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Offshore blooms of the red tide dinoflagellate, *Alexandrium* sp., in the Gulf of Maine

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Abstract

Paralytic shellfish poisoning (PSP) occurs nearly every year in the Gulf of Maine. In a study of dynamics of the causative organism, the toxic dinoflagellate *Alexandrium* sp., we conducted three surveys of the coastal and offshore waters of Gulf of Maine during the summer of 1998, sampling more than 200 stations during each cruise in June, July and August. Hydrographic data were collected and concentrations of phytoplankton chlorophyll, inorganic nutrients and densities of *Alexandrium* cells were measured in discrete water samples. The distributions of *Alexandrium* at the surface and in subsurface waters displayed maximum cell densities in the offshore waters of the Gulf on all three cruises. Highest cell densities in surface waters (ca. 5.5×10^3 cells l^{-1}) were observed in two broad patches: one in the Bay of Fundy and another in shelf and offshore waters of the central and eastern Gulf of Maine in association with the Eastern Maine Coastal Current. Highest subsurface densities of cells appeared to be associated with the frontal edges beyond the cold surface waters associated with the Eastern Maine Coastal Current. As the summer progressed, the highest surface densities of *Alexandrium* receded toward the eastern portions of the Gulf and the Bay of Fundy. We suggest that the offshore distributions of relatively high densities of *Alexandrium* are naturally occurring and can be related to inorganic nutrient fluxes, and to the ambient light field as it varies seasonally and vertically. Locations of high cell densities were described and interpreted using a nondimensional light-nutrient parameter, computed as the ratio of the depth of the 10% surface irradiance to the depth of 4 μM NO_3 concentration. Possible mechanisms responsible for periodic development of PSP outbreaks in nearshore shellfish beds are discussed.

Keywords: Gulf of Maine; Red Tides; *Alexandrium*; Nutrients; Phytoplankton; Hydrography

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1. Introduction

Paralytic shellfish poisoning (PSP) results when humans consume molluscan shellfish that have ingested toxic dinoflagellates of the genus *Alexandrium* (Anderson, 1997; Bricelj and Shumway, 1998), a taxon common in the Gulf of Maine region and known to occur throughout much of the world (Wyatt and Jenkinson, 1997). Blooms of these dinoflagellates are often referred to as red tides because of the discoloration of the surface waters at times of high cell densities, although PSP can result when cell densities are well below that required to color the water (as few as 100–200 cells per liter; Anderson, 1997; J. Hurst, pers. comm.). In the past few decades episodes of PSP in the Gulf of Maine region would appear to have become chronic, appearing nearly every year since 1974 when monitoring activities intensified, although the problem is known to be much older. For example, human deaths attributable to PSP in the Gulf of Maine/Bay of Fundy region date back to 1889 (Ganong, 1889). In addition, as many as 45 people are known to have become ill with PSP in Nova Scotia in 1936, and two people died (Bond, 1975). It was only in relatively recent years, as a result of these episodes, that monitoring and management activities commenced. The first PSP management program was enacted by the Canadians in the Bay of Fundy region of the Gulf of Maine in 1945. Following a PSP outbreak in New Brunswick in 1957, the state of Maine began to monitor for PSP, but almost exclusively in shellfish collected from Maine's eastern-most coastal areas adjacent to New Brunswick (Hurst, 1975). In some years, when toxicity was especially high in the eastern Maine site, testing was conducted along the entire coast of Maine; an example was 1961 when PSP was detected along most of the Maine coast, although the levels were not high enough to close shellfish harvesting areas. Especially high toxicity recorded in the 1960 s in shellfish collected from Maine's outer islands, Matinicus and Monhegan Islands (Fig. 1), led to their being permanently closed to shellfish harvesting; as a result, routine monitoring for PSP is no longer performed there.

Perhaps the most infamous PSP outbreak in the Gulf of Maine outside of the Bay of Fundy occurred in mid-September 1972, affecting areas of Massachusetts, New Hampshire and western-most Maine. Patches of colored water were reported inshore at the height of the bloom, with cell densities between 7×10^5 and 2.6×10^6 cells l^{-1}; the cells were identified then as *Gonyaulax tamarensis,* now known as *Alexandrium tamarense* (Sasner et al., 1975). (As many as three species of *Alexandrium* may be present in the Gulf of Maine (Anderson, 1997), and we refer here only to *Alexandrium* sp.) Primarily in response to the 1972 bloom, an expanded, state-wide monitoring program for PSP on Maine's coast was started in 1974 (Hurst, 1975) and continues today.

The 1972 red tide event was perceived by many to have been the first significant PSP outbreak in the western Gulf of Maine (Bicknell, 1975), but neither the causes of the 1972 bloom nor of the PSP events that have followed nearly every year on the Maine coast since that event have been adequately explained. This communication presents results of field work conducted in 1998 which, for the first time, allows a direct comparison of aspects of the oceanography of the Gulf of Maine with abundances and distributions of *Alexandrium*.

2. Methods

We conducted oceanographic surveys of the coastal and offshore waters of the northern Gulf of Maine from New Hampshire to the outer Bay of Fundy during the summer 1998, collecting data

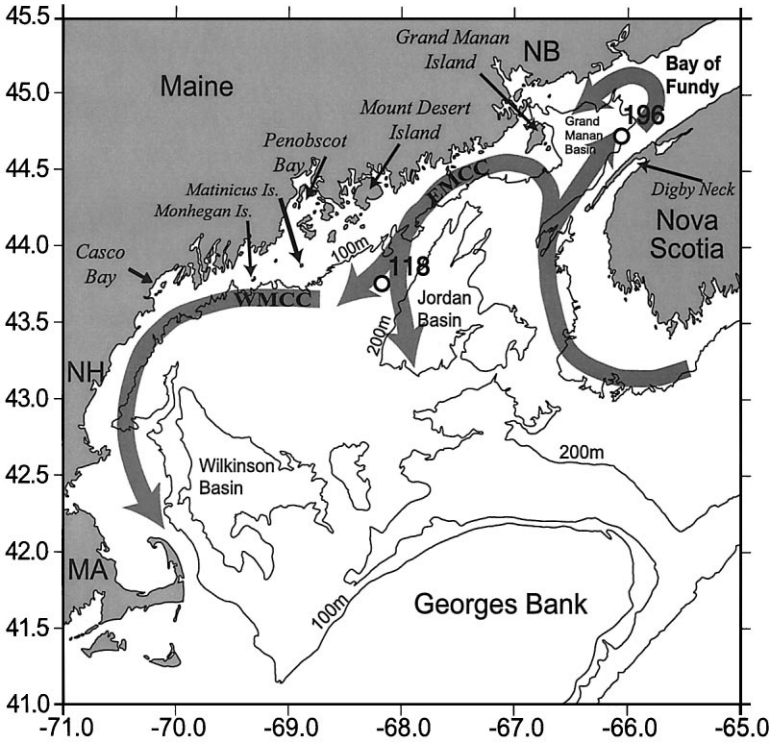

Fig. 1. Map of the Gulf of Maine and Bay of Fundy region, showing the 100 m and 200 m isobaths, and locations referred to in the text. Arrows approximate the residual coastal surface circulation; the Eastern Maine Coastal Current (EMCC) and Western Maine Coast Current (WMCC) are indicated. The locations of Stations 118 and 196, referred to in the text, are given.

from more than 200 stations on each of three cruises (6–16 June and 6–16 July on the R/V *Cape Hatteras*, and 4–17 August on the R/V *Oceanus*). On each cruise CTD casts were made at all stations and water samples were collected using a rosette sampler and Niskin bottles. Stations were sampled around the clock, meaning that some were sampled during daylight hours and others at night. An underwater PAR (photosynthetically active radiation) sensor and an in situ fluorometer were mounted on the CTD package; PAR data were used only at stations sampled between 0800 and 1800 h. Water samples from various depths were collected for analyses of phytoplankton chlorophyll (fluorometric analyses of acetone extracts of particulate material collected from 100 ml on GF/F glass fiber filters; Parsons et al., 1984) and inorganic nutrients. Nutrient samples were filtered through Millipore HA filters, placed immediately in a sea water-ice bath for 5–10 min, and frozen at $-18^{\circ}C$ to be analyzed following the cruises for $NO_3 + NO_2$, NH_4, $Si(OH)_4$ and PO_4 using a Technicon II AutoAnalyzer and standard techniques. Water samples for the enumeration of *Alexandrium* cell densities were collected from the surface (2 m depth) and a deeper depth; this second sample was collected at the depth of the subsurface chlorophyll maximum layer, if present as indicated by the in situ fluorometer trace; when no subsurface maximum was apparent it was collected at 20 m. Two liters of water from each of the two sample depths at each station were sieved through a 20 μm mesh screen, the concentrate preserved in a

5% formaldehyde sea water solution, and stored in 20 ml vials in a refrigerator. Two stations sampled during the July survey (Fig. 1) included vertical profiles of *Alexandrium* cell densities, as well as *T*, *S*, chlorophyll and nutrients, from 12 depths. Quantitative counts of *Alexandrium* cells were based on epifluorescence microscopy and an immunological stain specific to the genus *Alexandrium* (provided by D.M. Anderson, Woods Hole Oceanographic Institution, based on the method of Adachi et al., 1993). A subsample of 5 ml (from the 20 ml vial) was filtered onto a 5 μm pore size polycarbonate filter, stained, and placed on a microscope slide; a drop of 80% glycerin was placed on the filter and covered with a coverslip. All *Alexandrium* cells on the filter were counted; in cases where there were more than about 1000 cells per filter, a new slide was prepared with a smaller subsample volume. Areal contour plots of the above parameters were made using Surfer software (Golden Software, Golden, Co., USA), with checks against actual data to ensure fidelity. Sea surface temperature measurements during each cruise were made by AVHRR (Advanced Very High Resolution Radiometer) satellite data received and processed at the University of Maine's ground station.

3. Results

Contours of the surface water distributions of *Alexandrium* and the corresponding satellite images of sea surface temperature for each of the survey cruises are shown in Figs. 2–4. Maximum surface cell densities were observed primarily in offshore waters for all three surveys, and not immediately adjacent to the shoreline as one might initially expect, based on historically reported patterns of shellfish toxicity. Highest cell densities were observed in two broad patches: one in the Bay of Fundy, and another in the Gulf of Maine proper which was relatively confined to shelf and offshore waters south of Penobscot Bay and the eastern Maine coast. We will refer to each of these patches of cells as Bay of Fundy and Gulf of Maine populations. Figs. 2–4 show that as the summer progressed the highest surface densities of *Alexandrium* receded toward the eastern portions of the Gulf and the Bay of Fundy; that is, cell densities increased from June to August in the Bay of Fundy population, while Gulf of Maine cell densities decreased and contracted toward the east from June to August. Comparing the *Alexandrium* surface distributions with sea surface temperatures we see that highest cell densities in the Gulf of Maine were correlated spatially with the cold surface waters that characterize the Eastern Maine Coastal Current system. Maximum surface cell densities in the Bay of Fundy were located more in the southern half of the outer Bay, perhaps in association with cooler, but stratified waters flowing into the Bay and carrying elevated nutrients from vertical mixing in the western Nova Scotian shelf region.

