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Alongshore transport of a toxic phytoplankton bloom in a buoyancy current: *Alexandrium tamarense* in the Gulf of Maine

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Abstract. We examined the mechanisms controlling blooms of the toxic dinoflagellate *Alexandrium tamarense* Lebour and the concomitant patterns of shellfish toxicity in the southwestern Gulf of Maine, USA. During a series of cruises from 1987 to 1989, hydrographic parameters were measured to elucidate the physical factors affecting the distribution and abundance of dinoflagellates along this coast. In 1988 and 1989 when toxicity was detected in the southern part of this region, *A. tamarense* cells were apparently transported into the area between Portsmouth, New Hampshire, and Cape Ann, Massachusetts, in a coastally trapped buoyant plume. This plume appears to have been formed by the outflow from the Androscoggin and Kennebec Rivers. Flow rates of these rivers, hydrographic sections, and satellite images led us to conclude that the plume persisted for about a month, and extended alongshore for several hundred kilometers. The distribution of cells followed the position of the plume as it was influenced by wind and topography. When winds were downwelling-favorable (to the southwest), cells were moved alongshore to the south, and were held to the coast; when winds were upwelling-favorable (to the northeast), the plume sometimes separated from the coast, advecting the cells offshore. In 1987 when no plume was present, *A. tamarense* cells were scarce, and no toxicity was recorded at the southern stations. The alongshore advection of toxic cells within a coastally trapped buoyant plume can explain the details of the temporal and spatial patterns of shellfish toxicity along the coast. We hypothesize that (1) the source of the *A. tamarense* populations is in the north, possibly associated with the Androscoggin and Kennebec estuaries, that (2) toxicity patterns follow a predictable relationship with river flow volume and timing of flow peaks and that (3) wind stresses directly influence the distribution of low salinity water and the dinoflagellate cells. Local, in situ growth of dinoflagellates can be an important factor initiating toxic dinoflagellate blooms. However, these data demonstrate the significant role of alongshore transport of established populations of *A. tamarense* in controlling the location and timing of paralytic shellfish poisoning (PSP) outbreaks in May and June along the southwestern coast of the Gulf of Maine.

Introduction

Blooms of the toxic dinoflagellate *Alexandrium tamarense*[1] are a recurrent feature of the southwestern coast of the Gulf of Maine. Blooms of this dinoflagellate have occurred since 1958 between May and October along the southern coast of Maine, and, with the exception of 1987, since 1972 along the north shore of Massachusetts. The economic importance of locating, and restricting the harvest of toxic shellfish has led to the development of regional monitoring programs (e.g. Shumway et al. 1988). These programs have demonstrated that toxicity in the mussel *Mytilus edulis* is a good indicator of the presence of *A. tamarense* populations. The toxic shellfish outbreaks in the southern section of this region typically show a north-to-south progression (Franks and Anderson 1992); for example, a twenty-day lag is common between the first measurable toxicity at Lumbos Hole, Maine, and the first occurrence of toxicity at Cape Ann, Massachusetts.

This pattern, also seen by Hurst and Yentsch (1981) and Shumway et al. (1988), has been assumed by some to reflect a southward sequence of discrete nearshore blooms of *Alexandrium tamarense*, possibly as a result of wind-driven upwelling (Mulligan 1973, 1975, Hartwell 1975, Seliger et al. 1979). These studies were motivated by the first occurrence of paralytic shellfish poisoning

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[1] *Alexandrium tamarense* and *Alexandrium fundyense* were formerly included in the genera *Protogonyaulax* or *Gonyaulax* but are now accepted as *Alexandrium* (Steidinger and Moestrup 1990). Both species bloom in the Gulf of Maine (Anderson unpublished data), but since discrimination between them is impossible for large-scale field programs or when referring to shellfish toxicity, only the more familiar name *Alexandrium tamarense* will be used here

(PSP) in the southwestern Gulf of Maine in September 1972. The origin of this massive bloom was linked to the passage of Hurricane Carrie, which may have swept an established bloom of *A. tamarense* from the Bay of Fundy to the Massachusetts coast. It was further hypothesized that late-summer blooms of *A. tamarense* in the Cape Ann region in subsequent years were caused by germination of cysts in local waters, followed by growth and accumulation nearshore as a result of delivery by wind-driven upwelling. These studies did not, however, directly address the question of the source of PSP toxicity in the spring (April to June).

Martin and Main (1981) were among the first to attempt to identify the source of the annual toxic outbreaks. Their field work just north of Cape Ann led them to conclude that *Alexandrium tamarense* cells were advected into the study area from the north by the prevailing currents. This was the first suggestion that episodes of toxicity in the spring could be related to alongshore advection of cells rather than local growth. A source of cells in Maine waters was implied, but no mechansim was identified for the alongshore advection.

Several physical mechanisms could generate alongshore currents in the Gulf of Maine. These include wind-driven upwelling and estuarine discharge (Graham 1970) and tidal forcing (Garrett et al. 1978, Greenberg 1979, Loder and Greenberg 1986). Balch (1986) noted a weak association of PSP outbreaks with the lunar cycle, and Yentsch et al. (1986) explored the association of blooms of *Alexandrium tamarense* with tidal fronts as has been observed in other regions (e.g. Pingree et al. 1975). Holligan et al. (1984) found enhanced concentrations of *A. tamarense* ~35 km off the Maine coastline, but did not speculate on the causes of the horizontal patchiness.

Clearly, the coastal waters of the Gulf of Maine are subject to a variety of physical forcings, and PSP toxicity in southern sections progresses in a north-to-south pattern each year. The purpose of the present study was to elucidate the factors controlling the distribution of *Alexandrium tamarense* populations, and the concomitant shellfish toxicity, along the Massachusetts coast. Based on sampling over three bloom seasons, 1987 to 1989, we demonstrate that the blooms of *A. tamarense* seen in the Cape Ann area were not of local origin, but were advected alongshore in a coastally trapped buoyant plume created by enhanced river outflow in Maine.

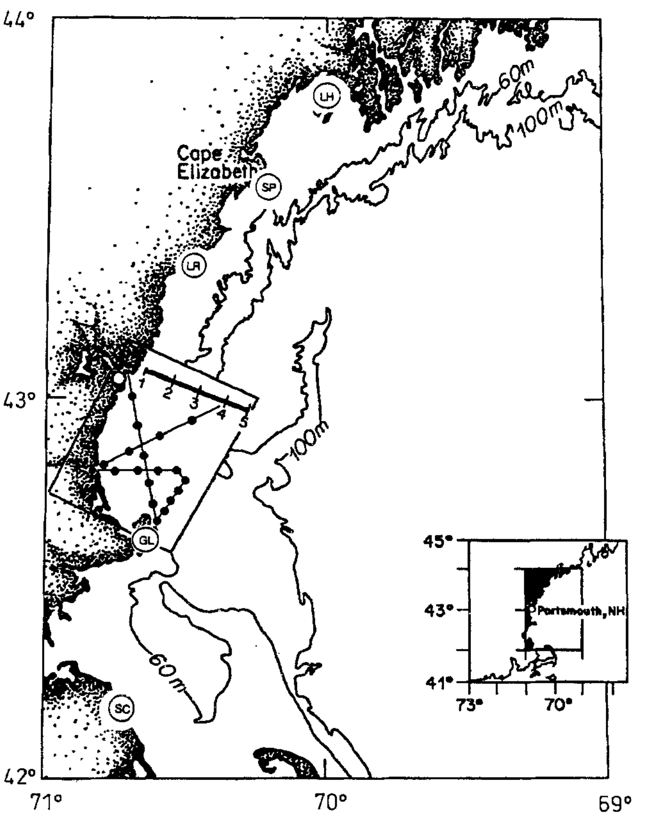

Fig. 1. The study area. The coast of the Gulf of Maine, USA, is shown, from Casco Bay, south to Cape Cod Bay. Stns 0 to 5 comprise the regular cruise transect, sampled from 1987 to 1989. These stations are ~7 km apart. The additional stations are those sampled aboard the C.V. "Unity". The box indicates the region plotted in Fig. 7. Toxicity sampling stations are LH: Lumbos Hole, SP: Spurwink River, LR: Little River, GL: Gloucester and SC: Scituate

Materials and methods

Most sampling in 1987 to 1989 was along a six-station transect extending from Portsmouth, New Hampshire, 30 km into the Gulf of Maine (Fig. 1, Stns 0 to 5) on the 45′ vessel R.V. "Jere A. Chase". Stations were ca. 7 km apart, with depths of 10 m at Stn. 0 (in Portsmouth Harbor) to 175 m at Stn. 5. In 1989, the charter vessel C.V. "Unity" was used on three occasions (19 May, 8 June, 27 June) for more detailed horizontal mapping of the hydrography and of *Alexandrium tamarense* Lebour cell concentrations in the region from Cape Ann, Massachusetts to Portsmouth, New Hampshire, covering 25 stns in 8 h (Fig. 1; Stns 0 to 4, and small circles).

