Preface

The Gulf of Maine (GOM) is a continental shelf sea in the northwest Atlantic, USA that supports highly-productive shellfisheries that are frequently contaminated by toxigenic *Alexandrium fundyense* blooms and outbreaks of paralytic shellfish poisoning (PSP), resulting in significant economic and social impacts. Additionally, an emerging threat to these resources is from blooms of toxic *Pseudo-nitzschia* species that produce domoic acid, the toxin responsible for amnesic shellfish poisoning (ASP). Nearshore shellfish toxins are monitored by state agencies, whereas most offshore stocks have had little or no routine monitoring. As a result, large areas of federal waters have been indefinitely closed or their shellfish beds underexploited because of the potential risk these toxins pose and the lack of scientific understanding and management tools.

Patterns and dynamics of *Alexandrium* blooms and the resulting shellfish toxicity in nearshore waters were examined in a number of research projects, the largest being the Ecology and Oceanography of Harmful Algal Blooms (ECOHAB)-Gulf of Maine (GOM), a five-year regional program emphasizing field surveys, laboratory studies and numerical modeling. At the completion of the ECOHAB-GOM program (documented in Anderson et al., 2005), great progress was made in understanding *A. fundyense* blooms and resulting shellfish toxicity in nearshore waters, but there were major unknowns that still required investigation. For example, little was known about *A. fundyense* bloom dynamics in the waters south and east of Cape Cod, Massachusetts, and in particular, about the link between blooms in surface waters and toxicity in deep offshore shellfish. Large areas of offshore shellfish beds were off limits to harvest, including a 40,000 km^2 region closed during the 2005 bloom and a much larger zone (~80,000 km^2) including portions of Georges Bank was closed in 1990 after high levels of PSP toxicity were detected. In recent years, pressures were mounting from industry to open those offshore areas and to develop management strategies so that surfclam (*Spisula solidissima*), ocean quahog (*Arctica islandica*), and roe-on sea scallop (*Placopecten magellanicus*) fisheries could be opened.

In response to these unknowns and societal needs, a new multi-investigator program, GOMTOX (Gulf of Maine Toxicity), was formulated and ultimately funded through the NOAA ECOHAB program. GOMTOX was a regional observation and modeling program that investigated the patterns and mechanisms underlying *A. fundyense* and *Pseudo-nitzschia* blooms and the resulting toxicity in shellfish in the southern GOM and its adjacent New England shelf waters, with special emphasis on the delivery pathways, mechanisms, and dynamics of offshore shellfish toxicity. The GOMTOX team of investigators included 16 principal investigators from eight institutions and, continuing in the ECOHAB-GOM tradition, strong participation from federal and state resource managers as well as representatives of the shellfish industry.

This team worked together for over five years, running numerous large-scale survey cruises of *Alexandrium* cells and cysts, and also supporting industry cruises to collect shellfish from offshore sites including Georges Bank. Other efforts included participation in National Marine Fisheries Service surveys for shellfish (sea scallops, surfclams, and ocean quahogs), numerical modeling studies, deployment of sediment traps, and laboratory and ship-based experiments to investigate grazing and other processes that might regulate blooms and deliver toxins to shellfish in deeper waters. A smaller-scale but concurrent effort collected samples to characterize *Pseudo-nitzschia* species and their potential toxicity in the region. This volume consists of a series of papers describing the results of the program, which constitute 26 of the 69 GOMTOX papers to date.

The following sections summarize the major scientific contributions to be found in this special issue.

Cyst and sediment dynamics. In recognition of the critical role played by cysts in bloom initiation and termination, there are eight papers in this issue that deal with this topic. Prior to GOMTOX, we knew that cysts were present in the GOM in two major seedbeds or accumulation zones, but we did not know how the size or location of those seedbeds varied through time, nor how the overall abundance of cysts varied in the Gulf. Anderson et al. present a 9-year time series of large-scale cyst surveys, an unprecedented dataset that documents more than 10-fold differences in overall cyst abundance between years, as well as the appearance, and then rapid disappearance of a seedbed extension following a "red water" bloom of *A. fundyense* near Portsmouth, New Hampshire (McGillicuddy et al.). This paper also establishes statistically significant linkages between cyst distribution patterns and metrics of *A. fundyense* bloom geographic extent and intensity in the years immediately before and after each cyst mapping survey. Martin et al. examine 30 years of *A. fundyense* cyst and motile cell dynamics in the Bay of Fundy, Atlantic Canada and find no linkages between cyst distributions and *A. fundyense* metrics for that system. Together, these results represent an important step toward understanding the relationships between excystment and encystment in *A. fundyense* bloom dynamics in the GOM, and augment our predictive capability for blooms of this important species.