The distributions of *Alexandrium* cells beneath the surface (Fig. 5) were dissimilar to the near surface distributions. Subsurface cell densities in June were not as high as at the surface, and reached densities greater than 600 cells l^{-1} at only a few stations; maximum surface cell densities were 4×10^3 cells l^{-1}, while maximum subsurface densities were 2×10^3 cells l^{-1}. Also, the distinction between a Gulf of Maine and Bay of Fundy population was not as clearly defined as for the surface waters, with the Bay of Fundy population having much lower subsurface cell densities than the surface waters. The pattern of subsurface cell densities in the Gulf of Maine in June extended farther to the southwest and offshore than the surface distributions did, and may be related to the frontal edges of the Eastern Maine Coastal Current and its offshore plume as

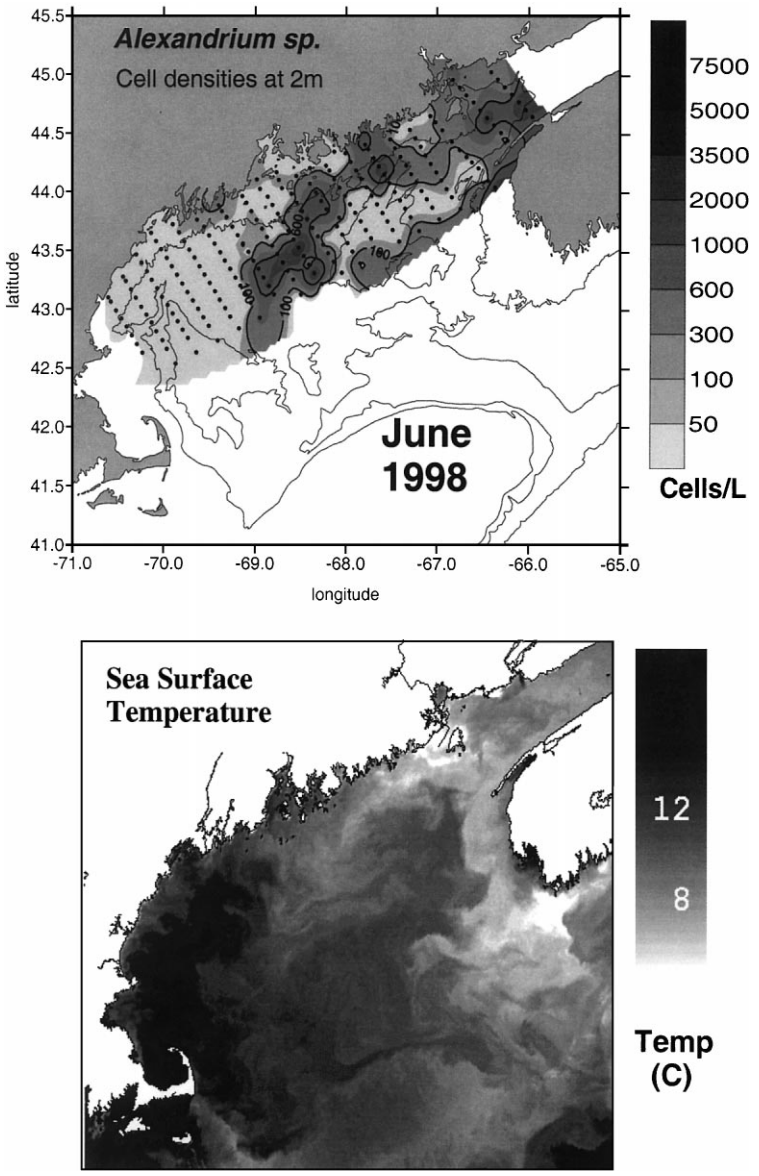

Fig. 2. Contours of cell densities (number of cells l^{-1}) of *Alexandrium* sp. at 2 m depth for the June 1998 survey cruise along with the corresponding AVHRR satellite image of sea surface temperature (Yearday 153). Note compressed scale for *Alexandrium* plot. The 100 and 600 cells l^{-1} contour lines are given. Station locations are indicated.

suggested by inspection of the sea surface temperatures in Fig. 2. In July the two populations could be discerned from one another as cell densities in the Gulf of Maine and Bay of Fundy increased markedly (Fig. 5). Like the June subsurface distributions, relatively high densities of subsurface cells in July appeared to be located farther offshore and to the southwest than cells at the surface. Maximum cell densities in July were ca. 5×10^3 cells l^{-1} at the surface and $> 10^5$ cells l^{-1} subsurface (at one station 29 m depth; Fig. 5). Subsurface cell densities in August

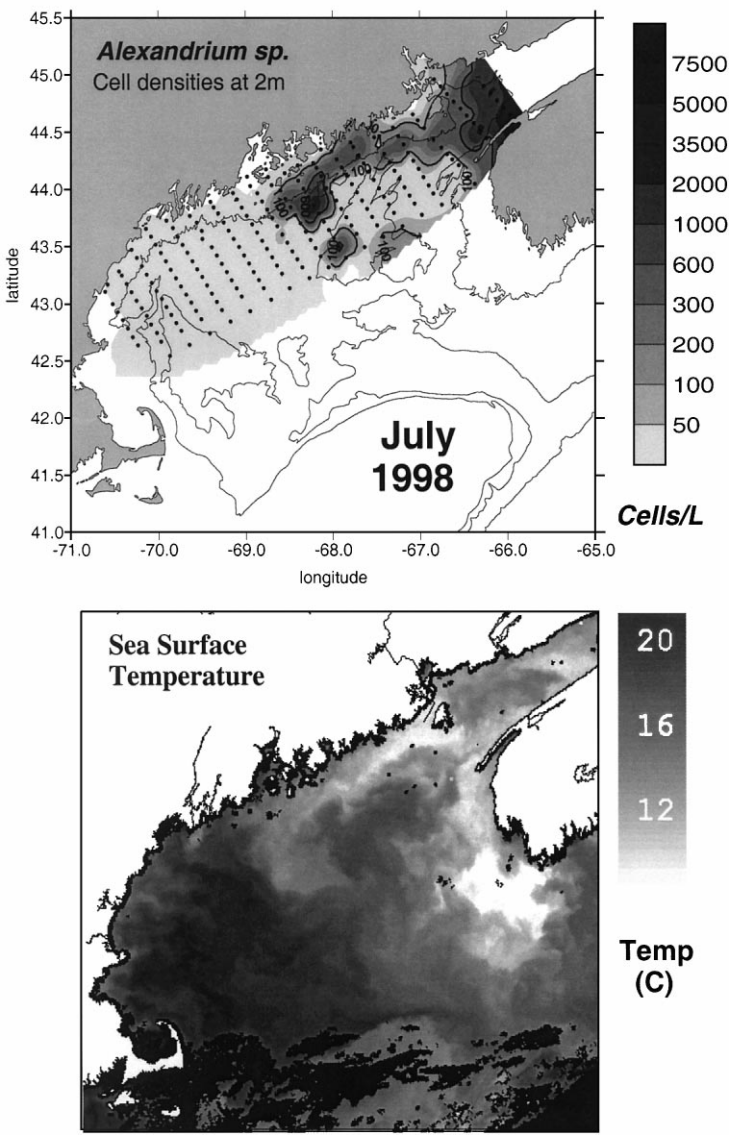

Fig. 3. Contours of cell densities (number of cells of l^{-1}) of *Alexandrium* sp. at 2 m depth for the July 1998 survey cruise along with the corresponding AVHRR satellite image of sea surface temperature (Yearday 200). Note compressed scale for *Alexandrium* plot. The 100 and 600 cells l^{-1} contour lines are given. Station locations are indicated.

remained high in the Bay of Fundy but decreased in the Gulf of Maine; the subsurface cell distributions again extended farther to the southwest and offshore than the surface distributions. Maximum densities in August were 5.2×10^3 cells l^{-1} and 8.6×10^3 cells l^{-1} at the surface and subsurface, respectively.

Because our survey cruises sampled around the clock, some cell density data were collected at stations sampled during the daylight hours and some during darkness. This difference in sampling

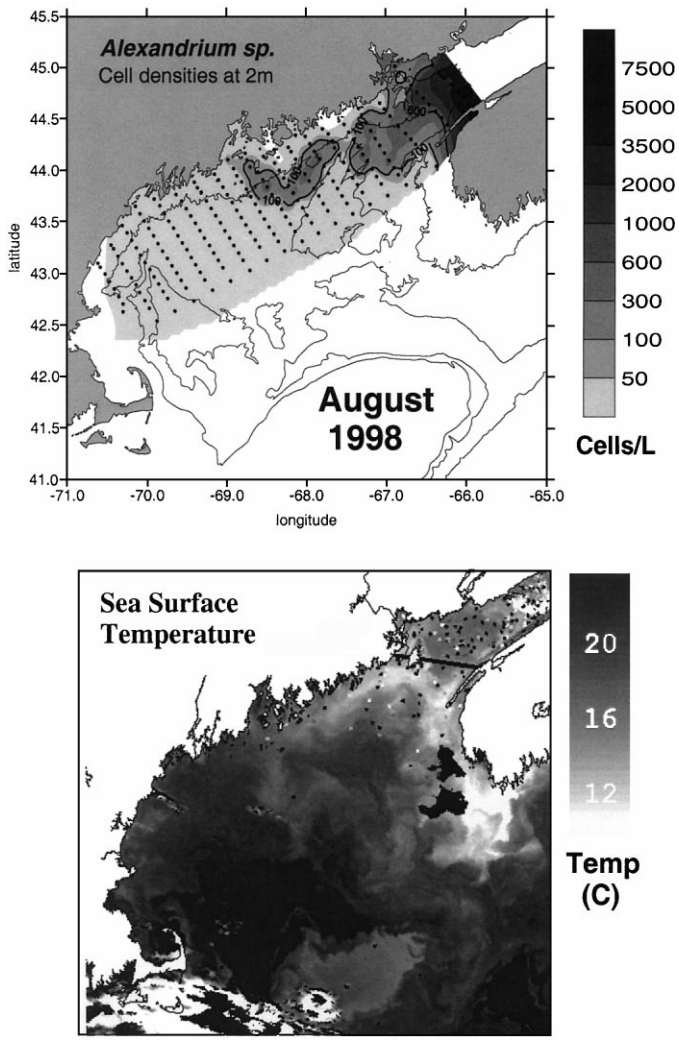

Fig. 4. Contours of cell densities (number of cells l^{-1}) of *Alexandrium* sp. at 2 m depth for the August 1998 survey cruise along with the corresponding AVHRR satellite image of sea surface temperature (Yearday 218). Note compressed scale for *Alexandrium* plot. The 100 and 600 cells l^{-1} contour lines are given. Station locations are indicated.

times could potentially introduce artifacts in the distribution plots should the populations of *Alexandrium* we were studying be exhibiting diel vertical migratory behavior. However, inspection of the three cell density plots (Figs. 2–4) and the locations of stations sampled during daylight hours (between 0800 1800 h; e.g., Fig. 10) reveal no apparent coherence. That is, the patch structures revealed in the surface cell distributions do not appear to be dependent in any clear way on the time of day that they were sampled, which would indicate a lack of diel migratory behavior.

