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# Diel vertical distributions of the red tide dinoflagellate *Alexandrium fundyense* in the Gulf of Maine

David W. Townsend*, Stephanie L. Bennett, Maura A. Thomas

*School of Marine Sciences, 5706 Aubert Hall, University of Maine, Orono, ME 04469, USA*

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**Abstract**

Two 24-h experiments, designed to test whether the toxic dinoflagellate *Alexandrium fundyense* exhibited significant changes in vertical distribution, were performed in offshore waters of the Gulf of Maine in June 2000. Standard hydrocasts with a CTD/carousel water sampler package were made hourly on-station while following a drogue set at 25 m depth. Continuous measurements of T, S, and chlorophyll fluorescence were made on each down cast, and discrete water samples were collected at 5-m intervals from 55 m depth to the surface on the up cast, for analyses of extracted phytoplankton chlorophyll, inorganic nutrients and cell densities of *Alexandriu*m In the first experiment we observed a bimodal vertical distribution of cells, with relatively high cell densities near the surface ($<15$ m depth) and a second peak of relatively high cell densities at depths between 25 and 40 m, coincident with the depth of the pycnocline and nitricline. Internal waves of 10–15 m amplitude appeared to exert control over the depth distribution of the deep population. Approximately 12 h into the first experiment, a relatively warm surface water mass with low *Alexandrium* cell densities intruded over the drogue station, leaving only the deep population. In the second experiment overall cell densities of *Alexandrium* were much lower, but again we observed initially a bimodal depth distribution of cells. As in the first experiment, the surface population effectively disappeared after a few hours, leaving only the deep population; in this case, however, there was some evidence of an initial downward movement of the surface population prior to its complete disappearance. Evidence for intrusion of a surface-water layer was not as clear in the second experiment as in the first. In addition to higher-frequency internal waves, as was observed in the first experiment, we also observed a low-frequency internal tidal wave of greater than 20 m amplitude that controlled the vertical distribution of the deep population of cells. We were unable to discern evidence of diel vertical migratory by the *Alexandrium* population in either of the two experiments.
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*Keywords:* *Alexandrium*; Red tide; Vertical distributions; Diel migration; Gulf of Maine

## 1. Introduction

The oceanography and population dynamics of the toxic dinoflagellate *Alexandrium fundyense* (hereafter referred to simply as *Alexandrium*), which is responsible for periodic outbreaks of Paralytic Shellfish Poisoning (PSP) throughout the Gulf of Maine–Bay of Fundy region (Anderson, 1997), have been the subject of intense study as part of the Gulf of Maine ECOHAB Program. As part of this research program, Townsend et al. (2001) reported on distributions of *Alexandrium* surveyed during

*Corresponding author. Tel.: +207 581 4367; fax: +207 581 4388.
*E-mail address:* davidt@maine.edu (D.W. Townsend).

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three research cruises that covered much of the coastal and offshore waters of the Gulf of Maine in June–August 1998. They found that the highest cell densities in general were confined to two broadly distributed patches: one in the western Bay of Fundy, similar to observations reported earlier by Martin and White (1988), and a second patch in the offshore waters of the east-central Gulf of Maine, in close association with the eastern portion of the Maine coastal current (EMCC) system (Townsend et al., 1987; Brooks and Townsend, 1989; Bisagni et al., 1996; Pettigrew et al., 1998). In each case, the Bay of Fundy and the EMCC patches, the relatively high concentrations of cells were explained in relation to hydrographic regions of relatively high flux rates of inorganic nitrogen and conditions that allowed the cells to be exposed to relatively high levels of ambient light (Townsend et al., 2001).

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; Maranda, 1985; Langdon, 1987; Flynn et al., 1996; Chang and McClean, 1997). The dependence on elevated concentrations of nitrogenous nutrients later in the summer when near-surface waters throughout much of the Gulf of Maine become vertically stratified and relatively nutrient depleted, would preclude high phytoplankton growth rates and thus high cell densities of *Alexandrium*, but high cell densities do indeed appear at certain times and locations throughout the Gulf region. Martin and White (1988) reported that the peak season for high cell densities in the Bay of Fundy is typically late summer, during the time of maximal density stratification of the upper water column in the Bay. Likewise, Townsend et al. (2001) reported an increase in *Alexandrium* cell densities in 1998, from June to July to August, in the western Bay of Fundy, while densities declined over the same period in the Gulf of Maine proper. Instead, they reported that highest cell densities later in the summer in the Gulf of Maine were confined to subsurface layers, apparently coincident with pycnocline and nitricline depths. Unfortunately, Townsend et al. (2001) limited their sampling to only two depths: the near surface waters (ca. 2 m depth) and at either the depth of the subsurface chlorophyll maximum, when present, or when not present, at 20 m depth. Nonetheless, the observed subsurface distributions of high cell densities of *Alexandrium* appeared to be related to frontal features surrounding the cold core waters of the EMCC, reaching in some instances cell densities $>100{,}000\,\text{cells}\,\text{L}^{-1}$. More recent and complete surveys of the vertical distributions of *Alexandrium* throughout the Gulf of Maine are presented in this issue (Townsend et al., 2005). The observation that *Alexandrium* cells aggregate at surface frontal features is well known (Rasmussen and Richardson, 1989; Incze and Yentch, 1981; Franks and Anderson, 1992); such aggregations reflect either physical accumulation processes (advection coupled with buoyancy and/or weak vertical swimming capabilities), or local growth effects in the case of increased nutrient fluxes at fronts. Subsurface distributions of *Alexandrium* populations are less well studied.

