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Assessing the Potential for Range Expansion of the Red Tide Algae Karenia Brevis

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By

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Table of Contents

ABSTRACT:
Phytoplankton communities are vital to oceanic ecosystems. While most are harmless or beneficial, a select group possesses the capability to produce toxins and cause mass die-offs of marine organisms. Florida red tide, caused by blooms of the dinoflagellate *Karenia brevis*, is common in the Gulf of Mexico, although blooms have been transported to the Atlantic coast and impacted estuaries where *K. brevis* is not normally found. An in-depth overview of compiled estuary research evaluated the possibility of the continued spread of Florida red tide blooms to Southeastern Atlantic estuaries and the likelihood of establishment in non-native regions. A rank-scoring system was used to better depict the potential for red tide expansion. With inland river systems providing estuaries with freshwater, excessive nutrient build-up supports eutrophication. Waterflow dynamics prove to be a contributing factor in bloom establishment. Florida and North Carolina estuaries, which tend to have poor flowrates and excessive anthropogenic nutrient loading, have had documented cases of red tide blooms. Georgia and South Carolina estuaries, in contrast, have high flowrates and little nutrient loading, and few algal blooms have occurred. Although bloom populations of *K. brevis* have been successfully transported beyond native ranges, complete establishment has not yet occurred. Based on key environmental factors, the possibility of red tide expansion to Southeast Atlantic estuaries is low to moderate, but climate change and rising sea levels may result in an increased risk of further expansion.

KEY WORDS: Harmful algal blooms, *Karenia brevis*, Florida red tide, Southeastern Atlantic estuaries

1. Introduction

Phytoplankton are a cornerstone of marine ecosystems. These primary producers form the base of oceanic food webs and contribute to oxygen production via photosynthesis in the water column. Phytoplankton community composition is remarkably expansive and includes the two main groups of diatoms and dinoflagellates. Diatoms are characterized by a protective silica shell, while dinoflagellates have one or two flagella that enable movement throughout the water column. There are roughly 4000 species of marine microalgae in the world oceans, and each species can occupy a vast oceanographic range (Smayda and Reynolds 2003, Masó and Garcés 2006). Both diatoms and dinoflagellates can survive in a multitude of locations when conditions are favorable.

At times, environmental conditions can result in an algal bloom. A bloom is perceived as an increase in cellular biomass, creating an unbalance between phytoplankton growth and loss processes (Carstensen et al. 2007). The specific set of conditions that can fuel the exponential growth of an algal community can consist of multiple factors, such as excess nutrient runoff and water column stratification (Paerl and Scott 2010). This overgrowth of algae can become problematic for other species of algae and larger marine animals, especially during periods of exponential algal growth (Arzul et al. 1999).

While most species of marine microalgae are harmless and beneficial, at least 200 species are capable of producing harmful toxins in response to external stressors such as low nutrient availability (Smayda and Reynolds 2003). Therefore an overgrowth of these species is termed a Harmful Algal Bloom (HAB). HAB's are a well-known phenomenon in waters throughout the world, in both fresh and marine waters. Approximately 90% of these 200 harmful species are dinoflagellates (Smayda and Reynolds 2003). One key species of harmful dinoflagellate in the Eastern Atlantic and the Gulf of Mexico is *Karenia brevis*, and blooms of this algae are familiarized as Florida red tide. Specific to the U.S. southern coastline, it is recognizable due to the reddish-brown water discoloration associated with it.

1.1 Cellular characteristics:

Cell size in *K. brevis* ranges between 20 to 40 µm in diameter. This unicellular phytoplankton is surrounded by four cellulose plates, which are secreted by membrane-bound vesicles below the cell membrane. Two transverse and longitudinal grooves occur between the cellulose plates, and a pair of flagellum are attached within these grooves. One flagella is wrapped around the cellular body within the transverse groove, while the second flagella extends from the longitudinal groove. This second flagella produces the forward locomotion that dinoflagellates are known for. Movement through the water column enables movement towards essential energy sources and nutrients.

What makes *K. brevis* such a formidable species of harmful algae is the production of brevetoxin (PbTxs), which are lipid-soluble polyether neurotoxins that disrupt sodium channels in vertebrates (Poli et al. 1986, Baden et al. 2005). Exposure to brevetoxin results in depolarization of sodium channels in nerve cell membranes, leading to distorted functioning of muscle groups and cardiac complications (Alcock 2007). There are several different structural forms of brevetoxins, but the most common is Brevetoxin B (PbTx-2) (Pierce et al. 1986). Despite having cellulose plates, the organism itself is rather fragile and easily ruptures, releasing brevetoxin into the water and air.

1.2 Growth conditions:

Understanding the growth conditions that are suitable for the survival and exponential growth of *K. brevis* is key to forecasting the occurrence of blooms, both within and outside the known range of this species. By examining the factors which contribute to existing growth patterns of *K. brevis* algae, it is possible to identify similar conditions that lead to new locations for optimal growth. *Karenia brevis* is typically found on the shallow coastal shelf in the upper and lower water column, within a temperature range of 9ºC (48ºF) to 33ºC (92ºF) and a salinity range of 24 PSU to 37 PSU. The optimal range for exponential growth is 22ºC (72ºF) and 28ºC (82ºF), and 31 PSU to 37 PSU (Steidinger et al. 1998).

Blooms begin offshore and are eventually carried to inshore inlets by wind and ocean currents, where nutrients of terrestrial origin are fully exploited for growth (Tester and Steidinger 1997). Rainfall and river flow can significantly increase the terrestrial nutrient runoff total (Dixon 2003). Inlets mimic the specific water density gradients of offshore conditions, where different gradient factors of salinity and temperature can replicate favorable conditions for Florida red tide, creating an easy transition point for bloom transport (Alcock 2007).

The conditions under which *K. brevis* grows are typically nutrient-poor, and the blooms make use of recycling or regenerating nutrients from multiple sources which vary over time (Alcock 2007). Groundwater and bottom sediments can contain essential nutrients that are released through disturbance events such as cases of extreme weather conditions (Hu et al. 2006). Collective nutrients in sediments originate from surface waters as sinking detritus, or groundwater seepage of porewater pumping downstream of topographic features, which can be broken down into compounds to be utilized by the phytoplanktonic community (Sinclair et al. 2009, Vargo et al. 2007). Fluctuations in available nutrients can also come from coastal upwelling of deep nutrient-rich waters. Nutrients are thus available in different quantities throughout different cellular life stages but can be inconsistent from year to year (Alcock 2007). It remains unclear which nutrient combinations are key to consistent blooms (Walsh et al. 2007)

Florida red tide algae are not restricted to surface water; *K. brevis* cells can be distributed throughout the water column (Walsh et al. 2003). Individual cells operate on a diel cycle, migrating to the surface at night to uptake nutrients and consume microalgae, then retreating to a meso-layer range of 0-25 m during the day (Henrichs et al. 2015). The cellular duplication process is slow compared to other phytoplankton. *Karenia brevis* may go through one cellular division in 2-3 days, possibly due to larger cell size, while most phytoplankton can divide three to four times in a single day (Alcock 2007). Studies have found that *K. brevis* cells living at depths of 60 m replicate on an extended time scale, where cells near the substrate replicate every 6-10 days, which is three times the normal time scale (Sinclair et al. 2009). *K. brevis* cell size can also be a contributing factor to the few successful East coast acclimation events. The large size of cells occurring at depth indicates the ability to sustainably reserve energy for when populations are prone to long distances (Mckay et al. 2007).

The slow growth cycle leads to the prediction of the existence of a slow nutrient uptake process. However, this dinoflagellate can outcompete other community phytoplankton species given an extended cellular growth cycle. While certain phytoplankton specialize in optimizing the uptake of organic nutrients and low amounts of inorganic nutrients (Bronk et al. 2014), *K. brevis* is well-adapted to thrive in such locations (FWRI 2007c). The inorganic forms of nitrogen, ammonium (NH_4^+) and nitrate (NO_3^-) are the most important nutrients for estuarine systems where blooms take place (Bronk et al. 2014). Both nutrient forms play a crucial part during the beginning and intermediate growth phases of *K. brevis* blooms, however, it is unknown what amounts trigger the growth phases.

One of the leading environmental factors that initiate algae blooms is the introduction of excess nutrients, often from an anthropogenic source. The major source of anthropogenic nutrients is the use of agricultural and recreational (gardens, golf courses, etc.) fertilizer. Fertilizer is chemically composed of ammonia and carbon dioxide. While its uses are invaluable, it severely alters the nutrient balance in estuaries. Surface water concentrations of nitrogen have been measured at ~0.42 mg/L in southwest Florida, which is higher than the average amount of available nitrogen (<0.1 mg/L) (Thompson et al. 2012, Kennicutt II 2017). The nutrient ratio for marine water averages 1 phosphorus for every 16 nitrogen. Phosphorus concentrations on surface waters would calculate to be 0.026 mg/L, which is still above average for nutrient levels. The nitrogen concentration in Gulf coastal systems has gradually increased over the years, and can impact coastal bloom size as nitrogen is readily utilized by *K. brevis* (Anderson et al. 2002).

While *K. brevis* blooms outcompete much of the phytoplankton community, either by nutrient uptake or direct brevetoxin exposure, not all species of microalgae are negatively impacted by *K. brevis*. The algae group *Trichodesmium* is commonly found to coexist with the occurrence of *K. brevis* blooms. It provides an additional nitrogen source along with nitrogen-fixing bacteria. The excess nitrogen provides a supply source to further nourish *K. brevis* blooms. Iron is the nutrient that fuels the nitrogen fixation and one of the few nutrients where an abundant amount is supplied directly from its given source from across the Atlantic Ocean. African dust storms have been a relevant connection between the blooms of *Trichodesmium* and the Florida red tide (Mulholland et al. 2006). By studying *Trichodesmium*'s resistance to *K. brevis* brevetoxins, new species may be discovered within the same phytoplankton community that are also resistant to brevetoxins.

