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# Florida's Harmful Algal Bloom (HAB) Problem: Escalating Risks to Human, Environmental and Economic Health With Climate Change

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Harmful Algal Blooms (HABs) pose unique risks to the citizens, stakeholders, visitors, environment and economy of the state of Florida. Florida has been historically subjected to reoccurring blooms of the toxic marine dinoflagellate *Karenia brevis* (C. C. Davis) G. Hansen & Moestrup since at least first contact with explorers in the 1500's. However, ongoing immigration of more than 100,000 people year$^{-1}$ into the state, elevated population densities in coastal areas with attendant rapid, often unregulated development, coastal eutrophication, and climate change impacts (e.g., increasing hurricane severity, increases in water temperature, ocean acidification and sea level rise) has likely increased the occurrence of other HABs, both freshwater and marine, within the state as well as the number of people impacted by these blooms. Currently, over 75 freshwater, estuarine, coastal and marine HAB species are routinely monitored by state agencies. While only blooms of *K. brevis*, the dinoflagellate *Pyrodinium bahamense* (Böhm) Steidinger, Tester, and Taylor and the diatom *Pseudo-nitzschia* spp. have resulted in closure of commercial shellfish beds, other HAB species, including freshwater and marine cyanobacteria, pose either imminent or unknown risks to human, environmental and economic health. HAB related human health risks can be classified into those related to consumption of contaminated shellfish and finfish, consumption of or contact with bloom or toxin contaminated water or exposure to aerosolized HAB toxins. While acute human illnesses resulting from consumption of brevetoxin-, saxitoxin-, and domoic acid-contaminated commercial shellfish have been minimized by effective monitoring and regulation, illnesses due to unregulated toxin exposures, e.g., ciguatoxins and cyanotoxins, are not well documented or understood. Aerosolized HAB toxins potentially impact the largest number of people within Florida. While short-term (days to weeks) impacts of aerosolized brevetoxin exposure are well documented (e.g., decreased respiratory function for at-risk subgroups such as asthmatics), little is known of longer term (>1 month) impacts of exposure or the risks posed by aerosolized cyanotoxin [e.g., microcystin, β-*N*-methylamino-L-alanine (BMAA)] exposure. Environmental risks of *K. brevis* blooms are the best studied of Florida HABs and include acute exposure impacts such as significant dies-offs of fish, marine mammals, seabirds and turtles, as well as negative impacts on larval and juvenile stages of many biota. When *K. brevis* blooms are present, brevetoxins can be found throughout the water column and are widespread in both pelagic and benthic biota. The presence of brevetoxins in living tissue of both fish and marine mammals suggests that food web transfer of these toxins is occurring, resulting in toxin transport beyond the spatial and temporal range of the bloom such that impacts of these toxins may occur in areas not regularly subjected to blooms. Climate change impacts, including temperature effects on cell metabolism, shifting ocean circulation patterns and changes in HAB species range and bloom duration, may exacerbate these dynamics. Secondary HAB related environmental impacts are also possible due to hypoxia and anoxia resulting from elevated bloom biomass and/or the decomposition of HAB related mortalities. Economic risks related to HABs in Florida are diverse and impact multiple stakeholder groups. Direct costs related to human health impacts (e.g., increased hospital visits) as well as recreational and commercial fisheries can be significant, especially with widespread sustained HABs. Recreational and tourism-based industries which sustain a significant portion of Florida's economy are especially vulnerable to both direct (e.g., declines in coastal hotel occupancy rates and restaurant and recreational users) and indirect (e.g., negative publicity impacts, associated job losses) impacts from HABs. While risks related to *K. brevis* blooms are established, Florida also remains susceptible to future HABs due to large scale freshwater management practices, degrading water quality, potential transport of HABs between freshwater and marine systems and the state's vulnerability to climate change impacts.

**Keywords: HAB, Florida, *Karenia brevis*, climate change, risks, toxins**

# INTRODUCTION

Phytoplankton, the microscopic algae found in freshwater, estuarine and marine waters, are critically important to both human and the planet's health. They form the basis of aquatic food webs, and thus are essential for the secondary production of shellfish and finfish that provide ∼16% of the world's protein supply (Cato, 1998). They are responsible for ∼50% of global photosynthesis (Longhurst et al., 1995; Field et al., 1998; Beardall et al., 2009), producing between 50–85% of the $O_2$ in the atmosphere. Their role in sequestering atmospheric $CO_2$ through photosynthesis and transferring this carbon (C) to ocean sediments is considered a major buffer of climate change impacts (Falkowski, 2012). A small subset of the estimated 5,000 (Sournia et al., 1991; Sournia, 1995; Tett and Barton, 1995) to 100,000 (Round and Crawford, 1984) phytoplankton species in the ocean form blooms, an accumulation of cells of one or more species that occurs through physical concentration and/or *in situ* cell growth, with approximately 300 species involved in harmful bloom events (Berdalet et al., 2016). Blooms are considered to be a harmful algal bloom (HAB) when they become harmful to human, ecosystem or economic health. Harmful is a broad term, however, and can include both direct (e.g., damage due to cell morphology, toxins or other substances) and indirect (e.g., $O_2$ depletion due to respiratory demands of high biomass) impacts of cells. The concentration of cells of an individual species that constitutes a bloom is also highly variable. Smayda (1997) argues that biomass alone is insufficient to describe a bloom as harmful and that the environmental consequences of a bloom must be considered. A smaller subset of these HABs, ∼2% of total species (Sournia, 1995; Knap et al., 2002), produce secondary metabolites which can be toxic or fatal. Although the majority of toxic HAB species are Dinophyceae, species of Bacillariophyceae and Raphidophyceae, some Prasinophyceae as well as photosynthetic bacteria (Cyanophyceae/Cyanobacteria) can be toxic.

Within the past 30 years, there has been increasing scientific and public focus on and concern about HABs for several reasons. In the late 1980's and early 1990's, a trend of increasing frequency, geographical distribution and abundance of some HAB species, primarily dinoflagellates, was recognized (Anderson, 1989; Maclean, 1989; Smayda, 1989, 1990). These trends have increasingly been documented for additional species and groups (e.g., Cyanophyceae, Paerl and Paul, 2012; Harke et al., 2016) in subsequent years (Chinain et al., 2020a; Yñiguez et al., 2020; Anderson et al., 2021), and HABs are now an almost routine occurrence among much of the world's coastal waters. HAB increases are attributed to a variety of reasons that vary with the species and the geographical areas involved (Anderson, 1989; Hallegraeff, 1993; Burkholder, 1998; Glibert et al., 2005; Glibert and Burkholder, 2006). These include increasing coastal nutrient inputs and eutrophication, coastal development, industrial and agricultural intensification (Smayda, 1990; Anderson et al., 2002, 2008; Glibert et al., 2006; Heisler et al., 2008; Glibert, 2020), ballast water transport (Hallegraeff and Gollasch, 2006; Doblin et al., 2007; Smayda, 2007), increases in shellfish aquaculture (Shumway, 2011), climate change (Dale et al., 2006; Moore et al., 2008; Hallegraeff, 2010; O'Neil et al., 2012; Gobler, 2020) and a potential observer effect. In most cases, there is probably not a single cause underlying increases in a HAB's frequency, distribution or toxicity, but rather a complex interplay between these external pressures and the unique physiology of the HAB species involved which allows it to dominate under certain conditions.

Florida is arguably one of the global epicenters of HABs. Harmful and toxic micro- and macroalgal and cyanobacterial species are found in all of Florida's aquatic environments, from freshwater springs and lakes, to coastal lagoons, estuaries and shelf waters. Three algal toxins, brevetoxin, saxitoxin and domoic acid, have been detected in state waters, resulting in regulatory actions, including shellfish bed closures. One of the most predictable of global HABs, blooms of *K. brevis*, occur almost annually between August and November in southwest Florida coastal waters (Steidinger, 2009). These blooms are the cause of both neurotoxic shellfish poisoning (NSP) and respiratory irritation (**Table 1**) and are the focus of intensive state monitoring and management (Heil and Steidinger, 2009). Several Florida coastal regions (Indian River Lagoon, Tampa Bay, Charlotte Harbor) are also subject to blooms of the dinoflagellate *Pyrodinium bahamense*, which can contain saxitoxins that are responsible for both paralytic shellfish poisoning (PSP) and saxitoxin puffer fish poisoning (SPFP) (Landsberg et al., 2006; Abbott et al., 2009). The detection of domoic acid, a toxic, water soluble (Falk et al., 1991) amino acid produced by some species in the diatom genus *Pseudo-nitzschia*, has resulted in shellfish closures in St. Joseph Bay, Florida for the first time in 2013 and thereafter in 2014 and 2017 (O'Dea et al., 2013; Hubbard et al., 2015, 2017). Cyanobacterial toxins (e.g., microcystins and cylindrospermopsins) have also been detected in Florida fresh (Williams et al., 2007) and marine (Metcalf et al., 2021) waters at concentrations within EPA Drinking Water Health Advisory (HA) levels (United States Environmental Protection Agency, 2015). Other harmful blooms also occur with either uncharacterized toxins (e.g., undescribed *Karenia* species) or biomass related impacts [e.g., *Synechococcus* sp. blooms in Florida Bay (Glibert et al., 2009b,c, 2021), and *Aureoumbra lagunensis* D. A. Stockwell, DeYoe, Hargraves & P. W. Johnson blooms in the Indian River Lagoon (Gobler et al., 2013; Kang et al., 2015)].

Why are HABs so prevalent in Florida waters? There is no single explanation. Indeed, a number of unique biological, chemical and physical drivers as well as local, regional and global stressors are likely contributing to Florida's HAB prevalence, all of which may be occurring at different temporal and spatial scales. There are numerous freshwater, estuarine and marine potential HAB habitats available. Florida has a long coastline, 2,170 km, second only to Alaska in terms of length. This coastline borders two bodies of water, the Atlantic Ocean and the Gulf of Mexico (GoM) and is easily accessible from within 175 miles of any position within the state. Florida's coastal environments are characterized by widely varying environmental conditions, from marine lagoonal systems with restricted flows and residence times (e.g., the Indian River Lagoon, Florida Bay) to a north flowing river (e.g., St Johns River), to classical river driven estuaries (e.g., Charlotte Harbor and Apalachicola Bay). There are more than 7,800 lakes in Florida (Brenner et al., 1990), including the 4th largest United States natural lake, the 488,000-acre Lake Okeechobee, and numerous freshwater springs. The natural geology of Florida also plays a role in the prevalence of HABs. The sandstone and permeable limestone that characterize Florida karst topography produce a soil characterized by relatively poor nutrient retention (Slomp and Van Cappellen, 2004), which likely contributes to coastal eutrophication. The central west Florida region is also characterized by the Hawthorne Phosphatic Deposits, a natural phosphorus (P) rich geological feature that has been mined continually since the late 19th century (Filippelli, 2011) and results in elevated inorganic and organic P concentrations in central and southwest Florida coastal waters (Heil et al., 2007). Florida experiences a wide range of climate, from the warm temperate climate of the Panhandle to the Florida Keys, which constitute the northern boundary of the tropics. Florida's weather systems are characterized by two seasons, a wet season and a dry season, which can exacerbate nutrient retention and runoff conditions seasonally. Multiple anthropogenic stressors act on these diverse natural systems on different scales. Florida's human population is constantly increasing, an estimated 845 people move to Florida each day (Office of Economic and Demographic Research, 2021). In south Florida alone, population is projected to increase to over ten million by 2025 and possibly 15 million by 2050 (Obeysekera et al., 2011). Population increases have been accompanied by rapid, often unregulated, residential development. Urban and agricultural development and other associated anthropogenic activities lead to increasing water demands as well as stormwater, wastewater, and agricultural runoff to inland and coastal aquatic systems. In Florida, coastal development has been ongoing since 1912 when the Florida East Coast Railway linked to the Florida Keys, and has been characterized by both recent and historical marine and freshwater eutrophication (Brezonik et al., 1969; Lapointe and Clark, 1992; Havens and James, 2005; Turner et al., 2006; Barile, 2018; Lapointe et al., 2019, 2020). An additional anthropogenic activity in Florida is the management of freshwater flows by both state and federal levels. Lake Okeechobee water levels are managed by the United States Army Corps of Engineers for human safety (Steinman et al., 2002), which in 2018 resulted in the release of *Microcystis* contaminated lake waters to both the eastern coast via the St. Lucie River and the west coast by the Caloosahatchee River (Krimsky et al., 2018). Indeed, South Florida is currently undergoing one of the largest flow restoration projects in the world, the Comprehensive Everglades Restoration Plan (CERP), which is impacting the amount, timing and distribution of freshwater flows and subsequent nutrient loading to the southern third of the state (Glibert et al., 2021). Overlying these natural features and anthropogenic stressors are the escalating effects of climate change. Florida is considered especially susceptible to the effects of climate change, from warming waters to sea

**TABLE 1 |** HAB Syndromes and associated marine HAB species and toxins reported from Florida.

| Syndrome | Toxin | Species | Vector | Regulatory level | Mode of action |
|---|---|---|---|---|---|
| Neurotoxic shellfish poisoning (NSP) | Brevetoxins | *Karenia brevis* | Shellfish, water | ≧0.8 mg/kg [20 mouse units (MU)/100 g] brevetoxin-2 equivalent or 5,000 cells/L | Voltage dependent Na channel, Site 5 |
| Paralytic shellfish poisoning (PSP) | Saxitoxin and derivatives | *Pyrodinium bahamense* var. *bahamense* | Shellfish | ≧0.8 mg/kg saxitoxin equivalents (80 mg/100 gm) | Voltage dependent Na channel, Site 1 |
| Amnesic shellfish poisoning (ASP) | Domoic acid and isomers | *Psuedo-nitzschia* spp. | Fish, shellfish, crustaceans | ≧20 mg/kg domoic acid | Glutamate receptors |
| Saxitoxin puffer fish poisoning (SPFP) | Saxitoxin and derivatives | *Pyrodinium bahamense* var. *bahamense* | Fish | ≧0.8 mg/kg saxitoxin equivalents (80 mg/100 gm) | Voltage dependent Na channel, Site 1 |
| Ciguatera fish poisoning (CFP) | Ciguatoxins | *Gambierdiscus toxicus* | Reef fish | Caribbean ciguatoxins: >0.1 mg/kg Caribbean Ciguatoxins-1 (C-CTX-1) equivalents | Voltage dependent Na channel, Site 5 |
| Diarrheic shellfish poisoning (DSP) | Okadaic acid and derivatives | *Dinophysis* spp.<br>*Prorocentrum* spp. | Shellfish | ≧0.16 mg/kg okadaic acid equivalents | Serine/threonine protein phosphatases |

level rise to increasing storm intensities (Obeysekera et al., 2011; Reece et al., 2013).

Harmful Algal Blooms and their associated toxins thus represent significant risks to human and environmental health as well as local and state economies within Florida in ways that are unique to the state. The goal of this review is to provide an overview of major HAB species of specific concern in Florida waters, including a brief review of the ecology and associated risks of these species, and an evaluation of the potential impacts of climate change on these species and their associated risks in the future. As such, it is structured to include an overview of the human, environmental and economic risks associated with HABs in Florida, followed by a review of the different HAB groups and major species, then a discussion of the potential impacts of climate change on these HAB species and future challenges posed for HAB research and management by these impacts. How climate change is impacting HABs now and in the future in Florida represents a major challenge for local, state and federal HAB researchers and managers. By highlighting the ecology and impacts of the major HABs and the potential impacts of the local (e.g., water quality), regional and global stressors (e.g., climate change) on Florida's HABs, our hope is to provide potential direction on relevant future research efforts to reduce these risks.

