Can offshore HABs hinder the development of offshore mussel aquaculture in the northeast United States?

Darien D. Mizuta* [a], Gary H. Wikfors [a]

* Corresponding author: darien.mizuta@noaa.gov

[a] NOAA Fisheries Service, Northeast Fisheries Science Center, 212 Rogers Ave Milford, CT 06460 USA

Abstract

Shellfish aquaculture is predicted to expand from nearshore locations into US federal waters in response to increased seafood demand and domestic food security concerns. As the industry moves into new areas, risk from offshore harmful algal blooms (HABs) focuses attention on new needs for summary background information about past algal bloom events to guide management decisions and monitoring programs. Indigenous *Alexandrium* and *Pseudo-nitzschia* species both have triggered shellfish harvest closures in offshore areas of New England after toxins were measured in bivalve tissues.

Keywords: offshore shellfish aquaculture; toxic algae; New England (USA); shellfish harvest closures; historical blooms

1. Introduction: Harmful algal blooms in the Northeast region of United States

Coastal waters of the northeast United States are historically known as a hub of fishery activities, with bivalve aquaculture, mostly Eastern oysters (*Crassostrea virginica*), blue mussels (*Mytilus edulis*) and softshell clams (*Mya arenaria*), playing an increasing role in local seafood economies (NOAA, 2015). A challenge in the area has been recurring harmful algal blooms (HABs) that produce toxins that can affect physiology of many animals feeding on phytoplankton, including filter-feeding bivalves (Landsberg, 2002). Although HAB monitoring programs have been established for near-shore areas, monitoring in Atlantic offshore areas has not been conducted so far, and the limited data available have been derived from emergency and isolated research cruises after nearshore toxicity outbreaks. The current, growing interest in moving shellfish farming operations to US federal waters within the Exclusive Economic Zone (or EEZ, 3 to 200 nautical miles) is partially motivated by the intention to avoid numerous conflicts of use (and the higher shellfish toxicities) nearer the coast. Establishment of monitoring programs for harmful algae is undoubtedly necessary to support the cultivated fisheries industry in the US EEZ. To date, the lack of standards for this activity has impeded the harvest of shellfish from federal waters (Abbott, 2017). Notably, some toxic blooms can originate offshore and be transported to near-shore areas (McGillicuddy Jr. et al., 2003). Thus, routine, offshore monitoring of toxic algae is essential for the establishment of shellfish aquaculture in federal waters. Indeed, areas used for commercial shellfish farming are required by US Federal law to be routinely sampled (Langlois and Morton, 2018).

Two main, toxic microalgal taxa can be found in New England waters. The first is the dinoflagellate *Alexiandrium* spp.*;* however, note that all previous references published about *A. fundyense* and toxic *A. tamarense* on East and West coast of the US currently are referred to *A. catenella* (Litaker et al. 2018). Accordingly, future references to these aforementioned species will be as *A. catenella*. Globally, *Alexandrium* spp. can produce a suite of neurotoxic compounds referred to as saxitoxins that can cause a syndrome known as Paralytic Shellfish Poisoning (PSP) in consumers of contaminated seafood (Hégaret et al., 2009). On the other hand, *Pseudo-nitzschia* spp. are known to produce a neurotoxic amino acid, domoic acid, which can cause a reaction referred to as Amnesic Shellfish Poisoning (ASP) when ingested from contaminated seafood (Hégaret et al., 2009). The aforementioned toxic dinoflagellates can reach concentrations so high as to discolor the waters offshore to reddish brown (McGillicuddy Jr. et al., 2014); whereas, the harmful diatoms can form highly-dense, visible blooms in bays and less-dense, invisible blooms offshore (Trainer et al., 2012). Although blooms of *Alexandrium* spp*.* are always toxic in the Northeast, not all blooms of *Pseudo-nitzschia* spp. develop toxicity, and not all species of this genus are known to be toxigenic (Villac et al., 1993) as domoic acid synthesis in these species depends upon environmental conditions such as temperature, nutrients, salinity, and grazing (Mos, 2001; Fuentes and Wikfors, 2013).

Nevertheless, the presence, usually in high concentration, of either of these toxigenic microalgal groups often triggers conservative shellfish-harvest closures pending follow-up toxicity tests, although for *Alexandrium* spp. In the developed world, the presence, even in low concentrations, can be enough to result in conservative harvest closures (Trainer et al., 2012; FDA, 2018; Table 1). Bivalves are more likely to become contaminated to unsafe levels when exposed to high population densities of toxic phytoplankton, but the mere presence of toxigenic algae in the water does not imply above-limit toxic concentrations in harvested organisms.

HABs cause notable ecological and economic disruptions through responses such as shellfish harvest closures, marine wildlife mortalities, marine fish kills, long-term consumer fear of consumption of seafood products, and public health risks (Hoagland and Scatasta, 2006). The events also cause hidden, indirect costs when development and investment in aquaculture are restricted based upon perceived risks associated with the blooms (Anderson et al., 2000). The prospective bivalve species for offshore culture in

New England is the blue mussel, which has been included in local, experimental farming trials (Langan and Horton, 2003; Karney et al., 2009; Lindell et al., 2012; Buck et al., 2017; Maney et al., 2018) and is already being commercially cultured offshore on the American west coast (Lester et al., 2018). Although market price is lower than for other shellfish species, mussels are the main, imported bivalve shellfish in the U.S. (FAO, 2019); thus, offshore farming can lessen dependency upon foreign production considering that market conditions are favorable (Fairbanks, 2016). Offshore-grown mussels have reportedly overall higher quality and can be sold as premium product and green product (see details and references in Mizuta et al., 2019). Additionally, local customers are willing to pay more for a domestic product (Atlantic Corporation, 2019).

Considering concerns that the presence of toxic algae offshore could hinder offshore mussel farming off the coast of southern New England, this overview provides a compilation of the most-recent, open-source data of *in situ* sampling and assessment of harvest closures in the region of interest to provide general knowledge about the offshore distribution and characteristics of *Alexandrium catenela* and *Pseudo-nitzschia* spp. blooms. It also discusses the possible effects of the shellfish farms upon the environment, in relation to harmful algal blooms.

Table 1: Sanitary specifications of the main toxic algae genus in the US NE in relation to shellfish harvest and aquaculture (based upon Shumway, 1990; James et al., 2010; Langlois and Morton, 2018).

Harmful algae	**Phytoplankton Group**	**Toxin**	**Effect on Shellfish**	**Human Disease**	**Symptoms in humans**	**Closure thresholds for shellfish harvest**	
						Sanitary threshold in meat (per 100 g meat)	**Concentration in the sea water (cells/L)**
Alexandrium spp.	dinoflagellate	Paralytic Shellfish Toxins Saxitoxins (STXs)	Shell closure, immunodeficiency; low growth, filtration inhibition; (mass mortalities are rare)	Paralytic Shellfish Poisoning	numbness, muscular paralysis, respiratory difficulty, death	80 µg saxitoxin equivalents	Not officially established*
Pseudo-nitzschia spp.	diatom	Neurotoxin Domoic Acid (DA)	(mass mortalities are rare)	Amnesic Shellfish Poisoning	Abdominal cramp, disruption in the brain, memory loss, death	2 mg DA	Not officially established**

* For reference: presence at any concentration in Washington State (Langlois and Morton, 2018)

** For reference: 5.10^4 cells.L^{-1} in Washinton State (Langlois and Morton, 2018); 10^5 cells.L^{-1} suggested by Bates et at. (1998)

2. Materials and methods

The study area is shown in Figure 1. Available data on phytoplankton population densities off the coasts of Rhode Island, Massachusetts, and New Hampshire were obtained from the Woods Hole Oceanographic Institution (WHOI) cell count inventory database covering the period from 2005 to 2017, which includes years identified by Pershing and co-authors (2015) as representing a remarkable warming trend. Data originated either from deployments of Environmental Sample Processors (ESPs) at different locations along the coast of these states or vessel cruises. ESPs automatically collect water samples from subsurface at 1.5 m depth, and sensors test phytoplankton molecular biology (DNA and biotoxins), providing estimates of concentrations of *Alexiandrium* spp. and *Pseudo-nitzschia* spp. ESPs are moored in selected locations on vertical lines providing real-time phytoplankton data. Monitoring cruise surveys were performed at pre-determined stations with multiple vessels. During sampling cruises, at each location 2 L of seawater was sampled at surface (1 m), middle layer (10 m), and increased depth (20 m) on a CTD rosette and processed for cell counts or abundance estimates. There was not a determined frequency at which the HAB sampling cruises were scheduled because most oceanographic samplings were scheduled based upon necessity, as rapid response surveys when there was a warning that a bloom could be occurring. To gain more information and possible relevant details about the blooms, a review of the descriptions of each “bloom season” (available at: http://www.whoi.edu/website/northeast-psp/previous-bloom-seasons) from WHOI data also was performed and summarized.