1.3 Impacts:

Coastal estuaries along the eastern Gulf of Mexico have experienced Florida red tide before urban development. Once construction began in the early 1900s, Florida red tide remained a present issue. With continued coastal urban development and improper coastal management, anthropogenic sources of nutrients sustain much larger blooms than that which would occur naturally, with Florida red tide events have increased in frequency and duration (Anderson et al.

2008). This has resulted in ongoing negative impacts for residents of urban and environmental communities in the coastal zone. Hazards to terrestrial organisms occur when the waterborne brevetoxin becomes airborne through disturbances at the air-sea boundary (such as white-capped waves) (Pierce et al. 1989, Pierce et al. 2005). Wildlife, such as birds, fish, and marine mammals are affected by both waterborne and airborne brevetoxin (Flewelling et al. 2005). Inhalation, ingestion, and physical contact with brevetoxin can lead to illness and, in some rare cases, death. An early warning sign of Florida red tide is mass fish mortality, which results from the ingestion of either direct consumption of brevetoxin, *K. brevis*, or other contaminated foods leading to muscle paralysis and respiratory failure (Kirkpatrick et al. 2004). Direct exposure to Florida red tide brevetoxin is not the only cause. Depending on toxin concentration, primary and secondary consumers can accumulate and transfer toxigenic phytoplanktonic chemicals throughout the trophic levels of pelagic food web structures (Bricelj et al. 2012), creating severe physiological incapacitations for those primary grazers (Cohen et al. 2007). Full recovery of fish communities from one seasonal red tide event could take several years, and multiple harmful bloom events within a given season could substantially extend the recovery process.

Humans are equally susceptible to the negative impacts of brevetoxins. Waterborne brevetoxin can occur when individuals make contact with red tide water, which could theoretically be prevented simply by avoiding the bloom. Airborne toxins are less avoidable and can be widely dispersed. In humans, airborne toxin exposure is primarily characterized by respiratory irritation (Pierce et al. 2005). It is advised for those with medical lung conditions, such as asthma, to avoid public beaches and coastlines during an active Florida red tide event. The risk escalates when airborne toxins travel inland, possibly as far as a mile from waves breaking on the shoreline, depending on the intensity and direction of the wind (Kirkpatrick et al. in prep). Another form of brevetoxin exposure is through the consumption of contaminated seafood. Commercial harvesting of shellfish is an important industry in coastal economies and supports community livelihoods. Bivalves feed on the microalgae suspended throughout the water column, and toxins can persist in invertebrate tissue for an average of 2-8 weeks for native species (Echevarria et al. 2012, Mcfarland et al. 2015). Contaminated shellfish that aren’t properly treated by depuration can cause neurotoxic shellfish poisoning (NSP) or other related illnesses in consumers (Naar et al. 2002).

Economic damages are inevitable when toxic algal blooms occur. To better understand the severity of the damages, four points of economic interest are analyzed for impact: public health, commercial fisheries, recreation and tourism, and monitoring and management (Anderson et al. 2000; Hoagland et al. 2002). Tourism and recreation in Florida coastal communities alone generates most of the state's revenue. While the economic losses caused by Florida red tide blooms are estimated in the millions, it is difficult to calculate an accurate assessment of total costs. One study estimated $82 million in economic impact from all HABs across the United States between 1987 and 2000 (Hoagland and Scatasta 2006). In Florida, roughly $240 million in economic impact was estimated for the Tampa region alone during a 2005 HAB, according to the St. Petersburg/Clearwater Visitors and Area Convention Bureau (Moore 2006). These two examples of impact costs are a few of many variations of economic loss and displacement caused by Florida red tide blooms.

1.4 Management strategies:

To counter the damage caused by Florida red tide, certain management strategies have been tested to decrease the impact. There are three categories of management strategies: Prevention (stop blooms from occurring), control (focus on killing or neutralizing the harmful algae and removing it from the water), and mitigation (limit the impact without dealing directly with the red tide) (Boesch et al. 1997). Not every strategy can combat every Florida red tide event, any given occurrence requires careful planning to properly handle the situation. The following collection of strategies have seen success in the field, but are not yet proven to be broadly applicable to future cases.

1.4.1 Prevention:

While the practicality of prevention methods are disputed, they can be effective when properly executed. The central challenge is informing and educating the public regarding proper practices to minimize anthropogenic effects. One issue that may arise is the reliability of relevant research to support claims of impact. If urbanization and nutrient pollution from human activity is not supported by scientific research, then it is unlikely that coastal operations will adjust their actions based on mere speculation. Besides the evidence provided by research, public support is essential to prevention planning. Exercising precautions will help reduce the incidence and extent of Florida red tides (Alcock 2007). Public education and outreach to those greatly affected by Florida red tide will receive immediate attention. Further prevention measures can be extended to HAB contributors further inland such as agriculture,

Nutrient pollution from agricultural operations is difficult to monitor directly. Non-point nutrient pollution sources vary from watershed to watershed and from basin to basin (Alcock 2007). Reductions in nutrient pollution will often require certifications and permits to limit the amount of discharge, and permit programs such as the National Pollution Discharge Elimination System (NPDES) are crucial in maintaining water quality standards. Coastal discharge is one of several sources of nutrients that support blooms and the actions taken throughout coastal watersheds can greatly reduce nutrient pollution. Any given source does not contain every nutrient required by a full-scale bloom, however, a combination of several non-point sources can provide the nutrient amounts and types needed (Walsh et al. 2007). This highlights the importance of implementing prevention methods regardless of the difficulty inherent in monitoring nutrient pollution.

1.4.2 Control:

The presence of *K. brevis* is constant but only becomes an issue when the population grows to a size where brevetoxins are produced. When prevention strategies either fail or are never implemented, new strategies must combat the existing blooms, including changing nutrient ratios, limiting nutrient availability, and diluting water masses (Alcock 2007).

One strategy is the use of flocculant clays to clump algae cells together without disrupting the cellular integrity, with the clumps proceeding to sink to the bottom sediments. In theory, the cells die and the brevetoxin is buried in the sediments where it degrades over time. While a successful method, flocculants can only be applied during certain tidal cycles in small-scale locations. Phosphatic clay is the ideal flocculant, but alternatives of sand and chitin composite are being researched (Sengco and Anderson 2004).

A second strategy is ozone injection, which is commonly used to treat and sterilize drinking water as it kills bacteria and other harmful microorganisms. It also kills *K. brevis* cells and destroys brevetoxin (Pierce et al. 2003). The issue with this strategy is the lack of specific targeting when dispersing ozone. Upon injection, it takes several seconds for high concentrations of ozone to kill any organism within its dispersed range. This leads to unnecessary casualties to untargeted organisms (Schnieder et al. 2004). Thousands of other chemical compounds have been and are continually tested to find new combinations that are effective in controlling Florida red tide blooms, but few have proven effective (Marvin and Proctor 1964).

The presence of a natural bacterial-algal interaction of *K. brevis* blooms has given rise to new strategies of controlling Florida red tide. By both direct and indirect contact, select strains of *Cytophagal*/*Flavobacterium*/*Bacteroidetes* (CFB)-bacterium cause algicidal lysis of *K. brevis* cells (Roth et al. 2008). Observations after contact with the bacterium has revealed cyst-like growths on the exterior of *K. brevis* cells. The effectiveness of this strategy depends on the requirement of direct contact with the algal cells. so it can be effective but consequently unpredictable between bloom populations.

1.4.3 Mitigation:

It is vital to maintain constant surveillance of bloom activity at all stages of cellular growth. Technology has proven an effective means to monitor activity; satellite tracking and intensive monitoring programs are indispensable for collecting vital data on bloom growth and transport. The use of FlowCAM cytometers can be very useful for identifying specific cells and collective sizes in water samples. By narrowing the algal species present within a phytoplanktonic community, finding a specific species is made easier. Implementing cell recognition software is especially beneficial for identifying important cell groups (Buskey and Hyatt 2006). New technological advancements have proved successful in supporting monitoring programs, providing the ability to cover more regions. The Harmful Algal Blooms Observing System (HABSOS), a national program under NOAA, provides updates on existing blooms for coastal states. Under its guidelines, locations of existing blooms, alerts regarding bloom development, and predictive probabilities of bloom occurrence became more expedient.

HAB’s cause several negative impacts, and new branches of research develop to investigate new potential strategies to combat them. The Humans Dimensions Research strategy for Harmful Algal Blooms (Bauer 2006) considers aspects of socio-economic and human health impacts with a distinct focus on water quality. The results correlate with the prevention strategy of outreach programs to public audiences. By communicating risks associated with HAB’s in an easy-to-understand manner to the public, media trust and engagement will be better organized. Even though there are continual challenges with consistency and public feedback, public education about the impacts and prevention of red tide is the most important strategy to combat Florida red tide.

1.5 History:

Harmful algal blooms occur on an annual basis, but do not always cause direct or indirect damage. It is thus beneficial to have a detailed record of HAB events to better understand the frequency and level of intensity. The oldest cases of Florida red tide in the Gulf of Mexico were documented in 1948-1949, and further evidence implies that blooms have been native to the West Florida Shelf for hundreds if not thousands of years (Alcock 2007). There has been a considerable change in Florida red tide abundance from the 1954-1963 period to the 1993-2003 period (Brand and Compton 2006). It is difficult to research the intensity of past blooms without sufficient data or sediment records, however. Once documentation of Florida red tide cases began, HAB research has continually progressed. Based on historical data, it was hypothesized that an increase in terrestrial-sourced nutrients was the cause of the Florida red tide phenomenon. Past research implies that land-use activity is strongly correlated with nutrient concentration and red tide bloom activity (Alcock 2007). Currently, new initiatives to monitor new blooms and the potential impacts they cause have proven successful. One example is the Coastal Zone Management Act and the addition of the Harmful Algal Bloom and Hypoxia Research and Control Act. The 1998 joint effort became the forerunner for maintaining coastal water quality, with an increasing focus on research.

