

The cover features several watercolor-style illustrations of birds in flight, scattered across the white background. The birds are rendered in various colors including teal, orange, purple, green, pink, and blue. Some are positioned near the top teal band, while others are spread across the lower half of the page. The style is soft and artistic, with visible brushstrokes and blended colors.

ENVIRONMENTAL THREATS TO THE STATE OF FLORIDA—CLIMATE CHANGE AND BEYOND

EDITED BY: Frank S. Gilliam, James W. Fourqurean, Wade H. Jeffrey and
Hilary M. Swain

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ENVIRONMENTAL THREATS TO THE STATE OF FLORIDA—CLIMATE CHANGE AND BEYOND

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Table of Contents

- 04** *Editorial: Environmental Threats to the State of Florida—Climate Change and Beyond*
Frank S. Gilliam
- 06** *Impacts of Tropical Cyclones on Longleaf Pine Ecosystems of Florida: Tropical Cyclogenesis, Landfall Frequencies, and Climate Change*
Frank S. Gilliam
- 21** *Coastal Ecosystem Vulnerability and Sea Level Rise (SLR) in South Florida: A Mangrove Transition Projection*
Fred H. Sklar, Christine Carlson, Carlos Coronado-Molina and Ana Carolina Maran
- 38** *Viable Putative *Vibrio vulnificus* and *parahaemolyticus* in the Pensacola and Perdido Bays: Water Column, Sediments, and Invertebrate Biofilms*
Trupti V. Potdukhe, Jane M. Caffrey, Mackenzie J. Rothfus, Carrie E. Daniel, Michael E. Swords III, Barbara B. Albrecht, Wade H. Jeffrey and Lisa A. Waidner
- 56** *Florida's Harmful Algal Bloom (HAB) Problem: Escalating Risks to Human, Environmental and Economic Health With Climate Change*
Cynthia Ann Heil and Amanda Lorraine Muni-Morgan
- 94** *Ranking 67 Florida Reefs for Survival of *Acropora cervicornis* Outplants*
Raymond B. Banister and Robert van Woesik
- 104** *Impact of Extreme Disturbances on Suspended Sediment in Western Florida Bay: Implications for Seagrass Resilience*
Jonathan R. Rodemann, W. Ryan James, Rolando O. Santos, Bradley T. Furman, Zachary W. Fratto, Valentina Bautista, Jan Lara Hernandez, Natasha M. Viadero, Joshua O. Linenfelser, Lulu A. Lacy, Margaret O. Hall, Christopher R. Kelble, Christopher Kavanagh and Jennifer S. Rehage
- 117** *Microplastics in Florida, United States: A Case Study of Quantification and Characterization With Intertidal Snails*
Jordan M. Kleinschmidt and Alexis M. Janosik



Editorial: Environmental Threats to the State of Florida—Climate Change and Beyond

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Keywords: climate change, global warming, environmental threats, marine ecosystems, Florida

Editorial on the Research Topic

Environmental Threats to the State of Florida—Climate Change and Beyond

There is an ancient legacy of human alteration of natural ecosystems on a global scale, with an anthropogenic signature indelibly etched on many natural systems (Gilliam, 2016). Ecosystems of Florida are no exception, wherein human occupation by indigenous people dates back to >12,000 years BCE (Hine, 2013; Milanich, 2017). In the 16th century, watercourts—sub-rectangular constructions of shell and sediment for fish storage—were created by the Calusa, a fisher-gatherer-hunter society that managed surpluses of aquatic resources (Thompson et al., 2020).

Although human activities of previous millennia exerted lasting effects on terrestrial and aquatic ecosystems, more recent anthropogenic changes are more profound. The period from the latter part of the 20th century to the new millennium has witnessed unprecedented ecosystem degradation. Some of this has been mitigated via federal environmental legislation and international cooperation, whereas others, especially anthropogenic climate change, are becoming increasingly more serious.

Although effects of climate change are not unique to Florida, the state is uniquely susceptible to many of them because of several interactive factors. Among the 10 most populated states in the USA, Florida has the highest current growth rate. Florida is second only to Alaska in absolute distance of marine shoreline, but has a far higher ratio of shoreline to surface area. Florida has the second lowest mean elevation among states—30.5 m—with a high relative surface area <5 m in elevation (Hine, 2013). Thus, Florida comprises a distinct confluence of environmental concerns: a large, rapidly growing human population with high connectivity to and reliance on marine ecosystems, all increasingly vulnerable to effects of climate change.

This Research Topic addresses seven widely-varied issues, all with ties to climate change. These include tropical cyclones and longleaf pine ecosystems, microplastics in marine environments, sea level rise and mangrove ecology, harmful algal blooms, seagrass ecosystems, *Vibrio* bacteria, and coral reef restoration and survivorship.

Gilliam reported a long-term climate-mediated increase in both frequency and intensity tropical cyclones in the North Atlantic Ocean. Historically, these make landfall more often in Florida in any other state, especially in the southern extreme of the Florida Peninsula. The more intense storms have a long-lived influence on the structure and function of Florida's longleaf pine ecosystems. Although the connection may not be immediately apparent, increases in tropical cyclones also contribute to enhancing microplastics in the environment. Kleinschmidt and Janosik examined microplastic concentrations in waters and snail tissue within the Gulf of Mexico, focusing on two predatory species—*Stramonita haemastoma* (red-mouth rock snail) and *Melongena corona* (crown conch)—common in food webs of the Gulf. They found notable concentrations of microplastics,

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virtually all microfibers, in water and snail tissue samples, confirming the ubiquitous nature of microplastics. Sklar et al. estimated impacts of sea level rise on a variety of site types in southern Florida using three scenarios (increases of 0.27, 0.76, and 1.13 m by 2070) made by NOAA and the IPCC. Predictably, projected impacts were directly related to degree of increase. For the lower two scenarios, however, mangrove accretion and migration was able to mitigate effects of sea level rise on coastal wetland ecosystems. Harmful algal blooms (HABs) are occurring at increasing frequencies in coastal areas globally. Heil and Muni-Morgan provided a state-of-the-science review and synthesis of HABs as they affect human, environmental, and economic health of impacted regions of Florida. Although several microorganisms and the numerous toxins they produce cause HABs, the dinoflagellate *Karina brevis* is principally responsible for more serious events and the brevetoxins they produce can become widespread in the environment. Climate change can exacerbate effects of HABs, suggesting challenges for the future. Numerous factors, many related to climate change, interact to threaten the structure and function of another critical component of the ecology of coastal Florida—seagrass ecosystems. Rodemann et al. combined satellite imagery and field measurements to monitor two distinct disturbances on seagrass communities of Florida Bay, Florida, namely, a drought-induced die-off in 2015 and a hurricane (Irma) in 2017. Massive loss of seagrasses from both events resulted in a persistent sediment plume. Among the more immediate threats to the health and safety of human populations is the pathology of two species of waterborne *Vibrio* bacteria: *V. vulnificus*, which causes necrotizing fasciitis, and *V. parahaemolyticus*, which causes gastrointestinal illness. To establish a critical baseline, Potdukhe et al. extensively surveyed water, sediments, and biofilms around Perdido and Pensacola Bays in Florida, finding notable occurrence of both *Vibrio* species that correlated with wind and suggesting resuspension as an important driver and

establishing a connection with climate change via tropical cyclones and increases in water temperature. Coral reefs, with their impressive biodiversity, are declining globally, resulting from thermal stress, disease, and pollution. Restoration efforts are underway to mitigate these declines. Banister and van Woesik assessed the efficacy of restoration for the Florida reef tract, from the coast of extreme southeast Florida and extending southwest around the Florida Keys, using outplanted colonies of *Acropora cervicornis*. The success of such efforts appears promising. On the other hand, they found that survivorship of these outplants was highly spatially variable, with low survivorship often associated with high wave energy.