The occurrence of subsurface concentrations of *Alexandrium* and other dinoflagellates in the Gulf of Maine has been documented (Mulligan, 1975; Holligan et al., 1984; Franks and Anderson, 1992). Mulligan (1975) noted that populations of dinoflagellates in subsurface chlorophyll maxima in the Gulf of Maine increase in cell densities at a time roughly coincident with the decrease in surface phytoplankton populations. Holligan et al. (1984) found that *Alexandrium* spp. cells occurred in elevated densities either at the surface or at the depth of the pycnocline, and at some stations they observed populations of cells at both depths, forming a double peak in vertical profile, which is similar to that reported by Townsend et al. (2001) for the only two stations where they sampled multiple depths.

Many species of dinoflagellates are known to be capable of using their weak swimming abilities to exploit deeper pools of nutrients, and dinoflagellates such as *Alexandrium* are capable of swimming at rates up to $1\,\text{m}\,\text{h}^{-1}$ in laboratory columns (Eppley et al., 1968). Thus, diel vertical migration behavior might facilitate the cells acquiring both high light and high nutrient levels, by maintaining near surface distributions by day, and near pycnocline and nutricline depths by night.

MacIntyre et al. (1997) tested for diel vertical migration behavior in the laboratory using a clone of *Alexandrium tamarense* from the St. Lawrence estuary. They showed that as the dissolved nitrogen in the surface layer of their 2-m experimental columns was depleted, the *Alexandrium* population began a pattern of migration. The cells descended across an artificially created thermocline into a nutrient-replete bottom layer just before dark, and then began to ascend before first light the next

morning. The pattern continued until the nitrogen was depleted in the bottom layer as well, at which time all migration ceased. Anderson and Stolzenbach (1985) documented vertical migratory behavior by *Alexandrium* spp. in a salt pond on Cape Cod, USA. In the shallow, semi-enclosed salt pond, the *Alexandrium* populations appeared to undergo vertical migration coinciding with the tides. The downward migration kept cells from being swept out of the ponds as the surface water flowed out with the ebb tide (Anderson and Stolzenbach, 1985). It was not clear if that behavior was also linked to nutrient and light availability, however, and indeed, anecdotal evidence from work performed by ourselves and others in more coastal and offshore locations has shown that while there certainly appear to be discrete vertical distributions of *Alexandrium*, there are no clear indications that cells are actively migrating (Townsend et al., 2001; Martin and White, 1988; see also Martin et al., 2005).

The purpose of this communication is to present the results of field experiments designed to test whether *Alexandrium* populations alter the vertical distributions over diel cycle. We sampled the vertical distributions of *Alexandrium* cells over two 24-h periods at a pair of stations in the Gulf of Maine in June 2000. In each case we were unable to discern any vertical distributional changes that could be interpreted as vertical migratory behavior related to nutrient gradients or the day-night light cycle.

## 2. Methods

We conducted an oceanographic survey of the northern Gulf of Maine from 5 to 15 June 2000 aboard the R/V *Cape Hatteras*, during which we sampled hydrographic properties and distributions of *Alexandrium* Hydrocasts casts were made at the stations shown in Fig. 1 using a SeaBird CTD with an in situ fluorometer, PAR sensor (photosynthetically active radiation) and carousel water sampler equipped with 5-L Niskin bottles. Stations were sampled around the clock, meaning that some were sampled during daylight hours and others at night. The CTD package was lowered to within 5 m of the bottom at all survey stations and water was collected during the upcast. Details of the survey data are presented elsewhere (Townsend et al., 2005), and only surface *Alexandrium* cell densities (at 2 m depth) are presented here.

