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Bloom dynamics of the red tide dinoflagellate *Alexandrium fundyense* in the Gulf of Maine: a synthesis and progress towards a forecasting capability

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ABSTRACT

Paralytic shellfish poisoning (PSP) is a recurrent and widespread problem in the Gulf of Maine (GOM) caused by the dinoflagellate *Alexandrium fundyense.* Blooms of this species have been the subject of more than a decade of investigation through the ECOHAB-GOM and GOMTOX research programs. Multiple large-scale field surveys have provided data that were combined with mooring observations, satellite-tracked drifters, and numerical model simulations to document the complex dynamics of *A. fundyense* blooms within this region. A detailed conceptual model of *A. fundyense* bloom dynamics and PSP toxicity in the region is summarized here, highlighting where possible the key physiological, behavioral, and environmental or oceanographic factors involved. A numerical model has also been developed and evaluated against cruise observations and other data. The status of those modeling efforts is discussed, including recent efforts to provide seasonal forecasts of *Alexandrium* bloom magnitude, and near-real time hindcasts and forecasts of use to resource managers.

INTRODUCTION

Paralytic shellfish poisoning (PSP) is a recurrent and serious problem caused by blooms of toxic dinoflagellate species within the genus *Alexandrium*. The neurotoxin saxitoxin and its congeners is produced by these organisms and accumulated by filter-feeding shellfish and other grazers who ultimately pass the toxin on to humans and animals at higher trophic levels, leading to illness, incapacitation, and even death.

PSP toxicity is a recurrent and widespread problem in the Gulf of Maine (GOM), affecting vast expanses of the region's nearshore and offshore shellfish (Shumway et al., 1988; Anderson, 1997). Toxicity was historically restricted to the far eastern sections of Maine and the Bay of Fundy (Fig. 1; Hurst, 1975; Shumway et al., 1988) until a massive, visible red tide of *Alexandrium fundyense*[1] stretched from southern Maine through New Hampshire and into Massachusetts in 1972, causing toxicity in southern and western areas for the first time. Virtually every year since the 1972 outbreak, western Maine has experienced PSP outbreaks, and on a less-frequent basis, New Hampshire and Massachusetts have as well. This pattern has been viewed as a direct result of *Alexandrium* cysts being retained in western GOM waters once introduced there by the 1972 bloom (Anderson and Wall, 1978).

PSP is not uniform across the GOM, but instead reflects *Alexandrium* growth and toxin accumulation in several separate zones defined by circulation patterns and the temporal distribution of the dinoflagellate. As described in Anderson (1997), each of these "habitats" is thought to have a unique set of environmental and oceanographic forcings that determines the timing and extent of bloom development and transport within that zone, and that regulates the extent of genetic exchange with adjacent zones.

Within the GOM region, five "habitats" can be identified in which toxic *Alexandrium* blooms occur (Anderson, 1997; Fig. 1). These can be defined as: 1) eastern Maine - the eastern Maine coastal

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[1] Both *A. tamarense* and *A. fundyense* occur in the Gulf of Maine. We consider these to be varieties of the same species (Anderson et al. 1994; Scholin et al. 1995). Neither antibody nor oligonucleotide probes can distinguish between them, and only detailed analysis of the thecal plates on individual cells can provide this resolution. This is not practical for large numbers of field samples. Accordingly, for the purpose of this study, the name *A. fundyense* is used to refer to both forms.

current (EMCC) region; 2) western Maine, New Hampshire, and northern Massachusetts – the western Maine coastal current (WMCC) region; 3) Massachusetts and Cape Cod Bays; 4) Georges Bank (GB), the Great South Channel (GSC), and Nantucket Shoals (NS); and 5) isolated salt ponds and embayments. Our knowledge of *Alexandrium* dynamics within each of these habitats varies greatly as a result of unequal research emphasis and different levels of shellfish monitoring. It is nevertheless clear that despite the geographic proximity of these areas, the mechanisms of bloom formation and toxicity development for each vary significantly. One example of the different timing and patterns of shellfish toxicity at selected sites within the region is described in Anderson (1997).