The articles in this Research Topic comprise sharply contrasting environmental threats, of both regional relevance (i.e., Florida) and global significance, pointing to the complexity of ecological processes and recalling the classic quote from plant ecologist, Frank Egler (Egler, 1977): “Ecosystems are not only more complex than we think, but more complex than we can think.” These studies also emphasize the current and future challenges we face in mitigating the most damaging effects of these threats, as well the seriousness of directly addressing the cause of climate change by shifting from fossil fuel consumption to sustainable, renewable non-fossil fuel alternatives, such as wind and solar power.

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Impacts of Tropical Cyclones on Longleaf Pine Ecosystems of Florida: Tropical Cyclogenesis, Landfall Frequencies, and Climate Change

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Tropical storms and hurricanes (collectively hereafter, *tropical cyclones*) are among the most destructive forces in nature. These threats are of particular concern to human populations and ecosystems of coastal areas of the southeastern United States, most especially in the State of Florida. This review begins with an overview of the effects of tropical cyclones on Florida's most conspicuous terrestrial ecosystem—longleaf pine. Environmental factors leading to tropical cyclogenesis will also be reviewed, with a specific focus on (1) landfall history in Florida, and (2) the potential relationship between climate change and the frequency/intensity of tropical cyclones in the North Atlantic Ocean. Given its geographical distribution, it is not surprising that longleaf pine has long been impacted by tropical cyclones of the North Atlantic. Tropical cyclones are formed from a complex combination of meteorological conditions, driven initially by the release of excess heat from the surface waters of the ocean, along with an unstable atmosphere comprising air temperatures decreasing and wind speeds increasing with altitude. Among the coastal counties from Texas to Maine, those of Florida have experienced by far the highest frequency of tropical cyclones, especially the southern tip of peninsular Florida, with its most populous county (Miami-Dade) receiving 25 hits from 1900 to 2010, second only to Monroe County (32 hits) during that period. Frequencies of all categories of cyclones have increased significantly from 1850 to the present. Cyclone frequencies were significantly correlated with increases in air and ocean temperatures, both of which have increased over the past, suggesting a causal relationship with anthropogenic climate change. Of future concern is how increases in frequencies and intensities of tropical cyclones will negatively affect the structure and function of these ecologically and economically important longleaf pine ecosystems.

Keywords: tropical cyclogenesis, global warming, Florida, tropical storms, hurricanes, longleaf pine

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INTRODUCTION

Tropical storms and hurricanes (also called typhoons, but collectively hereafter, *tropical cyclones*) comprise among the most formidable, destructive forces in nature. As dramatic an event as was the 1980 eruption of Mt. St. Helens (Washington State, United States), its total energy yield was 1,000-fold lower than a typical single tropical cyclone. To wit, the initial pyroclastic blast of

Mt. St. Helens was 2.93^{16} J of energy (United States Geological Survey [USGS], 2005), whereas the average tropical cyclone is $>1.10^{19}$ J of energy. Even the energy associated with the mean annual seismic activity (nearly 1.10^{18} J) falls short of that by over an order of magnitude (Emanuel, 1999; Leeder and Perez-Arlucea, 2006). The destructive forces of tropical cyclones are manifold, including high winds, excessive rain, and storm surge, with the latter two often combining to create extensive, deep flooding. All of these comprise serious threats to human life and built structures, and are unsurprisingly of particular concern to coastal areas, including the southeastern United States. They also represent an existential threat to the flora and fauna of impacted areas of this region (DuBois et al., 2020; Gang et al., 2020).

The State of Florida is second only to Alaska in absolute distance of marine shoreline, but it has a far higher ratio of shoreline to surface area than Alaska, making it all the more susceptible to damage from tropical cyclones. Florida also has the second lowest mean elevation among states (30.5 m), with a high relative surface area <5 m in elevation, enhancing the threat of cyclone-generated flooding. Finally, the rate of human population growth in Florida—the third most populous state in the United States, behind California and Texas—is highest among the 10 most populated states. All these factors combine to make Florida particularly vulnerable to tropical cyclone-mediated impacts. Although such vulnerability is understandingly primarily focused on impacts on human populations, considerable damage occurs to Florida's terrestrial ecosystems, especially those dominated by longleaf pine (Gang et al., 2020; Zampieri et al., 2020).

Longleaf pine is a major forest type in Florida, and its distribution covers most of the state (Figure 1). Despite the naturally low biodiversity of the overstory, wherein longleaf pine is typically the sole species, longleaf ecosystems exhibit an extremely high level of plant diversity in the ground cover (Gilliam et al., 2006). Once covering approximately 37 million ha in its original range throughout the southeastern United States, it currently occupies $<3\%$ of this extent (Gilliam and Platt, 2006). Thus, threats to extant longleaf stands represent a loss of biodiversity. Among the more expansive tracts of old-growth longleaf pine is in Florida, particularly under the protection of the federal government on United States Air Force bases (AFBs), such as Eglin AFB and Tyndall AFB (Hiers et al., 2007; Kirkman and Jack, 2018). Currently, extensive efforts are underway to restore degraded longleaf stand in Florida (Hogland et al., 2020).

As will be described later, the main source of energy needed to create and sustain tropical cyclones is heat absorbed by and released from surface ocean water. Because of this, it is possible that the current trend of increasing air and ocean temperatures (Figure 2) related to anthropogenic climate change may be having an impact on the frequency of tropical cyclones. On the other hand, as of the new millennium, this has been a topic of some debate amongst climatologists.