Pilskaln et al. provide two papers, one presenting a unique time series dataset on the water column flux and deep-water delivery rates of *A. fundyense* cysts in the GOM and the other presenting maps of the extent and thickness of pervasive benthic nepheloid layers (BNLs) and the inventories of suspended *A. fundyense* cysts within these near-bottom layers. Understanding the timing and magnitude of downward cyst fluxes throughout the water column provides the critical link between *A. fundyense* bloom termination and the formation of underlying sedimentary seedbeds. The existence of widespread BNLs containing substantial cyst inventories indicates that these near-bottom layers may represent a significant source of germinating *A. fundyense* cysts providing seasonal bloom inoculum.

Other papers focus on cysts in the sediments and the way they might be buried (Shull et al.), eroded (Butman et al.), or transported laterally (Aretxabaleta et al.) in the dynamic near-bottom environment. Butman et al. present observations of sediment erodibility and modeling results that suggest that about 1 mm of the surface sediment can be resuspended by bottom stress caused by tidal- and wave-induced currents. Aretxabaleta provides additional information on the distances this resuspended material might travel. With trajectories simulated for a single year, only 18% of the resuspended material was transported more than 20 km from the mid-coast Maine seedbed source and about 5% traveled in excess of 50 km. Where previously we thought that large northeast storms were important in transporting established motile populations of *Alexandrium* to shore, Butman et al. now suggest a second important mechanism, namely that in some years, resuspension events could episodically introduce cysts into the water column in spring where germination is likely to be facilitated at the time of bloom formation.

Looking deeper into the sediments, Shull et al. present data and model results demonstrating that the shape of cyst profiles in the sediments are the result of complex bioturbation processes. Deeper portions of these profiles are relatively stable and independent of cyst depositional history whereas cyst profiles in the top few cm of the sediment show strong seasonal and interannual variation due to the timing and magnitude of cyst deposition and germination. Profiles in the sediments show persistent deep subsurface maxima which may serve as long-term reservoirs. These deep maxima are created by several species of benthic top-down deposit feeders that ingest cysts at the sediment surface and bury them at depth. Additionally, bioturbation by deep-dwelling species of other polychaetes deliver these cysts to the sediment surface where they can germinate. Germination in spring and summer tends to deplete the cysts at the sediment-water interface.

Vahtera et al. took on the challenging task of estimating the survival of cells that germinate from cysts in the deep GOM basin, and present experimental laboratory results that suggest a significant fraction of germling cells may die in the dark during their ascent to the illuminated surface waters. More studies of this type are needed, as the inoculum from a cyst population in bottom sediments is a critical aspect of bloom initiation and needs to be well parameterized for numerical model hindcasts and forecasts.

Ecology and bloom dynamics. Ecology and bloom dynamics of *Alexandrium* spp. in the GOM / Georges Bank region are inextricably related to the larger phytoplankton communities inhabiting these areas. Gettings et al. describe the distribution, abundance, and species succession of the major phytoplankton groups on Georges Bank during the late-spring to early-summer of 2008, and document the transition from a diatom-dominated phytoplankton community in late spring (April-May) to a dinoflagellate community, including *A. fundyense*, by early-summer (May-June). They observed another transition to a community of both heterotrophic and mixotrophic dinoflagellates by mid-summer (June-July). Depletions of dissolved inorganic nutrients, especially nitrate and silicate, accompanied the transition from diatoms to dinoflagellates; both populations appeared to have been supported by recycled ammonium. Patches of recycled silicate on the Bank in mid-summer, and recycled ammonium, accompanied a mid-summer diatom community on the crest of the Bank. Multivariate statistical analyses allowed the identification of several distinct phytoplankton assemblages in space and time, and suggested that in addition to physical and chemical drivers, ecological interactions between *A. fundyense* and diatoms act together to determine their abundances and distributions on the Bank.