## HAB ASSOCIATED RISKS

The impacts of HABs fall into three categories: harmful effects upon human health, detrimental environmental impacts including impacts to aquatic biota, and economic losses to a range of sectors and stakeholders. Of these three, the assessment of risks associated with HABS has focused primarily on human health (Hitzfeld et al., 2000; Carmichael, 2001; Van Dolah et al., 2001; Krahl, 2009; Cheung et al., 2013; Ibelings et al., 2014; Janssen, 2019). These effects can be significant, even life threatening, depending on the particular HAB species, the toxin involved and the route of exposure (Berdalet et al., 2016). Global estimates of HAB related human intoxification incidences range from 6,000 per year (Hallegraeff, 1993; Van Dolah, 2000) to more than 500,000 per year (Quod and Turquet, 1996).

These routes of HAB exposure to humans vary with the species involved, the toxin, and even the location, but all fall into one of three exposure routes: (1) ingestion of contaminated fish, shellfish or drinking water, (2) exposure to aerosolized HAB toxins, or (3) dermal contact with a HAB. All of the human health syndromes associated with HAB exposure in Florida (**Table 1**) result from one of these three routes. Regulatory effects have primarily focused on the ingestion route, particularly that of shellfish, which through feeding efforts can act to biomagnify toxins in their tissues. The three toxins that are the primary focus of HAB monitoring in Florida, brevetoxin, saxitoxin, and domoic acid, all have regulatory levels established by the FDA [FDA and EPA Safety Levels in Regulations and Guidance, A5 – 12 (March 2020)]. This is because the risks associated with ingestion of these toxins are most closely defined by the formal framework for Risk Assessment outlined by the National Research Council in 1983 (National Research Council [NRC], 1983), which include 4 sequential steps: (1) identification of the hazard, (2) a dose-response assessment of the hazard, (3) exposure assessment of the hazard, and (4) a risk characterization of human exposure. Brevetoxin, saxitoxin and domoic acid have been identified and chemically characterized and the dose required for impacts has been estimated from natural events and epidemiological studies. Exposure assessment establishes the extent and routes of potential toxin exposures, namely ingestion, inhalation or dermal contact. Effect risk characterization merges the last 2 steps to determine the probability of toxin exposure in sufficiently high concentrations to have a clinical effect (Van Dolah et al., 2001; Krahl, 2009). This is most easily assessed for ingestion of identified toxins. For the majority of HAB species, however, the information required to assess risk, from identification of the toxin and its chemical structure to determining potential biomarkers of exposure is poorly understood or unknown. Thus, the assessment of human risk associated with most HABs is in its early stages, especially for inhalation and dermal contact exposure routes.

Health risk assessment of HABS is further hampered by many additional factors, including a lack of toxin identification for some species as well as lack of knowledge of toxin transformations in the environment, lack of biomarkers of exposure, and even the dynamic physical nature of blooms which makes both predicting and determining exposure difficult. Determination of the human health impacts of HAB toxin exposure has largely focused on acute impacts of limited exposure. In Florida, there is a large emphasis on brevetoxins associated with *K. brevis* blooms due to frequency and the number of individuals impacted (e.g., Kirkpatrick et al., 2004; Fleming et al., 2011). For many HAB routes of exposure, the health effects of chronic exposure are unknown and require further research. For example, the impacts of short-term inhalation of aerosolized brevetoxins from *K. brevis* blooms is established (Backer et al., 2003; Fleming et al., 2007, see Fleming et al., 2011 for review). Blooms of *K. brevis* may persist in southwest coastal waters for periods of up to 30 months (Steidinger, 2009) and the impacts of this longer term exposure of aerosolized brevetoxins are unknown. Even less is known about both the acute and chronic impacts of exposure to aerosolized cyanotoxins. Increases in the frequency of blooms of the toxic cyanobacteria *Microcystis* in Lake Okeechobee (Havens and Steinman, 2015; Havens et al., 2019), especially in 2018 when a large *Microcystis* bloom in the Lake was transported to the east and west coasts via release through the St. Lucie and Caloosahatchee Rivers, combined with the detection of microcystin in nasal swabs from people exposed to this *Microcystis* bloom (Schaefer et al., 2020), suggests that this toxin route merits further investigation.

The environmental impacts of Florida HABs are diverse and significant. Reviews of the impacts of HABs on biota and the environment are provided by Landsberg (2002); Landsberg et al. (2009), Basti et al. (2018); Shumway et al. (2018), Zohdi and Abbaspour (2019), and Brown et al. (2020). Impacts range from direct, acute impacts of toxins on freshwater and marine biota (e.g., fish, marine mammal and sea turtle mortalities) to indirect effects through food web transfer of toxins (Landsberg, 2002; Landsberg et al., 2009) and/or bloom-associated anoxia such as occurred with larger *K. brevis* blooms on the central west Florida shelf in 1974 (Smith, 1975, 1979) and 2005 (Hu et al., 2006). The HAB species and toxins involved are especially important in predicting environmental impacts associated with blooms. In many cases, e.g., *K. brevis* blooms, acute bloom impacts are well documented, while routes of toxin transfer are still being elucidated (Abraham et al., 2021). In other cases, e.g., other *Karenia* species, these impacts are yet to be determined. Sublethal impacts, especially during extended blooms, are poorly understood and are dependent on our identification and understanding of the toxin(s) involved, including their structures and modes of action.

Harmful Algal Blooms are costly. Global estimates of HAB impacts on human health alone are over $4 billion dollars per year (United Nations Environment Programme, Joint Group of Experts on the Scientific Aspects of Marine Environmental Protection, 2001, references in Berdalet et al., 2016). Estimates of HAB related losses in the United States have been steadily increasing over time. Anderson et al. (2000) and Hoagland et al. (2002) put annual losses related to HABs in the United States at $20 million dollars at the start of the 21st century. These estimates have increased from $50 to $82 million dollars annually (Hoagland and Scatasta, 2006; Anderson et al., 2012). These economic costs generally are attributed to losses in four sectors: public health, commercial fisheries, tourism and recreation, and HAB monitoring and management. They include economic losses from relevant markets (e.g., seafood, labor, and coastal tourism), costs associated with the HAB and its impacts (e.g., public health) and the cost of mitigating these impacts (e.g., costs of cleaning dead fish from beaches, monitoring) (Hoagland and Scatasta, 2006). Losses attributed to each of these sectors will vary greatly with the HAB involved and its impacts.

Quantifying the economic risks of HABs and HAB associated losses has proven to be challenging. One difficulty in evaluating HAB economic risks lies in their differences from other natural hazards. HABs differ from other large natural hazards such as hurricanes or earthquakes in that their impacts are not necessarily immediate (Bechard, 2020b) or restricted to a limited area. HABs can last for an extended period. The longest duration *K. brevis* bloom occurred for 30 months from 1994 to 1997 (FWRI HAB Historical Database) while blooms of *Synechococcus* have persisted intermittently in Florida Bay since 1999 for periods of up to 3 years (Glibert et al., 2009b,c). HABs can also impact large regions: the 1986–1987 *K. brevis* bloom impacted most of the coastline of Florida and the eastern seaboard as far north as North Carolina (Tester et al., 1991; Tester and Steidinger, 1997). Economic impact estimates rarely account for economic 'halo' effects, which are collateral losses resulting from human perceptions related to HABs, such as consumer avoidance of goods (e.g., shellfish) perceived as tainted by HAB toxins (Jensen, 1975; Kuhar et al., 2009; Adams et al., 2018). This can be a significant risk for sectors such as Florida's tourism industry, which relies upon images of pristine beaches to draw people globally and are heavily impacted by public perception (Kuhar et al., 2009; Cahyanto and Liu-Lastres, 2020). This social amplification of risk, which may potentially be intensified by the media (Li et al., 2015), is an extensive problem with Florida red tide specifically (Hoagland et al., 2020).

Within both the United States and Florida, the scientific focus of assessing economic losses related to HABs has been primarily on *K. brevis* blooms. Adams et al. (2018) in their review of existing literature, research methods, data, and information gaps of current HAB-economic research, point out that 18 of the 36 relevant HAB economic papers focus on *K. brevis* blooms in Florida. This is not unexpected as *K. brevis* blooms reoccur annually, generally impact larger areas of the state relative to other HABs and affect the greatest number of people and businesses. Initial estimates of economic losses associated with these blooms range from $20 million dollars for a 1971 bloom in southwest Florida (Habas and Gilbert, 1974) to $18.45 million dollars for a 2000 Texas *K. brevis* bloom (Evans and Jones, 2001). Interestingly, Habas and Gilbert (1974) suggest that their estimate is likely a significant underestimate of true bloom costs due to an array of costs that were masked by substantial economic growth during the bloom period. These studies focused primarily on losses within the fisheries and tourism sectors. It is now understood that the economic impacts of these blooms, especially the infrequent, longer duration, high impact *K. brevis* blooms such as occurred in 2017–2019, are complex, diverse, and long-lasting. Direct economic losses via negatively impacted businesses are predominantly marine (e.g., fisheries and aquatic dependent businesses) or tourism related, and costs to local governments associated with bloom mitigation costs. But significant losses are also associated with the costs of bloom associated human health care as well as impacts on property values and government revenues (Adams et al., 2018).

Other bloom associated economic losses include losses to the fishery (both wild harvest and aquaculture) and seafood sectors. Anderson et al. (2000) estimated that 37% of HAB related economic losses were attributable to commercial fisheries in the United States, which Hoagland and Scatasta (2006) increased to 48%. These are likely underestimates as they account primarily for direct economic losses and do not include the halo effect (Hoagland and Scatasta, 2006). Béchard (2020a) found that in one Florida County alone, taxable sales receipts for the fishery and seafood sectors experienced a $20,000 monthly loss, or 4.8% below normal, when a *K. brevis* bloom was present. These estimates also represent 'acute' impacts during the time of the bloom, generally when extensive fish kills occur. Blooms of *K. brevis* have recently been shown to impact fish community diversity for extended periods (Gannon et al., 2009; DiLeone and Ainsworth, 2019), with severe blooms such as occurred in 2005 and 2018 resulting in declines in annual recruitment of commercially important species such juvenile spotted seatrout (*Cynoscion nebulosus*), sand seatrout (*Cynoscion arenarius*), and red drum (*Sciaenops ocellatus*) (Flaherty and Landsberg, 2011), and multiyear closures of some commercial fisheries that are especially sensitive to brevetoxin impacts [e.g., snook (*Centropomus undecimalis*)], red drum and sea trout (Gillis, Feb 19, 2020).

Florida's economy is heavily dependent upon tourism revenue. In 2017–2018 alone, visitors to Florida accounted for from $1.84 billion dollars economic impact (Visit Sarasota County, 2019) to $22 billion dollars in beach related tourism. Much of the attractiveness of Florida to tourists results from its environment, including warm weather and a long coastline with beautiful beaches and a healthy ocean. Any threat to Florida's environment is a threat to its tourism industry. As such, the economic losses due to tourism from HABs can be considerable (Habas and Gilbert, 1974; Adams et al., 2002; Larkin and Adams, 2007; Morgan et al., 2009, 2010). Larkin and Adams (2007) report reductions in monthly revenue of restaurants and lodging of $2.8 and $3.7 million dollars, respectively (29 and 35% declines, respectively) in Ft. Walton Beach and Destin areas of the Florida Panhandle for 1995–1997 when a *K. brevis* bloom was present. Three beachfront restaurants reported reductions in revenue due to red tide from $646 to $3,734 (13.7–51.3% on average) per day (Morgan et al., 2009). Adams et al. (2000) was unable to demonstrate a negative effect upon beach attendance during a red tide but suggested this may reflect inadequate data resolution or the selection of alternative entertainment by business patrons. Bechard (2019) reported a 15% decrease in sales in Sarasota County during persistent blooms, while the food and restaurant sector losses averaged 1.75%. Similar reductions in adjacent, unimpacted counties were not evident. Further research over an extended 6 county area from Pinellas to Collier Counties in southwest Florida (Bechard, 2020d) reported that each additional day of red tide per month in excess of 17 days drove lodging sales down 1–2% and restaurant sales down 0.5–1%. While these results suggest that economic impacts may be localized to the areas of the bloom, they also demonstrate that these impacts can be significant.

Health care costs during *K. brevis* blooms are related to digestive, gastrointestinal and respiratory impacts (Hoagland et al., 2014; Patel et al., 2020). Kirkpatrick et al. (2006) utilized hospital records to compare the number of patients admitted with respiratory disease during red tide periods with non-bloom periods and found a significant increase in the ER admissions for respiratory diseases during the 2001 red tide compared to the 2002 non-red tide period, with elevated rates among individuals living within 1.6 miles of the shore. A 40% increase in gastrointestinal diagnoses and admissions were also found (Kirkpatrick et al., 2010). Hoagland et al. (2009) estimated the costs of respiratory illness associated with *K. brevis* blooms in Sarasota County alone to be between $0.5 and $4 million depending on bloom severity. Increased health costs were associated with older cohorts (>55 years of age) in 6 southwest Florida counties and ranged from $60,000 to $700,000 annually depending on bloom severity (Hoagland et al., 2014). The authors suggest that capitalized costs of future *K. brevis* related illnesses could be up to $24 million dollars.

Although they reoccur each year, Florida red tides vary greatly in their severity, duration, impacts and spatial extent. The 2017–2019 *K. brevis* bloom was especially severe, lasting for 17 months and impacting most of Florida's 23 Gulf counties. This bloom has provided an opportunity to estimate the higher end economic impacts possible with a severe *K. brevis* bloom. A Gulf of Mexico Alliance Report (The Balmoral Group., 2020) documented the total losses attributable to this bloom in Florida Gulf counties of $1 billion dollars, with an additional tax revenue decline of $178 million dollars. The tourism sector had by far the greatest loss, $455 million dollars in direct loss and a $113 million dollar loss in tax revenue, followed by property values ($343 and $32 million dollars, respectively) then boat sales ($55 and $21 million dollars, respectively) and recreational and commercial fisheries. Economic losses attributable to human health impacts were not figured into these losses, nor were losses attributed to marine mammal strandings ($198 million dollars, The Balmoral Group., 2020). Bechard (2019) reported monthly losses to lodging and restaurant sectors to be between 1 and 15% and 0.5 and 1.7%, respectively, during the 2006 and 2018 blooms in counties where red tide was present. Property values within 1 mile of the coast sold for up to 30% less compared with similar homes in areas with no red tide, and (Bechard, 2021; Bechard, 2020c) reported that during a 16 year period that included the 2018 bloom, property values decreased by 10% during the bloom with an additional decline of 1–2% for each additional bloom month, with steeper decreases experienced by waterfront homes.

Little is known of the economic costs associated with HABs other than *K. brevis* in Florida. Hoagland and Scatasta (2006) attributed public health costs of $250,000 and $525,000 per year for reported and unreported cases of ciguatera poisoning, respectively, in Florida from 1987 to 1992. Todd (1985) quantified the economic losses resulting from ciguatera poisoning (medical costs and lost labor) at $2.7 million dollars per year, suggesting that Florida's costs are potentially greater than $775,00 per year if lost labor costs are factored in. Given that significant revenue losses associated with ciguatera continue to exist for fish dealers who produce grouper on Florida's east coast (Raizin and Meaburn, 1988), these estimates are likely low. In the south Pacific region where it is endemic, ciguatera poisoning has been shown to result in increases in health care costs (Lewis, 1986), labor productivity losses (Bagnis et al., 1992) and tourism (Lewis, 1992) and fish sale (Yeeting, 2009) losses ranging from $1.1 million (Bagnis et al., 1992) to $22 million dollars annually (Hoagland et al., 2002). Other HABs, such as *Synechococcus* spp. blooms in Florida Bay, and cyanobacterial blooms statewide, undoubtedly have significant negative impacts on both tourism and fisheries but economic losses have not yet been quantified.