For example, Emanuel (2005c) created an index of potential destructiveness of tropical cyclones that he based on the total dissipation of energy and integrated over the duration of a cyclone event. He reported temporal patterns of increases in the destructiveness index of cyclones over a 30-year period, from

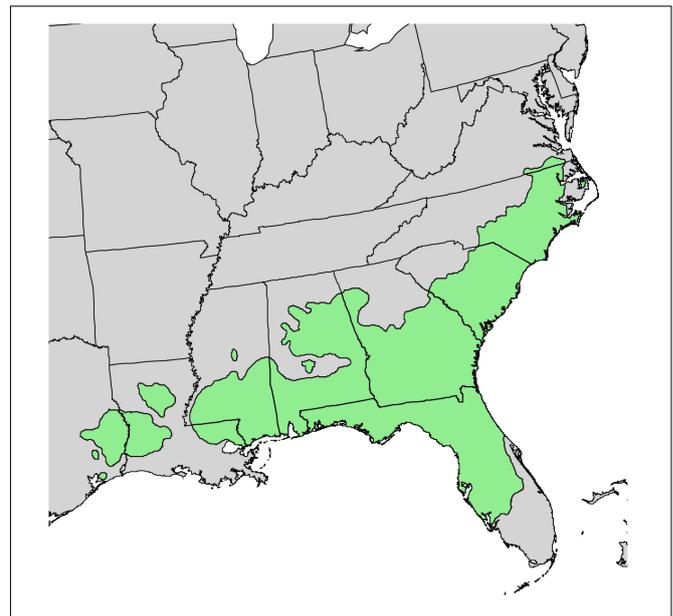


FIGURE 1 | Geographic range of longleaf pine (www.plants.usda.gov).

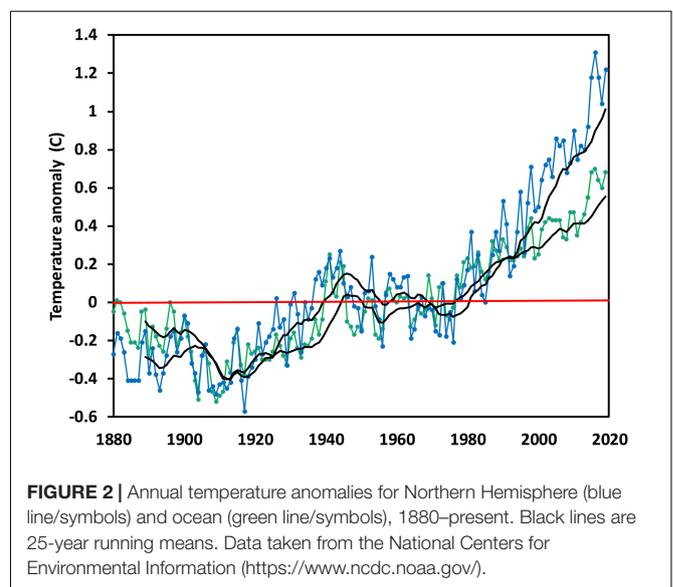


FIGURE 2 | Annual temperature anomalies for Northern Hemisphere (blue line/symbols) and ocean (green line/symbols), 1880–present. Black lines are 25-year running means. Data taken from the National Centers for Environmental Information (<https://www.ncdc.noaa.gov/>).

1975 to 2005, concluding that this was driven significantly by increases in sea surface temperatures (SSTs). He further noted that increased dissipation of energy over this period was likely to have been from either more intense cyclones, longer duration of peak intensities, or both (Emanuel, 2005c).

These conclusions were challenged by Pielke (2005), who based his metrics on storm-mediated loss/damage; he found that these did not vary significantly over a similar time period. Landsea (2005) also questioned the findings of Emanuel (2005c) by downplaying the impact of increasing SSTs in enhancing the intensity of tropical cyclones. Emanuel (2005b) defended his original conclusions, citing theory, and modeling predicting that, for an increase of 2°C in tropical SST, there would be

increased wind speeds by 10% and power dissipation by 40–50% (Knutson and Tuleya, 2004).

More recent studies (e.g., Mann and Emanuel, 2006; Shepherd and Knutson, 2007; Zhao and Held, 2010; Hosseini et al., 2018) have taken various approaches, many quite sophisticated, to address this important question of whether there is a link between global warming and tropical cyclones. This article, which is particularly focused toward a student and/or non-atmospheric scientist readership, will take a more heuristic approach by utilizing readily accessible data and simpler statistics.

The objectives of this review are multi-faceted: (1) characterize the recent effects of tropical cyclones on longleaf pine ecosystems of Florida by synthesizing current literature, (2) outline the general mechanisms of tropical cyclogenesis, (3) describe the tropical cyclone scenario for Florida, including frequencies of occurrence for coastal counties and general summaries of tropical cyclones in the past 30 years, and (4) examine historical data for tropical cyclone frequencies in the North Atlantic Ocean, particularly as related to air and ocean temperatures, to assess potential relationships between cyclone frequency and climate change.

TROPICAL CYCLONES: EFFECTS ON LONGLEAF PINE IN FLORIDA

Longleaf pine clearly represents one of the better examples of a disturbance-maintained ecosystem (Platt et al., 1988; Frost, 1993), with one disturbance—fire—having long been known as essential in maintaining the structure and function of these ecosystems (Chapman, 1932; Heyward, 1939), a role noted even by 18th century naturalist William Bartram (Bartram, 1791). Among its numerous effects, fire simultaneously exposes mineral soil required for successful germination of copious seed production and eliminates potentially competing vegetation, thus allowing for establishment and early growth of seedlings. Under typical fire frequencies, longleaf stands are thus maintained in an open savanna-like physiognomy (Platt, 1997). Under chronic fire exclusion, however, hardwood species, especially southern oak species, establish in the open matrix of the savanna and greatly inhibit, or even essentially eliminate, longleaf reproduction (Gilliam and Platt, 1999).

More recently, the role of tropical cyclones in shaping longleaf pine ecosystems has been increasingly understood (Provencher et al., 2001), with cyclonic events in the southeastern United States during the past 25 years having stimulated research on direct effects on longleaf stands (Stone and Finkl, 1995; Batista and Platt, 2003). Gilliam et al. (2006) proposed a phenomenological model for longleaf pine savanna comprising two natural disturbances: fire and tropical cyclones. This model considers that these two disturbances exert contrasting effects on stand physiognomy. Fires are more frequent and less intense, whereas tropical cyclones are periodic and often of extreme intensity. Fire exerts direct effects on juvenile stages of longleaf regeneration and indirect effects on ground cover via consumption of fine fuel and selective mortality among plant species that are potential competitors of longleaf juveniles.

Tropical cyclones influence the overstory directly via wind-caused damage and mortality, indirectly influencing ground cover by changing the spatial distribution of shading and litter accumulation. Such differences in effects of disturbances can result in widely different physiognomies for longleaf stands. In the absence of disturbance, especially fire, vegetation structure changes dramatically with the increased establishment of hardwood shrubs and tree species (Gilliam et al., 2006).

This model suggests that tropical cyclones comprise an integral component of longleaf pine ecosystems. As will be discussed later in this review, however, some global climate change scenarios have suggested increases in both frequency and intensity of future events, thus greatly affecting pine stands, and ultimately entire pine savanna ecosystems. To address this on a synoptic scale, Gang et al. (2020) used satellite observations to assess forest resilience to 12 hurricanes making landfall in the northern Gulf of Mexico from 2001 to 2015, most of which had direct impacts on Florida. These included two that were Category 1 (Saffir-Simpson Scale—Landsea et al., 1999), three that were Category 2, six that were Category 3, and one that was Category 4. Thus, over half of the storms during this period were major hurricanes (Category 3 or higher). Using standard vegetation indices, they concluded that structural recovery of vegetation impacted by a single major hurricane could take decades to return to pre-hurricane conditions.