A qualitative phytoplankton net sample was collected at each survey station using a 25-cm

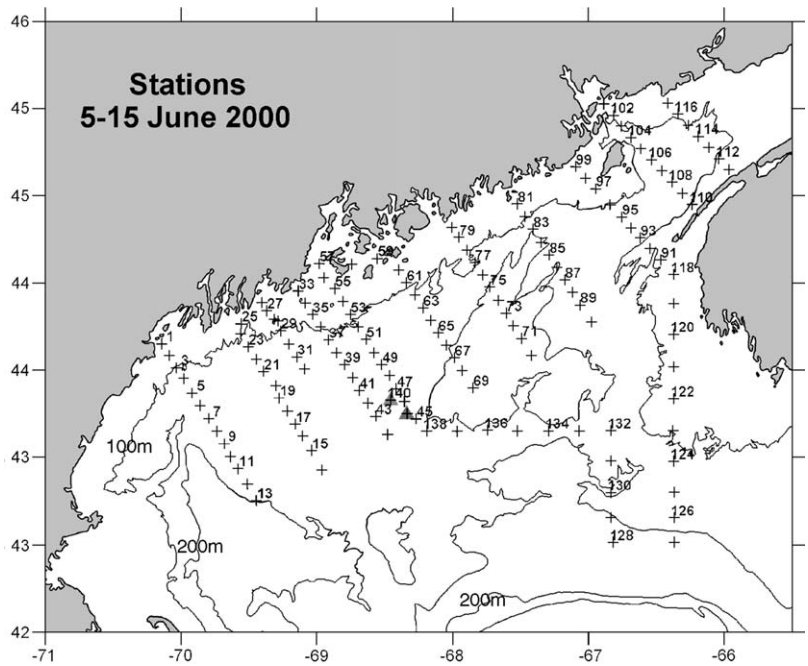


Fig. 1. Station locations for 5–15 June 2000 Gulf of Maine cruise on the R/V *Cape Hatteras* (only every other station is labeled). The two 24-h experiment stations (Stations 46 and 140) are indicated by the triangles. The 100 and 200 m depth contours are indicated.

diameter, 20-μm mesh net lowered to about 20 m depth. It was examined immediately upon collection under a compound microscope to determine the presence and relative cell densities of *Alexandrium* This information was used to select suitable sites (e.g., with relatively high cell densities) for our detailed 24-h vertical distribution studies.

Two 24-h vertical profile experiments were performed at the stations shown in Fig. 1 to examine the change in *Alexandrium* vertical distributions over time. The first experiment (Station ♯46; 43.33° N, 68.35° W) began at 0400 h on 8 June 2000 and finished at 0410 h the following morning. The second experiment (Station ♯140; 43.33° N, 68.46° W) began at 1418 h on 13 June 2000 and finished at 1422 h the next afternoon. We selected these two stations based on the presence of relatively high densities of *Alexandrium* in the qualitative net tow. A subsurface drogue (25 m depth) with a surface float was followed throughout the experiments; the drogue drifted approximately 2.3 km during the first 24-h experiment and less than 0.7 km during the second. The ship followed the movements of the drifter, and standard CTD-bottle casts were taken along side it every hour for a total of 25 casts over a 24 h period. Twelve water samples were collected on each cast at 5-m intervals from 55 m to the surface (1 m depth). *Alexandrium* samples were taken at each depth, following the procedure above, at every hour, but not all samples were counted; actual samples counted for the two experiments can be gleaned from examination of Figs. 3 and 4. Samples for chlorophyll *a* determinations were taken at 2, 10, 20, 30 and 50 m every hour; all samples were processed. Water for nutrient assays was collected and processed from all 12 depths on every third cast.

Phytoplankton chlorophyll was determined fluorometrically on acetone extracts of particulate material filtered from 100 ml onto GF/F glass fiber filters (Parsons et al., 1984). Nutrient samples were filtered through Millipore HA filters, placed immediately in a sea water-ice bath for 5–10 min, and frozen at −18 °C to be analyzed following the cruises for $NO_3+NO_2$, $NH_4$, $Si(OH)_4$ and $PO_4$ using an autoanalyzer and standard techniques. Enumeration of *Alexandrium* cell densities was performed by sieving two liters of water from each sample depth through a 20-μm mesh screen; the concentrate was preserved in a 5% formaldehyde sea water solution and stored in 20-ml vials in the dark in a refrigerator.

