate actual sampling times over each season. Although there are differences between individual stations, the primary purpose of these data is to highlight interannual differences in overall toxicity.
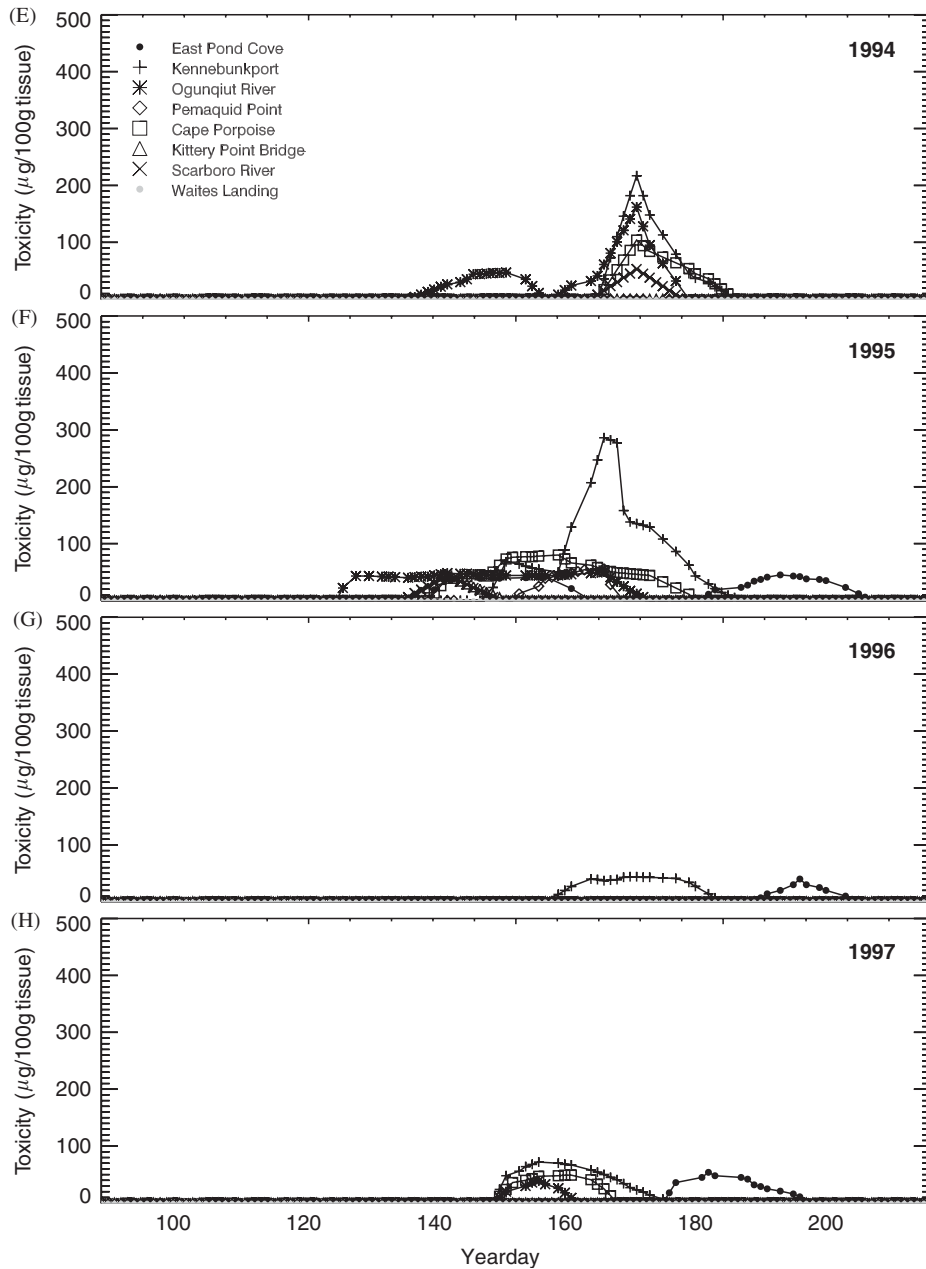
Fig. 5. (*Continued*)

region of interest, starting relatively early in the season (early to mid-June). This implies reduced surface connection between the EMCC and western Gulf of Maine, potentially limiting the delivery of cells from eastern and offshore locations. As these strong SST gradients persist throughout the summer, any early-season period of weak gradients represents the only window for delivery of cells from an eastern source to the western Gulf of Maine.