By accessing extensive pre-storm data, Zampieri et al. (2020) provided clear, empirical data on the immediate effects of Hurricane Michael in 2018—the first Category 5 hurricane to make landfall this millennium and the third most intense North Atlantic hurricane ever, with maximum sustained winds of ~257 km/h and a minimum barometric pressure of 919 mb (Figure 3A). One of their principle areas of focus was on the longleaf pine ecosystem as a global biodiversity hotspot (Blaustein, 2008; Noss et al., 2015). By directly comparing pre-versus post-storm data at four sites within the impacted area, they concluded that such high intensity storms reduced the extent of mature longleaf habitat (Figure 3B), a reduction that threatens both the innately high biodiversity of these hotspots, as well as the existence of endangered species endemic to the habitat (Zampieri et al., 2020). In another study of the effects of Hurricane Michael on longleaf stands, Rutledge et al. (2021) used observations of >3,000 stems of different species—primarily longleaf but also other pines and oaks species—to confirm that longleaf was in the lower range of treefall probability, but that this pattern varied greatly with soil type. They concluded that tropical cyclones can greatly alter landscape-scale structure and composition of impacted stands. This response also interacts with storm-mediated changes in fire regimes in longleaf pine ecosystems (Rutledge et al., 2021).

Clearly, these are neither the types of storms, nor the responses, envisaged in the phenomenological model of Gilliam et al. (2006). As will be discussed later, the frequency and intensity of tropical cyclones impacting longleaf pine ecosystems is far higher in the current millennium than what was used to conceptually develop the model. Thus, the question for the future of longleaf pine ecosystems in Florida, and throughout its range (Figure 1), is what existential threat is posed by tropical cyclones

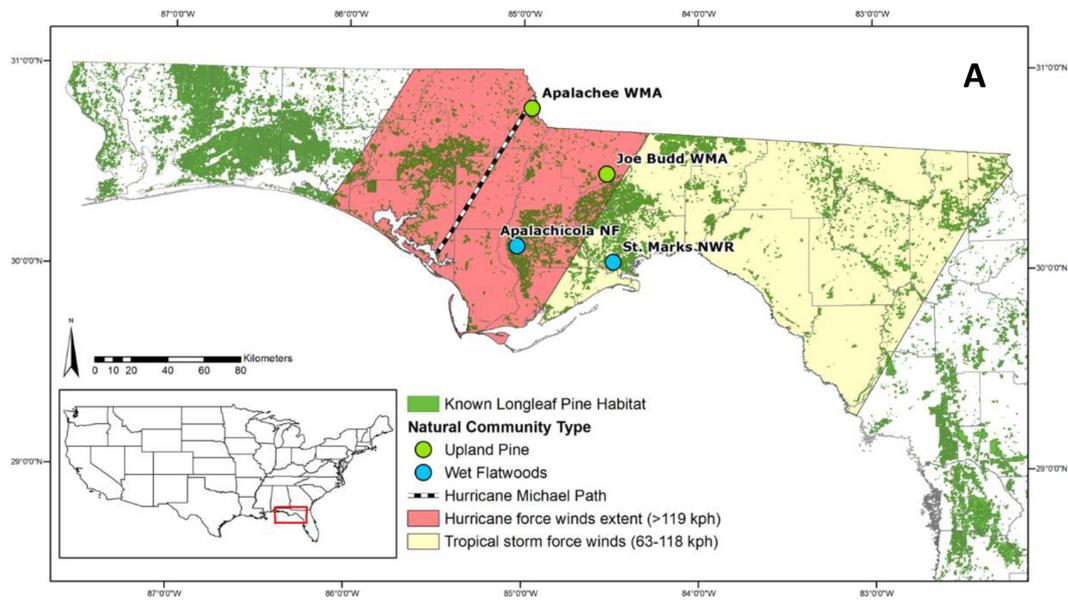


FIGURE 3 | (A) Map showing trajectory of Hurricane Michael, which made landfall on October 10, 2018 as a Category 5 hurricane. Shown also are the affected areas and study sites from Zampieri et al. (2020); used with permission. **(B)** Pre- and post-storm longleaf pine savanna, Apalachee Wildlife Management Area, Florida (Zampieri et al., 2020); used with permission.

that may increase in frequency and intensity with climate warming? To address this, it is first imperative to understand the process of tropical cyclogenesis, along with implications for the state of Florida and relationships with temporal patterns of surface and ocean temperatures.

TROPICAL CYCLOGENESIS

Especially because of increasingly sophisticated meteorological instruments, the factors that interact to lead to formation of tropical cyclones are generally well understood, if not relatively complex (Emanuel, 2005a). Several variables and factors comprise this list, without any of which tropical cyclones will fail to form. Below are six, as originally articulated by Zehr (1992), with brief further discussion:

High Sea Surface Temperature

Graham and Barnett (1987) estimated that surface sea temperature (SST) should be at least 27.5°C at the surface and remain warm to a depth of ~50 m to initiate tropical cyclogenesis. This is because the rapid loss of heat from warm surface ocean waters provides the initial energy to drive the heat engines of tropical cyclones. Higher SSTs indicate a higher heat content of surface ocean water and, thus, result in release of more heat energy.

High Relative Humidity in the Mid-Troposphere

Because dry air has lower energy than humid air, dry air up to 5 km in altitude can absorb the energy dissipated in the early stages of cyclogenesis. Conversely for humid air, condensation of water vapor into cloud droplets and rain releases a considerable amount of energy to the developing system, something which does not occur with dry air. In addition, condensation of water vapor associated with air of high relative humidity releases considerable energy as latent heat, further driving heat engines of tropical cyclones (Rosenberg et al., 1983).

Large Surface-to-500 mb Lapse Rates of Equivalent Potential Temperature

Lapse rates quantify the rate of change (in this case, decrease) of temperature between pressure levels or fixed layers above the surface (Rosenberg et al., 1983). Lapse rates between 6 and 9.6 C/km are considered “conditionally unstable.” It is this range that is required for the deep convection contributing to tropical cyclone formation.

Small Tropospheric Vertical Wind Shear

Wind shear is the change of wind speed and direction over relatively short distances in the atmosphere, with vertical wind shear referring to such variation with change in altitude. A small degree of vertical wind shear between the surface and the upper troposphere enhances thunderstorm formation, providing more energy for tropical cyclones. The requisite convection for thunderstorms is disturbed and weakened by excessive vertical wind shear (Wong and Chan, 2004).

