Population dynamics of *Alexandrium fundyense* in the Gulf of Maine: outlook for improved management and forecasting

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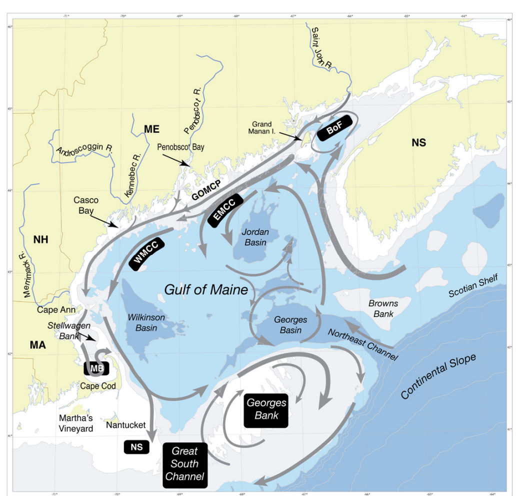
Abstract

Paralytic shellfish poisoning (PSP) is a recurrent and widespread problem in the Gulf of Maine (GOM) caused by the dinoflagellate *Alexandrium fundyense*. Blooms 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 conceptual model of *A. fundyense* bloom dynamics and PSP toxicity in the region is summarized here, highlighting key physiological, behavioral, and environmental or oceanographic factors underlying blooms. 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 *A. fundyense* bloom magnitude, and near-real time hindcasts and forecasts of use to resource managers.

Introduction

Paralytic shellfish poisoning (PSP) toxicity is a recurrent and widespread problem in the Gulf of Maine (GOM; Fig. 1), affecting vast expanses of the region's nearshore and offshore shellfish (Shumway *et al.* 1988; Anderson 1997). Toxicity is not uniform, but instead reflects *Alexandrium fundyense*[1] growth and toxin accumulation in several separate zones or habitats defined by circulation patterns and the temporal distribution of the dinoflagellate (Anderson 1997).

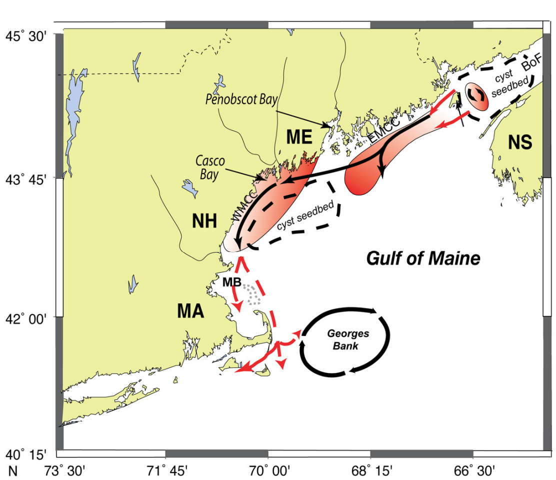
This biogeographic diversity in *A. fundyense* blooms has been the subject of sustained investigation through the ECOHAB-GOM (Anderson *et al.* 2005d) and GOMTOX (www.whoi.edu/gomtox/) research programs. A series of large-scale field surveys provided data that were combined with mooring observations, drifter tracks, and numerical model simulations to document the complex dynamics of blooms within this region. This paper highlights major features and mechanisms underlying the widespread, coastal blooms that can close hundreds of kilometers of coastline for shellfish harvesting. A numerical model that provides realistic simulations of these blooms is also presented, emphasizing progress towards short-term (weekly) and seasonal (annual) forecasts of bloom dynamics and toxicity.



[1] Both *A. tamarense* and *A. fundyense* occur in the Gulf of Maine region. We consider these to be varieties of the same species (Anderson et al. 1994; Brosnahan et al. 2010). 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 field samples. Accordingly, for this study, the name *A. fundyense* is used to refer to both forms.