In 2005 and 2018, Florida red tide blooms were some of the most severe on record (Alcock 2007). The 2018 red tide bloom in particular grew large enough for a population to break off and move around the Florida peninsula. It became one of the rare instances where the Gulf-native algae contaminated the Florida Atlantic coast. Over the course of surveying the bloom's movement, a high-density concentration was sampled in the Indian River Lagoon (IRL) (Figure 1). The lagoon is a shallow, narrow, bar-built estuary averaging ~0.8m deep and ~3km wide (Steward and VanArman, 1987) that stretches North to South for 248km. Freshwater river-runoff enters from submarine groundwater discharge and inflows from tributaries and local canals (B.E. Lapointe et al. 2015). The build-up of nitrogen and phosphorus in the north portion of the IRL is adequate to support substantial blooms. Because of the geographical structure of the inlets and the long water residence time, the IRL has become highly susceptible to eutrophication caused by water discharge from near-by urban and agricultural land use, making the region prone to algal blooms (Lapointe et al. 2015).

According to the survey map (provided by the Florida Fish and Wildlife Conservation Commission), *K. brevis* concentrations within the IRL were as dense as the Gulf of Mexico populations at >1,000,000 cells per liter. South of the IRL, population densities were lower, with average counts of >10,000-100,000 cells per liter in the lower 4 counties of St. Lucie, Martin, Palm Beach, and Broward. North of the IRL, however, *K. brevis* densities were much lower (<1,000 cells per liter). It is likely that the IRL was the initial starting point from which the Florida red tide expanded, but due to the lack of tidal mixing and shallow depths of the lagoon, HABs are not able to travel further north from the northern inlet.

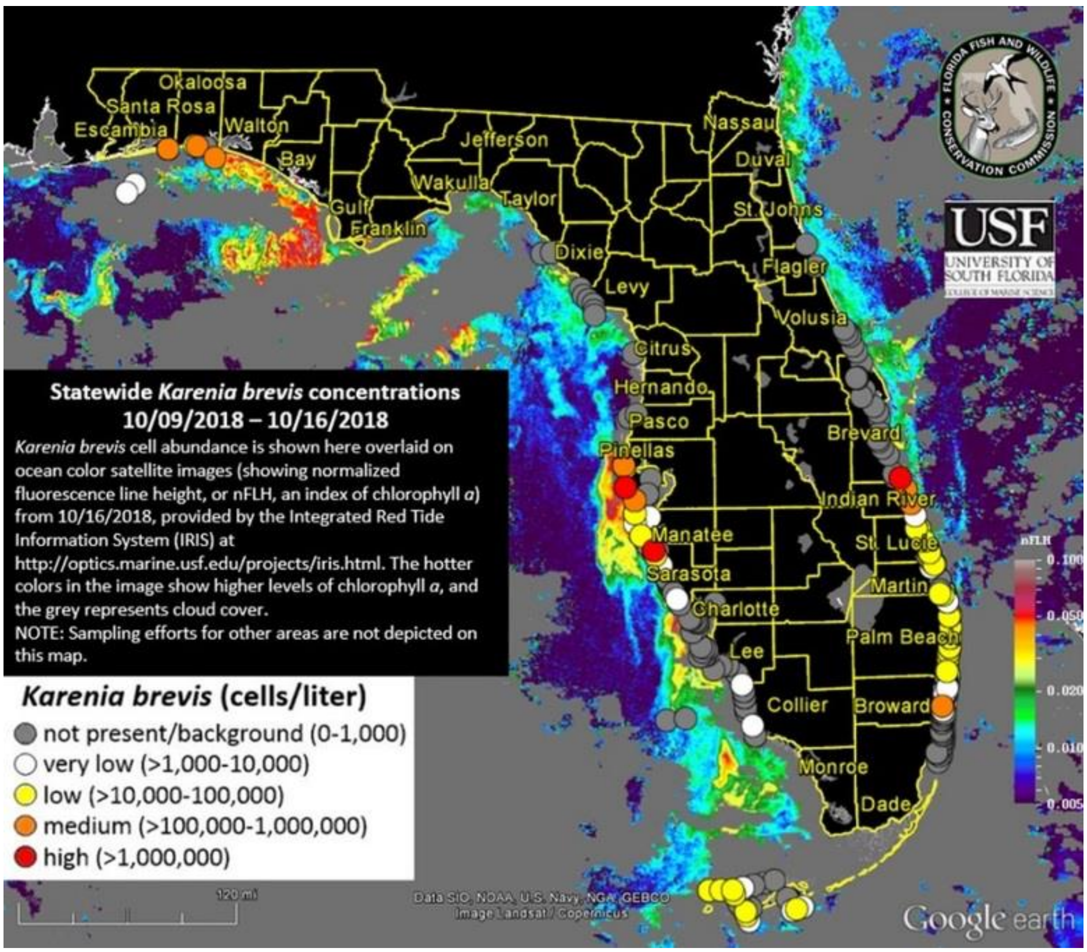

Figure 1. Map showing the cell concentrations of *Karenia brevis* in October 2018 across the coastline of Florida (Photo credit: Florida Fish and Wildlife Conservation Commission).

1.6 Monitoring conditions:

Blooms of harmful algae species have devastating effects on marine ecosystems and coastal communities. When taking sample collections of Florida red tide, it is important to remain unbiased and consistent for monitoring purposes; sampling strategies and patterns must be equally distributed whether a bloom is present or not. The acquisition of water quality data pertaining to Florida red tide algae concentrations has only been established since 1998 (Alcock 2007), thus it is unclear whether patterns in past data are based on event response data or systematically collected data. Because past data is possibly unreliable, it is often advised to disregard any data collected before 1998.

2. Objectives:

The main objectives of this research were threefold. First, what are the environmental factors that support the formation of red tide in Florida? The environmental factors that both trigger and support historical Florida red tide blooms were evaluated, based on a compilation of the known history of Florida red tide, as well as the furthest range that any bloom has expanded. Conditions that contribute to blooms including salinity, temperature, water flow, and nutrient loading were evaluated. This research required extensive compilations of water quality, nutrient pollution, and Florida red tide outbreak data from published literature and from federal/state water quality databases of the USGS and the National Estuarine Inventory.

Second, what neighboring coastal regions hold similar environmental factors that would be suitable for red tide expansion? Adjacent areas where contributing conditions exist in regions outside the Gulf of Mexico were assessed. Based on historic evidence, Florida red tide has been tracked as far north as North Carolina; therefore, coastal water quality data from South Florida to North Carolina was included.

Finally, can *K. brevis* population blooms become successfully established if introduced to new regions? The potential for the successful expansion of red tide (if introduced) to nearby regions was evaluated, and coastal regions with risk factors deemed vulnerable to Florida red tide were identified. Data was implemented into predictive assumptions, and the overall potential success of red tide introduction was based on a comparison score with the native region of Florida red tide.

3. Methods:

An overview of the Southeastern Atlantic coast was compiled by Dame et al. 2000. It is comprised of a well-detailed analysis of the status of estuaries of the south Atlantic coast of North America. Estuaries from Florida, Georgia, South Carolina, and North Carolina (Figure 2) were reviewed based on location, influential physical parameters, biotic components, and anthropogenic influences. The specific locations discussed served as references for this study since the description of each location is an informational starting point in understanding these ecosystems. Additional estuary sites from the Gulf of Mexico were compared with Southeastern Atlantic estuaries to examine potential differences in estuaries that are within the native range of Florida red tide. Estuaries from the Florida Gulf coast and Southeast Texas were reviewed based on their past exposure to the native Florida red tide (Figure 3). Further analysis of the estuaries was achieved by compiling similar works indicating the changes in data following 20 years since initial data collection.

Figure 2. Map of the Southeastern Atlantic Coast illustrating coastal sedimentary deposits of the Atlantic coastal plain (yellow highlights). The red marks indicate the locations of interest within the study. (Photo credit: USGS public domain).

Florida: Estuaries in review (From southern coast to northern coast): Biscayne Bay, Indian River Lagoon, and the St. Johns River.
Georgia: Estuaries in review (From southern coast to northern coast): St. Marys River and Cumberland Sound, St. Andrew Sound/St. Simons Sound/ Satilla River, Altamaha River, Ossabaw Sound/Ogeechee river, and Savannah River.
South Carolina: Estuaries in review (From southern coast to northern coast): Helena Sound/S. Edisto River/Coosaw River, Charleston Harbor/Wando River/Cooper River/Ashley River, North/South Santee River, and Winyah Bay/Pee Dee River/Black River/North Inlet.

North Carolina: Estuaries in review (From southern coast to northern coast): Cape Fear River, New River, Bouge Sound, Neuse River, Pamlico River/Pungo River, and Albemarle Sound/Chowan River/Roanoake River.

Figure 3. Map of the Southern United States Coast along the Gulf of Mexico. The red marks indicate the locations of interest within the study. (Photo credit: Empty Lighthouse Magazine).