High Low-Level Relative Vorticity

Vorticity describes the tendency for fluids (in this case, air) to rotate. Thus, relative vorticity describes the vorticity of air relative to the Earth induced by the velocity field. Earth vorticity is zero at the Equator and maximal at the poles (Bierly, 2005). Vorticity is considered positive when air moves in a counterclockwise direction, seen as looking down to the surface of the earth. In the Northern Hemisphere, positive vorticity is called cyclonic rotation (and is associated with low-pressure systems), whereas negative vorticity is anticyclonic rotation (and is associated with high-pressure systems). In the Southern Hemisphere, an opposite nomenclature applies (e.g., negative vorticity and clockwise rotation is cyclonic). The high low-level relative vorticity required for formation of tropical cyclones initially arises from heat energy rising from surface waters of the ocean, creating low pressure which causes inward movement of air. When this movement interacts with the Coriolis force (see below), a vortex forms.

Sufficiently High Coriolis Force

The Coriolis force (also called the Coriolis effect, named after Gaspard-Gustave de Coriolis, who initially described it in 1835 as a theory for water wheels) is an inertial force that deflects movement of fluids (i.e., air and water) toward right angles to the right in the Northern Hemisphere and right angles to the left in the Southern Hemisphere. Varying proportionally with latitude, the force is greatest at the poles and zero at the equator; it only reaches enough strength to create the spin required for tropical cyclone formation 480 km from the equator. As this spin is typically required for cyclones to organize, tropical cyclones closer to the equator than 480 km are extremely rare (Figure 4). Finally, the Coriolis force is what causes tropical cyclones (and all low-pressure systems) to rotate counter-clockwise in the Northern Hemisphere, and clockwise in the Southern Hemisphere, as described previously for vorticity.

Not all of these factors are equal in their contribution toward cyclone formation. Some variables comprise numerical values

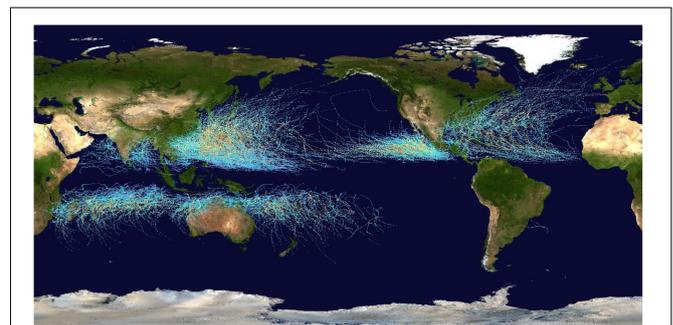


FIGURE 4 | Tracks for global tropical cyclones, 1985–2005. Data for the North Atlantic and East Pacific are from the National Hurricane Center. Tracking data for storms in the Indian Ocean, the Northwest Pacific, and the South Pacific are from the Joint Typhoon Warning Center. Tracking data for Cyclone Catarina in the South Atlantic was published in Gary Padgett’s April 2004 Monthly Tropical Cyclone Summary and was originally produced by Roger Edson, University of Guam. Public domain.

unlikely applicable for determining cyclogenesis for individual events. For example, SSTs and Coriolis forces vary at spatial-temporal scales that preclude diurnal fluctuations for a given potential cyclone. By contrast, other variables, especially vertical wind shear, can vary at diurnal scales (Wong and Chan, 2004). Indeed, development of wind shear is a common factor that disrupts tropical cyclone formation in the Atlantic basin (Landsea et al., 1999). Furthermore, wind shear is a principle mechanism for why the occurrence of El Niño/Southern Oscillation (ENSO) events typically suppress tropical cyclogenesis in this area (Goldenberg and Shapiro, 1996). Note that, in addition to ENSO-generated wind shear, Tang and Neelin (2004) demonstrated that another mechanism for tropical cyclone suppression in the North Atlantic arises from anomalous tropospheric temperatures communicated from the Pacific Ocean from ENSO.

Much of the preceding discussion regarding tropical cyclogenesis can be exemplified in global maps (Figures 4, 5A,B), both by where tropical cyclones form and where they do not, especially regarding SSTs and the Coriolis force. Tracks of global cyclones from 1985 to 2005 show the greatest frequency of storms in the western Pacific, with a similarly high density of cyclones in the eastern Pacific (Figure 4). For the North Atlantic Ocean—and comprising the cyclones of interest in this article—there are notably fewer tracks relative to the Pacific Ocean, yet they occur over a greater area of ocean. Fewer still are the cyclones of the Southern Hemisphere, with perhaps the most notable pattern being the essentially complete absence of tracks in a band around Equator (Figure 4).

The density of cyclones is clearly driven by spatial patterns of SSTs that are widely higher in corresponding regions of the Pacific Ocean (Figure 5A). The lower number of tracks in the North Atlantic Ocean also results from a proclivity of the jet stream to create wind shear there (Landsea et al., 1999). The widespread absence of cyclones along the west coasts of South America and Africa below the Equator arises from low SSTs (Figure 5A) which are maintained by cold ocean currents, namely the Peru Current (also called the Humboldt Current) and the Benguela Current for South America and Africa, respectively (Figure 5B). Similarly, the northern limit of tropical cyclone tracks in the eastern Pacific Ocean is limited by the cold waters of the California Current (Figure 5B).

The distinctive equatorial band lacking cyclones displays the clear importance of the Coriolis force, which is absent at the Equator and only gains enough strength ~480 km north and south of it to initiate and maintain tropical cyclogenesis. Finally, the uneven distribution of cyclonic tracks north versus south of the Equator arises from a combination of interactions of ocean currents with land masses and the profound asymmetry of land mass, wherein that of the Northern Hemisphere (67.3%) is approximately twice that of the Southern Hemisphere (32.7%).

