

Marine harmful algal blooms (HABs) in the United States: history, current status and future trends

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ABSTRACT

Harmful algal blooms (HABs) are diverse phenomena involving multiple species and classes of algae that occupy a broad range of habitats from lakes to oceans and produce a multiplicity of toxins or bioactive compounds that impact many different resources. Here, a review of the status of this complex array of marine HAB problems in the U.S. is presented, providing historical information and trends as well as future perspectives. The study relies on thirty years (1990–2019) of data in HAEDAT - the IOC-ICES-PICES Harmful Algal Event database, but also includes many other reports. At a qualitative level, the U.S. national HAB problem is far more extensive than was the case decades ago, with more toxic species and toxins to monitor, as well as a larger range of impacted resources and areas affected. Quantitatively, no significant trend is seen for paralytic shellfish toxin (PST) events over the study interval, though there is clear evidence of the expansion of the problem into new regions and the emergence of a species that produces PSTs in Florida – *Pyrodinium bahamense*. Amnesic shellfish toxin (AST) events have significantly increased in the U.S., with an overall pattern of frequent outbreaks on the West Coast, emerging, recurring outbreaks on the East Coast, and sporadic incidents in the Gulf of Mexico. Despite the long historical record of neurotoxic shellfish toxin (NST) events, no significant trend is observed over the past 30 years. The recent emergence of diarrhetic shellfish toxins (DSTs) in the U.S. began along the Gulf Coast in 2008 and expanded to the West and East Coasts, though no significant trend through time is seen since then. Ciguatoxin (CTX) events

caused by *Gambierdiscus* dinoflagellates have long impacted tropical and subtropical locations the U.S., but due to a lack of monitoring programs as well as under-reporting of illnesses, data on these events are not available for time series analysis. Geographic expansion of *Gambierdiscus* into temperate and non-endemic areas (e.g., northern Gulf of Mexico) is apparent, and, fostered by ocean warming. HAB-related marine wildlife morbidity and mortality events appear to be increasing, with statistically significant increasing trends observed in marine mammal poisonings caused by ASTs along the coast of California and NSTs in Florida. Since their first occurrence in 1985 in New York, brown tides resulting from high-density blooms of *Aureococcus* have spread south to Delaware, Maryland, and Virginia, while those caused by *Aureoumbra* have spread from the Gulf Coast to the east coast of Florida. Blooms of *Margalefidinium polykrikoides* occurred in four locations in the U.S. from 1921–2001 but have appeared in more than 15 U.S. estuaries since then, with ocean warming implicated as a causative factor. Numerous blooms of toxic cyanobacteria have been documented in all 50 U.S. states and the transport of cyanotoxins from freshwater systems into marine coastal waters is a recently identified and potentially significant threat to public and ecosystem health.

Taken together, there is a significant increasing trend in all HAB events in HAEDAT over the 30-year study interval. Part of this observed HAB expansion simply reflects a better realization of the true or historic scale of the problem, long obscured by inadequate monitoring. Other contributing factors include the dispersion of species to new areas, the discovery of new HAB poisoning syndromes or impacts, and the stimulatory effects of human activities like nutrient pollution, aquaculture expansion, and ocean warming, among others. One result of this

multifaceted expansion is that many regions of the U.S. now face a daunting diversity of species and toxins, representing a significant and growing challenge to resource managers and public health officials in terms of toxins, regions, and time intervals to monitor, and necessitating new approaches to monitoring and management. Mobilization of funding and resources for research, monitoring and management of HABs requires accurate information on the scale and nature of the national problem. HAEDAT and other databases can be of great value in this regard but efforts are needed to expand and sustain the collection of data regionally and nationally.

Keywords: HAB; harmful algal bloom; red tide; eutrophication; time series; HAEDAT

Highlights:

- The first effort to quantitatively analyze trends in U.S. marine HAB events
- Some HABs (PSTs and NSTs) show no trend over 30 years; DSTs show no trend over 12 years
- Others (AST, CTXs, *Margalefidinium*, brown tides, cyanotoxins) increased in frequency and/or geographic extent
- A statistically significant increasing trend is seen for all U.S. HAB events combined

- 91 ● Part of the expansion is a realization of the true scale of the problem, long obscured by
92 inadequate monitoring
- 93 ● Increases also linked to species dispersion and stimulation from nutrient pollution,
94 aquaculture, and ocean warming
- 95

1 Introduction

Harmful algal blooms (HABs) are a significant problem in U.S. coastal waters, dating back hundreds of years when explorers and early west-coast settlers were poisoned from what we now know were toxins in the seafood they consumed (e.g., Fortuine 1975). The species that cause HABs in the U.S. are diverse, as are the habitats in which they occur. Impacts are equally diverse and include multiple human poisoning syndromes associated with the consumption of molluscan and crustacean shellfish, fish, and other marine animals that have accumulated algal toxins. Human exposures to aerosolized or water-borne toxins, and dermatological contact with HABs can also have negative impacts. Other effects include mortalities of fish and wildlife, ecosystem disruption, hypoxia and anoxia from high biomass blooms, and noxious impacts associated with the accumulation and decay of massive micro- and macroalgal blooms.

HABs affect economic and health sectors that include commercial and recreational fisheries, aquaculture, coastal tourism, and wildlife and human health. Potentially impacted resources include commercially harvested fish and shellfish with a value of \$5.6 billion in 2018, and aquaculture production valued at \$1.5 billion in 2017 (NMFS 2018). Of all species of fish and shellfish harvested, shellfish are most severely impacted by HABs due to the retention of toxins in their tissues. The delay of the Dungeness crab season due to a massive domoic acid event on the U.S. West Coast in 2015 caused an estimated \$48.3 million in direct economic impacts and resulted in an appropriation by Congress of \$25 million in disaster aid. The direct economic impacts of a 2005 *A. catenella* bloom on commercial fisheries, in terms of lost gross revenues,

were \$2.4 million in Maine and \$16-18 million in Massachusetts (Jin et al., 2008). Economic impacts on the recreational razor clam fishery that brings tourists to remote regions of the Washington State coast range from a loss of 3 to 339 full-time job equivalents and from \$110,000 to \$10.6 million in coastal income (Huppert and Trainer, 2014). HABs can also contribute to the stranding of numerous marine mammals, impacting ecosystem health (e.g., McCabe et al., 2019; Flewelling et al., 2005).

HAB phenomena in the U.S. are one component of the global problem currently being assessed through the GLOBALHAB Status Report (Hallegraeff et al. this volume). As countries and regions throughout the world assess the current status and future trends of HABs using common datasets and approaches, a comprehensive view of the nature and global impact of these phenomena will emerge. Here, a review of the status of marine HAB problems in the U.S. is provided using historical information and trend analysis. Brief summaries of the key drivers for bloom dynamics are presented as well. This compilation of information is of value not only to assist in current management strategies for fisheries, tourism, human health and other impacted sectors, but it will also provide the baseline against which future changes can be assessed, particularly those associated with climate change, nutrient pollution, and other global trends.

2 Methods

One challenge with a study of the trends of HAB events through time is that the datasets available at the local, state, and national levels are highly variable in terms of years of coverage,

parameters measured, and the nature of bloom events that are recorded. Although these records are valuable and are used to some extent herein, this study relies predominantly on HAEDAT - the IOC-ICES-PICES¹Harmful Algal Event database (<http://haedat.iode.org/>). HAEDAT was originally established by the ICES-IOC Working Group on Harmful Algal Bloom Dynamics in the 1990s to compile bloom data from ICES countries bordering the North Atlantic. In 2000, PICES began adding bloom records from the Pacific region (though U.S. West Coast HAB events have been recorded in HAEDAT since 1989). The database now contains 880 bloom events from the U.S.

All reports entered into HAEDAT must meet a strict definition of a ‘harmful algal event’. Specifically, the bloom must be associated with a negative impact or management action. These could include: 1) toxin accumulation in seafood above levels considered safe for human consumption; 2) water discoloration, scum or foam sufficient to cause ecosystem damage or a socio-economic impact; 3) any event where humans, animals or other organisms are negatively affected by the bloom; or 4) precautionary closures of harvesting areas based on predefined thresholds of toxic phytoplankton cells in the water. Note that a single HAEDAT event can

¹ IOC – International Oceanographic Commission; ICES – International Council for Exploration of the Seas; PICES -North Pacific Marine Science Organization

represent dozens of individual toxin measurements that exceed regulatory levels when a bloom extends along a coast and lasts weeks or months.

A small number of freshwater cyanobacterial events have been entered in the HAEDAT dataset for the U.S., but the vast majority are for events that affect estuarine or coastal marine waters. Even those records are limited in coverage, so this review only uses peer-reviewed literature to discuss cyanoHAB problems in coastal waters. It does not directly address cyanoHABs and other blooms in freshwater systems. A similar situation pertains to records of CTXs and macroalgal blooms, both of which are currently not included in the U.S. HAEDAT records.

The U.S. National Office for Harmful Algal Blooms coordinates the collection of annual bloom data through a survey form submitted by multiple scientists and managers spanning 29 coastal regions defined for the U.S. and its territories (Fig. 1). Event information includes: the nature of the event, what was affected, the associated syndrome, species involved in the transmission, whether the report is the outcome of a monitoring program, date, location and zone, contact information, environmental conditions, and toxin assay information. HAEDAT records have evolved through time and in some instances, particularly in older records, not all information is available. All data are evaluated for accuracy and clarity prior to being entered into the database. Recently, a major effort was made to review all of the U.S. HAEDAT records to identify and remove those that did not meet the above criteria or were redundant.

To assess changes over time in the geographical extent of bloom events, for each of the toxin families associated with a human poisoning syndrome (PSTs, ASTs, DSTs, and NSTs), a linear logistic regression model of the proportion of monitoring zones in each year that experienced at least one event was fit, with time as the regressor. All analyses were performed using the glm function from the R statistics package (version 4.0.2). The function also provides an observed significance level (or *p* value) for the fitted model. This approach was also used for the combination of all HAB toxins and impacts described herein to provide an overall national HAB trend.

This analysis was run for 30 years for PSTs and NSTs, and for shorter intervals for ASTs and DSTs, starting with the first year of a documented event for that toxin (1991 and 2008, respectively). It was assumed that in all years during these periods, all HAEDAT zones were monitored for the effects of these toxins. This means either phytoplankton observations or shellfish flesh testing, or management oversight were used to decide whether a specific toxin was or was not a risk within that zone. States do not monitor for all HAB toxins – each must conduct a risk assessment and then monitor for the HAB species and toxins that might occur at dangerous levels with a given zone. With the statistical approach taken here, lack of monitoring for a given toxin is not a problem if management oversight for that zone generally ensures that there were unlikely to be significant events from that toxin.

3 U.S. HABs

3.1 Poisoning syndromes

The impacts from HABs in the U.S. are diverse, with the most significant associated with the accumulation of algal toxins in shellfish, leading to poisoning of humans and animals that consume or ingest contaminated seafood. The resulting human poisoning syndromes linked to consumption of shellfish have been given the names paralytic, diarrhetic, neurotoxic, amnesic, and azaspiracid shellfish poisoning (PSP, DSP, NSP, ASP, AZP) to describe primary symptoms or the toxins involved. Except for ASP, all are caused by biotoxins synthesized by dinoflagellates; the ASP toxin, domoic acid, is produced predominantly by diatoms within the genus *Pseudo-nitzschia*. This review will refer to the toxins (e.g., PSTs, DSTs, NSTs, ASTs and AZTs) rather than the syndromes because the HAEDAT records are of toxin concentrations above regulatory concentrations² and not human poisonings. A sixth human illness, ciguatera poisoning (CP) is caused by toxins produced by benthic dinoflagellates (*Gambierdiscus* and

² States along the Gulf Coast, including Florida, Alabama, Mississippi, Louisiana and Texas, conduct monitoring for NSTs following federal public health safety policies set by the National Shellfish Sanitation Program (NSSP), which recently changed from using a cell threshold (5000 *Karenia brevis* cells L⁻¹) or a toxin threshold in shellfish measured using an approved method (20 MU/100 grams or 0.8 mg brevetoxin-2 equivalents kg⁻¹ of shellfish tissue) to using only the toxin threshold. Many older HAEDAT NST events thus reflect cell count criteria, not direct toxin measurements.

Fukuyoa spp.) that live on substrates or surfaces in many coral reef communities. Ciguatoxins (CTX) are transferred through the food web from herbivorous reef fishes to larger, carnivorous finfish. Additional CP vectors include giant clams and other invertebrates. Unfortunately, HAEDAT records for CTXs do not exist for the U.S. and its territories. This reflects a lack of routine monitoring of ciguatera toxins in fish, which is in turn attributed to the lack of commercially available toxin standards and analytical approaches for toxin detection that are feasible and affordable. Human poisonings do occur in the U.S. and its territories from CTXs (see e.g., Friedman et al., 2017; Chinain et al., 2020), but the true nature of the problem is hindered by misdiagnosis and under-reporting of CP cases to health authorities. Collection of data from hospitals, clinics, and medical professionals would be a significant undertaking far beyond the current effort to compile U.S. HAB event data into HAEDAT. These issues are reviewed in greater detail by Chinain et al. (2020).

AZTs, though a problem in other parts of the world (e.g., EC, 2002), are not yet a serious concern in the U.S. and thus are not addressed here in any detail. In 2002, the European Commission established a regulation for the maximum levels of AZTs, defined as the combination of AZA-1, 2, 3 in shellfish, at $160 \mu\text{g kg}^{-1}$ (EC, 2002). Although *Azadinium poporum* has been identified in the northern Gulf of Mexico (Luo et al., 2016), no AZT HAEDAT events have been reported in the U.S., except on the East Coast in Washington State where a new toxin, named AZA-59, was identified and characterized in *A. poporum* from Puget Sound in 2016, with a potency approximately 3-fold lower than AZA-1 (Kim et al., 2017). Based on deployment of passive solid-phase resin samplers throughout Puget Sound during 2014–2015 and detection of

measurable but low amounts of AZA-59 in shellfish in 2016 and 2017, the current risk of human exposure to AZA in Washington State is low (Kim et al., 2017). Two azaspiracids, AZA-1 and AZA-2, were more recently detected for the first time on the East Coast, in Chesapeake Bay and in Virginia coastal bays (Onofrio et al., in press). While AZTs showed broad spatiotemporal distribution in these estuarine and coastal waters during a study in 2017-2018, toxin amounts detected on solid-phase resin samplers were uniformly low, suggesting a minimal threat to seafood safety.

3.2 Other impacts

Another type of HAB impact occurs when marine plants and animals are killed by algal species that release toxins and other bioactive compounds into the water. HABs also cause mortalities of fish and wildlife (e.g., seabirds, whales, dolphins, and other marine animals), typically as a result of the transfer of toxins through the food web or when aquatic toxins are ingested or transferred across gills (see e.g., Shumway, 1990; Landsberg, 2002). Physical damage of fish gills has been caused by phytoplankton with spiny processes, e.g. *Chaetoceros* spp. (Horner et al., 1997).

Several HAB species are highlighted herein even though they do not fall under the poisoning syndromes; they are significant in terms of areas affected and nature of impacts. Some of these cause plant and animal mortalities and are sufficiently important nationally to be described separately. They include the brown tide species *Aureococcus anophagefferens* and *Aureoumbra lagunensis*, as well as the dinoflagellates *Margalefidinium polykrikoides* and

Karenia mikimotoi and the raphidophyte *Heterosigma akashiwo*. Some of these species produce poorly defined bioactive compounds, but for most, impacts derive from the high biomass that some blooms achieve. These may cause reduced light penetration in the water column and subsequent decreased densities of seagrass beds that can have dramatic impacts on coastal ecosystems, as these serve as nurseries for the young of commercially important fish and shellfish. Additionally, when large blooms of non-toxic species die, bacterial breakdown of the biomass can lead to reduced oxygen levels and subsequent mortalities of plants and animals in the affected area. High biomass blooms are sometimes linked to excessive nutrient inputs but can also occur in pristine waters.

Macroalgae (seaweeds) also cause significant problems. Over the past several decades, blooms of macroalgae have been increasing along many of the world's coastlines (e.g., Lapointe and Bedford, 2007; Keesing et al., 2011; Wang et al., 2019). These have a broad range of ecological effects and can affect human health as well through the production of H₂S as the biomass washed onto shorelines decays. Macroalgal blooms can be particularly harmful to coral reefs where under high nutrient conditions, opportunistic macroalgal species out-compete, overgrow, and replace the coral. A significant and developing problem with macroalgae involves the transport of huge floating masses of seaweeds and deposition of that material on beaches. In the U.S., problems with *Sargassum* are becoming serious in the Caribbean territories as well as along the coasts of Florida (Wang et al., 2019). These events are not covered here since they have not been recorded in HAEDAT. Plans are underway, however, to include these phenomena in the database going forward.

A discussion is also included on toxic cyanobacterial blooms that can affect estuarine and nearshore coastal waters.

3.3 U.S. HAB species

All potentially toxic or harmful marine microalgal HAB taxa observed in the U.S. are listed in Table 1, along with an indication of where in the country they occur. Many salinity-tolerant freshwater phytoplankton species are impacting marine coastal waters (see 4.6.6), but Table 1 is restricted to marine HAB species. Among the major genera, the diatom *Pseudo-nitzschia*, dinoflagellates *Alexandrium*, *Dinophysis*, *Gonyaulax*, and *Karenia*, and the raphidophyte *Heterosigma* are present along the East, Gulf, and West Coasts. The dinoflagellates *Amphidinium*, *Karlodinium*, *Pfiesteria*, *Phalachroma*, *Pheopolykrikos*, *Prorocentrum*, *Pseudopfiesteria*, and *Pyrodinium*, the pelagophyte *Aureoumbra*, and raphidophytes *Chattonella* and *Fibrocapsa* occur along the East and Gulf Coasts. Toxic dinoflagellates in the genera *Gambierdiscus* and *Fukuyoa* occur in Florida, the U.S. Virgin Islands, Puerto Rico, Hawai'i, Guam, and other Pacific Island territories. More details on the species responsible for the U.S. HAB poisoning syndromes and impacts are given in the sections below.

4 U.S. HAB history and trends

4.1 PSTs

4.1.1 Background.

Paralytic shellfish poisoning (PSP) is caused by the saxitoxin family of biotoxins, hereafter termed paralytic shellfish toxins (PSTs). Taxa known to produce PSTs in the U.S. are dinoflagellate species in the genera *Alexandrium* and *Pyrodinium*. The species *Alexandrium catenella* (historically called *Gonyaulax excavata*, *G. tamarensis*, *A. fundyense*, *A. tamarense* Group I, and *A. tamarense* North American Strain) is the most widespread, responsible for outbreaks along the U.S. East and West Coasts, including Alaskan coastal waters. PSTs have also been reported in *A. peruvianum* in Rhode Island (Borkman et al., 2012) though outbreaks are limited in scale and toxin levels are low. Isolates of *Alexandrium ostenfeldii* from the Gulf of Maine produce spirolide toxins, but not PSTs (Gribble et al., 2005), while *Pyrodinium bahamense* causes PST incidents on both coasts of Florida (Landsberg et al., 2006; Lopez et al., 2019). Several other *Alexandrium* species that can produce saxitoxins are also present in U.S. waters and are included in Table 1, but they have not been linked to PST events.

4.1.2 History of PSTs from *Alexandrium catenella*.

On the East Coast of North America, PSP (which we can now reliably attribute to *A. catenella*) was reported in northeastern Canada over 100 years ago (Ganong, 1889), but in the New England region of the U.S., PSTs were first documented in 1958 in far-eastern sections of

Maine near the Canadian border (Hurst, 1975; Shumway et al., 1988). In 1972, a massive, visible red tide of *A. catenella* stretched from southern Maine through New Hampshire and into Massachusetts, causing PST-related shellfish toxicity in southern areas for the first time. Virtually every year since the 1972 outbreak, Maine, New Hampshire, and Massachusetts have experienced PST outbreaks, a direct result of *Alexandrium* cysts being retained in bottom sediments of southern New England following their introduction by the massive bloom (Anderson and Wall, 1978; Anderson et al., 2014). Low levels of toxicity had occasionally been reported in Maine west of Penobscot Bay prior to 1972 (Shumway et al., 1988), but present-day outbreaks in that area are far more numerous and involve much higher levels of toxicity, consistent with a dispersal event.

Further to the south, PSTs and *A. catenella* cells and cysts were first documented in small embayments in Connecticut and Long Island in the early 1980s (Anderson et al., 1982; Schrey et al., 1984). Despite the presence of cysts at some sites in Connecticut, there have been very few closures due to PSTs in that state, the most recent being in 2003. On Long Island, New York, the first PST outbreak and shellfish bed closure occurred in 2006 when blooms first became significant issues in Northport Harbor (Hattenrath et al., 2010). Since then, PST-induced shellfish bed closures have occurred at more than six different locations across Long Island, with closures becoming annual events. Cysts and motile cells of *A. catenella* have been reported as far south as New Jersey (Cohn et al., 1988), but no PSTs have been reported in that region.

Recent history is thus suggestive of a gradual expansion of the PST problem from north to south in the northeastern U.S., in part due to major species dispersal events like the 1972 bloom, but also small-scale dispersal events, as may have occurred on Long Island. Some of this apparent expansion can also be attributed to the detection of indigenous, low-toxicity populations that had long existed in southern waters (Anderson, 1997).

On the U.S. West Coast, the oldest putative PST incident associated with *A. catenella* occurred in Alaska in 1799 when approximately 100 crew members of a fur-trading ship died after eating blue mussels in an area near Sitka, now appropriately called Peril Strait (Khlebnikov, 1837, Fortuine, 1975). In fact, saxitoxins were originally extracted from their namesake butter clams (*Saxidomus giganteus*) harvested from this Peril Strait region (Lewitus et al., 2012). Elsewhere on the West Coast, human poisonings from PSTs were apparently common among European settlers in California (Meyer et al., 1928), but the first recorded incident occurred in 1903 when twelve people became ill and five died after eating mussels (Sommer and Meyer, 1937). PSTs were finally recognized as a serious health risk in that state in 1927 when a major outbreak near San Francisco led to more than 100 illnesses and multiple deaths (Price et al., 1991). This led to the establishment of a PST shellfish monitoring program, the first in the U.S.

Three fatalities due to PSP were recorded in Washington State in 1942 (Quayle, 1969) resulting in seasonal closures for all shellfish harvest, except razor clams, on the outer coast. That state has also instituted a routine shellfish monitoring program for HAB toxins, as have Oregon and Alaska, though the latter focuses on commercial harvesting sites while keeping the

remainder of the massive coastline permanently closed. Tribal entities now have their own monitoring and testing programs, run through SEATOR – Southeastern Alaskan Tribal Ocean Research.

The PST problem along much of the U.S. West Coast thus has a long history. Monitoring has been somewhat limited, however, due to seasonal, coastwide closures of shellfish harvest areas in several states. There is evidence for regional expansions in severity and geographic extent in Oregon and Washington, as indicated by the increase in harvesting closures along the Oregon coast from 1990 to the 2000s (Lewitus et al., 2012), and the increase in shellfish closures in Puget Sound WA that paralleled the gradual incursion of *A. catenella* into the Sound since monitoring first began in the 1940s and 1950s (Trainer et al., 2003).

PSTs have also long been a problem in Alaska, particularly along much of the Gulf of Alaska coast from the British Columbia border in the southeast to the Aleutian Islands (RaLonde et al., 2001; Vandersea et al., 2018). Between 1973 and 2012, over 200 cases of PSP and several deaths from consuming PST-contaminated shellfish were reported in Alaska (Gessner, 1996, with updates from AK Epidemiology bulletins). Because of the huge coastline, lack of comprehensive toxicity testing and underreporting of illnesses, the historical and geographical extent of PST and the number of people affected by PSP in Alaska have been grossly underestimated (Gessner and Middaugh, 1995; Gessner and McLaughlin, 2008; Trainer et al., 2014). The historical record of PSTs in Alaska from 1991-2012 shows several measurements of PSTs in shellfish in southeast Alaska at $>5000 \mu\text{g } 100\text{g}^{-1}$, more than 50x the regulatory level. A

record of $>30,000 \mu\text{g } 100\text{g}^{-1}$ was measured in mussels from Ketchikan in May 2011, when several people became ill with PSP (Trainer et al, 2014). The PST problem stretches north into the Bering Sea and beyond. Recent research studies have documented huge blooms of *A. catenella* just north of the Bering Strait and in the Chukchi Sea areas of the Alaskan Arctic (Natsuike et al., 2017; D. M. Anderson, unpub. data.) There are records of *A. catenella* (as *Goniaulax tamarensis*) in far northern Alaska near Pt. Barrow more than 60 years ago (e.g., Bursa, 1963), but it is not known if the distribution, frequency, and magnitude of blooms of this species have expanded due to the rapid warming of waters in that region, though this seems likely given the recent changes in bottom and surface water temperatures that are now supportive of germination and growth (Danielson et al., 2020; D. M. Anderson, unpub. data).