Management efforts are necessary to prevent or lessen economic, environmental and human health impacts of HABs and these generally focus on HAB mitigation. Mitigation of HABs is comprised of 3 categories: prevention of HABs, control of HABs and associated toxins and mitigation of the impacts of HABs (Boesch et al., 1996; CENR, 2000; Sengco, 2009a,b). Prevention focuses on strategies to prevent bloom occurrence or to limit their scope. These include limiting nutrient supply to blooms, management of the physical conditions that play a role in initiation and preventing HAB introductions to new areas (Anderson, 2004) and requires critical knowledge of the biological, chemical and physical factors contributing to bloom initiation which may not be known. Control strategies focus on efforts to destroy or remove both the HAB cells and associated toxins and include both application of chemical controls [e.g., copper sulfate (Sengco, 2009b) and removal technologies (Hallegraeff et al., 2017)]. Mitigation has received the greatest scientific and funding focus with both HABs in general and with Florida HABs, especially *K. brevis* blooms, and includes efforts to limit the impact of blooms through monitoring, education and communication outreach (Kleindinst and Anderson, 2004; Fleming et al., 2007; Kirkpatrick et al., 2008; Nierenberg et al., 2011) as well as development and application of HAB forecasting models (Walsh et al., 2001; Stumpf et al., 2003, 2009; McGillicuddy, 2010; Kavanaugh et al., 2013). For HABs in Florida, monitoring related technologies are rapidly advancing and being applied, from molecular and optical detection methods (e.g., HABscope for *K. brevis* monitoring, Hardison et al., 2019) to improved impact predictions (e.g., NOAA respiratory predictions, Stumpf, 2008).

Florida has perhaps the earliest attempt to mitigate the risks associated with a marine HAB when in 1947, during one of the most severe *K. brevis* blooms on record in southwest Florida, Florida Senator Claude Pepper requested that the Navy send planes to bomb the dead fish and Rear Admiral Davidson telegraphed Senator Pepper that this was '*inadvisable as likely to disperse present concentration and involve additional beach communities*' (Sarasota Herald Tribune, 1947). Subsequent collaborative state and federal efforts focused on the use of copper sulfate to control *K. brevis* blooms in the 1950's (see Sengco, 2009b for review) with additional research on potential algicidal control (Mayali and Doucette, 2002; Roth et al., 2007, 2008; Lin et al., 2016; Kinley-Baird et al., 2021) and clay flocculation thereafter (Sengco et al., 2001; Lewis et al., 2003; Pierce et al., 2004). At the state level, Florida's recent reinvigoration of the HAB and Red Tide State Task Forces has led to an increasing scientific, management and public focus on HAB mitigation research and application within the state. Florida's Red Tide Mitigation and New Technology Initiative Program (2019–2025) also represents a substantial unique state effort to fund the development of new technology and mitigation research and application efforts related to *K. brevis* blooms.

## FLORIDA HABs

The state of Florida routinely monitors for more than 75 HAB species in freshwater to marine environments. While the agencies directly involved are primarily Florida Fish and Wildlife Conservation Commission's Fish and Wildlife Research Institute for estuarine and marine HABs and the Florida Department of Environmental Protection for freshwater HABS, many local municipalities and counties, especially those in southwest Florida that experience annual *K. brevis* blooms, maintain some monitoring and management capabilities, especially with beach cleanups, or directly collaborate with the state agencies. The following sections summarize the main Florida HAB species of concern for human, environment and economic health in the state. It is by no means an exhaustive list, but is meant to provide a summary of the relevant state of knowledge of each HAB species to allow evaluation of the potential risks associated with each, especially in light of Florida's ongoing demographic and environmental challenges.

### Dinoflagellate HAB Species

#### *Karenia brevis* (Florida Red Tide)

Blooms of the toxic dinoflagellate *Karenia brevis* represent perhaps the most widely known and potentially greatest HAB threat to the state. Known colloquially as Florida Red Tide, these blooms reoccur annually in southwest Florida, impact the greatest number of people and biota both directly and indirectly, and have the largest, most widespread economic impacts of all Florida HABs (Heil and Steidinger, 2009; Steidinger, 2009). Considered among the most predictable of global HABs, *K. brevis* (formerly *Gymnodinium breve, Ptychodiscus brevis*, and *Gymnodinium brevis*) blooms have a long and extensive history which predates the taxonomic identification and description of the causative dinoflagellate after one of the most destructive blooms on record in 1947 (Davis, 1948). Galtsoff (1948) reported of the 1947 bloom that '*All the beaches in the Fort Myers area became littered with dead (fish) bodies which were reported to* *accumulate at a rate of more than 100 pounds per linear foot of shore line.*' But the existence of *K. brevis* blooms is known to predate this 1947 bloom based on records of its unique human symptomology (Steidinger, 2009). Respiratory irritation, which occurs in humans exposed to aerosolized brevetoxins at or near bloom impacted beaches or in the vicinity of blooms offshore, was first noted in 1917 (Taylor, 1917). The unique human symptomology of Neurotoxic Shellfish Poisoning (NSP), the syndrome associated with consumption of shellfish exposed to *K. brevis* which have concentrated brevetoxins, was noted in 1880 in Tampa Bay in association with local oyster saloons (Steidinger, 2009). *K. brevis* bloom history likely extends much further back in GoM history based on anecdotal reports and ship logs which describe extensive fish kills in the region (Steidinger, 2009).

The more recent record of *K. brevis* blooms has received much public attention. With the onset of formal state red tide monitoring in the 1980's and the establishment of an extensive monitoring network, the recent bloom record is extensive, with well documented blooms of varying extent, duration and impacts occurring almost annually. The state HAB Historical Database of Florida currently includes >85,000 georeferenced entries for *K. brevis* concentrations dating from 1952 to current times, and was originally compiled in 2000 from more than 70 different entities and sources (e.g., academia, non-profit, local state, and federal agencies) (Haverkamp et al., 2004). This database reflects the temporal, spatial and depth biases associated with these disparate data sources and the event response nature of *K. brevis* sampling prior to formal monitoring efforts in the 1990's. Although Brand and Compton (2007) have interpreted the database as supporting an increasing frequency of *K. brevis* blooms in southwest Florida, statistical analysis of the database for long term trends remains problematic (Heil et al., 2014a). Walsh et al. (2006) examined the long term records of *K. brevis* blooms off both Texas and southwest Florida in conjunction with available nutrient data and concluded that while increasing incidences of blooms off Texas were likely related to nutrient discharges from the Mississippi River, those off Florida were not directly related to nearshore nutrient inputs. Regardless of prior bloom history, however, coastal development continues, as does ongoing immigration to the state and the eutrophication of Florida's freshwater, estuarine and coastal waters. The net effect of this is that more Florida residents and visitors are experiencing and being exposed to Florida Red Tide and its environmental and economic impacts over time than ever before.

*Karenia brevis* cells are a natural feature of the GoM and cells are found year round throughout the GoM at background concentrations of 1,000 cells $L^{-1}$ or less (Geesey and Tester, 1993). Although blooms occur throughout Florida coastal waters, including the Panhandle and the east coast, blooms in these regions are preceded by established blooms in southwest Florida waters in the region between Tarpon Springs and Naples (Heil and Steidinger, 2009; Steidinger, 2009). In this southwest region blooms occur almost annually, initiating in late summer to early fall and lasting anywhere from 3 to 4 months to greater than 30 months in 1994–1997.

To understand why blooms are most common in southwest Florida, there is a need to understand the physical and chemical oceanography of this region as well as the coastal morphometry. Vargo (2009) reviewed the 24 theories proposed to explain *K. brevis* blooms from the 1880's to 2009. Many early red tide studies attempted to associate coastal blooms with local nutrient, weather or physical conditions. Ingle and Martin (1971) attempted to correlate bloom occurrence with an Iron-index of riverine conditions while Slobodkin (1953) related blooms to low salinity, coastal water masses. Even in the 1950's controversy existed surrounding the role of local nutrient inputs such as the Caloosahatchee River on blooms, with Murdock (1954) arguing that '*The continuing high rate of water release from the Caloosahatchee River may be a contributing cause to Red Tide Outbreaks,*' while Graham et al. (1954) pointed out that '*Neither the rivers, nor the bottom of the Gulf, nor the deep water of the Gulf can be held as a source of phosphorus sufficient to increase the concentration in the body of coastal water to the values which are found in red tide samples.*' None of these studies successfully explained how an organism characterized by relatively slow growth rates, 0.2–0.3 divisions $day^{-1}$ (Vargo, 2009), was able to dominate phytoplankton biomass in these coastal blooms so rapidly until Steidinger (1975) recognized and documented the four stages of *K. brevis* blooms: initiation, growth, maintenance and termination. Blooms initiate 18–74 km offshore in 12–37 m depths on the mid-shelf of the southwest Florida coast, most often between Tarpon Springs and Naples (Steidinger, 1973). While offshore initiation has been documented in 1966, 1976, 1979, 1985, 1998, and 2008 (Steidinger, 2009; Heil et al., 2014a), identifying this stage remains problematic due to the low concentrations of subsurface *K. brevis* cells which are difficult to detect, either remotely or with autonomous technology, and the large potential offshore geographical area over which the blooms potentially initiate. At this stage, physical drivers are crucial to bloom development. Offshore upwelling related to Loop Current intrusion plays an important role in bloom initiation, with some upwelling required for initiation (Liu et al., 2012; Weisberg et al., 2014). Too much upwelling, however, delivers sufficient upwelled $NO_3^-$ to the shelf bottom waters to favor diatom development and impede *K. brevis* growth (Heil et al., 2001; Weisberg et al., 2016). Cells then grow slowly and are transported cross-shelf via the bottom Ekman layer (Weisberg et al., 2009, 2016), driven by wind-driven and upwelling-related transport. Winds, frontal systems and longshore currents act to concentrate increasingly dense *K. brevis* populations shoreward (Tester and Steidinger, 1997; Vargo et al., 2001, 2004; Weisberg and He, 2003; Janowitz and Kamykowski, 2006) where the blooms may persist for months to years (Steidinger, 2009). Weisberg et al. (2019) demonstrated that the dramatic increase in cell counts off the Pinellas County coastline in September 2018 which contributed to the unusually severe 2017–2019 *K. brevis* bloom was shown to be due to advection from the offshore formative region (Weisberg et al., 2019). This 2018 southwest Florida bloom was subsequently advected to the Florida Panhandle and east coast in a similar manner later in the bloom as has been demonstrated for *K. brevis* blooms in 2005 (Carlson and Clarke, 2009).

The nutrient sources that sustain *K. brevis* blooms as well as the nutrient physiology of *K. brevis* are complex. *Trichodesmium* blooms have long been observed to immediately precede and often co-occur with *K. brevis* blooms on the west Florida shelf and a relationship between the two species was suggested (Chew, 1955; Steidinger, 1973; Taylor and Pollingher, 1987). Walsh and Steidinger (2001) documented their co-occurrence over a 41 year period on the west Florida shelf from 1957 to 1998 and hypothesized that these two species were nutritionally linked through the transport and deposition of Fe-rich Aeolian dust from north Africa, which supplied the Fe required for *Trichodesmium* $N_2$ fixation. Lenes et al. (2001) documented increases in Fe concentrations in surface water after dust deposition, with subsequent increases in DON and *K. brevis* concentrations. *Trichodesmium* can release up to 50% of fixed N to the environment as $NH_4^+$ and dissolved organic N (Capone et al., 1994; Glibert and Bronk, 1994). This N, in turn, is taken up by *K. brevis* (e.g., Lenes et al., 2001; Mulholland et al., 2002, 2006, 2014; Sipler et al., 2013; Heil et al., 2014c; Killberg-Thoreson et al., 2014).

As blooms grow and are transported nearshore, the nutrient sources available to cells increase and can include (1) benthic nutrient flux (Dixon et al., 2014a); (2) photochemical nutrient production (Bronk et al., 2014); (3) nitrification (Bronk et al., 2014), (4) zooplankton grazing (Walsh and O'Neil, 2014); and (5) nearshore coastal sources from estuarine and river runoff and inputs (Vargo et al., 2008; Dixon et al., 2014b; Heil et al., 2014c). As bloom concentrations increase nearshore to concentrations $>10^6$ cells $L^{-1}$ (Heil and Steidinger, 2009), nutrient regeneration from dead fish also can play an increasingly important role (Walsh et al., 2009; Killberg-Thoreson et al., 2014; Heil et al., 2014c). The exact sources which contribute to bloom maintenance nearshore depends upon bloom latitude as well as distance offshore and bloom age (Heil et al., 2014a). Nutrient stoichiometry calculations (Vargo et al., 2008; Heil et al., 2014c) have shown that sufficient nutrients are present to support moderately sized, nearshore *K. brevis* blooms, during average estuarine flow years: combined estuarine sources contribute up to 17 and 69% of the N and P needs of these blooms, although only $N_2$ fixation and release and decay of seasonal *Trichodesmium* bloom biomass are sufficient to provide for the N needs of larger blooms (Lenes and Heil, 2010).

The factors that control *K. brevis* bloom expansion and termination are less understood. Favorable physical and sufficient nutrient sources are required to expand blooms and increase their biomass. Potential nutrient sources that are important to these bloom stages may include additional nutrient sources derived from excessive freshwater inputs linked to hurricanes or water management practices. Hu et al. (2006) suggested that a series of hurricane inputs in 2004 contributed to the severity of the 2005 *K. brevis* bloom. The severe 2017–2019 bloom was preceded by intense flooding and runoff following Hurricane Irma in fall of 2017, along with an extremely wet season in 2018 which resulted in management decisions to release high volumes of nutrient-laden Lake Okeechobee water through the Caloosahatchee and St. Lucie Rivers. Both a $\delta^{15}N_{particulate}$ value at the Caloosahatchee River mouth (Yentsch et al., 2008) and statistical tests with convergent cross mapping and upriver N concentrations (Medina et al., 2020) suggest that *K. brevis* blooms at the Caloosahatchee River mouth can utilize some fraction of inland agricultural nutrient sources. Uhlenbrock (2009) examined nutrient concentrations within the river during 2005 releases and concluded that nutrient loading rates into San Carlos Bay from the River provided sufficient DON and DIN to support the *K. brevis* bloom at the river mouth during the study. Note that these blooms often extend well to the south and north of the river mouth, and when the larger bloom areas are taken into account, there are insufficient nutrient inputs from the Caloosahatchee River to support the larger blooms. Heil et al. (2014c) utilized nutrient stoichiometry to examine the potential role of Caloosahatchee River N and P loading rates, in comparison with other known nutrient sources for blooms, to support small, medium and large estuarine, coastal and offshore *K. brevis* blooms. River inputs were significant for small estuarine blooms at the river mouth but decreased significantly for larger estuarine blooms and small coastal blooms. These results suggest that the input of river N and P, while significant for smaller *K. brevis* blooms at or near the river mouth, are insufficient to account for blooms of higher concentrations or larger spatial extent.

The mechanisms controlling bloom termination likely include physical, chemical and biological processes. Blooms may be transported offshore, entrained in offshore fronts, and transported out of the area (Steidinger, 2009). Blooms frequently transport south to the Ten Thousand Island area in southwest Florida, then migrate either east through the Florida Straits and up the east coast (15 times from 1972 to 2018) or westward into the central Gulf. Chemical and biological factors may include nutrient impoverishment as well as bacterial and viral processes. Lenes et al. (2013), in a bloom simulation which examined factors important in *K. brevis* bloom termination, reported a modeling efficiency of 0.68 when a bacterial lysis term was introduced to nutrient limited *K. brevis* populations. Algicidal bacteria (Mayali and Doucette, 2002; Roth et al., 2007, 2008) as well as viruses (Paul et al., 2002) have been documented for *K. brevis*, but their role in bloom dynamics and bloom termination is unknown.