A hose-pumping system was used when sampling from the R.V. "Jere A. Chase". A "Li'l Giant" submersible pump brought water through 40 m of 2-cm i.d. garden hose which was raised from 40 m depth to the surface at 2 m min^{-1}. Water flowing at a rate of a 2 liter min^{-1} was directed through a bubble trap, and through the flow cell of a Turner Designs Model 10 fluorometer. The fluorometer was linked to a portable computer which plotted and recorded the fluorescence every 2 s. From the fluorometer, the water passed into buckets used to integrate samples over 5 m depths. From each bucket one liter was filtered through 20-μm mesh, backwashed with 50 ml of filtered seawater, and preserved in 5% formaldehyde for cell counts, while 500 ml were filtered through GF/A filters for chlorophyll analysis.

Samples for cell counts were settled in 50 ml chambers and counted on a Zeiss inverted microscope. Half a slide was counted if there were fewer than 200 cells, otherwise 20 fields were counted at 160 ×. Fluorometric chlorophyll analysis followed Strickland and Parsons (1972), corrected for phaeopigment.

A CTD (Sea Cat Profiler, Sea-Bird Electronics) was attached below the hose inlet with sensors oriented upward in order to take the upcast data. This was necessary as the hose had to be completely submerged to prime the pump. The CTD data were smoothed using an objective mapping routine (after Levy and Brown 1986) to remove salinity spikes. Using the transit time of the water in the hose (1.8 min; calculated by tracing a chlorophyll spike), the fluorescence vs time data were converted to fluorescence vs depth. These data were then merged with the CTD data to examine the relationship of fluorescence with temperature and salinity. A SeaTech 25-cm path-length transmissometer was attached to the CTD during the 1988 and 1989 field seasons. The signal from this instrument was converted to beam attenuation (beam-c: m^{-1}) to facilitate comparison with the fluorescence profiles.

When sampling from the C.V. "Unity", vertical CTD/transmittance casts were made down to 40 m, but to minimize the time taken at each station, no hose-pumping system was deployed. Surface (0.5 m) and 10 m water samples were taken using a 2-l Niskin bottle. Subsamples from the Niskin bottle were processed and preserved as above for cell counts.

Flow data for the Androscoggin, Kennebec and Merrimack Rivers were obtained through the United States Geological Survey. Data for Stn 01059000 on the Androscoggin near Auburn, Maine, Stn 01049265 on the Kennebec River at North Sidney, Maine, and Stn 01100000 at Lowell, Massachusetts, on the Merrimack River were analyzed.

Wind data from Logan Airport, Boston, Massachusetts, were obtained through the National Climatic Data Center. These data were rotated into the coordinate system of the coast north of Cape Ann by subtracting 30°, and resolved into across and alongshore stresses using the algorithm of Large and Pond (1981).

Shellfish toxicity data were made available by the Department of Environmental Quality Engineering (Massachusetts), and the Department of Marine Resources (Maine). Data from Lumbos Hole, Spurwink River and Little River (Maine), and Gloucester and Scituate (Massachusetts) were processed for analysis. Differences in PSP toxin analysis sensitivities between Maine and Massachusetts necessitated conversion of the toxicity data to binary time series: 1 = toxicity present, 0 = no measurable toxicity. This conversion allows comparison of the different data sets without the confounding influences of assay sensitivity and shellfish species sampled.

Nine cruises were made during 1987, 12 in 1988, and 11 in 1989. These cruises spanned the toxic dinoflagellate bloom season, from April to September, with the majority of the cruises from early May to late June. Only those cruises which occurred during the initial stages of a bloom will be described below.

Results

Density and fluorescence distributions, 1988

Data for 1988 appear to represent typical May to June conditions along the southwestern coast of the Gulf of Maine, and are presented in detail (Figs. 2 and 3). A strongly-sloping pycnocline was seen from at least 27 May to 9 June, (Fig. 2) intersecting the bottom inshore and the surface offshore, giving a pattern typical of a water mass or buoyant plume front. The lack of a well-mixed region inshore indicates that this was not a tidally-generated front. The pycnocline slopes in the wrong direction for a wind-driven upwelling front, while a wind-driven downwelling system would be expected to show a horizontal region of the pycnocline offshore.

The fluorescence contours (Fig. 2) show isolated regions of high fluorescence offshore of the front. There was a gradual decline in fluorescence from 14 May to 3 June, followed by a sudden increase on 9 June. The fluorescence peak on 14 May was associated with spring-bloom diatom species of the genera *Thalassiosira*, *Stephanopyxis*, *Nitzschia*, and *Fragilaria*. The extremely high fluorescence values seen on 9 June and 16 June were related to a bloom of a diatom of the genus *Eucampia*. This bloom appears to have been separated from inshore waters by the front. The depth of peak fluorescence values increased by ca. 1 m d^{-1} from 3 June to 16 June possibly due to sinking of the diatoms.

The temperature contours (Fig. 3) were similar to the density contours, with warmer water inshore. Surface temperatures of ~8 °C increased slowly with time, until a strong warming period between 9 June and 16 June. The horizontal surface temperature gradient was 2 to 3 °C from inshore to offshore for most cruises, with the maximal gradient between Stns 1 and 3.

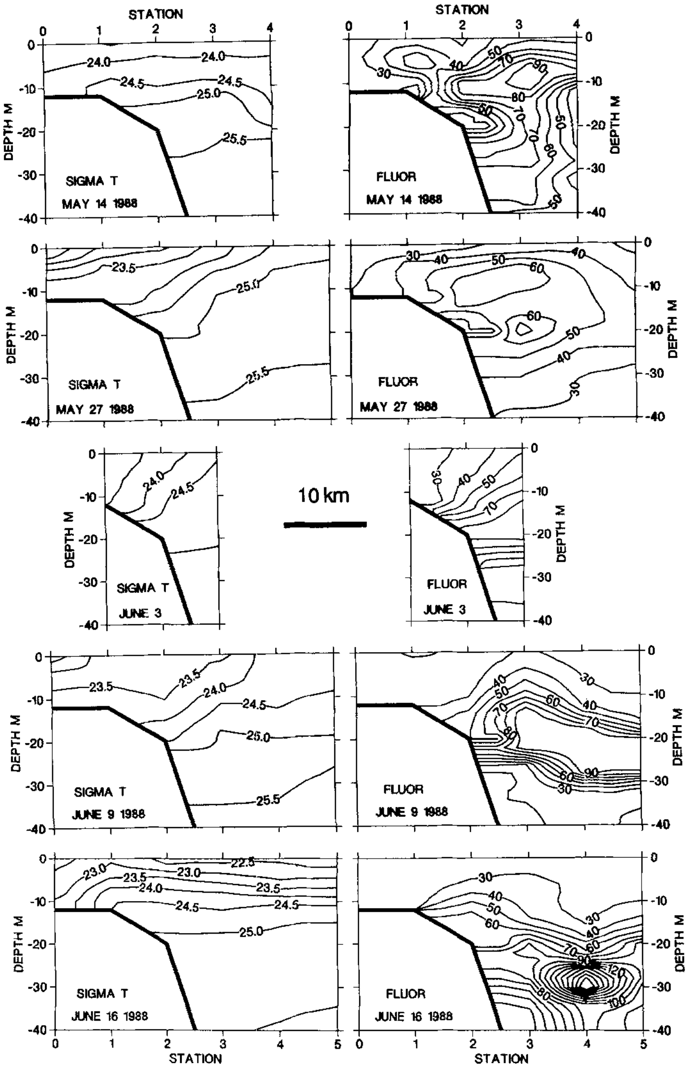

Fig. 2. Hydrographic sections from 1988. Time series of contour plots of σ_T (left panels) and in situ fluorescence (right panels) from the regular cruise track. The cruise date is shown at the bottom left of each panel. Thick black line indicates bottom profile. Stns 1 to 5 are ~7 km apart, while Stn 0 is in Portsmouth Harbor