Cell counts were performed within 14 months of collection, and were based on epifluorescence microscopy and an immunological stain specific to the genus *Alexandrium*, based on the method of Adachi et al. (1993). Slides were prepared by drawing a 5-ml subsample of the formalin-preserved, 20-μm-seived sample through a 5-μm Nucleopore filter. The particles retained on the filter were stained in a two-step process. First, the filters were incubated in a solution containing a primary antibody specific to *Alexandrium* cell surface proteins, M8751 (MAB); the antibody was provided by D.M. Anderson, Woods Hole Oceanographic Institution. The filters were then incubated with a secondary antibody that was bonded with FITC, a fluorescent molecule. The filters were washed free of excess antibody and placed on a microscope slide and covered with a cover slip onto which a drop of 80% glycerin had been added. This procedure makes *Alexandrium* cell surface proteins fluoresce green when excited by light of 494 nm wavelength, thus easing microscopic identification and enumeration. The entire area under the cover slip was counted using a Nikon epifluorescent microscope at a magnification of 100x or 200x. All slides were counted within four days of being made, as the fluorescence fades over time.

Three toxic species of the dinoflagellate genus *Alexandrium* have been identified in the Gulf of Maine: *Alexandrium tamarense, A. fundyense,* and *A. ostenfeldii* (Anderson, 1997; Gribble et al., 2005). *A. ostenfeldii* is a larger cell than either *A. tamarense* or *A. fundyense*, and both *A. ostenfeldii* and *A. tamarense* are significantly less abundant than *A. fundyense*. The immunofluorescence technique does not distinguish between *A. fundyense* and *A. ostenfeldii* (Anderson et al., 2005), and while we did not attempt to distinguish among these three species, we excluded larger cells that we suspected were A. ostenfeldii. Thus we assume that the vast majority of the cells we counted in this study are *A. fundyense*.

Contour plots of *Alexandrium* spp. cell densities and hydrographic parameters were made using a commercial software package (Surfer, produced by Golden Software, Golden, Co., USA). All contour plots were checked 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 by A.C. Thomas.

## 3. Results

Contour plots showing the surface distribution of *Alexandrium* cell densities in the Gulf of Maine for the entire survey cruise are given in Fig. 2 along with a corresponding eight-day composite satellite image of sea-surface temperature (cloud cover during the period of our cruise obscured individual images). The areal distribution of cells is uneven, with highest surface (2 m depth) cell densities ($>1000$ cells $L^{-1}$) occurring in several patches between the Bay of Fundy in the east and the central Gulf of Maine. The general pattern of surface cells is one that encircles the northern Jordan Basin area of the Gulf of Maine, forming an inverted cup-like shape roughly coincident with a frontal zone encompassing the warmer waters offshore, as seen in the satellite image of sea-surface temperature. A second patch of cells is seen in the Bay of Fundy just east of Grand Manan Island. Additional details of cruise results not immediately germane to this paper are presented in Townsend et al. (2005).

Densities of *Alexandrium* cells during the first of our two vertical profile experiments (at Station 46)