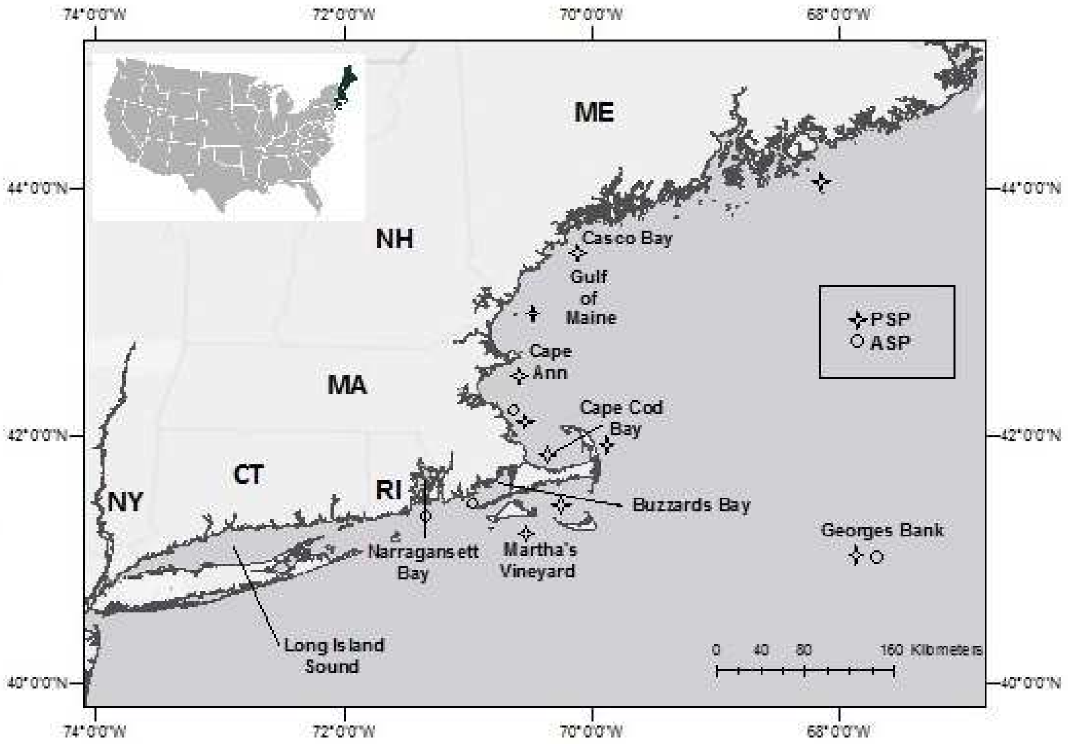

Figure 1: Study area and locations affected by harmful algal blooms caused by dinoflagellates *A. catenella* (risk of Paralytic Shellfish Poisoning, PSP) and diatoms *Pseudo-nitzschia* spp. (risk of Amnesic Shellfish Poisoning, ASP). The symbols do not indicate absolute location of blooms but rather represent occurrence in the adjacent area.

Currently, there is no official established monitoring program for HABs offshore. Official harvest closures are established in the states' coastal areas, and data of HAB-related coastal closures enable more-inclusive estimates of the dimensions of inshore algal blooms in waters of the Northeast. Coastal harvest closures attributable to HABs were quantified for yearly average days of closure from data obtained directly from the responsible governmental institution in each state: the Department of Environmental Services (DES) for New Hampshire, The Division of Marine Fisheries (DMF) for Massachusetts, and the Department of Environmental Management (DEM) for Rhode Island[1]. The total period between harvest closure and re-opening was quantified for "blue mussels" only when species identification was available; in cases wherein shellfish species were not specified, the period was determined for "shellfish." Data of shellfish harvest closures were calculated as yearly average days of closure (days.year^{-1}; d.y^{-1}) for each state to enable inter-state comparisons. The average days of closure for each state was calculated based upon a sum of closure periods for separate areas within that state, but accounting for concomitant days of closure not to overestimate the number of days. The mean number of days of harvest closure per each state for the studied period (2006-2017) was also calculated and expressed as a "threshold" (Figure 2). A linear regression was applied for the studied period (2006 to 2017) combining harvest closure data from all states to determine possible changes in harvest-closure days in the recent past in the New England region. The calculations for the studied period excluded the year of 2005 because an *Alexandrium catenella* bloom that year was characterized as 'exceptional' with regard to high toxicity, spatial extent, and cell count (Anderson et al., 2005). The year of 2005 was declared a "red tide disaster," federal assistance was requested, resulting in closure of a large spatial area of 40,000 km^2 of federal waters (Anderson et al., 2005). As the nature of the bloom was very particular in 2005 compared to all the other years in the studied period, quantitative data of that year were not used in regional quantitative trend analysis. For Rhode Island, harvest closure data were available for offshore and inshore areas, which allowed comparison of HAB-related issues between both areas.

---

[1] To increase the study area, the Department of Environmental Conservation for Long Island sites in New York was also contacted for data about coastal harvest closures attributable to HABs. However, as data were restricted to monitoring within the inner part of Long Island Sound and enclosed Shinnecock Bay, they were of limited use for extrapolation to offshore areas and ultimately were not included in the statistics.

3. Results

3.1 Characteristics of recent blooms

HABs are seasonal problems in the region, with most events occurring from April to late October (during the warm season), with some yearly fluctuations. Bloom events related to *Alexandrium catenella*, or *Pseudo-nitzschia* spp., or both organisms, occurred every year from 2005 to 2017, with fluctuating intensities and areal coverage (Figure 1; Table 2). The highest counts of cells were in 2005 (> 60,000 cells.L^{-1}) for an *Alexandrium catenella* bloom and in 2016 (> 500,000 cells.L^{-1}) for *Pseudo-nitzschia australis*. The average coastal harvest closure for the area was 58 ± 24 d.y^{-1}, excluding the atypical year of 2005. In recent years, Massachusetts was the state with the highest incidence and intensity of detected and reported toxic blooms, with both PSP- and ASP-related harvest closures; whereas, PSP has not been reported in Rhode Island to trigger harvest closures, and similarly ASP has not been detected in New Hampshire, according to respective official state reports (DES; DMF; DEM). In each state, the duration of most yearly harvest closures remained at or below the state's historical average days of closure, especially in New Hampshire (Figure 2). In percentages, the days of HAB-related closure in the New England area corresponded to 15% of the year for PSP, and 8% of the year for ASP. Using the values related to closures (d.y^{-1}) in recent years, a declining trend in closure duration was observed between the period of 2006 to 2017, although this trend was not significant (slope of equation = -3.60, $p = 0.08$). Based upon Rhode Island official shellfish harvest closure data, thus considering only ASP, offshore and inshore closures did not differ in duration, with annual average days of closure being 50 and 54 days, respectively.

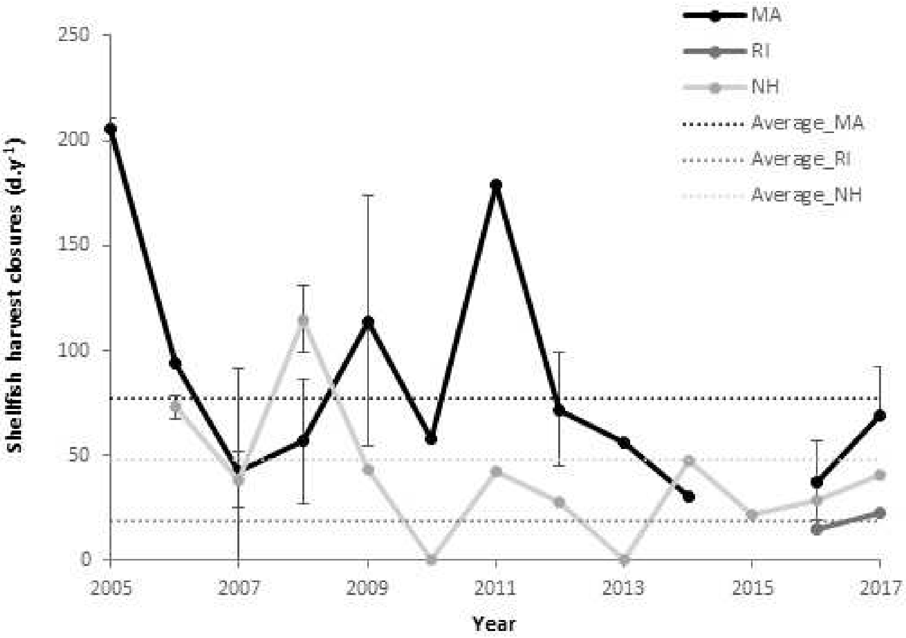

Figure 2: Number of days of shellfish harvest closures per year, especially for blue mussel, in coastal waters of Rhode Island (RI), Massachusetts (MA) and New Hampshire (NH). Dotted lines indicate the historical average number of days of closure for each state during the studied period (the atypical year of 2005 was excluded in the calculation of average for MA).