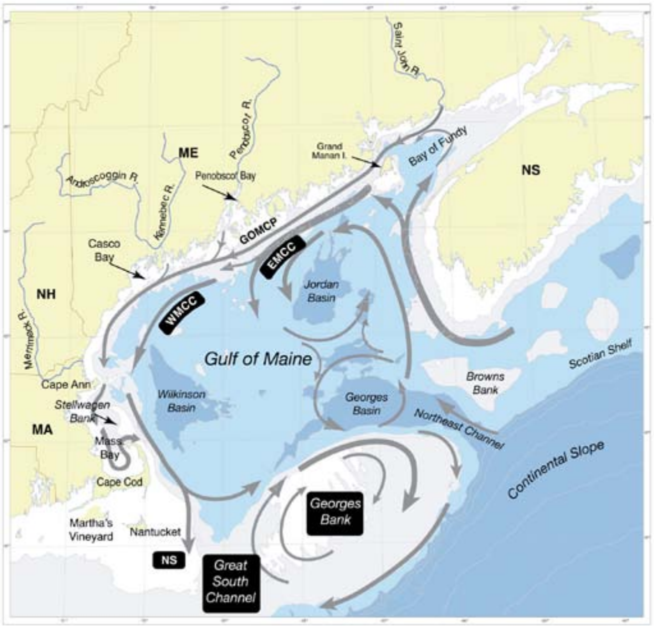

Figure 1. Map of the Gulf of Maine, showing dominant circulation patterns (arrows) and *Alexandrium* habitats.

This biogeographic diversity in *A. fundyense* blooms in the GOM has been the subject of sustained investigation through the ECOHAB-GOM (Anderson et al., 2005d) and GOMTOX (www.whoi.edu/gomtox/) research programs. A series of large-scale field surveys provided data that were combined with mooring observations, drifter tracks, and numerical model simulations to document the complex dynamics of blooms within this region. This paper summarizes the findings of these programs in the form of a detailed conceptual model that highlights major features and mechanisms underlying blooms in the five different habitats described above. A numerical model that provides realistic simulations of these blooms is also presented, emphasizing progress towards short-term (weekly) and seasonal forecasts.

Gulf of Maine Circulation. The patterns of PSP within the region are best viewed in the context of the large- and small-scale hydrographic characteristics of the GOM and adjacent waters. One key feature is the Maine Coastal Current system (MCC), described by Lynch et al. (1997) as a composite of seven legs or segments with multiple branch points (Fig. 1). The upstream, eastern segment of the MCC extends from Grand Manan basin in the BOF to Penobscot Bay. This current, hereafter termed the EMCC, derives from inflow from the Scotian Shelf and freshwater from the Saint John River (Bisagni et al., 1996). The EMCC often veers offshore south of Penobscot Bay, which defines a branch point. Some EMCC water continues offshore, and some returns shoreward to form the western segment or WMCC, which is then augmented by freshwater outflow from the Penobscot, Kennebec/Androscoggin, Saco, and Merrimack Rivers. Near Cape Ann, Massachusetts, another branch point is found, with some WMCC water entering Massachusetts Bay, and some traveling along the eastern flank of Stellwagen Bank. Downstream, the Stellwagen segment undergoes another bifurcation into a Nantucket segment, exiting the GOM at the Great South Channel, and a Georges Bank segment that travels to and around Georges Bank.

A related hydrographic feature that figures prominently in *A. fundyense* blooms has been termed the Gulf of Maine Coastal Plume or GOMCP (Fig. 1; Keafer et al., 2005b). This transport pathway is shoreward of the EMCC and carries low salinity water from the BOF and eastern Maine across the mouth of Penobscot Bay and into the western GOM where it merges with western river plumes. This transport is density-driven and influenced by wind as well as the large-scale GOM circulation.

Massachusetts Bay (which includes Cape Cod Bay) is a semi-enclosed basin bounded on the east by the relatively shallow waters of Stellwagen Bank (Fig. 1). The dominant circulation regime in the bay is a counterclockwise flow that enters the bay just south of Cape Ann, travels south through most of Massachusetts Bay, and exits through a deep channel between the southern end of Stellwagen Bank and Provincetown at the tip of Cape Cod, heading offshore toward Georges Bank and southern waters via the Great South Channel (Geyer et al., 1992). Superimposed on this pattern are episodic intrusions of low-salinity water from the WMCC, which enter Massachusetts Bay around Cape Ann (Butman, 1975; Franks and Anderson, 1992). This area represents another fork or bifurcation point in the MCC system. Depending on the local wind stress, water from the WMCC can either enter the bay or bypass it entirely, traveling instead along the eastern flank of Stellwagen Bank toward Georges Bank.