Years with moderate toxicity (1994, 1995, 1998) and those years of weak toxicity (e.g., 1997 and 2001) that appear to have relatively weak frontal zone development, represent either the intermediate situation, local (and presently unknown) environmental conditions that override large-scale circulation as a controlling influence, or a combination of these. In many of these years, a strong front develops later in June than the years with little
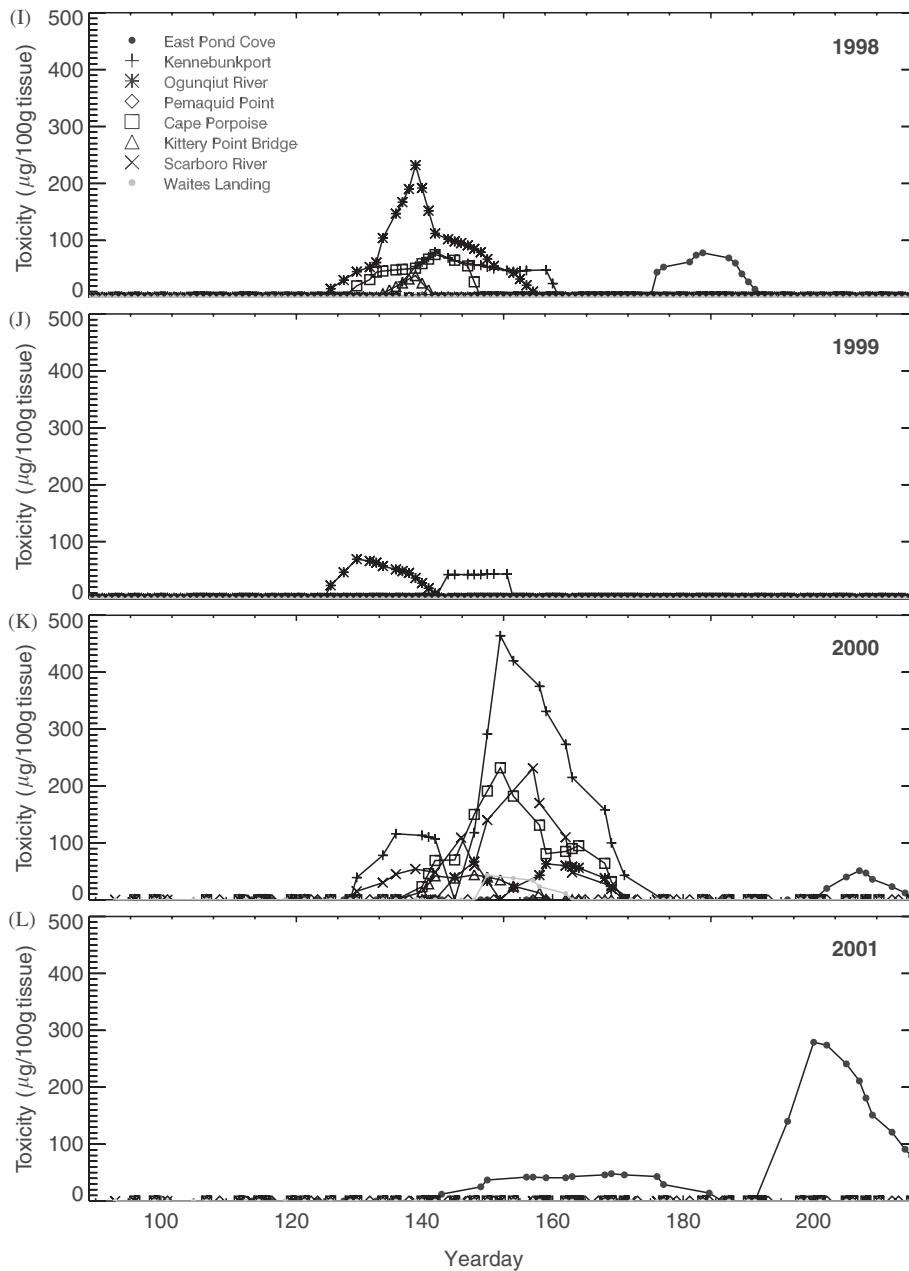
Fig. 5. (*Continued*)

toxicity, allowing an early period of enhanced connectivity but then restriction. Subsequent development of toxicity in these intermediate years would then depend on interactions between the cells and local environmental conditions and be less directly connected to circulation. For example, surface-nutrient concentrations decrease over the season due to uptake by phytoplankton while SST, stratification and solar insulation increase, creating chan-

ging temporal windows of advantageous conditions. Thus, timing of the development and/or breakdown of the front in relation to the occurrence of optimal growth conditions for *A. fundyense* is one explanation of the variability observed in the magnitude of toxicity events during these years, masking the direct impact of transportation/connectivity.