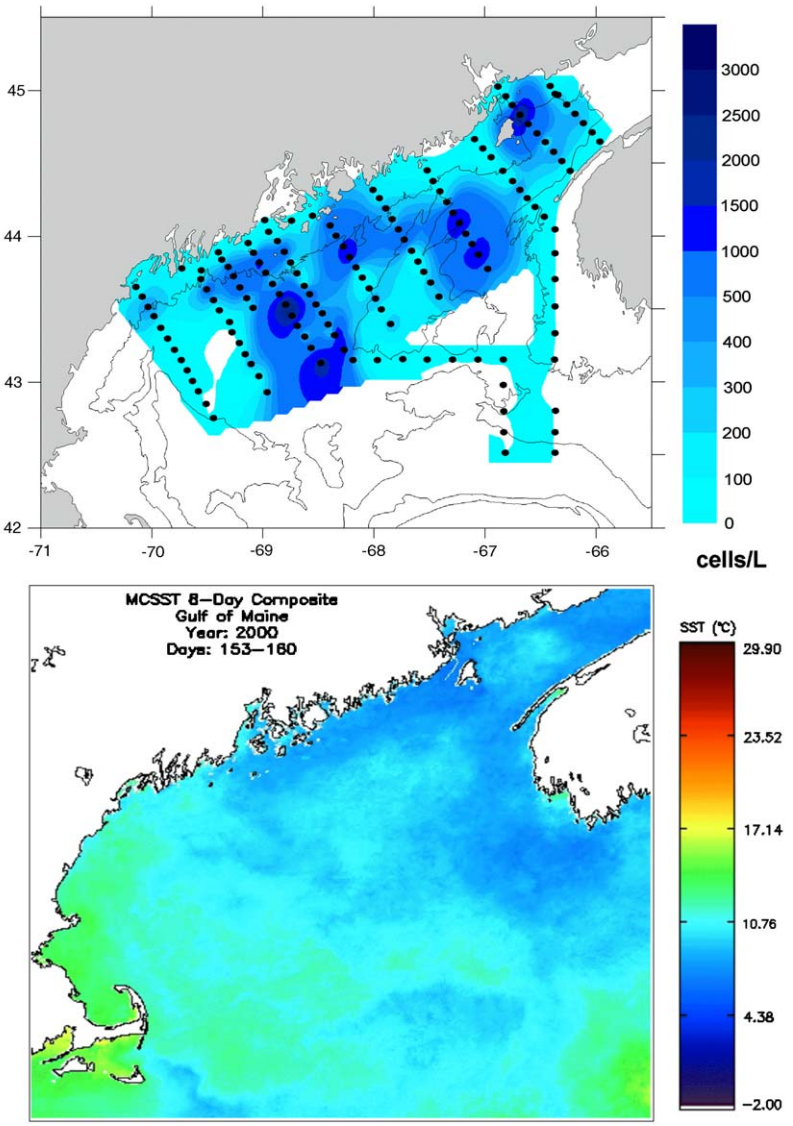


Fig. 2. Top Panel: Cell densities of *Alexandrium* at surface (2 m depth), 5–15 June 2000; note compressed scale. Bottom Panel: eight-day composite AVHRR satellite image of sea surface temperature for year days 153–160. Temperature scale (°C) is given.

were relatively high, as compared with earlier published accounts for the Gulf of Maine (Anderson, 1997; Townsend et al., 2001) with a maximum density of over 2400 cells $L^{-1}$ (Fig. 3). At the beginning of the experiment the cell densities appear to be grouped into two vertical maxima: one near the surface and the other within the thermocline, similar to patterns we and others have seen in the past (Holligan et al., 1984; Townsend et al., 2001). While the *Alexandrium* cell densities are relatively high, they are nonetheless too low to be responsible for the observed chlorophyll concentrations, which are more than likely due to other phytoplankton species (based on phytoplankton carbon:chlorophyll ratios and average phytoplankton cell densities in the Gulf of Maine this time of year). Fifteen hours into the experiment, corresponding to a time of day of 1800 h, the top 20 m of the water column appear to have been replaced by a different water mass. The new water mass was warmer, more depleted in nitrate, and had a low concentration of phytoplankton chlorophyll and *Alexandrium* cells. It appears that while the ship was following the drogue at 25 m, the top 20 m of water moved in a different direction. While the ship maintained its position above the deep population of *Alexandrium*, fewer cells in the shallower layers resulted in lower overall cell abundance (number of cells beneath a unit area of sea surface), which dropped by more than half when compared to profiles earlier in the experiment. The presence of what appear to be high-frequency internal waves (versus low-frequency internal tides) in this first experiment probably exerted significant control over the vertical distributions of cells in the deeper layer (Fig. 3). These waves are clearly visible in the temperature and density profiles of Fig. 3. Vertical fluctuations in concentrations of phytoplankton chlorophyll,