Vertical profiles of *Alexandrium* cell densities, temperature, salinity, density (σ_t), *in situ* chlorophyll fluorescence, and dissolved inorganic nutrients at Stations 118 and 196 in July (Fig. 1) are given in Fig. 6. Both stations were sampled during daylight hours; Station 118 at 14 : 32 and

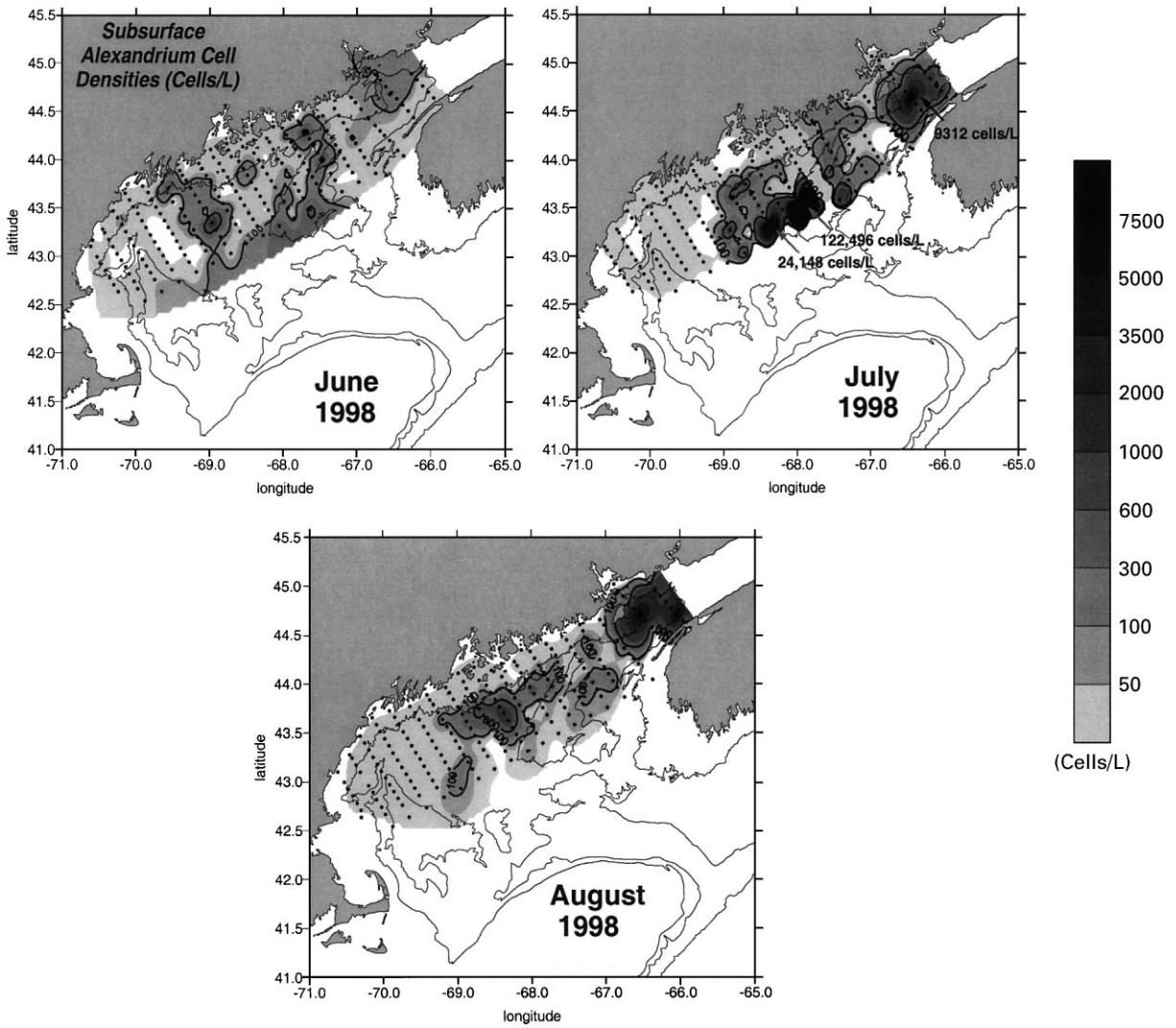

Fig. 5. Contours of cell densities (number of cells l^{-1}) of *Alexandrium* sp. at either the depth of the subsurface chlorophyll maximum, or 20 m depth (for those stations that did not exhibit a subsurface chlorophyll maximum) for the June, July and August 1998 survey cruises. The 100 and 600 cells l^{-1} contour lines are given. Densities of cells (off the scale) at three stations are indicated.

Station 196 at 14 : 20 local time, each about 1.5 h after local apparent noon. Station 118 was located south of the outer front delineating the Eastern Maine Coastal Current and displayed moderate vertical stratification, with a pycnocline between 10 and 20 m. Inorganic nutrients were depleted in the upper 20–25 m and increased sharply between 25 and 40 m. Densities of *Alexandrium* cells at Station 118 were low, displaying a double peak of about 3×10^2 cells l^{-1} at 2 and 20 m. Station 196 was located in the Bay of Fundy (Fig. 1), where there was a sharp thermocline and pycnocline between 5 and 10 m. Nutrient concentrations were also depleted at the

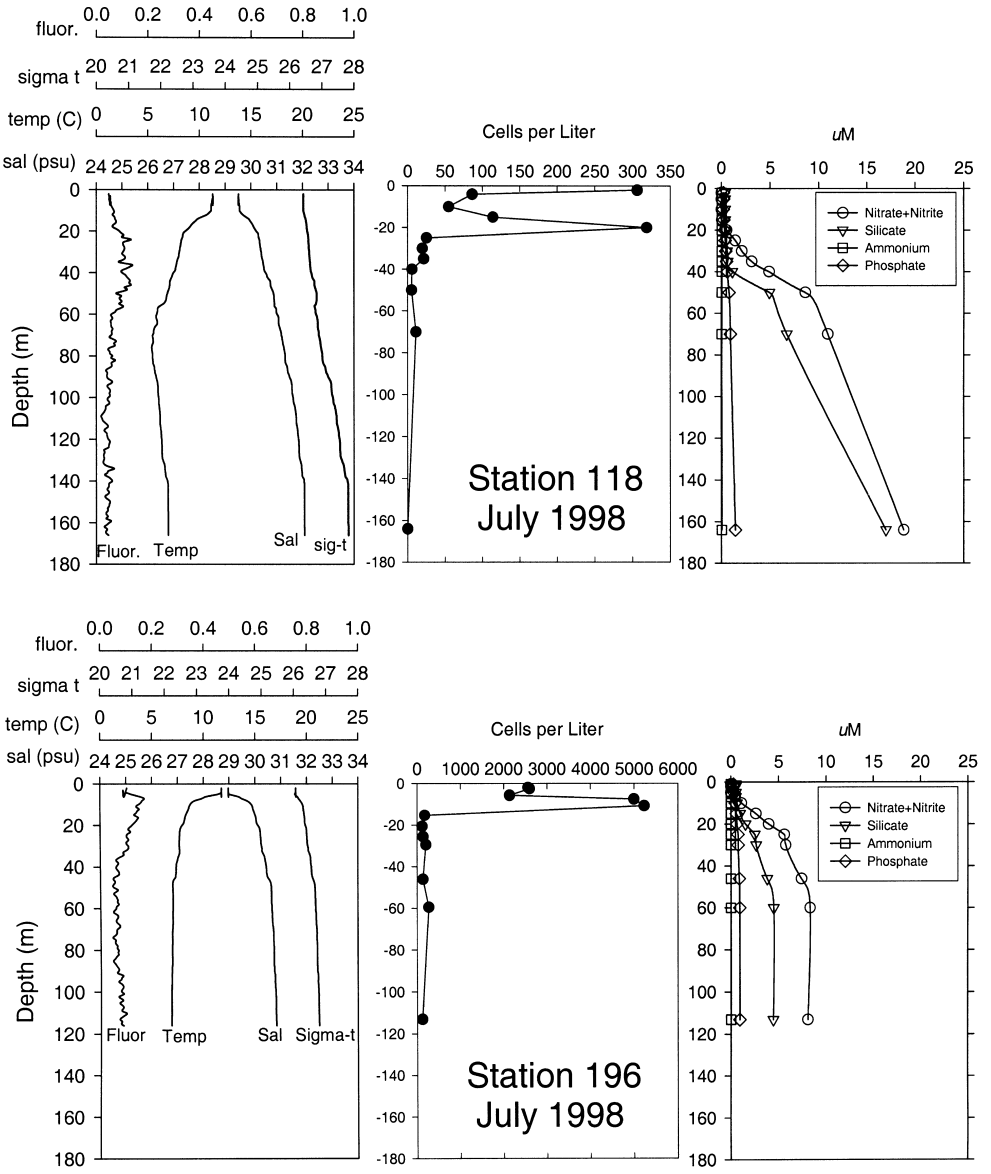

Fig. 6. Vertical profile plots of temperature, salinity, sigma-t, in situ chlorophyll fluorescence, *Alexandrium* cell densities, and concentrations of inorganic nutrients ($NO_3 + NO_2$, NH_4, $Si(OH)_4$ and PO_4) at Stations 118 and 196 (Fig. 1) in July 1998.

surface there, but unlike Station 118, concentrations increased with depth beginning at 10 m. *Alexandrium* cell densities at Station 196 were much higher than at Station 118, between 2 and 2.5×10^3 cells l^{-1} at the surface and more than 5×10^3 cells l^{-1} at the base of the pycnocline (10 m).