3.2 PSP

In the northern part of the studied area, *A. catenella* cell counts during blooms were maximal at the surface. For Massachusetts, the years of 2005 and 2011 were the most anomalous, namely when the number of days of algal bloom events far exceeded the yearly average. These extended blooms have not been repeated in more-recent years. In particular, the development of the event in 2017 is worth noting because it complies with previous models wherein blooms initiated offshore and were transferred inshore (McGillicuddy Jr. et al., 2003; Anderson et al., 2014). Sampling stations located at progressive distances offshore followed a distinct concentration pattern. A sampling station located 5.4 nautical miles offshore southeast of Cape Ann with an initial cell count above 2,000 cells.L^{-1} on June 21 declined in cell count to values of less than 100 cells.L^{-1}, while stations closer to shore experienced increases in *A. catenella* population density, both in surface and middle layers (Figure 3).

3.3 ASP

Pseudo-nitzschia spp. events are not as common as PSP events in the northeast US area, but recently have caused shellfish farming areas to close in 3 different years (2006, 2016 and 2017; Table 2). Reports of *Pseudo-nitzschia* spp. blooms in the study area are recent, starting in 2016 in Rhode Island as well as in Massachusetts, but blooms did not expand northward to New Hampshire. Nonetheless, the US east coast has been less susceptible to ASP occurrences than the west coast, where seasonal bloom events have been affecting both shellfish and fish harvest, with a major recent outbreak of *Pseudo-nitzschia australis* in 2015 (McCabe et al., 2016). The 2016 events at different sampling stations in Buzzards Bay in

Massachusetts showed that, during the most intense blooms, the cell-density of *Pseudo-nitzschia australis*. was highest at the bottom layer, followed by the middle and surface. This is not surprising as transport of cells of this species to the bottom can be rapid, with concentration of cells usually reflecting patterns of phytoplankton abundance in the surface layers above (Dorch et al., 1997; Sekula-Wood et al., 2009). Domoic acid (DA) can become associated with sediments, which can have a particularly long-lasting effect upon benthic food webs (Dorch et al., 1997; Burns and Ferry, 2007), as animals are able to obtain DA by ingesting live, dying, or dead DA producing *Pseudo-nitzschia* spp. cells (Lefebvre et al., 2002).

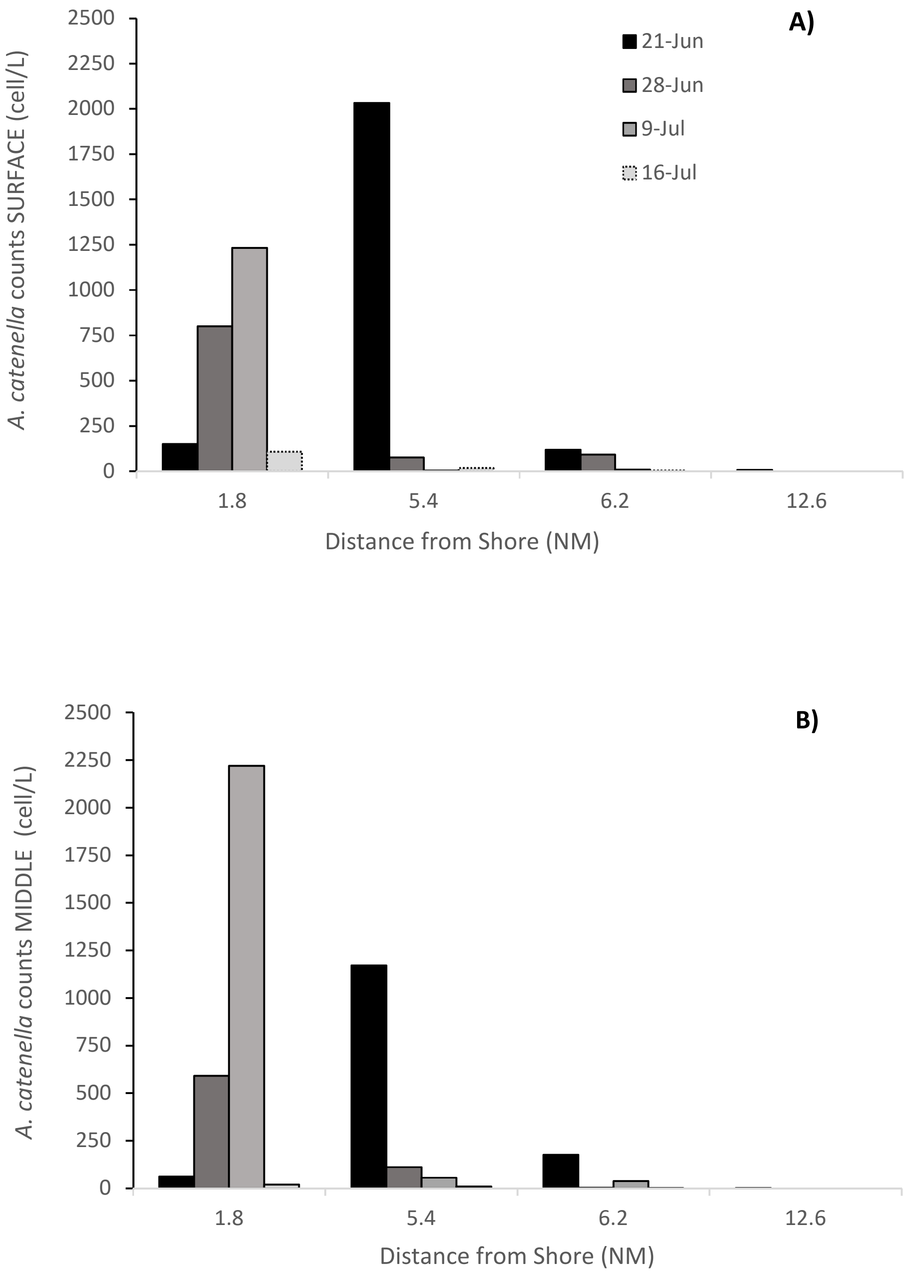

Figure 3: Development of the *Alexandrium catenella* bloom in the 2017, (A) at surface and (B) middle layer (10 m depth) offshore Cape Ann. Horizontal axis shows distance from shore in nautical miles (NM).

Table 2: Recent *Alexandrium catenella* and *Pseudo-nitzschia* spp. bloom events in the region of Rhode Island (RI), Massachusetts (MA) and New Hampshire (NH), US NE, both costal and offshore (Source: WHOI cell count inventory database). The symbol (*) denotes unidentified species.