It is important to note that this connectivity between the EMCC and the western Gulf of Maine
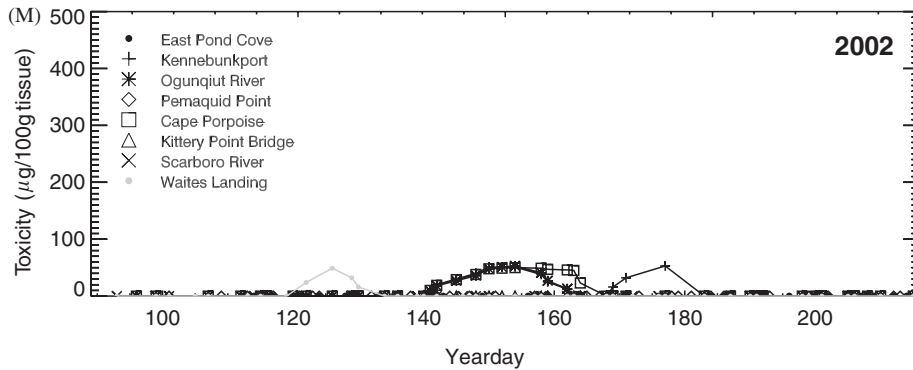
Fig. 5. (*Continued*)

4. Discussion

does not always control the occurrence of a HAB. Anderson et al. (2005) found that in 1993 and 1994, HABs developed from two separate possible sources. In 1993, the bloom was likely formed from the cells contained in the EMCC that were delivered to the western Gulf of Maine early in the season when the front was not as strong. Alternatively, the 1994 bloom most likely developed from a cyst bed population offshore of Casco Bay. Stock et al. (2005) suggest the mechanism seen in 1993 to be more important late in the spring and into the summer and the local cyst beds offshore of Casco Bay to be capable of providing the bulk of the cells that make up the blooms earlier in the spring.

4. Discussion

One observation from the data is a delayed annual onset of toxicity in the eastern station (East Pond Cove, Fig. 5) compared to those in the west. Although this single eastern station requires analyses of additional stations to verify regional trends, it is consistent with proposed hypotheses explaining east–west Gulf of Maine *A. fundyense* ecology differences. One hypothesis explaining differences in the annual timing of toxicity events in the western and eastern Gulf of Maine is that the two regions have separate source populations of *A. fundyense*. Anderson (1997) hypothesized that populations in the eastern and western regions could be independent from one another with respect to *A. fundyense* populations. Franks and Anderson (1992) suggest that the onset of toxicity in the western Gulf of Maine is due to a source population of *A. fundyense* located in the Androscoggin and Kennebec River estuary that is advected alongshore in a buoyant freshwater plume. The association of the plume with

the coastline is controlled by local wind forcing. In April, river discharge is maximum, resulting in an increase in the potential delivery of toxic cells. If the source population for eastern portions of the Maine coast is in the Bay of Fundy, then alongshore advection of these cells is controlled by influx of Scotian Shelf water into Jordan Basin that drives the EMCC (Smith, 1983). This hypothesis suggests that differences in source populations and advective mechanisms account for differing times of toxicity events.

A number of additional mechanisms also would result in delayed seasonal toxicity events in eastern relative to western Gulf of Maine shorelines. A strong difference in the temperature regime of the two regions exists throughout spring, summer and fall. Vertical mixing and the colder surface waters of the EMCC means that seasonal warming in spring–summer of eastern Maine lags behind that of western Gulf of Maine, reducing cell growth rates and delaying the possibility of large populations of *A. fundyense*. This temporal pattern is evident in overall chlorophyll concentrations in the Gulf of Maine (Thomas et al., 2003). Also, alongshore transport within the EMCC is strongest in June (Xue et al., 2000). *A. fundyense* cells growing in the EMCC early in the season are rapidly advected along the coast preventing extensive build-up of cell numbers. By late July, the front separating surface waters of the eastern and western Gulf of Maine becomes well defined and the strength of flow within the EMCC declines. Cells growing in the EMCC are no longer advected as rapidly downstream, increasing residence time and the possibility of a toxic event.