Surface (2 m) spatial patterns of each of the dissolved inorganic nutrient concentrations were similar to one another ($NO_3 + NO_2$, NH_4, $Si(OH)_4$ and PO_4) for all three cruises; all were highest

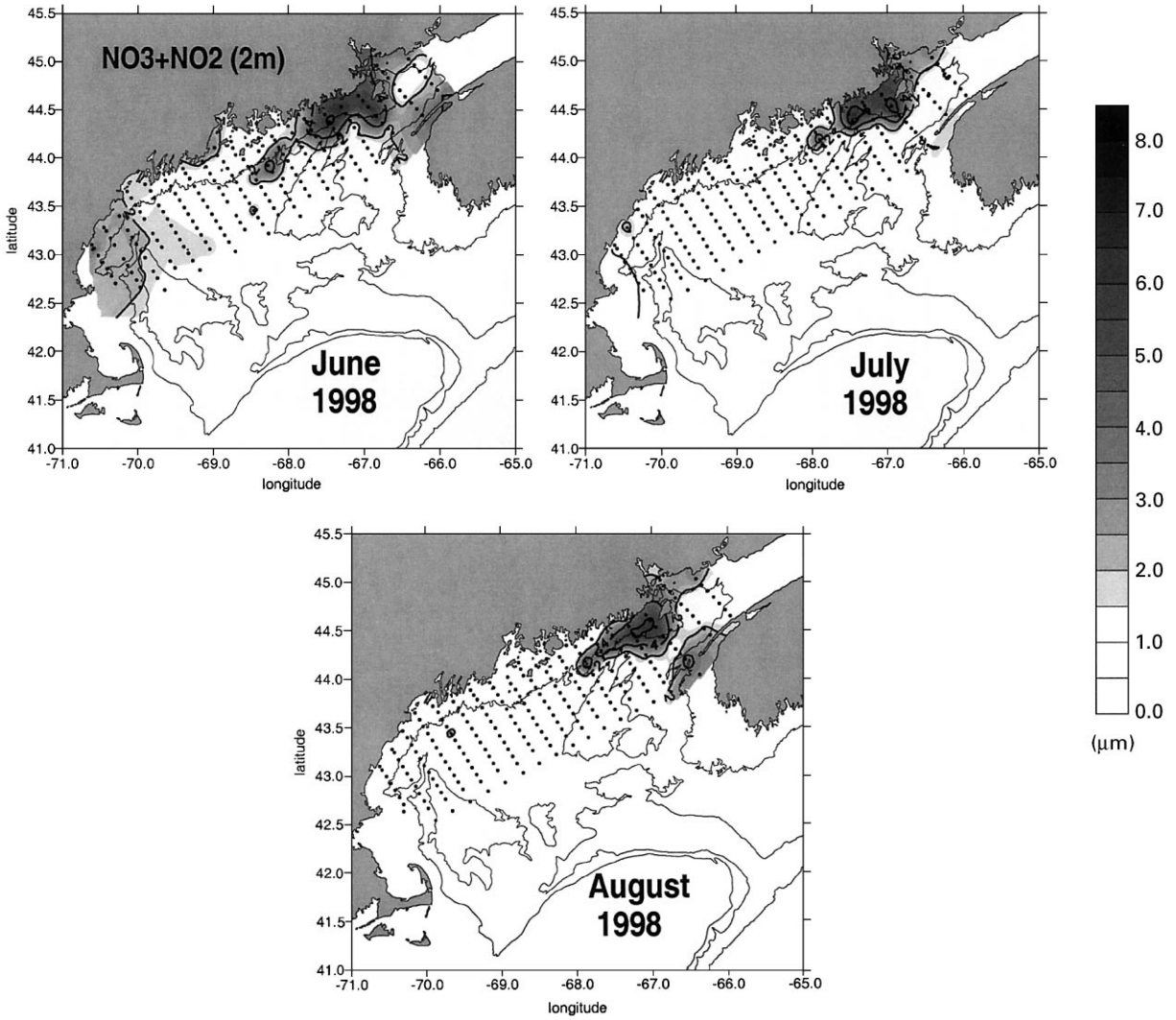

Fig. 7. Surface (2 m) concentrations of nitrate + nitrite for the June, July and August 1998 survey cruises.

in the eastern Gulf of Maine and near the western Nova Scotian shelf and southern Bay of Fundy in the vicinity of Digby Neck. This pattern is shown in Fig. 7 for surface nitrate + nitrite on each survey. Levels greater than 6 μM $NO_3 + NO_2$ were confined to the eastern Gulf of Maine, described earlier as a region of intense vertical mixing at the upstream end of the Eastern Maine Coastal Current (Townsend et al., 1987; Brooks and Townsend, 1989; Pettigrew et al., 1998). Elevated nitrate + nitrite concentrations off Nova Scotia and the southern Bay of Fundy reached 4–5 μM in surface waters. Because surface nutrient concentrations provide little information on potential nutrient availability to near-surface phytoplankton populations, we have also plotted the integrated nitrate + nitrite from the surface to 25 m, based on a polynomial fit to the profile

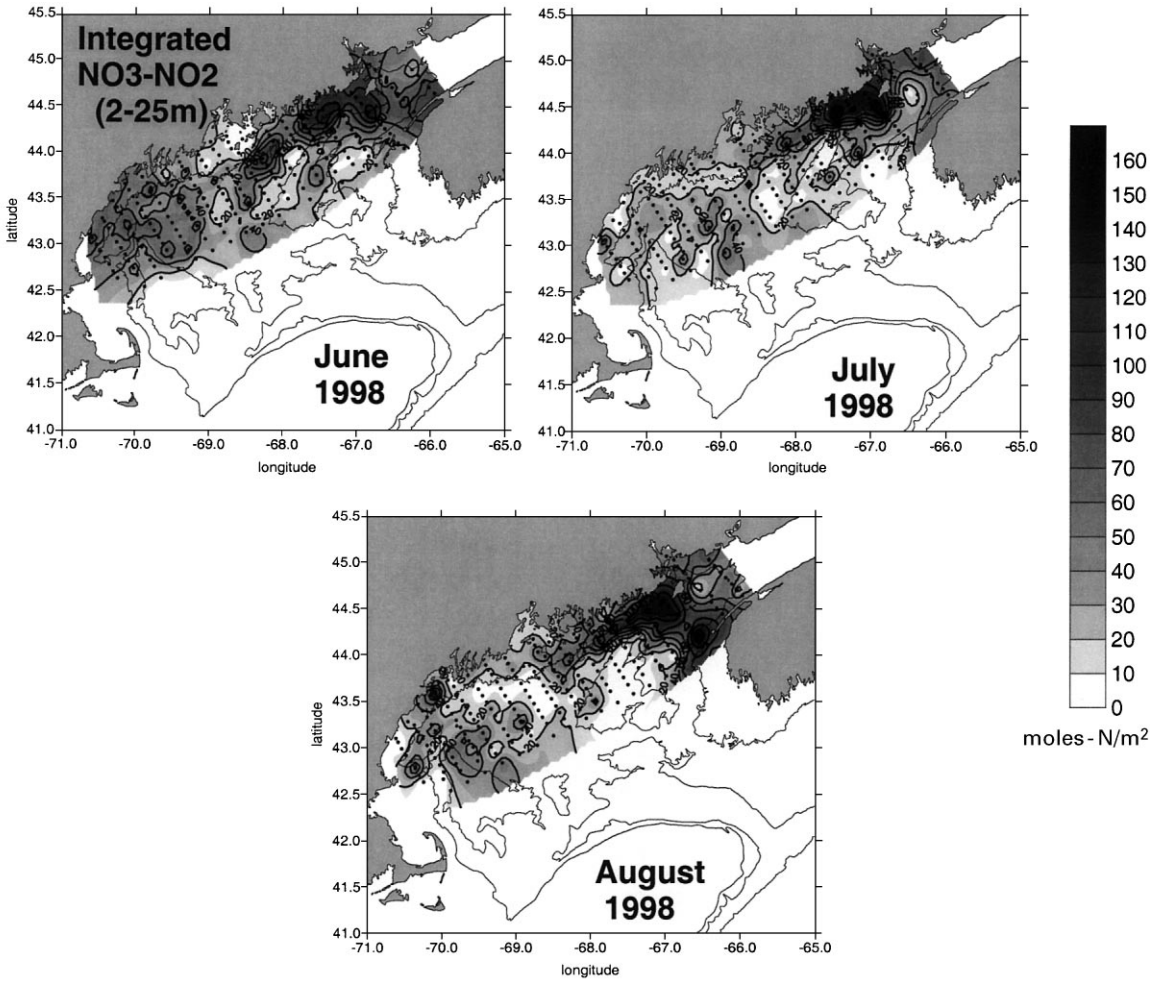

Fig. 8. Integrated nitrate + nitrite from the surface to 25 m for the June, July and August 1998 survey cruises.

data for each station. Contours of integrated nitrate + nitrite illustrate the delivery of high nutrient waters to the central and western Gulf of Maine, as part of the Eastern Maine Coastal Current, and show more clearly the elevated nutrients in the southern Bay of Fundy (Fig. 8).

Phytoplankton chlorophyll concentrations were highest along the Maine coast during all three survey periods, with relatively high levels ($>4\,\mu g\,l^{-1}$) extending farthest offshore south of Penobscot Bay (Fig. 9). High offshore chlorophyll levels may be related to elevated nutrient concentrations and advective features of the Eastern Maine Coastal Current (Fig. 1) as has been described earlier (Townsend et al., 1987). There was no apparent correlation between chlorophyll concentrations and *Alexandrium* cell densities (compare Fig. 9 with Figs 2–4). Highest chlorophyll concentrations were located shoreward of maximum *Alexandrium* cell densities and, based on the low densities of other phytoplankton species in our $>20\,\mu m$ *Alexandrium* samples, these high