The beam-c fields (Fig. 3) were almost identical to the fluorescence fields, indicating that most of the beam attenuation was associated with living phytoplankton. For the most part, the beam-c field maps the distribution of diatoms. As with the fluorescence, the highest beam-c values were found offshore of the front.

Salinity and *Alexandrium tamarense* distributions, 1987–1989

The salinity fields of 1987 showed weak stratification, with ca. 1 psu (practical salinity unit) difference from the surface to 40 m (Fig. 4). The isohalines were relatively horizontal, with little structure except near the surface on 5 June. The temperature and σ_T fields showed identical structure (not shown). The *Alexandrium tamarense* cell

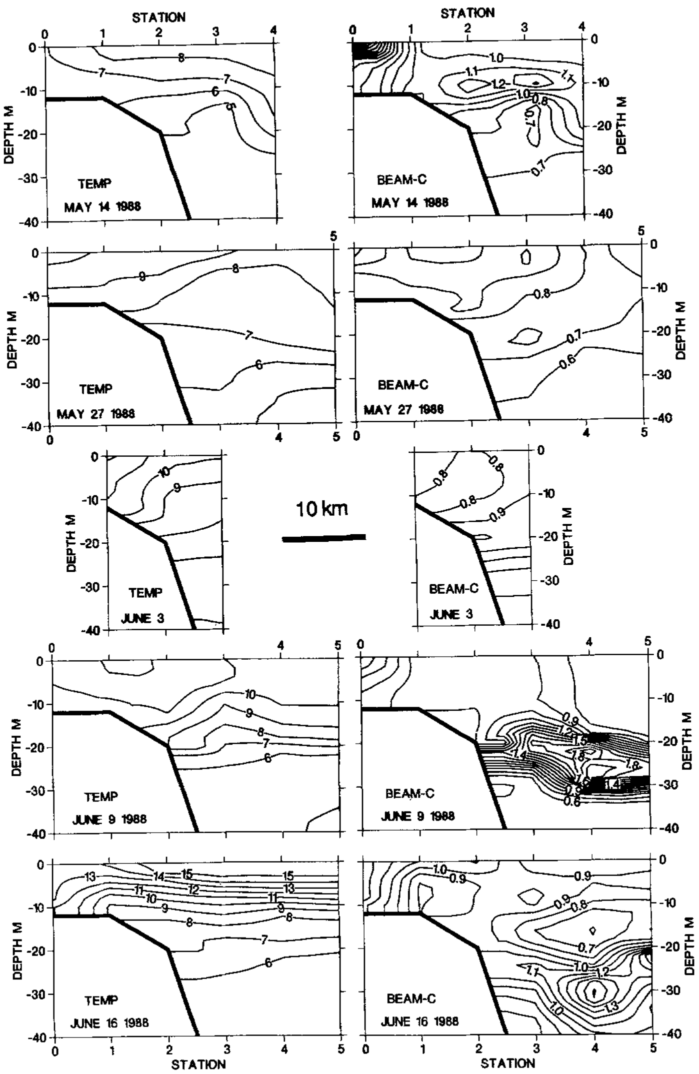

Fig. 3. Hydrographic sections from the regular cruise track, 1988. Same as Fig. 2, but sections of temperature (°C, left panels) and beam-c (m^{-1}, right panels)

concentrations were unusually low during 1987, reaching maximum values of ~150 cells l^{-1} after 27 May. The cells were found in an isolated patch inshore, associated with the pycnocline. Almost no cells were found offshore of Stn 3.

In striking contrast to the 1987 data, the 1988 salinity fields were similar to the temperature and σ_T fields, with strongly-sloping isohalines and salintiy differences of up to 3 psu from the surface to 40 m (Fig. 5). Surface salinities of less than 30.5 psu were measured in inshore waters from 14 May to 3 June, after which slightly more saline waters of 31 psu were seen inshore. The deeper waters were ca. 0.5 psu saltier in 1988 than in 1987. During the initial stages of the bloom (14 May, 27 May, 3 June 1988), the *Alexandrium tamarense* cells were found mainly in waters of <31.5 psu (Fig. 5). On 27 May, in particular, the cells were strongly restricted to the inshore, low salinity water mass. After 3 June, high concentrations of *A. tamarense* were measured offshore of the front, in areas which had previously shown cell concentrations of <1000 cells l^{-1}.

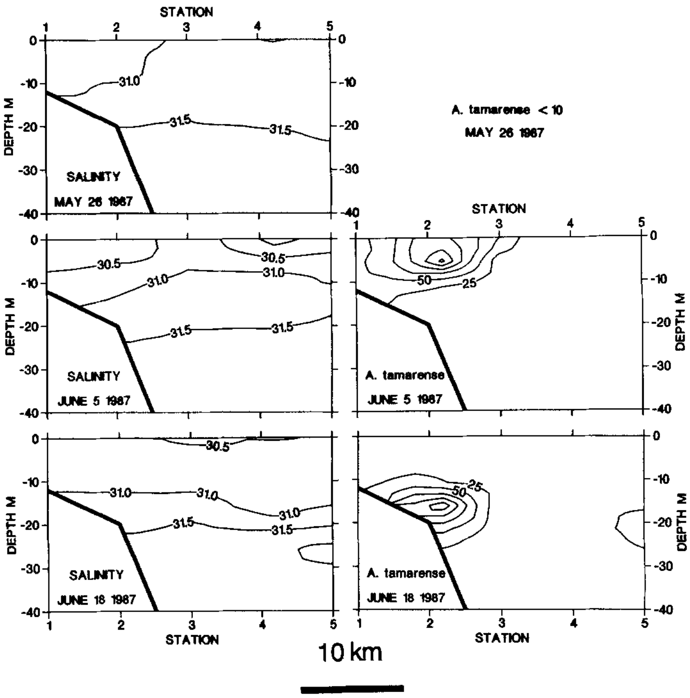

Fig. 4. *Alexandrium tamarense*. Hydrographic sections from the regular cruise track, 1987. Same as Fig. 2, but sections of salinity (psu, left panels) and cell concentrations (cells l^{-1}, right panels)

The vertical salinity gradients during 1989 were similar to, or greater than, those measured during 1988 (Fig. 6). Surface salinities as low as 23 psu were seen on 19 May. These unusually low values were caused by extremely high flow rates of the Androscoggin and Kennebec Rivers in the week prior to this cruise. The salinity contrast from the surface to 40 m was 2 to 3 psu. As with 1988, in 1989 the highest *Alexandrium tamarense* cell concentrations were associated with water <31.5 psu. However, the location of the low salinity water was quite variable: on 19 May it formed a 5-m thick lens which intersected the coast, whereas on 9 May, 23 May and 1 June it was found offshore. On 23 May, in particular, it formed an isolated offshore lens, with a pycnocline which sloped downwards and offshore. The *A. tamarense* cells show the same distributions as the low salinity water: on 19 May the cells are found in inshore surface waters, while on 23 May and 1 June, the cells formed restricted patches in offshore waters. The cell concentrations were almost an order of magnitude lower than at the same time of year in 1988.