Yearly Blooms	Harmful algae	Sampling	Blooming date (approx.)	Area	Development area	Finish date (approx.)	Final area	Maximum cell counts (cells/L)
2005	*Alexandrium catenella*	Cruise	10-15 May	Gulf of Maine Offshore Massachusetts Bay and Cape Ann	Offshore Massachusetts Bay, Cape Cod Bay, Nantucket Bay and Martha's Vineyard.	28-29 June	Offshore waters outside shelf	60,296 (surface, 9 June, Orleans, Cape Cod)
2006	*Pseudo-nitzschia* sp.*	Cruise	26 May	Unknown	Massachusetts Bay	Unknown	Unknown	10,000
	Alexandrium catenella		26 April	Massachusetts Bay, offshore Cape Ann, Cape Cod Bay	Cape Ann, Cape Cod Bay, Stellwagen, New Hampshire and Nantucket	29 June (still blooming)	Nantucket, Great Round Shoals, Cape Ann	6,410 (surface, 14 June, division New Hampshire and Maine)
2007	*Alexandrium catenella*	Cruise	21 May	Georges Bank	Georges Bank, South of Nantucket	18 October (still blooming)	Georges Bank, Western Maine offshore	13,000 (surface, 20 May, Southern Flank, George's Bank)
2008	*Alexandrium catenella*	Cruise	28 April	Gulf of Maine as offshore New Hampshire	Coastal and offshore New Hampshire, Massachusetts, Nantucket Sound, Georges Bank	End of June	Cape Cod Bay, Georges Bank	7,364 (surface, 29 May, East of Cape Ann)
2009	*Alexandrium catenella*	Cruise	Early May	Gulf of Maine bordering Maine and New Hampshire	East of Cape Ann, offshore	23 July	Offshore New Hampshire and Maine	7,257 (surface, 12 July, East of Cape Ann)
2010	*Alexandrium catenella*	Cruise	1-10 May	Coastal Cape Cod, offshore Gulf of Maine	Western Gulf of Maine and New Hampshire	End of May	-	
			30 June - 8 July	Offshore New Hampshire (previous bloom in Maine)	From Boston to Isle Au Haut (offshore Maine)	End of July	-	5,383 (surface, 5 July 2010)
2011	*Alexandrium catenella*	--	*Mid-May*	Casco Bay (Maine)	Maine, New Hampshire, south to Plymouth, Massachusetts.	-	-	676
2012	*Alexandrium catenella*	Coastal Water Samplings; ESP	*March*	Casco Bay (Maine)	New Hampshire, Massachusetts, Isles of Shoals	Beginning May	-	-
2013	*Alexandrium catenella*	Coastal Water Samplings	*April*	Nauset Marsh System, North Massachusetts	Nauset Marsh System, North Massachusetts	June	Unknown	100
2014	*Alexandrium catenella*	ESP	*Mid-May*	Casco Bay (Maine), Pemaquid Point	New Hampshire, Massachusetts	July	Unknown	2,000
2015	*Alexandrium catenella*	ESP	*May*	Offshore Maine	Gulf of Maine, New Hampshire, Massachusetts	July	Gulf of Maine	2,400
2016	*Alexandrium catenella*	Coastal Water Samplings; ESP	*April*	Gulf of Maine	Coastal flats in open ocean in Cape Cod	June	-	200
	Pseudo-nitzschia australis	Cruise	*7 October*	Narragansett Bay, Mount Hope Bay, Nantucket Sound, South Cape Cod	Nantucket Sound, South Cape Cod	31 October	-	-
			6 -13 October	Inner Buzzards Bay	Inner Buzzards Bay	Middle November	Inner Buzzards Bay	> 500,000 (surface, 6-10 October)
2017	*Pseudo-nitzschia australis*	Cruise	End of February	Lower Narragansett Bay	Lower Narragansett Bay	End of March	Lower Narragansett Bay	Unknown
	Alexandrium catenella		21 June	Southeast Cape Ann	Southeast Cape Ann	11 July	Southeast Cape Ann	(middle layer, 9 July)

4. Plan for federal waters

Monitoring programs, similar to those in coastal waters, for federal waters are challenging because of distance from shore and areal extent, which could raise safety concerns for seafood produced in offshore areas. Nevertheless, there have been precedents of toxicity in bivalve shellfish harvested in offshore areas that include economically-important, wild harvested species, such as sea scallops (*Placopecten magellanicus)*, Atlantic surfclams (*Spisula solidissima*) and ocean quahogs (*Artica islandica*). In an attempt to allow capture fisheries of shellfish from infrequently-monitored federal waters, the National Shellfish Sanitation Program approved a protocol for onboard screening and dockside testing of shellfish meats for biotoxins (DeGrasse et al., 2014). The offshore, shallow area of Georges Bank that in the past had been completely closed to harvest of shellfish because of recurrent, toxic algal blooms was partially re-opened following the adoption of the Protocol, which established that harvesting could occur only after 5 samples (1 sample consists of 30 whole mussels) from the area tested negative or below the safe threshold level (Table 1) for toxins onboard the harvesting vessel, and that two layers of testing (onboard and dockside; the latter consisting of 7 samples) should be performed before product commercialization (DeGrasse et al., 2014). The national approved methods for marine biotoxin testing by the National Shellfish Sanitation Program (NSSP) are divided into categories: "approved for use" and "approved for limited use", such as mouse assays, Receptor Binding Essay, HPLC-PCOX, and limited use of ELISA (shipboard) and Scotia Rapid Test for PSP; and HPLC and limited use of Reveal 2.0 ASP for ASP (see details of tests and categories in the NSSP Guide for the Control of Molluscan Shellfish - 2017 revision; FDA, 2018).

To account for sanitary needs and guarantee food safety of offshore aquaculture products, amendments were proposed to the National Shellfish Sanitation Plan (ISSC, 2017), establishing the same previously mentioned Protocol to be used for landing of products deriving from any offshore farm. The updates recently entered into effect with the publication of the NSSP Guide for the Control of Mollusca Shellfish - 2017 Revision (FDA, 2018). The history of harmful algal occurrences in a specific area determines the necessity of biotoxin sampling for different kinds of toxins, in a way that biotoxin tests should be performed only for known biotoxins occurring in the considered area (FDA, 2018). The State Authority in the landing State is responsible for enforcing the Code for Shellfish Sanitation and is in charge of biotoxin analysis and receipt of onboard test results. The sanitary control and surveys of shellfish grown in federal waters, which is at present limited to blue mussels, lies within the responsibility of the US Food and Drug Administration (FDA), and FDA will classify areas as approved for shellfish harvesting. The authority to declare harvest closures of biotoxin-contaminated areas, however, lies within the National Marine Fisheries Service. As in the capture fisheries, the costs of the tests are expected to be assumed by the farmers.

An obstacle to management response to toxic blooms is that the current verification of marine biotoxins is based upon animal tissue analysis for wild-caught seafood and cultured seafood rather than environmental monitoring. In the most recent National Shellfish Sanitation Plan (04. B Page 50), there is a description that water samples ‘may be assayed’ for the presence of toxin-producing phytoplankton but water samples are referred to as a recommendation, not a requirement (FDA, 2018). The approach makes it difficult to determine if blooms originate in different locations at the same time, or the exact origin of blooms offshore before reaching the coastline, and does not serve the goal of early detection (Price et al., 1991; Horner et al., 1997). Water sampling for phytoplankton could help in the aforementioned issue, but should be complementary to the already established animal tissue analysis because the relationship between toxic phytoplankton and shellfish toxicity is not direct, and there is no trigger for regulatory action based upon cell density in the NSSP (Langlois and Morton, 2018; Table 1) for the toxins studied in the present work. An established, delineated marine farm could provide support for practical environmental monitoring, as discussed below.

5. Implications of HABs for offshore shellfish aquaculture

Because algal blooms in the region of interest usually initiate offshore (McGillicuddy Jr. et al., 2003), planned locations for offshore bivalve farms should avoid the most historically-affected areas and should adopt frequent toxin monitoring to assure safe harvests. Although blooms in New England are diverse in development and spatial coverage (Anderson et al., 2008), the analysis of recent events can provide guidance and identify research gaps related to the risks associated with expansion of bivalve aquaculture in open waters. For example, the 2017 PSP event developed in a typical way for the Gulf of Maine, initiating offshore and later extending to inshore locations, which exemplifies how monitoring for offshore farms can possibly serve as early warning for the existing, coastal aquaculture industry, although toxicity should not be expected to reach inshore areas in every bloom event. The presence and toxicity status of both toxigenic algal genera suggests that EEZ areas off the coast of Massachusetts present a relatively high risk of HAB effects. Considering its coastline extension and corresponding offshore area compared to the other studied states (with coast lines of 192 miles for Massachusetts; 13 miles for New Hampshire and 40 miles for Rhode Island; Beaver, 2006), the probability of Massachusetts being affected by HAB was relatively high within the larger region.

The extent to which toxins affect shellfish is species-dependent (Hégaret et al., 2007), in relation to both the phytoplankton and cultured shellfish, even though closures, which are directly based upon toxicity of affected local shellfish, in the northeast region were, in average, less than 60 days in duration. Furthermore, shellfish usually are able to depurate toxins, and blooms very often have sub-lethal effects upon shellfish that degrade performance, such as lower growth, feeding inhibition, and other sublethal effects (Shumway, 1990; Landsberg, 2002, Table 2). Accordingly, for farmers, the risks posed by HABs are often not related to loss of production, but rather economic disruptions caused by delays in harvests.