Florida: Estuaries in review (From southern coast to northern coast): Ft. Myers, and Tampa Bay.
Texas: Estuaries in review: Corpus Christi Bay

Gulf of Mexico Estuaries:

1) **Tampa Bay (FL)** – A large harbor on the west central coast of the Florida peninsula. The bay is divided into sections with the ocean connecting with Lower Tampa Bay, followed by Middle Tampa Bay then splitting into Old Tampa Bay to the north and Hillsborough Bay to the northeast.
2) **Corpus Christi (TX)** – Southeast Texas holds a chain of barrier islands that stretches more than 113 miles along the coast. The collection consists of seven barrier islands that encloses a series of estuaries with few inlet connections both natural and man-made. Corpus Christi Bay has past reports of *K. brevis* blooms along with other sites among southeast Texas, but the city of Corpus Christi is centralized among the estuaries and experiences high anthropogenic impact though port activity. Surrounding land-use operations are concentrated on agriculture, leading to high nutrient loading (Quenzer 1998).

East Florida Estuaries:

1) **Biscayne Bay** – A large southern bay and central drainage point for Florida that has a slightly lower salinity than the surrounding saltwater due to surface freshwater inputs. The amount of groundwater entering the bay has decreased as urbanization and canal construction increased (Stalker et al. 2009). The bay contains shallow seagrass beds and fringing mangrove swamps. It is a popular tourist destination for recreational activities. While reports of algal blooms in Biscayne Bay exist (Collado-Vides et al. 2013), there are no instances of extended periods of high concentrations of Florida red tide.
2) **Indian River** – A large-scale coastal inlet that is located in the Central District of Florida East Coast. It stretches north and south providing an array of estuary habitats and drainage points. Seagrass beds provide shelter for hundreds of marine species, providing species-rich habitat systems (Gilmore 1995). Anthropogenic impacts are common due to local urbanization and habitat destruction.
3) **St. Johns River** – The longest river in Florida draining approximately one-fifth of the water from St. Lucie and Indian River Counties into the Jacksonville/Mayport area (Demort 1991). It is a coastal plain with a northward-flowing river.

Georgia Estuaries:

1) **St. Marys River / Cumberland Sound** – Constitutes extensive salt marshes and sand flat. St. Marys River provides freshwater input to the sound, although it supports a low discharge rate into a well-mixed estuary system (Fagerburg et al. 1992). The tidal changes provide mixing and constant salinity changes.
2) **St. Andrew / St. Simons Sound / Satilla River** – A series of rivers leading to salt marsh estuaries protected by barrier Islands (Cia et al. 2000). Satilla River comes from the coastal plain further inland.
3) **Altamaha River** – A coastal plain estuary with salt marshes and low-lying islands. The river flow peaks during spring and is driven by freshwater discharge, tidal mixing, and wind/wave flow (Kang and Iorio 2005).
4) **Ossabaw Sound / Ogeechee River** – Ogeechee river is broken into a North and South channel that supplies freshwater from a 7000 km^2 watershed (Wenner et al. 2005).
5) **Savannah River** – The river bordering the state lines of Georgia and South Carolina. It is approximately 320km long before discharging into the Atlantic (Mendelsohn et al.1999). The watershed basin covers 27,500 km^2 throughout Georgia, South Carolina, and inland North Carolina.

South Carolina Estuaries:

1) **Helena Sound / S. Edisto / Coosaw River** – A complex estuarine river system where the Coosaw river connects the overall region. The interconnecting rivers throughout the sound are important habitats for shellfish fisheries. With a steady increase in population, this location is gradually becoming impaired with anthropogenic pollution (Conrads et al. 2002).

2) **Charleston Harbor / Wando / Cooper / Ashley Rivers** – The Charleston Harbor is fed by the Wando, Cooper, and Ashley's freshwater discharge. The surrounding areas consist of salt marshes where tidal action affects the salinity of the river upstream. Being the site of several river re-diversion projects, the salinity increased and altered sediment suspension (Althausen Jr. and Kjerfve 1991).
3) **North/South Santee Rivers** – A small river delta system that was once the fourth largest river system on the east coast. In 1941, the water discharge was diverted to the southern Coopers River to provide hydroelectric power to an established dam (Pearlstine et al. 1985).
4) **Winyah Bay / Pee Dee River / Black River / North Inlet** – This is part of the upper physiographic region of South Carolina (Patchineelam et al. 1999). Winyah Bay is the drainage point for the surrounding rivers and the shared watershed basins. Salt marshes are the dominant environment.

North Carolina Estuaries:

1) **Cape Fear River** – A large-mouthed river estuary with overlying marshes. It controls several factors including salinity, temperature, and sediment (Xia et al. 2007).
2) **New River** – Consists of a series of broad and shallow lagoons. It was once one of the most eutrophic estuary systems among the Southeastern Atlantic, suffering from phytoplankton blooms (Mallin et al. 2005).
3) **Bogue Sound** – One of the locations impacted by the 1987 red tide event (Summerson and Peterson 1990). Cell concentrations of red tide were at its highest over the course of its permeation. Its geography is similar to the Indian River Lagoon; a large-scale coastal inlet that stretches East to West.
4) **Neuse River** – A river system prone to high eutrophication, algal blooms, low oxygen zones, and fish killings (Stow et al. 2001). The nutrient loading is strongly based on rapid population growth and agricultural development.
5) **Pamlico River / Pungo River** – The Pamlico River is a shallow, turbid system that is also well oxygenated (Kuenzler et al. 1979). It is a major fishery location with strong water circulation powered by wind and freshwater discharge (Copeland et al. 1984). The two rivers feed freshwater discharge into the Pamlico Sound, the largest sound in the state.
6) **Albemarle Sound / Chowan / Roanoake River** – Impacted by increasing population and poor agricultural practices. Its shallow nature makes it highly susceptible to eutrophication and nutrient build-up (Hazen and Esch 1983).

An analysis of introduction success was conducted by using a ranking system to compare similarities between Southeastern Atlantic estuaries and the native region of *K. brevis*, as *K. brevis* cells have specific conditions in which populations can thrive. These conditions were compared for commonalities in other regions and assigned a rank indicative of successful commonalities. The more similar categories are, the higher the rank of score for a potential success of bloom introduction within that given region. Certain factors were likely to be less important than others due to the nature of phytoplankton survival. For example, since *K. brevis* can exist in a wide range of salinities, most estuaries will score a “successful” rank in the salinity category. This makes categories such as temperature and salinity less important in the overall potential success rating.

Seven environmental factors served as categories: Salinity [Practical Salinity Unit (PSU)], Temperature (ºC), Tidal Flow (m), Water Flow (m^3/s), Turbidity [Nephelometric Turbidity Unit (NTU)], Nitrogen (mg/L), and Phosphorus (mg/L). Topographic features and coastal geography were not taken into account for the ranking. *Karenia brevis* is known to survive in certain environmental conditions; salinity of 24-37 PSU, temperature of 22-26ºC, tidal range of <1m, water flow of 8.5-37 m^3/s, turbidity of 3.6-9.6 NTU, nitrogen of 0.31-0.5 mg/L, and phosphorus of 0.026 mg/L (Steidinger et al. 1998, USGS Caloosahatchee River). These specific categories are based on data collected from the Ft. Myers area, which experiences a red tide event on an annual basis. Environmental factors from each estuary site were given a rank score for each category, which varied depending on that factor’s placement within the ranged conditions of *K. brevis*. Temperature and salinity are important factors to the scoring system but are likely to experience similarities when comparing estuary sites due to the wider temperature and salinity ranges. Based on this assumption, the score range for the temperature and salinity categories go from 0, where the factor is not within *K. brevis* survivability range, to 1, where the factor is within *K. brevis* survivability range. Flow-based categories (tidal flow, water flow, turbidity) follow a 0-2 score range for its environmental factors. If an environmental factor is within the range, the given score is two. If an environmental factor is placed out of range but within the inter-quartile range, the given score is one. If an environmental factor is placed beyond inter-quartile range, the given score is zero. The nutrient categories for nitrogen and phosphorus followed a different set of guidelines as well as a different score range. Excess nutrient runoff is a leading cause of phytoplankton blooms, with higher nutrient levels fueling larger bloom sizes. This lead to a gradual increase in score with an increase in nutrient concentration. Therefore, low-level nutrient concentrations that are below the known concentrations that exist during Florida red tide will receive lower scores of 0 or 1. Nutrient concentrations that are within the average range for Florida red tide blooms will receive a score of 2. Further nutrient concentrations greater than the average range for Florida red tide blooms will receive high scores of 3 or 4. The category score for each estuary was then summed to provide an overall rank score out of 16. A score of 16 indicated that an introduced population of *K. brevis* would be very likely to succeed in establishment, whereas a lower score would indicate that an introduced population of *K. brevis* would be unlikely to successfully establish.

Data was not available for every environmental factor for most of the estuary sites. In these cases, instead of a single score for these sites, a ranged score was used based on the potential outcomes of the missing data points and resulted in a minimum and maximum score range.

4. Results:

Gulf of Mexico Estuaries:

Corpus Christi Bay, TX:

Florida red tide events do not occur every year, but past reports have speculated that blooms are transported to the Southeastern Texas coastline. Although Corpus Christi Bay is located in the Western Gulf, estuary conditions are favorable for Florida red tide blooms. Salinity and water temperature are consistent with ranges of 32-27 PSU and 29-21ºC (Lee and Dunton 1996). Much of the water stratification is wind-driven, with little addition from river water flow (6.33 m^3/s) or tidal range (0.5 m) (Quenzer 1998, Islam et al. 2014). This causes the turbidity to remain low at 7.7 NTU (Montagna and Froeschke 2009). Concentrations of nitrogen average 0.34 mg/L while concentrations of phosphorus average 0.35 mg/L (Quenzer 1998). Overall score: 14/16.