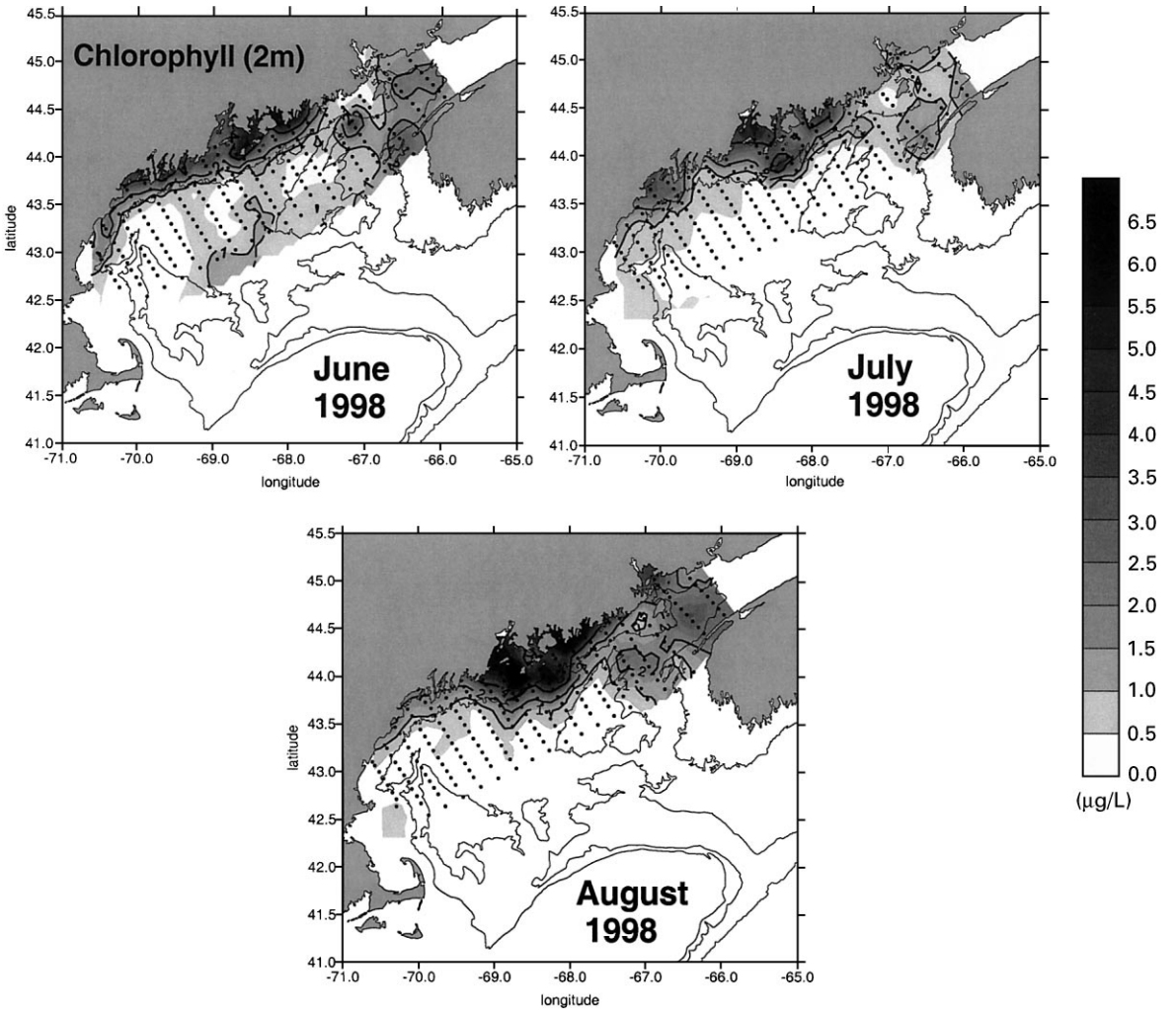

Fig. 9. Surface (2 m) concentrations of phytoplankton chlorophyll *a* for the June, July and August 1998 survey cruises. The 1, 2 and 4 $\mu g l^{-1}$ concentration contour lines are indicated.

chlorophyll levels likely reflect the contribution of the nanophytoplankton and smaller size fractions (e.g., $<20\,\mu m$).

Water transparency, expressed as percent of surface irradiance, was greatest in the offshore waters of the Gulf, especially in the eastern Gulf and over Jordan Basin (Fig. 10). Light penetration in the eastern Gulf and Bay of Fundy did not change markedly between June and July, but it decreased some in the western Gulf, as shown by the position of the 30 m isopleth in Fig. 10. Because of instrument problems in August, fewer data are available with which to draw conclusions; however, it did appear that light penetration generally decreased between July and August.

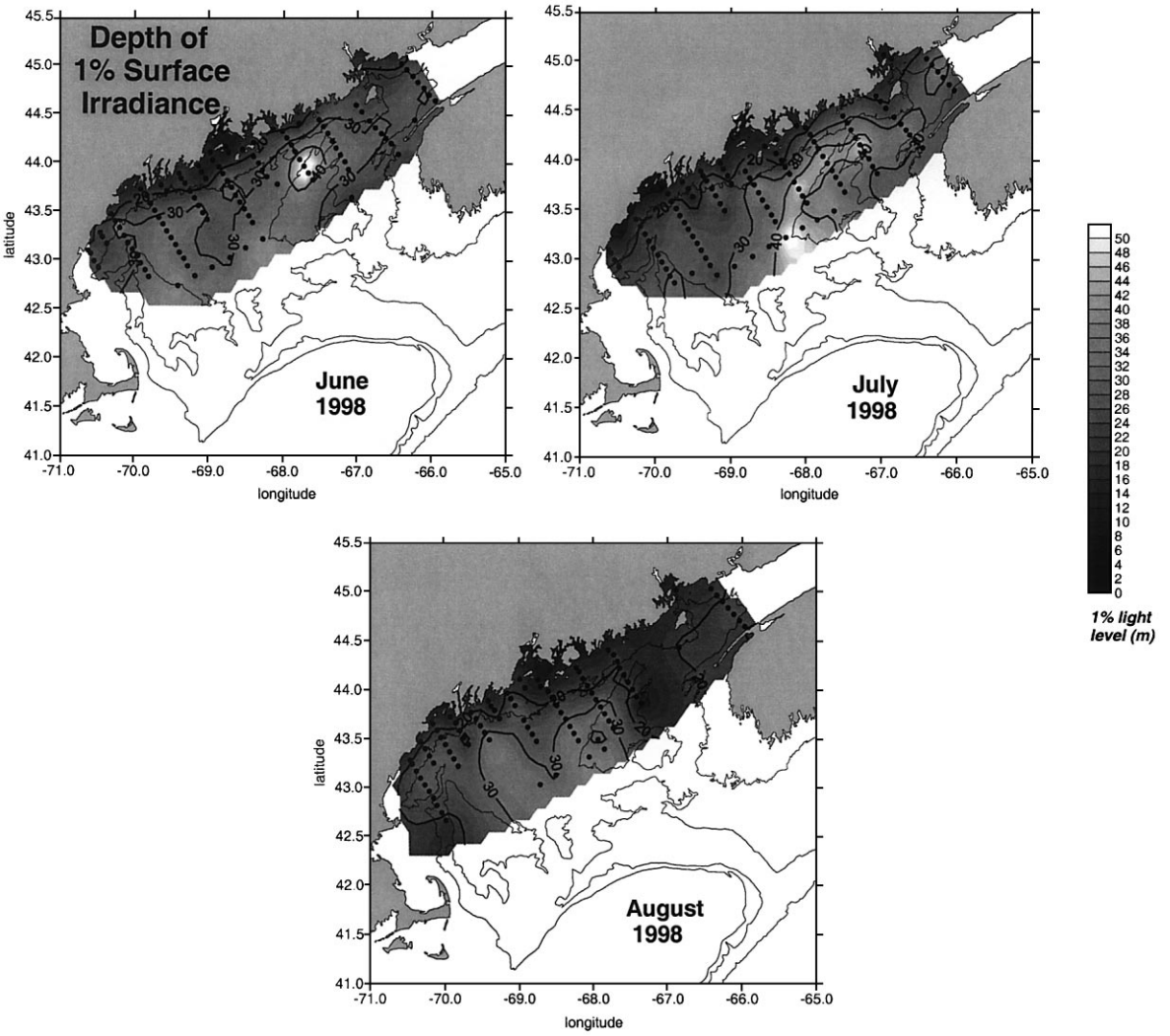

Fig. 10. Depth of the 1% surface irradiance for all stations sampled between 0800 and 1800 h in during the June 1998 survey cruise, based on CTD profiles with an attached PAR sensor. Station locations are indicated.

4. Discussion

Our observations of relatively high densities of *Alexandrium* sp. cells offshore is consistent with results reported by Martin and White (1988). They observed high densities of *Alexandrium* sp. (10^5–10^6 cells per liter) within the Bay of Fundy in four of the five years of their study, and in one of the two years that they extended their sampling into the Gulf of Maine, they observed similarly high cell densities in a band of water offshore in the eastern Gulf of Maine. Although Martin and White (1988) did not report hydrographic results, the patch of cells they observed in the eastern Gulf was roughly coincident with the location of the core of the well-mixed, cold, and nutrient-

rich Eastern Maine Coastal Current system (Townsend et al., 1987; Brooks and Townsend, 1989; Bisagni et al., 1995; Pettigrew et al., 1998; Fig. 1), and is similar to our observations reported here.

The coincidence of high densities of *Alexandrium* cells with the Eastern Maine Coastal Current could explain the "sandwich" phenomenon reported years ago by Hurst and Yentsch (1981) and Yentsch et al. (1986) and Shumway et al. (1988). The "sandwich" phenomenon is the commonly observed lack of PSP along a stretch of the Maine coast between the western edge of Penobscot Bay and an area east of Mount Desert Island, Maine (Fig. 1), while sampling sites to the east and west of this stretch of coastline usually do exhibit PSP. The "sandwich" portion of the Maine coast is generally coincident with the location of the offshore-directed flow of the Eastern Maine coastal Current (Brooks and Townsend, 1989; Bisagni et al., 1995; Pettigrew et al., 1998; Fig. 1). Our observations of highest densities of *Alexandrium* in the offshore waters suggest their advection within the Eastern Maine Coastal Current, which, upon deflecting away from the coastline, transports cells farther offshore, thus denying a portion of the Maine shoreline, and its shellfish resources, access to *Alexandrium* cells. Because part of this offshore-directed flow of the Eastern Maine Coastal Current branches back toward the coastal waters of the western Gulf of Maine (Bisagni et al., 1995; Pettigrew et al., 1998) the usually high PSP levels known to occur on Matinicus and Monhegan Islands might be so explained. Close inspection of Fig. 2 shows a filament of cold surface water that appears to have flowed toward shore on the western side of Penobscot Bay, carrying *Alexandrium* cells with it. Pettigrew et al. (1998) have shown that the degree of this connection between the eastern and western components of the coastal current is highly variable, making it difficult to generalize the nature of the connection between high densities of *Alexandrium* in offshore waters of the eastern Gulf with inshore shellfish beds in the western Gulf.