The candidate species for offshore aquaculture, namely the blue mussel *M. edulis*, can use both *A*lexandrium spp. and *Pseudo-nitzschia* spp. as food sources in periods of low food availability (Bricelj et al., 1993) and were shown to accumulate toxins faster than other bivalves, which makes the species a suitable, and commonly-used, sentinel species (Bricelj and Shumway, 1998; Langlois and Morton, 2018). It is known that detoxification in blue mussels can be affected by factors that are also different depending upon the toxin, such as season for saxitoxins (Prakash et al., 1971), and temperature and shellfish size for DA (Novaczek et al., 1992). Nevertheless, mussels also eliminate toxins and recover quickly from the effects of toxicity after ingesting other, non-toxic phytoplankton (Novaczek et al., 1992; Galimany et al., 2008) in comparison to other bivalves such as oysters that accumulate and eliminate toxins at slower rates (Shumway, 1990). For DA, recovery is in a matter of days, as the half-life of that toxin in mussels was estimated to be in average 55 hours using a 2-compartment model fit, as the concentration of toxin profiles by time appeared bi-exponential and declined following a log-linear manner as the mussels depurated (see details in Shultz et al., 2008). Mussels are less able to recover if they had recently spawned (Galimany et al., 2008).

For other shellfish species, some previous lessons should be considered. Shellfish harvest re-openings following HAB closures showed that recovery from toxins, for both PSP and ASP, usually occurred in the following order for the local shellfish in data we accessed: softshell clams, blue mussels, ‘other shellfish’, razor clam (*Siliqua costata*), surfclam, moon snails (*Euspira heros*), indicating already scientifically-known differences between species depuration rates. But although both softshell clams and blue mussels are considered fast detoxifiers (Bricelj and Shumway, 1998), usually, blue mussels detoxify at a faster rate than softclams (Prakash et al., 1971), and HAB harvest re-opening data should be considered with caution. Considering STXs, the blue mussel reportedly detoxifies at an average of 10.6% day^{-1} and lose up to 15% of accumulated toxin per day, but *Mya arenaria* has detoxification rates up to 9.8 %.day^{-1} (see Table 4 in Bricelj and Shumway, 1998). In the studied region, clams may have had different toxicity levels for reasons such as different exposure to toxins related to different locations because the number of detoxification days required to reach the regulatory level may reflect differences in the peak of toxicity achieved by animals.

Sea scallops are divided into two categories for harvest bans, namely "sea scallops whole" and "sea scallops adductor muscle". Bans are readily applied and lengthy for the commercialization of whole scallops. In the case of PSP toxins, scallops can biotransform biotoxin into more toxic products that accumulate in the viscera, especially in the digestive gland (Shimizu and Yoshioka, 1981) and take months to years to detoxify (Bricelj and Shumway, 1998). However, commercialization of adductor muscles, which is the commonly consumed product in US, usually is not suspended by bans because muscles do not accumulate toxins as do other tissues (Shumway and Cembella, 1993). With this advantage, and because an ear hanging technique brought from Japan in which vertical ropes are used to hang scallops is being tested in New Hampshire and Maine for sea scallops, the sea scallop is the second possible target species, after blue mussels, for offshore aquaculture in the region (FFAR, 2018).

As in coastal areas, toxic algal blooms could temporarily impose offshore commercial farm harvest closures. One would expect that offshore blooms may be of shorter duration because of water advection and currents in open ocean environments compared to enclosed, coastal bays where water residence time is longer and can influence the occurrence of blooms (Anderson, 1997). This assumption, however was not confirmed based upon Rhode Island inshore and offshore data. Thus, offshore farms may have no advantage with regard to HAB closure duration compared to inshore environments, but on the positive side, closures also do not appear to last longer, at least in Rhode Island. Nevertheless, knowledge of offshore bloom characteristics and culture management are expected to help in management of disruptions from toxic algal blooms. This fact highlights the need for knowledge of historical blooms and reinforces the importance of the present work. Recently, HAB events seem to be increasing in number globally (Edwards et al., 2006; Gobbler et al., 2017), with even local reports documenting increases in enclosed, local bays (Crespo et al., 2011). For the two genera studied in the present work and region of interest, however, this trend was not observed. This indicates differences can occur locally, as previously acknowledged by Bricelj and Shumway (1998); therefore, world-wide trends cannot always be applied locally, and trends may not be occurring worldwide. Additionally, as bivalve offshore aquaculture systems are submerged to different depths, the temperature to which shellfish are exposed can be managed to a certain extent according to vertical temperature profiles to facilitate depuration and avoid reproduction (Mizuta and Wikfors, 2019), thus possibly enabling quicker recovery of harvestable stocks.

On the US northeast coast, harmful algal blooms were first detected in 1975 in the Gulf of Maine, where the bloom was caused by *Alexandrium catenella*. Subsequently, the southward expansion of *A. catenella* established blooms in Massachusetts (Franks and Anderson, 1992) and toxicity in offshore shellfish as whole animals, such as sea scallops, Atlantic surfclams, ocean quahogs and Northern horse mussels (*Modiolus modiolus*) was first reported in 1988 (White et al., 1993). *Pseudo-nitzschia* event records in the east coast are more recent, following the blooms of *P. seriata* in Canadian waters that date from 2002 (Trainer et al., 2012) but only more recently causing closures in the USA (Bates et al., 2018).

Nevertheless, regional harmful algal outbreaks in the east coast of US remain less disruptive compared to the US west coast where blooms, especially of *Pseudo-nitzschia*, are frequent and intense (McCabe et al., 2016), and several species of *Alexandrium* and *Pseudo-nitzschia* have been causing economic losses in the fisheries industry since as early as 1793 (Horner et al., 1997; Trainer, 2002; Table 3).

In spite of HAB disruptions, the US west coast has an active shellfish aquaculture production industry and is the national leader in offshore shellfish farming development, hosting the first commercial offshore blue mussel farm in the US (Lester et al., 2018). In contrast, on the east coast there have been longstanding concerns among stakeholders about feasibility of offshore shellfish farming because of possible harmful algal bloom disruptions.

Table 3: Species of toxic *Alexandrium* and *Pseudo-nitzschia* reportedly found in the West and Northeast coast of United States (Hargraves et al., 1993; Anderson et al., 1994; Villareal et al., 1994; Horner et al., 1997; Trainer, 2002; Gribble et al., 2005; Trainer et al., 2012; Fuentes and Wikfors, 2013; Borkman et al., 2014; Fernandes et al., 2014; Bates et al., 2018).

	Species	
Genus	**West Coast**	**Northeast Coast (New England area)**
Alexandrium	*A. catenella ; A. hiranoi;* *A. ostenfeldii*	*A. catenella;* *A. ostenfeldii*
Pseudo-nitzschia	*P. australis; P. delicatissima;* *P. fraudulenta; P. multiseries;* *P. pseudodelicatissima; P. pungens*	*P. australis; P. delicatissima; P. fraudulenta;* *P. granii; P. multiseries;* *P. pseudodelicatissima; P. pungens;* *P. seriata; P.subpacifica; P. turgidula*

6. Implications of suspension-feeding shellfish farming for HAB dynamics

An important prospect is that offshore aquaculture facilities can support coastal aquaculture by serving as early bloom detectors, because of potentially strategic locations, a feature called upon to be explored in a previous publication (Langlois and Morton, 2018). Early warnings allow harvesting prior to intoxication and better planning following a bloom-initiation report (Shumway, 1990). In a recent document of the Interstate Shellfish Sanitation Conference, there is a strong call for implementation of an early-warning system for marine biotoxin management (ISSC, 2017). For instance, at various sites on the Newfoundland coast in Canada (north of US New England area), the PSP toxicity *from A. catenella* in blue mussels correlated positively with abundance of cysts in sediments (Schwinghamer et al., 1994). Within species reported as being within the *A. tamarense* complex (Litaker et al. 2018), *A. tamarense* resting cysts were shown to be even more toxic than vegetative cells (Oshima et al., 1992), and locally-germinated vegetative cells of *A. catenella* can be transported to coastal waters during favorable downwelling events (McGillicuddy Jr. et al., 2003). Consequently, blooms in inshore waters can result from offshore initiation and potentially lead to coastal shellfish toxicity. Inshore cysts can also germinate but contributed to less than 15% of the total germination flux (McGillicuddy Jr. et al., 2003). Although the processes governing offshore-inshore interactions, including bloom dynamics and especially the role of cysts (Anderson, 1997), need to be further explored, the offshore *Alexandrium* bloom initiation hypothesis was previously highlighted by Martin and Richard (1996). Those authors suggested that, in the offshore Bay of Fundy, spatially large *A. catenella* cyst beds resulted in high numbers of vegetative cells offshore, and advected offshore populations were considered responsible for most subsequent coastal blooms and shellfish toxicity.