The *Alexandrium fundyense* conceptual model

A dominant feature underlying *A. fundyense* regional bloom dynamics is the Maine Coastal Current or MCC (Fig. 1; Lynch *et al.* 1997) - a composite of multiple segments and branch points. The two major transport features in this system are the eastern and western segments of the MCC, hereafter termed the EMCC and WMCC. Conceptual models of *A. fundyense* bloom dynamics within the MCC have been provided by Anderson *et al.* (2005c) and McGillicuddy *et al.* (2005). Key features in the models are two large cyst "seedbeds"- one in the Bay of Fundy and the other offshore of mid-coast Maine (Fig. 2; Anderson *et al.* 2005c). Cysts germinate from the BOF seedbed, causing recurrent coastal blooms that are self-seeding with respect to future outbreaks in that area. In effect, the BOF is an incubator for localized populations in that area, but the incubator is leaky, as cells escape into the EMCC, where they bloom, particularly at the distal end of that coastal current, where waters warm and stratify (Townsend *et al*. 2001). Some cells travel south and west with the EMCC, while others deposit cysts in the mid-coast Maine seedbed. In subsequent years, these latter cysts (combined with vegetative cells from populations within the EMCC) inoculate WMCC blooms that cause toxicity in western portions of the Gulf and in offshore waters as well. Toxicity in southerly and western regions of the GOM such as Massachusetts Bay is regulated by coastal current transport, with northeasterly winds accelerating the alongshore and cross shor movement of the populations (Anderson et al. 2005a).



Hindcasting and forecasting efforts

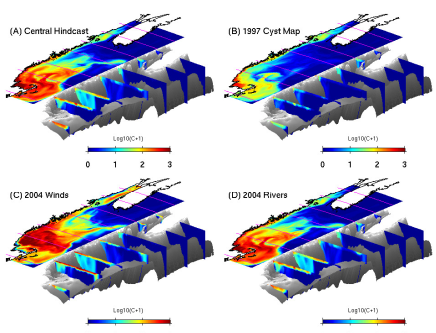
A coupled physical/biological model of *A. fundyense* population dynamics in the Gulf of Maine has been developed that is consistent with the above conceptual model (e.g., McGillicuddy *et al.* 2005; Anderson *et al.* 2005c; He *et al.* 2008; Li *et al.* 2009). The model is initiated from large-scale 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.

In a novel application of this model, observations were combined with model hindcast simulations to identify the dominant factor leading to a 2005 *A. fundyense* bloom considered to be the largest in at least three decades (He *et al.* 2008). Anderson *et al.* (2005b) proposed three factors to explain the historic 2005 outbreak: 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. 3A). Recently germinated cells swimming upward from the western GOM and BOF 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.

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 suggested 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. Anomalously high river runoff enhanced alongshore transport near the coast. 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.