Tampa Bay, FL:

Tampa Bay is frequently exposed to Florida red tide and is around 50 miles north of the initial bloom site of Ft. Myers. Several environmental factors are similar to the specific ranges found in the Ft. Myers area with water temperatures at 30ºC-21.1ºC and salinity at 26-34 PSU (SeaTemperature.org, Weisberg and Zheng, 2006). The lower bay area experiences a high tidal range at 2 m (Goodwin 1989). Water flow can vary during the year concomitant with rainfall, causing waterflow speeds between 10-90 m^3/s and resulting in a water-mixed turbidity level of 2.4-15.4 NTU (Weisberg and Zheng 2006, Moreno-Madrinan et al. 2010). Nutrient concentrations are highly affected by anthropogenic impacts to the bay. Nitrogen and phosphorus are in much higher concentrations then natural levels, with nitrogen at 0.8875 mg/L and phosphorus at 0.2875 mg/L (Greening et al. 2014). Overall score: 13/16.

Southeastern Atlantic Estuaries:

Biscayne Bay, FL: Biscayne Bay is a large lagoon 35 miles long and 8 miles wide. The current within the bay travels at a rate of 121 m^3/s. Tidal range in this region is minimal, ranging between ~0.6 m throughout the year (Dame et al. 2000). Water enters the bay region through several small waterways, but most water enters and exits from a 14 km wide gap between Biscayne Key and the Ragged Keys called the Safety Valve Region (Pitts and Smith 1997). The width of this gap paired with current and tidal action mixes the water column to provide a salinity range of 18-30 PSU, averaging 22 PSU (USGS). Nutrient concentrations are variable throughout the bay. Average nitrogen concentrations are 0.378 mg/L, and average phosphorus concentrations are 0.17 mg/L (National Estuarine Inventory, 1989). This provides a medium level of nutrient concentrations, where the sources are primarily agricultural. Summer temperatures average 30ºC and fall temperatures average 25ºC, making this range similar to the Gulf of Mexico (Seatemperature.org). While this location would seem to be the large bay area on the east coast most likely to experience Florida red tide expansion, the region does not provide long-term support for Florida red tide blooms. Overall score: 11/16.

Indian River Lagoon, FL: The Indian River Lagoon has a record of Florida red tide occurrence in the inland channels, indicating that the environmental factors of this location may represent an ideal potential expansion area. Turbidity reaches 13.91 NTU, salinity averages 27.6 PSU, and temperatures range from 29ºC-25ºC. The tidal action is higher than Biscayne Bay by .5 m, with water flow at 34 m^3/s, which allows bloom concentrations to travel within the inland channels (Dame et al. 2000). The nutrient concentration is low with 0.05 mg/L nitrogen and 0.017 mg/L phosphorus, but area has a high susceptibility to nutrient concentration build-up. Most of the non-point sources come from urban developments and agricultural operations. Overall score: 8/16.

St. Johns River, FL: The St. Johns River has high turbidity (29 NTU) and low salinity (12-18 PSU) (St. Johns River report, 2019). While the tidal range is high at ~1.6 m, the strong river flow of 151m^3/s is sufficient to counter the oceanic tidal inflow (Dame et al. 2000). The water temperature ranges from 28.5ºC in the summer to 21.5ºC in the fall. Nutrients inputs from agriculture and wastewater sources are high (0.12 mg/L nitrogen, 1.54 mg/L phosphorus), but disperse into the ocean, making the nutrient concentration a medium level susceptibility (St. Johns River report 2019). While freshwater harmful algal blooms exist upriver, no records of saltwater blooms are found, making it unlikely that Florida red tide can become established. Overall score: 10/16.

St. Mary's River and Cumberland Sound, GA: The tidal range of Cumberland Sound averages ~1.6m in height, allowing substantial mixing, with a salinity range of 26-32 PSU (Dame et al. 2000, Granat 1990). The water flow is fairly low at 20 m^3/s. Turbidity can vary widely, from 1.7 to 351 NTU (Kozel 1989). Nitrogen concentrations range from 0.004 mg/L to 0.162 mg/L, and phosphorus ranges from 0 to 0.17. mg/L (Alber et al. 2005). The St. Mary's River is part of a much more extensive river system that feeds into the sound, thus without direct water quality testing in specific river sites, it is difficult to identify non-point nutrient sources. There are few areas where still water exists, as many openings to the ocean provide constant mixing. Overall score: 9.5/16.

St. Andrew Sound/St. Simons Sound/Satilla River, GA: The water temperature begins to decrease slightly as coastal waters are transported further north from the tropics. Summer water temperatures average 28ºC and fall water temperatures average 20.5ºC, which is suitable for *K. brevis* populations. Tidal action has a max of ~2.2 m. The overall water flow for these sounds is 65 m^3/s (Dame et al. 2000). The Satilla River originates deep inland and empties directly into St. Andrews Sound at what is known as The Hole, a large oceanic gap between barrier islands. The length of the river encompasses numerous major sources of nutrients, which are cumulatively carried downriver . This causes the nutrient concentration susceptibility to be high, with nitrogen at 1.336 mg/L and phosphorus at 0.153 mg/L (National Estuarine Inventory, 1989). St. Simons Sound is not directly connected with the Satilla River or St. Andrews Sound, but is a large river/marsh system that experiences high tidal mixing creating varied nutrient levels and salinities (Dame et al. 2000). Overall score: 11/16.

Altamaha River, GA: The Altamaha River is variable in salinity, ranging from 10-20 PSU (Dame et al. 2000). Tidal range averages ~2.2 m and the incoming water flow from the Altamaha

River is strong at 396 m^3/s, allowing substantial mixing of the water column and resulting in a turbidity of 7-11 NTU (Dame et al. 2000). Nitrogen concentration is 0.25 mg/L and phosphorus is 0.034 mg/L, therefore the concentration susceptibility is a medium level (National Estuarine Inventory, 1989). Water temperatures average 28ºC in summer and 20.5ºC in fall. The sound the Altamaha River empties into is not large and does not support the existence of still water. A passing bloom would simply be removed by river flow and high tidal forces. Overall score: 6/16.

Ossabaw Sound and Ogeechee River, GA: The Ogeechee River divides into smaller rivers that empty into the Ossabaw Sound. The river flow of 86 m^3/s paired with a tidal range of ~2.2 m results in variable salinity levels (Dame et al. 2000). Nutrient concentrations are 0.325 mg/L nitrogen and 0.052 mg/L phosphorus. Multiple sources of upriver, urban, forest, and agriculture contribute to the nutrient loading, causing a high level of concentration susceptibility (National Estuarine Inventory, 1989). Similar to the Altamaha River, the sound is not large and has very few boundaries to block water flow. Overall score: 6.5/16.

Savannah River, GA: The Savannah River does not empty into a sound or a series of channels, it discharges directly into the Atlantic. With a tidal range of ~2.2 m and water flow of 344 m^3/s , the salinity near the river mouth averages ~15 PSU (Dame et al. 2000, Mendelsohn et al. 2020). The water temperature is similar to the rest of the sites in Georgia, with 28.5ºC in summer and 20ºC in fall. Nitrogen levels are nearly identical to the Ogeechee River with 0.374 mg/L nitrogen and 0.051 mg/L phosphorus. The majority of nutrients come from upriver, causing a medium level of concentration susceptibility (National Estuarine Inventory, 1989). With no locations viable for algae to bloom, it is not likely for Florida red tide to become established. Overall score: 6/16.

Helena Sound/South Edisto River/Coosaw River, SC: The water temperature for Helena Sound is 28.5ºC in the summer and 20ºC in the fall. Tidal range averages ~2.2 m and the water flow averages 85 m^3/s, resulting in an average salinity of 3-10 PSU (Dame et al. 2000). Nutrient levels are 0.233 mg/L nitrogen and 0.034 mg/L phosphorus. Most of the sources come from upriver, creating a medium level concentration susceptibility (National Estuarine Inventory, 1989). There are no boundaries to create areas of still water. Overall score: 5/16.

Charleston Harbor/Wando River/Cooper River/Ashley River, SC: The Wando, Cooper, and Ashley River all feed into Charleston Harbor, providing collective discharge flow of 159 m^3/s and a tidal range of ~2.2m. Turbidity measures 25 NTU (South Carolina Coastal Resources, Dame et al. 2000), and nutrient readings are 0.132 mg/L nitrogen and 0.065 mg/L phosphorus. A major percentage of the phosphorus comes from agriculture, wastewater, and industrial facilities. The nutrient concentration susceptibility is at a medium level. Water temperature readings range from 28.5ºC in the summer and 22ºC in the fall, adequate for populations of *K. brevis*. Overall score: 5/16.

North Santee River/South Santee River, SC: The North and South Santee Rivers are smaller rivers that do not discharge into a bay or sound. Average salinity is 5-10 PSU with a water temperature during late summer of 20 ºC (Christie et al. 1981, Kjerfve and Greer 1978). The tidal action is ~1.5m and the river water flow is 366 m^3/s (Dame et al. 2000). The nutrient loading is high with 1.956 mg/L nitrogen and 0.146 mg/L phosphorus. There is a high level of nutrient concentration susceptibility with major upriver input sources (National Estuarine Inventory, 1989). Florida red tide could utilize the high nutrient loading in this area, but establishment would be difficult depending on the river flow and tidal action. Overall score: 8/16.

Winyah Bay/Pee Dee River/Black River/North Inlet, SC: Winyah Bay is an inland bay with input from the Pee Dee and Black Rivers. The collective water temperature is 28.5ºC in the summer and 20ºC in the fall. Salinity within the center bay ranges from 11-24 PSU (Wingar 2019). Tidal range averages ~1.5m with a water flow of 465 m^3/s (Dame et al. 2000). Nutrient levels are 0.887 mg/L nitrogen and 0.094 mg/L phosphorus . There is a medium level concentration susceptibility with nutrient sources mostly from nearby urban development (National Estuarine Inventory, 1989). Overall score: 9/16.