As described by Langlois and Morton (2018), the responsibility of monitoring and sampling would be primarily borne by the shellfish industry, and agreed-upon responsibilities would be part of the regulatory biotoxin contingency plan. At this stage, offshore shellfish aquaculture in the US targets blue mussels that, as mentioned, accumulate and depurate toxins quickly, aside from being extremely resilient. As (most) blooms originate offshore, the establishment of offshore blue mussel farms, where frequent, biweekly regulatory monitoring is already implemented (Maney et al., 2019), would allow for easy local, open ocean HAB monitoring and early detection within the farming site. Setting stations within the farm would allow for both water sample collection and farmed mussel samples from the longline at different depths (for details of offshore farming design refer to Buck, 2007; Buck et al., 2017) of offshore mussel farms. Water samples for phytoplankton analysis would allow for species identification and algal taxonomy. The offshore mussel farm itself would constitute a sentinel station, as the arrangement permits ready access to frequent sample collection and early detection of biotoxins with a recognized sentinel bivalve species, eliminating the need for more laborious, routine samples of, for example, other benthic species harvested offshore (Langlois and Morton, 2018). The frequency of monitoring can be adjusted as the offshore aquaculture activity and monitoring needs develop, considering that frequency interval is not prescribed in the NSSP, as it should take into account the unpredictability of toxin events and variability of phytoplankton populations in terms of species and abundance in the area (Langlois and Morton, 2018).

Taking into account the available, local hydrological knowledge, coastal areas “downstream” or where downwelling could occur (Anderson, et al., 2008; McGillicuddy Jr. et al., 2014), could be warned in advance of the possibility of a bloom reaching the coast. The ability to understand and predict HABs in coastal areas will depend upon coastal-offshore interaction, even though processes are complex (McGillicuddy Jr. et al., 2003). Coastal farms in New England produce mainly the Eastern oyster, which is currently a more valuable product than the blue mussel; thus, the economic service an offshore farm can provide is extended beyond the revenue of mussel commercialization.

A possible negative side effect of offshore shellfish culture in connection with HABs is that shellfish could be vectors if transported from offshore phycotoxin-contaminated areas to areas where a toxic bloom is not concurrently occurring (Scarratt et al., 1993; Hégaret et al., 2008), as shellfish begin to self-depurate and can seed a future bloom (Shumway et al., 1990). In the case of PSP, some studies show the *Alexandrium catenella* cells remain viable and resume normal growth following egestion in feces (Bricelj et al., 1993), but more recent studies (Hégaret et al., 2008) showed that within 24 hours of depuration in clean water after exposure to toxicity, the feces produced by mussels did not contain viable *Alexandrium catenella* cells. Although the potential transport of PSP is not fully understood, control of movement of shellfish can prevent possible transfer of toxic phytoplankton with shellfish.

Data for offshore areas should be interpreted as preliminary because, in the case of *Pseudo-nitzschia,* the high concentration of potentially-harmful algal taxa does not always mean that cells are toxigenic, as that requires additional investigation and data that were not available. Nor can the algal cell density directly translate to levels of toxicity in the exposed shellfish, a fact that is true for both harmful algae discussed in this study. Available data remain very scarce and sporadic, thus generalization is provisional.

7. Conclusions

This summary of recent harmful algal blooms in the Northeast area is intended to help in planning for future research and fisheries management of a nascent offshore mussel-farming industry. Regionally, the frequency and intensities of blooms did not show increasing tendencies based upon shellfish harvest closures in recent years. Offshore farming may experience closures with similar length as active, coastal farming areas, with particular higher frequency in Massachusetts than in the other areas. Blue mussels are already the primary sentinel species for shellfish harvest closures, and because they can recover quickly from toxicity, mussel farming offshore is advantageous, both as an alternative farming location and as a service to traditional, coastal farming areas. Although offshore aquaculture locations will most probably overlap the areas where blooms start, it should not discourage offshore shellfish aquaculture development. Evidently, the development of offshore aquaculture will require extension of phytoplankton and shellfish toxicity monitoring programs with higher sampling frequency and strong aquaculture regulations of HABs, as offshore environmental monitoring results will be essential to ascertain the safety of products, including possible benefits of early warning to coastal areas, and thus reliability and sustainability of the overall northeast US shellfish aquaculture industry.

8. Acknowledgements

The authors would like to acknowledge Dr. Quay Dortch from the Ecology and Oceanography of Harmful Algal Blooms (ECOHAB) – Program (NOAA), Dr. Donald M. Anderson, Dr. Dennis McGillicuddy, Bruce Keafer, Olga Kosnyrev from WHOI, Kristin DeRosia-Banick from the Bureau of Aquaculture - Connecticut Department of Agriculture and Dr. Stacey McLeroy from the Center for Food Safety and Applied Nutrition – US Food and Drug Administration for providing database guidance during the initial data gathering for this manuscript. We also thank the 4 state government departments for supplying HAB-related harvest closure information. We acknowledge the 3 anonymous reviewers for their valuable suggestions to improve this manuscript. This research was supported by a postdoctoral fellowship award from the NOAA Fisheries Office of Aquaculture through the National Academy of Sciences National Research Council.

9. References

Abbott, M. 2017. Sanitary control of molluscan shellfish harvested from federal waters, 101-102. *In:* ISSC, 2017. Task Force I Report. International Shellfish Sanitation Conference. South Carolina, 11-19 October 2017.

Anderson, D.M., D.M. Kulis, G.J. Doucette, J.C. Gallagher, E. Balech. 1994. Biogeography of toxic dinoflagellates in the genus *Alexandrium* from the northeastern United States and Canada. Marine Biology 120, 467-478.

Anderson, D.M. 1997. Diversity of harmful algal blooms in coastal waters. Limnology Oceanography 42(5, part 2), 1009-1022.

Anderson, D.M., Y. Kaoru, A.W. White. 2000. Estimated annual economic impacts from harmful algal blooms (HABs) in the United States. Woods Hole Oceanographic Institute technical report 2000-11.

Anderson, D.M., B.A. Keafer, D.J. McGillicuddy Jr., M.J. Mickelson, K.E. Keavy, P.S. Libby, J.P. Manning, C.A. Mayo, D.K. Whittaker, J.M. Hickey, R. He, D.R. Lynch, K.W. Smith. 2005. Initial observations of the 2005 *Alexandrium fundyense* bloom in southern New England: general patterns and mechanisms. Deep-Sea Research II 52, 2856-2876.

Anderson, D.M., J.M. Burkholder, W.P. Cochlan, P.M. Glibert, C.J. Gobler, C.A. Heil, R. Kudela, M.L. Parsons, J.E.J. Rensel, D.W. Townsend, V.L. Trainer, G.A. Vargo. 2008. Harmful algal blooms and eutrophication: Examining linkages from selected coastal regions of the United States. Harmful Algae 8(1), 39–53.

Anderson, D.M., D.A. Couture, J.L. Kliendinst, B.A. Keafer, D.J. McGillicuddy Jr., J.L. Martin, M.L. Richlen, J.M. Hickey, A.R. Solow. 2014. Understanding interannual, decadal level variability in paralytic shellfish poisoning toxicity in the Gulf of Maine: The HAB Index. Deep-Sea Research II 103, 264-276.

Atlantic Corporation. 2019. Consumer attitudes and preferences about farm-raised shellfish, finfish and seas vegetables in the Atlantic coast states, Waterville, ME.

Bates, S.S., D.L. Garrison, R.A. Horner. 1998. Bloom dynamics and physiology of domoic-acid-producing *Pseudo-nitzschia* species. In: Anderson, D.M., A.D. Cembella, G.M. Hallegraeff (Eds.) Physiological ecology of harmful algal blooms, 267-292. Springer-Verlag, Heidelberg.

Bates, S.S., K.A. Hubbard, N. Lundholm, M. Montresor, C.P. Leaw. 2018. *Pseudo-nitzschia*, Nitzschia, and domoic acid: New research since 2011. Harmful Algae 79, 3-43.

Beaver, J.C. 2006. US International Borders: Brief Facts. CRS Report for Congress, RS 21729.