The SST gradient data (Fig. 6) suggest that the development of the cross-shelf front between
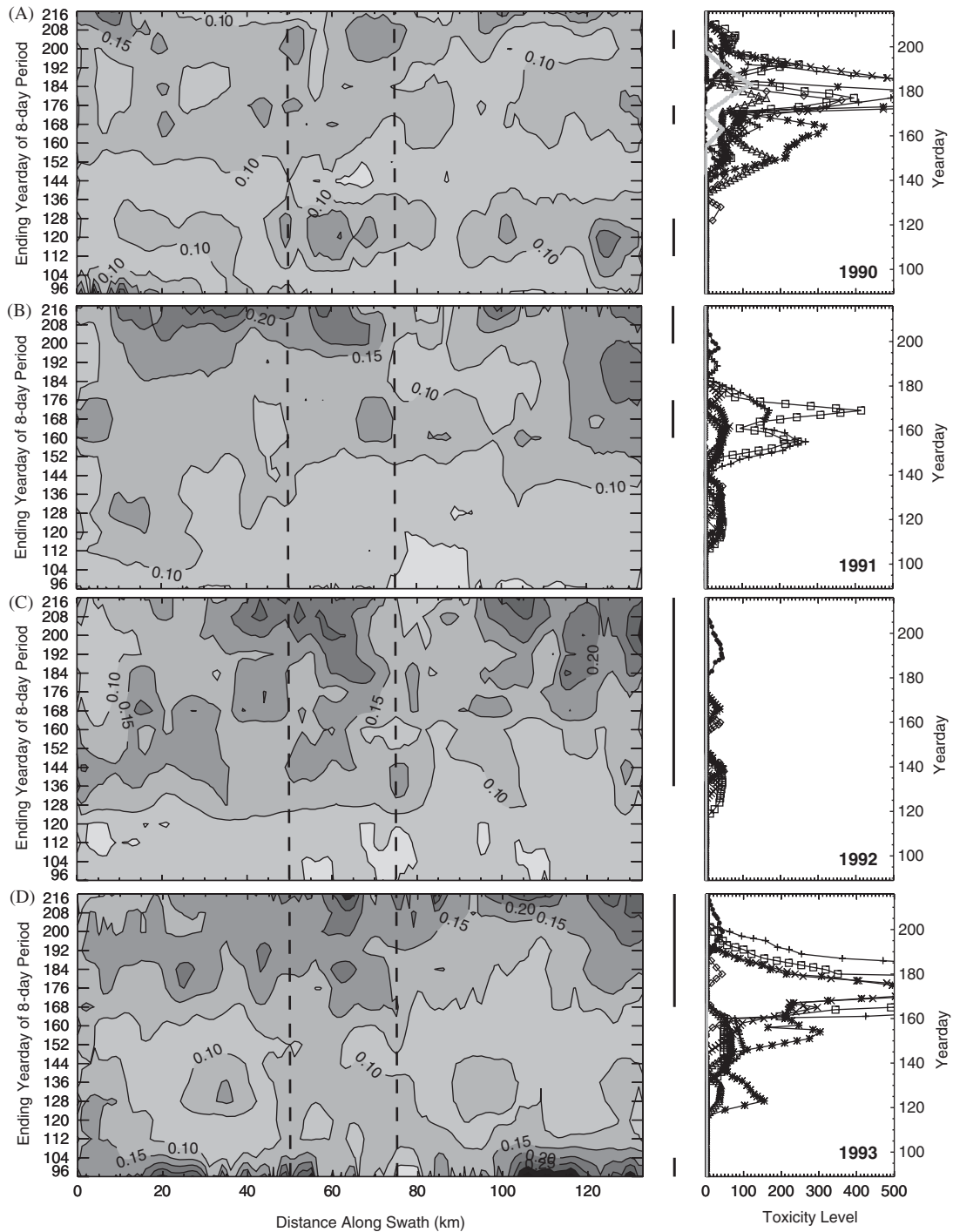
Fig. 6. (A)–(M) The maximum SST gradients (°C/km) contoured as a function of time (April 6–August 4) and distance alongshore (from west to east, within the box defined in Fig. 4) for the 13 years of available data (1990–2002). Coincident toxicity timelines (μg toxin/100 