Cyst Seedbeds. A key element of *A. fundyense* bloom dynamics is the existence of two large, benthic accumulations of dormant cysts, termed "seedbeds". These were revealed in survey cruises that mapped out the concentrations of cysts in bottom sediments from Massachusetts Bay to the Bay of Fundy (Anderson et al., 2005c). Two large areas of accumulation are typically evident – one at the mouth of the Bay of Fundy, and the other offshore of Penobscot and Casco Bays in mid-coast Maine. These are seen as dashed, outlined areas in Fig. 2. In between these deposition sites, cysts are found, but at much lower concentrations. Likewise, in shallow, nearshore waters along the coast, *A. fundyense* cysts are found, but at concentrations that are typically 10-100 times lower than in the offshore seedbeds (Anderson et al., 2005c).

THE *ALEXANDRIUM FUNDYENSE* CONCEPTUAL MODEL

Anderson (1997) first described the different *A. fundyense* habitats in the GOM and highlighted some of the oceanographic and biological processes that lead to toxicity in each. Additional data was provided by the 5-year ECOHAB-GOM program, which in turn led to a revision in our thinking in some respects. Several conceptual models were proposed for the region (Anderson et al., 2005c; McGillicuddy et al., 2005; Townsend et al., 2001), derived from different approaches, but with many features in common, and some differences as well. Here, these models are presented in the context of the five habitats, as that proves to be a useful framework within which to view the complex workings of the entire GOM system.

Localized blooms in embayments, salt ponds, and sounds. The GOM has many small bodies of water that are linked to the open coast, but often through narrow, constricted channels that restrict exchange. Several of these salt ponds, embayments or sounds have been studied extensively on Cape Cod (e.g., Anderson et al., 1983), and provide the data needed to generalize the bloom dynamics for such systems elsewhere in the GOM.

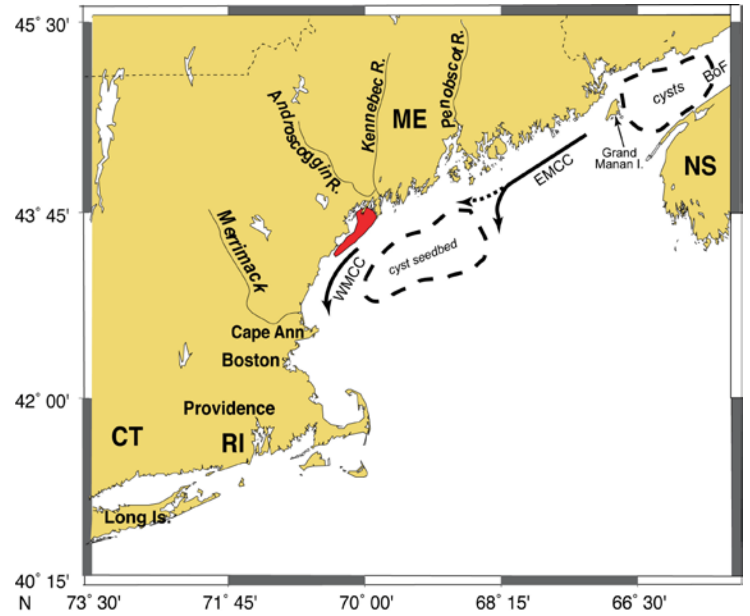

Figure 2. *A. fundyense* blooms in localized embayments such as Lumbo's Hole in Maine are largely independent of populations in the open GOM, but some exchange (red area) is possible with certain types of outflow events.

These locations can be viewed as "point sources" of toxicity, in that *A. fundyense* populations originate within the embayments or estuaries from in situ germination from isolated cyst seedbeds. Because of limited tidal flushing or exchange, the resulting blooms are localized, and as a result, upon bloom termination, they are self-seeding as well, leading to recurrent, annual outbreaks. In the GOM, localized blooms of this type are scattered but common, perhaps best exemplified by the outbreaks that occur in Lumbo's Hole near Casco Bay. This embayment typically develops toxicity earlier than is the case along the open coast of Maine. The toxicity that occurs within these localized embayments can reach very high levels, and is thus very important in the overall pattern of PSP toxicity in the region, but it is evident that these outbreaks are largely independent of the broad-scale blooms that occur along the open coast. Figure 2 depicts the manner in which these blooms can communicate with open coastal waters if they grow sufficiently large and if transport occurs though tidal exchange or rainfall-induced outflow events. This is, of course, dependent on their proximity to the open coast, and the extent of water exchange.