A separate group of harmful algae present in the region includes multiple species of the diatom genus *Pseudo-nitzschia* that can produce the neurotoxin domoic acid (DA). During GOMTOX field efforts, *Pseudo-nitzschia* species were observed to coexist in space and/or time with *A. fundyense* (Fernandes and Hubbard et al.). To gain further knowledge of the taxonomic composition and toxicity of *Pseudo-nitzschia* species in this region, over 100 new isolates were cultured from samples collected during research cruises in 2007-2008. Nine species were identified using electron microscopy in tandem with genetic analyses, permitting the classification of a new toxic species in the *P. pseudodelicatissima* species complex. The confirmation of DA production in seven *Pseudo-nitzschia* spp., the broad spatial and temporal distribution of these species, and the potential for concurrent exposure to multiple algal toxins in the GOM have substantial implications for ecosystem health, as well as the regional management of nearshore and offshore shellfisheries.

Dynamics of *A. fundyense* populations on Georges Bank was a major focus of the GOMTOX program. It had been known for decades that *A. fundyense* proliferates on Georges Bank, based on shellfish toxicity measurements dating back to the 1960s. The initial hypothesis guiding the GOMTOX field program was that the Georges Bank population was an extension of the coastal population, fed by the advective pathway that connects them. Georges Bank populations of *A. fundyense* appear, however, to be quasi-independent of those in the adjacent coastal GOM, insofar as they occupy a hydrographic niche characterized by lower temperatures and higher salinities (McGillicuddy et al.). Moreover, in contrast to coastal populations that rely on abundant resting cysts for bloom initiation, very few cysts are present in the sediments on Georges Bank. We infer that bloom dynamics must therefore be primarily controlled by the balance between growth and mortality processes, which are at present largely unknown for this population. Based on correlations between cell abundance and nutrient distributions, ammonium appears to be an important source of nitrogen for *A. fundyense* blooms on Georges Bank.

In addition to the GOMTOX focus on the offshore region of Georges Bank, there were also important findings pertaining to inshore populations of *A. fundyense*. In early July 2009, an unusually high concentration of *A. fundyense* occurred in the western GOM, causing surface waters to appear reddish brown, a very unusual occurrence in this region (McGillicuddy et al.). Maximum observed concentrations exceeded two million cells per liter, 2-3 orders of magnitude higher than is observed in typical blooms in the GOM. The discolored water appeared to be the southern terminus of a large-scale event that caused shellfish toxicity along the entire coast of Maine to the Canadian border. Rapid-response shipboard sampling efforts together with satellite data suggest that the water discoloration in the western GOM was a highly ephemeral feature that lasted less than two weeks. Cyst fluxes downstream of the discolored water were the highest ever measured in the GOM (Pilskaln et al.), and a large deposit of new cysts was observed that fall (Anderson et al.). Although the mechanisms causing this event remain unknown, its timing coincided with an anomalous period of downwelling-favorable winds that could have played a role in aggregating upward-swimming cells. This event highlights the importance of short-term episodic phenomena on regional population dynamics of *A. fundyense*.

New tools also were developed during the GOMTOX program that facilitate novel insights into bloom dynamics. Brosnahan et al. describe modifications to an imaging flow cytometer system (Imaging FlowCytobot) enabling DNA measurements and oligonucleotide probe-based identifications of *A. fundyense* cells within natural populations. The system was used to analyze samples taken from the development, peak, and termination phases of an inshore *A. fundyense* bloom in Salt Pond, Massachusetts and samples taken during the red water event in the western GOM described by McGillicuddy et al. Results showed that in both cases, large proportions of the *A. fundyense* populations underwent sexual fusion during bloom termination. This finding is particularly significant in terms of the 2009 red water episode, as it is, to our knowledge, the first direct observation of a regional-scale encystment event that links observations of planozygotes in the water column with a sinking flux of cysts and their deposition in sediments.