g tissue) for the eight sampling stations (from Fig. 5) are shown on the right of each to illustrate relationships between frontal development and toxicity. Solid black bars between the plots indicate time periods having gradients greater than 0.15 °C/km in the area of interest (50–75 km along the transect, between dashed lines).
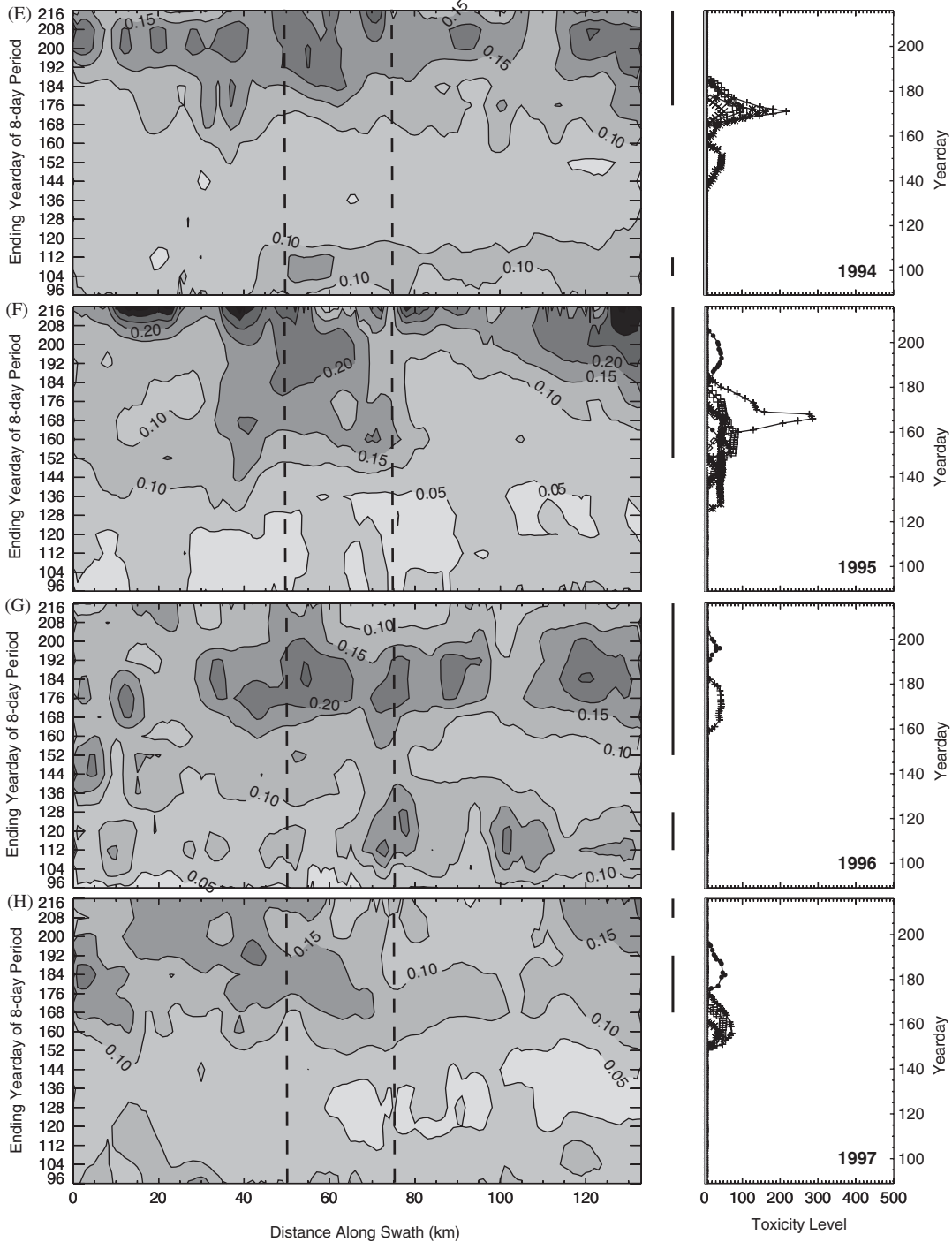
Fig. 6. (*Continued*)