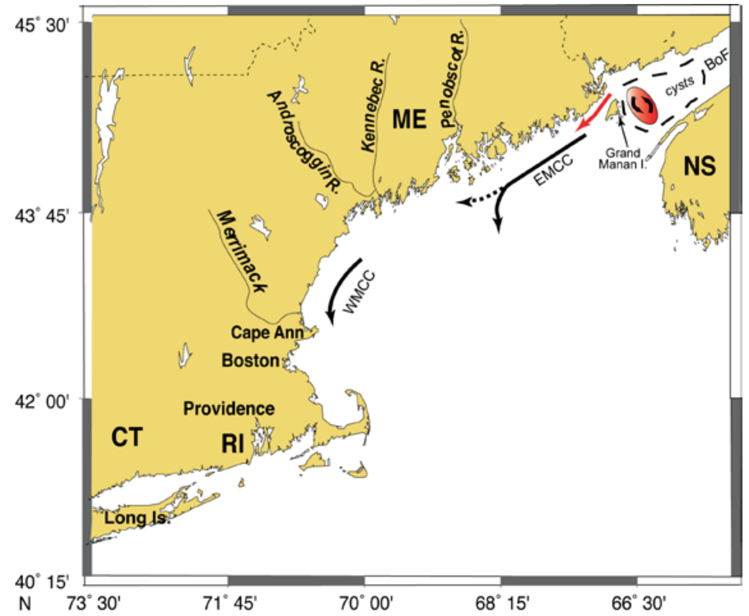

Figure 3. *A. fundyense* cells originate from in situ cyst germination in the BOF, with cells accumulating in a retentive gyre that leads to large blooms, and a new deposit of cysts each year.

<u>The Bay of Fundy.</u> The Bay of Fundy is critically important to the large-scale PSP problem in the GOM. The large cyst seedbed at the mouth of the bay produces motile cells that divide and accumulate within a retentive gyre of water that circulates to the east of Grand Manan Island (Fig. 3). A combination of localized cyst germination and this eddy feature leads to the growth and accumulation of large populations of *A. fundyense* cells, resulting in high levels of toxicity in that region year after year. At the termination of these blooms, new cysts are deposited in the large seedbed at that location, providing the inoculum for future blooms. It is thus a self-seeding area, but as highlighted below, it is leaky or "propagatory" as well (Anderson et al., 2005c; Aretxabaleta et al. 2009).

Eastern Maine the EMCC region. As shown in Fig. 4, some cells that originate and grow within the Bay of Fundy escape around Grand Manan Island and enter the eastern segment of the Maine coastal current (EMCC). Initially, these cells do not grow very fast, due to the cold temperatures and turbulent mixing of this water mass (Townsend et al., 2001). As these cells are transported to the west in the EMCC, the water mass begins to warm and stratify, creating more favorable growth conditions. Cells accumulate in greatest abundance at the distal end of the EMCC, and along its boundaries.

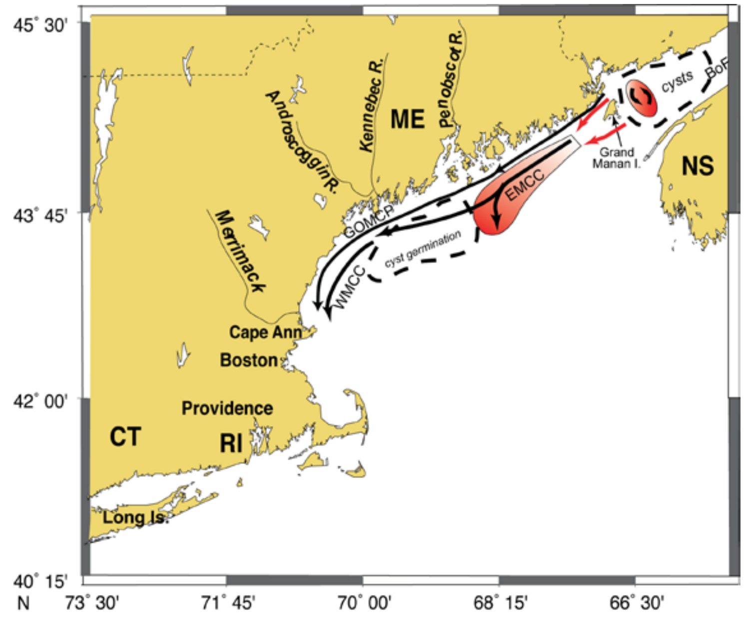

Figure 4. Blooms in the EMCC region originate from cells that escape from Bay of Fundy blooms. The EMCC and its associated cells often veer offshore near Penobscot Bay.