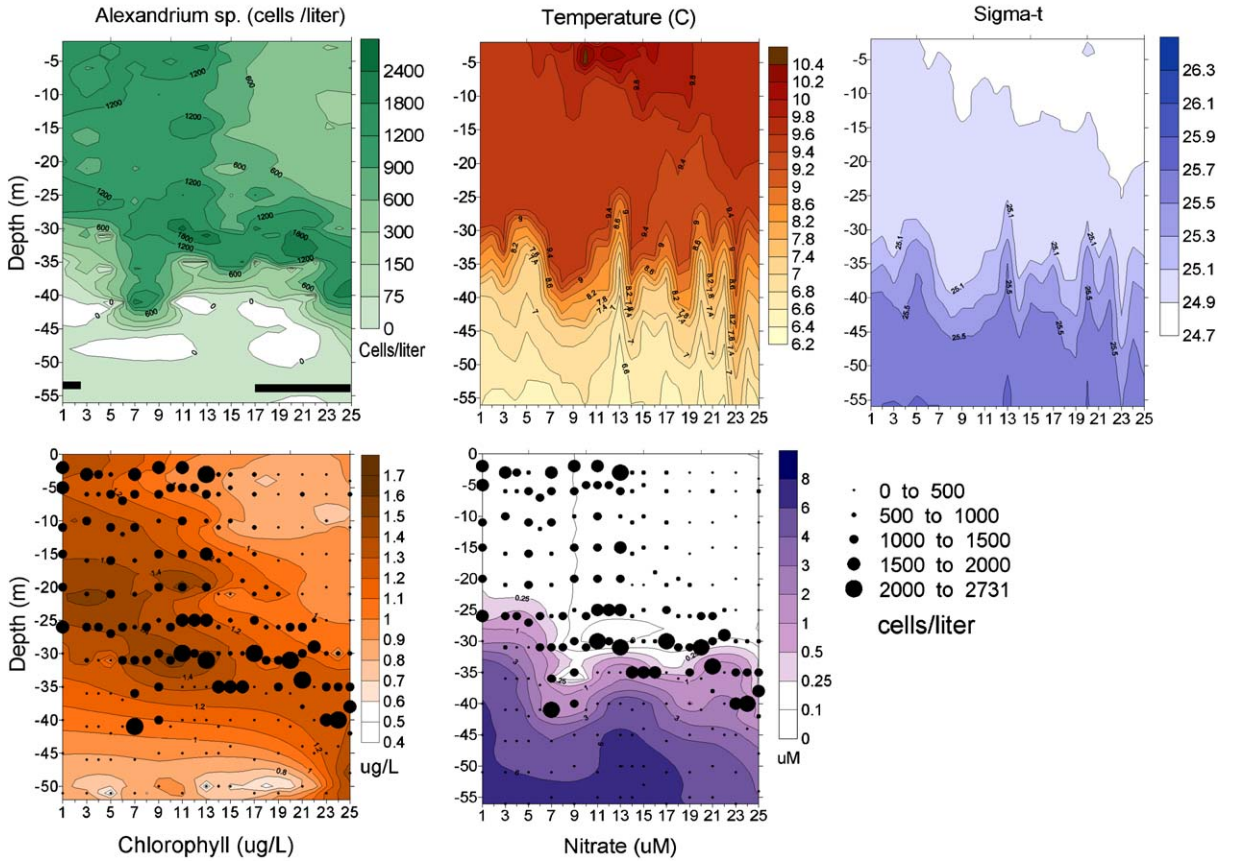


Fig. 3. Experiment 1, Station 46: Depth (m) versus sample number (once each hour for 24 h) contour plots of *Alexandrium* cell densities, temperature, density anomaly (sigma-theta), phytoplankton chlorophyll, and nitrate + nitrite concentrations. *Alexandrium* cell densities are also superimposed as dots on the chlorophyll and nitrate + nitrite panels; the scale is given on the right. The black bars at the base of the first panel indicate nighttime hours of darkness.

nitrate + nitrite and *Alexandrium* cell densities, while not as striking as for temperature and density, are also present. Each shows a general coherence with the internal wave patterns, but not as clearly as for the temperature and sigma-t data. These variables, chlorophyll, nutrients and cell counts, were not measured with the same frequency as the CTD data, as discussed in our methods section, which may explain this apparent aliasing. The frequencies of these internal waves are on the order of 2–8 min (Brickley, 2000), while the frequency of our sampling was 1 h, which means that all our data are likely aliased to some unknown extent.

Our second vertical profile experiment, at Station 140, had an initially high surface population of *Alexandrium* cells (~3000 cells $L^{-1}$) when the sampling began at 14:30 (Fig. 4). As in the first experiment, there was also a second, subsurface population of cells at the depth of the thermocline and nitricline, although the cell densities at depth were relatively low (~300 cells $L^{-1}$). Similar to the first experiment, the *Alexandrium* cells at the surface effectively disappeared after hour 3 (between 16:30 and 18:30) after which the overall cell abundances were significantly lower (Fig. 4). Unlike the first experiment, there was no obvious change in water properties over time, which might suggest advective interleaving of layered water masses; temperature and salinity were relatively unchanged and the nitrate + nitrite also changed only very slightly (by 0.1–0.2 μM). Interestingly, the disappearance of the surface cell population early in the second experiment did show some evidence of a possible downward movement of cells through hour 7 of the experiment, after which the surface population disappeared altogether.