eastern and western Gulf of Maine is linked to toxicity events, at least during extreme years of either very large or very reduced toxicity. One possible mechanism is a regulation of the amount of

A. fundyense cells that are transported into western regions from the EMCC population identified in Fig. 3. The consistency of the relationship between maximum toxicity and timing of frontal develop-
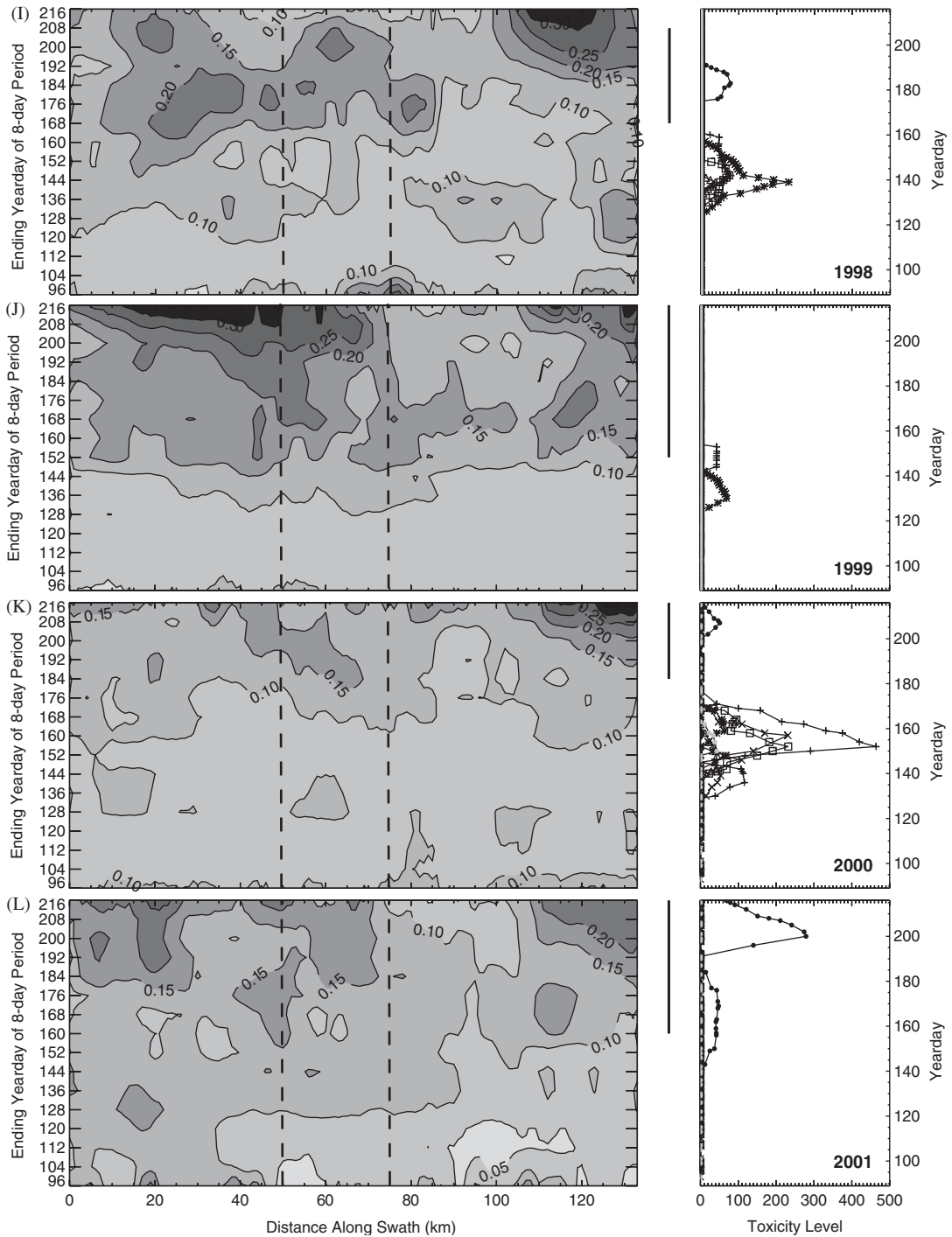
Fig. 6. (*Continued*)