Cape Fear River, NC: The water temperature of the Cape Fear River is relatively cooler, 28ºC in summer and 19.5ºC in fall. Tidal range is ~1.5m with the water flow produced by the river at 221 m^3/s (Dame et al. 2000). The flow of the river inland results in a turbidity of 10 NTU, and increases to ~50 NTU near the river discharge into the ocean. (Analysis, UNCW). The base river salinity measures ~5-10 PSU and increases towards the ocean. The nutrient levels are 0.4 mg/L nitrogen near the river source, gradually decreasing to 0.15 mg/L towards the ocean. The phosphorus levels are high, ranging between 0.1-0.2 mg/L (Mallin et al. 1999). The increase in salinity correlates with a decrease in nutrients. Overall score: 8/16.

New River, NC: The New River does not empty directly into the ocean. It discharges into first Morgan Bay and then Stones Bay before reaching the ocean. The tidal range is ~1m (Dame et al. 2000). Turbidity is low, averaging 7 NTU. Salinity within the bays measures 3-12 PSU, but increases nearer the coast (New River Quality Report, 2008-2009). Nutrient levels average 0.5 mg/L nitrogen and 0.07 mg/L phosphorus, but both nutrients decrease to 0 nearer to the coast. , There is a high level of nutrient concentration susceptibility due to the restrictive entryway to oceanic waters, which is important where sources originate from agriculture, wastewater, and industrial facilities (National Estuarine Inventory, 1989). The coastal gap that leads into the bay is slim and slightly curved, making tidal mixing difficult. Given the right environmental factors, an introduced bloom population could enter the bay and become easily established in the surrounding channels. Overall score: 6/16.

Bogue Sound, NC: Bogue Sound is structured similarly to the Indian River Lagoon; a large sound separated from the ocean by miles of barrier islands with few connecting gaps. These gaps are however sizable, allowing large amounts of seawater to enter the sound. With a low tidal range of ~1 m, there is little counterforce against outward water flow (Dame et al. 2000). Salinity for the sound is similar to oceanic water at 27-35 PSU (BCO-DMO), and the average water temperature is 28-24ºC (Burreson et al. 2004). Nutrient levels average 0.104 mg/L nitrogen and 0.008 mg/L phosphorus. While nutrient levels are low, the concentration susceptibility is high due to nutrient accumulation over time (National Estuarine Inventory, 1989). This area had exposure to populations of Florida red tide during a 1987 event, thus it is possible an establishment can reoccur. Overall score: 7/16.

Neuse River, NC: The Neuse River empties into the large Pamlico Sound, and the river itself is wide when entering into the sound. It is far from direct oceanic water sources, and the salinity of the river mouth is 11-15 PSU (Jia and Li 2012). Water temperature averages 20.8 ºC (Peierls and Paerl 2010). Tidal range is ~1 m, with water flow averaging 118 m^3/s (National Estuarine Inventory 1989, Dame et al. 2000). Nitrogen levels are 1.3 mg/L and phosphorus is 0.4 mg/L

(Peierls and Paerl 2010). If Florida red tide establishment occurs, it would affect the Pamlico Sound before reaching the river. Overall score: 8/16.

Pamlico River/Pungo River, NC: The Pamlico and Pungo Rivers enter Pamlico Sound in a similar way to the Neuse River. The salinity at the estuary mouth is 20 PSU (Hobbie 1970). Tidal range for the area is ~1 m with a water flow of 69 m^3/s (Dame et al. 2000). Water temperature is an average of 20.8 ºC (Peierls and Paerl 2010). The nutrient levels for this set of rivers are 0.395 mg/L nitrogen and 0.05 mg/L phosphorus. The nutrient concentration susceptibility is at a medium level, due to sources originating from wastewater and agriculture (National Estuarine Inventory, 1989). Overall score: 9/16.

Albemarle Sound/Chowan River/Roanoake River, NC: The Chowan and Roanoake Rivers feed into the Albemarle Sound. Tidal range for the sound is ~1 m with a strong water flow of 317 m^3/s (Dame et al. 2000). This creates a wide variety of low salinities. Water temperature ranges from 28.5ºC in the summer to 22ºC in the fall (Haeseker et al. 1996). Nutrient levels are 0.395 mg/L nitrogen and 0.05 mg/L phosphorus, equating to a medium concentration susceptibility level. Depending on water flow, salinity, and mixing potential, an introduced bloom could become established. Overall score: 9/16.

A compilation of the environmental factors of estuary sites described above is provided in Table 1. Most sites had sufficient data to determine a rank score, but one site, The New River (NC), had three missing data points and does not support a relevant score. Only five estuary sites had enough existing data to successfully determine a rank score (Indian River Lagoon FL, St. Johns River FL, Altamaha River GA, Charleston Harbor SC, Cape Fear River NC). The remaining estuary sites are missing 1-2 data points. The cumulative rank scores for each estuary and category are shown in Table 2, thus providing an overall score of bloom establishment potential. The input data was sourced from available information and in some cases the specific data points were not available, which significantly affected the efficacy of the scoring system. Therefore, instead of a single score for these sites, a ranged score was used based on the potential outcomes of the missing data points, which resulted in a minimum and maximum score range representing the potential score if a complete data set was available. The median value, representative of the most likely possible score, was used in comparisons (Figure 1).

An important consideration was the reliability of nutrient data. Many of the data points for nutrient concentrations are representative only of a specific moment in time. Nutrient levels are known to fluctuate seasonally and as a result of weather-related forces, and this can cause a wide range in concentrations; it was not clear if each study or data point was influenced by external factors at the time of data collection. These other factors, such as changes in land use, can cause an increase in anthropogenic nutrient loading, resulting in fluctuating nutrient levels.

Table 1. Compilation of environmental factors of estuary sites throughout the Southeastern Atlantic study. '-' indicates lack of data pertaining to that estuary site.

	Salinity (PSU)	Temperature (ºC)	Tidal Flow (m)	Water Flow (m^3/s)	Turbidity (NTU)	Total N (mg/L)	Total P (mg/L)
Conditions for *Karenia brevis*	24-37 (31-37)	22-28 (25)	<1	8.5-37	3.6 – 9.6	~0.31 – 0.5	0.026
Corpus Christi Bay, TX	27-32	29-21	0.5	6.33	7.7	0.34	0.35
Tampa Bay, FL	26-34	30-21	2	10-90	2.4-15.4	0.8875	0.2875
Biscayne Bay, FL	18-30	30-25	0.6	121	-	0.378	0.17
Indian River Lagoon, FL	27.6	29-25	1.1	34	13.91	0.05	0.017
St. Johns River, FL	12-18	28.5-21.5	1.6	151	29	1.54	0.12
Cumberland Sound, GA	26-32	-	1.6	20	1.7-396	0.004-0.162	0-0.17
St. Andrew Sound, GA	10-20	28-20.5	2.2	65	-	1.336	0.153
Altamaha River, GA	10-20	28-20.5	2.2	396	7-11	0.25	0.034
Ossabaw Sound, GA	10-20	-	2.2	86	-	0.325	0.052
Savannah River, GA	15	28.5-20	2.2	344	-	0.374	0.051
Helena Sound, SC	3-10	28.5-20	2.2	85	-	0.233	0.034
Charleston Harbor, SC	26.2	28.5-22	2.2	159	25	0.132	0.065
N/S Santee River, SC	5-10	20	1.5	366	-	1.956	0.065
Winyah Bay/North Inlet, SC	11-24	28.5-20	1.5	465	-	0.887	0.094
Cape Fear River, NC	5-10	28-19.5	1.5	221	10	0.4	0.1-0.2
New River, NC	3-12	-	1	-	7	0.5	-
Bogue Sound, NC	27-35	28-24	1	-	-	0.104	0.008
Neuse River, NC	11-15	20.8	1	118	-	1.3	0.4
Pamlico/Pungo River, NC	20	20.8	1	69	-	0.395	0.05
Albemarle Sound, NC	1	28.5-22	1	317	-	0.395	0.05

Table 2. The score ranks of each estuary site based on the seven environmental factor categories. 'x' indicates lack of existing data. A higher score indicates that the site is likely more prone to the formation of Florida red tide based on its environmental factors. *- data points

	Salinity (PSU)	Temperature (ºC)	Tidal Flow (m)	Water Flow (m^3/s)	Turbidity (NTU)	Nitrogen (mg/L)	Phosphorus (mg/L)	Overall Score
Corpus Christi, TX	1	1	2	2	2	2	4	14
Tampa Bay, FL	1	1	0	2	2	4	3	13
Biscayne Bay, FL	1	1	2	0	x	2	4	10-12 (11*)
Indian River Lagoon, FL	1	1	2	2	1	0	1	8
St. Johns River, FL	0	1	1	0	0	4	4	10

Cumberland Sound, GA	1	x	1	2	1	1	3	9-10 (9.5*)
St. Andrew Sound, GA	0	1	0	1	x	4	4	10-12 (11*)
Altamaha River, GA	0	1	0	0	2	1	2	6
Ossabaw Sound, GA	1	x	0	0	x	2	2	5-8 (6.5*)
Savannah River, GA	0	1	0	0	x	2	2	5-7 (6*)
Helena Sound, SC	0	1	0	0	x	1	2	4-7 (5.5*)
Charleston Harbor, SC	1	1	0	0	0	1	2	5
N/S Santee River, SC	0	0	1	0	x	4	2	7-9 (8*)
Winyah Bay/North Inlet, SC	1	1	1	0	x	3	2	8-10 (9*)
Cape Fear River, NC	0	1	1	0	1	2	3	8
New River, NC	0	x	2	x	2	2	x	6*
Bogue Sound, NC	1	1	2	x	x	1	0	5-9 (7*)
Neuse River, NC	0	0	2	0	2	4	4	7-9 (8*)
Pamlico/Pungo River, NC	0	0	2	1	x	2	3	8-10 (9*)
Albemarle Sound, NC	0	1	2	0	x	2	3	8-10 (9*)