The physical/chemical setting. The dynamics of *A. fundyense* in the GOM and on Georges Bank are closely tied to various aspects of the physical oceanography and nutrient dynamics in the region, topics that are addressed by four papers in this issue.

Li et al. examine details of the coastal current system in the GOM, which has been shown in earlier studies to be important in the advection of bloom populations. Using particle tracking numerical models, they reconstructed the coastal current system for the six-year period 2004 to 2009, focusing primarily on the interannual variability in the continuity of flow between the Eastern Maine and Western Maine Coastal Currents. Their findings support the idea that the degree of east-west connectivity of the coastal current is fundamental to bloom advection, but they also point out that seasonal and interannual variability in the degree of that connectivity is large.

In another paper, Li et al. analyze mooring and shipboard survey data spanning the 9-year period 2002 to 2011 to examine interannual variability of surface winds, freshwater runoff, and hydrographic conditions in the GOM. They found significant variability among years in coastal surface water temperatures. For example, the summer of 2010 was 0.5–2 °C warmer than average, while 2004 was 2 °C colder. Coastal salinities also varied: in April 2010 they were the lowest in the 10-year study period; peak runoff that year occurred in early April as opposed to other years when it occurred between late April and mid-May. The coastal current system that year reflected those hydrographic anomalies. Direct current measurements using moored Acoustic Doppler Current Profilers as well as indirect measures based on geostrophic calculations using survey data both showed that the May–June period in 2010 had one of the weakest alongshore transports in the western GOM during the 10-year study period, which they suggest was also likely associated with anomalous deep water mass intrusions that year. Nutrient fluxes to the region, especially nitrate that supports *A. fundyense* blooms, are ultimately tied to these variable water mass fluxes and the dynamics of the coastal current systems in which the blooms develop.

Rebuck and Townsend provide a spatial climatology for nitrate in the GOM and Georges Bank region based on a historical database compiled for the years 1932 to 2011. They find that nitrate anomalies are coherent among different depths across the region, and suggest a dependence on inflowing water masses. The GOM nutrient fields are also shown to be coherent on seasonal and annual timescales, but within seasons and within years, the nitrate fields are more heterogeneous and localized. Nitrate anomalies during the annual spring drawdown and fall replenishment are shown to be dependent on the timing of the seasonal cooling and less dependent on preceding nutrient fields. They point out that based on lagged correlations of residuals, variability in seasonal convective mixing may be more important than actual nutrient concentrations at depth in terms of supplying surface waters with nutrients.

Townsend et al. analyzed all 10 of the GOMTOX cruises to relate patterns in *A. fundyense* blooms and the nutrient fields in the GOM and on Georges Bank, as determined by variable water mass fluxes into the gulf. They show that the locations and magnitude of *A. fundyense* blooms are controlled in part by variable nutrient fluxes to the interior GOM from offshore, and, that those interior gulf waters are, in turn, the main nutrient source to Georges Bank. They suggest that nitrate is the initial form of nitrogen that sustains *A. fundyense* blooms, but that it is quickly depleted to limiting concentrations, at which time continued growth and maintenance of the populations are likely fueled by recycled ammonium. They also suggest that under certain conditions, phosphate may become limiting on Georges Bank. Temperature-salinity analyses revealed spatial and temporal (seasonal and interannual) variability in the relative proportions of influxes of nutrient-rich Warm Slope Water and nutrient-poor Labrador Slope Water. In addition, they report evidence of episodic fluxes of relatively fresh and low-nutrient shelf waters from the Nova Scotian Shelf, which enter the gulf in pulses, displacing deep slope waters and diluting nitrate concentrations in the gulf's interior waters, which in turn affects the magnitude of *A. fundyense* blooms.