4.1.3 History of PSTs from *Pyrodinium bahamense*

Pyrodinium bahamense is a well-known PST producer in the tropical Indo-Pacific region (e.g., MacLean, 1989; Azanza and Taylor, 2001), but reports of toxic strains of this species in the Atlantic Ocean are relatively new (Landsberg et al., 2006; Philips et al., 2006). Until the early 2000s, it had been assumed that the Atlantic strain of *P. bahamense* (distinguished as *P. bahamense bahamense* from *P. bahamense compressum*) did not produce PSTs (Steidinger et al., 1980; Azanza and Taylor, 2001) until an extensive bloom in the Indian River Lagoon on the east coast of Florida coincided with pufferfish toxicity events in 2002 (Philips et al., 2004). Landsberg et al. (2006) later reported saxitoxin bioaccumulation in pufferfish from the same area, concurrent with *P. bahamense* blooms. Toxic *P. bahamense* blooms also occur regularly in

Tampa Bay and Charlotte Harbor on Florida's west coast (FWC HAB Monitoring Database, Lopez et al., 2019), with cells also present more sporadically in estuaries in the northern panhandle of Florida, as well as in Florida Bay and the Florida Keys (FWC HAB Monitoring Database; Accoroni et al., 2020). Puffer fish have tested positive for PTXs in all of these areas (Abbott et al., 2009).

To distinguish PST (saxitoxin) exposures in humans from consumption of toxic puffer fish, any public health incidents involving puffer fish rather than shellfish, are referred to as saxitoxin puffer fish poisonings (SPFPs) (Landsberg et al., 2006). Due to extensive monitoring of *P. bahamense* and the management of PSTs in shellfish in Florida, to date there have been no documented human cases of PSP since this link was discovered. Prior to this, 28 cases of SPFP in humans occurred from pufferfish harvested from January 2002 to May 2004, with further potential incidents managed by an indefinite ban on pufferfish harvesting implemented in June 2004 (Landsberg et al., 2006). If toxicity above the regulatory limit is detected, shellfish beds in areas managed by the state are closed (e.g., in the Indian River Lagoon in 2009). Note that cases of SPFP are not distinguished from shellfish-related PST events in HAEDAT.

The documented range of *P. bahamense* in the U.S. is currently restricted to the Florida coasts and Puerto Rico (Philips et al., 2004). Although known to be present in the Indian River Lagoon in the 1990s, *Pyrodinium bahamense* was not associated with toxicity as noted above. It is possible, but unverified, that PSTs were present in the Indian River Lagoon in the 1960s but were not linked to any poisoning events. As part of a study into the closely-related PST sodium-

channel blocker, tetrodotoxin (TTX), puffer fish research conducted in the early 1960s by Lalone et al. (1963) demonstrated by mouse bioassay that muscle from the southern puffer fish, *Sphoeroides nephelus*, was the most lethal to mice compared to other tissues (skin, gonad, liver). Researchers assumed (without other methods of analytical verification) that the toxicity was from TTX even though TTX is not typically accumulated in the muscle of puffer fish in the Indian River Lagoon. Recent work by Deeds et al. (2008) and Abbott et al. (2009) determined that high concentrations of PSTs are found there (up to 20,106 $\mu\text{g STX eq. } 100\text{g}^{-1}$ tissue).

The anecdotal data from the 1960s might hint of earlier PST presence in the Indian River Lagoon potentially originating from *P. bahamense*, but there was no indication of toxin levels reaching the high levels observed in puffer fish after the early 2000s. Theories for the apparent appearance of *P. bahamense* toxicity relate to an increase of bloom biomass from environmental triggers, high nutrient loadings, and increased water residency time (see below) rather than from the introduction or dispersal of a toxic strain, improved public health surveillance, or improved analytical methods. While there has been interest in conducting *P. bahamense* cyst analyses for retrospective toxin testing in sediment profiles, this has not yet been possible.

4.1.4 PST trends

PST event data for the U.S. in HAEDAT covering the last thirty years (1990–2019) are presented in Fig. 2. Panels A-D show the frequency of documented PST events in five-year increments beginning in 2000, panel E shows the pattern of events over a 30-year interval, and panel F shows a 30-year time series of the fraction of the 28 U.S. HAEDAT zones that had at

least one PST event each year. The five-year maps are provided for only the last 20 years because of space and clarity considerations.

It is evident from Fig. 2 that PST outbreaks over the last 20 years are annually recurrent on both coasts of the U.S. In the east, PSTs are a problem from Long Island north to the U.S. border with Canada. A clear biogeographic boundary of *A. catenella* exists near New York and New Jersey, as PST events have not been documented further to the south except for Florida where the causative species is *Pyrodinium bahamense*. On the West Coast, PSTs are recorded from Alaska to California, with the number of events each year decreasing from north to south.

One conclusion from the HAEDAT PST time series maps is the distribution of *Alexandrium*-related PST events in New England and along the coasts of California, Oregon, and Washington has not changed significantly over the last 20 years. Some of the expansions noted above in the Gulf of Maine, Long Island, and Puget Sound WA are not evident in this figure, either because the events occurred before the study interval or nearby PST events obscure the newer ones at the scale of these maps. In other parts of the country, expansions are evident. One is in Florida, where toxic *P. bahamense* blooms first appeared on the East Coast in the 2002 – 2007 interval (Fig. 2A and B), and then on the West Coast between 2008 and 2012. The lack of a HAEDAT record for the Florida west coast in the most recent interval (Fig. 2D) is because the *P. bahamense* blooms that occur are in an area where shellfish beds are closed for other reasons, or shellfish beds are outside areas with known blooms (Lopez et al., 2019) and thus no PST testing is occurring.

There is also a suggestion of an expansion in Alaska, toward the Bering Strait and northern waters, but the data are too sparse to say anything conclusive at this stage. Alaska is one of several states where commercially harvested and farmed products are routinely tested, but most recreationally harvested shellfish are not. Many PST events undoubtedly go unnoticed under this type of management program. Section 4.1.6 discusses PST and animal mortalities, with many new reports of PSTs in wildlife, but again, no time series data are available to reveal trends.

Between 2 and 14 PST events have been observed nationwide each year over the 30-year study interval, with 334 total events and a mean of 11.1 per year. No significant trend in the fraction of U.S. HAEDAT zones is evident for PST events over the last 30 years ($p > .05$), though there is a hint of multi-year cycling, with the lowest number of events around the years 1999, 2006, and 2010 (Fig. 2F). Note that there is also no significant trend in PST events if all those caused by *P. bahamense* are removed from the analysis. On the other hand, if only PST events caused by *P. bahamense* are examined, a significant increasing trend would be evident given the recent emergence of toxicity from this organism over the past 20 years and the increasing regulatory scrutiny this has engendered.

4.1.5 Other time series for PSTs

In the context of decadal trends or patterns, one of the longest and most comprehensive HAB toxicity time series in the U.S. is the monitoring program for PSTs conducted by the State of Maine, dating back to 1978. Using that dataset, a HAB Index was developed (Anderson et al., 2014) based on three measures of PST toxicity for each year (the percent of monitoring stations

showing detectable toxicity over the year, the cumulative amount of toxin per station measured in all shellfish samples during that year, and the duration of measurable toxicity). These metrics were combined into an index that provides a single measure of annual toxin severity. When viewed from 1978 to 2012, the Index reveals at least two, and perhaps three multi-year intervals or eras, each with different patterns and levels of toxicity (Fig. 3). Due to budget constraints, Maine dramatically reduced the number of monitoring stations in 2012, so it is not possible to calculate the Index to the present day. A new Index is currently being formulated that will use a smaller set of sampling stations to allow the Index time series to be sustained into the future.

4.1.6 PST Impacts in marine fish and wildlife

Thus far wildlife mortalities from PSTs in the U.S. involving shellfish (Shumway, 1990, Landsberg, 2002) and higher vertebrates have only been associated with *Alexandrium catenella*. In HAEDAT, PSTs were first reported to affect marine mammals, after the mortality of 14 endangered humpback whales (*Megaptera novaeangliae*) in November 1987 in Cape Cod Bay, Massachusetts. The whales were lethally exposed to PSTs after feeding on toxic mackerel, *Scomber scombrus* that had migrated south from the St. Lawrence River, Canada. This was the first documented case demonstrating the vectoring of PSTs to higher vertebrates via the food chain (Geraci et al., 1989). Earlier the same year, a mortality of 60 sea otters, *Enhydra lutris*, from PSTs in Alaska was suspected, but unproven (De Gange and Vacca, 1989). Concentrations of up to 9.9 ng PSTs g⁻¹ were recorded in bottlenose dolphin carcasses from the Indian River

Lagoon over a 10-year period, indicating that *P. bahamense* is a potential mortality risk factor (Fire et al., 2020).

Mortality events of birds involving PSTs originating from *A. catenella* and vectored through fish have occasionally been documented. In 1978, mortalities of common terns, *Sterna hirundo*, in Massachusetts (Nisbet, 1983) and of Kittlitz's murrelet, *Brachyramphus brevirostris*, in the last decade in Alaska, were caused by PSTs (Shearn-Boschler et al., 2014). Noteworthy because of other wildlife HAB toxicity events in Alaska (see ASTs), PSTs were also detected coincident with die offs of common murres, *Uria aalge* in the Gulf of Alaska from 2015-2016 (concurrent with ASTs) and in mortalities in the East Bering Sea of tufted puffins, *Fratercula cirrhata*, from 2016-2017, but lethal HAB toxicity was unproven (Jones et al., 2019, Van Hemert et al., 2020). The mortality of at least 13 endangered shortnose sturgeon, *Acipenser brevirostrum*, in Sagadahoc Bay, Maine, in the summer of 2009 occurred during a high biomass *A. catenella* bloom. Extremely high concentrations of PSTs were detected in local shellfish. PST-like activity was found in sturgeon tissues and stomach contents containing amethyst gem clams, *Gemma gemma*, were confirmed to contain PSTs (Fire et al., 2012).

4.1.7 Key drivers

One key factor underlying both the biogeography and bloom dynamics of *Alexandrium catenella* and *Pyrodinium bahamense* is that both species include a resting cyst stage in their life histories (Azanza et al., 2018). Cyst germination provides the inoculum for blooms, and the transformation back to the resting state can remove substantial numbers of cells from the bloom

population and act as a major factor in bloom termination. The timing of cyst germination (excystment) and the ultimate formation of new cysts (encystment) is regulated by both internal and external factors, and leads to highly episodic or seasonal outbreaks (Fischer et al., 2018; Lopez et al., 2019). Cysts are also important for population dispersal and can even be sources of toxin to shellfish and other benthic animals.

Once in the water column, the development of blooms of these species is driven by a range of environmental factors, the most important of which include temperature, nutrients, and water column stratification. Both PST-producing species migrate vertically in the water column and can form dense, near-surface aggregations during daylight hours and subsurface layers at night where higher nutrients are generally available. Salinity can play an important role in the blooms of both species through stratification and perhaps the provision of nutrients, humic substances and other growth enhancers from terrestrial sources. For example, blooms of *A. catenella* are closely associated with a buoyant coastal current formed by river outflow into the Gulf of Maine, providing a transport pathway to deliver cells to southern regions, while also providing a stratified layer that favors dinoflagellate growth and accumulation over non-motile diatoms (Franks and Anderson, 1992).

While the occurrence of HABs is controlled by multiple biological, chemical and physical processes, temperature is a central organizing factor determining the potential for HABs to occur (Smayda and Reynolds, 2001) and may have contributed to an expansion or continuance of *A. catenella* blooms in some regions of the U.S. As with many phytoplankton species, *A. catenella*

has maximal laboratory growth rates at temperatures higher than the annual maximum in some ecosystems within which it blooms. Ocean warming thus has the potential to promote blooms of *A. catenella* in the U.S., as shown by Gobler et al. (2017) who used models to indicate that ocean warming from 1982-2017 significantly increased the potential growth rate and duration of the bloom season from Cape Cod through Canada and the Gulf of Maine and within regions of southern Alaska and Puget Sound. Similarly, Moore et al. (2008; 2011) predicted a significant expansion of the bloom season in Puget Sound with the progressive warming predicted to occur this century, leading to longer blooms and higher toxicity. These two forecasts, however, focused solely on the growth of the motile, vegetative cells in the *A. catenella* life cycle. Brosnahan et al. (2020) recently explored the impacts of global warming on the germination dynamics of the cysts of this species and argued that cyst accumulation zones may persist longer in more seasonally-variable, shallow inshore habitats than in deep offshore ones, promoting HABs that are more localized and commence earlier. This work also suggests that *A. catenella* will be more resilient to future warming in habitats with high temperature seasonality (i.e., shallow embayments and estuaries). These types of climate-related forecasts are further complicated by the encystment process, as shown by Ralston et al. (2014) who demonstrated that warm winters did lead to earlier bloom development for *A. catenella* (as predicted by Gobler et al. (2017) and Moore et al. (2008)), but that blooms also ended earlier due to encystment driven by factors other than temperature. There was no expansion of the temperature window for rapid growth.

Pyrodinium bahamense var. *bahamense* is able to form blooms under low-salinity conditions (i.e., salinities from 13 to 35) that are found in many lagoons and estuaries in Florida (Phlips et al., 2006), but is usually restricted to the warmer months from April to October. The most intense *P. bahamense* blooms coincided with higher than normal rainfall from 2002-2006 (Phlips et al., 2015). *Pyrodinium bahamense* is hypothesized to have high nutrient requirements (Phlips et al., 2006) and blooms during elevated nutrient loading associated with high precipitation events that contribute to lower salinities (Phlips et al., 2015). In the Indian River Lagoon, one of the primary driving factors for blooms is the extended mean water residence period (Steward et al., 2005; Phlips et al., 2015), providing time for the accumulation of biomass, fueled by increased anthropogenic nutrient loading during elevated rainfall. However, in Tampa Bay, environmental factors only explain a small percentage of the variability in *P. bahamense* abundance (Corcoran et al., 2017) and life cycle dynamics play a primary role in seasonal patterns and recurrence of blooms (Lopez et al., 2019). Despite significant reductions in Tampa Bay N-loadings and recovery of other Bay segments, prolonged blooms of *P. bahamense* each summer continue to pose challenges for Old Tampa Bay (Sherwood et al., 2016). Blooms of *P. bahamense* in Tampa Bay occur primarily in the northern segment, Old Tampa Bay, which has high abundance of resting cysts in the sediments (Karlen and Campbell, 2012) and long water residence times (Meyers et al., 2017). Changes in top-down zooplankton pressure may also favor blooms of *P. bahamense* (Badylak and Phlips, 2008).

With increasingly likely variability in the frequency of hurricanes and precipitation events, it is possible that *P. bahamense* blooms will change in frequency or longevity in various areas of

Florida. The potential for an increase in temperature due to global warming may also provide optimal conditions for the range expansion of this species. As pointed out by Brosnahan et al. (2020) the bloom occurrence of *P. bahamense* extends beyond the known resting cyst distribution in the sediments, suggesting that an expansion may occur. However, this may be contingent upon the effects of temperature on dormancy and quiescence of the cysts (Lopez et al., 2019).

4.2 ASTs

4.2.1 Background

Amnesic shellfish poisoning is caused by domoic acid (DA) and its isomers, hereafter termed amnesic shellfish toxins (ASTs). In the U.S., taxa known to produce ASTs are multiple diatom species in the genera *Pseudo-nitzschia* (Table 1). Of the more than 50 *Pseudo-nitzschia* species identified, over 25 are known to produce ASTs at varying concentrations (Bates et al., 2018), dependent upon the species and the environmental conditions to which they are exposed (reviewed in Lelong et al., 2012; Trainer et al., 2012; Bates et al., 2018). Domoic acid has several means of entering the food web - through filter feeding molluscan shellfish, suspension-feeding finfish, and zooplankton. Shellfish closures to protect human health occur when DA concentrations exceed 20 ppm in most shellfish except Dungeness crab, for which the regulatory closure level is 30 ppm in viscera. The most highly toxic species of *Pseudo-nitzschia* on the U.S. West Coast are *P. australis* and *P. multiseriata*. On the East Coast, the species responsible for toxic episodes in the Gulf of Maine first reported in 2016 is *P. australis* and in the Gulf of

Mexico the *P. pseudodelicatissima* species complex (including *P. cuspidata*) has been associated with AST closures of shellfish harvest starting in 2013 (Bates et al., 2018).

4.2.2 AST history

Because of the relatively recent discovery of domoic acid as a HAB toxin (Bates et al., 1989), the 1990-2019 HAEDAT records show the complete story of the initial documented DA-related shellfish closures on the U.S. West Coast in 1991 and the more recent emergence of DA in the Gulf of Mexico and U.S. East Coast starting in 2014 and 2016, respectively. Soon after the first DA poisoning event was reported in 1987 in eastern Canada (Bates et al., 1989; Todd 1993), DA poisoning caused the illness and death of seabirds in Monterey Bay, California in 1991 (Work et al., 1993). Anchovies and sardines that had fed on the DA-producing *P. australis* (Buck et al., 1992; Fritz et al., 1992) were the vectors of toxin transfer to seabirds. Later that same year, DA was measured in razor clams (*Siliqua patula*) and Dungeness crabs on the Washington coast (Wekell et al., 1994). In May-June 1998, the first confirmed death of a marine mammal was recognized to be associated with the trophic transfer of DA from sardines and anchovies to sea lions (Gulland et al., 2000; Lefebvre et al., 1999; Scholin et al., 2000). ASTs continue to cause shellfish closures and marine mammal and bird deaths on the U.S. West Coast to the present day. A massive, coastwide bloom in 2015 has been linked to a warm water anomaly in the Pacific Ocean and resulted in record concentrations of DA in seawater, shellfish and planktivorous fish and numerous marine mammal and bird deaths (McCabe et al., 2016; McKibben et al., 2017).

In contrast to the recurring events observed on the U.S. West Coast, the first AST closures in the Gulf of Mexico and the U.S. East Coast occurred recently, in 2013 and 2016, respectively. Toxic *Pseudo-nitzschia* species and particulate DA were present in the Gulf of Maine prior to the first shellfish closure there in 2016, which coincided with the first observation of *P. australis* in that region after many years of monitoring (Fernandes et al., 2016; Bates et al., 2018). Since 2016, repeated AST closures associated with *P. australis* blooms have been observed. In the Gulf of Mexico, the first shellfish closures were imposed in April 2013 after eastern oysters (*Crassostrea virginica*) tested above the AST regulatory level (Bates et al., 2018). Since then, two additional closures have been warranted (2014, 2017); all three Gulf of Mexico closures occurred in the same embayment in northwest Florida (Bates et al., 2018).

4.2.3 AST trends in shellfish

HAEDAT records document an increasing trend of AST events in the U.S. (Fig. 4), with a hint of multi-year cycling. Initial events were only on the West Coast, occurring nearly every year from 2000–2019. Gulf of Mexico events first appeared in 2013 and thereafter occurred sporadically, compared to Gulf of Maine outbreaks which began in 2016 and recurred each year since. The overall pattern is one of relatively frequent outbreaks on the U.S. West Coast and far fewer on the East Coast and the Gulf of Mexico. This is most evident in Fig. 4E which shows the 30-year history, highlighting ASTs as a predominantly West Coast phenomenon, with emerging problems in the east. Figure 4F shows the fraction of HAEDAT zones with at least one AST event per year through time, documenting an increasing and significant trend in AST incidence

($p < .05$). There were 91 total AST events in the U.S. over the 30-year study interval, with a mean of 3.0 per year.

The increasing national trend is in part a reflection of growing management awareness of this new HAB toxin and its discovery in locations where it likely had occurred before but was undetected. Since the original discovery of DA in Canadian shellfish in 1987 (Bates et al., 1989), some U.S. states have been slow to set up comprehensive monitoring programs for this toxin, as qualitative risk assessments indicate that the likelihood of significant events is low. In some cases, shellfish flesh testing is not implemented until phytoplankton sampling indicates that *Pseudo-nitzschia* spp. cell abundance reaches certain thresholds. Interestingly, the recent AST events in the Gulf of Maine have been linked to *P. australis*, a species that had not been observed in decades of monitoring by U.S. and Canadian workers in that region (Bates et al., 2018). This therefore seems to be a clear example of the expansion of a HAB problem to a new region. Current thinking is that the species was introduced to the Gulf of Maine in 2016 with water masses from the Scotian shelf (Clark et al., 2019). It is not known whether recurrent events in that region since 2016 reflect the persistence of the species within the Gulf, or are due to additional water mass intrusions and introduction events. The link between these events and a warming climate is also unknown and is currently under investigation.

4.2.4 Other time series for ASTs

State shellfish safety programs such as those led by the Washington State Department of Health, the Oregon Department of Fish and Wildlife and California Department of Public Health

Services have provided useful shellfish time series data that help pinpoint trends and areas of concern. For example, DA time series data from both Dungeness crab and razor clams collected near Long Beach, Washington show the close linkage of toxin in these two species (Fig. 5). In almost every case, when razor clam DA increases, so does crab DA, illustrating the importance of clams as crab food. Other important data sets that provide insights into environmental drivers of DA events include the Olympic Region HAB (ORHAB; e.g. Trainer and Suddleson 2005) phytoplankton monitoring data, Monitoring Oregon's Coast for Harmful Algae (MOCHA; e.g. McKibben et al., 2015) and the California Department of Public Health Marine Biotoxin Monitoring Program monthly report (Smith et al., 2018; <https://www.cdph.ca.gov/Programs/CEH/DRSEM/Pages/EMB/Shellfish/Marine-Biotoxin-Monitoring-Reports.aspx>)

4.2.5 AST impacts in marine wildlife

Animal mortalities from DA exposure through the food web are common, with this syndrome being termed domoic acid poisoning or DAP. During DAP events in seabirds and marine mammals, the toxin moves rapidly through food webs by accumulating in filter-feeding invertebrates and planktivorous fish during blooms, and is then consumed by marine mammals and birds resulting in serious neurologic illness and death (Scholin et al., 2000; Work et al., 1993). Toxin concentrations detected in bivalve and fish vector species are high enough to cause documented illness and mortality in marine mammal and seabird predators, but unlike some other shellfish toxins, there are no reports of acute excitotoxic health impacts or die-offs due to

DAP in fish or bivalve vectors. Domoic acid is an excitotoxic agonist for glutamate, a primary neurotransmitter in the central nervous system (CNS) (Berman and Murray, 1997). As such, it exerts its toxicity through over-excitation of neurons in the CNS of mammals and birds, which may explain the lack of obvious neurotoxic impact in bivalves that lack this system. Planktivorous fish have been shown to have glutamate receptors in the CNS that are susceptible to DA over-excitation in laboratory studies (Lefebvre et al., 2001). However, oral gavage studies and field observations provide strong evidence that fish are more tolerant of oral consumption of DA than birds and mammals, and are not likely impacted acutely in the wild under the ecologically-relevant bloom conditions observed to date (Lefebvre et al., 2001, 2007, 2012).

DAP in seabirds and marine mammals via consumption of DA-contaminated planktivorous fish has been well documented on the U.S. West Coast (Fritz et al., 1992; Work et al., 1993; Lefebvre et al., 1999; Scholin et al., 2000). The highest incidence of DAP occurs along the coast of California. The first documented DAP event in the U.S. occurred in 1991 in Monterey Bay, California involving large numbers of brown pelicans (*Pelicanus occidentalis*) and Brandt's cormorants (*Phalacrocorax penicillatus*) that had consumed DA-contaminated Northern anchovies (*Engraulis mordax*) (Fritz et al., 1992). Behavioral excitotoxicity observed in DA-exposed birds consisted of head weaving, scratching and vomiting (Work et al., 1993). In 1998, a highly toxic *Pseudo-nitzschia* bloom in central California was linked to reduced interannual survival of the marbled murrelet (*Brachyramphus marmoratus*) (Peery et al., 2006). This highly toxic bloom also caused the first documented DAP event observed in a marine mammal species. Starting in May of 1998, hundreds of California sea lions began stranding on beaches exhibiting

signs of DAP such as scratching, disorientation, ataxia, and seizures as a result of consuming highly toxic anchovies (Lefebvre et al., 1999; Gulland, 2000; Scholin et al., 2000; Silvagni et al., 2005). Since this event, California sea lions have been experiencing DAP events on an almost yearly basis (Bejarano et al., 2008a). As a result of the regular occurrence, the highly visible neurotoxic symptoms, and the high numbers of animals affected, California sea lions have become a model system for studying mechanisms of DA toxicity.

In the absence of overt excitotoxic signs like seizures, it is difficult to diagnose DAP in stranded and dead marine mammals. As such, it is likely that more animals are impacted than have been reported. The toxin has been detected in many stranded marine mammal species along the entire U.S. West Coast (Landsberg et al., 2014) as well as in pygmy and dwarf sperm whales from southeastern and mid-Atlantic U.S. waters (Fire et al., 2009). Mortality events associated with DA have been reported in California sea lions (*Zalophus californianus*), Harbor seals (*Phoca vitulina*), Pacific harbor seal (*P. vitulina richardii*), Northern fur seals (*Callorhinus ursinus*), Southern sea otters (*Enhydra lutris nereis*), Long-beaked common dolphins (*Delphinus capensis*), Short-beaked common dolphins (*D. delphis*), Bottlenose dolphins (*Tursiops truncatus*), Risso's dolphins (*Grampus griseus*), Harbor porpoise (*Phocoena phocoena*), Dall's porpoise (*Phocoenoides dalli*), Minke whales (*Balaenoptera acutorostrata*), humpback whales (*Megaptera novaeangliae*), Cuvier's beaked whales (*Ziphius cavirostris*), and gray whales (*Eschrichtius robustus*) (Heyning, 2003; Kreuder et al., 2003, 2005; Torres de la Riva et al., 2009; Lefebvre et al. 2010; Fire and Van Dolah 2012; Fire et al. 2010).