A prominent feature of the EMCC is the manner in which it veers offshore near Penobscot Bay (Fig. 1). As explained by Pettigrew et al. (2005), this offshore deviation does not always occur, so under certain situations (such as with sustained downwelling-favorable winds), water from the EMCC continues in the alongshore direction, joining with and forming a substantial part of the WMCC. Blooms of *A. fundyense* in the EMCC region are thus linked to populations that develop within the Bay of Fundy, and their subsequent growth and delivery to shellfish via the EMCC. A related and potentially very important pathway is the Gulf of Maine Coastal Plume (GOMCP) that travels inshore of the EMCC (Keafer et al., 2005b). Derived from fresh water outflow from the Saint John River in the Bay of Fundy, as well as other Gulf of Maine rivers, this nearshore current provides an "inside track" with suitable growing conditions for *A. fundyense.* The relative importance of cells in the GOMCP versus the EMCC is not known. Both appear to be important transport pathways for *A. fundyense.*

Western Maine, New Hampshire and Northern Massachusetts – the WMCC region. As shown in Fig. 5, blooms within the western Maine region derive their cells from two different sources. One is from cells in the EMCC that are delivered to the WMCC through episodic transport events driven by downwelling-favorable winds and other forcings (Luerrssen and Thomas 2005; Keafer et al., 2005a). The second is from germination of cysts in the Casco Bay/Penobscot Bay offshore seedbed (Anderson et al., 2005c). Our view is that the later mechanism is dominant in the early bloom season (i.e. April, early May), whereas delivery of populations from the EMCC becomes more significant in late May, June, and July.

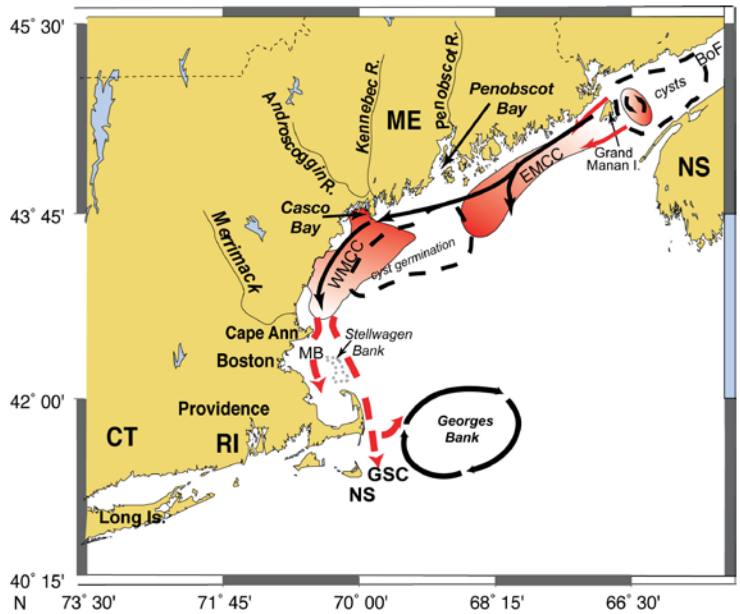

Figure 5. Blooms in the WMCC are initiated by cells delivered from the EMCC, as well as by germination of cysts from the seedbed offshore of Casco and Penobscot Bays.

The behavior of the WMCC, and in particular the extent to which it is influenced by upwelling-downwelling-favorable winds has been described previously (Franks and Anderson, 1992: Anderson et al., 2005a). Winds from the southwest cause upwelling that transports the WMCC offshore and thus removes the toxic cells in that water mass from the nearshore shellfish, reducing the threat of PSP toxicity. In contrast, winds from the east or northeast cause downwelling-favorable conditions that push the WMCC closer to shore and accelerate its movement to the south and west. This is associated with rapid increases in toxicity and propagation of the PSP outbreak to western and southern waters (the plume-advection hypothesis of Franks and Anderson, 1992 and Anderson et al., 2005a).

Also shown in Figure 5 is the importance of a branch point in the WMCC near Cape Ann, Massachusetts. At the northern entrance to Massachusetts Bay, WMCC water can either continue directly to the south along the eastern flank of Stellwagen Bank and then out to sea, or with downwelling-favorable wind forcing, can turn to the right and enter the Bay. The extent to which this latter pathway occurs is directly related to the patterns of toxicity within Massachusetts Bay. In essence, the cells that cause toxicity within the Bay originate in the north and are delivered to the bay by the WMCC. Development of toxicity can thus be very rapid, if the populations that are delivered are substantial in size, as happened in 2005 during a massive regional *A. fundyense* bloom (Anderson et al., 2005b). Localized, in situ development of *A. fundyense* blooms does not generally occur in Massachusetts Bay.