The association of *Alexandrium tamarense* cells with low salinity water is also apparent in the alongshore surface distribution on 19 May 1989 (Fig. 7). The 23 to 25 psu water shown in Fig. 6 is seen to extend in a band alongshore, throughout the region sampled. A band of *A. tamarense* cells with concentrations greater than 300 cells l^{-1} coincided with the 23 to 25 psu water distributed alongshore. An area of very fresh water at the mouth of the Merrimack River contained no *A. tamarense* cells. Similarly, very few cells were found in Portsmouth Harbor, which is the mouth of the Piscataqua River.

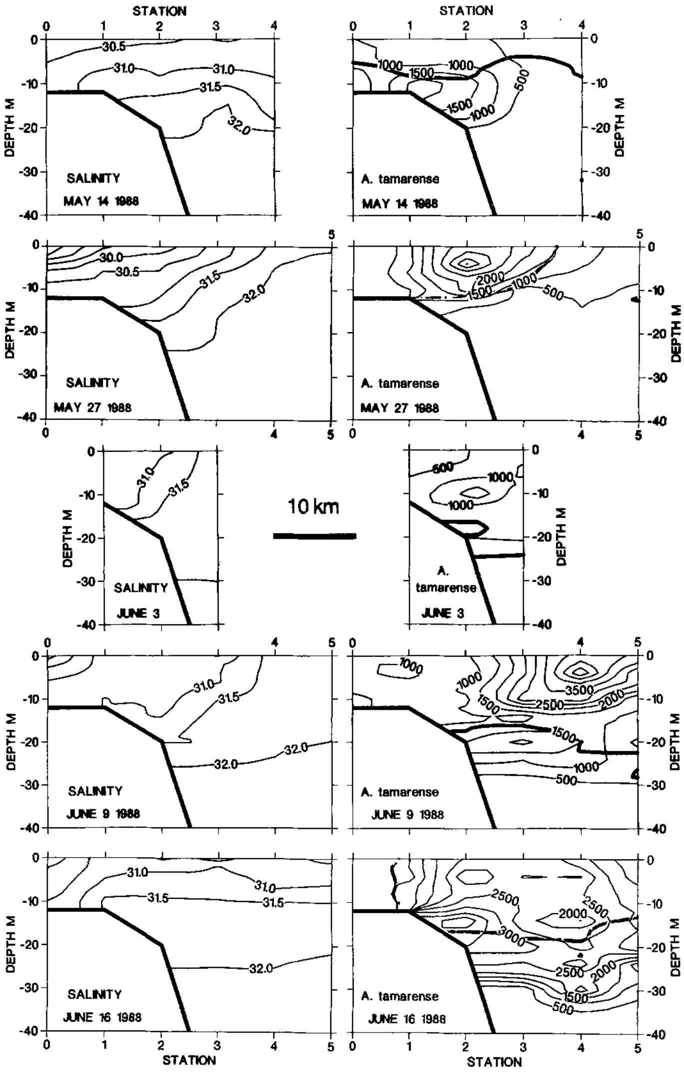

Fig. 5. *Alexandrium tamarense.* Hydrographic sections from the regular cruise track, 1988. Same as Fig. 2, but sections of salinity (psu, left panels) and cell concentrations (cells l^{-1}, right panels). The additional heavy line on the *A. tamarense* plots is the 0.5 μg-at N l^{-1} contour of nitrate + nitrite

The plume

The fresh inshore water in 1988 was warmer than the more saline offshore waters (Figs. 3 and 5), suggesting that the alongshore extent of the low salinity water should be visible in infra-red satellite images. The image shown in Fig. 8, for 8 June 1988 shows a distinct band of warm water extending from the Casco Bay area of Maine in the north of the image, southward into Cape Cod Bay. The heavy continuous line shows the regular cruise transect; the warm water front crosses the transect between Stns 2 and 3. The temperature contrast across the front in the image is ~2 °C in good agreement with the temperature section from 9 June 1988 (Fig. 3). It appears that the nearshore buoyant plume of low-salinity water extended in a band ~15 km wide from Casco Bay in Maine to Cape Cod Bay in Massachusetts, a distance of ~250 km alongshore.

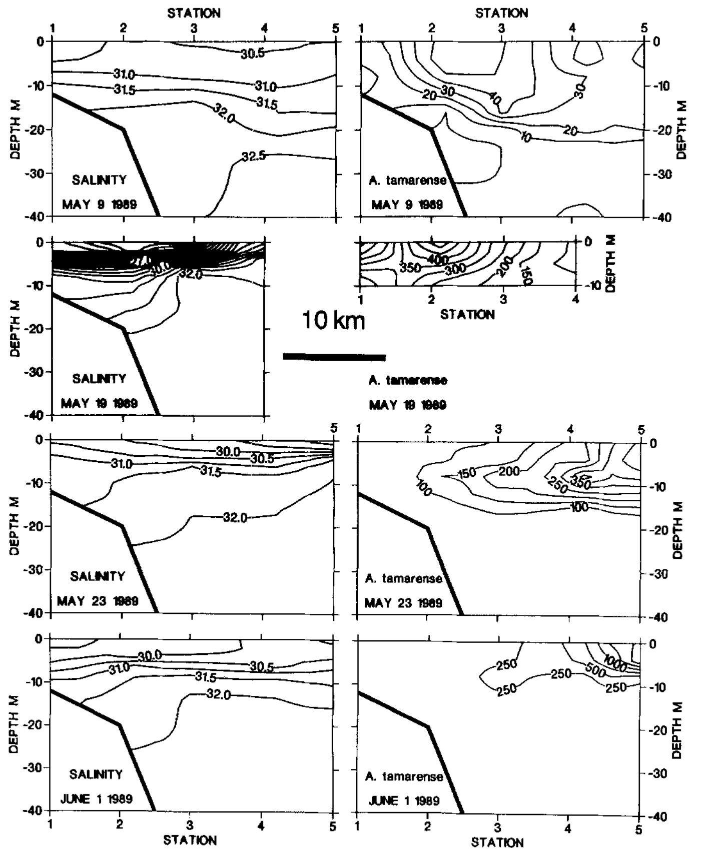

Fig. 6. *Alexandrium tamarense.* Hydrographic sections from the regular cruise track, 1989. Same as Fig. 2, but sections of salinity (psu, left panels) and cell concentrations (cells l^{-1}, right panels). The 19 May panels are results from a C.V. "Unity" cruise, and thus include cell counts from the surface and 10 m only

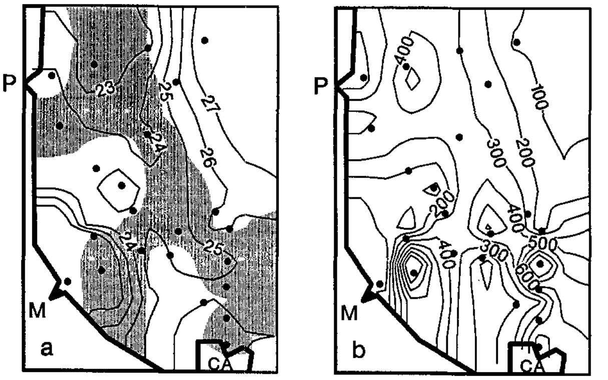

Fig. 7. *Alexandrium tamarense.* Surface maps of salinity and cell concentration, 19 May 1989. (a) Surface (1 m) salinity field (psu). Locations of the stations are shown in Fig. 1. The coastline is shown by the heavy black line, with the north shore of Cape Ann (CA) on the bottom of the plot. Shaded area denotes the region of > 300 cells l^{-1} of *A. tamarense.* (b) Surface cell concentrations (cells l^{-1}) of *A. tamarense.* P: Portsmouth Harbor, M: Merrimack River estuary, CA: Cape Ann