Relatively high *Alexandrium* cell densities in association with the Eastern Maine Coastal Current are probably associated with favorable growth conditions resulting from both greater water transparency and high nutrient concentrations. These eastern Gulf of Maine waters are known to have the highest surface concentrations of inorganic nutrients of any area of the Gulf of Maine region (Townsend et al., 1987; Townsend, 1998); furthermore, species of *Alexandrium*, and most large dinoflagellates in general, are known to have high light and high nutrient affinities (Eppley and Thomas, 1969; Eppley et al., 1969; Langdon, 1987; Chang and McClean, 1997). However, a comparison of patterns of surface nitrate + nitrite concentrations from 1998 (Fig. 7), water transparency (Fig. 10) and cell densities (Figs. 2–5) did not reveal any clear and direct correlations. In order to assess the potential combined effects of light and nutrients as they might affect *Alexandrium* growth dynamics and thus explain the distributions of high cell densities throughout the region, we computed a nondimensional light-nutrient parameter that represents the suitability of light and nutrient fields as they might relate to a phytoplankton population requiring high levels of each. We computed the ratio of the depth of the 10% surface irradiance (based on our PAR profiles at daytime stations) to the depth of the 4 μM nitrate concentration (based on a polynomial fit to the inorganic nitrogen profiles at each station). The value of each variable was selected to correspond with a relatively high light requirement (Langdon, 1987; Rasmussen and Richardson, 1989; Chang and McClean, 1997) and with earlier estimates of half saturation constants for nitrate uptake based on laboratory experiments on *Alexandrium* species (MacIsaac et al., 1979; Chang and McClean, 1997). Higher values of this light-nutrient parameter would be expected to correlate with areas of relatively higher growth rates of *Alexandrium*. The spatial distribution of the light-nutrient parameter in June (Fig. 11) shows two general areas of

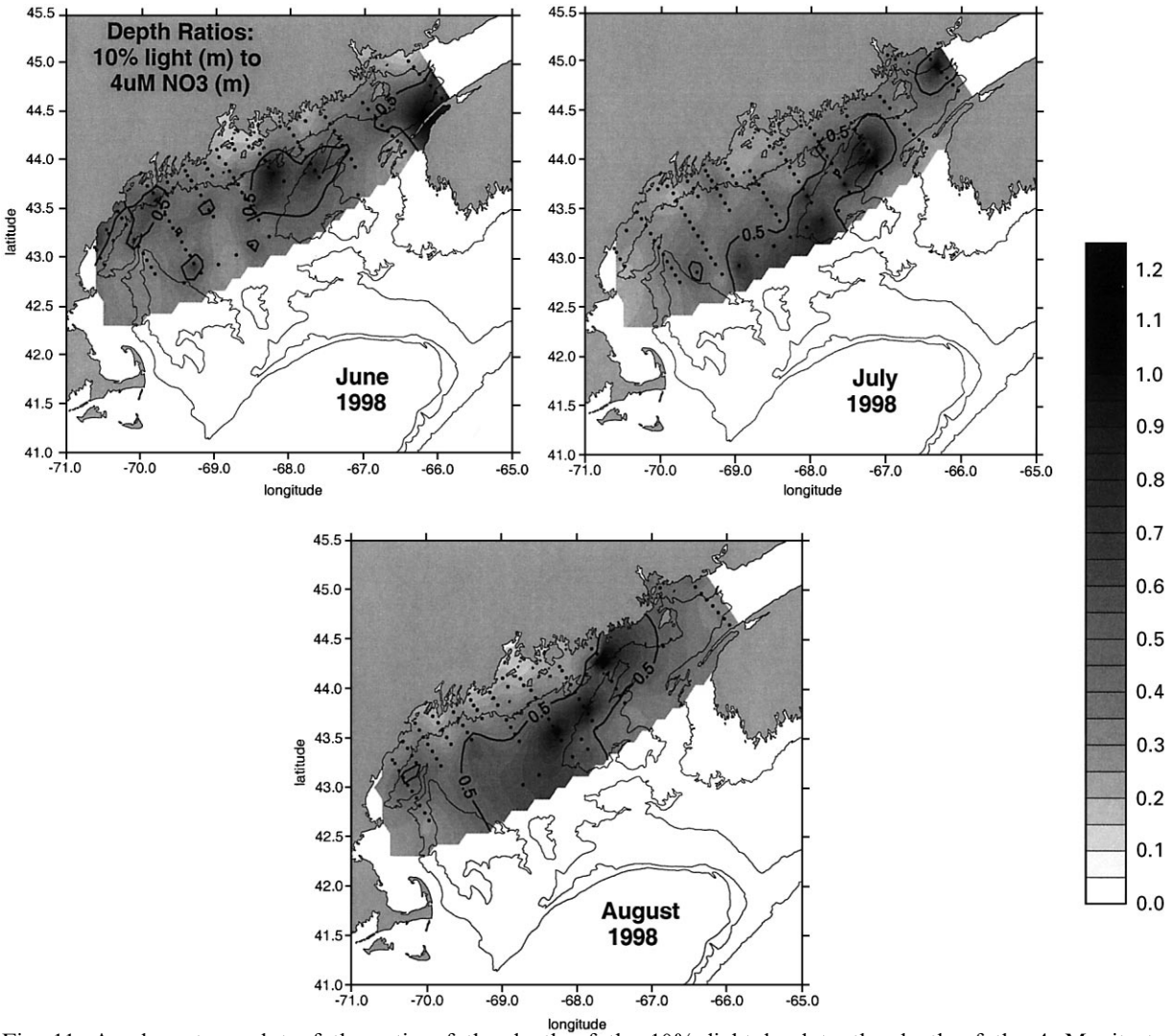

Fig. 11. Areal contour plot of the ratio of the depth of the 10% light level to the depth of the 4 μM nitrate concentration in the Gulf of Maine–Bay of Fundy region during the June, July and August 1998 survey cruises. Station locations are indicated.

higher values (e.g., indicated by the 0.5 contour, a value picked arbitrarily), one in the Bay of Fundy, and another off the mid-Maine coast. The light-nutrient parameter would appear to predict well the high surface densities of *Alexandrium* cells seen in the southern Bay of Fundy, which we presume result from relatively high growth rates in an area of favorable growth conditions. Waters in this part of the Bay receive inputs of nutrient-rich waters from the tidally well-mixed western Nova Scotian Shelf and the Digby Neck region (Denman and Herman, 1978). The vertical profile taken at Station 196 in July in the Bay of Fundy (Fig. 6) shows a shallow pycnocline and nutricline, which would promote growth of *Alexandrium* cells nearer the surface, in a stable surface layer of relatively high light yet still in waters where vertical fluxes apparently

maintain relatively high nutrient concentrations. The Gulf of Maine surface water population off the mid-Maine coast in June, however, displayed a distinct offset from the >0.5 light-nutrient parameter; highest cell densities occurred farther to the southwest (e.g., compare Figs. 2 and 11). This offset most likely reflects advection of cells within the Eastern Maine Coastal Current, which is carrying cells away from a region of intense vertical mixing and new nutrient fluxes farther upstream to the northeast. A vertical cross section of nitrate + nitrite with associated surface *Alexandrium* cell densities (Fig. 12) illustrates conditions upstream of the highest cell densities, and within the area of presumed optimal light-nutrient parameter values (e.g., in Fig. 11). Highest cell densities along that transect occur within and along the frontal edges of the high nutrient core of the Eastern Maine Coastal Current, although those cell densities are not as high as farther downstream (6 to 8×10^2 cells l^{-1} versus 1 to $>5 \times 10^3$ cells l^{-1}).

Current speeds in the Eastern Maine Coastal Current vary from about 25 cm s^{-1} (or about 20 km d^{-1}) near Grand Manan Island to about 10–15 cm s^{-1} (ca. 10 km d^{-1}) off Mount Desert Island (Pettigrew et al., 1998). On either side of the central core of the current the speeds drop off. Speeds continue to slow as the Eastern Maine Coastal Current extends into the warmer waters of the western Gulf where the flow begins to form eddies and perhaps undercuts the surface, as shown in the satellite SST images in Figs. 2–4. A population of *Alexandrium* cells at the position of the transect in Fig. 12 would be carried to the regions of highest cell densities, 50–70 km away, in approximately 5–10 days. At an estimated growth rate of 0.3 divisions d^{-1} (MacIntyre et al., 1997) the population of cells shown in Fig. 12 (6 to 8×10^2 cells l^{-1}) could divide on the order of 2–3 times and grow to densities from 1.2×10^2 to 6.4×10^3 cells l^{-1}, which would encompass the range of cell densities we observed. The subsequent fate of those cells at the distal end of the Eastern Maine Coastal Current is uncertain, however, and may include continued transport to the Western Maine Coastal Current, out over the central Gulf of Maine, or they may be advected beneath surface waters in the western Gulf, as the subsurface cell distributions suggest (Fig. 5). Cells emanating from these offshore surface and subsurface populations may at times be the source of cells responsible for western Gulf of Maine PSP events inshore; we discuss this possibility below.

In all three of our surveys, surface cell densities were uniformly low in the western portions of the Gulf of Maine, west of the most obvious influence of the Eastern Maine Coastal Current which extends only to a point approximately south of Penobscot Bay (Fig. 1). This demarcation between warmer western Gulf of Maine surface waters and the extent of the influence of the cold Eastern Maine Coastal Current is easily seen in satellite images of sea surface temperature. Low surface cell densities in the west is consistent with predictions based on our nondimensional light-nutrient parameter, which throughout the western Gulf had values generally below the arbitrarily defined 0.5 parameter threshold, indicating lower than optimal growth conditions there. The low values of the light-nutrient parameter in the west is due to lower nutrient concentrations rather than light transmission. Fig. 8 shows that integrated down to 25 m, nutrient levels drop off quickly beyond the influence of the Eastern Maine Coastal Current. A more sharply defined pycnocline in the western Gulf, evident as warmer surface waters in the satellite images, effectively retards the upward flux of deep nutrients.

The light-nutrient parameter did not correlate well with Gulf of Maine surface water *Alexandrium* populations in July and August (Fig. 11), while it continued to be an effective predictor of good growth conditions for the Bay of Fundy population, which continued to grow