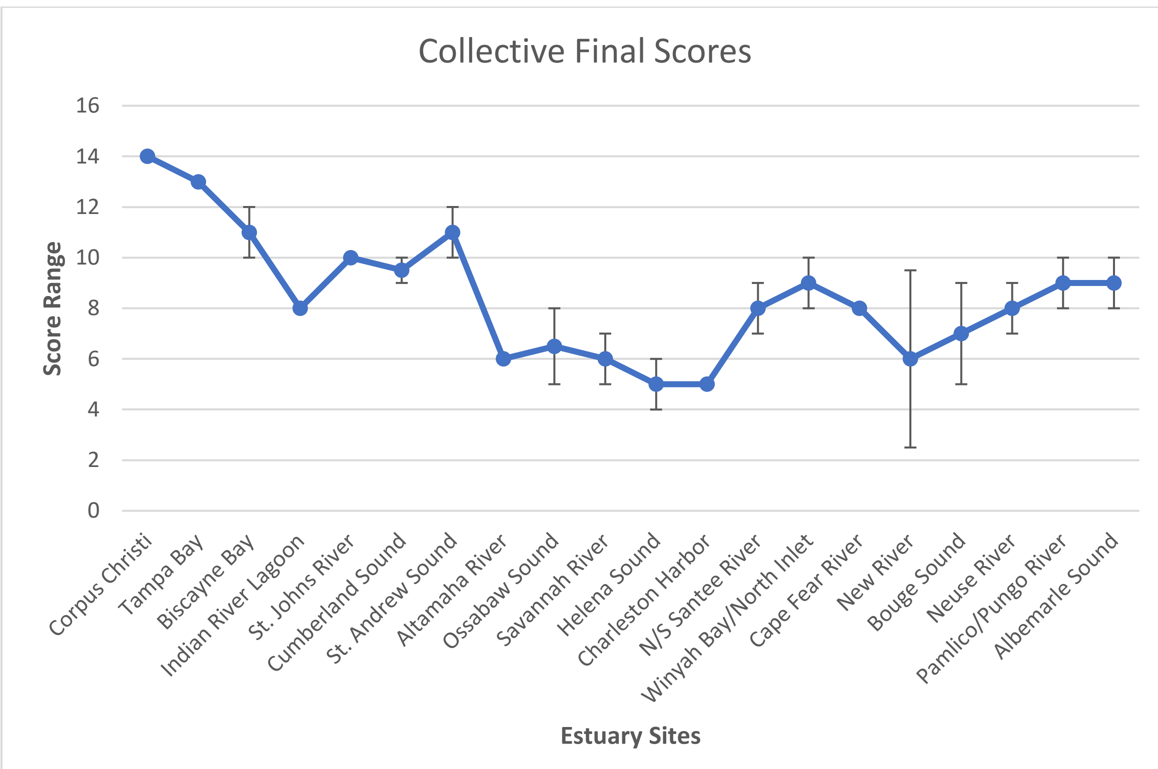

Figure 4. Scores for each estuary, from Biscayne Bay in south Florida to Albemarle Sound in North Carolina. The error bars indicate the range of scores possible given the missing data.

5. Discussion:

The Eastern Florida estuaries collectively had some of the highest scores among the Atlantic coast with totals of 11* and 10, expressing a medium/high level potential for Florida red tide bloom expansion. These estuaries were amongst the few sites that had a complete data set with which to determine complete scores. The high scoring estuaries are close to the red tide origin point, where many of the environmental factors are similar to the native Gulf of Mexico region. The Georgia estuaries received several medium/low scores of 6, with several medium/high scores of 11 and 9.5 due to high nutrient concentrations. The low scores from Georgia exist due to low scores in water flow and tidal action. South Carolina estuaries had medium-to-low scores of 5, 5.5, 8, and 9. This is due to 0 scores for water flow and tidal action as well as a lower average of nitrogen and phosphorus concentrations. Among the North Carolina estuaries, the New River scored 6, but with 3 missing data points, the applicability of this score is low. The rest of the scores are at medium levels between 6 and 9. The scores from Tampa Bay and Corpus Christi Bay are the highest with totals of 14 and 13, making these locations the most prone to bloom expansion, which is reinforced due to their location within the Gulf of Mexico.

5.1 Estuary Systems:

Inland river systems are the leading source of freshwater inputs to estuaries. Topography can cause a collection of several rivers to flow towards a single location. The Piedmont region (shown in Figure 2), dominates the inland areas from North Carolina to the northern coast of Georgia. This important region supplies the surrounding estuaries with substantial freshwater discharge from extensive watersheds (Dame et al. 2000). High flow estuaries carry high suspended sediment loads through riverine systems. North Carolina's Neuse and Cape Fear River, South Carolina's Santee River and Winyah Bay, and Georgia's Savannah and Altamaha Rivers are connected with the Piedmont region. Beyond the Piedmont systems, coastal plains form estuaries on the Southeastern Atlantic coast. North Carolina's New River, South Carolina's Cooper River, Georgia's Satilla River, and Florida's St. John River connect to the coastal plain watershed, and are often referred to as blackwater rivers due to discoloration from decaying vegetation (Dame et al. 2000). These riverine systems have characteristically sluggish flow rates, producing larger areas of estuary wetlands.

Estuaries are highly productive habitats that transport dissolved and partial nutrients to the ocean. Acting like giant filters, estuaries trap nutrients and other organic material that flow through the natural-made obstructions (Biggs and Howell 1984). The most common major nutrients found in estuary systems are carbon, nitrogen, and phosphorus, but concentrations of these nutrients can vary widely between estuaries. Several abiotic factors aid in translocating dissolved and particulate nutrients, such as tidal flow, river flow, and wind-powered waves, and a combination of mixing factors allows for even distribution of nutrients. However, most of the estuaries in the continental U.S. are impacted by human manipulation altering freshwater inflow (Dynesius and Nilsson 1994). An overabundance of nutrients causes several algal bloom-related issues. Sources of additional nutrients are point-based (industry wastewater) or non-point based (agriculture and lawn-based), with discharges creating direct effects (algal blooms) and indirect effects (impacts on fisheries and public health) (National Oceanic and Atmospheric Administration 1996). Some of the highest inorganic nutrient readings were from Cape Fear N.C., Pee Dee River S.C., and Savannah River GA; each system described was influenced by large amounts of fertilizer runoff (Dame et al. 2000). Cape Fear had the highest nutrient concentrations, nearly four times the average of the other seven rivers, originating from a highly industrial river basin with high agricultural land usage and swine farms. Estuaries in North Carolina and northern South Carolina contained the highest concentrations of dissolved inorganic material, reflecting the regions' high usage of land for agricultural and industrial operations. Summer months (July-September) in these regions had the highest concentrations, while winter months (January-March) had the lowest concentrations. Overall, North Carolina represented majority of discharges, but the highest specific discharge rate came from the highly populated coastal city of Savannah, Georgia (Dame et al. 2000).

5.2 Geographical Influence:

Coastal features such as barrier islands that create bays and inlets are a key factor to establishing a potential bloom. Where there are only a few open connections between the ocean and inlets, these natural barriers provide protection from infiltration of transported blooms. The inlets and associated barrier islands also restrict water flow, so if a transported bloom becomes introduced through these connections, the barrier islands can contain the bloom and allow it to continue growing. If there are no areas of still water, then the tidal force and river flow will remove any bloom that appears. While factors such as nutrient loading can support a bloom, establishment in a stable location is critical.

Powerful storms and tidal surges can devastate coastal estuary structure and alter riverine systems. The Southeastern Atlantic coast is prone to annual hurricanes, with the state of Florida having the greatest number of hurricane landfalls. River channel banks can erode and sediments are resuspended and carried down to the estuary mouth (Tissue et al. 1994). The intense effects of rainfall and river discharge can increase nutrient pollution and sediment deposits to the point of nutrient overload. Climate change and warming seas increase the frequency of hurricanes every year and impact all estuaries types, whether they are slow-flow, poorly flushed systems (North Carolina and Florida) or fast-flow, well-flushed systems (Georgia and South Carolina) (Mallin et al. 1999). The type of effect differs depending on the estuary system.

Sea level naturally changes within a season due to heating and cooling during summer and winter months (Patullo et al. 1955), however rising sea level is a global problem, and is projected to increase in height over time. Given the fact that different geographical locations face varying degrees of sea level rise, some regions will feel immediate effects and therefore this is becoming more relevant in issues regarding proper coastal management. Vogel et al. (1996) found that the sea level near North Inlet, South Carolina is increasing by 3.2 mm yr-1. As this trend continues to occur along the Southeastern Atlantic coast, the estuaries and barrier islands are projected to transgress upslope towards the inland coastal plain (Dame et al. 1992). Many estuaries, salt marshes, and mangrove swamps will be replaced with oceanic coastline, removing all of the natural factors that coastal ecosystems benefit from.

Coastal areas have also seen increasing human population density and infrastructure construction (Dame et al. 2000). Unchecked and unsupervised Coastal development causes harm to the delicate balance of the environment. As enticing as beachfront properties seem, the coastline is the main forefront facing sea-level rise and without natural protective barriers, coastal developments will face rising sea levels with little defense.