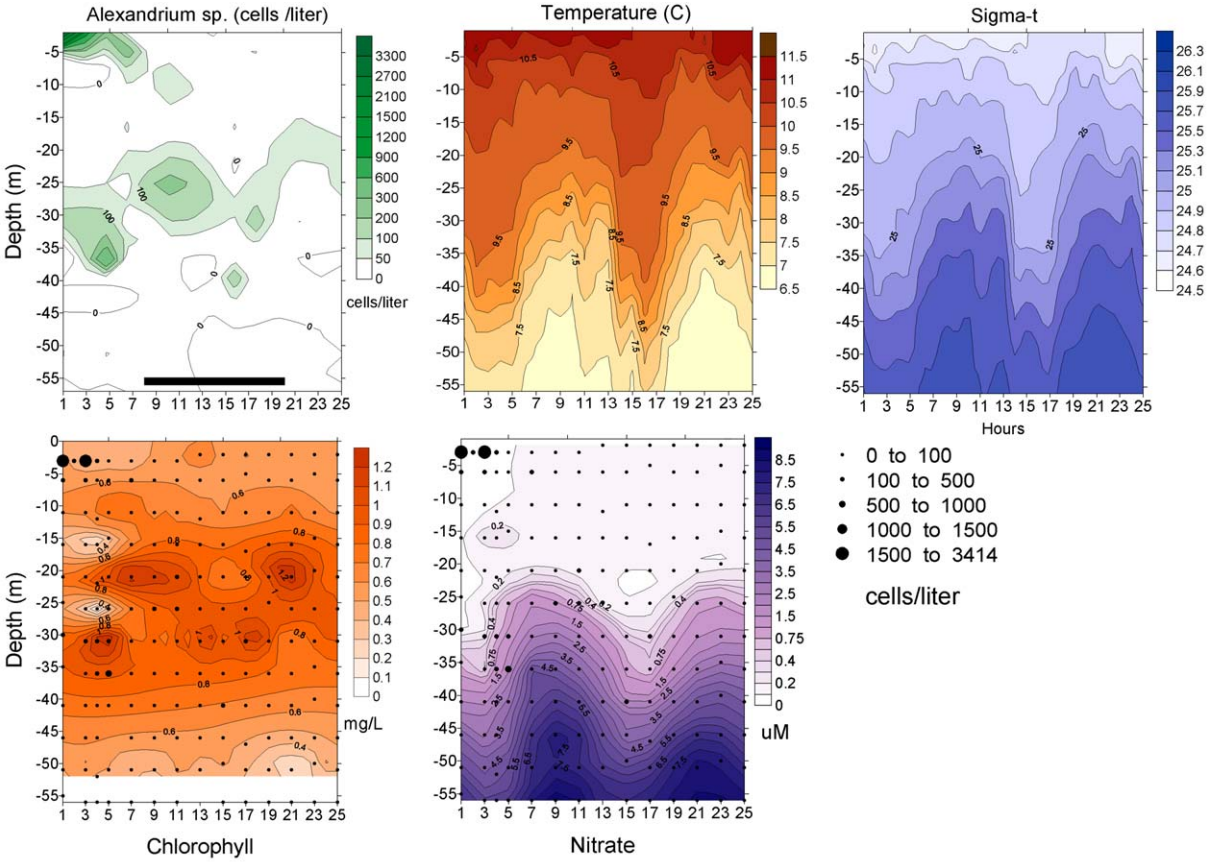


Fig. 4. Experiment 2, at Station 140: Depth (m) versus sample number (once each hour for 24 h) contour plots of *Alexandrium* cell densities, temperature, density anomaly (sigma-theta), phytoplankton chlorophyll, and nitrate + nitrite concentrations. *Alexandrium* cell densities are also superimposed as dots on the chlorophyll and nitrate + nitrite panels; the scale is given on the right. The black bar at the base of the first panel indicate nighttime hours of darkness.

## 4. Discussion

MacIntyre et al. (1997) showed in the laboratory that an *Alexandrium* clone from the St. Lawrence estuary was capable of diel vertical migrations when the cells were under nutrient stress, and Anderson and Stolzenbach (1985) found in situ evidence of vertical migration over a tidal cycle in *Alexandrium* populations in a salt pond. In each of these two examples, the environmental factors forcing swimming behavior (nutrient regimes and sheared tidal flows) were different. We would expect that in the open Gulf of Maine, sheared tidal flows are not as likely to exert a major influence on vertical movements of *Alexandrium* populations, as compared with much shallower systems such as salt ponds. Nutrient concentrations, on the other hand, may be very important; vertical nutrient concentrations are strongly stratified during the summer months, and with the obvious exception of being much deeper, the Gulf of Maine situation may be analogous to the laboratory experiments reported by MacIntyre et al. (1997). At our Gulf of Maine study sites, the depth of the nitricline (defined here as the depth of the 1.0 μM nitrate + nitrite concentration) varies with internal wave activity between depths of 25 and 40 m. The deep *Alexandrium* populations in both of our experiments resided just above these depths (Figs. 3 and 4), while the shallower populations resided in the upper 5–15 m. Vertical excursions of *Alexandrium* cells between these two depth zones would be of the order of 20 m each way, and assuming vertical swimming speeds on the order of only $1\,m\,h^{-1}$ (Eppley et al., 1968), it would be very unlikely that these two populations intermingle on a daily basis.