River flow

The strong salinity gradients which formed the plume in 1988 and 1989 suggest that the temporal dynamics of the plume should correlate with variations in freshwater in-

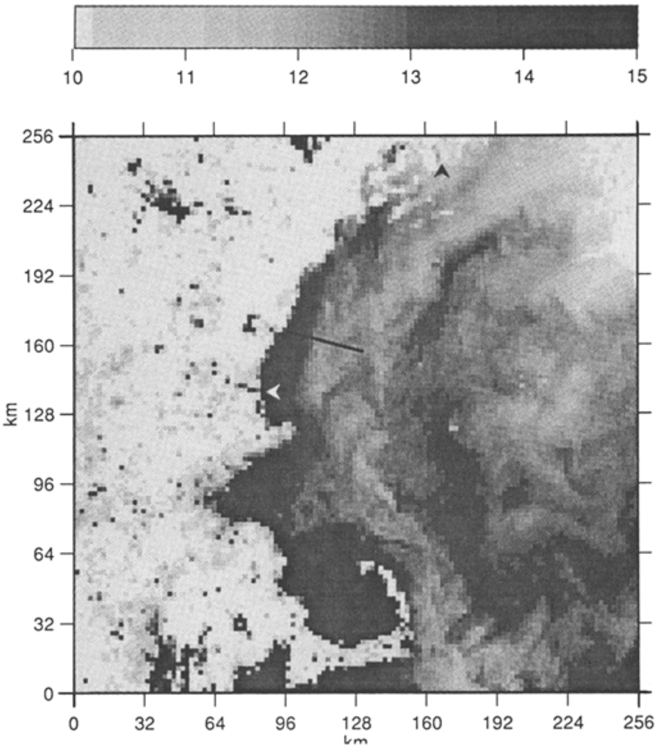

Fig. 8. Satellite image of the surface temperature field of 8 June 1988. Heavy continuous line denotes the regular cruise transect (Fig. 1). Black arrow indicates the approximate region of discharge of the Androscoggin and Kennebec Rivers, while white arrow indicates the mouth of the Merrimack River. Cape Ann and Cape Cod are clearly seen in this image. Note that the temperature scale (°C) at top of figure is not linear. Data courtesy of NORDA

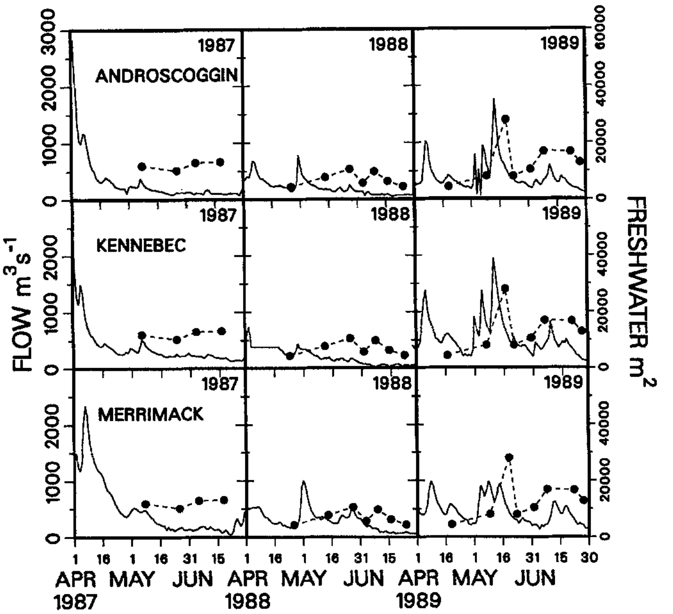

Fig. 9. Discharge (m^3 s^{-1}) of the Androscoggin River (top panels), Kennebec River (middle panels), and Merrimack River (bottom panels), for April to July of 1987, 1988 an 1989. The filled circles and dashed lines indicate A_{FW}, the area of fresh water which would have to be mixed into water of 32 psu to obtain the salinity distribution measured on that date

put to the coastal Gulf of Maine, in particular, river flow. The Androscoggin, Kennebec, and Merrimack rivers are the three largest rivers between the Penobscot area in Maine, and Cape Cod (Fig. 8). The flows of these rivers are plotted in Fig. 9 from April to July 1987, 1988 and 1989. Also plotted are rough estimates of A_{FW}, the amount of fresh water (0 psu) present in any given cruise transect. This value was calculated by first finding the average salinity ($\bar{S}_i$) between the surface ($z=0$) and the depth of the 32 psu isohaline (h_{S32}):

$$\bar{S}_i = \frac{1}{h_{S32}} \int_0^{h_{S32}} S(z)\,dz. \tag{1}$$

The fraction of fresh water, α_i, in that depth interval at the ith station was found according to:

$$\alpha_i = \frac{32-\bar{S}_i}{32}. \tag{2}$$

The areal amount of fresh water, A_{FW}, in the region bounded by the surface, the depth of the 32 psu isohaline (h_{S32}), the coast, and the farthest offshore station (n) can then be found from:

$$A_{FW} = \sum_{i=1}^{n} (\alpha D\, h_{S32})_i. \tag{3}$$

Here the sum is over n stations, with the ith station having an across-shelf scale D_i (m) based on the half-way points between adjacent stations. The value A_{FW} thus represents: the area of a transect cross section that would contain fresh water sufficient to dilute 32 psu water to the observed salinities. It would be more appropriate to compare a freshwater flux to the river flow rate; however, we have no good measurements of alongshore velocities with which to calculate a time-varying flux.

Changes in A_{FW} are most strongly related to changes in the flow rates of the Androscoggin and Kennebec Rivers, and less well correlated with changes in the flow of the Merrimack River. This is not surprising, as we expect the flow of the rivers to turn to their right after leaving the estuary. Thus the Merrimack River, which empties into the Gulf of Maine to the south of the study area, should not have a significant effect on the salt balance along the transect to the north (Stns 0 to 5, Fig. 1). The river flow patterns were quite similar to each other, but varied considerably from year to year. A peak in the flow rate typically occurs in early April, in response to the spring thaw. This early peak was particularly pronounced in 1987, when the flow rates reached record levels. The early April peak is usually followed by a peak in early May, reflecting rainfall at that time. Such a peak was absent in 1987, but was particularly well-developed in 1989.

The hydrographic sampling occurred on a coarser timescale than changes in river flow, yet it can be seen that large changes in A_{FW} are preceded by large changes in the volume of river discharge. The strongest correlations are seen in 1989, when the unusually high flows during early May led to very high proportions of fresh water in the transect. In 1987, following a major flood event, the river flows were low, and relatively constant,