Toxins: dynamics, food web transfer, and monitoring. One of the goals of GOMTOX was to gain a better understanding of the link between surface algal blooms and shellfish toxicity. The challenges of determining this link differed for nearshore versus offshore shellfish populations. For example, large historical datasets of nearshore shellfish toxicity exist. In this case, a format for comparative analysis between harmful algal blooms (HABs) and toxicity was needed. To address this data gap, Anderson et al. developed a novel HAB Index that collapses large amounts of data into a single measure indicative of annual severity. Using the extensive datasets of nearshore toxicity, Kleindinst et al. developed a bloom categorization tool to describe the severity of a bloom based on the extent of coastline closed in a given year due to PSP. Three specific levels and descriptors were created that can be used in bloom forecasts to provide scientifically-consistent and simply-defined information to the public, resource managers, and other stakeholders.

In contrast to nearshore areas, shellfish toxicity data from offshore regions are sporadic and limited. Shellfish toxicity surveys conducted during this project represent the most extensive offshore toxicity measurements to date (DeGrasse et al.). Extensive offshore and inshore federal waters have been closed to the harvest of bivalve molluscs for years due to the potential risk of PSP; however, it was not well known if PSP was persistent annually in the shellfish species of interest. Their research demonstrated that surfclams and ocean quahogs were safe for human consumption during the time period sampled (2007-2011), yet challenges remained regarding how to allow access to the resource in a way that would prevent contaminated shellfish from entering commerce if/when toxin levels rise again. The onboard screening dockside testing protocol was developed during the GOMTOX program to address this challenge. As a result of a successful pilot study (DeGrasse et al.), a biotoxin control strategy was developed that allows fishermen to screen their harvest at sea to ensure product safety before landing. This protocol requires subsequent confirmatory testing of landed product prior to its release in the market. This two-tier system of testing[1] provides a greater level of public health protection than had previously existed for seafood harvested from federal waters.

At the start of the GOMTOX program, most offshore waters were closed to the harvest of whole and roe-on sea scallops, *P. magellanicus*,even though data demonstrating the potential risk of this resource were few. Extensive offshore testing of sea scallops, described in DeGrasse et al., found that whole and roe-on sea scallops often contained toxins above the regulatory guidance level. For example, values as high as 198 and 996 µg saxitoxin equivalents (STX eq) 100 g^{-1} for scallop gonads and viscera were measured during the study, respectively. No temporal or spatial patterns were elucidated that would provide guidance as to when to expect hazardous levels. Several parameters (e.g., gonadosomatic index) were evaluated as potential predictive indicators of roe-on toxicity; however, no predictive indices for toxicity were found. These results supported and provided additional scientific basis for the current offshore closures that are in place for whole and roe-on sea scallop products.

In addition to field measurements, laboratory studies were undertaken to enhance our understanding of toxin kinetics in surfclams, *S. solidissima*. Bricelj et al. demonstrated the high *in vivo* capacity of this shellfish species to biotransform paralytic shellfish toxins (PSTs) from ingested *Alexandrium* cells of characterized toxin composition. Further, they determined the differential effects of temperature on toxin elimination rates in non-edible (viscera) and edible tissue compartments, which help to explain the overall slow detoxification in this species. Results of this study led to specific recommendations for future consideration in modeling the toxin kinetics in surfclams, most notably the importance of using two-compartment models.

Interannual variability over 21 years of toxicity readings from the blue mussel, *Mytilus edulis*, in the tidally mixed region of Cobscook Bay, Maine showed no correlation to oceanographic factors examined, local precipitation, or local river discharge (Horecka et al.). These records reveal correlations with local weather conditions characterized by dew point and atmospheric pressure. The correlations show an association between clearer skies/drier air and increased mussel toxicity. These, and the lack of association with precipitation, suggest a link between years of increased light availability and

[1] http://www.nero.noaa.gov/nr/doc/12/12scoqgeorgesbankareareopenphl.pdf

increased toxicity.