Anomalously warm ocean conditions have been linked to increased toxicity, geographic range, and duration of DA-producing algal blooms on the U.S. West Coast, resulting in exceptionally high DA contamination in vector species and sea lion mortality rates (McCabe et al., 2016). As waters warm, *Pseudo-nitzschia* blooms may expand and/or increase in toxicity, posing even greater risks to seabirds and marine mammals in new geographic regions. A recent long-term study of the presence of algal toxins in 13 marine mammal species from Arctic and subarctic regions revealed potential exposure risks in all species tested (Fig. 6). Although it could not be determined if these animals had high enough toxin doses to cause DAP, the data did confirm that DA was present in Arctic and subarctic food webs at levels high enough to be detected, regardless of feeding strategies, thereby posing increasing exposure risks as future ocean conditions warm (Lefebvre et al., 2016; McCabe et al., 2016).

4.2.6 *AST-related marine mammal mortality trends*

There were no reported marine mammal poisonings attributed to DA until 1998 in Central California (Scholin et al., 2000), but since then, DAP has impacted marine mammals almost every year, marking a definite increase in DAP-related mortality after 1998 along the California Coast (Fig. 7; Bejarano et al., 2008a; Bargu et al., 2010; McCabe et al., 2016). As a result of this common occurrence and well-defined symptomology, retrospective analyses of veterinarian records at The Marine Mammal Center in Sausalito, California were performed to identify DAP events prior to its initial discovery in 1998. Records revealed that at least one animal per year since 1990 has been impacted by DAP. The number of cases began increasing in 1998 (Fig. 7).

Dozens to hundreds of sea lions have been diagnosed with DAP or DAP-related mortality yearly along the California coast since 1998, with higher-than-average numbers recorded in 2015 during the widespread coastal bloom that year. In fact, the first sea lion documented to exhibit DA-related excitotoxic seizures north of California also occurred in 2015 in Long Beach, Washington, raising concerns of a northward expansion of intense DA-producing blooms (McCabe et al., 2016). Although confirmed DA toxicosis events in wildlife have not been documented on the East Coast nor in the Gulf of Mexico, there is an emerging trend for DA detection in stranded marine mammals from those areas (Fire et al., 2009, 2011).

4.2.7 Key drivers

Past field studies have shown that toxigenic *Pseudo-nitzschia* blooms often occur when macronutrients are not limiting; there is often no significant correlation between DA and ambient concentrations of macronutrients in situ (Trainer et al., 2009). However, toxin-producing *Pseudo-nitzschia* species have a unique capability of surviving extreme ocean conditions, including high temperatures and low macronutrients (e.g., Trainer et al., 2019). Certain *Pseudo-nitzschia* species appear to exhibit special strategies for survival under nutrient or trace metal stress. Some may have the ability to acquire strongly complexed iron, even when available at very low concentrations, using a high-affinity iron acquisition system that requires copper and the production of DA (Wells et al., 2005). In addition, the high affinity of at least one *Pseudo-nitzschia* species, *P. australis*, for nitrate and ammonium (Cochlan et al., 2008) provides it with a competitive advantage for acquiring nitrogen (N) under N-depleted conditions, but especially

following a N surge during upwelling when its maximal rate of nitrate uptake exceeds those of virtually all the other phytoplankton species commonly found in upwelling systems (Kudela et al., 2010). Recent genetic studies have shed light on the interplay of several genes involved in trace metal and vitamin acquisition on the ability of *Pseudo-nitzschia* species to cope with nutrient limitation (summarized in Bates et al., 2018). Toxic species often produce DA in culture under silicate limitation (e.g., Lelong et al., 2012), and field data suggests that interannual variability in the ratio of nitrogen to silicate may be important for DA production as well (Clark et al., 2019; Ryan et al., 2016). However, there is no consensus on any universal drivers for toxin production; in fact, geographical and species differences likely exist. However, long-term records are providing some clues. An analysis of the historical record of large-scale toxigenic *Pseudo-nitzschia* blooms has demonstrated a potential link to periods of anomalously warm ocean conditions such as El Niño, positive phases of the Pacific Decadal Oscillation (PDO), or record-setting marine heatwaves (McCabe et al., 2016; McKibben et al., 2017).

4.3 DSTs

4.3.1 Background

In the U.S., diarrhetic shellfish poisoning (DSP) is a relatively new threat to human health with only three confirmed illnesses in 2011 (Trainer et al., 2013). The lipophilic phycotoxins associated with this syndrome are okadaic acid (OA), dinophysistoxins-1 (DTX1) and -2 (DTX2) and their derivatives, hereafter referred to as diarrhetic shellfish toxins (DSTs). Eight toxigenic species of the genus *Dinophysis* are present in U.S. waters (Table 1) and initial culturing studies

have demonstrated that toxin profiles can vary at both the *Dinophysis* species and strain designation (Fux et al., 2011, Wolny et al., 2020). While a cross-regional comparison is still needed in the U.S., general trends can be identified amongst strains in culture thus far: East Coast *D. acuminata* contains both OA and DTX1 (Fux et al., 2011; Wolny et al., 2020); Gulf Coast *D. ovum* contains only OA (Fux et al., 2011), and only dihydro-DTX1 is present in *D. norvegica* from the Northeast Coast (Deeds et al., 2020). Less prominent are DST-producers *Prorocentrum lima*, an epiphytic/epibenthic dinoflagellate (Morton et al., 1999), and two species of *Phalacroma* (*P. rotundatum*, *P. mitra*), previously of the genus *Dinophysis* (Table 1). Yessotoxins and pectenotoxins are not regulated in U.S. seafood and so are excluded from this analysis

4.3.2 DST history

The earliest reports of DSTs in the U.S. date back over thirty years, to the mid 1980s, and first appeared along the East Coast. Multiple species of toxigenic *Dinophysis* and *P. lima* have been identified along this coastline and blooms can temporally overlap (Hargraves and Maranda, 2002). As such, the causative species of a DST event has not always been clear. In Narragansett Bay, Rhode Island, elevated cell concentrations of *D. acuminata* and a mixed assemblage of other toxigenic *Dinophysis* spp. coincided with the detection of DSTs in edible shellfish meat from 1984 - 1985 (Maranda and Shimizu 1987). Toxin levels, however, did not exceed FDA guidance levels of 16 µg okadaic acid eq. 100g⁻¹, thus shellfish and harvesting closures were not imposed. The first suspected human illness in the U.S., due to DSTs, parallels this timeline with

reports of gastroenteritis after the consumption of bivalves from New York (Freudenthal and Jijina 1985) and Maine (Maranda and Shimizu 1987) in the mid-1980s. The causative organism(s) could not be confirmed. New reports of DST did not occur for another decade, until 1998, when cases of gastroenteritis surfaced and DSTs were detected in low concentrations in shellfish collected off the coast of Maine (Morton et al., 1999). The causative organism was suspected to be *P. lima* due to the detection of DTX1 in epiphyte samples, a history of *P. lima* and associated DSP outbreaks in adjacent Canadian waters (Cembella 1989), and the presence of empty *P. lima* thecae in blue mussel digestive tracts. Potential DST-producers *D. norvegica* and *D. acuminata*, however, were also present, but plankton samples lacked DSTs as determined via multiple detection methods (Morton et al., 1999). Later field studies demonstrated that while *P. lima* abundance was correlated with DSTs in the epibiotic community, accumulation in shellfish was minimal (Maranda et al., 2007a,b), again suggesting low risk for DSP outbreaks and causative species along the coast of Maine. In 2002, a bloom of *D. acuminata* was detected in the East Coast estuary of Chesapeake Bay, Maryland (Tango et al., 2004). The elevated abundance led to a precautionary harvesting closure based on cell abundance that was lifted when DST levels in shellfish were confirmed to have been well below federal guidelines.

The events described between 1984–2002 are suggestive of a history of DST in the U.S., but reports were sporadic and DSP illnesses were not confirmed, nor was identification of causative organisms conclusive. DSTs in shellfish were not detected above FDA regulatory guidelines during this period so reports were not entered into the HAEDAT database. In 2008, however, toxigenic *D. ovum* was observed in the Gulf of Mexico (Texas) (Campbell et al., 2010, Deeds et

al., 2010). Toxin levels in the meat of the eastern oyster (*Crassostrea virginica*) exceeded the FDA regulatory guidance level, so harvesting for the species was prohibited for a month as product was recalled. To many, this notable event on the Texas Gulf Coast marked the emergence of DSP as a HAB concern in the U.S. This was the first DST entry into HAEDAT.

The first conclusive DSP illness in the U.S. was then documented in Sequim Bay, Washington, in 2011 with a bloom of *D. acuminata* and the sickening of three people who consumed blue mussels (*Mytilus edulis*) (Trainer et al., 2013). In a follow-up study in 2012, DSTs were also found above FDA guidance levels in the varnish clam (*Nuttalia obscurata*), California mussel (*Mytilus californianus*), Pacific oyster (*Crassostrea gigas*), and manila clam (*Venerupis philippinarum*), demonstrating that several seafood products were susceptible to contamination. This DSP event and subsequent study made it apparent that DSTs were a concern for the West Coast. On the same coastline, DSTs were detected in the California mussel above FDA guidance levels in Monterey Bay, California during a field study from 2013–2016 (Shultz et al., 2019).

While the East Coast had the earliest reports of DSTs in the U.S., the region did not experience a substantial event until 2011-2012 on Long Island, New York, when *D. acuminata* cells exceeded 2×10^6 cells L⁻¹ and DSTs in shellfish far surpassed FDA guidance levels (Hattenrath-Lehmann et al., 2013). Later, in 2015 and 2018, DST events were recorded for the first time off the coast of New England (Fig. 8D), with elevated concentrations of *Dinophysis* spp. and DSTs above FDA guidelines in shellfish collected from Massachusetts and Maine,

respectively. DSTs have also been found above FDA guidance levels between 2010-2016 in shellfish from the mid-Atlantic states of Delaware and Maryland where small embayments had *Dinophysis* spp. concentrations of 10^4 to 10^6 cells L^{-1} (Wolny et al., 2020). No closures resulted, however, as elevated DSTs were detected in areas already closed to harvesting or detected in noncommercial shellfish species. Together, this recent history indicates the threat of DSP now exists along all coasts of the U.S., with toxic shellfish detected in Texas, Washington, California, New York, Massachusetts, Maine, Delaware, and Maryland.

4.3.3 *DST trends*

Since the first documented DST event in 2008 (Fig. 8B), at least one event has been recorded in the U.S. every year, except 2009 (Fig. 8F). This is in stark contrast to the two decades prior, where reports were sparse and less intense (i.e., lower concentrations of *Dinophysis* spp. cells recorded and lower, unactionable levels of DSTs measured in edible shellfish meat). The 2008 DST event on the Gulf Coast and the subsequent events on the West and East Coasts (Fig. 8C,D), also more clearly identified the causative organisms, linking *Dinophysis* spp., and not *P. lima*, to a higher risk of DSP illness in the U.S. The entries in HAEDAT typically do not identify the species of *Dinophysis*, but when specified, the causative species has been *D. acuminata* or *D. ovum*, part of the *D. acuminata*-complex: a group of *Dinophysis* species currently undistinguishable using light microscopy (Reguera et al., 2014) or molecular methods (Raho et al., 2008). The importance of *P. lima* and related species in DST prevalence in the U.S. is still an unknown. The small dinoflagellate is considered benthic and

often epiphytic, and therefore, would likely be excluded from typical monitoring programs that enumerate cells in surface water samples.

The number of HAEDAT zones impacted by DSTs shows no significant trend with time since 2008 ($p > .05$; Fig. 8F). Since 2008, 34 events were recorded, with an average of 2.83 events per year. It is evident from Figure 8E that while DSTs are a problem on all three U.S. coastlines, the West Coast is the region with the most occurrences.

When comparing HAEDAT entries to the literature, it becomes apparent that multiple DST events were not included in the database despite the data meeting the criteria of “biotoxin accumulation in seafood above levels considered safe for human consumption” (e.g., Hattenrath-Lehmann et al., 2013; Trainer et al., 2013; Shultz et al., 2019; Wolny et al. 2020), suggesting an underreporting of these occurrences in the U.S. These DST events were likely excluded because a closure was not imposed in association with the elevated toxin levels in seafood. This may be because areas affected were already closed for other contaminants or toxins, or *Dinophysis* enumeration and DST quantification were not yet incorporated into shellfish monitoring programs. Toxins may also have been quantified in shellfish well after the DST event as part of a scientific study instead of a shellfish monitoring program.

Monitoring for *Dinophysis* and DSTs has been progressively incorporated into state shellfish monitoring programs over the last decade, as has been the case for AST over the last three decades. Regional thresholds have recently been defined to trigger enhanced phytoplankton and shellfish monitoring or precautionary harvesting closures based on the concentration of toxic

phytoplankton cells in the water, i.e., 2 – 10 *Dinophysis* mL⁻¹. Even with these improvements, however, DSTs may continue to be underreported, as harmful *Dinophysis* blooms typically do not reach cell concentrations capable of causing water discoloration, *Dinophysis* spp. may form subsurface layers evading detection (Velo-Suarez et al., 2008), and DSP symptoms can be confused with gastroenteritis in humans. To date, there are no unique behaviors or pathology in aquatic animals attributed to DSTs and so these types of entries have not yet been included in HAEDAT.

4.3.4 *DST impacts in marine wildlife*

DSTs have not solely been attributable to wildlife mortality events, but okadaic acid has been detected concurrently with other HAB toxins. Following a large-scale bottlenose dolphin mortality that occurred off the coast of Texas in the winter-spring of 2008, at least three dolphins were determined to be concurrently exposed to ASTs and DSTs (Fire et al., 2011). Although still unproven for possible effects on wildlife, it should be recognized that okadaic acid is a tumor promoter (Fujiki and Suganuma, 1993). Possible links with wildlife neoplasia and okadaic acid exposure via trophic transfer from benthic *Prorocentrum* have been investigated but potential connections remain equivocal (Landsberg et al., 1999, 2014).

4.3.5 *Key drivers*

Not enough information is available in the U.S. HAEDAT database yet to make conclusions regarding the drivers of DST events or to predict trends with climate change or eutrophication. The lack of DST events along the southern portions of the East or West Coasts (Fig. 8) may

provide some clues as to the parameters that constrict blooms. Outside of HAEDAT, drivers are being explored regionally with emphasis being placed on predator-prey dynamics (Hattenrath-Lehman et al., 2013, Harred and Campbell 2014), nitrogenous nutrients (Hattenrath and Gobler, 2015), and basic environmental parameters (Shultz et al., 2019). Models linking changes in surface temperatures to the growth rates of *D. acuminata* indicate that ocean warming from 1982-2017 has significantly increased the potential growth rate and duration of blooms in the northeast U.S. and Puget Sound (Gobler et al., 2017), both regions that have newly experienced these HABs during the past decade. More field studies are needed to determine drivers of DST events across species and regions including warm water anomalies, the Pacific Decadal Oscillation, El Niño, and the 2015 marine heatwave in the Pacific (McCabe et al., 2016; McKibben et al., 2017).

4.4 NSTs and *Karenia brevis* in the Gulf of Mexico

4.4.1 Background

Ingestion of neurotoxic shellfish toxins (NSTs, also known as brevetoxins), can cause Neurotoxic Shellfish Poisoning (NSP), and NSTs can cause other negative human health impacts when inhaled in aerosolized form (Backer et al., 2003; Kirkpatrick et al., 2006; Fleming et al., 2011). In the U.S., the vast majority of NST events are Gulf of Mexico blooms of the dinoflagellate *Karenia brevis* (historically known as *Gymnodinium brevis*, *Gymnodinium breve*, and *Ptychodiscus brevis*). *Karenia brevis* produces NSTs constitutively although to varying degrees (Baden and Tomas, 1988; Lekan and Tomas, 2010; Corcoran et al., 2014). Blooms of *K.*

898 *brevis* with associated NSTs cause recurring, frequent impacts and are observed nearly every
899 year in Florida and more sporadically in Texas. Events rarely occur in northern Gulf of Mexico
900 states (Alabama, Mississippi, and Louisiana) where they are linked to western advection of
901 northwest Florida blooms (Dortch et al., 1998; Maier Brown et al., 2006; Soto et al., 2018).
902 Blooms from southwest Florida – the area most frequently impacted by NSTs – are sometimes
903 transported to Florida’s Atlantic coast (Weisberg et al., 2019) and may become entrained in the
904 Gulf Stream. This impacts other U.S. Atlantic states, including North Carolina where one event
905 was documented (Tester et al., 1988), and Delaware where there was a putative event (Delaware
906 Department of Natural Resources and Environmental Control, DNREC,
907 <http://www.dnrec.delaware.gov/Pages/RedTideINformation.aspx>. Other observations of NST-
908 producing species in the U.S. include *Karenia papilionacea* found in the Gulf of Mexico, Florida
909 Straits, and Delaware (Coyne et al., 2015), and a flagellate, *Chloromorum toxicum*, identified in
910 Delaware and formerly reported as *Chattonella* cf. *verruculosa* (Bourdelaïs et al., 2002; Giner et
911 al., 2008). Recent phylogenetic analysis indicates that this species instead falls within a new
912 class of heterokonts that requires further taxonomic assessment (Medlin and Desdevises, 2018).
913 All other U.S. NST events have been attributed to *K. brevis*. Other *Karenia* spp. occur in the
914 Gulf of Mexico and are generally more broadly distributed but have been shown to produce
915 different toxins not considered to be NSTs (reviewed in Villac et al., 2020).

4.4.2 History of NSTs

Even with routine monitoring in place, impacts such as wildlife mortality, respiratory irritation, and water discoloration can provide some of the first indications of an NST event. Historical reports of these impacts suggest that *K. brevis* may have occurred prior to European settlement. Spanish explorers and early settlers provided some of the first accounts of recurring fish kills along the coasts of what are now eastern Mexico and Texas, yet most of these were not likely related to HABs (Gunte, 195; Magaña 2003), with only ~7% of fish kills in coastal Texas attributed to red tide from 1951-2006 (Thronson and Quigg 2008). Severe and widespread fish kills in Mexico (reviewed by Magaña, 2003) were noted in 1648 (with a foul odor), in 1792, and throughout the 1800s (1853, 1861, 1865, 1871, and 1875). Fish mortalities were first associated with respiratory impacts (a “dry cough”) in 1875. In southwest Florida, from the greater Tampa Bay region to the Florida Keys, extensive wildlife mortalities were first noted in the 1800s and early 1900s, and during this time, other impacts typically associated with NSTs began to be more consistently observed (Ingersoll, 1882; Feinstein et al., 1955; Rounsefell and Nelson 1966). Ingersoll (1882) described a series of unusual severe wildlife mortality events in southwest Florida in 1844, 1854, 1878, and 1880 and also recurring, less severe events (i.e., between 1854 and 1878). During the severe 1880 event, which followed a hurricane, a peculiar smell was associated with water discoloration, benthic fauna mortalities preceding pelagic species, and “spoiled” oysters in the greater Tampa Bay region (Ingersoll, 1882). In the early 1900s, further reports of wildlife mortalities and water discoloration also noted a “suffocating” or “acrid” gas (Taylor, 1917; Woodcock, 1948; Feinstein et al., 1955), likely aerosolized NSTs. In 1948,

following the particularly severe 1946-1947 bloom event in southwest Florida, *K. brevis* was first identified and associated with these phenomena (Gunter et al., 1947; Davis, 1948).

The first documented NST event in Texas was in 1935 with widespread fish mortalities and “irritating gas” that extended to Mexico, and this and another event in 1948 were subsequently attributed to *K. brevis* based on similarities to Florida events (Lund, 1936; Gunter 1952). In between those events, less severe but recurring localized impacts were reported in the Galveston Bay area (Connell and Cross 1950). Fish and mammal mortalities linked to *K. brevis* blooms were reported again in Florida from 1953-1955 (Landsberg 2002) and a severe fish mortality event occurred in Mexico and southern Texas in 1955 (reviewed by Buskey, 1996). These and subsequent events motivated more intensive monitoring by Gulf of Mexico states, demonstrating that in areas where blooms occur regularly, i.e., Texas and Florida, periodic severe events are interspersed with less severe events (Magaña et al., 2003; Walsh et al., 2006). Southwest Florida is the only U.S. area impacted nearly annually by blooms (defined as $\geq 100,000$ *K. brevis* cells L⁻¹), lasting months to years that result in shellfish harvest closures, marine mammal, turtle, bird, and/or fish mortalities, negative economic impacts, and human respiratory irritation and other symptoms associated with NST exposure (Rounsefell and Nelson, 1966; Steidinger, 2009; Diaz et al., 2019; see 4.4.5). Blooms of *K. brevis* are also known to occur regularly in northwest Florida (on average every 3 years), and less frequently on Florida’s east coast (with 10 events from 1972-2020; Florida Wildlife Commission HAB Monitoring Database, <http://myfwc.com/research/redtide/monitoring/database>).

Monitoring for *K. brevis* and brevetoxins in designated shellfish harvest areas by U.S. states around the Gulf of Mexico has been successful in that reports of human illnesses due to NSP are uncommon. Rare NSP outbreaks in southwest Florida (e.g., 1995, 1996, 2001, 2005, 2006) have been associated with unapproved recreational harvest from shellfish harvest areas during severe, prolonged blooms (Watkins et al., 2008; Florida Department of Health, 2011, [http://www.floridahealth.gov/diseases-and-conditions/disease-reporting-and-management/disease-reporting-and-surveillance/ documents/gsi-neurotoxic-shellfish.pdf](http://www.floridahealth.gov/diseases-and-conditions/disease-reporting-and-management/disease-reporting-and-surveillance/documents/gsi-neurotoxic-shellfish.pdf)). The 2006 outbreak was the second largest event on record in the U.S., with clusters representing at least 20 documented NSP cases related primarily to clam consumption, resulting in emergency room visits (Watkins et al., 2008). Regional scale advection of blooms in some years can cause the geographic extent to span multiple states and U.S. regions (Tester et al., 1988; Soto et al., 2018; Novoveská and Robertson, 2019). The first *K. brevis* bloom in the northern Gulf of Mexico that was associated with NSTs (in oysters) occurred in 1996 (Dortch et al., 1998; Maier Brown et al., 2006) when a northwest Florida bloom was advected west following a tropical storm, resulting in NST-related shellfish harvest closures as far west as Louisiana. Blooms have been noted infrequently since then in the northern Gulf (Soto et al., 2018). Western advection of northwest Florida blooms to Alabama and/or Mississippi has occurred at least six times (1996, 2000, 2005, 2007, 2015, and 2018) with varied impacts (Dortch et al., 1998; Maier Brown et al., 2006; Soto et al., 2018; Alabama Department of Public Health). The first and only reported observation of *K. brevis* in North Carolina occurred in 1987-1988 when a southwest Florida bloom was advected east around the southern tip of the state and transported north via the Gulf

Stream. A shoreward intrusion brought *K. brevis* cells into North Carolina coastal and estuarine waters (Tester et al., 1988). Human health impacts included reports of skin, eye, and respiratory irritation, as well as 48 documented cases of NSP, the largest recorded outbreak in the U.S., resulting in shellfish harvest area closures that lasted several months. The only other Atlantic observation outside Florida was in 2007, when *K. brevis* was putatively observed at low concentrations in Delaware, coincident with anecdotal reports of respiratory irritation (DNREC, <http://www.dnrec.delaware.gov/Pages/RedTideINformation.aspx>). While *K. brevis* appears to be endemic to the Gulf of Mexico, several other *Karenia* spp., including the NST-producing species *K. papilionacea*, occur in and outside the Gulf, but have yet to cause issues in the U.S. (Villac et al., 2020 and references therein).

Karenia papilionacea, initially described as *K. brevis*, was recognized as a separate species with differing morphotypes (i.e., “butterfly” and *K. brevis*-like) in 2004 (Haywood et al., 2004). This species has been documented in the North and South Pacific, North Atlantic, and Indian Oceans, as well as the eastern and western Gulf of Mexico, Florida Straits, and the Mediterranean Sea (summarized in Villac et al., 2020). Production of PbTx-2, one of the major forms of NSTs produced by *K. brevis*, was recently confirmed in strains from New Zealand and Delaware, but the levels produced by *K. papilionacea* strains tested were orders of magnitude less than *K. brevis*, and not all strains may be toxic (McNabb et al., 2006; Corcoran et al., 2014; Fowler et al., 2015). Production of NSTs by *K. papilionacea* has rarely been confirmed in nature, largely because this species occurs with other *Karenia* species that can produce NSTs (McNabb et al., 2006; Fowler et al., 2015). In the U.S., the recurring presence of low levels of *K.*

999 *papilionacea* in Delaware during late summer suggests that there may be a local or regional
 1000 population there (Coyne et al., 2015).

1001 Like *K. papilionacea*, *K. concordia* was initially described as *Karenia* cf. *brevis* (Chang and
 1002 Ryan, 2004; Haywood et al., 2004) but also has features similar to *K. mikimotoi* (Chang and
 1003 Ryan, 2004). This species has been observed only in New Zealand. In 2002, a bloom in the
 1004 Hauraki Gulf was associated with widespread fish mortalities (Chang et al., 2008) and in 2006,
 1005 *K. concordia* was confirmed to produce multiple NSTs with PbTx-2 as the dominant form
 1006 (Chang et al., 2006). Chang et al. (2006) suggested that the *K. brevis*-like cells observed in 1993
 1007 (when reported human health issues included respiratory distress and an NSP outbreak) were
 1008 actually *K. concordia*, however, multiple *Karenia* spp. were present during both events and this
 1009 could not be further confirmed.