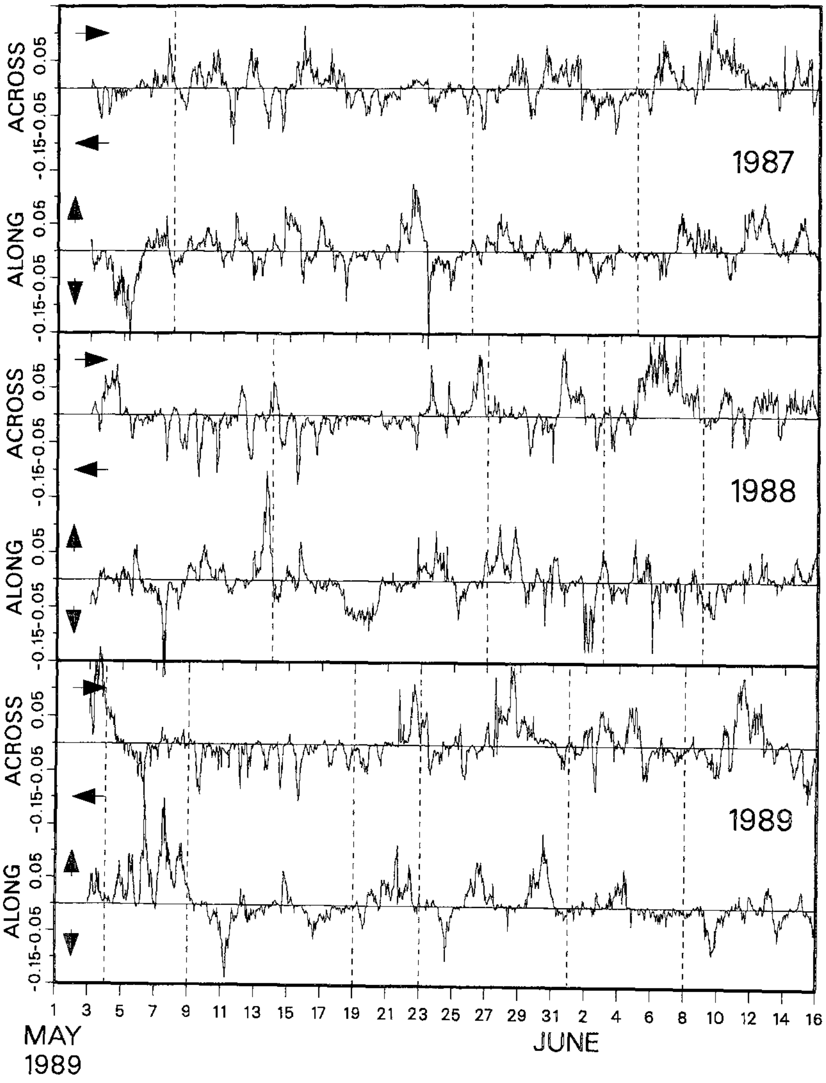

Fig. 10. Wind data from Logan Airport, Boston, for May to June 1987 (top panel), 1988 (middle panel) and 1989 (bottom panel). These data have been rotated into the coordinate system of the coast, so that the coastline runs vertically. The alongshore (ALONG) and across-shore (ACROSS) wind stresses (Pa) are plotted, with the arrows to the left of the plot indicating the direction the stress would act relative to the assumed coastline which is up/down along ordinate. Thus a positive alongshore stress acts to the north (upwelling-favorable). The vertical dashed lines indicate the cruise dates

which is reflected in the high but constant A_{FW} values. In 1988 there was an increase in A_{FW} after a peak in the river flows in late April. The highest amount of fresh water was seen on 19 May 1989 (see also Figs. 6, 7). The values of A_{FW} were generally much higher in 1987 than 1988 or 1989.

Wind patterns

In a coastal ocean, the across-shelf water motions are controlled by the alongshore wind stresses. In 1987, the alongshore wind stress was weak, but mainly upwelling-favorable (northeastward: positive alongshore stresses; Fig. 10). However, all cruises in May and early June of 1987 were preceded by weak or downwelling-favorable winds.

During 1988 the situation was somewhat different than in 1987, as the alongshore wind stress time series shows several strong downwelling-favorable events (19 May, 2 June). The 14 May cruise was preceded by a very strong upwelling-favorable wind (up to 0.15 Pa). The 27 May cruise showed only weak upwelling-favorable winds during a short interval prior to the cruise. The 3 June and 9 June cruises were preceded by strong downwelling-favorable wind stresses.

In 1989 the 9 May, 23 May, and 1 June cruises were preceded by strong upwelling-favorable winds of long duration. Of the cruises shown in Fig. 6, only the 19 May cruise took place after a period of relative calm. The alongshore wind stresses during May and early June 1989 were predominantly upwelling-favorable.

In 1988 and 1989, cruises which were preceded by strong upwelling-favorable wind events showed flat pycnoclines, or pycnoclines which sloped downwards and offshore (e.g. 14 May 1988; 9 May, 23 May and 1 June 1989; Figs. 4, 5 and 6). After strong downwelling-favorable winds, steep fronts sloping downwards and onshore were observed (e.g. 3 June 1988). Weak wind stresses (27 May, 9 June 1988; 19 May 1989) produced fronts sloping downward and onshore, with a broader horizontal extent than was seen after downwelling winds. Cruises during 1987 were generally preceded by weak winds, yet showed nearly horizontal pycnoclines.

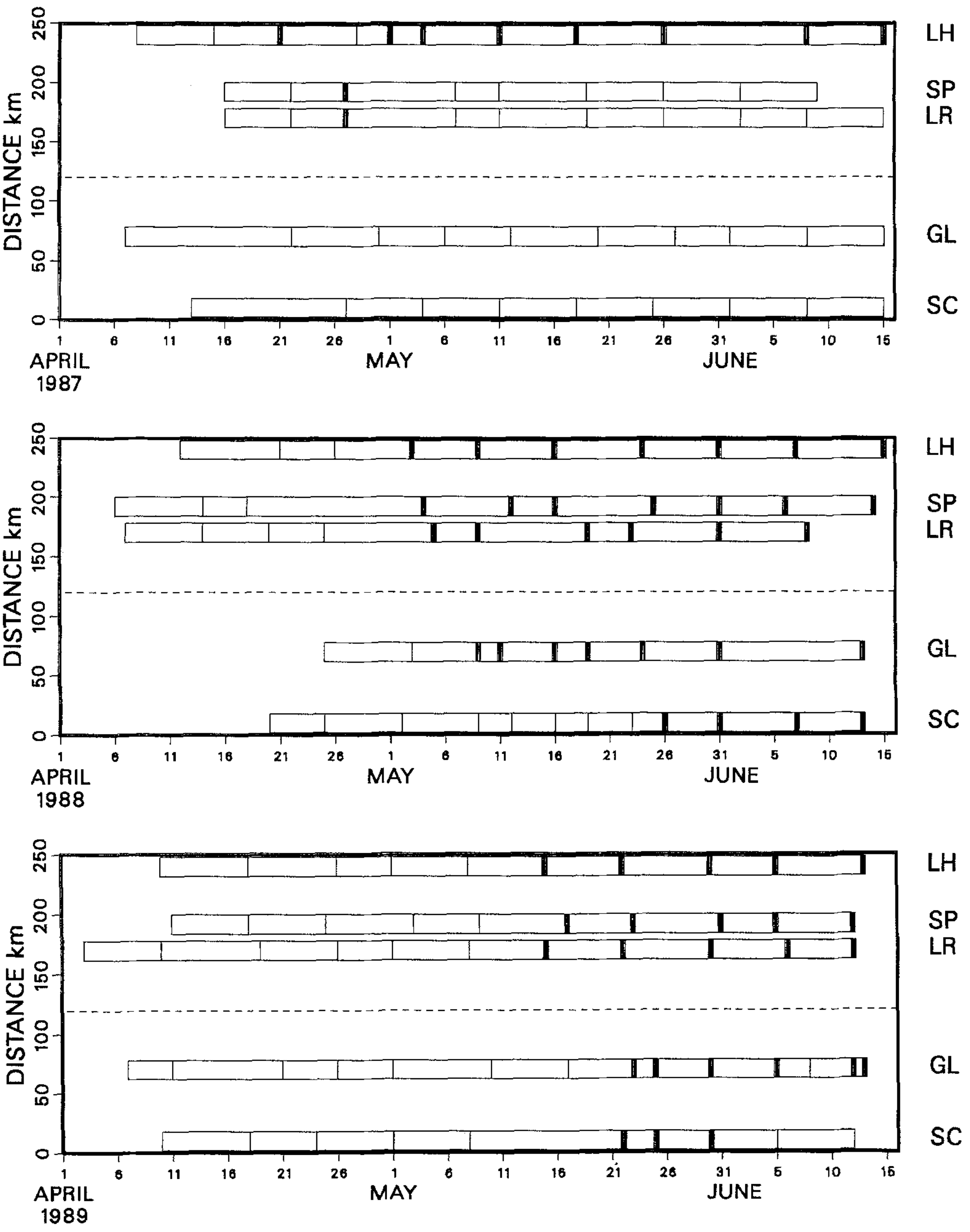

Fig. 11. Time series of binary toxicity at the five stations shown in Fig. 1, for 1987 (top panel), 1988 (middle panel) and 1989 (bottom panel). LH: Lumbos Hole, SP: Spurwink River, LR: Little River, GL: Gloucester and SC: Scituate. The alongshore distances of the stations relative to Scituate are shown on the vertical axis. Vertical bars indicate the sampling dates; heavy vertical bars indicate that the sample was toxic. Horizontal dashed line indicates alongshore location of Portsmouth, New Hampshire