ment over the 13-year study period is summarized in Fig. 7. These data show an overall positive relationship between the maximum toxicity in the western Gulf of Maine in each year and the yearday when the front develops and persists for more than two 8-day periods. This is consistent with the hypothesis that in years when the front does not develop until late in the season (yearday 168–216), there is an
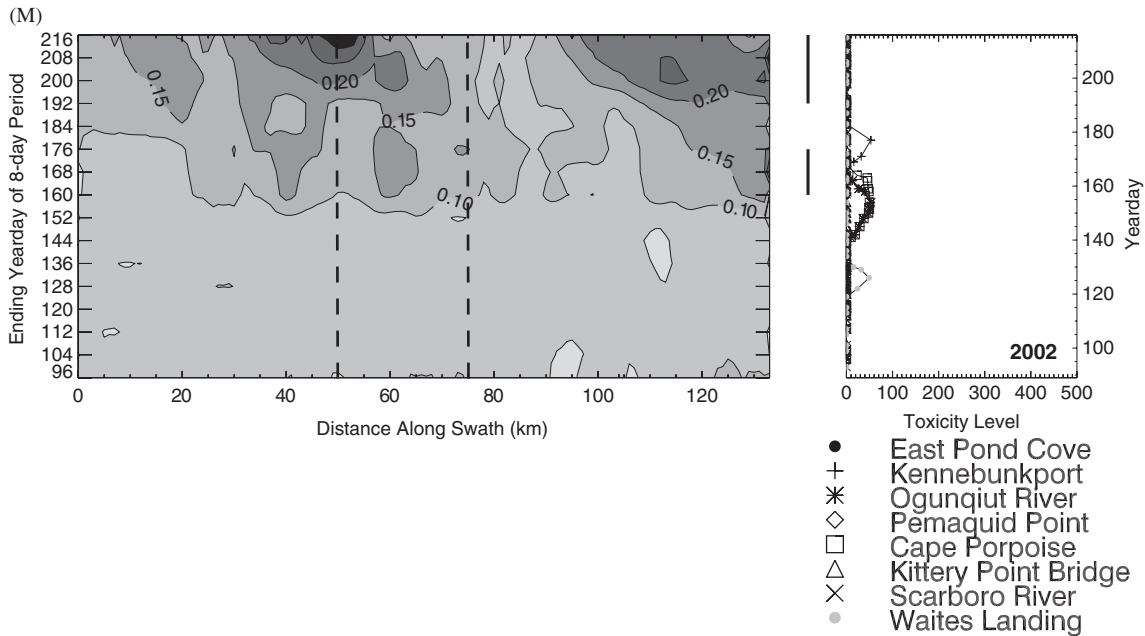
Fig. 6. (*Continued*)

extended period of connectivity allowing increased transportation of cells into the western Gulf of Maine from an EMCC source. With more cells entering the western Gulf of Maine earlier in the season, more cells are likely to encounter optimal growth conditions potentially resulting in elevated cell concentrations and a toxicity event. Years when the front develops quite early (yearday 128–152) and persists through the majority of the season are years of reduced connectivity and weak cell transport.

A second mechanism related to connections between the EMCC and the western Gulf of Maine is advection of optimal or even previously limiting environmental conditions into western coastal regions. Overall phytoplankton productivity in the Gulf of Maine depends primarily on nutrient-rich slope water and intense tidal mixing, especially in the EMCC (Brooks and Townsend, 1989), leading to strong spatial heterogeneity in phytoplankton seasonality (Thomas et al., 2003). In the stratified and nutrient-depleted surface summer waters of the western Gulf of Maine, the *A. fundyense* cell densities are uniform and low (ca. <50 cells/L, Townsend et al., 2001), indicating less than optimal growth conditions, at least offshore. Anderson (1997) suggests that transport of nutrient-rich EMCC waters to the stratified western gulf coastal

regions plays a significant role in the growth of *A. fundyense*. Introduction (or enhancement) of advantageous environmental conditions for *A. fundyense* through stronger alongshore transport could potentially lead to increased shellfish toxicity in the western Gulf of Maine.