1010 The only other producer of NSTs to date is a flagellate first described as *Chattonella* cf.
 1011 *verruculosa*, then proposed as the novel species *Chloromorum toxicum*, and now more recently
 1012 placed in a novel class of heterokonts most closely related to Raphidophyceae (Medlin and
 1013 Desdevises, 2018). This flagellate occurred widely in inland Delaware bays in 2000 and was
 1014 associated with extensive fish mortalities (Bourdelaïs et al., 2002, Giner et al., 2008). Pigment
 1015 and sterol analysis were unique but most similar to Raphidophyceae (Giner et al., 2008). Given
 1016 the absence of type material and new phylogenetic analysis, Medlin and Desdevises (2018)
 1017 suggest taxonomic reclassification at the class level is necessary which precludes assignment of
 1018 genus and species nomenclature. Analysis of field and culture material indicated the presence of

multiple NSTs, but further confirmation has not been conducted nor have subsequent events been reported.

4.4.3 NST trends

The HAEDAT dataset is focused on *K. brevis*—the only species known to cause recurring NST events in the U.S.—to provide further insight into bloom variability over the last 30 years (1990-2019; Fig. 9). HAEDAT also records aerosolized toxin impacts, but all of these were associated with NST event reports; aerosols are not discussed separately here to avoid double counting. This dataset primarily shows NST events across the four regions where repeated impacts have been described: the western Gulf of Mexico (Texas), the northern Gulf (Louisiana, Mississippi, and Alabama), Florida’s Gulf Coast, and Florida’s Atlantic Coast. The frequency of documented NST events is remarkably similar across these regions over time. This is shown in five-year increments from 2000-2019 (Fig. 9), capturing near annual occurrences in southwest Florida, frequent blooms in Texas, and rare events in the northern Gulf of Mexico and along Florida’s Atlantic Coast. A total of 58 NST events are recorded over 30 years, with a mean of 1.9. No significant trend over time is evident ($p > .05$; Fig. 9F). Although it appears that there might be a slight increase in the number of events over time, a greater than four-fold increase in monitoring effort occurred in Florida alone from 1990 to the present, and the possibility that some early events were missed or were not as comprehensively characterized cannot be excluded.

Reports of sporadic impacts from the northern Gulf of Mexico (Soto et al., 2018) should be similarly considered. Nevertheless, NST events occurred nearly annually with the exception of five years (1990, 1991, 1993, 1997, and 2010), of which the absence of a 2010 southwest Florida bloom was attributed to anomalous physical forcing that year (Weisberg et al., 2014). In HAEDAT records, the longest-lasting events—up to 30 months—occurred in southwest Florida (1994-1997, 2002-2004, 2004-2006, and 2017-2019), with a hint of multi-year cycling. Across the 30-year series, the greatest fraction of impacted zones occurred in 1996 and 2018, both of which are years with severe Florida blooms (Fig. 9). Integrating other metrics such as duration, spatial extent, and cell abundance could help further resolve spatiotemporal trends in bloom severity (i.e., Tominack et al., 2020).

4.4.4 Other NST time series

States along the Gulf Coast, including Florida, Alabama, Mississippi, Louisiana and Texas, conduct routine and event-driven sampling to inform management of shellfish harvest areas and testing for NSTs, and maintain time series data and information about bloom severity. Florida and Texas especially began to monitor more consistently for *K. brevis* in the mid-1900s with sampling intensity increasing over time (Steidinger, 2009; Tominack et al., 2020). Most of these *K. brevis* cell count data are available online (NOAA National Centers for Environmental Information, 2014, <https://data.nodc.noaa.gov/cgi-bin/iso?id=gov.noaa.nodc:0120767>), which is updated regularly, and is incorporated into other tools for tracking and predicting *K. brevis* blooms and their impacts. These include satellite chlorophyll imagery, oceanic and atmospheric

models for short-term forecasting of bloom transport and/or respiratory irritation impacts, wildlife mortality investigations (state and federal), and public health reporting systems (Abbott et al., 2009; Stumpf et al., 2009; review by Hu et al., 2015). States around the Gulf of Mexico provide *K. brevis* abundance data that feeds into a centralized respiratory irritation forecast produced by NOAA (Stumpf et al., 2009; Kavanaugh et al., 2016). Because of the impacts related to these blooms, there are also other records of fish, marine mammal, and other wildlife mortalities maintained by state and federal agencies.

4.4.5 *NST impacts in marine fish and wildlife*

The most devastating bloom-forming species in the U.S. with respect to diverse effects on wildlife and ecosystems is *K. brevis* whose blooms produce NSTs that directly affect an extensive range of marine and estuarine organisms, including marine mammals, birds, sea turtles, fish (osteichthyes and chondrichthyes), and invertebrates (Quick and Henderson, 1974; O'Shea et al., 1991, Kreuder et al., 2002; Landsberg et al., 2009, 2014; Flewelling et al., 2010; Twiner et al., 2012; van Deventer et al., 2012; Fauquier et al., 2013a, b). Even terrestrial organisms can be impacted, such as dogs or coyotes that have ingested beached toxic fish (Castle et al., 2013) or animals exposed to aerosolized NSTs or toxic rainwater (e.g., green tree frogs, spotted ground squirrels; Buttke et al., 2018). Aquatic organisms can be directly exposed to NSTs by ingestion of toxic cells or prey, through absorption of NSTs from the water through the gills, by drinking, or when cells lyse, releasing toxin on the gill filaments (Landsberg, 2002). NSTs are vectored to higher trophic levels through the food chain that can include filter-feeding phytoplankton,

zooplankton, fish, and shellfish, through to piscivores or vectored by benthic organisms such as seagrass with toxic epiphytes (Tester et al., 2000; Landsberg, 2002; Flewelling et al., 2005; Fire et al., 2008; Landsberg et al., 2009).

Fish kills associated with *K. brevis* red tides in the Gulf of Mexico have been documented since 1844 and observed routinely during almost annual red tides in the Gulf of Mexico usually lasting for months (Ingersoll, 1882; Landsberg, 2002; Magaña et al., 2003; Steidinger, 2009). The first dramatic widescale event documenting fish and invertebrate mortalities occurred along the west coast of Florida from November 1946-August 1947 (Gunter et al., 1947, 1948). It is only in prolonged bloom periods lasting for months to over one year (e.g. 2005) where noticeable short-term declines have been noted in finfish communities (Gannon et al., 2009; Flaherty and Landsberg, 2011; Walters et al., 2013), but these data are not reflected in HAEDAT. An almost total recruitment failure of bay scallops, *Argopecten irradians*, was documented during an unusual *K. brevis* bloom that impacted North Carolina coastal waters in 1987 (Summerson and Peterson, 1990).

Mortalities of other invertebrates such as shrimp, sponges, sea urchins, and stone crabs often occur during *K. brevis* blooms (Steidinger et al., 1973; Landsberg, 2002; Gravinese et al., 2018), with documented effects on larval molluscs (Leverone et al., 2006). Sustained persistent blooms can cause ecosystem-wide effects, as cascading toxins and dead bloom biomass influence water quality, leading to hypoxic and anoxic events and increased biological oxygen demand, that together with an increase in hydrogen sulfide from degrading blooms and decomposing dead

animals, can cause benthic mortalities. During intense and prolonged *K. brevis* blooms in 1971 and 2005, entire benthic communities over thousands of km² in the eastern Gulf of Mexico were effectively wiped out (Smith, 1975; Landsberg et al., 2009; Dupont et al., 2010). Many of these events have not been adequately reported in HAEDAT.

4.4.6 *NST-related marine animal mortality trends*

Other examples that may show a mortality trend are from *K. brevis* red tides killing endangered manatees, bottlenose dolphins, and sea turtles in Florida (Fig. 10). Impacts of *K. brevis* blooms to manatees were first documented in 1963, and the first mass mortality event was reported in 1982. Since 1996, and especially over the last two decades, mortalities of manatees have steadily increased but with some periodicity. This may be attributable in part to an increased population size, but it is also associated with increased frequency and longevity of blooms in coastal areas that manatee frequent. Extensive brevetoxicosis-associated mortalities affecting ~ 1000 manatees occurred in 2002, 2003, 2005-2006, 2007-2008, 2009, 2011-Feb 2012, Oct 2012-May 2013, 2015-April 2016, Oct 2016-May 2017, and Dec 2017-Jan 2019 (Landsberg et al., 2009; Fire et al., 2015; FWC 2020). Bottlenose dolphin mortalities have also been associated with brevetoxicosis (often temporally concurrent with manatee mortality events but not spatially) with ~ 500 hundred deaths reported since 1999 in the Gulf of Mexico, and mass die-offs occurring in 1999-2000, 2004, 2005-2006 (two events in SW and NW FL), and Oct 2007- Jan 2008 (east coast FL) (Van Dolah, 2003; Twiner et al., 2012, Fire et al., 2015). Suspected mortality events of bottlenose dolphins from brevetoxicosis also occurred in 1991 in

Florida and 1996 in Mississippi (concurrent with *K. brevis* blooms) and NSTs were detected at low concentrations in other mortality events with undetermined causes of death in Texas in 2008 and the central Gulf of Mexico from 2010-2014 (Litz et al., 2015).

For all the documented sea turtle strandings from all causes in the state of Florida from 1986-2013, Foley et al. (2019) reported some 2000 dead endangered loggerheads (*Caretta caretta*), green turtles (*Chelonia mydas*), Kemp's ridleys (*Lepidochelys kempii*), hawksbills (*Eretmochelys imbricata*) and leatherbacks (*Dermochelys coriacea*) from central west Florida (the high frequency zone with combined 100 months of red tide during this time period) as being directly attributable to brevetoxicosis. Statewide during the same years, some 2,900 turtles were killed by red tide. In 2005 (a red tide lasting all year), over a quarter of the turtle strandings statewide were attributed to brevetoxicosis (Foley et al., 2019).

4.4.7 Key drivers

Although much progress has been made in recognizing some drivers associated with recurring *K. brevis* blooms, the onset, duration, and severity of blooms and NST events are complex and vary from event to event (Vargo, 2009). Laboratory and field studies have been essential in revealing insights into *K. brevis* bloom dynamics. Unlike many HABs, a resting stage has not yet been described for *K. brevis* and the life cycle has not been fully resolved. A thin-walled resting cyst in the closely related species *Karenia mikimotoi* was described by Liu et al. (2020) as being similar to those described for other athecate dinoflagellates. Periodic observations of spherical *K. brevis* cells have been associated with salinity stress (e.g.,

1138 Novoveská and Robertson, 2019; Tilney et al., 2019). Even if a resting cyst is found for *K.*
 1139 *brevis*, vegetative cells occur throughout the Gulf of Mexico year-round (Geesey and Tester,
 1140 1993; Steidinger, 2009; Weisberg et al., 2019) and theoretically either or both could contribute to
 1141 bloom initiation.

1142 The low growth rates that *K. brevis* exhibits in culture suggests that other factors are
 1143 important in the formation of high biomass blooms (Steidinger, 2009; Vargo, 2009). Ecological
 1144 flexibility within the Gulf of Mexico seems to be key. Field and laboratory studies show that *K.*
 1145 *brevis* can tolerate a wide range of salinity, temperature, and light conditions (Maier Brown et
 1146 al., 2006; Vargo, 2009; Soto et al., 2018; Novoveská and Robertson, 2019), has the ability utilize
 1147 a broad array of nitrogen and phosphorus sources (Lenes et al., 2010; Heil et al., 2014;
 1148 Richardson and Corcoran, 2015), produces allelopathic chemicals (Kubanek et al., 2005),
 1149 inhibits grazers (Waggett et al., 2012), and undergoes diel vertical migration (Schaeffer et al.,
 1150 2009).

1151 Physical forcing has been identified as a key driver of bloom initiation and severity, and thus
 1152 observed interannual variability. Both Texas and Florida *K. brevis* blooms typically initiate
 1153 offshore in late summer or fall; regional hurricane and tropical storm activity typically peak
 1154 during the same window (i.e., August-October). These stochastic events have impacts on
 1155 blooms that are difficult to predict and have contributed to localized intensification, expansion to
 1156 new regions, and dissipation. Blooms of the nitrogen-fixing cyanobacterium *Trichodesmium*
 1157 often precede and coincide with *K. brevis*, and associated nitrogen fixation as well as bloom

decomposition potentially act as substantive nutrient sources. *Karenia brevis* can utilize an array of nutrient sources including those of anthropogenic origins (Heil et al., 2014).

Florida blooms are hypothesized to initiate on the West Florida Shelf, 18-74 km offshore, spanning from north of Tampa Bay to Sanibel (e.g., Steidinger, 1975; Weisberg et al., 2019). Interactions of the Loop Current with the West Florida Shelf are important for inoculating the inner shelf with deeper, nutrient-rich, oceanic water. Interannual variability in the location, duration, and intensity of Loop Current/slope interactions is important for *K. brevis* bloom severity in that blooms appear to require moderate upwelling but may be inhibited by strong upwelling events, as was observed in 2010 (Liu et al., 2016; Weisberg et al., 2014). Shoreward transport occurs via the bottom Ekman layer under upwelling favorable conditions typical of late summer/fall (Liu et al., 2016; Weisberg et al., 2009). Wind-driven forcing near shore coupled with the vertical swimming behavior of *K. brevis* can help transport cells to the surface and/or cause cells to aggregate at density fronts (Stumpf et al., 2008). Blooms in Florida typically endure for months to years, are patchy in space and time, and severity varies widely across events (Walsh et al., 2006; Liu et al., 2016).

Initiation in Texas is suspected to occur >15km offshore (Villareal et al., 2001), however, modeling studies point to a distant rather than local source (Hetland and Campbell, 2007; Stumpf et al., 2008; Thyng et al., 2013). Blooms occur regularly along the Mexican coast of the Gulf of Mexico during late summer/fall as well and often coincide with Texas events (Magaña et al., 2003; Núñez-Vázquez et al., 2016). Northeast transport along the shelf from Mexico to

1178 Louisiana typically occurs during upwelling-favorable conditions, which start in spring and
1179 summer. During fall, the switch to downwelling-favorable winds begins in the north and
1180 translates back down the coast, resulting in a reversal to the alongshore flow. Under strong
1181 downwelling conditions, a severe bloom is unlikely to develop along the Texas coast (Henrichs
1182 et al., 2015; Thyng et al., 2013); blooms are instead prevalent during years when alongshore,
1183 southwestern transport is weak. Shoreward Ekman transport—in tandem with vertical migration
1184 of *K. brevis*—helps create a convergence zone that concentrates cells near the coast (Hetland and
1185 Campbell, 2007; Thyng et al., 2013). A summary of HAB events in Mexico’s Yucatan coast
1186 along the Bay of Campeche from 1996-2014 indicated that NST impacts occurred in 14 of those
1187 18 years, and the Mexican state which borders Texas (Tamaulipas) had the most NST impacts
1188 relative to the rest of the Mexican Gulf states (Núñez-Vázquez et al., 2016); fewer events
1189 occurred in Texas during this same time (Fig. 6). The timing of many Mexico events relative to
1190 the seasonal transition to downwelling favorable conditions along the coast raise the possibility
1191 that advection along the U.S.-Mexico coast and/or localized processes are important drivers of
1192 blooms there. While genetically distinct populations of *K. brevis* have been identified over time
1193 and sometimes between the eastern and western Gulf of Mexico during years when blooms occur
1194 in both areas, there is no consistent indication that Florida and Texas populations are genetically
1195 distinct (Henrichs et al., 2013). Weisberg and Liu (2017) and more recently, Yang et al. (2020)
1196 highlight how intrusions of the Loop Current into the Gulf of Mexico may reach Texas,
1197 potentially providing one possible means of connectivity across these regions.

In the context of climate change, Errera et al. (2014) examined cultures under variable pCO₂ and temperature scenarios and did not find a response between pCO₂ or temperature and NST content but did find a response between pCO₂ and growth rate. Subsequently, Bercel and Kranz (2019) examined *K. brevis* growth in cultures at a constant temperature under future pCO₂ conditions and observed no change in growth, carbon or nitrogen cellular composition, or photosynthetic rates. NST content and pCO₂ were positively correlated, however. Both papers ultimately came to same conclusion – *K. brevis* blooms are likely to persist and NSTs might increase with a warmer, more acidic ocean, so toxin severity could increase. However, circulation changes and more storms in the region, also to be expected with climate change, make it difficult to assess whether conditions will support worsening blooms in existing areas, or whether the distribution of areas experiencing severe blooms will shift or expand.

4.5 CTX and CP

4.5.1 Background

Ciguatoxins (CTX) are a complex group of potent neurotoxins that can accumulate to dangerous levels in coral reef fish and invertebrates, and cause Ciguatera Poisoning (CP) in human consumers of seafood contaminated with these toxins. CTXs are produced by tropical dinoflagellate species in the genera *Gambierdiscus* and *Fukuyoa*, which are benthic and epiphytic, living on the surfaces of a variety of macrophytes as well as detritus on dead coral (Parsons et al., 2012; Cruz-Rivera and Villareal, 2006). CTXs enter the coral reef food web via grazing by herbivorous fishes and invertebrates, and can be bioaccumulated and concentrated in

fish at higher trophic levels. Toxin levels are frequently highest in carnivorous reef fishes, many of which are targeted by commercial and recreational fisheries, although a wide variety of species have the potential to be ciguatoxic. The CTXs associated with ciguatera are chemically diverse compounds composed of a ladder shape polyether structure, and differences in the number of ether rings and backbone structure are regionally specific (reviewed by Soliño and Costa, 2018). Of the more than 30 CTX congeners identified thus far, the main Pacific CTX (P-CTX-1) is most potent, producing clinical symptoms in humans at levels $>0.08 \text{ ng P-CTX-1 g}^{-1}$ fish flesh (Lehane and Lewis, 2000; Pasinszki et al., 2020). The main Caribbean CTX (C-CTX-1) is approximately ten-fold less potent than P-CTX-1. The U.S. FDA has proposed advisory levels of 0.10 ppb C-CTX-1 equivalent toxicity in fish from the tropical Atlantic, Gulf of Mexico and Caribbean, and 0.01 ppb P-CTX-1 equivalent toxicity in fish from Pacific regions (U.S. FDA, 2019). In addition to CTXs, some species of *Gambierdiscus* and *Fukuyoa* have been shown to produce other polyether compounds such as maitotoxins (MTXs), gambierol, gambieric acids, and gambierone, but their contribution to CP is not established (Soliño and Costa, 2020).

Taxonomic studies have identified two *Fukuyoa* species and at least 18 species within the *Gambierdiscus* genus, many of which co-occur and differ significantly in toxicity. At least ten of these species have been found in tropical and subtropical regions of the U.S., including Hawai'i, the Gulf of Mexico, the Florida Keys, Puerto Rico, and the U.S. Virgin Islands (Table 1). Not all species are globally distributed, and this includes the most toxic species identified thus far (Chinain et al., 1999, 2010; Longo et al., 2019; Robertson et al., 2018). For example, *G.*

polynesiensis has been reported in the Pacific (including Hawai'i) but not in the Caribbean, while *G. silvae* and *G. excentricus* have been found at locations in the Caribbean and Gulf of Mexico, but not in the Pacific or Indian Oceans. Several species – *G. carpenteri*, *G. caribaeus*, *G. carolinianus*– are widely distributed, and have been found at locations in both the Pacific Ocean and Caribbean Sea. Details regarding the current geographic distribution of *Gambierdiscus* species are reviewed by Chinain et al. (2020).

4.5.2 History of CTX and CP

CTXs have been found in fish from tropical or subtropical areas globally, and are endemic to coral reef ecosystems between 35° north and 35° south latitude. In the U.S., CP caused by CTX afflicts hundreds to thousands of people annually (Friedman et al., 2017), and outbreaks are most severe in Florida (Radke et al., 2015), the U.S. Virgin Islands (Radke et al., 2013), Puerto Rico (Azziz-Baumgartner et al., 2012), and Hawai'i, as well as U.S. affiliated territories (Copeland et al., 2014; Skinner et al., 2011). There have also been sporadic reports of CTX and CP from temperate waters of the U.S., and in 1987 ten cases of CP were reported from North Carolina during an outbreak involving several fish species, including barracuda (Pottier et al., 2001). CTXs are known to occur in the northwestern Gulf of Mexico, and have been found in fish caught near oil production platforms, which historically have not been regarded as risky areas for CP (Villareal et al., 2007). In addition to detecting CTX in fish, this study also found *Gambierdiscus* dinoflagellates in samples collected from the fouling community present on the platforms and from algae collected at these sites. In 2008, CP outbreaks were linked to grouper

and amberjack species caught near the Flower Garden Banks National Marine Sanctuary in the northern Gulf, prompting the U.S. FDA to issue guidance identifying several species of concern (e.g., hogfish, grouper, snapper, amberjack) for which ciguatera is a “reasonably likely hazard” when captured near the Sanctuary.

Of all the poisoning syndromes associated with HAB toxins, CP caused by CTX is the most prevalent globally, and is estimated to afflict tens of thousands of people each year, with many cases unreported. Unlike many other HAB poisoning syndromes, CP is not associated with large scale blooms of the causative organism, and monitoring programs to test fish for CTXs have been hindered by complex toxin chemistry and involvement of multiple toxins, as well as the lack of commercially available toxin standards and affordable and practicable methods for toxin detection. In the absence of monitoring programs, prevention of CP largely relies on avoidance of high-risk carnivorous fish species most commonly associated with outbreaks (e.g., barracuda, snapper, grouper) as well as local ecological knowledge regarding the distribution of toxic fish, which can function as an informal type of "closure," in which high risk locations are avoided.

4.5.3 CTX and CP trends

Although CP has been endemic to certain regions of the U.S. for decades, there are no sustained monitoring programs for *Gambierdiscus* or CTX, and HAEDAT datasets do not exist to establish time series trends. In the absence of routine monitoring, prevalence and trends for CTXs and CP can only be derived from state health department records, emergency room

reports, and other local systems used in CP surveillance. Obtaining complete data on CP is difficult and is an undertaking far beyond this current effort.

The scientific literature includes several efforts to examine CP incidence at local or regional levels in an effort to establish time series trends, and specifically to test hypotheses regarding climate-driven warming on CP incidence and extent. Based on these studies, CP and CTXs appear to be increasing in some locations where it is endemic, but declining in others. For example, Radke et al. (2013) found a possible decline in CP incidence on St. Thomas, USVI over a 30-year period (1980-2010) based on a review of emergency room reports and household surveys, despite the steady increase in sea surface temperatures (SSTs) during that same period. Similarly, CP incidence was estimated over a ten-year period in Florida based on an analysis of reports to the Florida Department of Health (FDOH), combined with a survey of recreational fisherman (Radke et al. 2015). This study also found that CP may have declined over the ten-year period. The study also determined, however, that the majority of possible cases of CP are never reported to the FDOH, illustrating the potential biases in current surveillance systems and the need for data-driven estimates of underreporting to more accurately determine prevalence and impact of CTXs and CP (Radke et al., 2015).

There is recent evidence of geographic range expansion of *Gambierdiscus* and CP into higher latitudes in U.S. waters, associated with climate-driven warming. Over the past two decades CP and CTXs were reported for the first time in the northern Gulf of Mexico, and ephemeral populations of *Gambierdiscus* have also been documented in North Carolina.

1298 Prolonged periods of elevated water temperatures at these locations and in northern Florida are
 1299 hypothesized to result in increased *Gambierdiscus* and *Fukuyoa* cell densities, and in turn,
 1300 increased CTX flux.

1301 In addition to shifts in CTX range, CP events throughout the U.S. are likely to increase due
 1302 to expanding seafood trade (supplying retail markets or restaurants), and importation of
 1303 ciguatoxic fish to temperate and land-locked locations for local consumption. CP outbreaks have
 1304 already been reported from multiple non-endemic locations such as Illinois, Maryland,
 1305 Massachusetts, New York, North Carolina, Vermont, District of Columbia, Texas, Kansas, and
 1306 California (Vogt, 1985; Juranovic, 1989; Barton et al., 1995; Graber et al., 2013).

1307 4.5.4 Key drivers

1308 Key drivers of CTX events and CP risk are not fully understood, but involve a combination
 1309 of: the species composition of *Gambierdiscus* and *Fukuyoa* populations, particularly the
 1310 presence of highly toxic species, and the environmental conditions that promote CTX
 1311 production and/or foster growth of toxigenic strains and species. Additionally, patterns of
 1312 toxicity and bioaccumulation are affected by CTX uptake by herbivorous fishes and
 1313 invertebrates, and trophic biotransformation and transfer in coral reef food webs.

1314 Temperature is a key factor controlling CTX occurrence, and laboratory experiments
 1315 investigating the influence of temperature on growth of various *Gambierdiscus* species have
 1316 shown that most species exhibit maximum growth rates between 24–30°C, but that growth
 1317 responses varied by species (Kibler et al., 2012; Xu et al., 2016). Thus, higher temperatures

1318 may favor growth of more thermally tolerant species (e.g., *G. belizeanus* and *G. caribaeus*) in
 1319 ciguatera endemic regions, and promote establishment of species shown to be less tolerant (e.g.,
 1320 *G. silvae*) in subtropical and temperate regions. Warm surface temperatures may also shift the
 1321 *Gambierdiscus* and *Fukuyoa* populations to deeper waters.

1322 Natural and anthropogenic damage to reef ecosystems have also been implicated in CTX
 1323 events, such as public or military construction activities involving dredging, explosives,
 1324 dumping of materials; coral bleaching, shipwrecks, and hurricanes (Randall, 1958; Ruff, 1989;
 1325 Hales, 1999; Lehane and Lewis, 2000). As the areal distribution and abundance of
 1326 *Gambierdiscus* and *Fukuyoa* dinoflagellates is largely a function of algal cover, it was
 1327 hypothesized that disturbances create free space on dead coral that is colonized by filamentous
 1328 algae, enabling the proliferation of epiphytic dinoflagellates (Randall, 1958; Yasumoto, 1977;
 1329 Yasumoto, 1980; Kohler and Kohler, 1992).