Toxicity

The binary toxicity time series for five stations along the coasts of Maine and Massachusetts have been plotted in Fig. 11 for the years 1987, 1988 and 1989. These time series show considerable variation from year to year. In 1987, toxicity was first detected in late April at the Maine stations. However, no toxic samples were found at any Massachusetts stations during 1987. In 1988, the pattern of toxic outbreaks followed a north-to-south trend: the first toxic sample was recorded in Lumbos Hole on 25 April, then at Gloucester on 8 May, and at Scituate on 26 May. The large sampling interval at Spurwink River early in the year makes it difficult to know the exact date of initiation of toxicity there.

In 1989, the toxicity began much later than in 1987 or 1988, the first toxic sample being recorded at Lumbos Hole on 15 May. As in 1988, the spread of toxicity followed a north-to-south trend, although the time between the initiation of toxicity at Lumbos Hole and at Scituate was only about 7 d. The interval between samples is approximately the same as the transit time of toxicity along the coast, making it difficult to interpret initiation patterns of toxic events for this year.

From the river flow data in Fig. 9 it can be seen that the initial toxic outbreaks are immediately preceded by a peak in the flow of the Androscoggin and Kennebec rivers. The isolated, patchy toxicity in Maine during May 1987 was not preceded by a significant peak in the flow rate, and for the first time since 1972 toxicity was absent from Massachusetts waters. In 1988 and 1989, toxicity followed flow peaks in early May. In 1988 the relatively low peak flow preceded a slow spread of toxicity from north-to-south. In 1989 the very high flow rates of early May preceded a very rapid southward spread of toxicity.

Discussion

In a region of complex coastal hydrography, measurements of a suite of physical and biological parameters for three years document the initial association of cells of *Alexandrium tamarense* with a buoyant plume along the southwestern coast of the Gulf of Maine. The cell distributions followed the distribution of low salinity water, which in turn was influenced by the surface wind stress and topography. The salinity balance of the plume suggests that the sources of this low salinity water were the Androscoggin and Kennebec Rivers, which also show peak flows prior to the detection of toxicity along the coast. These results do not rule out the possibility of in situ growth as a major source of cells in local toxicity; however, the alongshore advection of established populations in a coastally trapped buoyant plume can account for many of the observed patterns of dinoflagellate abundance and PSP toxicity in the study area.

Cell distributions and density structure

The patterns of *Alexandrium tamarense* cells and low salinity water in 1988 and 1989 were very different from 1987. In 1988 and 1989, isolated patches of cells were associated with patches of low salinity (<31.5 psu) water during May, regardless of the location of that water. This across-shelf relationship was also apparent alongshore, as data from 19 May 1989 demonstrate (Fig. 7). In 1987, low salinity water was found throughout the transect, but there was no plume and only low concentrations of *A. tamarense* were measured, late in the bloom season. These cells were found nearshore, within the pycnocline.

The lack of *Alexandrium tamarense* in 1987, despite significant fresh water nearshore, is likely related to the timing of a massive river flow in early April of that year. This huge flux of fresh water caused a freshening of the surface waters of the Gulf of Maine, visible as a thick layer of low salinity water at all stations and in the high proportion of fresh water, A_{FW}, that year (Fig. 9). The usual cyclonic circulation of the Gulf of Maine appears to have been disrupted in 1987, resulting in negligible geostrophic alongshore currents for the greater part of the spring and summer (Brown and Irish unpublished manuscript). Due to low rainfall in early May, no subsequent peak was seen in the river flow, and no sloping pycnocline was visible in the hydrographic surveys. Thus the alongshore transport mechanism of a coastally trapped buoyant plume was apparently weak or absent during the bloom season (May to August) of 1987, consistent with the lack of PSP toxicity in the south of our study area.

The plume

A simple model can be used to estimate the alongshore speed of the buoyant plume. Given the slope of the pycnocline on 27 May 1988, a cruise which was preceded by weak winds, an estimate of the velocities of the upper (low salinity) layer can be made using Margule's equation. This equation assumes a geostrophic balance of forces, homogeneous layers, and a lower layer which is at rest:

$$v = -\zeta \frac{g}{f}\left(\frac{\varrho'-\varrho}{\varrho}\right). \qquad (4)$$

Here v is the velocity of the upper layer (inshore water mass), ζ the slope of the pycnocline, g the acceleration due to gravity, f the Coriolis frequency, and ϱ and ϱ' the upper and lower layer densities, respectively. The slope of the 1024 kg m^{-3} ($\sigma_T=24$) isopycnal on 27 May 1988 gives $\zeta=10^{-3}$. With $g=10$ m s^{-2}, $f=10^{-4}$ s^{-1}, $\varrho=1023.5$ kg m^{-3} and $\varrho'=1025.5$ kg m^{-3}, we find $v\sim0.2$ m s^{-1}. Assuming alongshore uniformity to the plume (as suggested by the satellite image of Fig. 8), this speed is equivalent to a displacement of ~17 km d^{-1} alongshore to the south. At this rate, the plume would travel from Lumbos Hole, Maine, to Scituate, Massachusetts, a distance of 250 km, in ~15 d. The time between the initiation of shellfish toxicity at the two stations was ~23 d in 1988, and ~10 d in 1989, in fair agreement with the calculated velocity.

We can calculate the volume transport of fresh water in the plume, T, from:

$$T = vA_{\mathrm{FW}}. \qquad (5)$$

Using $v=0.2$ m s^{-1}, during 1988 the calculated flux was between 1000 and 2000 m^3 s^{-1}. From Fig. 9, we can see that the average sum of the flows of the Androscoggin and Kennebec rivers was 500 to 1000 m^3 s^{-1} in the spring of 1988. Thus about half of the fresh water in the plume can be accounted for by the discharge from these two rivers by this simple calculation. This is reasonable agreement given the uncertainty in the estimates of A_{FW} and the alongshore velocity, v, which assumed the lower layer to be at rest and neglected wind forcing, discharge rate of the river, shear, and other factors which may influence the alongshore velocities. Other methods of calculating the alongshore velocities (Franks 1990), suggest that 100% of the fresh water in the plume derives from the Androscoggin and Kennebec Rivers.

Wind effects

It was suggested above that the presence of a lens of low salinity water at the surface, offshore, was a result of strong upwelling-favorable winds forcing the coastal plume offshore. Such behavior has been reproduced in a three-dimensional primitive equation wind-forced model of a coastal plume (Chao 1987). In this model a 0.1 Pa upwelling-favorable wind stress was seen to cause detachment of buoyant water from the coast after less than two

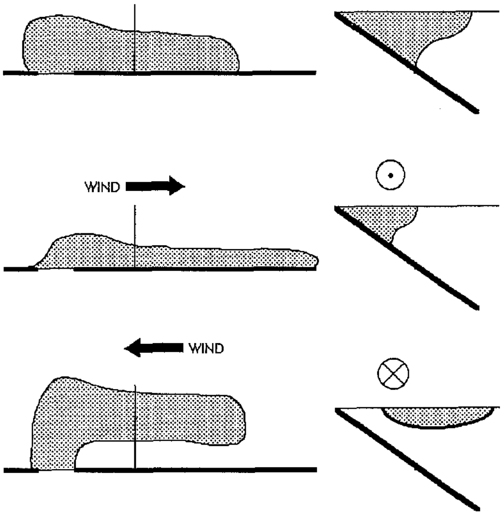

Fig. 12. Surface (left-hand plots) and across-shelf (right-hand plots) salinity distributions for a buoyant plume (stippled portion) under no wind stress (top plots), downwelling-favorable wind stress (middle plots), and upwelling-favorable wind stress (bottom plots). Vertical line indicates transect for section plots on right. Adapted from Chao (1987)

days (Fig. 12). In cross-section, the detached water mass appears as a lens of fresh water, separated from the coast by more saline water, much as was seen on 9 May and 23 May 1989 after major upwelling-favorable wind events (Fig. 6 and 10). The alongshore velocities of Chao's model plume were slowed by upwelling-favorable wind stresses, but the plume continued propagating alongshore against the prevailing wind.