Vargo (2009) summarized the physiological and ecological characteristics of *K. brevis* that contributes to its dominance of coastal phytoplankton communities during blooms. Cell motility may play a role, as *K. brevis* is capable of complex physiological regulation of its position in the water column (Heil, 1986; Kamykowski et al., 1998; Sinclair and Kamykowski, 2008; Heil et al., 2014b) as well as an effective photoadaptive strategy (Shanley, 1985; Shanley and Vargo, 1993; Millie et al., 1997; Evens et al., 2001; Evens and Leblond, 2004). *Karenia brevis* may gain a competitive advantage through the production of allelopathic substances (Kubanek et al., 2005; Prince et al., 2008, 2010; Poulson-Ellestad et al., 2014; Poulin et al., 2018) and a reduction in grazing losses due to the negative impacts of brevetoxins on higher trophic levels (Huntley et al., 1986; Turner and Tester, 1989, 1997; Lester, 2005; Waggett et al., 2012; Walsh and O'Neil, 2014). Not only is *K. brevis* able to utilize a variety of different nutrient sources, but nutrient physiology of *K. brevis* may also play a significant role in the dominance of these blooms. Recent evidence suggests that

*K. brevis* may also be capable of mixotrophic uptake of the picocyanobacteria *Synechococcus* (Jeong et al., 2005; Glibert et al., 2009a; Procise, 2012). Growth of marine picocyanobacteria in southwest Florida coastal waters is correlated with urea (Heil et al., 2007), which has been shown to increase with both large scale hurricane related inputs (Heil et al., 2007) and localized episodic, wind driven inputs (Ivey et al., 2020). Nutrient stoichiometry also may play a further role in *K. brevis* blooms as Walsh et al. (2006) suggested that the generally low DIN:DIP ratios that characterize southwest Florida rivers ($<4$) favor *K. brevis* as they select against diatoms which typically utilize oxidized N forms.

Human health impacts of *K. brevis* blooms are attributed to ingestion of brevetoxin contaminated shellfish (NSP), exposure to brevetoxin laden aerosols (see Kirkpatrick et al., 2004; Fleming et al., 2005, 2011 for reviews). Cases of NSP are now relatively rare due to effective monitoring of blooms and commercial shellfish beds within the state (Heil, 2009), but they do sometimes occur, especially when non-English speaking residents or tourists illegally harvest and consume contaminated shellfish. Respiratory irritation results from exposure to aerosolized brevetoxins contained within sea spray generated from the bloom (Pierce et al., 2003, 2005). Cells break apart at the water surface or in the surf zone, and dissolved brevetoxins are incorporated into sea spray. Human health studies have shown that in healthy adults, respiratory symptoms of bloom exposure disappear rapidly after removal from aerosol exposure, while in people with asthma and other respiratory issues, symptoms can persist for extended periods (Milian et al., 2007). Fleming et al. (2011) also point out how improvements in brevetoxin detection methodology have led to the detection of measurable brevetoxin loads within live fish, leading to potential "brevetoxin fish poisoning" (not just shellfish poisoning) with consumption of live fish. The potential risk of brevetoxin fish poisoning is further supported by increases in hospital admissions related to gastrointestinal issues during blooms (Kirkpatrick et al., 2010).

The majority of research on the environmental impacts of *K. brevis* blooms has focused upon acute organismal impacts. Brevetoxins are potent neurotoxic ichthyotoxins and both live cells and dissolved brevetoxins in seawater can be absorbed across fish gills (Landsberg, 2002; Naar et al., 2007), resulting in loss of muscle coordination, paralysis and eventually death via respiratory failure (Landsberg, 2002). Blooms frequently result in extensive fish kills as well as seabird and marine mammal mortalities (see reviews in Landsberg, 2002; Landsberg et al., 2009). Dead fish accumulate on beaches, and besides being an unsightly deterrent to beach dependent tourism industries, may also serve as a vector of brevetoxin to sea and shorebirds (Van Deventer et al., 2012). These kills can lead to local declines in fish stock (Landsberg et al., 2009) or in some cases impact multiyear classes of especially sensitive fish (DiLeone and Ainsworth, 2019), impacting longer term community structure and diversity (Gannon et al., 2009; DiLeone and Ainsworth, 2019). Because of these large, frequent fish kills associated with blooms, it was assumed that brevetoxins could not accumulate in fish at sublethal levels, or be transferred through food webs to different trophic levels. However, Flewelling et al. (2005) reported elevated brevetoxin levels in the tissue of live fish collected from the wild as well as in whole fish contained in the stomachs of dolphins (*Tursiops truncatus*) killed in a marine mammal mass mortality in the Florida Panhandle in 2004. Additionally, Naar et al. (2007) demonstrated that brevetoxins can accumulate in both omnivorous and planktivorous fish by dietary transfer in both the laboratory and in the natural environment and persist for up to a year after the bloom (Naar et al., 2007).

*Karenia brevis* blooms can also result in sea turtle and marine mammal moralities, including dolphins and manatees (Flewelling et al., 2005). In the 2002 bloom associated manatee mortality event, Flewelling et al. (2005), Fire et al. (2007, 2015) demonstrated that fish and seagrass served as the vector of brevetoxin to higher trophic levels after they accumulated high concentrations of brevetoxins during blooms. Sea turtles are also negatively impacted by *K. brevis* blooms with unusually high strandings reported for both east and west Florida coasts during blooms (Foley et al., 2019), especially from 2003 to 2006 (Capper et al., 2013; Fauquier et al., 2013). Sublethal impacts of on turtles have also been noted (Walsh et al., 2019), suggesting that sublethal brevetoxin impacts on these species may be pervasive during blooms and requires further study.

*Karenia brevis* blooms can also have secondary effects related to bloom associated hypoxia or anoxia (Smith, 1975, 1979; Hu et al., 2006). Large anoxic events were associated with a bloom in the early 1970's (Smith, 1975, 1979) as well as the severe 2005 bloom off central west Florida (Landsberg et al., 2009; Dupont et al., 2010). The 2005 event comprised more than 2,000 sq. miles in an area offshore of central west Florida and likely resulted from *K. b*revis cells trapped in bottom waters by a warm, stratified water column which over time (with bacterial decomposition of dead biota) resulted in a large area of bottom anoxia (Landsberg et al., 2009). The anoxia was only relieved when the water column was almost instantaneously mixed by the passage of Hurricane Katrina 200 miles to the west (Weisberg et al., 2009).

### *Pyrodinium bahamense*

The thecate dinoflagellate *Pyrodinium bahamense* is the HAB species responsible for the most HAB related paralytic shellfish poisoning (PSP) fatalities annually (Usup et al., 2012) since it first bloomed in Papua New Guinea in 1972 (Maclean, 1977). This species is generally considered a monospecies, currently with two accepted varieties, *P. bahamense* var. *compressum,* which is restricted to the Pacific Ocean, and *P. bahamense* var. *bahamense,* which occurs in the Atlantic Ocean and Caribbean Sea (Steidinger et al., 1980; Badylak et al., 2004) although there remains some taxonomic debate as to the validity of these two varieties (Balech, 1985; Matsuoka et al., 1989; Morquecho, 2008). Currently the two varieties are only reported to co-occur in the Arabian Sea (Glibert et al., 2002) and the Pacific coast of Mexico (Garate-Lizarraga and Gonzalez-Armas, 2011). Besides the taxonomic differences between the two varieties, Steidinger et al. (1980) also proposed that only the Pacific variety was toxic, while the Atlantic variety was not. In 2002, however, Landsberg et al. (2006) demonstrated that *P. bahamense* var. *bahamense* can produce paralytic shellfish toxins (PST) including saxitoxin (STX), decarbamoyl STX and *M*-sulfocarbamoyl toxins, in clonal cultures and in natural bloom samples from the Indian River Lagoon (IRL). Since 2002, frequent commercial shellfish bed closures have occurred in the IRL and more recently in Tampa Bay and Charlotte Harbor on Florida's west coast which also experience *P. bahamense* var. *bahamense* blooms (Phlips et al., 2006; Lopez et al., 2015, 2019).

*Pyrodinium bahamense* has a typical dinoflagellate life cycle, which includes a heterothallic sexual life cycle that results in an easily recognizable, large, round, spiny resting cyst (Usup et al., 2012). In the paleontological classification system the cyst of *P. bahamense* is referred to as *Polysphaeridium zoharyi* (Bujak et al., 1980). Cysts of *P. bahamense* exhibit a broader geographic distribution than the reported distribution of vegetative cells (Usup et al., 2012). Usup et al. (2012) further suggested that this widespread cyst distribution may underlie the expansion of *P. bahamense* var. *compressum* in the Pacific Ocean since the early 1980's (Maclean, 1989), likely in response to environmental changes rather than new introductions.

Badylak and Phlips (2004) and Phlips et al. (2004, 2006, 2011, 2015) have examined the bloom dynamics of *P. bahamense* var. *bahamense* in the IRL as part of a monitoring program. This species did not occur below 20°C (Phlips et al., 2006, 2011) and had a euryhaline salinity tolerance (10–45) (Phlips et al., 2006). *P. bahamense* var. *bahamense* is found year round in Florida Bay at low concentrations (Phlips et al., 2006), but higher biomass blooms exhibit a seasonality in more northern areas such as Tampa Bay and the IRL, appearing after temperatures exceed 20°C (Phlips et al., 2006). Blooms generally coincide with wet periods with heavy rainfall (Phlips et al., 2006) and Phlips et al. (2020) report a relationship between the peak biomass of *P. bahamense* var. *bahamense* blooms and high rainfall El Niño periods. Although this relationship with rainfall suggests that nutrient enrichment may be important in supporting these blooms, little is known about the nutrient requirements of *P. bahamense* var. *bahamense.* This species grows better in culture medium enriched in natural organic acids such as humic acids and soil extract supplements (McLaughlin and Zahl, 1961; Usup, 1996; Landsberg et al., 2006) and selenium (Usup, 1996; Landsberg et al., 2006). Usup et al. (2012) observed that *P. bahamense* is often found in areas adjacent to mangrove forests, which are a rich source of dissolved organic matter in Florida coastal waters (Jaffé et al., 2004).

A second route of potential human saxitoxin exposure (saxitoxin puffer fish poisoning, SPFP, **Table 1**) was described by Landsberg et al. (2006). From 2002 through 2004, 28 cases were reported from Florida, New Jersey, New York, and Virginia in which people became sick consuming pufferfish which originated in the Indian River Lagoon. Analysis of fish remains revealed saxitoxin in fish tissue (Quilliam et al., 2002) and *P. bahamense* was putatively identified as the toxin source (Landsberg et al., 2006). Monitoring of pufferfish in the IRL for saxitoxin (Abbott et al., 2009) recorded highest levels of saxitoxin in Southern and Bandtail puffer fish skin and elevated concentrations in the gut, gonads and liver. In July 2004, the Florida Fish and Wildlife Conservation Commission issued a permanent prohibition on take of puffer fish in waters of Volusia, Brevard, Indian River, St. Lucie, and Martin Counties.

## Ciguatera Dinoflagellates

Ciguatera fish poisoning (CFP) is a common human illness syndrome resulting from the consumption of large carnivorous marine finfish that have been contaminated with ciguatoxins (CTXs) originating from two benthic dinoflagellate genera, *Gambierdiscus* and *Fukuyoa* (Friedman et al., 2008). While Dawson et al. (1955) were the first to suggest that reef fish become toxic by feeding on poisonous algae, Yasumoto et al. (1977) first identified the dinoflagellate involved as *Gambierdiscus* based on type species of *Gambierdiscus toxicus* R. Adachi & Y Fukuyo described from the Gambier Islands in French Polynesia (Adachi and Fukuyo, 1979). Recently, several globularly shaped *Gambierdiscus* species have been re-classified into a new genus, *Fukuyoa*, based on their phylogenetic and morphological divergence (Holmes, 1998; Litaker et al., 2009; Gómez et al., 2015). Other genera have also been shown to be capable of producing less toxic ciguatera-like toxins, including *Prorocentrum*, *Amphidinium*, *Ostreopsis,* and *Coolia* (Nakajima et al., 1981; Tindall et al., 1984; Tindall et al., 1990; Babinchak et al., 1986). Representatives of all these genera have been reported from Florida coastal waters, especially in warmer south Florida waters in Florida Bay and Florida Keys (**Table 2**).

Ciguatoxins are lipid-soluble polyether compounds with skeletal structures comprised of 13–14 transfused ether rings (Parsons et al., 2012) which act on sodium ion channels causing cell membrane excitability and instability. More than 29 precursor ciguatoxins have been identified from *G. toxicus* cells and herbivorous and carnivorous fish from the Pacific Ocean Lehane and Lewis (2000) and a lesser amount, 12 congeners, identified from Caribbean and Atlantic Ocean fish (Dickey and Plakas, 2010). Significant variations in toxin production occur between *G. toxicus* clones (Dickey and Plakas, 2010).

Commonly associated with reef environments, these dinoflagellate genera are epiphytic, living associated with sand, coral and macroalgal substrates. Ciguatoxins are accumulated by herbivorous reef fish while grazing and these fat soluble toxins are subsequently biomagnified through trophic levels to large predatory fish. High concentrations of ciguatoxins in these fish are undetectable by appearance, taste or smell and are not destroyed by cooking or freezing. More than 400 species of fish are reported to be associated with ciguatera poisoning (Ahmed, 1991; Chateau-Degat et al., 2007; Azziz-Baumgartner et al., 2012; Soliño and Costa, 2020), but the majority of these species probably serve as vectors to higher trophic levels. The vast majority of outbreaks globally directly involve large carnivorous fish such as snappers, groupers, wrasses, and barracudas (Chinain et al., 2020a). In Florida, de Sylva (1994) reported that barracuda comprised 35 of 73 cases of CFS in Florida from 1954 to 1992, followed to a lesser extent by hogfish, groupers and jacks while Radke et al. (2015) report that barracuda and grouper were the most common fish involved in reported CSP cases, 18 and 31% of confirmed ciguatera outbreaks, respectively, between 2001 and 2011.