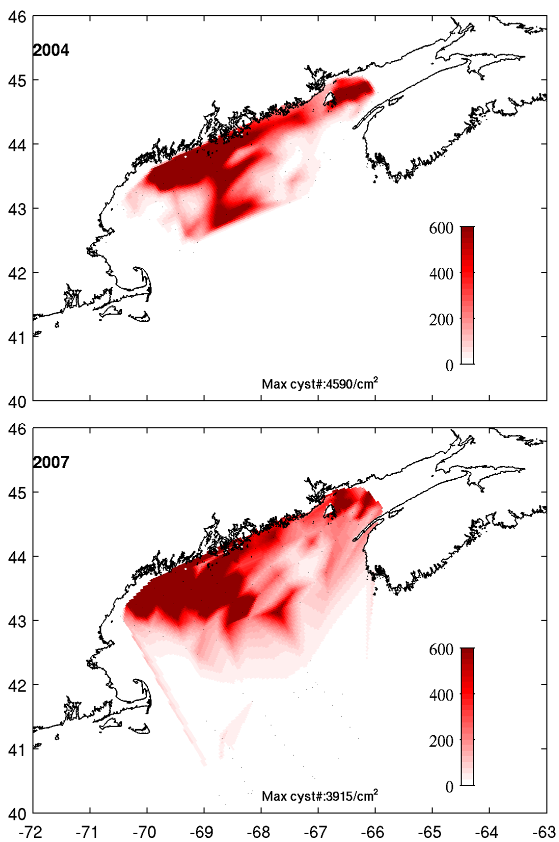


Weekly and annual forecasts

The model has been used to produce near-real-time quasi-operational nowcasts and forecasts for 2006 - 2010. Each of these synoptic simulations was initiated using a regional map of *A. fundyense* cyst abundance in the GOM (e.g., Anderson *et al.* 2005c) obtained in the winter before the next bloom season. Each year, weekly model 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 as one example of the skill of the model. Other analyses of model skill are given in Stock *et al.* (2005) and He *et al.* (2008).

The reception for this information has been highly positive, as it gave managers a view of the entire bloom in the Gulf through weekly updates during the bloom season. This information was complementary to shellfish toxicity measurements made on a weekly basis at scattered locations along the coast.

Seasonal or annual forecasts have also been made. This effort began when a cyst survey in late 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. Those cyst maps are shown in Fig. 4. 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 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 archived hydrographic simulations from 2004-2007 model runs. The ensemble forecast was 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 regional toxicity. All of the simulations indicated a severe bloom in the western GOM, 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 GOM, and to the sophistication and accuracy of our numerical model.

For 2009, a "moderately large" outbreak was forecast, based on the cyst abundance observed in fall, 2008 (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.

For 2010, the forecast that was issued was similar to that for 2008– i.e., a. "significant" *A. fundyense* bloom was anticipated since even more cysts were documented in late 2009 than were present in 2007, immediately before the large-scale 2008 outbreak (http://www.whoi.edu/page.do?pid=24039&tid=282&cid=69586). This forecast was, however, not borne out by the subsequent bloom that year. Relatively small sections of the Maine coast were closed because of toxicity, with no closures in coastal New Hampshire or Massachusetts. GOMTOX research cruises documented very low *A. fundyense* cell abundances in both nearshore and offshore waters of the GOM, so the issue was not a lack of onshore transport, but rather the overall lack of a bloom. Our working hypothesis is that a mesoscale GOM water mass change occurred that lies outside the envelope of observations from the six years used as the basis of the 2010 ensemble forecast.

This hypothesis is currently being evaluated using GOMTOX survey data for 2010, satellite measurements of ocean color, as well as moored observations from instrumented buoy networks (McGillicuddy *et al.* in prep.) Preliminary analyses suggest that the deep basins of the GOM were fresher and warmer than was observed in prior years. This water mass anomaly would have affected intermediate and surface waters, the latter being where *A. fundyense* resides. For example, surface waters were several degrees warmer than in 2008, when a large *A. fundyense* bloom took place. Stratification, nutrient concentrations, grazers, and other factors critical to *A. fundyense* growth could all have been affected.

Should we be able to deduce the mechanisms responsible for the lack of a bloom in the WGOM in 2010, those processes could then be included in the population dynamics model.

Furthermore, we note that the water mass changes mentioned above relate to the large-scale circulation of the northwest Atlantic, and therefore are observable months in advance of the *A. fundyense* season using moored instruments in ocean observing systems. Therefore, it is conceivable that forecasts can be made taking into account this type of variability. It is indeed fortunate that GOMTOX cruises were scheduled for 2010, as this will allow us to understand the factors that prevented a bloom and thereby allow us to improve our model.

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 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 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 the initial condition for physical/biological models for cyst-forming species. Grazing may need to be considered as well, but this is a difficult issue to parameterize in any detail. In our formulations, we have utilized a mortality rate that varies with temperature according to a Q_{10} formulation (He *et al.* 2008). It is simplistic, but thus far, does an adequate job with bloom termination judging from the match between our simulations and observations. This is one example where a simple approximation can replace a complex submodel and still provide acceptable simulations.

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 models in a particular region. However, as demonstrated in 2010 in the GOM, there may be years in which the nutrient fields differ dramatically from the climatology

Our numerical 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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