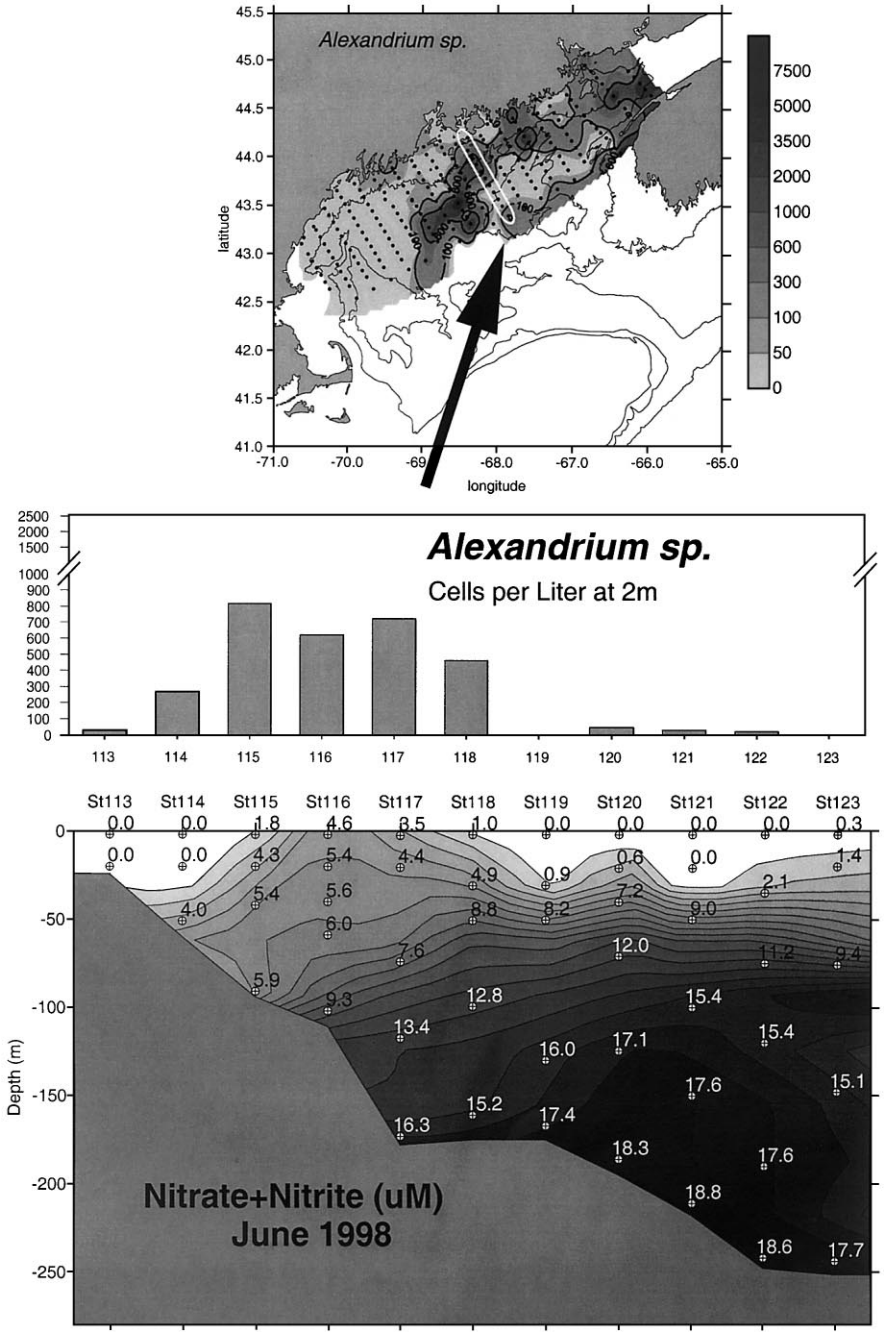

Fig. 12. Vertical cross section of nitrate + nitrite concentrations along the transect indicated on the contour plot of *Alexandrium* cell densities; bar graph shows surface (2 m) *Alexandrium* cell densities at each station along the transect, June, 1998.

throughout the summer. Because the light-nutrient parameter is relative and does not include actual ambient light levels, it does not account for differences in solar irradiance from the beginning to the end of our sampling period from June to August. Were it to incorporate actual light levels as they change with season we might expect it to predict a recession of cell densities, following the summer solstice, toward the eastern Gulf of Maine where nutrient levels remain high. Greater nutrient fluxes in the east would at least partially compensate for diminishing light as summer progresses; this interpretation is in keeping with our observations of surface cell densities. For example, Sverdrup et al. (1946) reported average light reaching the sea surface at 42°N 66–70°W (southern Gulf of Maine) as: $0.329\,\mathrm{gCal\,cm^{-2}\,min^{-1}}$ ($954\,\mu\mathrm{E\,m^{-2}\,s^{-1}}$) in June, $0.302\,\mathrm{g\,Cal\,cm^{-2}\,min^{-1}}$ ($878\,\mu\mathrm{E\,m^{-2}\,s^{-1}}$) in July and $0.267\,\mathrm{gCal\,cm^{-2}\,min^{-1}}$ ($776\,\mu\mathrm{E\,m^{-2}\,s^{-1}}$) in August, which is a 19% decrease from June to August. Overall highest cell densities in surface waters (e.g., more stations with elevated cell densities) occurred in June, which is when solar insolation is maximal. As summer progressed, cell densities decreased in the surface waters of the Gulf, remaining relatively high only in the eastern-most part of the Gulf proper where nutrient concentrations are highest. On the other hand, we observed that surface cell densities increased from June to August in the southern Bay of Fundy. This increase might be explained in terms of the relatively closed gyre-like circulation feature over Grand Manan Basin (Greenberg, 1983) which is thought to retain cells within that part of the Bay of Fundy (Martin and White, 1988). Greater vertical fluxes of nutrients in the southern Bay and a longer retention time in the Bay allow the population to grow to high cell densities. In addition, vigorous tidal mixing in the Bay of Fundy region (tidal range $>8\,\mathrm{m}$) maintains a shallow, steep pycnocline and a sharp nutrient gradient with relatively high nutrient concentrations at its base (Fig. 6). Retention of surface waters here for extended periods, as compared with the highly advective nature of the eastern Gulf of Maine, could thus allow an *Alexandrium* population to reach high densities by their either residing at or near the shallow nutricline or by vertically migrating between the shallower, high light depths and the relatively shallow nutricline (e.g., MacIntyre et al., 1997). We suspect that sufficiently high nutrient levels are too deep in the western Gulf for vertical migration behavior to be advantageous, given estimates of swimming speeds on the order of $5–10\,\mathrm{m\,d^{-1}}$ (Eppley et al., 1968).

The distributions of the Gulf of Maine *Alexandrium* population of cells beneath the surface did not correspond directly with the surface cell distributions for any of the three survey cruises. Instead, the subsurface distributions extended beyond those of the surface waters in a manner consistent with their being associated with the frontal edges of the Eastern Maine Coastal Current waters, both at the downstream end to the southwest, and along the southern edge. It is possible that *Alexandrium* cells in some parts of those subsurface distributions (Fig. 5) are actively growing, being located at depths of relatively high nutrient concentrations near and in the nutricline, while still experiencing sufficient light levels. Light penetration is greatest offshore of the maximum surface cell densities (Figs. 2–4), as indicated by the location of the 30 m isopleth for the 1% light depth (Fig. 10), and is roughly coincident with maximum subsurface cell densities (Fig. 5). However, some stations had very high cell densities (e.g., see Fig. 5) at depths below the 1% surface light intensity where we would expect growth to be light limited. We suspect that those high densities represent aggregations resulting from Eastern Maine Coastal Current water undercutting less dense surface waters to the south and southwest. The subsurface population of *Alexandrium* cells in the Bay of Fundy was in waters with less light penetration than in the

offshore Gulf of Maine, but nutrient levels were higher nearer the surface, suggesting that they were actively growing. Notwithstanding the forgone discussion, the general trends revealed in the light-nutrient parameter throughout the summer (Fig. 11) would not rule out the possibility of suitable growth conditions at depth where the high densities of subsurface *Alexandrium* cells were observed.

The ultimate source each year of the two seasonal *Alexandrium* populations we have been discussing is either resting cysts formed the previous year (Anderson and Wall, 1978) or vegetative cells that remain in the water column throughout the winter. As part of its life history *Alexandrium* cells, after dividing vegetatively for some time, will under the right (but poorly understood) conditions, produce resting cysts, which are negatively buoyant and which usually sink and become deposited in surficial sediments (Anderson, 1997). After a sufficiently long gestation period, usually by the beginning of the next year's growth season (Anderson and Wall, 1978), and in response to (again) poorly understood environmental cues, the cysts germinate. The resulting vegetative cell must then make its way to the surface to photosynthesize and begin the bloom cycle anew. *Alexandrium* cysts have been found in surficial sediments throughout the coastal and offshore Gulf of Maine (Thayer et al., 1983), with especially high densities occurring in Grand Manan Basin in the Bay of Fundy (White and Lewis, 1982). Either overwintering vegetative cells, resting cysts in the surficial sediments, or some other source of cysts, perhaps cysts that remain suspended in the tidally well mixed water column (e.g., Nehring, 1996), are required to initiate the populations we observed. In order to explain how the Gulf of Maine and Bay of Fundy *Alexandrium* populations reached the densities of cells we measured, and at the locations we observed them, we must know a number of things, including the locations and rates of supply of new cells, the vegetative growth rates, the advection rates, and the vertical migratory behavior of *Alexandrium*. Some of this information is available from earlier work. Laboratory experiments suggest the vegetative growth rate of *Alexandrium* to be on the order of 0.3 divisions d^{-1} (MacIntyre et al., 1997). We also know that resting cysts occur throughout the Gulf of Maine, but highest concentrations in surficial sediments are found in Grand Manan Basin (White and Lewis, 1982) and in deep (>80 m) offshore patches west of Penobscot Bay (Anderson, unpublished). We also know that while there appears to be a retention mechanism operating in the Bay of Fundy, which allows cells to grow to high densities before being flushed from that system, the Gulf of Maine population is growing in waters that are highly advective, as discussed earlier. Finally, vertical migratory behavior of *Alexandrium* has been demonstrated in the laboratory (MacIntyre et al., 1997), but field verification is lacking, making interpretations of data such as ours more difficult. For cells to reach densities of 1000 cells l^{-1} as seen offshore approximately 50 km west of Grand Manan Island in June (Fig. 2) they would have to do so in about 2–4 days as they are advected in the fast-moving (25 cm s^{-1}) Eastern Maine Coastal Current. For example, assuming a growth rate of 0.3 divisions d^{-1}, an initial supply of newly germinated cells, or overwintered vegetative cells, in the eastern Gulf (adjacent to Grand Manan Island) would need to total approximately 500 cells l^{-1} in the surface waters in order to reach 1000 cells l^{-1} by the time they are advected 50–70 km downstream; but actual cell densities observed in the Grand Manan area in June are nearer 100 cells l^{-1}.

Whether the source of cells for the Gulf of Maine population is excystment at the upstream portion of the Eastern Maine Coastal Current, cells that are lost to the Gulf of Maine from the Bay of Fundy population, or low background densities of overwintering vegetative cells

throughout the Gulf of Maine region, or some combination of each, is unknown. Furthermore, we do not know how *Alexandrium* cells in the eastern Gulf are vertically distributed. In addition to vegetative growth, swimming and changes in vertical mixing depth might work together to increase cell densities. Relatively low concentrations of cells distributed deeper in the water column in the more tidally-mixed eastern Gulf of Maine could, as a result of their limited swimming capabilities (e.g., Seliger et al., 1979; Rasmussen and Richardson, 1989), become more concentrated at the surface (or deep layers) at some point farther downstream as those waters become progressively more vertically stratified. This would create higher surface cell densities without the need to invoke high grow rates. A similar phenomenon could occur in the horizontal dimension as cells concentrate at convergences and eddies (Seliger et al., 1979; Rasmussen and Richardson, 1989); indeed close inspection of Figs. 2–4 reveal numerous complex eddy features that correspond closely with areas of highest cell densities. Further speculation about requisite source distributions and abundances is premature in the absence of addition information on the vertical distributions and vertical migratory behavior of *Alexandrium*.

