A mechanism for offshore initiation of harmful algal blooms in the coastal Gulf of Maine

D. J. McGillicuddy Jr.*, R. P. Signell1, C. A. Stock, B. A. Keaf er, M. D. Keller2, R. D. Hetland3 and D. M. Anderson

Woods Hole Oceanographic Institution, 1United States Geological Survey, Woods Hole, MA 02543, 2Bigelow Laboratory for Ocean Sciences, PO Box 475, West Boothbay Harbor, ME 04575 and 3Texas A&M University, College Station, TX 77843-3146, USA

*Corresponding Author: dmcgillicuddy@whoi.edu

A combination of observations and model results suggest a mechanism by which coastal blooms of the toxic dinoflagellate Alexandrium fundyense can be initiated from dormant cysts located in offshore sediments. The mechanism arises from the joint effects of oceanographic context in which these phenomena take place. In some cases, HABs are initiated and develop offshore and it is not until they impinge upon the coast that their most significant consequences are felt.

In the western Gulf of Maine, the offshore extent of the river plume during upwelling conditions is sufficient to entrain upward-swimming A. fundyense cells germinated from offshore cyst beds. Subsequent downwelling conditions then transport these populations towards the coast.

INTRODUCTION

Harmful algal blooms (HABs) occur in many regions of the global coastal ocean. The culprit organisms are taxonomically diverse, and produce a wide variety of deleterious effects—ranging from ecosystem disturbance to serious threats to human health. One of the major challenges to understanding the underlying controls on HABs stems from the oceanographic context in which these phenomena take place. In some cases, HABs are initiated and develop offshore and it is not until they impinge upon the coast that their most significant consequences are felt.

In New England, the most serious HAB issue is paralytic shellfish poisoning (PSP), a potentially fatal illness that occurs when humans eat shellfish that have accumulated toxins as they feed on dinoflagellates of the genus Alexandrium (Anderson, 1984). These organisms are responsible for human illnesses and occasional death due to PSP, repeated closures of shellfish beds in nearshore and offshore waters, the mortality of larval and juvenile stages of fish and other marine animals (White et al., 1989), and the death of marine mammals such as humpback whales (Geraci et al., 1989). Alexandrium has a complex life cycle (Wyatt and Jenkinson, 1997). Various aspects of the organism’s population dynamics can be pieced together from measurements in both the laboratory and the field, albeit based on a collection of studies that deal with different species. For example, Alexandrium can lie dormant as a resting cyst in the sediment for years (Anderson, 1984; Keafer et al., 1992). Germination is regulated by a complex set of processes, including an endogenous clock (Anderson and Keafer, 1987) and physiological responses to environmental factors such as temperature (Anderson, 1980), light and oxygen availability (Anderson et al., 1987). Once emerged from the sediment, cells swim towards the surface to begin a phase of vegetative growth. Photosynthetic production is fundamentally limited by light and the availability of nutrients; however, maximal growth rates occur only within a specific range of temperature and salinity conditions (Watras et al., 1982). When faced with environmental stress, such as nutrient limitation, the vegetative cells form gametes that subsequently fuse into a zygote (Anderson et al., 1984). The zygote then encysts and the cycle is complete. This intricate life history strategy has important ramifications with respect to both the timing of seasonal blooms and long-term persistence of the organism in specific geographic areas (Edlertsen and Wyatt, 2000).

The spatial distribution of benthic cysts may therefore...
be a key factor in initiating *Alexandrium* blooms. Although previous investigations have provided information on cyst abundance in some areas of the Gulf of Maine (Dale et al., 1978; White and Lewis, 1982; Thayer et al., 1983; Anderson and Keafer, 1985; Keafer et al., 1992), the regional-scale distribution remained obscure until the first systematic survey was undertaken in 1997 (documented below in the Results section). The cyst map reveals that highest abundances of *Alexandrium* cysts are located well offshore. This result is particularly noteworthy in light of the fact that blooms of vegetative cells in the western Gulf of Maine are observed in coastally-trapped river plumes (Franks and Anderson, 1995a,b). How might offshore cysts contribute to inshore blooms of *Alexandrium* in the western Gulf of Maine? This question is investigated with a coupled three-dimensional physical–biological model, and the results suggest a simple mechanism by which cells germinated from offshore cysts can become entrained into a buoyant coastal current.

**METHOD**

Cell abundance was measured in the western Gulf of Maine in 1993, 1994, 1998 and 2000. In the 1993 and 1994 data sets, cells were identified and counted in a Sedgewick–Rafter chamber using a standard light microscope at a magnification of ×100. In the 1998 and 2000 data sets, cells were counted using an immunological procedure based on an *Alexandrium*-specific monoclonal antibody probe used in a whole cell, indirect immunofluorescent format (Anderson et al., 1993; Turner et al., 2000). The M8751-1 hybridoma used in this procedure is not clear whether they were truly distinct deposits or the relatively coarse sampling between these two peaks, it is not clear whether they were truly distinct deposits or local maxima in a larger deposit spanning the area between Penobscot and Casco Bays. Because of the relatively coarse sampling between these two peaks, it is not clear whether they were truly distinct deposits or local maxima in a larger deposit spanning the area between Penobscot and Casco Bays.