<u>Georges Bank, Nantucket Shoals, and Southern Waters</u>. Since the mid-1960s, PSP toxins have occasionally been found in scallop digestive glands from Georges Bank, a shallow, well-mixed fishing ground located several hundred kilometers east of Cape Cod (Bourne, 1965; Jamieson and Chandler, 1983). In 1989, however, PSP toxins were detected in shellfish from the American sector of Georges Bank, (White et al., 1993). The source of the Georges Bank toxin remains unknown to this day. Recent measurements have also documented PSP toxins in sea scallops, ocean quahogs, and surf clams from nearby areas along the Great South Channel – including Nantucket Shoals (G. Day, R. Taylor, unpub. data).

This offshore area of the GOM is the subject of an ongoing program called GOMTOX. During survey cruises on Georges Bank in 2007, 2008 and 2010, considerable interannual variability has been observed in *A. fundyense* cell abundance over the Bank, ranging from widespread and long-lasting blooms in 2007 to small or short-lived outbreaks in 2008 and 2010 (unpublished data). The source of the cells that inoculate the Bank is unknown, but once introduced to those waters, bloom dynamics appears to be regulated by in situ growth and retention mechanisms (D. J. McGillicuddy, unpub. data).

HINDCASTING AND FORECASTING EFFORTS

A coupled physical/biological model of *A. fundyense* population dynamics in the Gulf of Maine has been developed that is consistent with the above conceptual model (e.g., McGillicuddy et al., 2005; Anderson et al., 2005c; He et al., 2008; Li et al., 2009). The model is initiated from large-scale maps of cyst distribution, with germination rates parameterized through laboratory experiments. Likewise, the growth of the resulting vegetative cells is regulated by light, temperature, and salinity, again parameterized using laboratory cultures.

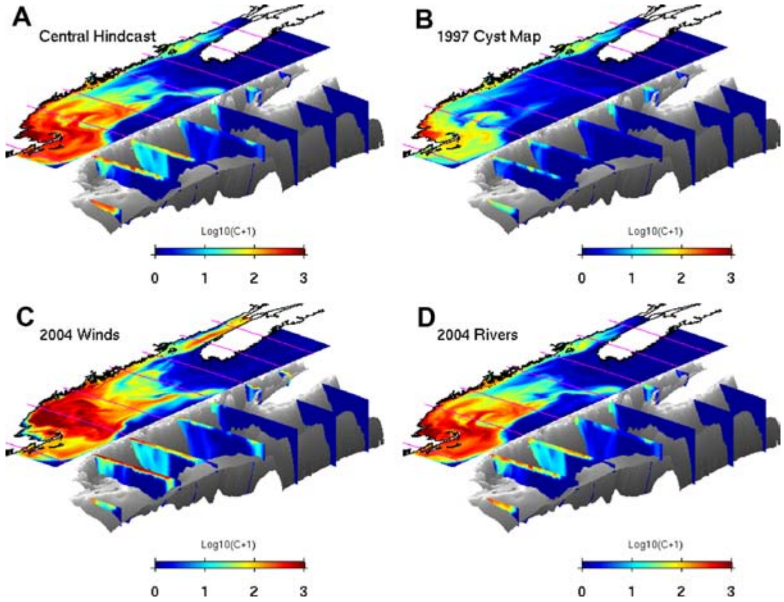

Fig. 6. Snapshots of model output on May 22, 2005 for the central hindcast for 2005 using the 2004 cyst map (A) and three sensitivity experiments that utilized: (B) the 1997 cyst map; (C) 2004 instead of 2005 winds, and (D) 2004 instead of 2005 river discharge. The left side of each panel shows the surface expression of the bloom, while the right portion shows vertical sections of cross-shore transects (purple lines) that reveal the input of cells from germinated cysts. Inoculation from the western Gulf of Maine and Bay of Fundy cyst seedbeds are evident in sections 2,3,4, and 6 counting from left to right. Colors denote *A. fundyense* abundance in [log10 (Cell concentration (cells l^{-1}) + 1). Figure was adapted from He et al. (2008b). An animated version of the central hindcast is available **at** http://omgrhe.meas.ncsu.edu/Redtide/Redtide_05/Redtide_2005_sensitivity.mov

In a novel application of this model, field observations were combined with numerical model hindcast simulations to identify the dominant factor leading to a massive 2005 *Alexandrium* bloom outbreak (He et al., 2008). Anderson et al. (2005b) proposed three factors to explain the 2005 bloom: 1) high abundance of resting cysts that provided a large inoculum; 2) storms with strong northeast winds that carried toxic cells towards, and along the coast; and 3) abundant fresh water runoff, providing macro- and micro-nutrients, a stratified water column, and an alongshore (towards the southwest) transport mechanism. These factors were evaluated using a sensitivity analysis that utilized field observations in the *A. fundyense* population dynamics model (He et al., 2008).