1330 Few studies have examined these linkages directly, however. In the U.S., Gingold et al.
 1331 (2014) examined the association between CP incidence and warming SSTs as well as tropical
 1332 storm frequency in the Caribbean Sea, based on calls made to U.S. National Poison Control
 1333 Centers over a ten-year time frame. These studies found that monthly CP calls to poison control
 1334 centers in the continental U.S. were associated with both tropical storm frequency and peak SST
 1335 in the Caribbean basin, with SST increases having a stronger association with CP compared with
 1336 the effect of storms. Additional data on cases with confirmed disease, perhaps focused on high

incidence areas, are needed to explore these findings further, and to pinpoint the proper lag time between weather and SST disturbance and CP.

4.6 Other HAB species

4.6.1 Brown tides

4.6.1.1 Background

Brown tides are caused by the pelagophytes *Aureococcus anophagefferens* Hargraves et Sieburth and *Aureoumbra lagunensis* DeYoe et Stockwell. Although *Aureococcus* and *Aureoumbra* are genetically distinct (DeYoe et al., 1995), they both are small (4-5 μm for *Aureoumbra* and 2-3 μm for *Aureococcus*), spherical, non-motile cells (DeYoe et al., 1997; Gobler and Sunda, 2012). Neither alga had been described prior to the onset of HABs in the U.S. caused by each species and both were originally assigned to the class Chrysophyceae (Sieburth et al., 1988; Buskey and Stockwell, 1993), although later examination led to their formal placement in a new class, Pelagophyceae (DeYoe et al., 1997).

Brown tides are considered ecosystem disruptive, as they are harmless to humans but are damaging to marine life and habitats. Brown tides are high biomass blooms with concentrations exceeding 10^6 ml^{-1} , which result in increased light attenuation and the destruction of seagrass meadows (*Zostera marina*; Cosper et al., 1987; Onuf, 1996; Gobler et al., 2013). Both pelagophytes produce extracellular polysaccharides which adversely impact larval, juvenile and adult hard clams (*M. mercenaria*; e.g., Bricelj et al., 2001; Newell et al., 2009), larval and adult bay scallops (*A. irradians*; Bricelj and Kuenstner, 1989; Gallagher et al., 1989), adult and juvenile

1357 blue mussels (*Mytilus edulis*; Bricelj and Kuenstner, 1989; Bricelj et al., 2001), and dwarf surf
 1358 clams *Mulinia lateralis* (Montagna et al., 1993). Brown tides are also harmful to micro- and
 1359 mesozooplankton (e.g., Buskey and Stockwell, 1993; Lonsdale et al., 1996; Smith et al., 2008).
 1360 *Aureococcus* has been shown to negatively affect bivalves at cell densities $> 3.5 \times 10^4$ cells ml⁻¹
 1361 (Bricelj et al., 2001).

1362 4.6.1.2 History of brown tides

1363 The first *A. anophagefferens* blooms in the U.S. occurred simultaneously in the summer of
 1364 1985 in Narragansett Bay, Rhode Island, Great South Bay, and the Peconic Estuary on Long
 1365 Island, New York, and putatively in Barnegat Bay, New Jersey (Fig. 11; Sieburth et al., 1988;
 1366 Cosper et al., 1989; Olsen, 1989). During the 1990s, blooms expanded south along the U.S. East
 1367 Coast into bays in New Jersey (Fig. 11; Barnegat Bay; Gastrich et al., 2004), Delaware (Fig. 11;
 1368 Little Assawoman Bay; Popels et al., 2003), Maryland, and Virginia (Fig 10; Chincoteague Bay;
 1369 Trice et al., 2004; Glibert et al., 2007; Mulholland et al., 2009a). Low abundances of *A.*
 1370 *anophagefferens* cells have been observed along the entire eastern seaboard of the U.S. from
 1371 Maine to Florida (Anderson et al., 1993; Popels et al., 2003).

1372 The first *A. lagunensis* brown tide bloom began in shallow lagoons in and around the
 1373 Laguna Madre and Baffin Bay, Texas in January 1990 and subsequently persisted for nearly
 1374 eight years, making it the longest continuous harmful algal bloom (HAB) event on record (Fig.
 1375 11; Buskey et al., 1997, 2001). Surveys across the Gulf of Mexico have detected low densities
 1376 of *A. lagunensis* through the entire Laguna Madre south into Mexico as well as in southern

Florida, specifically Florida Bay, but did not detect cells in Mississippi or along the northeast Texas coast (Villareal et al., 2004).

4.6.1.3 Brown tide time series

Since the onset of brown tides caused by *A. anophagefferens*, they have vanished from some ecosystems but have been annual occurrences in other locales. In Rhode Island's Narragansett Bay, the brown tide of 1985 never returned (Fig. 11A; Smayda, 2008). In New York, brown tides occurred in the Peconic Estuary from 1985-1998 but have not occurred since (up to 10^4 ml⁻¹; Fig. 11B; Nuzzi and Waters, 2004). In contrast, *Aureococcus* form dense blooms annually within the south shore lagoons of Long Island, with the intensity and frequency from 2007–2018 surpassing the blooms from 1985-2005 (Fig. 11C; Great South, Moriches, Shinnecock, and Quantuck Bays; Gobler et al., 2011). In New Jersey, monitoring has been inconsistent (Fig. 11D) but dense blooms ($> 10^5$ cells mL⁻¹) were recorded from 1998-2001 (Gastrich et al., 2004). Sporadic monitoring since then has revealed more modest densities (10^4 – 10^5 cells mL⁻¹; Bricelj et al., 2017). In Maryland, dense blooms have been occurring near annually in Chincoteague Bay since the mid-1990s (Fig. 11E). Brown tides were more intense and consistent in Maryland during the decade of 1999–2008 than the decade since, during which there have been only two events with densities exceeding 10^6 cells mL⁻¹ (Fig. 11E). This system represents the southern extent of *A. anophagefferens* blooms, perhaps partly due to warmer temperatures and lower salinities of lagoons south of this locale.

The first ever brown tide caused by *A. lagunensis* persisted from late 1989 through the fall of 1997 and then recurred during the summer and fall of 1998 in Laguna Madre and Baffin Bay, Texas (Buskey et al., 1997, 2001). Reporting of blooms was sporadic from 1999–2010, with at least one bloom occurring during that period (Fig. 11G; Wetz et al., 2017). Since 2012, the Wetz laboratory (Texas A&M University) has surveyed Baffin Bay annually and has reported dense blooms (10^5 – 10^6 cells mL⁻¹, Fig. 11G) annually. Over the past decade, the geographic extent of *A. lagunensis* has greatly expanded, with blooms in the northern Indian River Lagoon and Mosquito Lagoon on the east coast of Florida starting in 2012 (Gobler et al., 2013). This was the furthest east these blooms had ever been observed and the densest brown tides ever recorded, with cell concentrations exceeding 3×10^6 cells mL⁻¹ in 2012 and again in 2016 (Fig. 11F). Interestingly, in the year after the expansion to eastern Florida, *A. lagunensis* blooms were noted in Cuba for the first time (Koch et al., 2014a).

4.6.1.4 Key drivers

Although harmful algal blooms in coastal waters have been commonly attributed to nutrient loading, the role of nutrients in the occurrence of brown tides appears to be more complex than a simple excess inorganic nutrient stimulation of blooms (Sunda et al., 2006; Gobler and Sunda, 2012). Multiple lines of evidence demonstrate that *A. anophagefferens* is at a competitive disadvantage when the concentrations of inorganic nitrogen are elevated and instead blooms form when inorganic nutrient levels are low (Cosper et al., 1989; LaRoche et al., 1997; Keller and Rice, 1989; Gobler and Sanudo-Wilhelmy, 2001a; Gobler et al., 2002, 2004a,b; Taylor et al., 2006) due to its superior ability to utilize organic forms of C, N, and P (Berg et al., 2002;

1417 Mulholland et al., 2002, 2009a; Gobler et al., 2004, 2011; Kang et al., 2017). Similar
 1418 conclusions have been drawn regarding *A. lagunensis* (Buskey et al., 1997; Muhlstein and
 1419 Villareal, 2007; Sunda and Hardison, 2007, 2010) although there has been some evidence that
 1420 elevated ammonium levels might favor this alga (Buskey et al., 1997; DeYoe et al., 2007; Kang
 1421 et al., 2015).

1422 Regarding physical drivers, brown tides occur in estuaries, mainly lagoons, with long
 1423 residence times (weeks-months; Gobler and Sunda, 2012; Cira and Wetz, 2019) that permit the
 1424 accumulation of high algal biomass (10^6 cells mL⁻¹) and low light conditions (Gobler and Sunda,
 1425 2012; Cira and Wetz, 2019). Both brown tide species achieve near-maximum growth rates at
 1426 low light levels ($50 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$, ~ 2% of noon solar irradiance; MacIntyre et al., 2004;
 1427 Sunda and Hardison, 2010) which are common during dense blooms (Gobler and Sunda, 2012).
 1428 Within the sub-tropical estuaries of Texas and Florida, *A. lagunensis* blooms have been
 1429 associated with hypersaline conditions (40 – 90 PSU; Buskey et al., 1998; Gobler et al., 2013)
 1430 that may inhibit algal grazers and competing algal species (Buskey et al., 1998; Gobler et al.,
 1431 2013; Cira and Wetz, 2019). As warming accelerates during this century, hypersalinity is likely
 1432 to be a more frequent occurrence in sub-tropical and tropical estuaries with extended residence
 1433 times, favoring the occurrence of *A. lagunensis* blooms. This may have contributed to the
 1434 expansion of this species to Florida and Cuba during the past decade (Gobler et al., 2013; Koch
 1435 et al., 2014). Alternatively, warming may restrict the distribution and intensity of *A.*
 1436 *anophagefferens* blooms which have a significantly lower upper temperature threshold compared
 1437 to *A. langenensis* (24°C v 32°C; Gobler and Sunda, 2012). These warmer temperatures may be

driving *A. anophagefferens* blooms to occur and end earlier in ecosystems that commonly exceed this temperature, including those in New York, New Jersey, and Maryland.

Zooplankton grazing rates on brown tides are typically low due to unpalatability, toxicity, and/or physical interference with grazing, contributing to the initiation and persistence of blooms (Buskey et al., 1997; Gobler et al., 2002; Sunda et al., 2006; Smayda, 2008). Similarly, brown tides tend to inhibit filter feeding by bivalves in the shallow systems they occur (Bricelj and Kuenstner, 1989; Buskey et al., 1997; Bricelj et al., 2001; Harke et al., 2011) and an absence of benthic feeding may also enhance blooms (Cerrato et al., 2004). Grazing communities can evolve resistance to harmful algae over time via natural selection processes (Hairston et al., 2002), and the selective impact of blooms on more sensitive phenotypes within populations (Caron et al., 2004) could eventually lead to the establishment of grazer communities that are better adapted to co-exist with and consume *A. anophagefferens*. Recent studies have shown that in some New York estuaries a shift occurred in which zooplankton communities that formerly consumed *Aureococcus* at low rates during massive blooms have shifted to communities that actively graze *Aureococcus* at rates similar to those for other algal species (Deonaraine et al., 2006). Similarly, although *Aureococcus* inhibits grazing by mollusks, the filter feeding slipper limpet, *Crepidula fornicata*, robustly grazes *Aureococcus* (Harke et al., 2011). This limpet is now present at high abundance in estuaries that no longer experience brown tide blooms (e.g., the Peconic Estuary; Harke et al., 2011). Thus, the recent abatement or reduced magnitude of brown tides in some estuaries (Fig. 11) may, at least partly, reflect a shift in the grazing communities toward populations more capable of feeding on *A. anophagefferens*. Finally,

allelopathic interactions with other phytoplankton may facilitate the persistence of brown tide blooms, as both *A. anophagefferens* and *A. langenensis* have recently been shown to significantly reduce the cell densities and growth rates of multiple species of co-occurring phytoplankton (Kang and Gobler, 2018).

4.6.2 *Margalefidinium/Cochlodinium*

Dinoflagellates of the genus *Cochlodinium* were first identified in 1895 by Schütt (1895) and two species, *C. polykrikoides* and *C. fulvescens*, have been forming harmful algal blooms on the U.S. East Coast and West Coast, respectively, for several decades. These HAB species were recently renamed *M. polykrikoides* and *M. fulvescens* by Gomez et al. (2017) due to ribosomal DNA sequence differences from the type-species, *Cochlodinium strangulatum*. Blooms of *M. polykrikoides* have caused >\$100M in fisheries losses in Korea, the Gulf of Oman, and Canada (Kim, 1998; Whyte et al., 2001; Richlen et al., 2008) and have caused fish and wild and aquacultured shellfish kills in the U.S. (Gobler et al., 2008; Kudela and Gobler, 2012; Griffith et al., 2019a). Blooms of *M. polykrikoides* are macroscopically and microscopically distinctive but are also highly ephemeral and horizontally and vertically heterogenous (Koch et al., 2014b). Consequentially, consistent long-term monitoring records of these HABs in the U.S. are rare, and as such, the assessment here covers published occurrences of blooms that can be interpreted as reliable due to the visually distinctive nature of these HABs, commonly referred to as ‘rust tides’.

4.6.2.1 History and trends

The first reported blooms of *M. polykrikoides* were on the U.S. East Coast in Barnegat Bay, New Jersey (Silva, 1967), the York River, Virginia (Ho and Zubkoff, 1979), and Greenwich Cove, Rhode Island (Tomas and Smayda, 2008) in the 1960s, 1970s, and 1980s, respectively. Since these reports, there has been a significant expansion of blooms reported along the U.S. East Coast. On Long Island, New York, *M. polykrikoides* has formed dense blooms in the Peconic Estuary and Shinnecock Bay annually since 2004 through 2020 (Gobler et al., 2008; Tang and Gobler 2010; C. Gobler pers. obs.) and has recently (since 2011) expanded across Long Island into Great South Bay and Long Island Sound (since 2015; C. Gobler, pers. obs.). There were no reports of this alga prior to 2004 on Long Island despite robust HAB monitoring programs established decades prior (e.g. SCDHS, 1976-2020). To the north of this region, blooms have been observed this century in Point Judith Pond and Narragansett Bay, Rhode Island (Hargraves and Maranda, 2002). Within Buzzards Bay (Massachusetts), *M. polykrikoides* blooms were not observed until 2005, but now are observed annually (Rheuban et al., 2016). Since 2010, blooms of *M. polykrikoides* have emerged within both Martha's Vineyard and Nantucket Sound (Massachusetts; Leavitt et al., 2010). To the south of this region, blooms of *M. polykrikoides* had been sporadic events in the York River, Maryland, (Ho and Zubkoff, 1979) but have recently become regular, annual events within multiple tributaries of Chesapeake Bay in Maryland and Virginia (Marshall et al., 2005; Marshall, 2009; Mulholland et al., 2009b; Morse et al., 2011, 2013). Blooms of *M. polykrikoides* have also been newly reported in the southeast U.S. specifically within the Skidaway Estuary (Georgia, U.S.A; Verity, 2010) and the Indian

1499 River Lagoon (Florida; Philips et al., 2011). On the West Coast of North America,
 1500 *Margalefidinium* spp. cells had been observed in southern California coastal waters during the
 1501 twentieth century (i.e., La Jolla Bay, California; Kofoed and Swezy, 1921; Holmes et al., 1967).
 1502 Since that time, Curtiss et al. (2008) and Kudela et al. (2008) reported annual *M. fulvescens*
 1503 blooms in Monterey Bay (California), with recurrent sightings across central and Southern
 1504 California since 2004. While many of these studies have been strictly observational,
 1505 investigations in Virginia, New York, and Massachusetts have confirmed the ability of *M.*
 1506 *polykrikoides* to cause mass kills of fish and shellfish (Gobler et al., 2008; Mulholland et al.,
 1507 2009b; Levitt et al., 2010; Li et al., 2012; Griffith et al., 2019a).

1508 4.6.2.2 Key drivers

1509 Given the striking visual attributes of *M. polykrikoides* blooms (large, dense, surface patches
 1510 of rust-colored water), the occurrence of these events in multiple new regions on the U.S. East
 1511 Coast during the past two decades seems likely to be a real phenomenon rather than a function of
 1512 improved methods of detection. Several potential drivers for these trends have emerged. First, it
 1513 has been discovered during the past decade that *M. polykrikoides* populations on the U.S. East
 1514 Coast produce cysts in culture (Tang and Gobler, 2012) and cysts beds have been identified
 1515 within estuaries that experience recurrent blooms (Hattenrath-Lehmann et al., 2016) suggesting
 1516 anthropogenic and natural transport of cysts could facilitate the spread of this HAB (Smayda,
 1517 2007). Nitrogen loading has been associated with the intensification of *M. polykrikoides* blooms
 1518 in New York and Virginia (Gobler et al., 2012; Morse et al., 2011, 2013). Finally, the warming
 1519 of surface waters since 1982 has yielded significant increases in potential growth rates of *M.*

1520 *polykrikoides* and bloom season duration in coastal zones from Chesapeake Bay through Cape
 1521 Cod, areas where blooms have become newly established and/or intensified this century (Fig. 12;
 1522 Griffith et al., 2019b).

1523 4.6.3 *Heterosigma*

1524 4.6.3.1 Background

1525 The motile raphidophyte *Heterosigma akashiwo* (= *H. carterae*) is known for its dense
 1526 surface blooms, often leading to water discoloration. In the U.S., it occurs in the Gulf of Mexico
 1527 and on both the East and West Coasts, though it is considered harmful predominantly on the
 1528 West Coast due to its effects on fish farms. Reports of wild salmon and marine aquacultured fish
 1529 mortalities due to blooms of this species have been reported primarily in Washington State
 1530 inland waterways (Hershberger et al., 1997; Horner et al., 1997). Farmed fish are particularly
 1531 vulnerable when winds or currents move blooms into penned areas where the fish are unable to
 1532 escape. Consequently, *H. akashiwo* has caused the death of salmonids held in net pens in Puget
 1533 Sound since at least 1976 (Rensel, 2007; Rensel et al., 1989). These HABs were considered a
 1534 serious risk to site development for new net-pen facilities, particularly given that as few as 500
 1535 cells/L can cause fish deaths when cells are expressing toxicity (Horner, 1998). The salmon
 1536 aquaculture industry in Washington State has suffered economic losses of ~ \$2 to 6 million per
 1537 episode due to *H. akashiwo* blooms. Recent problems with net pen collapse have led to the
 1538 prohibition of aquacultured salmon operations in Puget Sound as of 2017, thus records of
 1539 mortalities due to *H. akashiwo* are no longer available. The most complete timelines of *H.*

1540 *akashiiwo* occurrence and associated aquacultured fish mortalities are recorded in nearby
1541 Canadian inland waterways (see Table 2 in Rensel et al., 2010).

1542 4.6.3.2 Key drivers

1543 *Heterosigma akashiwo* is considered a mixotroph as it can supplement its normal
1544 phototrophic physiology and nutrition through the ingestion of bacteria and other particles
1545 (Jeong, 2011). It also has a cyst stage that allows it to persist in a region when conditions are not
1546 suitable for growth (Imai and Itakura, 1999). In the Puget Sound region of the U.S., *H. akashiwo*
1547 blooms have been more frequently associated with specific times of year (early July and mid-
1548 September), warm water temperatures ($>15^{\circ}\text{C}$) and higher than normal riverine discharge from
1549 snowmelt, resulting in reduced salinity and a stable mixed layer in the coastal zone (Taylor and
1550 Haigh, 1993; Rensel, 1995; Connell and Jacobs, 1997; Li and Smayda, 2000; Anderson et al.,
1551 2001). In north Puget Sound, blooms are believed to initiate in the southern Strait of Georgia and
1552 U.S. waters north of San Juan Island in association with the brackish plume of the Fraser River
1553 in Canada (Rensel, 1995, 2007). The Fraser River, which empties into the southernmost portion
1554 of the Strait of Georgia, is the largest river contributing freshwater (Mackas and Harrison, 1997)
1555 to the Strait of Georgia, Puget Sound and Strait of Juan de Fuca region. Its effects on these
1556 marine waters and circulation therefore are pronounced, as *H. akashiwo* blooms in North Puget
1557 Sound and the Strait of Georgia have been strongly associated with its larger than normal
1558 discharge (Rensel, 2007).

4.6.4 *Karenia mikimotoi*

Blooms of *Karenia mikimotoi* have been observed on both the U.S. East and West Coasts. This species is globally distributed and is not known to produce toxins that impact human health or wildlife. It has, however, been associated with widespread fish and benthic mortality events. Although *K. mikimotoi* occurs regularly in the Gulf of Mexico, blooms or related impacts have not been identified in those waters (Villac et al., 2020). A high-density bloom occurred in Alaska in 2013 that caused water discoloration and fish kills, but was not detected in preceding or following years and the source is not known (Vandersea et al., 2020). This species also bloomed in the Gulf of Maine in 2017 at levels of 10^7 cells/L, and has been observed there in subsequent years. Recently, a resting stage was identified for *K. mikimotoi* (Liu et al., 2020), and thus the observation of recurring blooms in the Gulf of Maine could be a result of cyst germination giving rise to localized populations, though advection from another region can't be ruled out. Genetic differentiation has been observed among geographically distinct populations, which could be a useful diagnostic tool to better understand potential linkages with source populations, especially in areas with emerging events.

4.6.5 *Effects of other marine HABs on fish and wildlife*

From the 1930s onwards, sporadic kills affecting diverse estuarine and marine fish and invertebrates in the Gulf of Mexico (Texas) and in the Indian River Lagoon, east coast Florida were associated with *Alexandrium monilatum* (subsequently determined to produce goniodomin, but its role in kills was unknown) (Gunter, 1942; Howell, 1953; Wardle et al., 1975; Landsberg,

1579 2002). Since 2007, this species has bloomed almost annually in the Chesapeake Bay (Wolny et
 1580 al., 2020) and in that same year was associated with a mortality of veined rapa whelk, *Rapana*
 1581 *venosa*, presumptively attributed to exposure to goniiodomin causing respiratory paralysis
 1582 (Harding et al., 2009). *Takayama pulchella* was associated with fish and invertebrate kills in the
 1583 Indian River Lagoon in 1996 (Steidinger et al., 1998) and in 2004. A large shellfish kill in Maine
 1584 in 1988 was linked to *Gymnodinium aureolum*, and attributed to a combination of low dissolved
 1585 oxygen, possible toxicity, and production of mucus (Shumway, 1990; Heinig and Campbell,
 1586 1992). *Lingulodinium polyedra* (producing yessotoxins) had previously been associated with fish
 1587 and invertebrate kills in California (Torrey, 1902), and a fish kill in 2003 in the same state was
 1588 reported to HAEDAT, although a direct role for the toxins is unproven. Extensive study on
 1589 *Karlodinium veneficum* toxicity along the U.S. Atlantic eastern seaboard has shown multiple
 1590 strains producing polyketide karlotoxins that are cytotoxic, hemolytic, and ichthyotoxic (Deeds
 1591 et al., 2004, Van Wagoner et al., 2008; Bachvaroff et al., 2009; Place et al., 2012). Karlotoxins
 1592 bind to 4-desmethyl sterols (e.g., cholesterol) on cell bilayer membranes causing pore formation
 1593 in epithelial and chloride cells in fish gills leading to respiratory dysfunction and consequent
 1594 acute mortalities, as well as effects on shellfish larvae (Deeds and Place, 2006; Deeds et al.,
 1595 2006). As *Karlodinium* is a small unarmored dinoflagellate similar to *Pfiesteria*, multiple fish
 1596 kills attributed to the latter from 1991-1996 in North Carolina (Burkholder and Marshall, 2012)
 1597 are listed in HAEDAT as *Karlodinium*. HAEDAT has eight fish mortality events attributed to
 1598 *Karlodinium*, but some fish kills that were reported in the 1990s as *Pfiesteria* are not in the
 1599 database. *Karlodinium* has been reported killing diverse species of estuarine fish in mid-Atlantic

1600 coastal waters: Chesapeake Bay rivers and tributaries, aquaculture facilities in Maryland, the
 1601 Neuse and Pamlico Rivers, North Carolina, and in brackish retention ponds in South Carolina
 1602 (Deeds et al., 2002, 2006; Kempton et al., 2002; Goshorn et al., 2004), with increasing blooms of
 1603 *K. veneficum* and sporadic fish kills since the mid-2000s in the Chesapeake Bay (Wolny et al.,
 1604 2020). Not all events are in HAEDAT.

1605 Periodically, other HAB species are occasionally associated with a fish kill. In some cases,
 1606 toxicity is suspected but not known or kills are attributed to poor water quality because most
 1607 algal species at high biomass have the potential to be associated with low dissolved oxygen.
 1608 Examples of diverse fish kills in HAEDAT are from the dinoflagellates *Prorocentrum micans*
 1609 causing a fish kill in New Jersey in 1968, *P. minimum* and fish kills in Louisiana in 2001 and the
 1610 Potomac River, Chesapeake Bay in June 2016, *Katodinium rotundatum* fish and shellfish kills in
 1611 New Jersey in 1993 and 2000, and *Levanderina fissa* associated with fish and crab die-off in
 1612 Colonial Beach, Virginia in 2019.