TROPICAL CYCLONE FREQUENCIES AND FLORIDA LANDFALL EVENTS

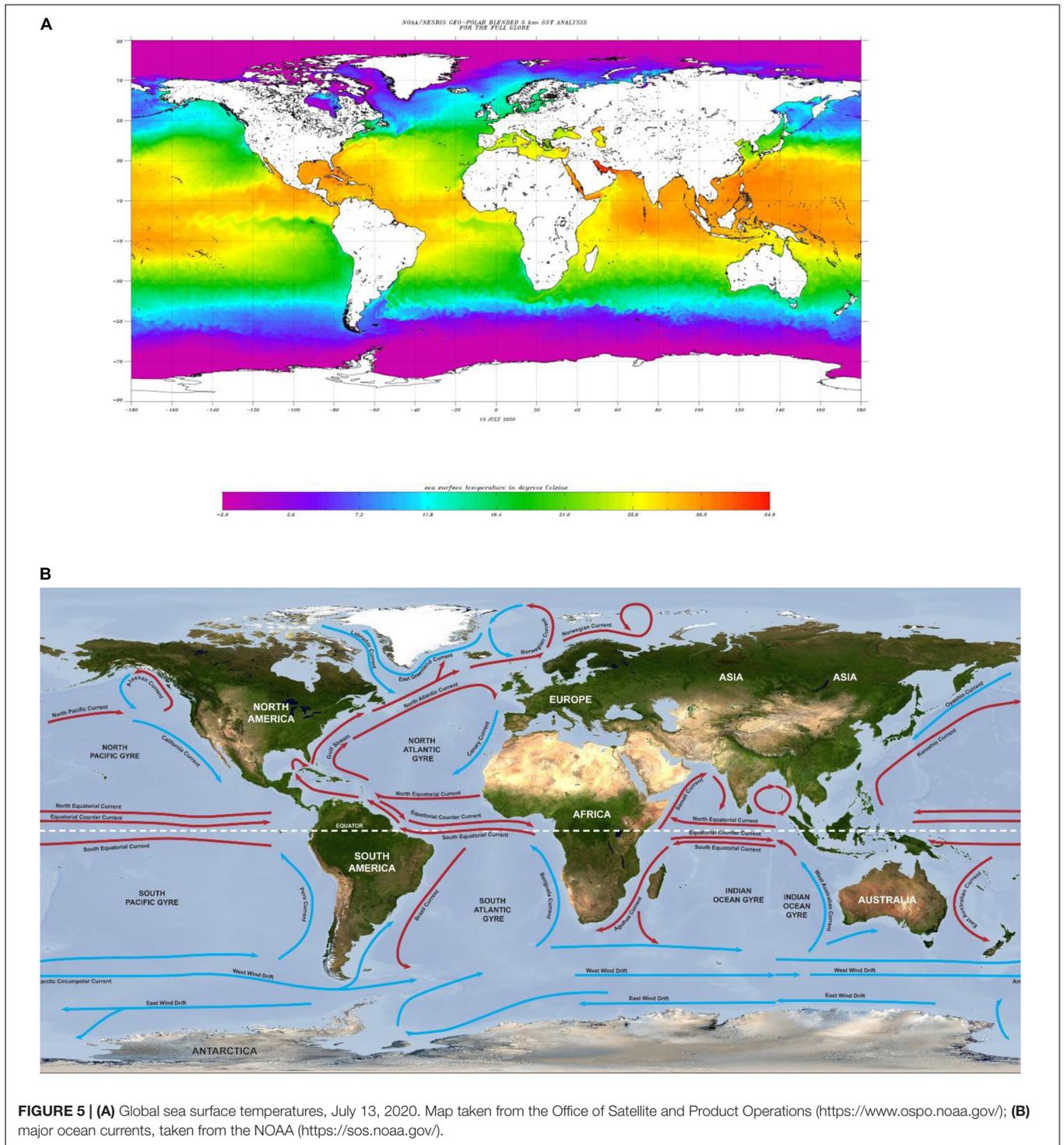
It is important to separate tropical cyclogenesis from the occurrence of cyclones that make landfall. Numerous factors

interact to control whether an individual cyclone reaches land, including many of the mechanisms previously discussed regarding cyclogenesis. In particular for the eastern United States and the North Atlantic Ocean is the North Atlantic Oscillation (NAO). The NAO arises from differences in sea-level air pressure between the Icelandic Low and the Azores High (which is also called the Bermuda High because of its shift toward Bermuda in summer months). The Azores/Bermuda High is also largely responsible for directing tropical cyclones that form off the west coast of Africa (the often-called Cabo Verde storms) in their west, north-west path toward the United States (Elsner and Bossak, 2004). The development of high-pressure systems over land, and in particular the dry air and wind shear commonly associated with them, often prevents tropical cyclones from making landfall. Storm tracks of all tropical and subtropical cyclones in the North Atlantic Ocean from 1851–2017 (Figure 6) reveal that most of these never made landfall.

In addition to the NAO, landfall events are also affected differentially by El Niño/La Niña cycles (i.e., ENSO) and the Atlantic multidecadal oscillation (AMO) (Klotzbach et al., 2018). As already discussed, ENSO-generated wind shear can greatly suppress tropical cyclogenesis (Goldenberg and Shapiro, 1996). Furthermore, there is current scientific debate regarding the origins of the AMO. Some studies (e.g., Grossmann and Klotzbach, 2009; Yan et al., 2017) suggest that the Atlantic meridional overturning circulation is the primary driver, whereas other studies identify sulfate aerosols (Booth et al., 2012) or stochastic midlatitude atmospheric forcing (Clement et al., 2015) as having a primary impact. Temporally, Klotzbach et al. (2018) reported no significant increase in landfall events for the continental United States from 1900 to 2017.

Spatially, considering both its geographic location and its geometric shape, it is unsurprising that Florida experiences a relatively high number of landfall tropical cyclones in the United States. That is, it is not only the most southeastern of all states, but most of Florida is a peninsula with a total shoreline distance second only to Alaska. Indeed, 40% of all landfall cyclones in the United States on record (1850–present) have hit Florida. Inspection of the total number of landfall hurricanes from 1900 to 2010 reveals that not only did Florida experience the highest number among coastal counties/parishes/boroughs from southern Texas to Maine, but that southeastern Florida and its southern-most tip was a particular “hot spot” during this period (Figure 7). Closer examination shows that Monroe, Miami-Dade, and Broward counties averaged 26 landfall hurricanes (Figure 8) in a period of time wherein the eastern United States experienced 73 landfalls.

Between 1990 and the present, there were 18 hurricanes to make landfall in Florida (Table 1). It is important to note that this list comprises only hurricanes and, thus, does not include tropical storms, which are named cyclones but do not reach the intensity of wind speeds of 33 m/s (119 km/h) or a minimum surface pressure of 980 mb (Landsea et al., 1999). Among the extremes of this list, the earliest and latest storms in a given year were Dennis (July) and Jeanne (November), respectively, which were also the months of least common occurrence. September was the most common month, with all but five hurricanes making landfall



in either September or October. Thus, nearly 75% of hurricanes making landfall in Florida over the past 30 years did so in either September or October.

Ten hurricanes made landfall as a Category 1, whereas two (Andrew in 1992 and Michael in 2018) made landfall as a Category 5. Notably, Andrew and Michael were two of only four hurricanes on record to make landfall as Category 5

storms anywhere on record in the United States [the Labor Day Hurricane (1935) and Camille (1969) were the other two]. All told, hurricanes making landfall in Florida created an estimated \$142 billion in damage or \$8.4 billion/storm.

Several factors intersect to suggest a challenging future for Florida regarding tropical cyclones, including that it has (1) a high coastline-to-surface area ratio (which exceeds that of Alaska,