**TABLE 2 |** Ciguatera associated dinoflagellate species reported from Florida waters.

| Species | Collection area | References |
|---|---|---|
| *Gambierdiscus* sp. | Florida Bay | Parsons et al., 2012 |
| *Gambierdiscus toxicus* Adachi & Fukuyo | Florida Keys | Taylor, 1979; Bergmann and Alam, 1981; Besada and Loeblich, 1982; de Sylva, 1982; Babinchak et al., 1986; Indelicato and Watson, 1986; Bomber, 1987; Bomber et al., 1988a,b; Morton et al., 1992 |
| *G. caribaeus* Vandersea, Litaker, Faust, Kibler, Holland & Tester | | Litaker et al., 2010; Accoroni et al., 2020 |
| *G. carolinianus* Vandersea, Litaker, Faust, Kibler, Holland & Tester | | Litaker et al., 2010; Rains, 2015 |
| *G. carpenteri* Kibler, Litaker, Faust, Holland, Vandersea & Tester | | Litaker et al., 2010; Rains, 2015 |
| *G. yasumotoi* Holmes | | Rains, 2015 |
| *G. belizeanus* Faust | Florida Keys | Litaker et al., 2017 |
| *Fukuyoa* sp. | Florida Keys | Accoroni et al., 2020 |
| *Coolia* sp. | Florida Keys | Besada and Loeblich, 1982; Accoroni et al., 2020 |
| *Coolia monotis* Meunier | Florida Keys | Morton et al., 1992 |
| *Coolia santacroce* Karafas, Tomas & York | Florida Keys | Accoroni et al., 2020 |
| *Ostreopsis* sp. | Florida Keys | Besada and Loeblich, 1982; Babinchak et al., 1986; Bomber et al., 1988a; Accoroni et al., 2020 |
| *Ostreopsis heptagona* Schmidt Norris, Bomber & Balech | Florida Keys | Bomber, 1987; Bomber et al., 1988a; Morton et al., 1992 |
| *Ostreopsis siamensis* | Florida Keys | Morton et al., 1992 |
| *Prorocentrum* spp. | Florida Keys | de Sylva, 1982; Accoroni et al., 2020 |
| *Prorocentrum lima* (Ehrenberg) Stein | Florida Keys | Bomber et al., 1985, 1988a; Morton et al., 1992; Accoroni et al., 2020 |
| *Prorocentrum hoffmanianum* Faust | Florida Keys | Accoroni et al., 2020 |
| *P. concavum* Fukuyo | Florida Keys | Bomber et al., 1988a; Morton et al., 1992 |
| *P. emarginatum* Fukuyo | Florida Keys | Bomber et al., 1988a; Accoroni et al., 2020 |
| *Prorocentrum rhathymum* Loeblich III, Sherley & Schmidt | Florida Bay | Accoroni et al., 2020 |
| *Sinophysis* sp. | Florida Bay | Accoroni et al., 2020 |
| *Amphidinium* sp. | Florida Bay | Accoroni et al., 2020 |

Ciguatera fish poisoning (CFP) is most common in tropical and subtropical environments (35°N to 35°S, Quod and Turquet, 1996; Pottier et al., 2001). Although ciguatera originally occurred primarily in the tropic and subtropics, the expansion of global travel as well as the importation of fish from the tropics (Van Dolah, 2000; de Haro et al., 2003) has expanded its range, and now CFP is the most frequently reported seafood illness in the United States (Fleming et al., 1997; Lipp and Rose, 1997). Annual estimates of individuals affected by ciguatera shellfish poisoning globally range from approximately 10,000 (Bruslé, 1997) to 50,000 (Gervais and Maclean, 1985) to greater than 500,000 per year (Fleming et al., 1998). Within Florida, there is a long history of reports of toxic fish that implicate ciguatoxins. de Sylva (1994) cites a report by Gudger of incidences of toxic barracuda off Key West in 1918 (Gudger, 1918) and subsequent reports of toxic barracuda in the 1940's (Colby, 1943), 1950's (Phillips and Brady, 1953; de Sylva, 1956), 1960's (Baratta and Tanner, 1970) and 1970's (Barkin, 1974; Deichmann et al., 1977). While CSP is more common in Florida's southern counties (Radke et al., 2015), given the large geographical range of predatory fish involved, populations throughout the state that consume these fish are at risk of CSP.

Reviews of the clinical, epidemiological and public health management of CFP are provided by Friedman et al. (2008, 2017), Dickey and Plakas (2010), and Chinain et al. (2020a,b). Ciguatera fish poisoning is characterized by gastrointestinal, neurological, and rarely, cardiovascular effects. Symptoms typically develop within 72 h after fish consumption, often in less than 6 h (Ahmed, 1991). The complexities of the toxins result in up to 355 different symptoms reported in ciguatera victims (Sims, 1987). Although fatalities are relatively rare (0.1–12%, Azziz-Baumgartner et al., 2012), neurological symptoms may persist and develop into a debilitating chronic condition (Mines et al., 1997; Palafox and Buenconsejo-Lum, 2001; Friedman et al., 2008) or may be re-initiated by further consumption of ciguateric fish (Poli, 1982).

The epidemiology of CFP is complex (Friedman et al., 2017; Chinain et al., 2020a,b), which has contributed to difficulties in reporting and management of risk for CFP both globally and locally in Florida. Cases are difficult to diagnose and often only a small percentage of cases are reported (Tester et al., 2010). Radke et al. (2015) examined the epidemiology of ciguatera poisoning in Florida between 2001 and 2011 and reported an incidence of 5.6 per 100,000 individuals, with Hispanic populations, primarily in southern Florida Monroe and Dade counties, having the highest incidence rate and risk. This is consistent with Lawrence et al. (1980)'s estimate of 5–500 cases per 100,000 individuals for 1974–1976 in Florida if the entire state population is considered. These annual caseloads are low compared with regions in the south Pacific Ocean such as French Polynesia, where CFP is highly endemic with 140 cases per 10,000 individuals (Chinain et al., 2010). However, both studies as well as Begier et al. (2006) suggest that these Florida incidence rates are underestimates of the true number of CFP cases in Florida due to underreporting, especially underreporting of non-outbreak associated ciguatera cases (Begier et al., 2006). Indeed, Poli (1982) estimated the annual total case load for combined Dade, Broward, Monroe, and Palm Beach counties at 1,300 cases annually.

There is some evidence that ciguatera is expanding into the northern GoM and north along the United States Atlantic seaboard (Villareal et al., 2007; Gingold et al., 2014). Rongo and van Woesik (2011) present two competing hypotheses to account for CFP outbreaks, the new surface hypothesis and the climate oscillation hypothesis, both of which could apply to Florida and are not mutually exclusive. CFP events are often associated with disturbances to coral reefs, including hurricanes, bleaching, blasting and eutrophication (see lists in Buslé, 1997; Lehane and Lewis, 2000), which theoretically result in additional substrate availability for macroalgal colonization and hence ciguatera dinoflagellate substrate. The spread of ciguatera north in the GoM via the spread of oil platforms which serve as artificial reef and fisheries enhancement structures (Villareal et al., 2007) supports the former hypothesis. Gingold et al. (2014) examined reports to the United States Poison Control Center for CFP from 2001 to 2011 and found an association between monthly CFP calls and both warmer sea surface temperatures and increased tropical storm frequency. This supports the findings of Tester et al. (2010) who reported the optimal temperature for growth for 5 of 6 *G. toxicus* strains was $>29°C$, and that the number of days with temperatures $>29°C$ in the Caribbean has more than doubled in the last 3 decades. Regional projections based on a model output (Kibler et al., 2017) indicated the highest *G. toxicus* growth potential was in the Caribbean Sea shelf waters, with moderate growth in southern Florida and the GoM; the lowest growth potential was in the northern GoM and along the United States south Atlantic coast. If climate change increases 2.5–3.5°C in the Caribbean as projected over the next 100 years, the Gingold et al. (2014) model suggests that the United States will see a 200–400% increase in CFP incidence. This agrees with patterns evident in the Pacific Ocean, where Hales et al. (1999) report strong positive correlations between CFP and sea surface temperatures in warming areas. Other variables that could underlie increases in CFP include south Florida's high immigration rates, changes in fisheries which decrease the relative abundances of larger ciguateric fish, consumer awareness and avoidance of known ciguateric fish species and laws prohibiting or restricting sale of these fish (de Sylva, 1994).

## Diatom HAB Species

### *Pseudo-nitzschia* Species

Diatoms can be harmful either directly, through toxicity, or indirectly through the secondary effects. This includes high biomass resulting in water column anoxia or hypoxia, mucilage production clogging gills, frustule spines irritating gills (Fryxell and Villac, 1999; Fryxell and Hasle, 2003; Sunesen et al., 2009) or a negative influence on aquaculture product taste (Sunesen et al., 2009). Toxicity is not a common feature of diatoms, only three genera, *Pseudo-nitzschia*, *Nitzschia,* and *Halamphora*, are known to be toxic (Sunesen et al., 2009). The first human poisoning directly linked to a toxic diatom occurred in November of 1987, when a group of people consumed mussels harvested from Prince Edward Island, Canada (Subba Rao et al., 1988; Bates et al., 1989) and became ill with gastrointestinal distress, confusion, disorientation, memory loss, and coma. Three individuals died. The causative toxin and responsible diatom was later identified as domoic acid (DA) from the species *Pseudo-nitzschia multiseries* (Kotaki et al., 2000; Lundholm and Moestrup, 2000) and its related human syndrome was called Amnesic Shellfish Poisoning (ASP).

Lefebvre and Robertson (2010) have suggested that DA containing diatom blooms are increasing globally. Of the three known toxic diatom genera, only one, *Pseudo-nitzschia*, a chain-forming, pelagic, cosmopolitan pennate diatom, has been associated with toxins in the GoM. Parsons and Dortch (2002) examined *Pseudo-nitzschia* in Louisiana waters and reported that *Pseudo-nitzschia* abundance has increased in the GoM since the 1950's, with sedimentary records suggesting that this increase may be related to increases in Mississippi River nutrient inputs. High *Pseudo-nitzschia* cell concentrations have also been reported in Alabama coastal waters linked to groundwater nutrient discharge (Liefer et al., 2009; MacIntyre et al., 2011). *Pseudo-nitzschia* species are a common component of marine phytoplankton communities in Florida's estuaries and coastal waters where blooms are common, especially in the spring and fall (Bates et al., 2018). Steidinger et al. (2018) reports that of the 20 known toxic *Pseudo-nitzschia* species identified from the GoM, 11 have been reported from Florida waters (**Table 3**).

*Pseudo-nitzschia* species potentially produce domoic acid (DA), a low molecular weight ($\sim$311 Da), water soluble (Falk et al., 1991) amino acid that is toxic to birds and mammals, including humans (see Todd, 1993; Bejarano et al., 2008; Lelong et al., 2012 for reviews). DA binds to glutamate receptors in the central nervous system, exciting neurons and causing $Ca^+$ input leading to neural death (Chand, 2009). While the impacts of acute exposure to DA in humans is established (Todd, 1993; Pulido, 2008; Lefebvre and Robertson, 2010; Saeed et al., 2017), the potential impacts of long-term low-level chronic exposure in "at risk" human populations are currently unknown (Lefebvre and Robertson, 2010). Biovalves filter *Pseudo-nitzschia* cells and concentrate DA with little impact on themselves but can serve as a vector to marine mammals and humans who consume the shellfish. Seabirds can also accumulate DA and be adversely impacted, likely through consumption of planktivorous fish such as mackerel (Sierra Beltrán et al., 1997). The first significant impacts of DA on wildlife occurred in Monterey Bay in 1991 (Work et al., 1993a,b) and mortality events involving DA and seabirds and marine mammals as well as toxic shellfish have become common on the west coast since 1991 (Scholin et al., 2000; see Trainer et al., 2012 for review), and more recently in the Gulf of Maine and adjacent waters (Hubbard et al., 2015; Bates et al., 2018). In Florida, filter-feeding mollusks such as mussels, cockles, oysters, hard and razor clams, scallops, squids and crustaceans have all been shown to accumulate DA (O'Dea, 2012). DA has also been shown to absorb to sediments (Burns and Ferry, 2007) suggesting that it may be present in benthic food chains. The detection of low levels of DA in dolphins (*T. truncatus*)

**TABLE 3 |** Toxic *Pseudo-nitzschia* species reported from Florida estuarine, coastal and marine waters.

| Species | References |
|---|---|
| *Pseudo-nitzschia brasiliana* Lundholm, Hasle & Fryxell | Parsons et al., 2012 |
| *Pseudo-nitzschia calliantha* Lundholm, Moestrup & Hasle | Phlips et al., 2011; O'Dea, 2012; Parsons et al., 2012 |
| *Pseudo-nitzschia cuspidata* (Hasle) Hasle | O'Dea, 2012; Parsons et al., 2012; Hubbard et al., 2014, 2015 |
| *Pseudo-nitzschia delicatissima* (Cleve) Heiden | Lehman and Wood, 1996; Moreno et al., 1996; Hernández-Becerril, 1998; Moreno-Gutiérrez, 2008; Gallegos-Martínez et al., 2009; Krayesky et al., 2009; Quijano-Scheggia et al., 2011; O'Dea, 2012; Parsons et al., 2012 |
| *Pseudo-nitzschia granii* (Hasle) Hasle | O'Dea, 2012 |
| *Pseudo-nitzschia linea* Lundholm, Hasle and G.A.Fryxell | Lundholm et al., 2002 |
| *Pseudo-nitzschia micropore* Priisholm, Moestrup & Lundholm | O'Dea, 2012 |
| *Pseudo-nitzschia multiseries* (Hasle) Hasle | O'Dea, 2012 |
| *Pseudo-nitzschia obtusa* (Hasle) Hasle & Lundholm | Sullivan, 1978; Krayesky et al., 2009 |
| *Pseudo-nitzschia pungens* (Grunow ex Cleve) Hasle | Saunders and Glenn, 1969; Lehman and Wood, 1996; Hernández-Becerril, 1998; Moreno-Gutiérrez, 2008; Krayesky et al., 2009; Gallegos-Martínez et al., 2009; Licea et al., 2011; O'Dea, 2012; Parsons et al., 2012; Hubbard et al., 2014 |
| *Pseudo-nitzschia pseudodelicatissima complex* (Hasle) Hasle | Conger et al., 1972; Hernández-Becerril, 1998; Moreno-Gutiérrez, 2008; Gallegos-Martínez et al., 2009; Krayesky et al., 2009; Licea et al., 2011; O'Dea, 2012; Parsons et al., 2012; Bargu et al., 2016 |
| *Pseudo-nitzschia turgidula* (Hustedt) Hasle | O'Dea, 2012 |

sampled live during health related surveys in Sarasota Bay (Twiner et al., 2011) and Florida's Panhandle region (Schwacke et al., 2010) and in menhaden and seawater off Louisiana (Del Rio et al., 2010) also supports its presence in pelagic food chains in the eastern GoM. Plasma and intestinal samples from a juvenile green sea turtle (*Chelonia mydas*) stranding event in southwest Florida coastal waters in 2014–2015 also found DA above regulatory limits (Flewelling et al., 2015).

Only three closures of commercial shellfish beds in Florida have resulted from the detection of DA above regulatory limits (20 $\mu$g gm$^{-1}$ tissue), all within St. Joseph Bay, a small enclosed embayment in the central panhandle (O'Dea et al., 2013; Hubbard et al., 2015, 2017). In May of 2013, a 2-month closure was enacted when DA was detected in eastern oysters (*Crassostrea virginica*) at concentrations of 76 $\mu$g g$^{-1}$ tissue (O'Dea et al., 2013). Other seafood, bay scallops (*Argopecten irradians*) and pen shells (*Atrina rigida*), also tested above regulatory limits over the course of the closure coincident with a bloom of *Pseudo-nitzschia cuspidata* (Hasle) Hasle. In October of 2014, DA was again detected in oysters in St. Joseph Bay, coincident with a mixed phytoplankton assemblage that included *P. cuspidata* (Hubbard et al., 2015) resulting in a 3 month closure. From July to September of 2017, a third closure was resulted from detection of DA in whole scallops and pen snails above regulatory limits (Bates et al., 2018). The coincident phytoplankton assemblage during the early stages of closure included *Pseudo-nitzschia pseudodelicatissima* (Hasle) Hasle (Hubbard et al., 2015).

Monitoring for toxic *Pseudo-nitzschia* species and the potential risks associated with DA is difficult for a variety of reasons. *Pseudo-nitzschia* is a ubiquitous member of coastal phytoplankton communities in Florida, but difficult to taxonomically identify to the species level without use of electron microscopy to define frustule morphology. Toxicity is highly variable between species, or even different strains of a *Pseudo-nitzschia* species (Thessen et al., 2009; Bates et al., 2018) and varies with environmental (e.g., upwelling and river runoff) and physiological [e.g., growth rate (Bates et al., 1998; Bates and Trainer, 2006; Howard et al., 2007)] conditions (see Trainer et al., 2012; Bates et al., 2018). Current reservoirs of DA in the environment are unknown but are likely as Bellinger and Hagerthey (2010) reported DA from periphyton in Everglades. While areas with an established history of DA regulatory closures are more routinely monitored (e.g., St. Joseph Bay), the increasing incidences of *Pseudo-nitzschia* spp. blooms globally and in the GoM, as well as links between blooms and river nutrient inputs (Parsons and Dortch, 2002) in the GoM, suggest that the frequency of *Pseudo-nitzschia* blooms and potentially DA occurrences will increase in the GoM and Florida.