1613 Diatom blooms, mostly in the Pacific Northwest, have been attributed to fish kills, both
 1614 natural and in aquaculture net pens. Usually intense blooms of *Chaetoceros*, *Skeletonema*, and
 1615 *Rhizosolenia* with morphological structures such as spines and setae can clog fish gills, causing
 1616 mechanical irritation, and puncturing of the surface gill lamellae can lead to secondary bacterial
 1617 infections. Fish trapped in the confines of net pens can succumb fairly quickly if the pens are not
 1618 moved (Landsberg, 2002). A mixed bloom of *Ceratium* spp., *Thalassiosira*, and *Nitzschia* sp. in
 1619 Kodiak Island, Alaska in September 2000 was reported to HAEDAT and associated with

1620 mortalities of flounder, dolly varden, and sea lance. Fish kills involving a mixed algal bloom of
 1621 *Skeletonema costatum*, *Thalassiosira gravida*, *T. nordenskioeldii*, *Cerataulina pelagica*,
 1622 *Rhizosolenia delicatula*, *Olisthodiscus luteus*, *Katodinium rotundatum*, *Prorocentrum* spp., and
 1623 *Eutreptia lanowii* in Raritan and Sandy Hook bays, New Jersey in late May-June and July 1995
 1624 and reported to HAEDAT, were attributed to associated low dissolved oxygen.

1625 Haptophytes, primarily *P. parvum*, are the biggest issue in brackish waters in Texas, with
 1626 occasional reports in other southern states. Only four events are documented in the HAEDAT
 1627 database, with three in Texas (2002, 2003, 2011), and one in Vero Beach, Florida (2004), but
 1628 additional widespread reports have been documented since the first associated fish kill in 1985 in
 1629 the Pecos River, Texas (James and De La Cruz, 1989; Roelke et al., 2016). Multiple toxins or
 1630 bioactive compounds characterized as prymnesins and polyunsaturated fatty acids have been
 1631 implicated in *Prymnesium* “ichthyotoxic” properties. As a low salinity tolerant species, the
 1632 spread of *P. parvum* blooms in inland, south-central U.S. was attributed to drought years and
 1633 increased salinities of various rivers and lakes (Roelke et al., 2016) with enhanced risks from
 1634 water management activities projected to boost the formation of coastal blooms (Lundgren et al.,
 1635 2015).

1636 In the 1970s-1980s, raphidophytes, principally *Heterosigma akashiwo* were associated with
 1637 fish kills, primarily of aquaculture fish (salmonids) in the Pacific Northwest. A kill was also
 1638 associated with *H. akashiwo* in 1994 in Puget Sound (see 4.6.3.1). There are several reports in
 1639 HAEDAT of *Chattonella*-associated fish kills in Virginia (*C. subsalsa*, 2010), New Jersey

1640 (*Chattonella* spp., 2017) and one in Core Sound, North Carolina in 2001. A closely-related
 1641 organism (formerly reported as *Chattonella* cf. *verruculosa*) was involved in ten fish mortality
 1642 events, killing over a million fish, primarily menhaden, in Rehoboth Bay, Delaware in 2000
 1643 (Bourdelaïs et al., 2002).

1644 In 1984 (Harper and Guillen, 1989), 1994, 2003, and 2007 (HAEDAT), blooms of the
 1645 dinoflagellate *Akashiwo sanguinea* (formerly *Gymnodinium sanguineum*) were occasionally
 1646 associated with fish kills in the Gulf of Mexico and attributed to consequential poor water
 1647 quality. In 2007, during a large-scale bloom, some 14 seabird species were killed in Monterey
 1648 Bay, California, demonstrating for the first time that at high biomass, *A. sanguinea* could
 1649 produce vast quantities of proteinaceous foam. The biosurfactant foam coated the birds' feathers
 1650 and affected their natural water repellency and insulation. Being unable to maintain body
 1651 temperature and forage, seabirds such as Pacific loons, *Gavia pacifica*, red-throated loons, *G.*
 1652 *stellata*, Clark's grebes, *Aechmophorus clarkii*, and western grebes, *A. occidentalis*, became
 1653 hypothermic and emaciated. Of 550 birds stranded alive, almost half were northern fulmar,
 1654 *Fulmarus glacialis* (Jessup et al., 2009). In the fall of 2009, another unusual *A. sanguinea* bloom
 1655 further north along the U.S. Pacific Northwest coast (Du et al., 2011; White et al., 2014),
 1656 affected several hundred loons, *Gavia immer*, common murre, *Uria aalge*, Pacific loons, red-
 1657 throated loons, surf scoters, *Melanitta perspicillata*, and western and Clark's grebes causing a
 1658 widescale dieoff (Phillips et al., 2011).

4.6.6 *Cyanobacteria*

While harmful cyanobacterial blooms (CHABs) have been reported in the scientific literature for more than 130 years (Francis, 1878), in recent decades, the incidence, intensity, and impacts of these blooms has increased in freshwater and marine systems (Hudnell, 2008; Paerl and Huisman, 2008; O'Neill et al., 2012). CHABs most commonly occur in water bodies that experience accelerated nutrient loading and can be promoted by elevated temperatures (O'Neill et al., 2012). Every state in the U.S. experiences CHABs, and while these blooms can be harmful by causing hypoxia, turbidity, and general ecosystem disruption, they also represent a serious human and animal health threat via their synthesis of hepatotoxins (microcystin, nodularin, cylindrospermopsin) and neurotoxins (anatoxin-a, saxitoxin; Paerl et al., 2001).

Beyond the effects of CHABs and their toxins within freshwater bodies across the U.S., there is now clear evidence that these toxins can become persistent contaminants when advected into estuarine and coastal ecosystems. Many CHAB events occur in close proximity to the land-sea interface on all coasts of the U.S. Miller et al. (2010) provided the first evidence of microcystins from land contaminating a marine ecosystem - specifically Monterey Bay, California. In this case, microcystins from rivers and lakes were flushed into Monterey Bay and accumulated in bivalves that were subsequently consumed by sea otters that died due to acute liver necrosis. Beyond identifying a novel source of marine mammal mortality, this study also revealed a striking potential human health threat, namely the bioaccumulation of microcystin in filter-feeding bivalves (as well as in secondary consumers including crabs and snails). Miller et

al. (2010) demonstrated that bivalves can concentrate microcystin from the water column more than 100-fold and that it takes weeks for contaminated bivalves to depurate themselves of that toxin, emphasizing the likely widespread nature of this scenario.

While this initial study identified a novel mechanism by which marine bivalves and marine mammals are exposed to harmful freshwater biotoxins, this finding was not necessarily a surprise. *Microcystis*, the most common CHAB in the U.S., is tolerant of brackish waters with most strains persisting at salinities between 10 and 15 (Preece et al., 2017), meaning that *Microcystis* cells can be expected to survive in brackish environments where many bivalves such as oysters thrive. Furthermore, senescent or dead intact cells are still toxic. This has been obvious in places like the Saint Lucie River Estuary where Florida has declared states of emergency in 2016 and 2018 when massive *Microcystis* blooms originating from Lake Okeechobee were flushed into estuarine regions with salinities up to 30 (Kramer et al., 2018). In addition, microcystins can be stable and persistent in saltwater and freshwater habitats (Harke et al., 2016). Moreover, while microcystin can be degraded by physical processes (Tsuji et al., 1994) or microbially (Rohrlack and Hyenstrand, 2007), 90% of microcystin is typically found within cells where the toxin is significantly more stable (Harke et al., 2016). Finally, the primary exposure route of HAB toxins to humans is via bivalves, yielding well-known syndromes such as PSP, ASP, etc. (Shumway, 1990). While the poisoning of humans from shellfish contaminated with microcystin has yet to be documented (hepatotoxic shellfish poisoning; HSP), evidence that has emerged since the Miller et al. (2010) study suggests such occurrences are likely common, but unreported.

Studies since Miller et al. (2010) have both affirmed the findings of that initial study and have demonstrated that filter-feeding bivalves on U.S. West and East Coasts regularly accumulate high levels of microcystin. Gobble and Kudela (2014) demonstrated that microcystins in and around Monterey Bay were widespread and found at moderate levels throughout the year and throughout the region. Across all of San Francisco Bay, microcystins were found to be chronically present in SPATT (solid phase absorptive toxin trackers) samplers over a five-year period and were also detected in mussel samples from sites across the entire bay, during all months (Peacock et al., 2018). One quarter of the mussels tested in this study exceeded the California Office of Environmental Health and Hazard Assessment guideline level to protect human health ($10 \mu\text{g kg}^{-1}$; Peacock et al., 2018). Further north, in Puget Sound, Preece et al., (2015) reported that mussels contained 2–15 $\mu\text{g microcystin kg}^{-1}$. Bukaveckas et al. (2018) recently reported on the accumulation of microcystin in shellfish in the oligohaline region of the James River, Virginia (>50 km from freshwater) to levels exceeding 100 $\mu\text{g microcystin kg tissue}^{-1}$ or an order of magnitude beyond the California guidance value. Similarly, Garcia et al. (2010) reported on blue crabs within the Barataria Estuary system (Louisiana) with > 100 $\mu\text{g microcystin kg}^{-1}$ in muscle and up to 820 $\mu\text{g microcystin kg tissue}^{-1}$ in the hepatopancreas. These observations demonstrate that the accumulation of microcystins and other CHAB toxins in shellfish is a phenomenon not isolated to California but rather represents an emerging human health threat across the U.S. that is poorly understood. Given the commonality of CHABs in water bodies that discharge into marine environments, the transport and accumulation of CHAB toxins in marine food webs may be a common occurrence.

5 Conclusions

The foregoing emphasizes that U.S. HABs are diverse phenomena involving multiple species and classes of algae that occupy a range of habitats and produce numerous toxins or bioactive compounds that impact a wide range of resources. This enormous diversity greatly complicates efforts to identify trends in bloom incidence, as some toxins (e.g., PSTs, NSTs) have been monitored on a routine basis for many years while others (e.g., ASTs, DSTs) have only emerged as threats in recent times, so monitoring efforts and entries in HAEDAT are less consistent and have a shorter history. The U.S. is also a large country with three major oceanic coastlines having very different plankton communities, hydrography, and habitats. Furthermore, many HAB species that do not threaten public health but that still cause harm (e.g., *M. polykrikoides*, *H. akashiwo*, *K. mikimotoi*) are not monitored on a routine basis, so events can be missed and are only entered into databases like HAEDAT on a sporadic basis. This is equally true for records of wildlife mortalities which also tend to be reported sporadically.

5.1 Trends for individual toxin families or HAB species

In the search for national trends and given these caveats, it is perhaps most meaningful to examine toxin families and individual HAB species and classes separately and to look for trends within each, as has been the focus throughout this review. The findings for these categories can be summarized as follows.

PSTs. PSTs are the most widespread of all HAB poisoning syndrome toxins in the U.S., affecting large areas of the East and West Coasts as well as small parts of Florida with annually

1741 recurrent blooms. Statistically, there is no significant national trend in PST incidence over the
1742 last 30 years, though there has been some geographic expansion of toxicity, such as with the
1743 emergence of *P. bahamense* in Florida and of *A. catenella* on Long Island, in Puget Sound, and
1744 in northern areas of Alaska, with major expansion events occurring in the western Gulf of Maine
1745 and in Puget Sound before the HAEDAT time series began. PSTs currently represent a sustained
1746 and persistent annual threat to U.S. coastlines in terms of the number of events, with individual
1747 blooms and years varying dramatically in scale and impact. At this time, the only suggestion of
1748 a link between changing PST distributions or dynamics in the U.S. and climate change is the
1749 apparent expansion of toxicity in the Bering and Chukchi Seas, though the latter is based on
1750 research cruises and is not yet evident in HAEDAT because of the lack of routine PST
1751 monitoring in that remote region. Theoretically, warming temperatures may lead to increases in
1752 the timing and severity of PST events in that region going forward, while the balance between
1753 localized estuarine blooms and those in deeper coastal waters may shift in other areas of the U.S.

1754 **ASTs.** ASTs are a relatively recent HAB problem in the US that can impact both humans and
1755 marine wildlife. The number and magnitude of AST events has been on the rise in the U.S. since
1756 the first reports in California in 1991 though there is strong evidence that the causative
1757 organisms were present on that coast decades before the discovery of domoic acid as the ASP
1758 toxin. The first events in the Gulf of Mexico were recorded in 2014 and in the Gulf of Maine in
1759 2016, the latter representing the apparent dispersal of highly toxic *P. australis* into this region for
1760 the first time. The national pattern is one of relatively frequent outbreaks on the US West Coast
1761 and emerging, recurring outbreaks on the East Coast, with sporadic incidents in the Gulf. The

1762 ability of *P. australis*, and perhaps other *Pseudo-nitzschia* species to survive in warmer, nutrient-
1763 depleted waters suggests that ASTs will likely be a persistent, recurrent problem in the future,
1764 warmer ocean.

1765 **DSTs.** HAEDAT entries for DST events in the U.S. begin in 2008, with no significant trend
1766 through time since then. The records provide evidence that the causative organism, *Dinophysis*
1767 spp. is now established on all three coasts. Comparison with the literature suggests an
1768 underreporting of DST events in HAEDAT and it is unclear if this problem will continue into the
1769 future, though reporting should improve as *Dinophysis* spp. enumeration and DST quantification
1770 are further incorporated into state and tribal monitoring programs. DST-related illnesses may
1771 remain inconspicuous, however, due to overlapping symptoms with other human diseases and
1772 unknown symptoms in wildlife. Not enough information is available to make conclusions
1773 regarding the drivers of DST events or predict trends with climate change or eutrophication.
1774 Field investigations into the drivers of DST events along all three U.S. coastlines are needed.

1775 **NSTs.** Like PSTs, there is a long historical record of NST events yet no significant trend was
1776 observed over the past 30 years. Instead, remarkably similar patterns were found in areas where
1777 events have recurred. The lack of a clear trend is at least partly due to sporadic severe events—
1778 which can last for multiple years—that are interspersed with less severe events. Incidents are
1779 documented nearly annually in the eastern Gulf of Mexico and can span international borders in
1780 the western Gulf. Ocean circulation appears to be a major driver of the recurring *K. brevis*
1781 blooms in the Gulf of Mexico and is important for bloom severity on event to interannual time

1782 scales (Stumpf et al., 2008). Culture and field studies that highlight the broad ecology of *K.*
1783 *brevis* suggest that this species may continue to thrive under future ocean conditions, however,
1784 changes in ocean circulation and storm frequency and intensity are likely to have impacts on
1785 bloom dynamics and distribution.

1786 **CTXs.** Due to a lack of monitoring programs for *Gambierdiscus* and CTXs as well as under-
1787 reporting of cases, data on these events are not available to establish time series trends.
1788 Epidemiological data have indicated possible declines at some locations (e.g., Florida, USVI),
1789 but these studies also identified significant underreporting and potential biases in current
1790 surveillance systems. Additional data-driven estimates of underreporting are needed to more
1791 accurately determine prevalence and impact of CTXs. Geographic expansion of *Gambierdiscus*
1792 spp. into temperate and non-endemic areas (e.g., northern Gulf of Mexico) appears to be
1793 occurring, fostered by ocean warming, and human health impacts from CTXs are expected to
1794 increase as this range expansion continues.

1795 **Wildlife toxicoses.** HAB-related marine wildlife morbidity and mortality events appear to be
1796 growing in number, with statistically significant increasing trends observed in marine mammal
1797 poisonings caused by domoic acid (ASTs) along the coast of California and brevetoxins (NSTs)
1798 in Florida. Sustained mortalities of other animals continue in parallel with the incidence of HAB
1799 events nationally, though events are not systematically recorded and reported. Some emerging
1800 HAB toxins (e.g., DSTs) will likely have fish and wildlife and ecosystem impacts, but more data
1801 and research on exposure effects are needed.

1802 **Brown tides.** Brown tides caused by *A. anophagefferens* have ceased to occur in some estuaries
 1803 in the Northeast U.S. (Rhode Island), have continued in other estuaries (New York, New Jersey),
 1804 and have expanded into the mid-Atlantic region (Maryland, Virginia). Brown tides caused by *A.*
 1805 *lagunensis* have regularly recurred in Texas since 1990 and have expanded into lagoons along
 1806 the east coast of Florida this decade. Brown tides caused by *Aureoumbra* are often coincident
 1807 with hypersaline events that are caused by warming and droughts in sub-tropical lagoons of
 1808 Texas and Florida which may be more common today and in the future.

1809 ***Margalefidinium.*** While blooms of this dinoflagellate were noted in the literature in four U.S.
 1810 locations during the twentieth century, there has been a significant expansion in the reported
 1811 occurrences and recurrence of these events in the recent past, now including > 15 previously
 1812 unimpacted estuaries. The unique macroscopic and microscopic nature of these blooms suggest
 1813 these are truly new occurrences in new locations. Eutrophication, ocean warming, and cyst-
 1814 facilitated dispersal may all have contributed to this trend.

1815 ***Heterosigma.*** *Heterosigma akashiwo* occurs in the Gulf of Mexico and on both the East and
 1816 West coasts, though it is considered harmful predominantly on the West Coast due to its effects
 1817 on farmed fish. Lack of routine monitoring and changes in the scale of fish aquaculture
 1818 operations obscure possible trends in national bloom frequency or magnitude.

1819 ***Karenia mikimotoi.*** This species occurs in many parts of the U.S., from Alaska to Maine,
 1820 including the Gulf of Mexico. Lack of routine monitoring prevents the identification of national

or regional trends, nor is there sufficient information on ecophysiology to suggest outcomes in a warming ocean.

Cyanobacteria. Toxic cyanobacterial blooms are widespread across the U.S., often identified in multiple locations in all 50 states. During the past decade, a new threat associated with cyanobacteria has been identified, specifically the ability of freshwater blooms and toxins to be transported to coastal ecosystems where they can accumulate in shellfish and subsequently intoxicate marine mammals or other shellfish consumers. These events are not yet recorded in HAEDAT, so trends cannot be identified. Given the strong link between CHAB events and anthropogenic nutrient increases and warm temperatures, however, the scale of this recently discovered HAB impact has likely expanded in recent years, and is likely to maintain that trend as global warming and global change continue.

5.2 All HABs combined

An effort was also made to identify national trends for all HAB types by combining HAEDAT records for PSTs, ASTs, DSTs, NSTs, marine mammal mortalities, and other HAB events into a single time series (“other” includes *Heterosigma*, *Aureococcus*, *Aureoumbra*, *Chattonella*, *Gymnodinium*, *Margalefidinium*, *Prymnesium*, and *Pyrodinium*). Results are presented in two forms. Fig. 13A shows the number of events through time, and for statistical purposes and trend analysis, Fig. 13B shows the proportion of the U.S. HAEDAT zones that experience one or more of these types of HAB events each year. Both panels reveal similar

patterns, with major interannual variability in events. In some years, the number of marine HAB events is 10 or less nationally, while in other years it is 30+.

Importantly, panel 13B shows a statistically significant increasing trend in the proportion of U.S. HAEDAT zones impacted by HAB events through time ($p < .05$). The U.S. HAB problem has therefore expanded during the study interval; HABs are affecting more regions with more toxins and impacts than was the case decades ago. Part of that expansion simply reflects a better realization of the true or historic scale of the problem, long obscured by inadequate or inconsistent monitoring. For example, two “new” toxins (DSTs and ASTs) emerged within the last several decades, leading to a progressively expanding national monitoring effort and thus to more findings of events in recent years. Prior to the discovery of those toxins in the U.S., there were no records of them and thus no events to tabulate. The absence of event data in the early years of the study does not, however, mean that there were no events. Indeed, the report by Bargu et al. (2012) demonstrating erratic and aggressive behavior of birds in California in 1961 is strong evidence that ASTs were present and causing harm nearly 30 years before domoic acid was documented as a toxin. Likewise, DST events probably did occur prior to 2008, but were not detected for reasons listed in section 4.3.3.

Also contributing to the overall trend in HAB incidence are events caused by the natural- or human-assisted dispersion of HAB species to new regions and the stimulatory effects of factors such as nutrient pollution, aquaculture expansion, and climate change, among others. There are multiple examples of species dispersion, such as the expansion of *A. catenella* and PSTs into

1860 southern New England, throughout Long Island, and within Puget Sound – all likely due to
1861 natural dispersion and subsequent colonization of the species via its encysted stage. Another
1862 example would be the identification of *P. australis* in the Gulf of Maine after decades of
1863 negative monitoring results for that species (Bates et al., 2019). Others would be the emergence
1864 of ciguatera dinoflagellates in the northern Gulf of Mexico or range expansions of non-toxic
1865 HABs like *Aureoumbra* and *Margalefidinium* along the U.S. East Coast in recent years.

1866 In terms of nutrient pollution-driven expansion, Anderson et al. (2008) examined U.S.
1867 HABs on a regional basis and concluded that most large-scale HABs along open coasts appear to
1868 be unrelated or weakly related to anthropogenic nutrient sources, whereas nutrient pollution is a
1869 much larger, and in some cases, dominant factor in HAB species success in certain estuaries,
1870 embayments, and sounds. The emerging cyanobacterial problem in the freshwater-to-marine
1871 continuum (e.g., Paerl et al., 2018) is one example of nutrient pollution-driven enhancement of
1872 HAB incidence. Another might be the severity of *K. brevis* blooms along the coast of Florida,
1873 though this warrants further examination to understand which of the many potential nutrient
1874 sources are utilized in the development and maintenance of massive but also spatiotemporally
1875 patchy blooms (Vargo et al., 2008, Heil et al. 2014).

1876 The role of climate or global warming-driven expansion is equally uneven, with some
1877 regions (e.g., the Alaskan Arctic and the northern Gulf of Mexico) showing signs of temperature
1878 increases that are supportive of HAB species expansion into or within the region, whereas such
1879 inferences are not yet as evident in other regions. Environmental influences on HABs are

1880 complex and not all species will become more problematic as the climate warms (Hallegraeff
1881 2010; Wells et al., 2015). For example, some species will thrive more than others as waters
1882 warm, while others may shift their geographic ranges (Kibler et al., 2015; Gobler et al., 2017).
1883 Recent extreme weather events, such as the 2015 marine heatwave on the U.S. West Coast and
1884 the subsequent widespread *Pseudo-nitzschia* bloom (McCabe et al., 2016) or the warm winter of
1885 2012 on the East Coast and its effect on *Alexandrium* blooms (Ralston et al., 2014) have
1886 provided insights into potential future responses by HABs to climate change, summarized by
1887 Wells et al. (2015).

1888 Note that the statistical approach using the proportion of zones with HAB events will reveal
1889 changes in event frequency and geographic range of HAB species, but says nothing about
1890 changes in the severity or duration of those events. This type of information is available in
1891 HAEDAT and other data sources and could be examined for trends in subsequent studies, as in
1892 the HAB Index approach of Anderson et al., (2014).

1893 One result of the multifaceted expansion documented here is that many regions of the U.S.
1894 face a daunting diversity of species and toxins compared to the past. This multiplicity presents a
1895 significant and growing challenge to resource managers and public health officials in terms of
1896 toxins, regions, and time intervals to monitor, necessitating new approaches to monitoring and
1897 management. Many programs have evolved to include both phytoplankton monitoring and flesh
1898 testing for HAB toxins, the former often used as a screening method to identify locations and
1899 times to implement the more time consuming and expensive targeted toxin analysis. The

1900 development of powerful sensors capable of detecting and quantifying HAB cells and toxins in
 1901 situ is a rapidly developing area that shows promise to expand the frequency, extent, and
 1902 efficiency of monitoring.