Regardless of whether *Alexandrium* populations in the Gulf of Maine use vertical swimming behavior to take advantage of light and nutrient distributions, our results do demonstrate what appear to be passive vertical motions of deep populations in association with internal waves, while the near-surface populations appeared to change in response to advection of shallow *Alexandrium* patches. Our two vertical distribution experiments were conducted in a relatively dynamic portion of the offshore Gulf of Maine, at the distal end of the eastern portion of the Maine coastal current (EMCC) and its offshore plume-like extension. During summer this region receives a mixture of both offshore (relatively oligotrophic) waters and relatively nutrient-rich waters emanating from the EMCC, which has been shown to support high densities of *Alexandrium* (Townsend et al., 2001). The results of our first experiment (Fig. 3) suggest that we sampled in both hydrographic regimes: relatively productive and slightly colder waters reflective of EMCC influence at the start of the experiment, followed by a displacement of those surface waters with warmer, nutrient-poorer offshore waters. Fig. 3 shows initially a water mass between the surface and 35–40 m that has relatively high cell densities of *Alexandrium* and phytoplankton chlorophyll. Halfway through the experiment, phytoplankton chlorophyll and *Alexandrium* cells in the upper water column effectively disappear, reflecting the displacement of those surface waters by a warmer and presumably lower-productivity surface water mass. As such, we assume that what would appear to be a downward displacement of cells, as seen in Fig. 3, did not represent an actual downward migration. Our second experiment effectively ran out of *Alexandrium* cells altogether in the shallow (<5 m) population a few hours after the experiment began (Fig. 4), leaving only a relatively low-density deep population. In both experiments, the deep population of cells experienced vertical displacements on the order of 10–15 m, which we interpret as being due to internal wave activity (Figs. 3 and 4), and not directional swimming by the *Alexandrium* cells.

Martin et al. (2005), in their study of the vertical distribution of Alexandrium in the bay of Fundy, also were unable to discern a diel vertical migration. They reported that cells were concentrated in the near surface waters (<5 m), and there was no subsurface maximum. The hydrographic structure at their study sites revealed only a very shallow surface mixed layer (<5 m) and pycnocline from near the surface to about 35 m, perhaps reflecting the vigorous vertical mixing by tides in that part of the Gulf of Maine.

The subsurface populations of cells in both our experiments were associated with pycnocline and nitricline depths, and each oscillated vertically with both high-frequency internal waves and the low-frequency internal tide. In both experiments, the surface waters were depleted of inorganic nitrogen, and the depth of the 1.0 μM nitrate concentration varied between 25 and 40 m (Figs. 3 and 4). Our vertical profiles of PAR indicate a diffuse attenuation coefficient in these offshore Gulf of Maine waters of about $0.11–0.14\,m^{-1}$, which translates to a 1% surface light depth of between 32 and 41 m, and a 10% light depth of between 16 and 21 m. Thus, in each experiment, the deep *Alexandrium* populations were residing just above the 1.0 μM inorganic

nitrogen concentration depth, at a corresponding light depth between the 1% and 10% surface light values. Oscillating vertically with the internal wave field, with amplitudes of 10–15 m, means that each wave crest would elevate both phytoplankton cells and dissolved inorganic nutrients into exponentially increasing light levels; such a light-amplifying phenomenon would be expected to augment photosynthesis and primary productivity. We might suggest, then, that vertical migrations from the relatively deep nitricline in the offshore Gulf of Maine are not only unlikely, but are unnecessary, given the light amplifying effect of the internal wave field. A vertical excursion on the order of that of the internal wave field (10–15 m) would be extreme, and we would conclude, unlikely for dinoflagellates that are purportedly capable of directed swimming on the order of only $1\,m\,h^{-1}$.

In the absence of diel vertical migratory behavior, we are left to reconcile the observed bimodal distribution of cells seen here and reported earlier by others (Holligan et al., 1984; Townsend et al., 2001). Higher concentrations of cells in the near-surface layers may be a reflection of higher light levels and concomitant growth rates there, although we have no direct evidence to support this. Likewise, such a distribution could result from random vertical excursions by cells unrelated to any diel rhythm. That is, cells that swim downward would most likely stop upon encountering the nitricline, perhaps giving the deep distribution we observed, and likewise, those swimming upward would concentrate near the surface. In between these two depth maxima we might expect to see lower cell densities, where cells would be expected to be swimming randomly in search of suitable light and/or nutrient regimes in this summertime period of high light at the surface and high nutrients at depth. Such behavior, of course, would constitute a form of vertical migratory behavior, but not diel migration. In this sense, much more remains to be learned about the dynamics of *Alexandrium* distributions, and we would expect that vertical distributions and migratory behavior will vary among environments with respect to specific hydrographic regimes and associated biological oceanographic processes.

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