One of the most significant findings in our study is that the highest densities of A*lexandrium* cells are offshore, not immediately adjacent to the shoreline. If PSP in shellfish along the shoreline results from cells delivered there from offshore populations, a physical mechanism needs to be invoked. PSP is rare in eastern Maine (producing the "sandwich" phenomenon discussed earlier), but it is common along the shores of the western Gulf. It is possible that part of the Eastern Maine Coastal Current continuing beyond Penobscot Bay along the Maine coast to become the Western Maine Coastal Current is responsible for advecting cells to the coastal waters of the western Gulf of Maine. Close inspection of Fig. 2 provides a hint of evidence of this phenomenon; a filament of cold water from the western-most end of the Eastern Maine Coastal Current plume can be seen connecting with the Maine coast, with apparently low densities of *Alexandrium* associated with it. The high toxicities at Matinicus and Monhegan Islands discussed earlier are likely one result of this connection between offshore *Alexandrium* blooms in the eastern Gulf and the western coastal current systems.

Episodic phenomena that could promote advection of more offshore waters toward shore would include Ekman transport resulting from east and northeast wind events. Such episodic events could seed the Western Maine Coastal Current with cells that could then be transported into nearshore environments. Indeed, it is interesting to speculate that the infamous 1972 red tide could have been one such event. The 1972 bloom was preceded two weeks earlier by Tropical Storm *Carrie*, which tracked directly across the center of the Gulf of Maine with winds speeds of about 50 knots. The direction and speed of those winds were such that they could have advected *Alexandrium* cells residing offshore late in the season toward the coast where they would become part of the coastal current system. Interestingly, winds from the opposite direction could also have an influence. Coastal upwelling-favorable winds, commonly observed in summer (Anderson, 1997) could facilitate shoreward transport of populations of cells residing at depths below the Ekman layer.

Finally, onshore transport of cells to nearshore shellfish beds is not the only mechanism responsible for PSP events. It is important to point out that local initiation of *Alexandrium* populations inshore is well documented and is thought to be responsible for events in the Casco Bay region and environments throughout the western Gulf of Maine (Anderson, 1997). Similar to our observed patterns of *Alexandrium* in offshore waters, we would also expect them to grow well in shallow waters with elevated nutrient concentrations, especially in waters under the influence

of urban freshwater runoff which would facilitate formation of a shallow, nutrient-rich surface layer.

In summary, offshore blooms of *Alexandrium* would appear to be naturally-occurring phenomena in the Gulf of Maine-Bay of Fundy region, based on our 1998 survey results, our mechanistic interpretation based on the combined influences of light and nutrients, and considering historical lines of evidence. Outbreaks of PSP in inshore waters may, at times, be related to episodic wind events that deliver offshore waters and *Alexandrium* cells into the coastal region where cells could be redistributed along the coast as part of the coastal circulation pattern.

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References

Adachi, M., Sako, Y., Ishida, Y., 1993. Application of monoclonal antibodies to field samples of *Alexandrium* species. Nippon Suisan Gakkaishi 59, 1171–1175.

Anderson, D.M., 1997. Bloom dynamics of toxic *Alexandrium* species in the northeast U.S. Limnology and Oceanography 42, 1009–1022.

Anderson, D.M., Wall, D., 1978. Potential importance of benthic cysts of *Gonyaulax tamarensis* and *G. excavata* in initiating toxic dinoflagellate blooms. Journal of Phycology 14, 224–234.

Bond, R.M., 1975. Management of PSP in Canada. In: LoCicero, V.R. (Ed.), Proceedings of the First International Conference on Toxic Dinoflagellate Blooms. Massachusetts Science and Technology Foudation, Wakefield, MA, pp. 473–482.

Bicknell, W.J., 1975. The first "red tide" in recorded Massachusetts history. In: LoCicero, V.R. (Ed.), Proceedings of the First International Conference on Toxic Dinoflagellate Blooms. Massachusetts Science and Technology Foudation, Wakefield, MA, pp. 447–457.

Bisagni, J.J., Gifford, D.J., Ruhsam, C.M., 1995. The spatial and temporal distribution of the Maine Coastal Current during 1982. Continental Shelf Research 16, 1–24.

Bricelj, V.M., Shumway, S.E., 1998. Paralytic shellfish toxins in bivalve molluscs: Occurrence, transfer kinetics, and biotransformation. Reviews in Fisheries Science 6, 315–383.

Brooks, D.A., Townsend, D.W., 1989. Variability of the coastal current and nutrient pathways in the eastern Gulf of Maine. Journal of Marine Research 47, 303–321.

Chang, F.H., McClean, M., 1997. Growth responses of *Alexandrium minutum* (Dinophyceae) as a function of three different nitrogen sources and irradiance. New Zealand Journal of Marine and Freshwater Research 31, 1–7.

Denman, K.L., Herman, A.W., 1978. Space-time structure of a continental shelf ecosystem measured by a towed porpoising vehicle. Journal of Marine Research 36, 693–714.

Eppley, R.W., Holm-Hansen, O., Strickland, J.D., 1968. Some observations on the vertical migration of dinoflagellates. Journal of Phycology 4, 333–340.

Eppley, R.W., Rogers, J.N., McCarthy, J.J., 1969. Half-saturation constants for uptake of nitrate and ammonium by marine phytoplankton. Limnology and Oceanography 14, 912–920.

Eppley, R.W., Thomas, W.H., 1969. Comparison of half-saturation constants for growth and nitrate uptake of marine phytoplankton. Journal of Phycology 5, 375–379.

Ganong, W.F., 1889. The economic Mollusca of Acadia. Bulletin of the Natural History Society of New Brunswick 8, 1-116 (cited in Bond, R.M., 1975).

Greenberg, D.A., 1983. Modelling the mean barotropic circulation in the Bay of Fundy and Gulf of Maine. Journal of Physical Oceanography 5, 886–904.

Hurst, J.W., 1975. History of Paralytic Shellfish Poisoning on the Maine Coast 1958–1974. In: LoCicero, V.R. (Ed.), Proceedings of the First International Conference on Toxic Dinoflagellate Blooms. Massachusetts Science and Technology Foundation, Wakefield, Massachusetts, pp. 525–528.

Hurst, J.W., Yentsch, C.M., 1981. Patterns of intoxication of shellfish in the Gulf of Maine coastal waters. Canadian Journal of Fisheries and Aquatic Sciences 38, 151–156.

Langdon, C., 1987. On the causes of interspecific differences in the growth-irradiance relationship for phytoplankton. Part I. A comparitive study of the growth-irradiance relationship of three marine phytoplankton species: *Skeletonema costatum*, *Olisthodiscus luteus* and *Gonyaulax tamarensis*. Journal of Plankton Research 9, 459–482.

MacIsaac, J.J., Grunseich, G.S., Glover, H.E., Yentsch, C.M., 1979. Light and nutrient limitation in *Gonyaulax excavata*: nitrogen and carbon trace results. In: Taylor and Seliger (Eds.), Toxic Dinoflagelate Blooms. Elsevier, Amsterdam, pp. 107–110

MacIntyre, J.G., Cullen, J.J., Cembella, A.D., 1997. Vertical migration, nutrition and toxicity of the dinoflagellate, *Alexandrium tamarense*. Mar. Ecol. Prog. Ser. 148, 201–216.

Martin, J.L., White, A., 1988. Distribution and abundance of the toxic dinoflagellate Gonyaulax excavata in the Bay of Fundy. Canadian Journal of Fisheries and Aquatic Sciences 45, 1968–1975.

Nehring, S., 1996. Recruitment of planktonic dinoflagellates: Importance of benthic resting stages and resuspension events. International Revue ges Hydrobiology. 81, 513–527.

Parsons, T.R., Maita, Y., Lalli, C.M., 1984. A Manual of Chemical and Biological Methods for Seawater Analysis. Pergamon, Oxford, 173 pp.

Pettigrew, N.R., Townsend, D.W., Xue, H., Wallinga, J.P., Brickley, P., 1998. Observations of the Eastern Maine Coastal Current and its Offshore Extensions in 1994. Journal of Geophysical Research 103 (C13), 30,623–30,639.

Rasmussen, J., Richardson, K., 1989. Response of *Gonyaulax tamarensis* to the presence of a pycnocline in an artificial water column. Journal of Plankton Research 11, 747–762.

Sasner, J.J., Ikawa, M., Barrett, B.E., 1975. The 1972 red tide in New Hampshire. In: LoCicero, V.R. (Eds.), Proceedings of the First International Conference on Toxic Dinoflagellate Blooms. Massachusetts Science and Technology Foudation, Wakefield, MA, pp. 517–523.

Seliger, H.H., Tyler, M.A., McKinley, K.R., 1979. Phytoplankton distributions and red tides resulting from frontal circulation patterns. In: Taylor, D.L., Seliger, H.H. (Eds.), Toxic Dinoflagellate Blooms. Elsevier, Amsterdam, pp. 239–248.

Shumway, S.E., Sherman-Caswell, S., Hurst, J.W., 1988. Paralytic shellfish poisoning in Maine: montoring a monster. Journal of Shellfish Research 7, 643–652.

Sverdrup, H.U., Johnson, M.W., Fleming, R.H., 1946. The Oceans: Their Physics, Chemistry and General Biology. Prentice-Hall, Englewood Cliffs, NJ, 1087 pp.

Thayer, P.E., Hurst, J.W., Lewis, C.M., Selvin, R., Yentsch, C.M., 1983. Distribution of resting cysts of *Gonyaulax tamarensis* var. *excavata* and shellfish toxicity. Canadian Journal of Fisheries and Aquatic Sciences 40, 1308–1314.

Townsend, D.W., 1998. Sources and cycling of nitrogen in the Gulf of Maine. Journal of Marine Systems 16, 283–295.

Townsend, D.W., Christensen, J.P., Stevenson, D.K., Graham, J.J., Chenoweth, S.B., 1987. The importance of a plume of tidally-mixed water to the biological oceanography of the Gulf of Maine. Journal of Marine Research 45, 515–529.

White, A.W., Lewis, C.M., 1982. Resting cysts of the toxic, red tide dinoflagellate *Gonyaulax excavata* in Bay of Fundy sediments. Canadian Journal of Fisheries and Aquatic Sciences 39, 1185–1194.

Wyatt, T., Jenkinson, I.R., 1997. Notes on *Alexandrium* populatiuon dynamics. Journal of Plankton Research 19, 551–575.

Yentsch, C.M., Holligan, P.M., Balch, W.M., Tvirbutas, A., 1986. Tidal stirring vs. stratification: Microalgal dynamics with special reference to cyst-forming, toxin-producing dinoflagellates. In: Bowman, M.J., Yentsch, C.M., Peterson, W.T. (Eds.), Tidal Mixing and Plankton Dynamics. Springer-Verlag, New York, pp. 224–252.