1903 Mobilization of funding and resources for research, monitoring and management of HABs
 1904 requires accurate information on the scale and nature of the national problem. As shown here,
 1905 HAEDAT and other databases can be of great value in this regard, but efforts are needed to
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1939

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Figure 1



Figure 2

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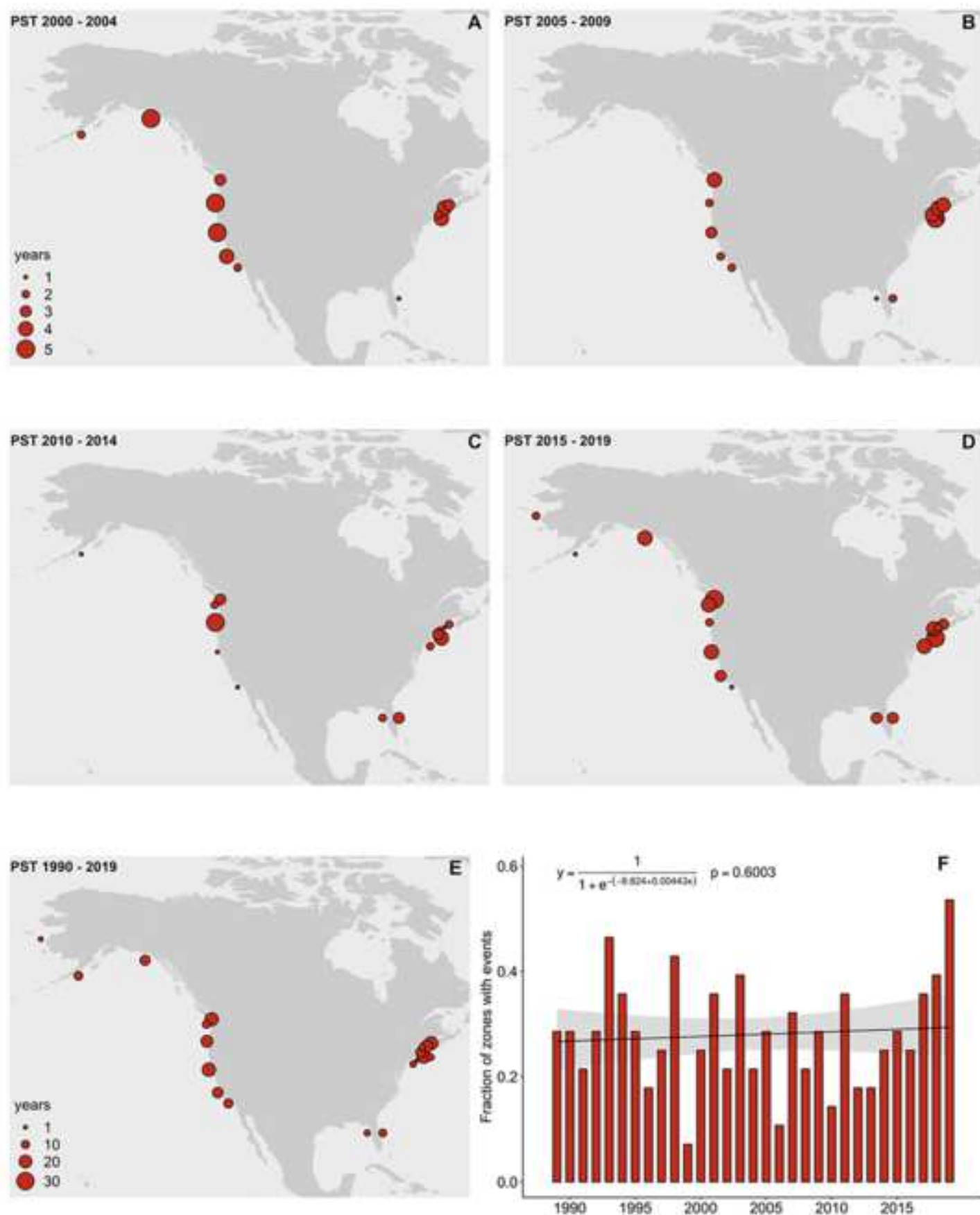


Figure 3

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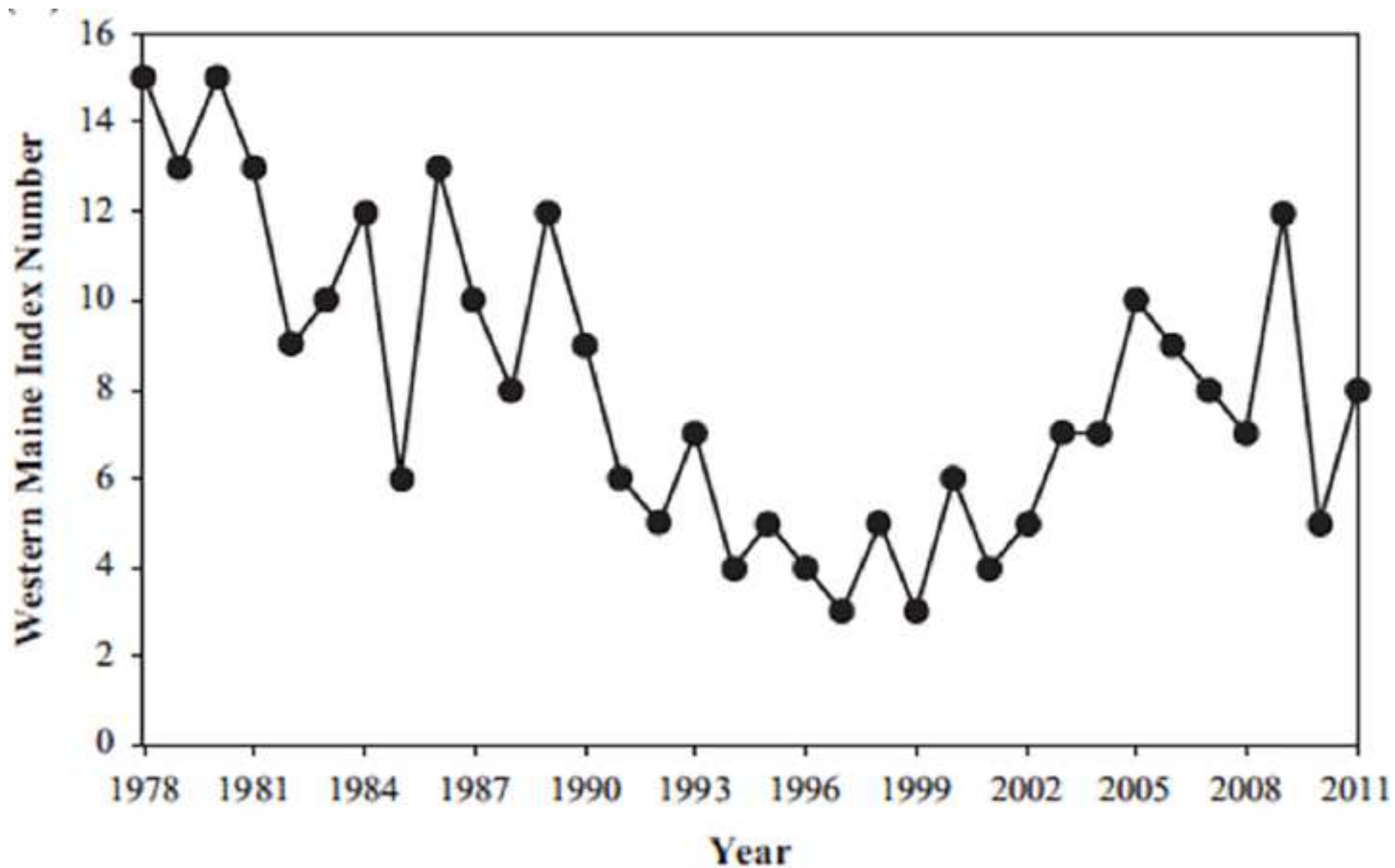


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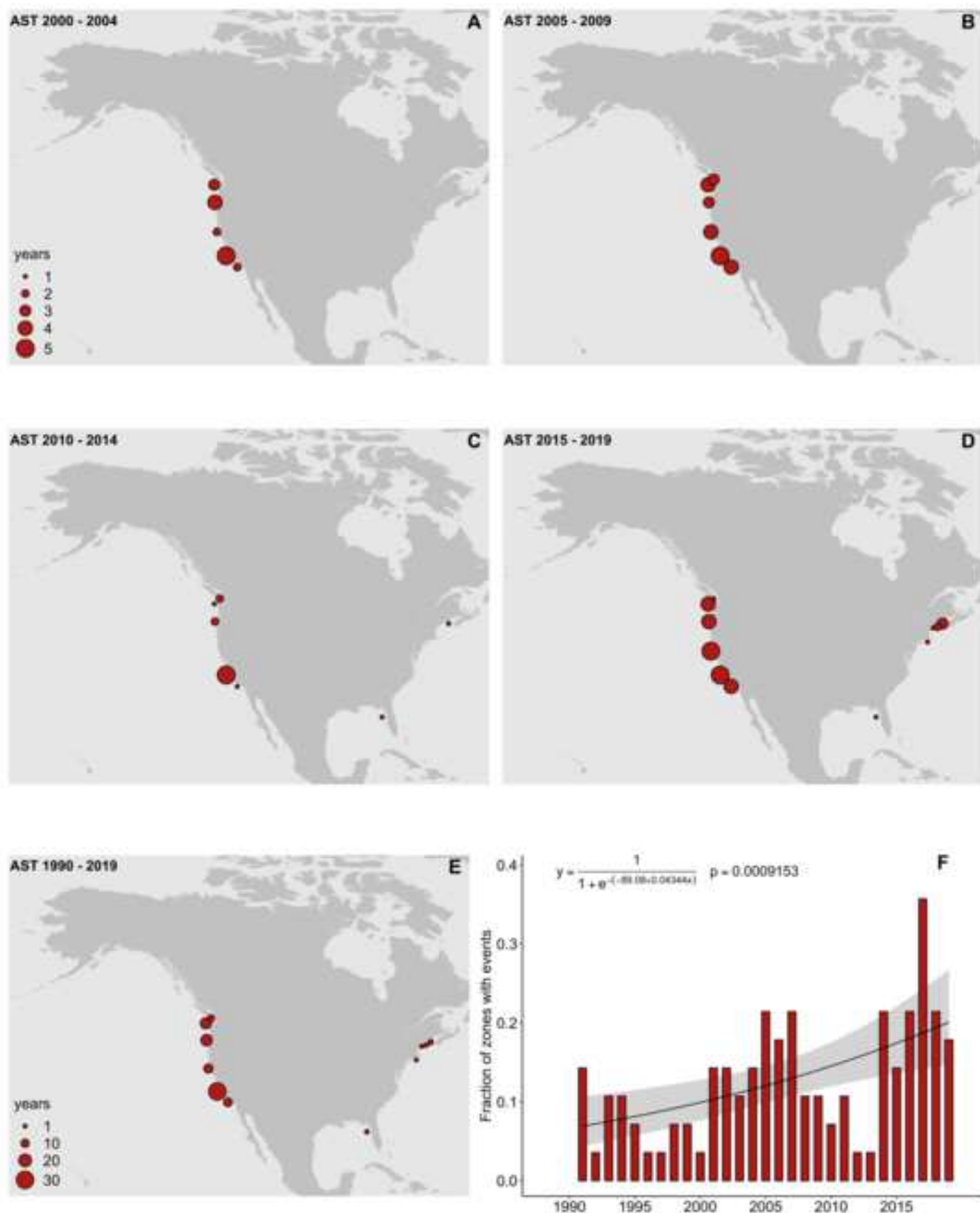


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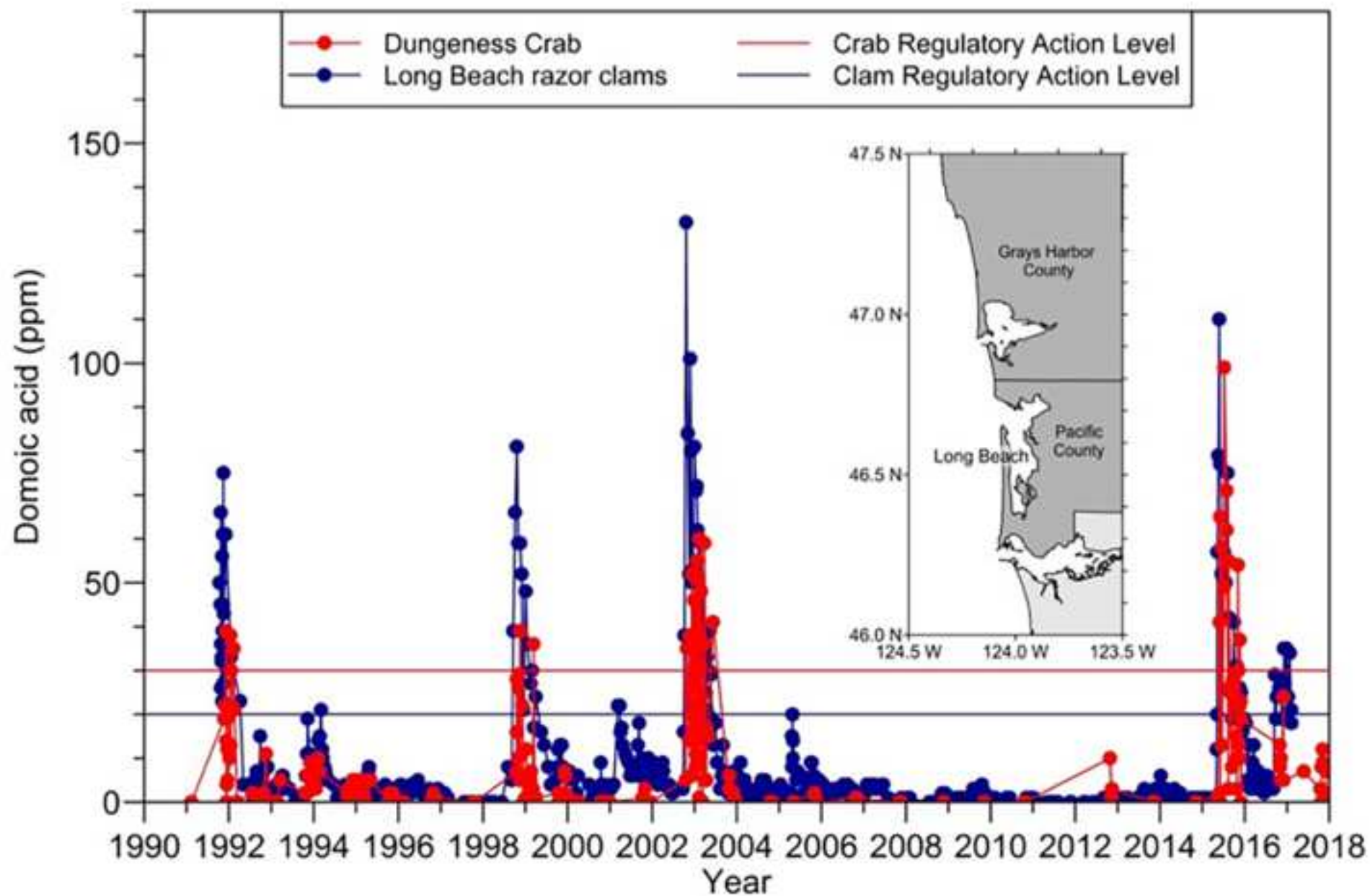


Figure 6

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Figure 7

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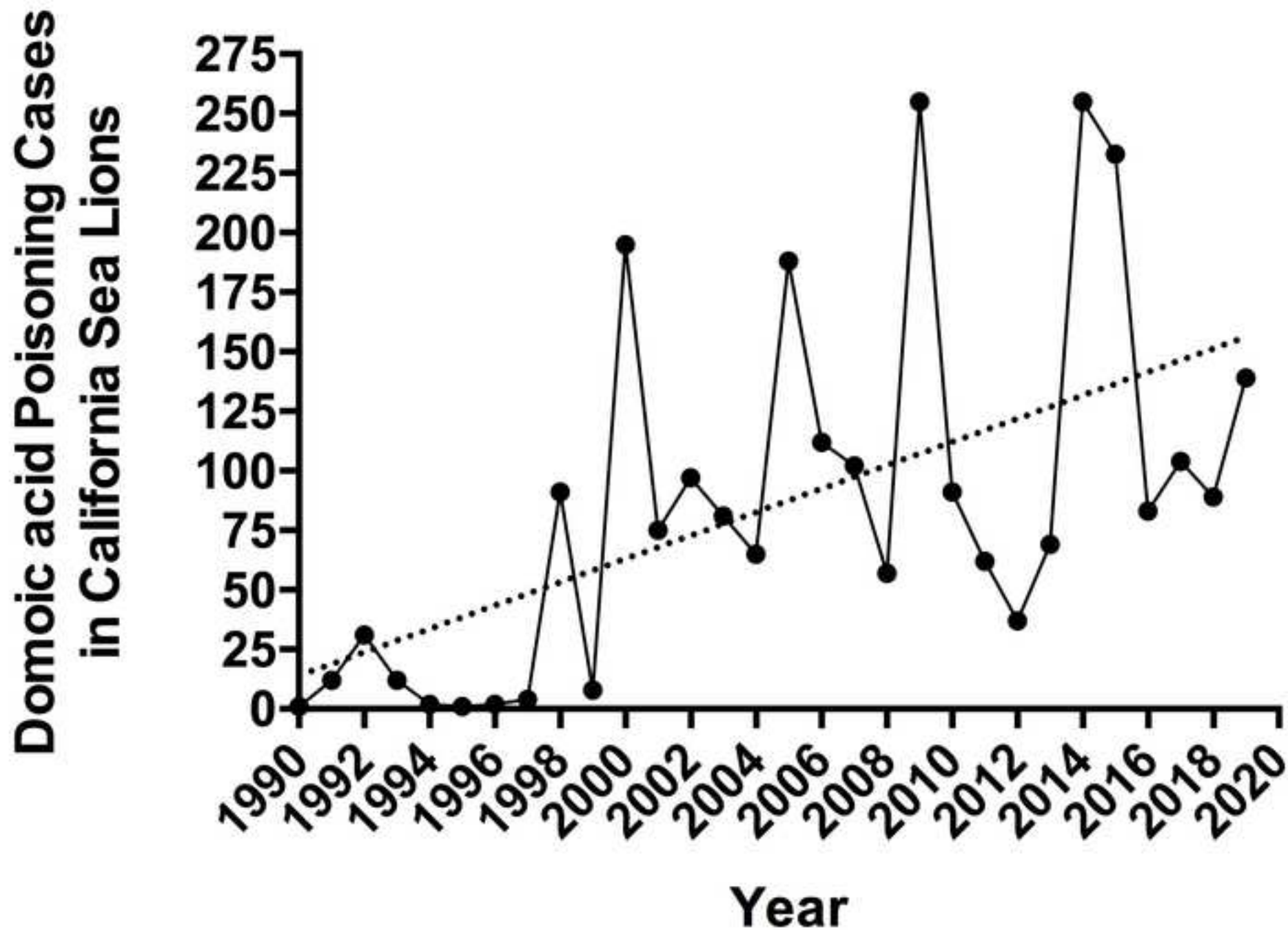


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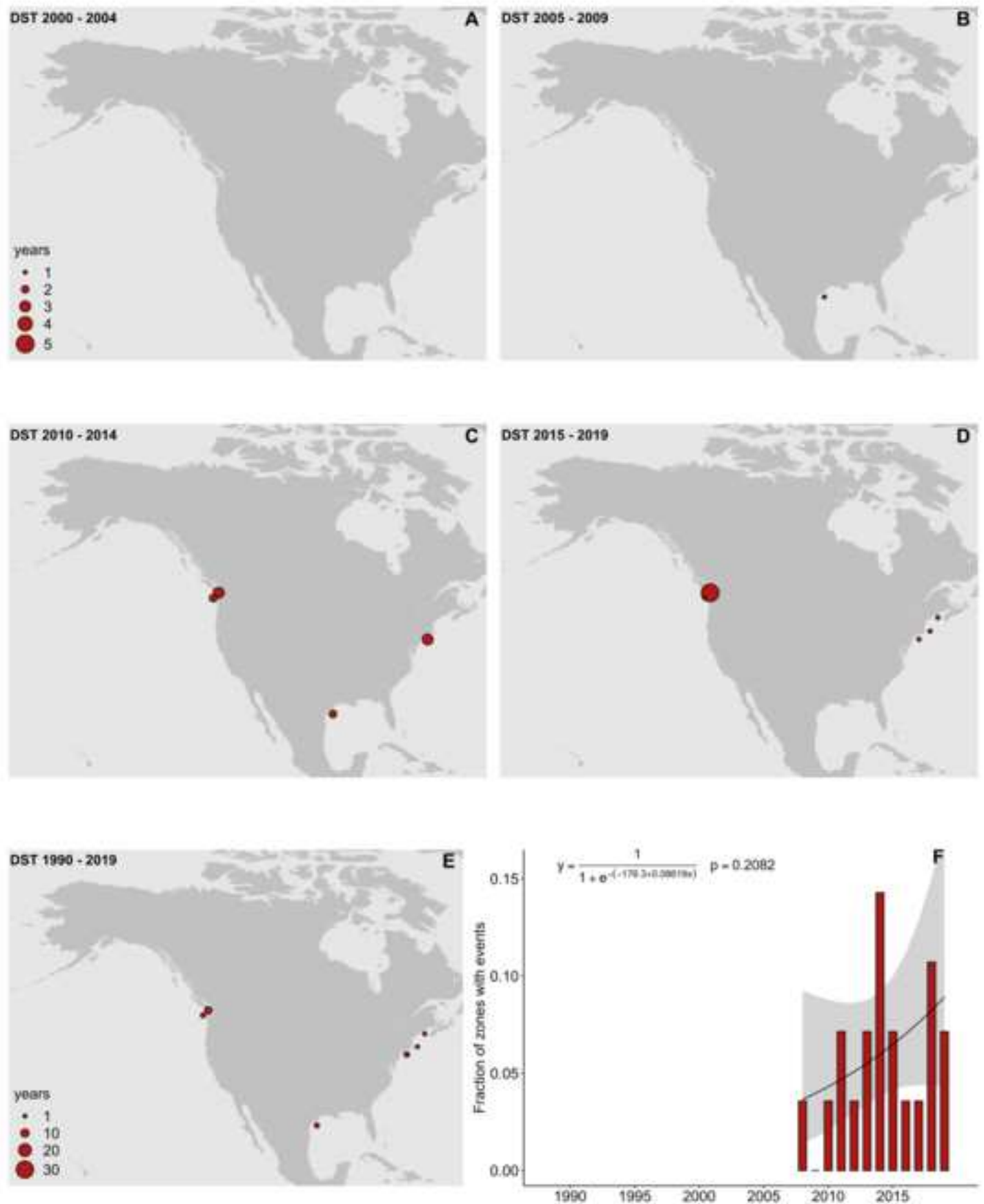


Figure 9

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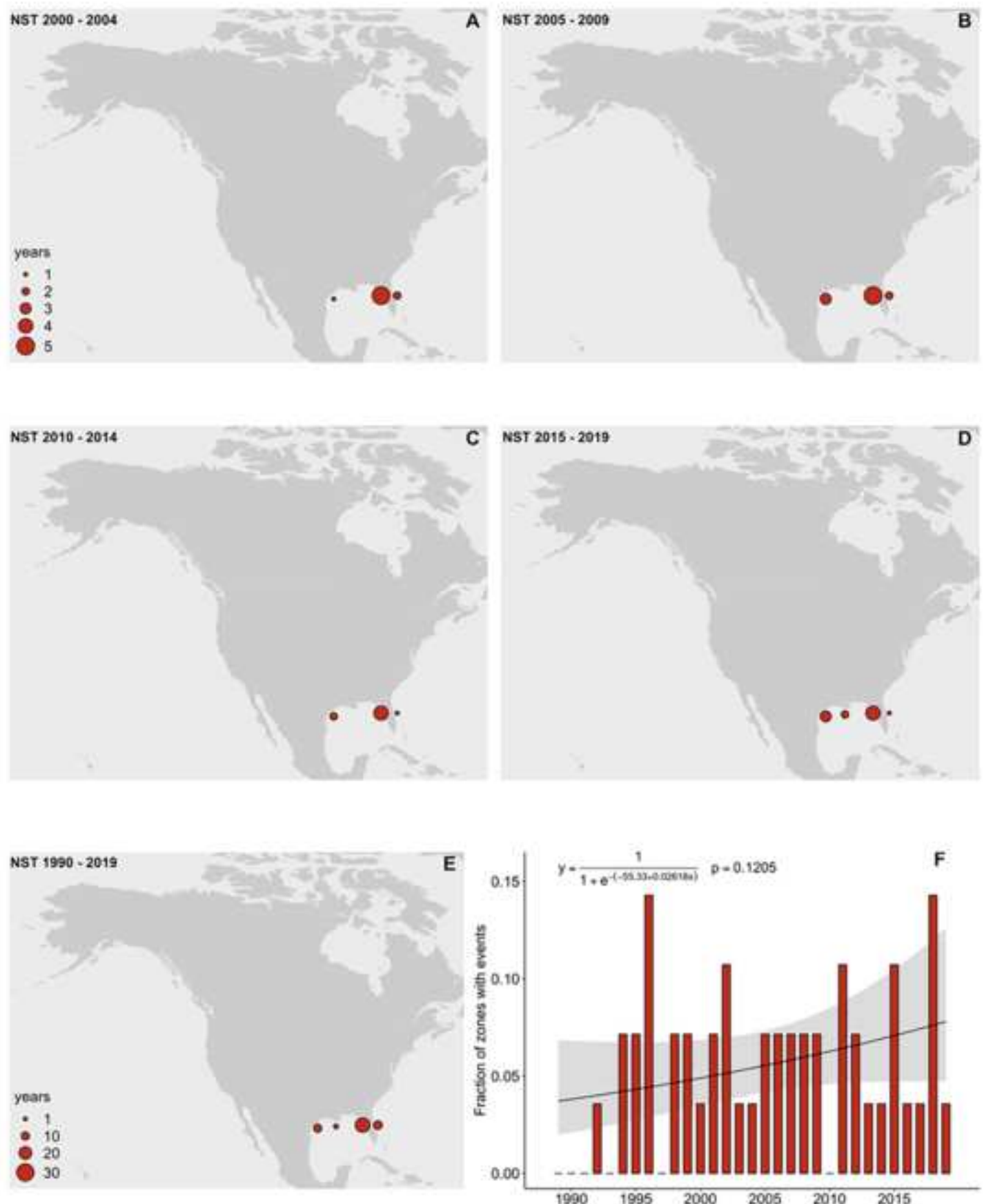
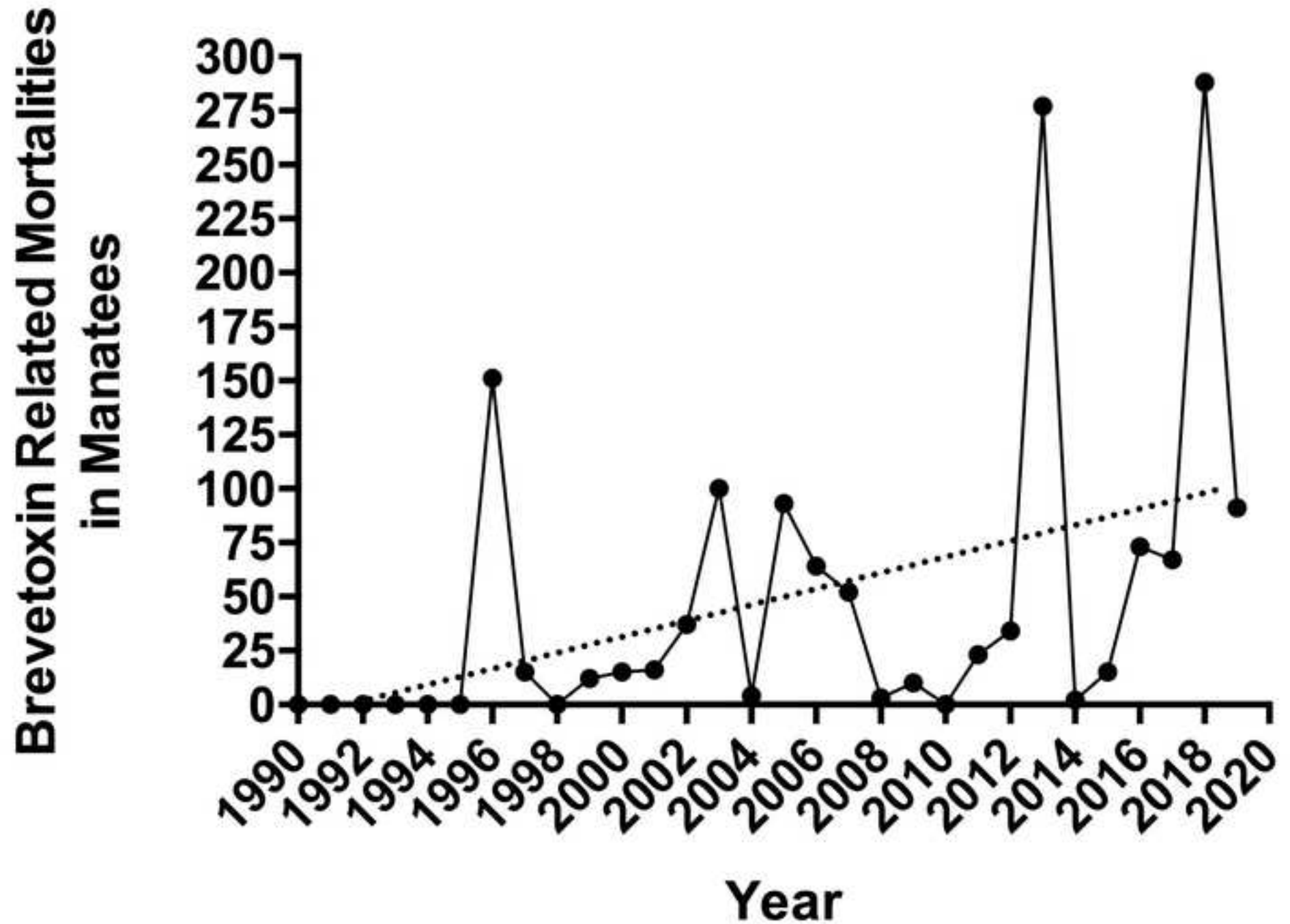