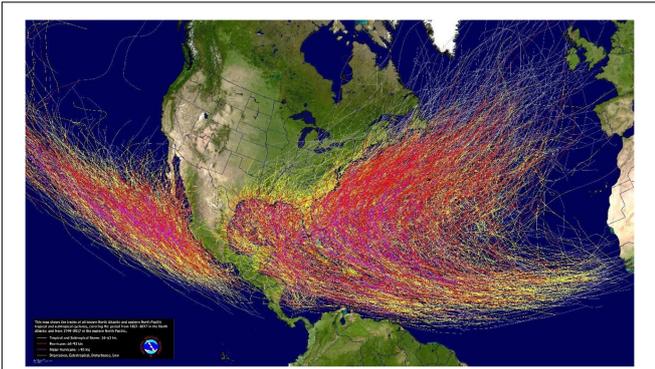
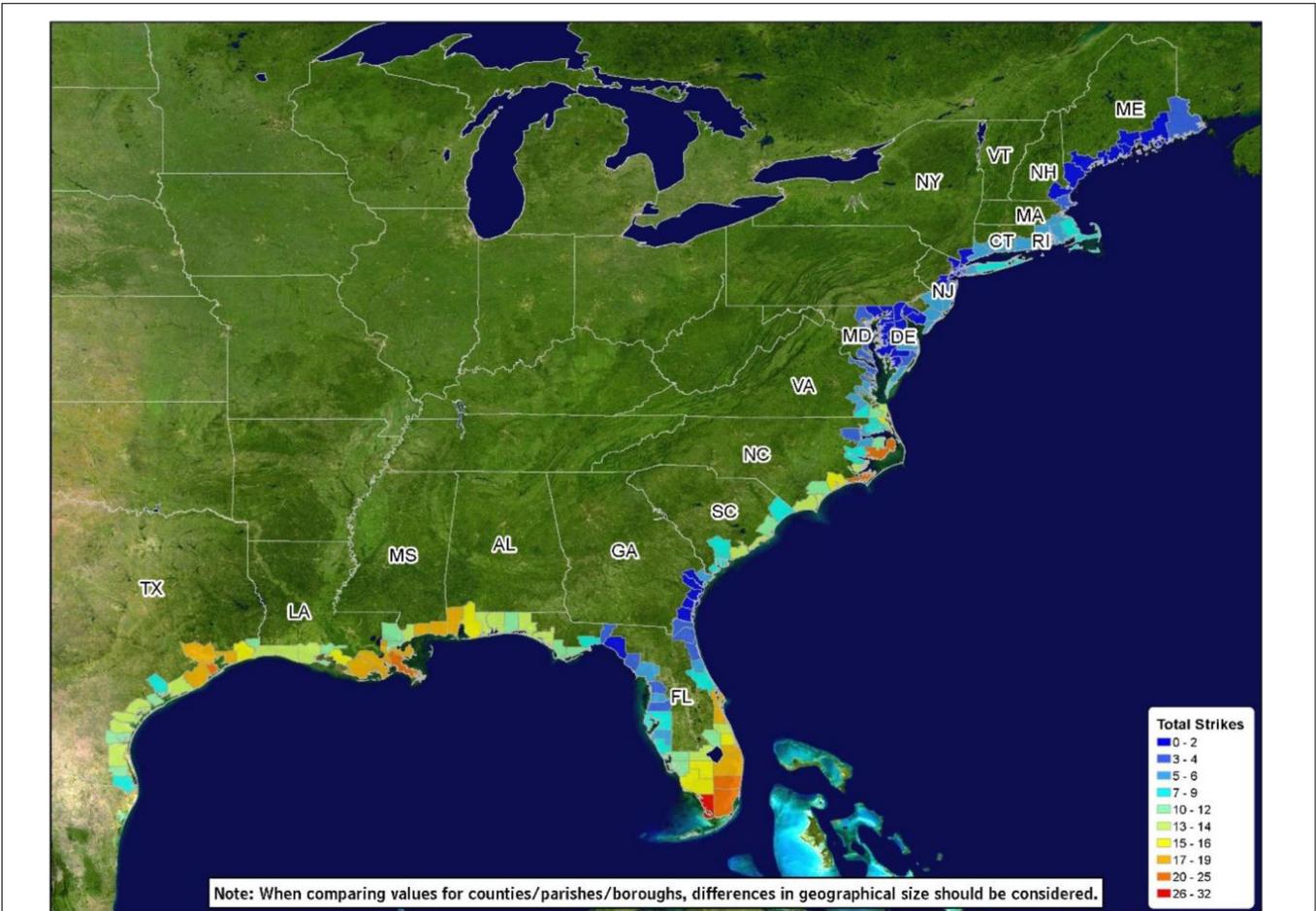


FIGURE 6 | Tropical cyclones, North Atlantic Ocean (1851–2017) and eastern North Pacific Ocean (1949–2017). Credit: NOAA/NHC.

rapidly growing human population. The population of Florida ranks third among United States states, behind California and Texas. With a current rate of 1.8%, however, Florida has the highest population growth rate among the top 10 states, which is over three times the current rate for the United States as a whole (0.5%).

Florida’s high coastline-to-surface area ratio—and its geographical location—are, of course, unchanging, ensuring a higher-than-average likelihood for landfall cyclones in the future. Low mean elevation is similarly unchanging, but mean sea level is rising. Global rise in sea level averaged 0.009 mm/year from 1880 to 1900, but from 1900 to 2009 averaged 1.7 mm/year, a nearly 200% increase in the rate of sea level rise (Church and White, 2011); it is predicted to continue to at least 0.3 m by the end of the century (Figure 9). Accordingly, storm surge from a tropical cyclone, which can be as much as 1.5 m for a Category 1 hurricane and 6 m for a Category 5 hurricane, will have an increasing impact via flooding. Finally, Florida’s increase in human population is part of an ongoing shift of the United States population toward the southeast region, with an

the state with the greatest distance of maritime coastline), (2) the second-lowest mean elevation (30 m, behind Delaware at 20 m) and a high proportion of the state <5 m, and (3) a large,