Bricelj, V. M., M. Greene, A.D. Cembella. 1993. Growth of the blue mussel *Mytilus edulis* on toxic *Alexandrium fundyense* and effects of gut passage on dinoflagellate cells, 371-376. In: Smayda, T.J., Y Shimizu (Eds.) Toxic Phytoplankton Blooms in the Sea. Developments in Marine Biology 3, New York: Elsevier Science Publishers.

Bricelj, V.M., S.E., Shumway. 1998. Paralytic shellfish toxins in bivalve molluscs: occurrence, transfer kinetics, and biotransformation. Reviews in Fisheries Science 6(4): 315-383.

Borkman, D.G., T.J. Smayda, E.N. Schwarz, L.J. Flewellin, C.R. Tomas. 2014. Recurrent vernal presence of the toxic *Alexandrium tamarense/ Alexandrium fundyense* (Dinoflagellate) species complex in Narragansett Bay, USA. Harmful Algae 32, 73-80.

Buck, B.H. 2007. Experimental trials on the feasibility of offshore seed production of the mussel *Mytilus edulis* in the German Bight: installation, technical requirements and environmental conditions. Helgoland Marine Research 61, 87-101.

Buck, B.H., N. Nevejan, M. Wille, M.D. Chambers, T. Chopin. 2017. Offshore and multi-use aquaculture extractive species: seaweeds and bivalves, 23-70. In: Buck, B.H., R. Langan (Eds.) Aquaculture perspective of multi-use sites in the open ocean: The untapped potential for marine resources in the Anthropocene. Springer Open, 404 p.

Burns, J.M., J.L. Ferry. 2007. Adsorption of domoic acid to marine sediments and clays. Journal of Environmental Monitoring 9(12), 1373–1377.

Crespo, B.G., B.A. Keafer, D. K. Ralston, H. Lind, D. Farber, D.M. Anderson. 2011. Dynamics of *Alexandrium fundyense* blooms and shellfish toxicity in the Nauset Marsh System of Cape Cod (Massachusetts, USA). Harmful Algae 12, 26-38.

DeGrasse, S. , S. Conrad, P. DiStefano, C. Vanegas, D. Wallace, P. Jensen, J.M. Hickey, F. Cenci, J. Pitt, D. Deardorff, F. Rubio, D. Easy, M.A. Donovan, M. Laycock, D. Rouse, J. Mullen. 2014. Onboard screening dockside testing as a new means of managing paralytic shellfish poisoning risks in federally closed waters. Deep Sea Research II 103, 288-300.

Dorch, Q., R. Robichaux, S. Pool, D. Milsted, G. Mire, N.N. Rabalais, T.M. Soniat, G.A. Fryxell, R.E. Turner, M.L. Parsons. 1997. Abundance and vertical flux of *Pseudo-nitzschia* in the northern Gulf of Mexico. Marine Ecology Progress Series 146(1-3), 249-264.

Edwards, M., D.G. Johns, S.C. Leterme, S. Svendsen, A. J. Richardson. 2006. Regional climate change and harmful algal blooms in the northeast Atlantic. Limnology and Oceanography 51(2), 820-829.

Fairbanks, L. 2016. Moving mussels offshore? Perceptions of offshore aquaculture policy and expansion in New England. Ocean and Coastal Management 130, 1-12.

FAO. 2019. Commodity trade and production. Fisheries and aquaculture information and statistics branch. Last access: Feb 14, 2019 at 1:52 pm.

FDA. 2018. Guide for the control of molluscan shellfish 2017 revision. National Shellfish Sanitation Program (NSSP). Food and Drug Administration. Available at:

https://www.fda.gov/food/federalstate-food-programs/national-shellfish-sanitation-program-nssp (Last access: May 8, 2019 at 10:20 am).

Fernandes, L.F., K.A. Hubbard, M.L. Richlen, J. Smith, S.S. Bates, J. Ehrman, C. Léger, L.L. Mafra Jr., D. Kulis, M. Quilliam, K. Libera, L. McCauley, D.M. Anderson. 2014. Diversity and toxicity of the diatom *Pseudo-nitzschia* Peragallo in the Gulf of Maine, Northwestern Atlantic Ocean. Deep Sea Research Part II: Topical Studies in Oceanography 103, 139–162.

FFAR. 2018. FFAR awards four grants totalling $1.5 million to enhance economic opportunity for clam, halibut, scallop, yellowtail and sea cucumber producers in United States. Available at: https://foundationfar.org/2018/04/23/ffar-awards-four-grants-to-enhance-american-aquaculture/

Franks, P.J.S., D.M. Anderson. 1992. Alongshore transport of a toxic phytoplankton bloom in buoyancy current: *Alexandrium tamarense* in the Gulf of Maine. Marine Biology 112, 153-164.

Fuentes, M. S., G.H. Wikfors. 2013. Control of domoic acid toxin expression in *Pseudo-nitzschia multiseries* by copper and silica: Relevance to mussel aquaculture in New England (USA). Marine Environmental Research 83, 23-28.

Galimany, E., I. Sunila, H. Hégaret, M. Ramon, G.H. Wikfors. 2008. Experimental exposure of the blue mussel (*Mytilus edulis, L.*) to the toxic dinoflagellate *Alexandrium fundyense*: Histopathology, immune responses, and recovery. Harmful Algae 7, 702-708.

Gobler, C.J., O.M. Doherty, T.K. Hattenrath-Lehmann, A.W. Griffith, Y. Kang, R.W. Litaker. 2017. Ocean warming since 1982 has expanded the niche of toxic algal blooms in the North Atlantic and North Pacific oceans. Proceedings of the National Academy of Science 114(19), 4975-4980.

Gribble, K.E., B.A. Keafer, M.A. Quilliam, A.D. Cembella, D.M. Kulis, A. Manahan, D.M. Anderson. 2005. Distribution and toxicity of *Alexandrium ostenfeldii* (Dinophycea) in the Gulf of Maine, USA. Deep Sea Research Part II: Tropical Studies in Oceanography 52(19): 2745-2763.

Hargraves, P.E., J. Zhang, R. Wang, Y. Shimizu. 1993. Growth characteristics of the diatoms *Pseudonitzschia pungens* and *P. fraudulenta* exposed to ultraviolet radiation. Hydrobiologia 269/270: 207-212.

Hégaret, H., G.H. Wikfors, S.E. Shumway. 2007. Diverse feeding responses of five species of bivalve mollusc when exposed to three species of harmful algae. Journal of Shellfish Research 26 (2), 549–559.

Hégaret, H., S.E. Shumway, G.H. Wikfors, S. Pate, J.A.M. Burkholder. 2008. Potential transport of harmful algae via relocation of bivalve molluscs. Marine Ecology Progress Series 361, 169-179.

Hégaret, H., G.H. Wikfors, S.E. Shumway. 2009. Biotoxin contamination and shellfish safety, 43-80. In: Shumway, S.E., G.E. Rodrick (Eds.) Shellfish safety and quality, Woodhead Publishing, Cambridge, 591p.

Hoagland, P., S. Scatasta, 2006. The economic effects of harmful algal blooms, 391-402. In: Granéli, E., J.T. Turner (Eds.), Ecology of harmful algae. Springer, Berlin, Heidelberg, 418p.

Horner, R.A., D.L. Garrison, F.G. Plumley. 1997. Harmful algal blooms and red tide problems on the US west coast. Limnology and Oceanography 42(5:2), 1076-1088.

ISSC, 2017. Task Force I Report. Interstate Shellfish Sanitation Conference. South Carolina, 11-19 October 2017.

James, K.J., B. Carey, J. O'Halloran, F.N.A.M van Pelt, Z. Škrabáková. 2010. Shellfish toxicity: human health implications of marine algal toxins. Epidemiology and Infection, 138(7), 927-940.

Karney, R.C., D. Robisnson, S. Stephens, A. Surier. 2009. Site permitting and market survey: preliminary tasks for the development of a mussel aquaculture industry in the offshore waters of Martha's Vineyard. Journal of Shellfish Research 28(3), 651-651. Abstracts of Technical Papers of the Milford Aquaculture Seminar February 23–25, 2009, Connecticut.

Landsberg, J.H. 2002. The effects of harmful algal blooms on aquatic organisms. Reviews in Fisheries Science 10(2), 113-390.

Langan, R., F. Horton. 2003. Design, operation and economics of submerged longline mussel culture in the open ocean. Bulletin of the Aquaculture Association of Canada 103, 3, 11-20.