Figure 10



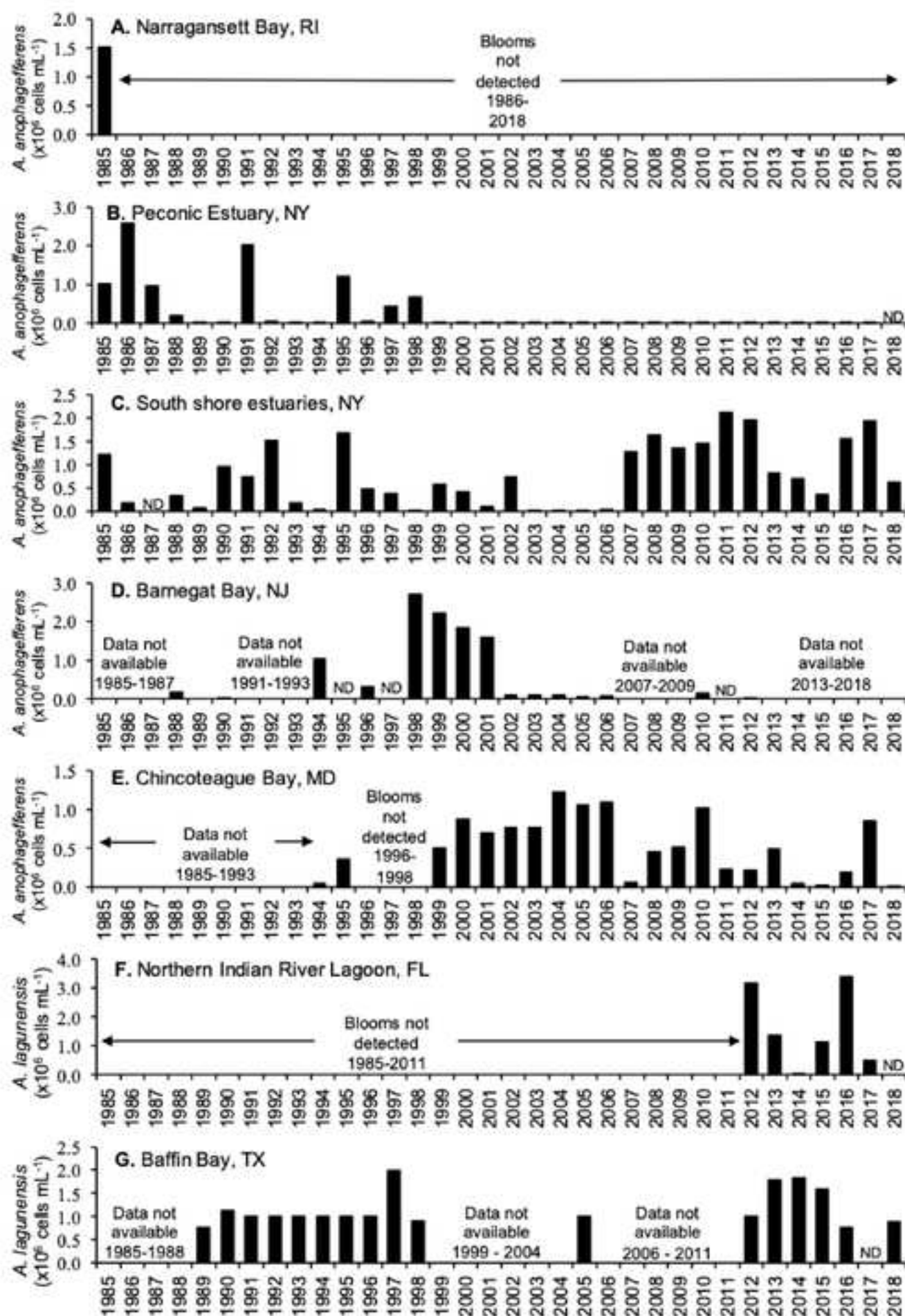


Figure 12

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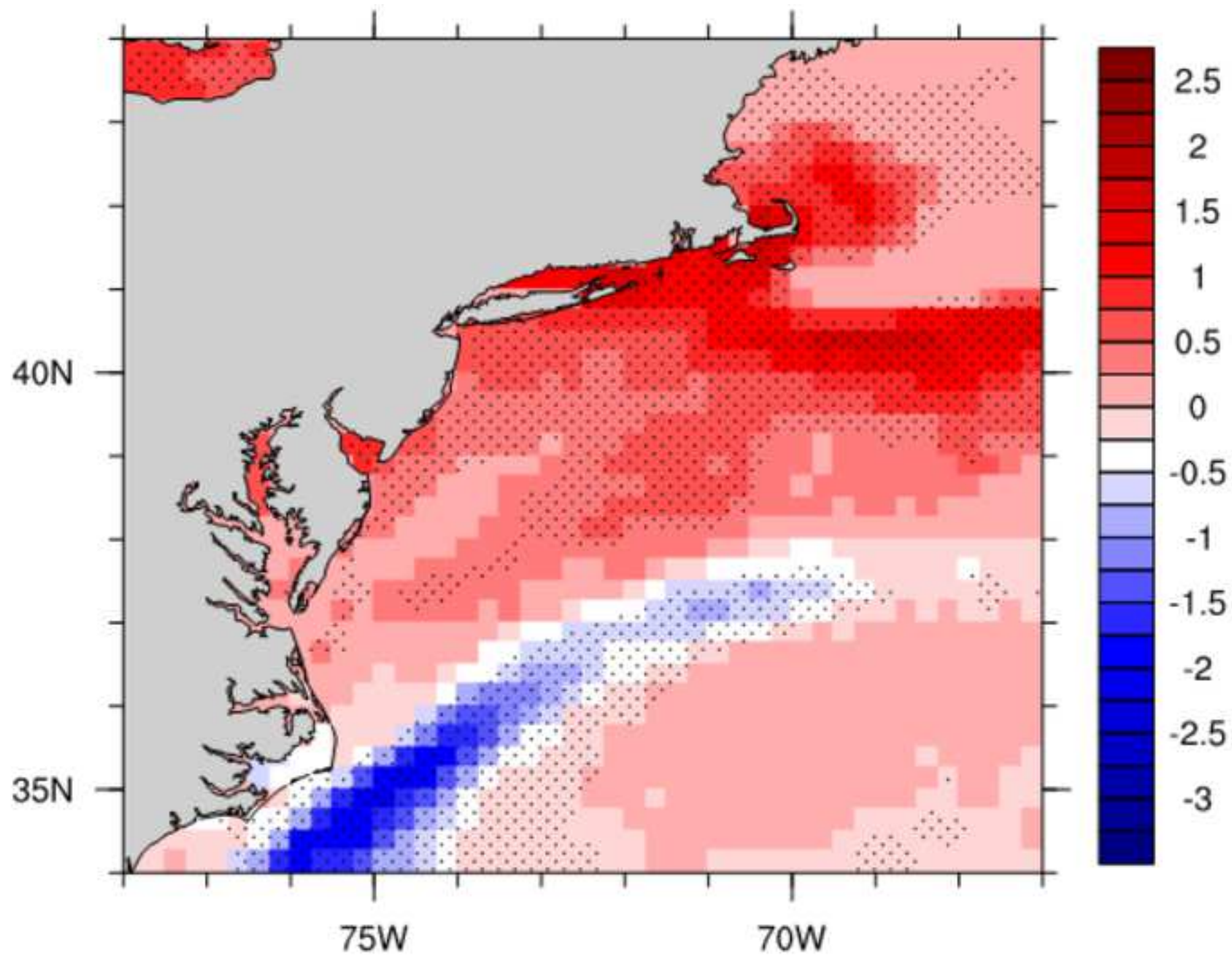


Figure 13

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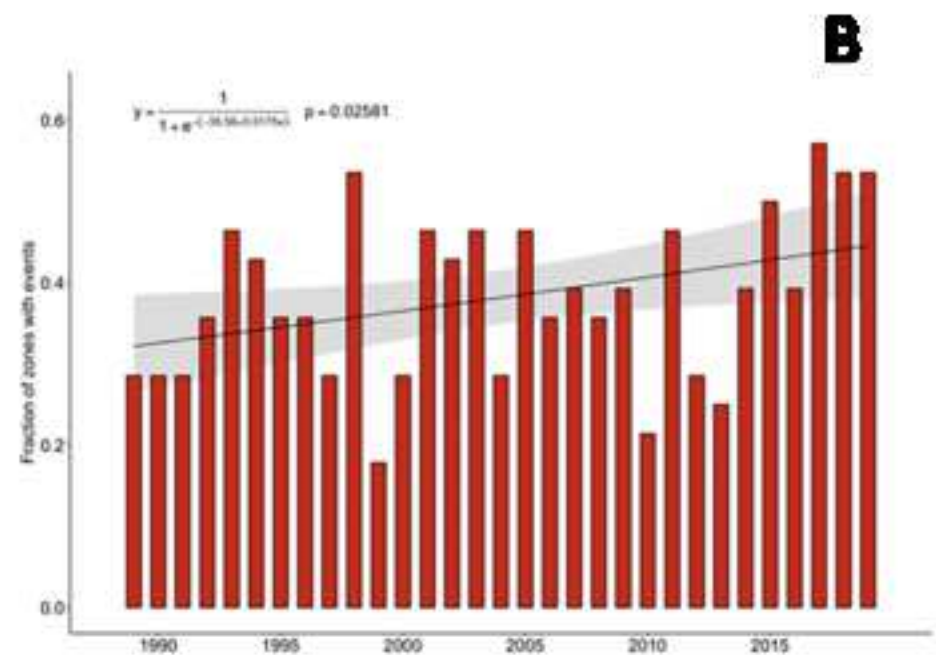
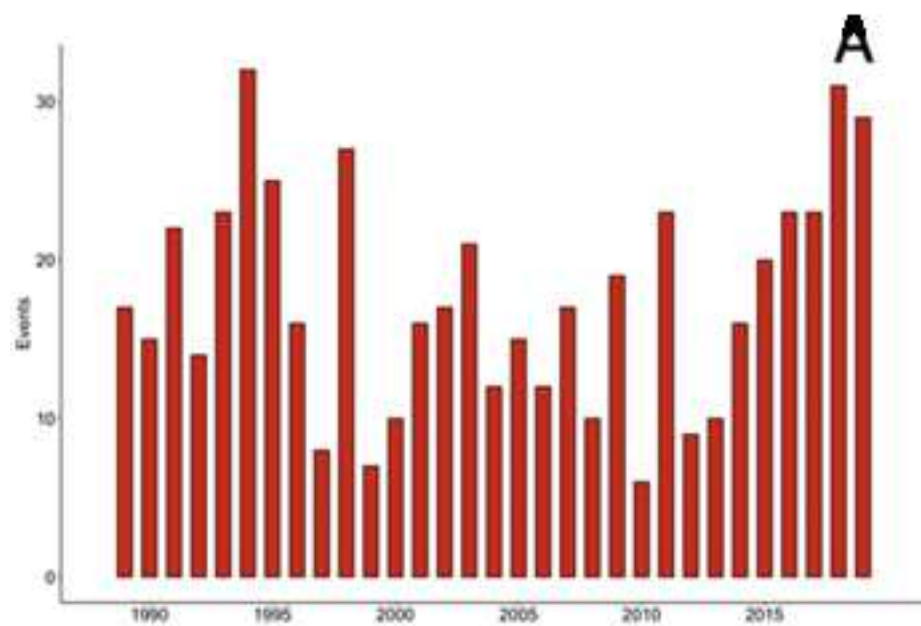


Figure Legends

Fig. 1. U.S. map showing HAEDAT zones. Some locations discussed in the text are also indicated.

Fig. 2. The frequency of PST events (defined as at least one closure in a defined region or HAEDAT zone in a given year) in the U.S. derived from HAEDAT. Data include events linked to either *A. catenella* or *P. bahamense*. A-D, five-year frequencies, with the size of the circle denoting the number of events during that interval; E, PST frequencies (events per year) for the entire U.S. over the 30-year study interval (1990 – 2019); F, time series of observed (bars) and modeled (line) proportions of monitoring zones with at least one event. Also reported is the fitted linear logistic model and its non-significant p value ($p > .05$).

Fig. 3. The HAB Index for western Maine. This metric combines multiple measures of PST toxicity to provide a single value that is indicative of overall severity for each year. Modified from Anderson et al., 2014.

Fig. 4. The frequency of AST events in the U.S. derived from HAEDAT. A-D, five-year frequencies, with the size of the circle denoting the number of events during that interval; E, AST frequencies (events per year) for the entire U.S. (1991 – 2019); F, time series of observed (bars) and modeled (line) proportions of HAEDAT monitoring zones with at least one event. Also reported is the fitted linear logistic model and its significant p value ($p < .05$).

Fig. 5. Time series of AST in Dungeness crab (red) and razor clams (blue) near Long Beach, WA. Monthly razor clam DA at Long Beach provides a 1-2 week early warning of Dungeness

crab DA. The crab and clam regulatory limits are shown with red and blue horizontal lines respectively. Source: Washington State Department of Health.

Fig. 6. Locations where algal toxins were detected in stranded (s) and harvested (h) marine mammals between 2004 and 2013. Red images represent species positive for domoic acid (DA) and purple images represent species positive for saxitoxin (STX). Many species contained both toxins confirming co-exposure. The 13 species that were sampled are listed on the side of the figure in gray (Source: Lefebvre et al., 2016).

Fig. 7. Increasing trend in cases of California sea lions diagnosed with domoic acid poisoning as recorded at the Marine Mammal Center in Sausalito CA. Dotted line shows the significant regression ($p < .05$).

Fig. 8 The frequency of DST events in the U.S. derived from HAEDAT. A-D, five-year frequencies, with the size of the circle denoting the number of events during that interval; E, DST frequencies (events per year) for 2008 – 2019; F, time series of observed (bars) and modeled (line) proportions of HAEDAT monitoring zones with at least one event. Also reported is the fitted linear logistic model and its non-significant p value ($p > .05$).

Fig. 9. The frequency of NST events in the US derived from HAEDAT. A-D, five-year frequencies, with the size of the circle denoting the number of events during that interval; E, DST frequencies (events per year) for the entire US over the 30 years study interval (1990-2019); F, time series of observed (bars) and modeled (line) proportions of HAEDAT monitoring zones with at least one event. Also reported is the fitted linear logistic model and its non-significant p value ($p > .05$)

Fig. 10. NST-related mortality in manatees from 1990-2019. Dotted line shows the significant regression ($p < .05$). (Data from FWC, 2020)

Fig. 11. Yearly maximum concentrations of *Aureococcus anophagefferens* in: **A.** Narragansett Bay (Rhode Island, RI), **B.** Peconic Estuary (New York, NY) **C.** the south shore estuaries (New York, NY), **D.** Barnegat Bay (New Jersey, NJ), and **E.** Chincoteague Bay (Maryland, MD), and *Aureoumbra lagunensis* in **F.** eastern Florida estuaries (FL) and **G.** Baffin Bay (Texas, TX) from 1985 – 2018. ND indicates no detection of brown tide alga. 'Data not available' means no data was collected / no data exists. In cases where there is no bar and no ND or 'data not available', the densities were detectable but low. Data sources for: Rhode Island (Anderson et al., 1993; Sieburth et al., 1988), all New York estuaries (Suffolk County Department of Health Services, 1985-2018; C.J. Gobler, unpublished), New Jersey (Anderson et al., 1993; Bricelj et al., 2017; Mahoney et al., 2003; M.D. Gastrich, unpublished), Maryland (Maryland Department Nuzzi et al., 1996; of Natural Resources, 2009-2018; Trice et al., 2004), Florida (St. Johns River Management District, 2012-2018), and Texas (Buskey et al., 1997, 1999, 2001; Villareal et al., 2004; Wetz et al., 2017; M. Wetz, unpublished).

Fig. 12. Change in the duration of the bloom season (days per year) from 1982 to 2016 for *M. polykrikoides* (American/Malaysian ribotype) along the US East Coast. Stippling (dots) indicates regions where trends were statistically significant ($p < .05$; Mann–Kendall test). Further analytical detail appears in Griffith et al., 2019b.

Fig. 13. Time series of all HAEDAT-recorded marine HAB events in the U.S., including PSTs, ASTs, DSTs, NSTs, marine mammal mortalities, and others (defined above). A) Number of events; B) Observed (bars) and modeled (line) proportions of U.S. HAEDAT zones with at least

one HAB event. Also reported is the fitted linear logistic model and its significant p value ($p < .05$).

Table 1 Harmful and potentially toxic marine HAB species observed along the East, Gulf, and West Coasts of the United States. E=East, G=Gulf, W=West

Diatoms		<i>Dinophysis acuminata</i>	E,G,W	<i>Ostreopsis siamensis</i>	G
<i>Chaetoceros concavicornis</i>	E,G,W	<i>Dinophysis acuta</i>	E,G,W	<i>Pfiesteria piscicida</i>	E,G
<i>Chaetoceros convolutus</i>	E,G,W	<i>Dinophysis caudata</i>	E,G	<i>Phalacroma mitra</i>	G
<i>Halamphora coffeaeformis</i>	E,G,W	<i>Dinophysis fortii</i>	E,G,W	<i>Phalacroma rotundatum</i>	E,G,W
<i>Pseudo-nitzschia australis</i>	G,W	<i>Dinophysis mitra</i>	G	<i>Pheopolykrikos hartmannii</i>	E,G
<i>Pseudo-nitzschia calliantha</i>	E,G,W	<i>Dinophysis norvegica</i>	E,G,W	<i>Prorocentrum belizeanum</i>	G
<i>Pseudo-nitzschia cuspidata</i>	E,G,W	<i>Dinophysis ovum</i>	E,G	<i>Prorocentrum borbonicum</i>	G
<i>Pseudo-nitzschia delicatissima</i>	E,G,W	<i>Dinophysis sacculus</i>	E,G	<i>Prorocentrum cordatum</i>	G
<i>Pseudo-nitzschia fraudulentata</i>	G,W	<i>Dinophysis tripos</i>	E,G,W	<i>Prorocentrum emarginatum</i>	G
<i>Pseudo-nitzschia galaxiae</i>	G	<i>Fukuyoa ruetzleri</i>	G,E	<i>Prorocentrum faustiae</i>	G
<i>Pseudo-nitzschia multiseriata</i>	E,G,W	<i>Fukuyoa yasumotoi</i>	G	<i>Prorocentrum hoffmannianum</i>	G
<i>Pseudo-nitzschia multistriata</i>	G	<i>Gambierdiscus belizeanus</i>	G	<i>Prorocentrum lima</i>	E,G,W
<i>Pseudo-nitzschia pseudodelicatissima</i>	E,G,W	<i>Gambierdiscus caribaeus</i>	G	<i>Prorocentrum maculosum</i>	G
<i>Pseudo-nitzschia pungens</i>	E,G,W	<i>Gambierdiscus carolinianus</i>	E	<i>Prorocentrum rhathymum</i>	G
<i>Pseudo-nitzschia seriata</i>	E,G,W	<i>Gambierdiscus carpenteri</i>	E	<i>Protoceratium reticulatum</i>	G,W
<i>Pseudo-nitzschia subpacifica</i>	E,W	<i>Gambierdiscus excentricus</i>	G	<i>Pseudopfiesteria shumwayae</i>	E,G
<i>Pseudo-nitzschia turgidula</i>	E,G	<i>Gambierdiscus silvae</i>	G,E	<i>Pyrodinium bahamense</i>	G,W,E
<i>Thalassiosira</i> spp.	E,G,W	<i>Gonyaulax spinifera</i>	E,G,W	<i>Takayama cladochroma</i>	G
Dinoflagellates		<i>Gymnodinium catenatum</i>	G	<i>Takayama pulchella</i>	E
<i>Akashiwo sanguinea</i>	G,W	<i>Heterocapsa circularisquama</i>	G	<i>Takayama tasmanica</i>	E
<i>Alexandrium andersonii</i>	G	<i>Karenia bicuneiformis</i>	G	Pelagophytes	
<i>Alexandrium balechii</i>	G	<i>Karenia brevis</i>	E,G	<i>Aureococcus anophagefferens</i>	E
<i>Alexandrium catenella</i>	E,G,W	<i>Karenia concordia</i>	G	<i>Aureoumbra lagunensis</i>	E,G
<i>Alexandrium minutum</i>	G	<i>Karenia cristata</i>	G	Prymnesiophytes	
<i>Alexandrium monilatum</i>	E,G	<i>Karenia digitata</i>	G	<i>Phaeocystis pouchetii</i>	E,W
<i>Alexandrium ostenfeldii</i>	E,G,W	<i>Karenia mikimotoi</i>	G,W	<i>Prymnesium parvum</i>	E,W
<i>Alexandrium peruvianum</i>	E	<i>Karenia papilionacea</i>	E,G	Raphidophytes	
<i>Alexandrium pseudogonyaulax</i>	G	<i>Karenia selliformis</i>	G	<i>Chattonella antiqua</i>	G
<i>Alexandrium tamiyavanichii</i>	G	<i>Karenia umbella</i>	G	<i>Chattonella marina</i>	G
<i>Amphidinium carterae</i>	E,G,W	<i>Karlodinium armiger</i>	G	<i>Chattonella subsalsa</i>	E,G
<i>Amphidinium gibbosum</i>	G	<i>Karlodinium corsicum</i>	G	<i>Chrysochromulina</i> spp.	E,W
<i>Amphidinium klebsii</i>	E	<i>Karlodinium veneficum</i>	E,G	<i>Fibrocapsa japonica</i>	E,G
<i>Amphidinium operculatum</i>	E	<i>Lingulodinium polyedrum</i>	G,W	<i>Heterosigma akashiwo</i>	E,G,W
<i>Azadinium poporum</i>	G,W	<i>Luciella masanensis</i>	E	<i>Olisthodiscus</i>	E
<i>Blixaea quinquecorne</i>	G	<i>Margalefidinium polykrikoides</i>	E,W	<i>Pseudochattonella verruculosa</i>	E,W
<i>Cochlodinium fulvescens</i>	W	<i>Ostreopsis lenticularis</i>	G	<i>Vicicitus globosus</i>	G
<i>Coolia santacroce</i>	G	<i>Ostreopsis mascarenensis</i>	G		
<i>Coolia tropicalis</i>	G	<i>Ostreopsis ovata</i>	G		

List of Table Captions

Table 1 Harmful and potentially toxic marine HAB species observed along the East, Gulf, and West Coasts of the United States. E=East, G=Gulf, W=West