## Cyanobacterial HAB Species

Cyanobacteria (also known as blue-green algae) are an evolutionarily old (Hoffman, 1999), diverse group of photosynthetic bacteria that have adapted to a wide variety of habitats, including soils and fresh, estuarine and marine waters (Chorus and Welker, 2021). They are biogeochemically important in marine waters as they contribute significantly to the global carbon and nitrogen (N) cycles via $N_2$ fixation (Graham and Wilcox, 2000; Castenholz et al., 2001) and they often dominate plankton assemblages in freshwater systems. They are of importance to human and environmental health because of the ∼2,000 to 8,000 species identified worldwide (Nabout et al., 2013), and many are able to form extensive blooms and can contain bioactive compounds (Dow and Swoboda, 2000), including a large array of potent toxic and bioactive compounds (Dow and Swoboda, 2000; Shimizu, 2003).

Cyanobacteria are responsible for the majority of freshwater HABs (cyanoHABs) globally (Lopez et al., 2008) and can contain a variety of hepatotoxins [e.g., microcystins (MC) and nodularins], cytotoxins (e.g., cylindrospermopsins), and neurotoxins [e.g., guanitoxin (formerly anatoxin-a(S), Fiore et al., 2020)] which can impact human health and have embryo-lethal, teratogenic, gonadotoxic, mutagenic, and tumor promoting impacts (Kirpenko et al., 1981; Carmichael, 2001; Zanchett and Oliveira-Filho, 2013). Recently, the isolation and identification of a non-proteinaceous amino acid with neurotoxic properties, β-*N*-methylamino-L-alanine (BMAA) (Cox et al., 2003; Metcalf and Codd, 2012), from cyanobacteria and microalgae in both freshwater and marine environments (e.g., Cox et al., 2005; Jiang and Ilag, 2014; Jiang et al., 2014; Lage et al., 2014; Violi et al., 2019) has been a cause for concern due to its identification as a risk factor for neurodegenerative diseases (Bradley and Mash, 2009; Chiu et al., 2011). Evidence supporting a potential link between BMAA exposure and clinical manifestations of Amyotrophic Lateral Sclerosis (ALS), Parkinsonism, and Alzheimer's disease (AD) globally have been variable due to inconsistencies in the analytical methodologies and poor reporting (see reviews by Faassen, 2014; Chernoff et al., 2017) as well as the potential impact of culture conditions and clone variability on alga and cyanobacterial BMAA production (Chernoff et al., 2017). For example, axenic cultures of the filamentous cyanobacteria *Leptolyngbya* PCC73110 exhibited high concentrations of BMAA, but similar measurements of field samples containing a consortia of cyanobacterial species registered two orders of magnitude lower (Spáèil et al., 2010). The detection of BMAA in some diatoms and dinoflagellates (Jiang et al., 2014; Lage et al., 2014) as well as freshwater and marine cyanobacteria (Metcalf et al., 2021) and biota (Brand et al., 2010) from Florida, including shark fin and shark fin supplements (Mondo et al., 2012, 2014) and stranded dolphins (Davis et al., 2019) suggests that the distribution and potential environmental and human health impacts of BMAA in Florida as well as its potential for biomagnification through aquatic food chains (Faassen, 2014) requires further study. Also unknown with regards to cyanobacterial related human health risks in Florida is the possible exposure to cyanotoxins resulting from irrigation of food crops with cyanobacteria-contaminated water (see references in Miller and Russell, 2017). Although many variables influence cyanotoxin accumulation (e.g., plant stage upon exposure, soil bacteria community, toxin concentration, irrigation volumes, and length of exposure), there is a growing body of evidence supporting the potential for cyanotoxin accumulation, especially microcystins, in food crops (Codd et al., 1999; McElhiney et al., 2001; Mohamed and Al Shehri, 2009; Hereman and Bittencourt-Oliveira, 2012; Liang and Wang, 2015; Cordeiro-Araújo et al., 2016; do Carmo Bittencourt-Oliveira et al., 2016; Machado et al., 2017).

Research on the human health impacts of cyanobacteria have largely focused on exposure to and effects of ingesting cyanotoxin contaminated drinking waters (Falconer, 1999; Fleming et al., 2002; Codd et al., 2005; Falconer and Humpage, 2005; Hoeger et al., 2005; Cheung et al., 2013; He et al., 2016; Chorus and Welker, 2021). The EPA established Health Risk Advisory (HRA) levels for the cyanotoxins, cylindrospermopsin and microcystin in drinking waters in 2015 (EPA-820R15101, June 2015, EPA-820R15100, June 2015) and water quality and swimming advisories in 2019 (EPA 822-R-19-001, May 2019). In Florida, Fleming et al. (2002) did report an association between possible exposure to surface water containing cyanotoxins and risk of primary haptocellular carcinoma (HCC), which was not present with ground water or in the general population, suggesting the health effects of cyanobacterial exposure in Florida need further study. Metcalf et al. (2021) has reported both microcystins and BMAA from a variety of freshwater, estuarine and marine environments in south Florida. Little is known of the potential human health impacts of aerosolized cyanotoxins, including BMAA, or the controls on the toxin aerosolization process. Plaas and Paerl (2020), in a recent review of inhalation specific threats associated with cyanotoxins, suggest that aerosolized cyanotoxin production associated with freshwater cyanoHABs may be more widespread than currently known and report values ranging from 91 fg $m^3$ to 50 + 20 ng $m^3$. There are many anecdotal reports describing illnesses related to cyanobacterial exposure in freshwater (Stewart et al., 2006a,b). Backer et al. (2008, 2010) demonstrated that *Microcystis* can be transferred to human nasal cavities during recreational activities (e.g., swimming and boating) in *Microcystis* blooms. Schaefer et al. (2020) reported measurable microcystins in the nasal mucosa of 95% of individuals in contact with *Microcystis* bloom waters in south Florida, with a statistically significant difference between individuals with direct bloom contact and those with no recent contact, and higher concentrations among occupationally exposed individuals. The environmental conditions and length of exposure that cyanotoxins are subjected to during aerosolization may also be important. Cheng et al. (2007) demonstrated that transfer of microcystins to air occurs via a bubble bursting process. Measurements of microcystin-LR aerosol degradation (Jang et al., 2020) have shown that it quickly decays from interactions with sunlight, hydroxyl radicals and ozone (54 min lifetime), although it can still be impactful. Additionally, Sutherland et al. (2021) has reported the aerosolization of anatoxin-a from cyanobacterial populations in a freshwater pond on Nantucket Island, Massachusetts (United States). Combined with reports of aerosolized nodularins (Wood and Dietrich, 2011; Gambaro et al., 2012) and BMAA (Banack et al., 2015), these reports suggest that aerosolization may be widespread among cyanotoxins and is of concern for human health, especially in light of a global increase in cyanoHABs in relation to climate change. The clinical impacts of this inhalation route of cyanotoxin exposures are unknown, as are the acute versus chronic exposure impacts and further study is warranted. Research on the identification and measurement of aerosolized cyanotoxins as well as their links with human health is in its infancy.

CyanoHABs with associated toxins have been reported from more than 50 countries and almost all states in the United States (Loftin et al., 2016). A diverse array of cyanobacterial species have been documented from many Florida waters, including freshwater springs, ponds and lakes, rivers, estuaries and marine environments. Increasingly, toxic cyanoHABs and/or their toxins are being documented in additional freshwater systems within the state, including the St John's River (Havens et al., 2019; Landsberg et al., 2020), Lake Okeechobee (Havens et al., 2003; Kramer et al., 2018), the St. Lucie River (Kramer et al., 2018) and the Caloosahatchee River (Metcalf et al., 2021) as well as some estuarine and marine environments within Florida (Paerl et al., 2008; Tiling and Proffitt, 2017; Lefler et al., 2021; Metcalf et al., 2021). These freshwater and marine cyanoHABs are not necessarily separate events. Some toxic freshwater cyanobacterial blooms, along with their toxins (e.g., toxic *Microcystis* blooms in Lake Okeechobee), are being transferred to estuarine and coastal waters (Oehrle et al., 2017; Metcalf et al., 2021; Tatters et al., 2021) through water management actions (Kramer et al., 2018), a trend for cyanoHABs that is occurring globally (Preece et al., 2017). Metcalf et al. (2021) reports that during analysis of a co-occurring 2018 bloom of *Microcystis* spp. in Lake Okeechobee and *Karenia brevis* in the Gulf of Mexico, brevetoxin was detected at low salinities (0.4 mS $cm^{-1}$) and microcystin-LR at higher salinities (41 mS $cm^{-1}$), indicating that there may be synergistic effects of co-occurring toxins at the freshwater-marine interface.

The first report of toxic cyanobacterial impacts in Florida is relatively recent. Carmichael (1992) reported the first incidence of cyanobacterial toxins associated with a cattle mortality near Lake Okeechobee, however Burns (2008) speculated that cyanoHABs have probably always been present in Florida freshwaters given the prevalence of underlying phosphatic deposits in the state. Shannon and Brezonik (1972) noted the widespread presence of *Microcystis, Dolichospermum,* and *Microseira* in 13 lakes in north central Florida and Nordlie (1976) noted *Anabaena* and *Aphanizomenon* in 3 eutrophied Florida lakes. Analysis of sediment cores from freshwater lakes within the state confirm the historical presence of cyanobacteria through pigment records (Whitmore et al., 2020), although the authors suggest cyanobacterial proliferation in recent decades has occurred in response to eutrophication (Riedinger-Whitmore et al., 2005). Many of Florida's freshwaters are increasingly being subjected to eutrophication (Riedinger-Whitmore et al., 2005; Havens et al., 2019), including Lake Okeechobee (Havens et al., 1996, 2001) and cyanoHABs have become more frequent in the state (Paerl and Huisman, 2008; Havens and Steinman, 2015; Urquhart et al., 2017; Havens et al., 2019).

## *Microcystis* Species

*Microcystis* is one of the most common bloom forming freshwater cyanobacterial genera globally (Fristachi and Sinclair, 2008) and in Florida (Burns, 2008). A coccoid, colonial genus, *Microcystis* cells do not form sheaths, but exist as either single cells, or more often in colonial form aggregated in large (up to 1 cm) colonies within a mucilage comprised of polysaccharide compounds (Xu et al., 2014). Often these surface populations are evident as a thick layer of bright green 'slime' on the surface of freshwater ponds and lakes. Cells contain gas vacuoles which allow them to regulate buoyancy and maintain populations in surface waters under optimal light conditions yet still access nutrients at depth (Walsby et al., 1997). They are also resistant to predation (Michalak et al., 2013; Harke et al., 2016), which can contribute to the dominance and persistence of these blooms.

*Microcystis* has been shown to produce over 100 microcystin (MC) isomers (Díez-Quijada et al., 2019), guanitoxin (Fiore et al., 2020), and BMAA (Fristachi and Sinclair, 2008). Toxin production in *Microcystis* is strain specific, and blooms have been reported to contain both toxic and non-toxic strains (Davis et al., 2009; Wood et al., 2011). Microcystin-LR is the most common microcystin variant and has been classified as possibly carcinogenic to humans (International Agency for Research on Cancer Working Group on the Evaluation of the Carcinogenic Risks to Humans, 2010). Microcystins are monocyclic heptapeptides composed of 5 D-amino acids and 2 variable L-amino acids, which bind with protein phosphatase enzymes, causing cell damage. The major exposure route for humans is through the consumption of contaminated waters (World Health Organization, 1993), although dermal transfer, primarily during recreational exposure, exposure during kidney dialysis (Azevedo et al., 2002), consumption of contaminated food and inhalation are also potential routes (Codd et al., 1997). Given their chemical stability, high water solubility and environmental persistence in Florida freshwaters (Burns, 2008), cyanotoxin exposure is a major public health threat in Florida.

*Microcystis* is prevalent in Florida freshwaters (Williams et al., 2007; Burns, 2008) although toxicity levels are highly variable (Lefler et al., 2020). It forms extensive, reoccurring blooms in the diverse freshwater environments throughout the state, including the St. Johns River (Williams et al., 2007) and Lake Okeechobee (Ramani et al., 2012; Kramer et al., 2018) where blooms are released through water management practices into its tributaries, the St. Lucie (Oehrle et al., 2017; Kramer et al., 2018) and Caloosahatchee (Urakawa et al., 2020; Metcalf et al., 2021) Rivers. Microcystins are found year-round in these systems (Williams et al., 2007). *Microcystis* is not capable of atmospheric $N_2$ fixation and relies upon the uptake of inorganic and organic N forms (Chen et al., 2019), including urea (Wu et al., 2015) and some amino acids (Dai et al., 2009). Increasing N concentrations generally increase the toxicity of both *Microcystis* cultures and blooms (see O'Neil et al., 2012 and references within). Kramer et al. (2018) found significant correlations between MC and total N in a bloom in Lake Okeechobee and suggested that high levels of N inputs favor *Microcystis* blooms. Increasing freshwater N inputs may thus favor the continued dominance of *Microcystis* blooms in Florida's freshwater systems.

## Picocyanobacterial HAB Species

Several cyanobacterial species have formed extensive blooms with associated environmental harm in various lagoonal estuaries in Florida, including both Florida Bay, a shallow (average depth ~1.5 m), 2,200 $km^2$ bay bordered by the Everglades to the north and the Florida Keys to the east, and the Indian River Lagoon, a shallow coastal lagoon on Florida's east coast. Blooms of *Synechococcus* sp., a small (~2 μm diameter) picocyanobacterial genus, was first noted in 1987 in Florida Bay when a bloom resulted in the destruction of 4,000 ha of *Thalassia* spp. (Robblee et al., 1991). These blooms ultimately resulted in a loss of 30% of Florida Bay's seagrass (Hall et al., 1999; Durako et al., 2002) when an extended bloom resulted in extensive seagrass die-offs and associated mortalities (Glibert et al., 2009b,c). These blooms have become a reoccurring feature of Florida Bay, taking place in 1991 and frequently thereafter (Boyer et al., 1999; Phlips et al., 1999; Stumpf et al., 1999; Richardson and Zimba, 2002; Glibert et al., 2004, 2009b,c, 2010) through 2018 (Glibert et al., 2021). Although not directly toxic *per se*, these blooms reach such dense concentrations that light attenuation is diminished, affecting other primary producers such as seagrass. These blooms can be directly harmful to sponges through impacts on filter feeding (Lynch and Phlips, 2000; Peterson et al., 2006; Stevely et al., 2010).

### Benthic and Epiphytic Cyanobacterial Proliferations

*Lyngbya* and *Microseira* (formerly *Lyngbya*) are epiphytic bloom forming cyanobacteria genera that have been characterized as cyanoHABs in Florida. These species exhibit long branching filaments enclosed in mucilaginous sheaths that can form large, smothering, mats in both freshwater (Cowell and Botts, 1994; Stevenson et al., 2007) and marine (Paul et al., 2005; Paerl et al., 2008) environments, including Florida. *Microseira wollei* (Farlow ex Gomont) G.B. McGregor & Sendall ex Kenins (formerly *Lyngbya wollei*) has an increasingly widespread distribution in Florida's freshwater springs and spring fed rivers, including the Silver Glen Springs and Blue Hole Springs (Foss et al., 2012) and Crystal (Cowell and Botts, 1994), and Homosassa (Harr et al., 2008) Rivers. *Lyngbya majuscula* has been reported extensive from estuarine and coastal environments in south Florida (Capper and Paul, 2008; Paerl et al., 2008; Sharp et al., 2009; Tiling and Proffitt, 2017). In addition to being aesthetically displeasing, these genera can contain an array of potential toxins and bioactive compounds (Carmichael et al., 1997; Singh et al., 1999; Milligan et al., 2000; Osborne et al., 2001; Berry et al., 2004; Foss et al., 2012) and their mats can be directly harmful to biota through their smothering impacts (Brinkhuis et al., 2008; Tiling and Proffitt, 2017) or indirectly by displacing more desirable biota within the system. They are also more resistant to chemical controls (Phlips et al., 1992; Dubose et al., 1997; see review by Wood et al., 2020). Their taxonomy is currently under extensive revision (Berthold et al., 2020; Lefler et al., 2021) with multiple new genera descriptions (e.g., *Affixifilum, Neolyngbya, Leptochromothrix, Vermifilum*, and *Ophiophycus*). Recent genetic analysis has also split the genus *Lyngbya* into new genera [e.g., *Moorena* (Engene et al., 2012), *Limnoraphis* (Komárek et al., 2013), *Okeania* (Engene et al., 2013), *Microseira* (McGregor and Sendall, 2015), and *Dapis* (Engene et al., 2018)] so it is likely that the current nomenclature of *Lyngbya* and *Microseira* species identified from Florida fresh and marine waters will be revised.