A snapshot from the 2005 hindcast simulation that used the 2004 cyst data (hereafter termed the central hindcast illustrates the bloom's regional-scale characteristics (Fig. 6A). Recently germinated cells swimming upward from the western Gulf of Maine and Bay of Fundy cyst seedbeds are evident in vertical transects. Germinated cells inoculate the coastal current system, which flows from northeast to southwest and then spreads offshore in the south. Large-scale characteristics of the simulation are generally consistent with field observations (Fig. 6).

Initial conditions of the three sensitivity experiments were identical to the central hindcast in all respects except: experiment 1 utilized the 1997 cyst map instead of 2004; experiment 2 was forced by winds from a more typical year (2004) instead of the strong downwelling-favorable winds of 2005; experiment 3 used riverine discharge from a typical year (2004) instead of the anomalously large discharge of 2005.

This sensitivity analysis suggesed that high cyst abundance in the WGOM was the main cause of the 2005 bloom. Wind forcing was an important regulator, in the form of both episodic bursts of northeast winds and the downwelling-favorable mean condition, causing onshore advection of offshore populations. The anomalously high river runoff enhanced alongshore transport near the coast, but had limited impact on the gulf-wide bloom distribution.

These and other results demonstrate that model simulations initiated from *A. fundyense* cyst distributions capture large-scale seasonal patterns in the distribution and abundance of vegetative cells. Cyst abundance is a first-order predictor of regional bloom magnitude the following year in the WGOM, suggesting that cyst abundance may hold the key to interannual forecasts of PSP severity, recognizing that other factors will determine the extent of population growth and delivery to shore. This is a major finding that is of significant importance in terms of bloom management and forecasting in the region.

Synoptic and seasonal forecasts

The model was used to produce near-real-time quasi-operational nowcasts and forecasts for 2006, 2007, 2008, 2009, and 2010. Weekly updates were made available to a listserve of more than 150 managers and other officials and scientists involved with PSP outbreaks in the northeastern US. These weekly updates allowed the listserve members to go to a website where they could view the latest model simulations of that year's *Alexandrium* bloom, extended one week forward in time using weather forecasts. An example forecast can be seen at http://omglnx3.meas.ncsu.edu/yli/08forecast/dino_08.htm. Forecasts were also sent to researchers at sea to aid in the planning of sampling activities. Readers are also encouraged to visit the forecasting web site cited above to scrutinize the comparisons between simulated and predicted *A. fundyense* concentrations in 2008. Manuscripts describing these results are in preparation, and a brief report is available online at http://www.whoi.edu/oceanus/viewArticle.do?id=47406&sectionid=1021 .

The reception for this information was highly positive, as it gave managers a view of the entire bloom in the Gulf each year, rather than just the scattered, alongshore shellfish toxicity records they receive from their own monitoring efforts. Each of these synoptic simulations was based on a regional map of *A. fundyense* cyst abundance in the Gulf of Maine. Results from a cyst survey in fall 2007 revealed that cyst abundance offshore of mid-coast Maine was 30% higher than in fall 2004, just prior to the historic bloom of 2005. The 2008 field season thus offered an exceptional opportunity for testing the hypothesis that the magnitude of the bloom in the western Gulf of Maine and southern New England is set by the abundance of resting cysts. In advance of the bloom season, the coupled physical-biological model was used to make a seasonal forecast using an ensemble of scenarios based on conditions from 2004-2007, made available to resource managers on the web at http://omglnx3.meas.ncsu.edu/yli/simulation_new/08forecast/dino_08.htm . The simulations were initialized with zero cell concentration throughout the domain and the cyst map prescribed from fall 2007 observations. Each member of the ensemble was based on the hydrodynamic hindcast for each specific year, which affected the abundance and distribution of *A. fundyense* cells through environmental influences on germination, growth, mortality, and transport.