We show that years of strong and weak toxicity are years of late and early strong frontal development, respectively. However, due to the likely complex and still poorly understood factors that potentially trigger increased local *A. fundyense* population growth, we do not expect the inverse relationship to be as robust. All years of strong (weak) fronts are not necessarily weak (strong) toxicity years. Although interannual extremes of toxicity event occurrence appear related to large-scale circulation patterns, local conditions likely dictate much of the intermediate toxicity variability. In years of moderate toxicity, the development of the front occurs some time in the middle of the sampling season, allowing partial, early connectivity and cell transport. Differences in the magnitude of the toxicity in these years are likely dictated by local environmental conditions in the western Gulf of Maine once the cells have arrived. The timing of frontal development and/or breakdown in relation to optimal growth conditions only partially explain the variability of the magnitude of toxicity events
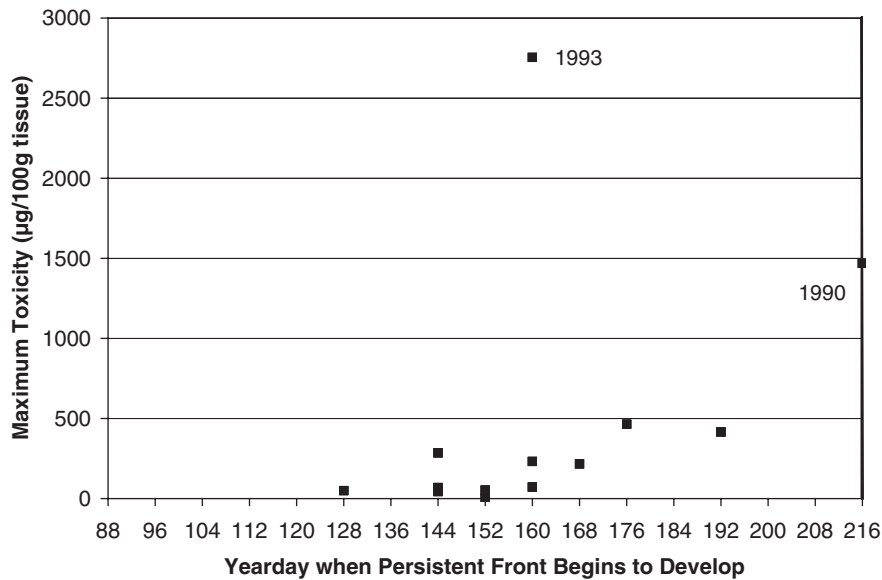
Fig. 7. The positive relationship between timing of frontal development (characterized as the yearday of development of a front which persists for more than two 8-day periods) and the maximum toxicity level observed at the western Gulf of Maine monitoring stations, over the 13 years of coincident SST and toxicity data. Two specific years are marked, 1993 with exceptionally high toxicity and 1990 with very weak fronts when the "persistent front" criteria was never met over the summer sampling period.

during these years of intermediate toxicity. Optimal conditions that occur before or significantly lagging a major transportation of cells might not support extensive growth and weaker toxicity events would result.

5. Conclusions

Surface *A. fundyense* cell distributions in the Gulf of Maine are strongly linked to surface hydrographic properties. We show that these are identifiable in satellite SST data such that maximum cell concentrations are within the colder EMCC waters. Comparisons of interannual variability in surface frontal dynamics and toxicity present a consistent story linking interannual variability of toxicity events in the western Gulf of Maine to large-scale hydrographic features. Toxicity events in the western Gulf of Maine are related to the connectivity of EMCC to western Gulf of Maine either through direct cell transport or advection of advantageous environmental conditions. This connection is characterized here as a cross-shelf-oriented front, located offshore of Penobscot Bay, determined using satellite-measured frontal features. Years of reduced toxic events are years when the frontal "door is closed" (Luerssen, 2001) because the front develops and persists early in the

sampling season. In years when the "door is open" (Luerssen, 2001) because the front is weak for a majority of the season, cells or advantageous conditions are delivered to the western Gulf of Maine where local environmental conditions determine their success and the magnitude of the toxicity events that result.

This study indicates the utility of satellite-derived SST data in defining hydrographic patterns associated with elevated *A. fundyense* cell concentrations and in the detection and monitoring of oceanographic features that are conducive to toxicity events along the coast of western Maine. Future work making use of additional years, stations and sample species of toxicity information, wind data and other SST products will likely improve the utility of satellite data in understanding the ecology of *A. fundyense* and toxic events in the Gulf of Maine demonstrated in a preliminary fashion here.

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