Langlois, G.W., S.L. Morton. 2018. Marine biotoxin and harmful algae monitoring and management, 377-417. In: Shumway, S.E., J.M. Burkholder, S.L. Morton. Harmful algal blooms: a compendium desk reference. 667 p.

Lefebvre, K.A., S.Bargu, T. Kieckhefer, M.W. Silver. 2002. From sanddabs to blue whales: The pervasiveness of domoic acid. Toxicon 40, 971-977.

Lester, S.E., R.R. Gentry, C.V. Kappel, C. White, S.D. Gaines. 2018. Offshore aquaculture in the United States: Untapped potential in need of smart policy. Proceeding of the National Academy of Science 115(28), 7162-7165.

Lindell, S., R. Karney, B. Silkes, E.G. Beach, B. Rathjen. 2012. Offshore mussel farming in Southern New England: research plans for optimizing economic yield. Journal of Shellfish Research 31(1), 312-312. Abstracts 104th Annual Meeting, March 24-29, 2012, National Shellfisheries Association, Seattle, Washington.

Litaker, R.W., S. Fraga, M. Montresor, M. Brosnahan, D.M. Anderson, M. Hoppenrath, S. Murray, J. Wolny, Uwe John, N. Sampedro, J. Larsen, A.J. Calado. 2018. Harmful Algae News 61, 13-15.

Maney E. Jr., M. Fregeau, B. Lee, 2018. First year results from offshore shellfish aquaculture in Federal waters of the Atlantic. 38Th Milford Aquaculture Seminar, 8-10 January, NOAA Fisheries, Shelton.

Maney E. Jr., M. Fregeau, B. Lee. 2019. Minimizing interactions with protected species through gear design and monitoring efforts at an offshore shellfish farm in federal waters in the Gulf of Maine, 9-11 January, Northeast Aquaculture Conference & Exposition and the 39th Milford and Aquaculture Seminar, Boston, Massachusetts.

Martin, J.L., D. Richard. 1996. Shellfish toxicity from the Bay of Fundy, eastern Canada: 50 years in retrospect. In: Yasumoto, T., Y. Oshima, Y. Fukuyo (Eds.) Harmful and Toxic Algal Blooms. UNESCO, Paris, pp.3-6.

McCabe, R., B.M. Hickey, R.M. Kudela, K.A. Lefebvre, N.G. Adams, B.D. Bill, F.M.D. Gulland, R.E. Thomson, W.P. Cochlan, V.L. Trainer. 2016. An unprecendent coastwide toxic algal bloom linked to anomalous ocean conditions. Geophysical Research Letters 43(19), 10366-10376.

McGillicuddy Jr., D.J., R.P. Signell, C.A. Stock, B.A. Keafer, M.D. Keller, R.D. Hetland, D.M. Anderson. 2003. A mechanism for offshore initiation of harmful algal blooms in the coastal Gulf of Maine. Journal of Plankton Research 25(9), 1131-1138.

McGillicuddy Jr., D.J., M.L. Brosnahan, D.A. Couture, R. He, B.A. Keafer, J.P. Manning, J.L. Martin, C.H. Pilskaln, D.W. Townsend, D.M. Anderson. 2014. A red tide of *Alexandrium fundyense* in the Gulf of Maine. Deep Sea Research Part II: Topical Studies in Oceanography 103, 174-184.

Mizuta, D.D., M.S. Dixon, E.J. Maney Jr., M. Fregeau, G.H. Wikfors. 2019. Offshore mussel aquaculture strategies for farming in the changing environment of the Northeast U.S. shelf EEZ. Bulletin of Japan Fisheries Research and Education Agency 49, 111-119.

Mizuta, D.D., G.H. Wikfors. 2019.

Mos, L. 2001. Domoic acid: a fascinating marine toxin. Environmental Toxicology and Pharmacology 9, 79-85.

NOAA. 2015. Marine Aquaculture Strategic Plan FY 2016-2020. US Department of Commerce. Available at: https://www.fisheries.noaa.gov/aquaculture-library. Last access: August 9, 2018.

Novaczek, I., M.S. Madhyastha, R.F. Ablett, A. Donald, G. Johnson, M.S. Nijjar, D.E. Sims. 1992. Depuration of domoic acid from live blue mussels (*Mytilus edulis*). Canadian Journal of Fisheries and Aquatic Sciences 49, 312–318.

Oshima, Y., C. J. Bolch, G. M. Hallegraeff. 1992. Toxin composition of resting cysts of *Alexandrium tamarense* (Dinophyceae). Toxicon 30(12), 1539–1544.

Prakash, A., J.C. Medcof, A.D. Tenant. 1971. Paralytic shellfish poisoning in eastern Canada. Bulletin of Fisheries Resource Board of Canada 177: 87.

Pershing, A.J., M.A. Alexander, C.M. Hernandez, L.A. Kerr, A. Le Bris, K.E. Mills, J.E. Nye, N.R. Record, H.A. Scannell, J.D. Scott, G.D. Sherwood, A.C. Thomas. 2015. Slow adaptation in the face of rapid warming leads to collapse of the Gulf of Maine cod fishery. Science 350(6262), 809-812.

Price, D.W., K.W. Kizer, K H. Hansgen. 1991. California's paralytic shellfish poisoning prevention program, *1927-89.* Journal of Shellfish Research 10, 119-145.

Scarratt, A.M., D.J. Scarratt, M.G. Scarratt. 1993. Survival of live *Alexandrium tamarense* cells in mussel and scallop spat under simulated transfer conditions. Journal of Shellfish Research 12(2), 383–388.

Schwinghamer, P., M. Hawryluk, C. Powell, C.H. MacKenzie 1994. Resuspended hypnozygotes of *Alexandrium fundyense* associated with winter occurrence of PSP in inshore Newfoundland waters. Aquaculture 122, 171–179.

Sekula-Wood, E., A. Schnetzer, C.R. Benitez-Nelson, C. Anderson, W.M. Berelson, M.A. Brzezinski, J.M. Burns, D.A. Caron, I. Cetinic, J.L. Ferry, E. Fitzpatrick, B.H. Jones, P.E. Miller, S.L. Morton, R.A. Schaffner, D.A. Siegel., R. Thunell. 2009. Rapid downward transport of the neurotoxin domoic acid in coastal waters. Nature Geoscience 2, 271-275.

Shimizu, Y., M. Yoshioka. 1981. Transformation of paralytic shellfish toxin as demonstrated in scallop homogenates. Science 212, 546-549.

Shultz, I.R., A. Skillman, D. Woodruff. 2008. Domoic acid excretion in dungeness crabs, razor clams and mussels. Marine Environmental Research 66, 21-23.

Shumway, S.E. 1990. A review of the effects of algal blooms on shellfish and aquaculture. Journal of the World Aquaculture Society 21(2), 65-104.

Shumway, S.E., J. Barter, E. Sherman-Caswell. 1990. Auditing the impact of toxic algal blooms on oysters. Environmental Auditor 2, 41-56.

Shumway, S.E., A.D. Cembella. 1993. The impact of toxic algae on scallop culture and fisheries, Reviews in Fisheries Science 1(2), 121-150.

Trainer, V.L. 2002. Harmful algal blooms on the US west coast, 89-119. In: Taylor, F.J., V.L. Trainer (Eds.), Harmful Algal Blooms in the PICES Region of the North Pacific. PICES Scientific Report 23.

Trainer, V.L., S.S. Bates, N. Lundholm, A.E. Thessen, W.P. Cochlan, N.G. Adams, C.G. Trick. 2012. *Pseudo-nitzschia* physiological ecology, phylogeny, toxicity, monitoring and impacts on ecosystem health. Harmful Algae 14, 271-300.

Villac, M.C., D.L. Roelke, F.P. Chavez, L.A. Cifuentes, G.A. Fryxell. Pseudo-nitzchia autrslis Frenguelli and related species from the west coast of the U.S.A.: occurrence and domoic acid production. Journal of Shellfish Research 12(2), 457-465.

Villareal, T.A., D.L. Roelke, G.A. Fryxell. 1994. Occurrence of the toxic diatom *Nitzschia pungens f. multiseries* in Massachusetts Bay. Marine Environmental Research 37, 417e423.

White, A.W., J. Nassif, S.E. Shumway, D.K. Whittaker. 1993. Recent occurrence of paralytic shellfish toxins in offshore shellfish in the northeast United States, 435-440. In: Toxic Phytoplankton Blooms in the Sea. Proceedings of the Fifth International Conference on Toxic Marine Phytoplankton. Elsevier Science Publishers, Amsterdam.