Marine *Lyngbya* can produce over 70 different toxins (Harr et al., 2008) that are irritants to eyes, skin and the respiratory system, as well as neuroparalytic and cytotoxic compounds (Osborne et al., 2001; Shimizu, 2003; Capper et al., 2013). Foss et al. (2012) reported the presence of PSTs decarbamoylgonyautoxin 2&3 (dcGTX2&3) and decarbamoylsaxitoxin (dcSTX) in *M. wollei* mats in Florida springs as well as evidence supporting the presence of all *M. wollei* toxins (LWT 1–6) and Berry et al. (2004) reported that *Lyngbya* sp. isolated from the Everglades contains pahayokolide A. While there is evidence that marine *Lyngbya* in Florida coastal waters is less toxic other marine *Lyngbya's* globally (e.g., Australia, Dennison et al., 1999), Metcalf et al. (2021) recent report of BMAA production from *Lyngbya* populations in Sarasota Bay suggests that this assumption should be reassessed.

### *Trichodesmium* Species

*Trichodesmium* is a pelagic marine cyanobacterial genus that occurs worldwide in oligotrophic tropical and subtropical waters (Capone et al., 1997). Within the eastern GoM, *Trichodesmium* can form extensive surface blooms in early spring through the fall (Lenes and Heil, 2010), which resemble sawdust on the ocean surface (hence its nickname 'sea sawdust'). This genus is colonial, with cells joined in long filaments called trichomes, which can group together into macroscopic (up to 1 cm) 'tuft' or 'puff' forms (Capone et al., 1997). Cells regulate their buoyancy, often forming surface populations dense enough to be detected by satellite (Hu et al., 2010; Hu and Feng, 2014). These blooms infrequently impinge upon west Florida beaches, where they are mistaken for sewage spills due to their brown coloring.

*Trichodesmium* is an important component of biogeochemical nutrient cycling within the ocean, including the GoM. *Trichodesmium* is a diazotroph and utilizes a specialized Fe-requiring enzyme called nitrogenase to 'fix' atmospheric $N_2$ gas into $NH_4^+$. The scale of $N_2$ fixation by *Trichodesmium* is globally significant (Carpenter and Capone, 1992); it is estimated to account for up to 50% of the N fixed globally in marine systems, between 60 and 80 Tg of N per year (Bergman et al., 2013). Although globally some strains of *Trichodesmium* can produce toxins (Hawser et al., 1992; Kerbrat et al., 2011; Detoni et al., 2016). While not directly toxic, *Trichodesmium* has been implicated as an important nutrient source for offshore initiation stages of *K. brevis* blooms (see "*K. brevis*" section).

## Other Florida Nuisance HAB Species

### Macroalgal HABs ("Drift Algae," "Red Drift Algae," and "Golden Tides")

Large floating mats of a variety of macroalgal genera (e.g., *Gracilaria, Hypnea, Botryocladia, Eucheuma, Sargassum*) have long been recognized to provide critical habitats to a variety of estuarine and marine biota in Florida (Thorhaug and Roessler, 1977; Gore et al., 1981). Recent large accumulations of these macroalgal mats, popularly known as 'drift algae' or 'red drift algae' have, however, become increasingly problematic in Florida estuarine and coastal marine waters. Many species of macroalgae respond to increasing nutrient supply by increasing their biomass (Lapointe et al., 1994; Morand and Briand, 1996; Valiela et al., 1997). Early reports of drift algae accumulations of *Gracilaria* and *Ulva* spp. in Tampa Bay from the 1960's to the early 1980's were attributed to eutrophication within the Bay (Humm, 1973; Guist and Humm, 1976; Avery, 1997). In 2003–2004, Lee County beaches in southwest Florida began to experience large Rhodophyte blooms which washed ashore on beaches in large quantities which was attributed to local increases in nutrient inputs (Lapointe and Bedford, 2007). While not directly toxic, these mats resulted in a variety of environmental problems including dissolved oxygen depletion, displaced species, habitat destruction, increases in arsenic and fecal coliform counts, changes in biogeochemical cycling and seagrass and coral die-offs (Lapointe et al., 1994, 2020; McGlathery, 1995; Valiela et al., 1997; Board and National Research Council, 2000). Large macroalgal accumulations on beaches result in unpleasant odors and are aesthetically displeasing to beachgoers, negatively impacting tourism and incurring significant costs by local municipalities for their repeated physical removal (Morand and Briand, 1996; Lapointe and Thacker, 2001). Their continuing annual reappearance on beaches in south Florida during summer months suggests that they have become an ongoing environmental problem. Although the effects of climate change on drift algae is unknown, it is likely that increasing temperatures and coastal nutrient inputs may increase the frequency and spread of the phenomena north and southward from the tropics. This may indirectly impact the spread of other HAB species as Besada and Loeblich (1982) and Bomber et al., 1988a,b suggest that these drift algal mats may also play a role in the circumtropical dispersal and spread of ciguatera dinoflagellates in the region by providing a drifting substrate of epiphytic ciguatera causing dinoflagellates.

The macroalgal genus *Sargassum* has become particularly problematic in the Caribbean Sea and southern Florida coastal region since 2011 (Franks et al., 2011; van Tussenbroek, 2011; Smetacek and Zingone, 2013), forming massive blooms termed "golden tides" (Smetacek and Zingone, 2013) for their gold-colored pigments. Wang et al. (2019) described the great Atlantic *Sargassum* belt, a 8,850 km area of *Sargassum* extending from the African coast to the GoM that has been reoccurring since 2011, and which in 2018 contained more than 20 million metric tons of biomass with significant associated environmental and economic issues. Although the causes and dynamics of the belt are not well understood, Wang et al. (2019) hypothesize that it is supported by nutrients derived from west African coastal upwelling in the winter, and Amazon River discharge in the spring and summer. Johns et al. (2020) analysis of drifter groundings demonstrated that *Sargassum* present in this belt from 2011 to 2012 was transported into the GoM to the Florida Keys. *Sargassum* was particularly problematic in 2018, when large *Sargassum* masses drifted onto Miami's beaches.

### Ecosystem Disruptive Algal Bloom (EDAB) Species

Since 2012, 'super blooms' of the brown tide pelagophyte *Aureoumbra lagunensis* have occurred in the IRL, a narrow, shallow, poorly flushed (Smith, 1993) 240 km long estuary on Florida's east coast (Gobler et al., 2013; Kang et al., 2015; Lapointe et al., 2015, 2017; Judice et al., 2020). Although not toxic, these blooms are an example of an ecosystem disruption algal bloom (EDAB, Sunda et al., 2006; Gobler and Sunda, 2012), or an algal bloom which significantly alters or degrades ecosystem function. *Aureoumbra lagunensis* is a small (2–5 $\mu$m), non-descript (Koch et al., 2014) phytoplankton that contains the accessory pigment fucoxanthin (DeYoe et al., 1997) and reaches sufficiently high concentrations (200 $\mu$g $L^{-1}$ Chl *a*, $>10^6$ cells $L^{-1}$ in the 2012 IRL bloom, Gobler et al., 2013) to attenuate light, resulting in seagrass loss. High cell concentrations in the 2012 IRL bloom resulted in finfish and shellfish kills due to the bloom-induced near hypoxic conditions resulting in a decline of these organisms and/or reductions in shellfish clearance rates (Gobler et al., 2013).

*Aureoumbra lagunensis* blooms have been a recurring feature of the Laguna Madre and Baffin Bay in Texas for more than 20 years (Buskey and Hyatt, 1995; Buskey et al., 1998; Buskey et al., 2001; Villareal et al., 2004) prior to their spread to the IRL in 2012 (Gobler et al., 2013) and Cuba in 2013 (Koch et al., 2014; Hall et al., 2018). This species is resilient in hypersaline conditions (Buskey et al., 1998; Liu and Buskey, 2000) and outcompetes phytoplankton under conditions of reduced N, especially dissolved organic N, low P (Kang et al., 2015) and high N:P ratios (Liu et al., 2001). The IRL is hypereutrophic (Bricker et al., 2007), with nutrient inputs shifting from point-source dominance in the 1980's to non-point source inputs such as sewage enriched in reduced N forms (Virnstein and Carbonara, 1985; Barile and LaPointe, 1999; Barile, 2018). This species has been shown to preferentially take up $NH_4^+$ and urea in the IRL where the bloom was characterized by lower $\delta^{15}$N stable isotope values, suggesting support by regenerated N compounds (Kang et al., 2015). Nutrient enrichment alone may not explain the dominance of *A. lagunensis* in the IRL, however. Grazing avoidance has also been demonstrated for *A. lagunensis* in the IRL (Kang et al., 2015) as has allelopathy (Kang and Gobler, 2018). A resting stage has also been documented for *A. lagunensis* (Kang et al., 2017), which may allow this species to avoid adverse environmental conditions as well as facilitate the spread of these blooms.

## CLIMATE CHANGE AND FLORIDA HABs

Climate change represents the ultimate anthropogenic stressor in Florida. Levels of $p\text{CO}_2$ have risen from pre-industrial age levels of 280 ±10 ppm to current levels of over 400 ppm, largely due to fossil fuel burning and deforestation (Pörtner et al., 2019). Climate change is undoubtedly influencing aquatic systems worldwide in many nuanced, complex and interacting ways, resulting in increasing water temperatures, lower pH, changes in vertical mixing, stratification and upwelling, as well as changes in storm intensities and freshwater inputs (McMichael et al., 2006; Patz et al., 2006; Laws, 2007). How climate change is potentially influencing HABs globally is an important issue and poses many challenges to resource managers, but has only recently received significant scientific examination (Geesey and Tester, 1993; Hallegraeff, 1993, 2010; Tester, 1993; Wells et al., 2015; Gobler, 2020; Yan et al., 2020 and references therein). One reason for the lack of research has been the difficulty in differentiating the effects of climate change on HABs from other anthropogenic stressors (e.g., eutrophication, ballast water introductions, Moore et al., 2008). Tester and co-authors suggested potential impacts of climate change on the Florida red tide dinoflagellate *K. brevis* in the early 1990's (Tester, 1993) and scientists have increasingly linked a variety of both freshwater and marine HABs to climate change globally (Dale et al., 2006; Edwards et al., 2006; Moore et al., 2008; Paerl and Huisman, 2008; Hallegraeff, 2010; O'Neil et al., 2012; Glibert et al., 2014; Havens and Paerl, 2015; Wells et al., 2015; Gobler, 2020 and articles contained within). However, only in 2019 have HABs been directly linked to climate change by the United Nations' Intergovernmental Panel on Climate Change's (IPCC) Special Report on the Ocean and Cryosphere in a Changing Climate (Pörtner et al., 2019). The links between climate change and HABs are explored in a recent special issue of the journal Harmful Algae (see Gobler, 2020 and references within).

Florida is considered especially susceptible to the impacts of climate change (Obeysekera et al., 2011), with its warmer, nutrient rich waters. Eight of the 10 cities in the United States identified as most susceptible to climate change costs are in

Florida (Muro et al., 2019). Generalized as warming, acidification and deoxygenation (Gobler, 2020), the specific climate change impacts likely to impact Florida include sea-level rise (Reece et al., 2013), increasingly intense weather and heavy precipitation events (Knutson et al., 2010; Emanuel, 2013; Contento et al., 2018, 2019; Marsooli et al., 2019), marine fishery declines (Cheung et al., 2009), water pollution (Moss et al., 2011; Glibert, 2020), and reef and habitat loss (Snedaker, 1995; Manzello et al., 2007; Tobey et al., 2010; Okazaki et al., 2017). There is a general consensus that climate change is predicted to increase the frequency of both freshwater (O'Neil et al., 2012; Havens and Paerl, 2015) and marine HABs (Hallegraeff, 2010) through a variety of direct and indirect mechanisms. The impacts of climate change on Florida HABs are likely to vary with species involved, and range from direct impacts at the cellular level (e.g., cell metabolism) to regional impacts on spatial and temporal range expansions. Additionally, indirect effects of climatic associated changes, such as the impacts of changing hurricane intensities on local rainfall and runoff, may supply additional nutrients to blooms or alter the physical characteristics of the water column through increasing stratification. At the same time, alterations in food webs and nutrient cycling and trophic interactions resulting from changing temperatures and $CO_2$ levels add additional layers of complexity to both studying and predicting the impacts of climate change on HABs.

Climate change has been predicted to impact HABs in Florida in a number of ways. Warming waters may act to expand the geographical range and bloom duration of some HAB species, pushing tropical and subtropical species northward and extending their bloom seasons. This was suggested as a potential impact for both GoM *K. brevis* blooms by Tester (1993) as well as for ciguatera dinoflagellates (Tester et al., 2010). Transport of *K. brevis* blooms from southwest Florida to the east coast of Florida has frequently occurred (Tester and Steidinger, 1997) with subsequent transport as far north as North Carolina in 1986 (Tester et al., 1991) where the bloom persisted for 4–5 months and resulted in closures of shellfish harvesting areas with an estimated $25 million loss (Tester and Fowler, 1990). Unlike *K. brevis*, most of the 11 other *Karenia* species present in the Gulf [e.g., *Karenia mikimotoi, Karenia papilionaceae, Karenia selliformis, Karenia umbella* (Steidinger et al., 2018)] have a widespread distribution globally, suggesting that the potential exists for an increase in their occurrence in the GoM. Within the United Kingdom, *K. mikimotoi* has spread northward, possibly due to change in the timing of stratification (Davidson et al., 2009; Bresnan et al., 2013; Townhill et al., 2018) and Turner et al. (2015) suggest that warming waters may favor other *Karenia* species in United Kingdom waters. Ciguatera dinoflagellates may be especially responsive to increasing water temperatures. A correlation between abundance of the ciguatera dinoflagellate *G. toxicus* and increased sea surface temperatures during El Niño has been reported for the south Pacific (Hales et al., 1999; Chateau-Degat et al., 2005), where ciguatera has been recognized to be spreading since the 1970's (Maclean, 1989; Hallegraeff, 1993). Villareal et al. (2007) documented how the prevalence of offshore oil rigs in the GoM has allowed the expansion of ciguatera dinoflagellates northward by providing substrate. Although Florida does not have oil rigs within its coastal waters, Villareal et al. (2007)'s documentation of *G. toxicus* associated with *Sargassum*, which is increasing in abundance in both the Atlantic Ocean and the GoM (Dierssen et al., 2015; Wang et al., 2019), suggests that other vectors for transport of ciguatera dinoflagellates northward in Florida waters exist. Warmer waters may also influence the spread of ciguatera indirectly through impacts on the coral substrate itself. Ciguatera has been noted to increase in tropical and subtropical regions where reef systems have experienced some form of anthropogenic disturbance, such as physical reef destruction due to storm damage or coral bleaching due to rising temperatures (Skinner et al., 2011; Rongo and van Woesik, 2013). Reef destruction can lead to increasing microalgal colonization, providing additional substrate for benthic dinoflagellate species, including *G. toxicus*. In south Florida, ongoing degradation of the Florida Key reef tract (Kemp et al., 2011; Colella et al., 2012; Lapointe et al., 2020) and southeast Florida reefs (Lapointe, 1997) with increasing associated macroalgal colonization has been well documented.