Although the hindcasts for 2004-2007 did not span the range of all possible outcomes, they provided contrasting conditions including one with strong downwelling-favorable winds and anomalously high river discharge in May (2005) and one with near climatological conditions (2004). They also spanned the range from major PSP outbreak (2005) to moderate (2006, 2007) to low (2004) levels of toxicity. All of the simulations indicated a severe bloom in the western Gulf of Maine, on par with the historic bloom of 2005. A press release was issued (http://www.whoi.edu/page.do?pid=9779&tid=282&cid=41211&ct=162). This information was used by resource managers in staffing decisions in advance of the bloom and was seen by many as a major factor in the controlled and moderate response of the public and press during the outbreak, and thus in the reduced economic impacts compared to the 2005 event. The seasonal forecast was confirmed when a major bloom occurred, extending from Maine through New Hampshire and much of Massachusetts, leading to federal emergency assistance to these three states because of the "failed fishery".

This seasonal forecast of the 2008 outbreak is a major breakthrough, as it represents the first prediction of a red tide or HAB on a regional scale, and speaks to the advanced nature of our understanding of the *A. fundyense* bloom dynamics in the Gulf of Maine, and to the sophistication and accuracy of our numerical model.

In 2009, a "moderately large" outbreak was forecast, based on the lower cyst abundance observed in the fall, 2008 (see http://www.whoi.edu/page.do?pid=24039&tid=282&cid=56567). This forecast was generally accurate, since the toxicity was more limited in scale than in the previous year, extending only to the middle of Massachusetts Bay. However, a resurgence of toxicity in June and July occurred in Maine, leading to very high and prolonged toxicity in that state. This second wave of toxicity could not have been anticipated in the seasonal forecast, and reflected unusual wind patterns in June and July.

OVERVIEW

The conceptual and numerical models described herein are a result of more than a decade of detailed study of *A. fundyense* dynamics over a large area in the GOM. The models are extraordinarily useful research and management tools that help to guide decisions about closures and re-openings of harvest sites, support forecasts and predictions that are of use to shellfish industry and resource managers, and that in general, provide a context against which blooms and toxicity observations can be viewed.

Looking back, one can highlight the information needs and analytical approaches that can help other countries or regions develop similar conceptual models for HABs and their waters. First and foremost, one needs a detailed understanding of the hydrography of the area under investigation, including adjacent waters that influence the localized flows. Major current systems need to be identified and characterized, as well as the episodic movements of water associated with storm runoff, upwelling, downwelling, and other factors. Moored instruments and survey cruises are needed to characterize this hydrography to provide data to numerical models that are critical in the development of an understanding of HAB dynamics. Initially, the numerical models should focus entirely on the physics of the region, but ultimately, biological elements can be added (e.g. Stock et al., 2005) that can be very useful in understanding HAB dynamics. For a cyst-forming HAB species like *Alexandrium fundyense*, much of the biological model formulation has already been accomplished, and can be adapted to the strains of this or related species in a different area following some laboratory studies to derive growth rate and germination rate as a function of temperature, light, and salinity. More sophisticated efforts might include nutrient uptake kinetics, as this can be useful in forecasting the decline of blooms in the locations where cysts will be formed and deposited. This is important as initial conditions for physical/biological model-forming species. Grazing may need to be considered as well, but this is a difficult issue to resolve in any detail. In our formulations, we have utilized a constant grazing rate of ten percent per day, with a temperature function (Q10). It is simplistic, but does do an adequate job with bloom termination based on the match between our simulations and observations.

Another key feature in the development and application of conceptual models like that described here is the documentation of the nutrient environment that the HAB species will occupy. Survey cruises will provide large-scale snapshots of the nutrient fields, but these change constantly, and are quickly out of date. We have found it useful to utilize "climatological" or long term average nutrient fields for the modeling efforts. These have been derived for the GOM region on the basis of numerous shipboard surveys conducted throughout the years, with those data being compiled and related to parameters such as temperature and salinity. The development of climatological nutrient fields is thus an important priority for those wishing to develop conceptual models in a particular region.

Our conceptual model for *A. fundyense* in the GOM will undoubtedly be refined and modified through time. In its present form, however, it is already proving very useful as a management tool and as a means to communicate the nature of the HAB phenomenon to the public, the press, and to agency officials. Development of such models for HABs in other regions requires a systemic approach whereby the key hydrographic and biological features of the system are identified, characterized, and ultimately modeled. Conceptual models and numerical models are best formulated in parallel, as each provides information and insights to the other. Effective management and mitigation of HABs are greatly facilitated by these efforts.

Acknowledgements

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