To further understand trophic transfer and the link between toxic *Alexandrium* and shellfish toxicity, GOMTOX focused on the contribution of size-fractioned particulates in the water column to the vertical flux to the benthos (Deeds et al; Petipas et al). This work was conducted both nearshore and offshore, demonstrating differences in *Alexandrium* cell concentrations and cellular toxicity levels (Petitpas et al.). Data demonstrate that when *Alexandrium* cells are present in surface waters, they are also found throughout the water column. The *Alexandrium*-containing 20-64 µm size fraction appears to be the primary source of PSTs to all depths (Deeds et al.). Size-fractioned particle measurements also reveal that PSTs were widespread throughout all size classes of zooplankton. Diverse assemblages of zooplankton grazers were identified as PSP toxin vectors, including microzooplankton such as tintinnids, heterotrophic dinoflagellates such as *Protoperidinium* spp., and mesozooplankton grazers such as barnacle nauplii, harpacticoid and calanoid copepods, the marine cladoceran *Evadne nordmanni*, and hydroids of the genus *Clytia*.

While limited examples of toxin biotransformation in larger grazer fractions were observed, the PST composition in the bulk of the particulate samples tested remained fairly consistent during the study with gonyautoxins (1,2,3, & 4) dominating (>90%), followed by the carbamate toxins saxitoxin and neosaxitoxin (7.7%), followed by the N-sulfocarbamoyl toxins (C1 & 2, GTX 5) (1.3%). Differences between PST profiles, mainly within the composition of the gonyautoxin and carbamate toxin components, were observed between coastal GOM sampling stations and offshore Georges Bank stations in two of the three years sampled. This suggests that populations of *A. fundyense* in the coastal GOM and offshore on Georges Bank are distinct, a conclusion also reached by McGillicuddy et al.

Unique research opportunities also arose during this study that provided insight into how PSTs impact humans. Reported human intoxications associated with PSP are typically anecdotal and are based on symptoms and dietary history. DeGrasse et al. describe analysis of meal remnants and patient urine and serum samples to determine if PSTs were responsible for the observed clinical manifestations in a 2007 PSP case. It was confirmed that PSTs were present at high levels (>13,000 µg STX eq 100 g^{-1}) in mussels that had been consumed as well as in the patient urine and serum samples. Toxin profiles differed for the mussels, serum, and urine, indicating differences in residences times and/or metabolism/biotransformation. This dataset represented the first report of PST-specific excretion rates in human urine.

Management implications. The scientific accomplishments of GOMTOX investigators are broad-ranging and significant, as documented in the papers contained herein. From a management perspective, however, three major outcomes are of special note. The first is that the population dynamics model for *Alexandrium* developed during ECOHAB-GOM was further tested, evaluated (He et al. 2008; Li et al. 2009; McGillicuddy et al. 2011), and refined to the extent that it is now being actively transitioned to operational use by NOAA as a HAB forecast system for the GOM. The second major management outcome is that in January, 2013, surfclam and ocean quahog resources worth an estimated $10-15 million per year were opened to harvesting under the onboard screening, dockside testing protocol, described in detail in DeGrasse et al. GOMTOX research demonstrates that Georges Bank is home to a separate and distinct population of *A. fundyense*, described in McGillicuddy et al. The third key management outcome was the completion of a comprehensive inventory of *Pseudo-nitzschia* species in the region. As described by Fernandes and Hubbard et al., nine species were identified using electron microscopy in tandem with genetic analyses, permitting the classification of one new toxic species in the *P. pseudodelicatissima* species complex. The confirmation of DA production in seven *Pseudo-nitzschia* spp., the broad spatial and temporal distribution of these species, and the potential for concurrent exposure to multiple algal toxins in the GOM have substantial implications for ecosystem health, as well as the regional management of nearshore and offshore shellfisheries.

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Dedication: This issue is dedicated to Quay Dortch, a scientist and program manager who has worked tirelessly in support of US HAB research. She has been a valued colleague during the ECOHAB-GOM and GOMTOX projects. Since 2003, Quay has been the ECOHAB Program Coordinator for NOAA and has fought to provide funding to HAB researchers throughout the country during a time of dwindling science budgets within NOAA. She understands the need for regional research programs like GOMTOX, involving multiple PIs in an interdisciplinary effort that integrated field, laboratory, and modeling approaches to address a specific HAB problem. Throughout the GOMTOX program, she has been a valued resource, always mindful of the needs of the end users while recognizing and endorsing the fundamental science needed to provide those deliverables. Thank you Quay for all of your support and encouragement.

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