Climate change has been cited as one of the factors contributing to the increase in cyanoHABs globally (Paerl and Huisman, 2008; O'Neil et al., 2012; Paerl and Paul, 2012; Yan et al., 2020) as well as within Florida (Paerl and Huisman, 2008; Havens and Paerl, 2015; Urquhart et al., 2017; Havens et al., 2019). Climate change influences cyanobacteria directly through temperature effects on metabolism as well as environmentally through impacts on the physical and chemical characteristics of the cyanoHABs environment. Cyanobacteria have a higher temperature optimum for growth than do eukaryotes (Paerl and Huisman, 2008), suggesting that they have a competitive advantage over other algae as temperatures increase. A relationship between water temperature and cyanobacterial dominance has been noted for many systems (de Figueiredo et al., 2006; Paerl et al., 2011). Carey et al. (2012) suggested that there are many other physiological advantages that favor cyanobacteria to effectively outcompete other algae under warming conditions, including buoyancy, P storage affinity, atmospheric $N_2$ fixation and efficient light harvesting ability. The increases in rainfall and frequency of extreme rainfall events predicted to result from climate change (Groisman et al., 2012) may also favor cyanobacteria through increased N and P nutrient loading to freshwaters, as well as changes in the quality and quantity of this loading, the volume ratio of inputs to receiving waters and its seasonal timing (Reichwaldt and Ghadouani, 2012). Additionally, increasing temperatures have a direct effect upon the physical characteristics of freshwater systems, resulting in earlier (Winder and Schindler, 2004) and stronger stratification and reducing vertical mixing (Xu et al., 2010) and longer residence times (Lehman et al., 2013; Cross et al., 2014). This may lead to potential oxygen depletion at depth and P enrichment from sediments, thus enhancing nutrient recycling (Søndergaard et al., 2003; Wilhelm and Adrian, 2008). The net effect of these climate change associated changes in freshwater systems, including those in Florida, is favoring of cyanobacteria over other algae.

Many HAB species, especially dinoflagellates, have life cycles characterized by benthic resting stages or cysts, stages that allow a species to survive adverse environmental conditions. Within Florida, both *P. bahamense* and *A. lagunensis* have resting stages. Cysts of *P. bahamense* have a much broader global geographic distribution than do vegetative cells of this species (Zonneveld et al., 2013; Brosnahan et al., 2020), suggesting that there are many areas globally, and within Florida, that currently do not experience *P. bahamense* blooms but may be primed to do so by the presence of cyst beds. Cyst beds of *P. bahamense* have been documented from the Indian River Lagoon, Tampa Bay and in Charlotte Harbor (Phlips et al., 2006), with highest vegetative cell concentrations occurring in the area where resting cysts are concentrated ($>10^3$ cysts gm wet weight$^{-1}$ of sediments) in Tampa Bay (Lopez et al., 2015). Concentrations of 300–900 cysts gm wet weight$^{-1}$ of sediments have been reported from the IRL (Brosnahan et al., 2020). The environmental conditions under which *P. bahamense* resting cysts are produced and excyst in Florida populations is unknown. Brosnahan et al. (2020) suggests that as warming changes species ranges, cyst beds may persist longer in shallow nearshore areas that exhibit more seasonally variable temperatures, contributing to the potential for increasing *P. bahamense* blooms and associated PSP or SPFP events northward within Florida as warming occurs. Florida state HAB monitoring data suggest that currently a bloom maximum of $10^6$ cells L$^{-1}$ of *P. bahamense* exists within Florida waters (Brosnahan et al., 2020).

An additional indirect impact of climate change is ocean acidification. As $p\mathrm{CO_2}$ concentrations rise in the atmosphere, increasing $\mathrm{CO_2}$ concentrations dissolve in seawater. $\mathrm{CO_2}$ in seawater dissolves to form carbonate species which disassociate and produce hydrogen ions, leading to a decrease in the pH of seawater, termed ocean acidification (OA). Changes in pH can influence both growth and toxicity in some HAB species (Griffith and Gobler, 2020). Several early studies of natural systems (Yoo, 1991) and natural populations within mesocosms (Hinga, 1992) report a positive correlation between pH and dinoflagellate abundance. Although this is counter-intuitive to an increase in HABs resulting from the decreasing pH associated with OA, the relationship does not hold for diatoms (Hinga, 2002) and there are significant clonal and species differences in the dinoflagellate responses (Hinga, 2002). Under low pH and high $p\mathrm{CO_2}$ concentrations, *Pseudo-nitzschia multiseries* (Hasle) Hasle increases domoic acid production (Sun et al., 2011; Tatters et al., 2012), although this has been shown to be strain specific with some producing domoic acid under high pH conditions (Lundholm et al., 2004; Trimborn et al., 2008). Reported effects of increasing $p\mathrm{CO_2}$ on *K. brevis* are somewhat contradictory. Errera et al. (2014) reported higher growth rates at higher $p\mathrm{CO_2}$ concentrations, but did not find any relationship between toxin concentrations and either temperature or $p\mathrm{CO_2}$ concentrations. In contrast, Hardison et al. (2014) reported reduced growth and enhanced toxicity under reduced $p\mathrm{CO_2}$ concentrations. Bercel and Kranz (2019) however, did not find a significant response in growth, cellular carbon and N quotas, nor in photosynthetic rates over a $p\mathrm{CO_2}$ concentration range from 150 to 780 μatm. They reported no statistically significant, correlation between $p\mathrm{CO_2}$ and brevetoxin content, but a strong effect on *K. brevis* acquisition of inorganic carbon, with an increase in half saturation values for $\mathrm{CO_2}$ (from 1.5 to 3.3 μM), a switch in inorganic carbon preference from $\mathrm{HCO_3}$- to $\mathrm{CO_2}$, and downregulation of external carbonic anhydrase activity. They concluded that *K. brevis* employs an efficiently regulated carbon concentration mechanism to maintain constant carbon fixation and growth across $p\mathrm{CO_2}$ levels. Although Bercel and Kranz (2019) conclude that net photosynthesis of *K. brevis* is not impacted by $p\mathrm{CO_2}$, the work of Errera et al. (2014) and Hardison et al. (2014) suggests that at the very least there are significant clonal differences in *K. brevis* response to pH and $p\mathrm{CO_2}$ concentrations which require further study before a reasonably assured prediction can be made of the impacts of changing $p\mathrm{CO_2}$ and pH can be made for *K. brevis* blooms.

Climate change impacts HAB species on spatial scales ranging from subcellular metabolism to oceanic gyres and on temporal scales from nanosceconds to decades. These large and variable scales involved as well as complex trophic interactions and feedbacks make predicting the response of Florida HABs to climate change problematic. While the conclusions that climate change will result in HAB range expansion and increased frequency, changes in abundances and seasonal growth windows and secondary effects for marine food webs (Hallegraeff, 2010) are generally agreed upon by scientists, extensive strain- and strain-specific responses, dynamic interactions between species as well as non-linear responses in HAB growth and toxin production to climate related stressors (Griffith and Gobler, 2020) suggest that predicting these impacts is currently problematic and presents an immense challenge for HAB researchers, monitoring programs and managers.

## FUTURE CHALLENGES ASSOCIATED WITH FLORIDA HABs AND HAB RISK MANAGEMENT

There are many unknowns regarding HABs in Florida, the most immediate of which are those related to human health risks. Transfer of algal toxins to humans via consumption (e.g., contaminated shellfish) is well documented for many toxins, but emphasis has been on acute health impacts of exposure. The chronic impacts and health risks associated with low level toxin exposures in shellfish and finfish are unknown. With the increasing importance of seafood in diets (Love et al., 2020), this exposure route is predicted to become increasingly important. This is especially important for new and emerging toxins, such as the cyanobacterial toxin BMAA. Little is known of the environmental and physiological factors influencing its production, transfer through aquatic food webs, route(s) of transmission to humans and clinical impacts and biomarkers of exposure. Study of potentially important toxin transfer routes, such as aerosolization of brevetoxins and cyanobacterial toxins, are in their infancy. Study of these routes is especially important given the increase in freshwater cyanobacterial blooms in Florida, and the transport of these blooms and associated toxins to estuarine and marine waters (Preece et al., 2017), such as occurred in 2018 when the Lake Okeechobee *Microcystis* bloom was released down the St. Lucie and Caloosahatchee Rivers.

Harmful Algal Blooms species other than those described in the text above have been noted or bloomed within Florida waters, including some with known toxins. An example is the dinoflagellate *Peridinium quinquecorne* T.H. Abé, which has bloomed in coastal areas with restricted circulation and elevated nutrient inputs, resulting in localized anoxia. Although these blooms are often viewed as isolated events, with Florida's ongoing anthropogenic stressors, including changing demographics, coastal development, eutrophication and climate change impacts, conditions may be changing in such a manner as to potentially make environmental conditions more favorable for HAB species in Florida waters in the future. Toxicity is variable in some HAB species, but has also been shown to vary with nutrient supply as well as environmental conditions [e.g., *Pseudo-nitzschia* spp. (Tatters et al., 2012), *K. brevis* (Hardison et al., 2012; Hardison et al., 2013)] and thus is also potentially impacted by changing conditions. Indirect impacts of current HABs, e.g., altered food webs, may potentially contribute to new HAB occurrences. New HABs may also occur through the promotion of species present in the "hidden" plankton (Steidinger et al., 2018), through invasive species brought to Florida waters by currents or from ballast water or sediment introductions. The 'unknown HAB', an unidentified bloom forming species or one that has yet to present itself as a threat due to unidentified toxicity, is impossible to predict and remains a major challenge for management and monitoring agencies. Perhaps the best example of this to date in Florida is the appearance of toxicity associated with *P. bahamense* in the Indian River Lagoon, where it had never previously been noted for this species in the Atlantic.

Ascribing different HABs to causative or contributing anthropogenic and natural stressors and identifying and developing appropriate mitigation strategies to address these stressors and curb their impacts require establishing trends in bloom frequency, magnitude and duration, which in turn, requires a timeline of relevant measurements, collected in a statistically valid manner. Given their often episodic occurrence and the event response nature of HAB monitoring, these types of long term data sets are rarely available for HABs. Bloom history can be recorded in sediment cores if a suitable proxy for the HAB of interest is available. In Florida's estuarine and marine systems, which are generally characterized by non-depositional carbonate or limestone sediments or subjected to extensive reworking due to anthropogenic activities, establishing this sedimentary record is especially problematic. Turner et al. (2006) examined the sedimentary record from Charlotte Harbor and found a threefold increase in N loading to the estuary over the past 200 years. Increased carbon loading from the N-limited phytoplankton has resulted in increasingly anoxic bottom sediments as a result. However, a more detailed analysis of total phosphorus (TP), total N (TN), and $NO_3^-$ and $PO_4$ at the mouth of the Caloosahatchee River (Anderson et al., 2008) from 1949 to 2005 clearly shows the influence of shifting state agricultural trends (e.g., the shift to sugar agriculture in southwest Florida post Cuban Revolution) as well as municipal and federal laws restricting or banning P in detergents from the 1970's onward (ReVelle and ReVelle, 1988) on shorter time periods.

Although a long-term record exists for *K. brevis* blooms in Florida and has been used to argue a link between a potential trend in increasing frequency and coastal eutrophication (Brand and Compton, 2007), the database upon which the argument is based was compiled in 2000 (Haverkamp et al., 2004) and consists of records of *K. brevis* cell concentrations compiled from >70 entities, with water samples collected at irregular intervals over variable time and spatial scales, often in event response mode. This makes statistical analysis of this database extremely problematic (Steidinger, 2009; Heil et al., 2014a). It is only with an established monitoring program of stations sampled at regular intervals during both bloom and non-bloom conditions that statistically valid conclusions may be drawn.

As stated previously, the ongoing, continual immigration of people into Florida translates into more potential HAB exposures from current known HABs. As more people move to Florida, whether for economic reasons or for access to Florida's rich coastal resources, more people are potentially exposed to existing HABs and their toxins. Florida's economy is heavily reliant on tourism, and much of this tourism is focused on the coastal environment, including clean beaches and available resources. This lack of public knowledge of HABs may be especially dangerous in a state in which a high percentage of the population is transient, e.g., tourists with stays of limited duration, with little knowledge of HABs, their potential impacts or how to avoid exposure. Regardless of long-term HAB trends, the demographics of Florida populations suggest that more people are experiencing and being exposed to these blooms than ever before.

Within Florida, demographic, developmental and environmental changes have been ongoing for over 100 years. These continual changes make establishing a realistic predevelopment baseline for both water quality and HABs problematic, which in turn may give false impressions of past environmental conditions surrounding HABs, making it difficult for policy makers and environmental managers to set appropriate restoration and management guidelines. This difficulty in establishing a water quality and HAB baseline is similar to the concept of a 'shifting baseline,' originally proposed by Pauly (1995). Developed to explain the inability of fisheries scientists to incorporate historical fisheries data to be used as a reference point between generations of fisheries scientists, and the tendency for scientists to use inappropriate reference points as a baseline for the state of the science at the beginning of their careers, the concept has been expanded into the shifting baseline syndrome (SBS) and applied to many other disciples [e.g., ethnobotany (Hanazaki et al., 2013), habitat loss (Humphries and Winemiller, 2009), pollution (Lyytimäki, 2013), and climate change (Herman-Mercer et al., 2016)]. It describes a gradient change in the accepted environmental 'norm' over time due to lack of experience, memory or knowledge (Soga and Gaston, 2018) and how people can falsely perceive environmental change over time. The concept is readily applicable to the perception of environmental change and HABs in Florida, especially both in assessing long-term changes in HABs over time as well as their relationship to climate change and degrading water quality. As an example, new Florida resident's experience of *K. brevis* blooms date to their first experience, which with recent immigrants, is the severe 2017–2019 *K. brevis* bloom which lasted for 17 months and resulted in extensive respiratory irritation, fish kills and marine seabird and mammal mortalities. The perception of this bloom as the 'status quo' for red tides has tempered public responses to the bloom itself as well as subsequent blooms and management practices (e.g., management related Lake Okeechobee releases) perceived to have influenced this bloom.

Recent studies on media exposure, risk perceptions and visitor behavioral responses (e.g., Cahyanto and Liu-Lastres, 2020) has underscored the need for effective outreach to visitors and residents alike regarding risks associated with HABs in Florida. Indeed, knowledge of Florida red tide was found to be widely inconsistent and incorrect (Nierenberg et al., 2010) with the media framing red tide as a largely environmental issue (Li et al., 2015). Advances in knowledge of HAB human health impacts and mitigation have not been effectively communicated to the public and the risk perception regarding shellfish consumption during red tides has declined (Kuhar et al., 2009; Kirkpatrick et al., 2014). In some cases, both risk perceptions and misconceptions have been socially amplified, which has been identified as a contributor to many Florida Red Tide messaging issues (Kuhar et al., 2009; Nierenberg et al., 2010). Social media undoubtedly plays a role in risk perception and social amplification regarding misconceptions with regards to HABS in Florida, but has not been assessed. Targeted messaging and unique products developed early in projects and utilizing appropriate media for the targeted stakeholders has been shown to be an effective communication strategy for HABs (Nierenberg et al., 2011). However, effective communication of HAB associated human health, environmental and economic risks in Florida remains challenging.

## AUTHOR CONTRIBUTIONS

All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

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