Hydrodynamic simulations were constructed using a primitive equation model (Blumberg and Mellor, 1987) with a variable horizontal resolution of 2–4 km and 12 terrain-following vertical levels. Vertical mixing is internally generated from the Mellor–Yamada level 2.5 turbulence closure, and subgrid-scale horizontal mixing is parameterized with the Smagorinsky formulation. The model is initialized with climatological temperature and salinity profiles. Freshwater discharge is specified from USGS gauges in the Kennebec/Androscoggin, Saco, Merrimack and Charles rivers. Wind stress and heat fluxes are computed from observations at NOAA buoy 44807 offshore of Portland, Maine using bulk formulae described in Large and Pond (Large and Pond, 1981, 1982). Surface insolation is prescribed from land-based sensors in Woods Hole, Massachusetts. Tidal forcing at the offshore open boundary is provided by a larger-scale finite-element model of the region (Lynch et al., 1991).

The biological model explicitly represents vegetative cells that swim upward at 10 m day⁻¹, once germinated from resting cysts. Swimming speed decreases linearly to zero in the upper 10 m of the water column. Germination input is calculated from the observed cyst distribution and laboratory measurements of the dependence of specific germination rate on light, temperature and the endogenous clock of *A. fundyense*. The time period of the simulation is nearly coincident with the maximum germination potential set by the endogenous clock, so the waters overlying the cyst beds are inoculated with a relatively steady input of newly germinated cells. Typical germination rates range from 5% per day in the relatively warm, well-illuminated shallow sediments, to 1% per day, which is more characteristic of the colder and darker conditions associated with deeper cyst beds offshore. Vegetative growth is not included, as our objective here is focused on bloom initiation rather than its development. Thus, once germinated from the cyst beds, cells in this model behave as passive tracers with an upward swimming velocity. Simulations using a more complete biological model are being quantitatively evaluated with observations as part of ongoing research.

**RESULTS**

*Alexandrium* cysts were present in bottom sediments throughout the entire regional domain that was sampled (Figure 1). However, the highest abundances occurred in large deposits offshore, beyond the 75 m isobath. The largest peaks in the mapped distribution appeared offshore of both Penobscot and Casco Bays. Because of the relatively coarse sampling between these two peaks, it is not clear whether they were truly distinct deposits or local maxima in a larger deposit spanning the area between Penobscot and Casco Bays.

It is not known how the large-scale distribution of cysts varies over time, given that only a single survey of this geographic scope is available. However, repeat surveys in a smaller domain south and west of the present survey domain show ‘no significant change in cyst abundance’ from November 1983 to November 1984 (Anderson and Keafer, 1985). Moreover, those observations documented high abundance of cysts in sediments 30–40 km northwest of Cape Ann, near the southern extent of the present survey. Although differences in sampling methodology preclude direct evaluation of interdecadal variability,
these results suggest the offshore maximum is a persistent feature of the cyst distribution.

Highest concentrations of vegetative cells occur in the relatively fresh waters of the coastal current (Figure 2). Moreover, the salinity of the waters overlying the offshore maximum in the cyst distribution is significantly higher than that where peak concentrations of vegetative cells exist. It is striking that, in a mean sense, inshore blooms are spatially disconnected from this large source located offshore. Clearly, the higher abundance of cells at characteristic plume salinities is a result of conditions inside the plume that are more favorable for bloom development than the surrounding waters. The question is, what initiates these blooms? It could be that cells germinated from the very low concentrations of cysts present in inshore sediments provide an initial inoculum of cells that is sufficiently large enough to trigger a bloom. However, it is reasonable to inquire as to whether or not the large cyst deposits observed offshore have any relevance to inshore blooms.

The numerical model was used to investigate potential links. Starting from an initial condition in which *Alexandrium* concentration is zero everywhere in the domain, the model is integrated forward with the physical forcing shown in the upper two panels of Figure 3. The results highlight offshore initiation of an *Alexandrium* bloom via germination from offshore cyst beds (Figure 4; see supplementary data http://plankt.oupjournals.org/ for an animated presentation of the results). Cysts also germinate inshore, but they contribute <15% of the total flux due to germination.

Spatio-temporal evolution of cell distribution is dominated by wind-forced river plume dynamics. Fresh water inputs originating at the Kennebec/Androscoggin and Merrimack rivers result in a buoyant coastal current that flows southwestward down the coast in the direction of Kelvin wave propagation. In addition, the plume undergoes significant cross-shore displacement due to wind forcing. Upwelling-favorable winds (from the southwest) drive the plume offshore (e.g. April 22), whereas downwelling-favorable winds (from the northeast) confine it near the coast (e.g. April 14 and May 2). The overall
simulated on May 2 (Figure 4).