Downwelling-favorable winds were seen to narrow the model plume, and accelerate its propagation alongshore (Chao 1987, Fig. 12). In cross-section, the front forming the plume steepened, and moved shoreward. This is analogous to 3 June 1988 (Fig. 5), when a steep front was observed nearshore after a strong downwelling-favorable wind event. Thus the model of Chao (1987) supports the inference that the across-shelf hydrographic structure of the plume was closely related to the prevailing wind stress. Strong upwelling-favorable wind stresses flattened the sloping front, or separated the plume from the coast and slowed its alongshore progression, while downwelling-favorable winds forced the plume into the coast and sped it alongshore.

Conceptual model

The results discussed above suggest the following conceptual model for the development and spread of toxic dinoflagellates and concomitant shellfish toxicity in the study area between Penobscot Bay, Maine and Massachusetts Bay, Massachusetts:

Source: A source population of cells to the north, possibly associated with the outflow of the Androscoggin-Kennebec estuary

We infer a source population of *Alexandrium tamarense* cells to the north of our study area based on the southward alongshore movement of the Androscoggin-Kennebec plume waters. These cells might originate within the estuary or be concentrated or entrained by its outflow as it enters the Gulf of Maine. Incze and Yentsch (1981) found concentrated populations of *A. tamarense* in an adjacent estuary of relatively low freshwater discharge, and *A. tamarense* cysts are abundant offshore, to the north-east of the Androscoggin-Kennebec estuary (Lewis et al. 1979). Thus the potential for seed populations exists in that area. In contrast, *A. tamarense* cells were undetectable in Portsmouth Harbor, the Merrimack River estuary, or offshore waters early in the bloom. Frontal systems of estuaries have been shown to be sites of dinoflagellate accumulation in a variety of locations (Tyler and Seliger 1978, Incze and Yentsch 1981, Tyler et al. 1982, Tyler 1984). Furthermore, the large estuary (Penobscot) to the north of the Androscoggin-Kennebec estuary (Fig. 1) has historically been devoid of PSP toxins (the "PSP sandwich"; Shumway et al. 1988). This again implies a source population of cells to the south of that estuary.

Timing and volume of outflow: A pulse of freshwater in May carries the growing Alexandrium tamarense population out of the estuary or entrains nearshore populations, causing initiation of toxic events alongshore.

It is likely that years with a large peak flow in May would show extensive alongshore spread of toxicity, with short transit times for initiation of PSP outbreaks the coast. Years of low flow in early May should show longer alongshore transit times, and a close relationship between toxicity patterns and wind stress. Unusually high river flows early in April may suppress the development of the seed population near the estuary, reducing the risk of toxic outbreaks. This occurred in 1987, when record river runoff in early April was followed by relatively low flow. A very early outbreak of toxicity in Maine (21 April 1987) was followed by patchy toxicity, and little alongshore spread. The Massachusetts coast to the south was toxin-free. In 1988 and 1989, the pulse of freshwater was in early May and was immediately followed by extensive toxicity along the coast.

Wind effects: Upwelling-favorable winds force the plume and cells offshore, potentially causing separation of the plume from the coast and a removal of cells from intertidal shellfish. Downwelling-favorable winds hold the plume to the coast, and speed it to the south.

Our hydrographic data follow the predictions of Chao's (1987) model with respect to the formation of offshore lenses, and the influence of surface wind stress on frontal slope. Furthermore, major changes in *Alexandrium tamarense* cell distributions and concomitant shellfish toxicity followed wind events in a predictable manner. The occurrence of toxicity in 1988 at Scituate, Massachusetts, the southernmost station shown in Fig. 11, followed a strong downwelling-favorable wind stress (Fig. 10, 18 May to 20

May) which would have accelerated the plume and cells alongshore to the south. In 1989, the wind events were primarily northward and upwelling-favorable, but were apparently overcome by the large freshwater flux. An alongshore wind stress should generate an alongshore current velocity (Janowitz and Pietrafesa 1980) given approximately by:

$$v = \frac{\tau}{\varrho r}\left(1 - \exp\left(-\frac{rt}{h}\right)\right) \tag{6}$$

where r is,

$$r = \frac{1}{40}\left(\frac{|\tau|}{\varrho}\right)^{1/2}. \tag{7}$$

Thus a wind stress, τ, of 0.05 Pa, a water density, ϱ, of 1024 kg m^{-3}, a water depth, h, of 20 m, and a 1 d duration, t, would produce $v \sim 0.15$ m s^{-1}. This is slightly less than the 0.2 m s^{-1} calculated for the plume velocities using equation (4). Thus in years of high river flow, the plume velocities might overcome the retarding effects of sustained upwelling winds, while in years of low flow, the wind-forced currents may dominate the plume advection. The relatively short time scale of wind events ($\sim$1 d) relative to changes in river flow ($\sim$20 d) also suggest that the plume should show a predominantly southward progression.

Post-initiation bloom structure: Once delivered to the study area, the across-shelf distribution of the Alexandrium tamarense cells can change dramatically.

In 1988, the distribution of *A. tamarense* cells changed from an isolated patch restricted to low-salinity water, to an extensive population associated with the pycnocline and offshore waters. This change may have been due to a variety of mechanisms, including advection of cells across the front, or enhanced growth of populations in offshore waters. Such mechanisms are discussed in Franks (1990).

Summary

The conceptual model described above provides specific hypotheses that can be tested. These include: the presence of a population of *Alexandrium tamarense* in or near the Androscoggin-Kennebec estuary in April; enhanced flow of the Androscoggin and Kennebec Rivers prior to outbreaks of toxicity along the coast; short transit times of initial detection of toxicity along the coast in years of high peak flow; and relatively strong influence of alongshore wind stress in years of low peak flow. These are site-specific hypotheses that do not apply to areas of the Gulf of Maine north of Penobscot Bay. Furthermore, we do not expect our model to explain the pattern of toxic outbreaks that occasionally occur in the fall in our study area; it is likely that different mechansims are acting such as the delivery of offshore populations to inshore waters. This mechanism would be consistent with the observations of Mulligan (1973, 1975) and Hartwell (1975), who suggested that local offshore populations were advected inshore during wind-driven upwelling in the fall of 1972. The present data show that a population of *A. tamarense* existed offshore of the plume front late in the summer (e.g. Fig. 5). This population may have derived from the inshore population present in early May, and could provide the biomass for late-season toxicity.

Data are presented linking the initial distribution of *Alexandrium tamarense* cells in the study area to the alongshore transport of a coastally trapped buoyant plume of water. Many of the implications and hypotheses raised by these data remain to be tested, but our conceptual model explains many of the observed features of blooms in different years, as well as the temporal trends in shellfish toxicity (Hurst and Yentsch 1981, Martin and Main 1981, Shumway et al. 1988). Our data cannot directly assess the relative importance of in situ growth of localized, nearshore populations as hypothesized by Mulligan (1973, 1975), or physical accumulation of dinoflagellates at frontal convergences (Tyler and Seliger 1978, Tyler 1984), but they do emphasize once again the importance of long-distance transport in the general phenomenon of dinoflagellate blooms and shellfish toxicity.

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