5.3 Algal Blooms:

Phytoplanktonic communities are difficult to assess in terms of composition and group diversity. The Southeastern Atlantic covers a large area of coastline and the species-specific composition of any given region depends on salinity distribution, turbidity, light penetration, nutrient loading, and mixing characteristics (Dame et al. 2000). One common factor found throughout the Southeastern Atlantic coast is that nitrogen availability limits the growth potential of phytoplankton populations (NOAA 1996). Shallow and turbid waters can also be a limiting factor to phytoplankton growth. South Carolina and Georgia estuaries are good examples, with characteristic shallow waters and high turbidity (Pomeroy et al. 1981).

Phytoplanktonic blooms occur mainly in North Carolina and Florida estuary systems (Mallin 1994). For North Carolina, phytoplankton populations peak in March-May and July-September (Carpenter 1971). In Florida, red tide is common between August and November. Dinoflagellates dominate in terms of population mainly during the summer, while diatoms dominate during the spring (Mallin 1994). South Carolina and Georgia have similar temporal patterns in algal group dominance and bloom growth; diatoms are the dominant phytoplankton group during the winter months, and phototrophic flagellates surpass the diatoms during the summer months (Marshall 1985). As stated earlier, the agricultural nutrient loading within North Carolinas estuaries is fairly high and is major driving force for phytoplankton blooms. The high abundance of dinoflagellates throughout the year in North Carolina is largely due to the weather-driven anthropogenic nutrient loading which causes many regions to be highly eutrophic (Dame et al. 2000, Bricker et al. 1999). Eutrophic-prone estuaries have poorly flushed conditions; North Carolina consists mostly of poorly flushed areas, while Georgia and South Carolina are strongly flushed and therefore poorly eutrophic (Dame et al. 2000).

Harmful algal blooms (HABs) are not uncommon in the Southeastern Atlantic, especially when eutrophication has occurred. It has been documented that half of the Southeastern Atlantic estuaries have outbreaks of red or brown tides as a result of eutrophication (Bricker et al. 1999). A combination of similar nuisance algal blooms, hypoxia/anoxia, and mass fish and shellfish kills can result from eutrophication. Most HABs reported in the Southeastern Atlantic occur in Florida and North Carolina. Florida is prone to red tides by the toxic dinoflagellate *K. brevis*, along with blue-green cyanobacteria blooms. North Carolina is plagued by several toxic dinoflagellate species throughout several estuaries (Burkholder et al. 1992). The algae group *Pfiesteria* caused nearly 50% of fish kills in the Pamlico, New, and Neuse River estuaries in the 1990s (Burkholder and Glasgow 1997). One case in 1987 reported substantial concentrations of Florida red tide transported by the Gulf Stream to Onslow Bay, North Carolina (Tester et al. 1991), although no reports exist of Florida red tide transported that far north following that event.

Surprisingly, few HABs are reported in Georgia and South Carolina estuaries. The only reported cases in Georgia took place in 1956 and 1972, where blooms of the dinoflagellate

Kryptoperidinium were documented in the salt-marsh estuaries of Sapelo Island (Pomeroy et al. 1956, 1972). South Carolina HAB events are equally rare. The first recorded incidents of Florida red tide took place in the spring of 1998 and 1999, consisting of the dinoflagellate *Scrippsiella carolinium* covering several locations over 100 miles apart from North Inlet to Hilton Head Island (Lewitus et al. 2002).

Overall, there is little evidence of HAB events in South Carolina and Georgia, while numerous occurrences are documented in Florida and North Carolina. This is due to high tidal flushing, short water residence times, and low anthropogenic nutrient loading in Georgia and South Carolina estuaries, in contrast to low tidal flushing, long water residence times, and high anthropogenic nutrient loading in North Carolina and Florida estuaries (Dame et al. 2000). Short water residence times and high tidal flushing are important factors in the prevention of HAB occurrence.

Another environmental characteristic shared by Florida and North Carolina estuaries is the presence of seagrass beds. Found in the northern estuaries of North Carolina and throughout coastal Florida, seagrass serves as an indicator of environmental quality. Seagrass is highly sensitive to water quality, and is often limited by light exposure (Day et al. 1989). With rapid breakdown of organic plant matter, nutrient-rich sediment provides additional resources for microalgae blooms. Seagrass is not as common in South Carolina and Georgia, as light penetration is limited by the region's high turbidity (Pomeroy et al. 1981).

5.4 Future Predictions:

For Florida red tide to spread successfully, vulnerable estuaries must be consistently exposed to sizable transported blooms. Two essential factors that support development of bloom-size concentrations of *K. brevis* are the presence of low-flow water and nutrient loading in freshwater discharges. Combining both in a non-native region could, in theory, recreate scenarios similar to the North Carolina red tide event of 1987. Since 1987, no similar red tide cases have been reported in that region. This leads to the conclusion that while the bloom was supported, the *K. brevis* population was not able to fully acclimate to the North Carolina region. However this case offers valuable insights into how the transported algal population managed to survive. Low-flow rates are a feature of coastal inlets and sounds, where bodies of water are surrounded by barrier islands or banks. A substantial number of sounds are found within the state borders of North Carolina and Florida and these states are the only east coast states with reports of Florida red tide blooms. Inlets and sounds in South Carolina and Georgia lack the structural factors that support algal blooms. Reports of blooms are therefore rare and occur only when ideal conditions exist. For *K. brevis* blooms to occur in South Carolina and Georgia, the data suggests that inlets in this region would have to be larger, have restricted water flow, and have higher concentrations of anthropogenic nutrients in river discharge.

Global warming and sea level rise are changing habitats and altering ecosystem function (Pyšek and Richardson 2010). Coastal areas are some of the world's most vulnerable regions to impacts from climate change. One of the biggest threats is rising sea levels (Poulter et al. 2009), and low-lying coastal features such as salt marshes and wetlands are especially vulnerable. Low-lying regions have a substantial influence on watersheds, and North Carolina and Florida are among the lowest-lying regions in the United States (Titus and Richman 2001). There is very little to protect these areas from flooding from a geographical standpoint and they will be the first affected by sea-level rise. Estuaries that have large inlets with little water flow and large quantities of nutrient loading are vulnerable to the establishment of Florida red tide blooms. As climate change and sea-level rise weakens barrier islands and inlets, the potential for *K. brevis* to naturalize in new areas increases.

6. Conclusion:

Karenia brevis is a nuisance and harmful algal species. Populations may have successfully migrated to non-native regions, but have never established a year-round presence as the Southeastern Atlantic estuaries simply do not have the required factors to fully support *K. brevis*' life cycle. Florida red tide therefore only remains established in the Gulf of Mexico.

This species requires a salinity of 31-37 PSU, warm yearly water temperatures of ~30ºC, low water flow-rates of 8.5 m^3/s, and high nutrient loading of nitrogen at 0.31 mg/L and phosphorus at 0.026 mg/L. A combination of similar environmental conditions should provide ample support for bloom growth, and Florida red tide has occasionally been documented beyond its native range, in the inlets/bays of southeastern Florida and the sounds of North Carolina (Tester et al. 1991). It is easier for red tide to infiltrate the estuaries of Florida as they share many similar environmental factors with the Gulf of Mexico. The specifics on the duration and magnitude of red tide blooms are not well documented for North Carolina, but it is clear that the 1987 event had enough impact to affect local estuary systems. The 1987 red tide bloom decimated the bay scallop (*Argopecten irradians concentricus*) recruitment population and impacted the recruitment population the following year in Bogue Sound (Summerson and Peterson 1990). To reach a distant location such as Bogue Sound would require a large-scale bloom population to split from the main population in the Gulf of Mexico and be transported northward by the Gulf Stream, passing estuaries in Florida, Georgia, and South Carolina along the way. During this time, there were no reports of Florida red tide impacts in these estuaries as a harmful algal bloom. One possible reason is that the passing bloom was far offshore; however, even if the bloom has shifted closer to shore, establishment would have been difficult simply due to the estuaries' environmental characteristics. Based on the rank score system presented here, most Southeastern Atlantic estuaries lack the essential environmental factors and coastal structure needed to support a Florida red tide bloom. The estuaries of Georgia and South Carolina are well flushed, have low water residence times, and little anthropogenic nutrient pollution. All factors that would promote harmful algal bloom growth do not exist on a level that would sustain an existing bloom. In contrast, North Carolina estuaries have low flush rates, high water residence time, and high anthropogenic nutrient pollution; these are key to sustaining an introduced bloom. If South Carolina and Georgia had more urbanization and agricultural activities, nutrient pollution would become a serious concern.

Sea level rise is an inevitable issue for all coastlines. Estuaries with low-lying salt marshes and wetlands will be inundated, becoming indistinguishable from oceanic inlets. Coastal flooding can create new sounds, depending on the geographic location. Loss of sediment supply from river input will cause coastline structures to be more vulnerable to changing sea levels. The newly created banks, created by alternative sediment sources, that surround the inlets can be unstable and even dangerous to local communities. Given the fact that sea-level rise is a slow process, the creation of new inlets and sounds would take decades of flooding. Newly formed inlets would lack sufficient flow and a base primary production, but those systems will become established naturally over time.

Algae species are adapted to survive in a wide range of conditions, and *K. brevis* is well suited to its native range within the Gulf of Mexico. For the present time, it is highly unlikely that Florida red tide blooms will become established in Georgia and South Carolina estuaries, although past occurrences indicate that it is possible for Florida and North Carolina. Assessment of risk factors for estuaries on the Southeastern Atlantic coast concluded that most are not currently at risk of Florida red tide expansion, but identified a sizable knowledge gap for a number of environmental factors which could increase the probability of blooms in those regions. Dedicated monitoring programs are therefore essential to understanding the scope of potential Florida red tide bloom expansion, and in managing the spread of this harmful algae.

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