...exemplified by the patch of cells northeast of Cape Ann in the salty waters of the ambient coastal current, as surface during downwelling conditions take up residence outside the plume. Upward-swimming cells arriving at the east of the line in Figure 4). Cells entrained into the plume occurring towards the end of the upwelling period. When the winds subsequently shift to favor downwelling, cell abundance in the low-salinity water appears to drop. However, this is primarily a consequence of the cells being advected out of the ‘source region’ in which the budgets shown in Figure 3 are quite low relative to observed values (Figure 2). This results from two factors. First, the cell concentrations reported in Figure 3 are computed by dividing the total number of cells in a salinity interval by the total volume of water in that interval. The absolute concentrations are therefore low because the cells occupy a small fraction of the total volume in each interval (upward swimming confines them to the surface layers). Secondly, vegetative growth is not included in the model, so cell concentrations are not expected to reach the levels observed in the field. Thus, it is only the relative changes in salinity-normalized cell concentration that are of primary interest here.

**DISCUSSION**

These results suggest that the response of the river plume to fluctuating wind forcing provides a mechanism for cross-isobath transport of *Alexandrium* cells (Figure 5). Under upwelling conditions, the plume thins and extends far offshore where it is inoculated by upward-swimming light-seeking cells germinated from the offshore cyst bed. When the winds shift to favor downwelling, the plume moves onshore and thickens, thereby exposing the coast to offshore populations of *Alexandrium* (albeit downstream of the cyst bed from which the cells were germinated).

What is the observational evidence that can be used to determine the extent to which this mechanism is operative in the natural system? Indirect support comes from the Franks and Anderson retrospective analysis of wind records and shellfish toxicity data (Franks and Anderson, 1992b), indicating that downwelling precedes PSP outbreaks along the coast. However, this line of evidence speaks more to the delivery of mature blooms to shellfish beds rather than the initiation of the blooms themselves. Unfortunately, direct observation of bloom initiation via synoptic surveys of the vegetative cell distribution is problematic for a number of reasons. To begin with, it is difficult to separate the processes of bloom initiation (stimulated by germination) and development (dominated by growth) in the natural system. This stems from the fact that there is no way to distinguish between input of cells into the system via germination and simple vegetative growth of the existing population. Moreover, these processes occur in a dynamic fluid medium in which three-dimensional transport plays a fundamental role in creating substantial patchiness in the observed distributions. Therefore, evaluation of the efficacy of this mechanism will require a more complete analysis of the population dynamics of *Alexandrium* (including germination, growth and mortality) in the context of a three-dimensional hydrodynamic model. Once a realistic simulation of the observed vegetative cell distribution has...
Fig. 3. Upper two panels: time series of river discharge and winds used to force the model. Thick horizontal bars indicate time periods of upwelling-favorable (south-westerly) and downwelling-favorable (north-easterly) winds. Bottom panel: mean cell concentrations in various salinity intervals diagnosed from the source region of the model (see text). Arrows indicate the dates of model snapshots shown in Figure 4. Only the cells germinated from cysts deeper than 75 m are included in order to highlight the mechanism by which offshore cells are entrained in the plume.
been created, it will be diagnosed to ascertain the underlying controls on both initiation and development of blooms. This is the central focus of our ongoing research. Nevertheless, the simple model presented here demonstrates a physical–biological interaction that could facilitate a connection between the spatially distinct distributions of the dormant cysts and vegetative cells of *Alexandrium* in the Gulf of Maine. Although the basic elements of this cross-shore transport mechanism are clear, additional pathways of offshore cell entrainment into the plume are possible. Idealized two-dimensional simulations suggest a quasi-lateral entrainment process that occurs when upwelling conditions cause the plume to ride up and over pre-existing surface patches of cells offshore (Hetland et al., 2003). Subducted cells then enter the plume through upward swimming, and the degree of entrainment depends strongly on swimming speed. The same could be true for cells originating from cyst beds further upstream, subsequently subducted by the larger-scale flow of the Eastern Maine Coastal Current (Townsend et al., 2001). Indeed, some evidence links cells observed underneath the plume to upstream water masses (Anderson et al., 2000). Fed either by germination directly underneath the plume or by a source further upstream, the mechanism illustrated in Figure 5 constitutes a pathway through which near-shore blooms of *Alexandrium* can be initiated offshore. Similar mechanisms might well be operative for other cyst-forming HAB species worldwide. The cross-shore flux arises from the combination of organism behavior and the response of a buoyant plume to tran-

![Fig. 4](image_url)
sient wind forcing. Its implications are substantial, in that the processes linking coastal and offshore environments are subtle, complex and non-linear (Tyler and Seliger, 1978; Steidinger and Haddad, 1981; Fraga et al., 1988; Bakun, 1996; Brink and Robinson, 1998; Shanks et al., 2002; Walsh et al., 2002). Our ability to understand and eventually predict HABs and other coupled physical–biological phenomena in the coastal ocean depends critically on the elucidation of these links.

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