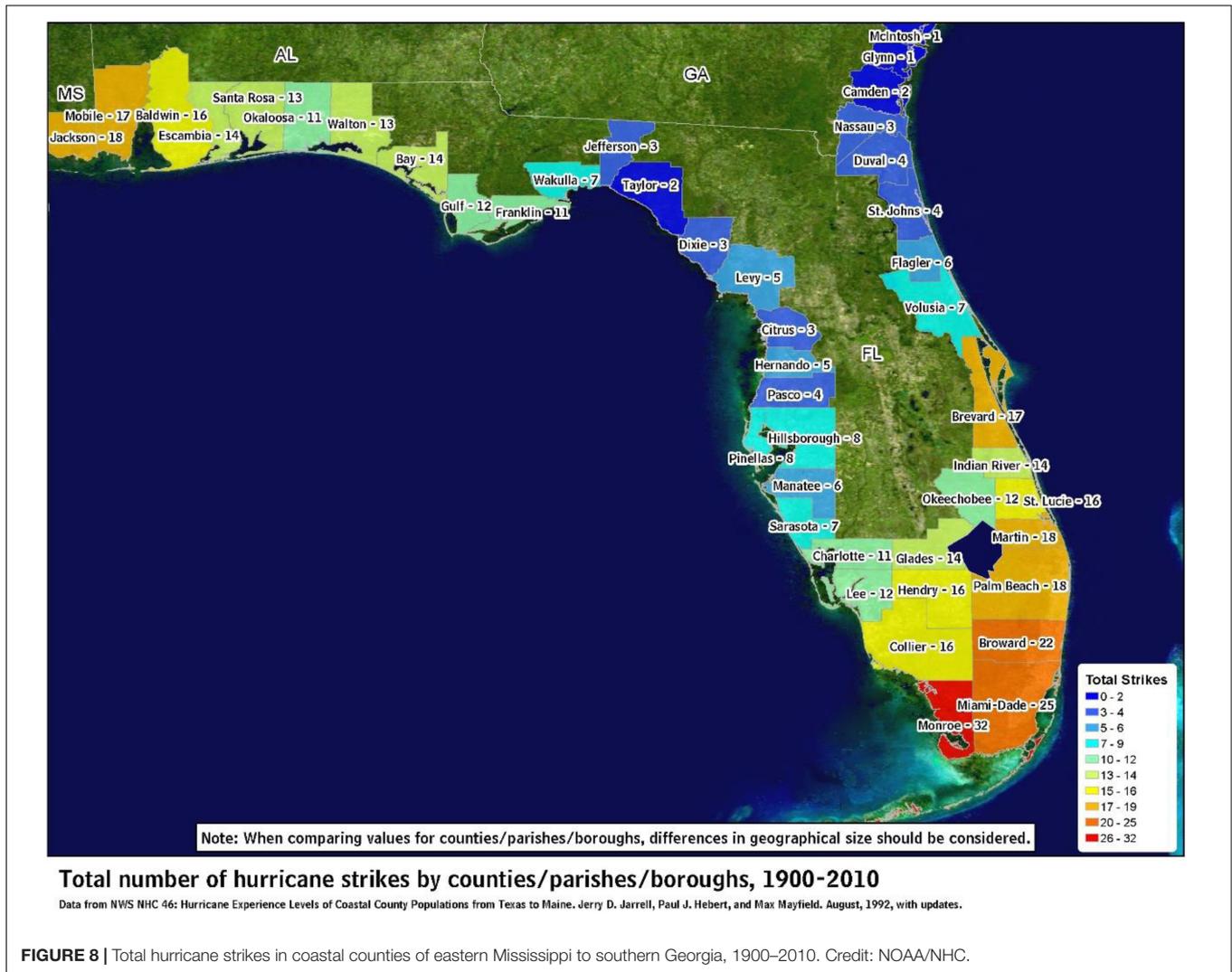


Note: When comparing values for counties/parishes/boroughs, differences in geographical size should be considered.

Total number of hurricane strikes by counties/parishes/boroughs, 1900-2010

Data from NWS NHC 46: Hurricane Experience Levels of Coastal County Populations from Texas to Maine. Jerry D. Jarrell, Paul J. Hebert, and Max Mayfield. August, 1992, with updates.

FIGURE 7 | Total hurricane strikes in coastal counties/parishes/boroughs, 1900–2010. Credit: NOAA/NHC.



annual growth rate of just under 1% in 2010s (twice that of the United States in general and 10 times that of the northeast at 0.1%). This translates into more property that is susceptible to cyclone-mediated damage and—far more important—more lives threatened by tropical cyclones. The question of what this may mean for the future is covered in the next section.

TROPICAL CYCLONES AND CLIMATE CHANGE

Anthropogenic climate warming—driven primarily by exponential increases in global emissions of CO₂ that enhance the heat-trapping greenhouse effect—has long been acknowledged in the scientific community, particularly among environmental and atmospheric scientists (Oreskes, 2004; Doran and Zimmerman, 2009; Goldberg et al., 2019), with warming for this century projected to be of an unprecedented magnitude (Hansen et al., 1981). A landmark study at the time, the National Research Council (1979) estimated the Earth’s “climate sensitivity” (i.e.,

susceptibility of Earth’s climate to anthropogenic influence) was between 1.5 and 4.5°C per doubling of global atmospheric CO₂. Over 40 years later, Sherwood et al. (2020) examined all lines of evidence—feedback processes and historical/paleo climate records—and improved the uncertainty around climate sensitivity, suggesting values toward the middle and upper limits of this range.

Hansen et al. (1988) made several specific predictions regarding climate change using a three-dimensional model developed at the Goddard Institute for Space Studies. Among their predictions was that greenhouse warming would be clearly identifiable in the decade of the 1990s, reaching a level at least three standard deviations above that of the 1950s. They also predicted that such increases in temperature would be enough to have profoundly detrimental impacts on humans and the biosphere, including increases in frequencies of extreme events, e.g., hot versus cold, wet versus dry, as well as extremes of intensity of storm events. Over the >30 years since Hansen et al. (1988), evidence fully supports these predictions, as revealed in temporal patterns of temperature

TABLE 1 | Landfall hurricanes for the State of Florida, 1990 to present.

Name	Year	Month	Region/category	Highest category	Pressure (mb)	Wind (kt)	Damage (\$million)
Andrew	1992	August	SE5, SW4	5	922	145	25,500
Erin	1995	September	NW2, SE1	2	973	85	700
Opal	1995	October	NW3	3	942	100	>1,000
Earl	1998	September	NW1	1	987	70	70
Georges	1998	September	SW2	2	964	90	70
Irene	1999	October	SW1	2	964	95	800
Charley	2004	August	SW4, SE1, NE1	4	941	130	13,500
Frances	2004	September	SE2, SW1	2	960	90	8,320
Ivan	2004	October	NW3	3	946	105	8,000
Jeanne	2004	November	SE3, SW1, NW1	3	950	105	3,500
Dennis	2005	July	NW3	3	946	105	1,500
Katrina	2005	August	SE1, SW1	3	920	110	523
Rita	2005	September	SW1	3	937	100	
Wilma	2005	October	SW3, SE2	3	950	105	20,000
Hermine	2016	September	NW1	1	981	70	176
Matthew	2016	October	NE2	2	963	85	2,770
Irma	2017	September	SW4, SE1	4	931	115	50,000
Michael	2018	October	NW5	5	919	140	6,500

Included are the region of the state impacted and Saffir-Simpson category at impact, highest category of storm, central pressure, maximum wind speed, and damage estimates.

(Figure 2) and global occurrences of storms, droughts, and floods (Figure 10).

Although the veracity of global warming is widely accepted among scientists (Oreskes, 2004; Doran and Zimmerman, 2009), current debate remains regarding the environmental repercussions of increasing surface and ocean temperature on terrestrial and aquatic ecosystems, including both biotic processes, such as life cycles and phenology, and abiotic processes, such as weather patterns, hydrology, and fire cycles (Parmesan and Yohe, 2003; Marlon et al., 2009; Mackey et al., 2012; Gilliam, 2016). Once again, there is a broad consensus among scientists that anthropogenic climate change

has detrimentally affected numerous Earth systems (Oreskes, 2004; Doran and Zimmerman, 2009).

Not surprisingly, given the central role of heat release from surface seawater in tropical cyclogenesis (sometimes even referred to as a “heat engine,” Renno and Ingersoll, 1996), part of this debate includes whether global warming is causing increases in the frequency and/or intensity of tropical cyclones. In addition to the dialogue chronicled earlier between Emanuel (2005b,c) and Pielke (2005)/Landsea (2005) regarding the potential for such relationship, recent work has suggested a direct connection between warming-enhanced increases in surface temperatures and increases in frequency/intensity of tropical cyclones (Shepherd and Knutson, 2007; Zhao and Held, 2010).

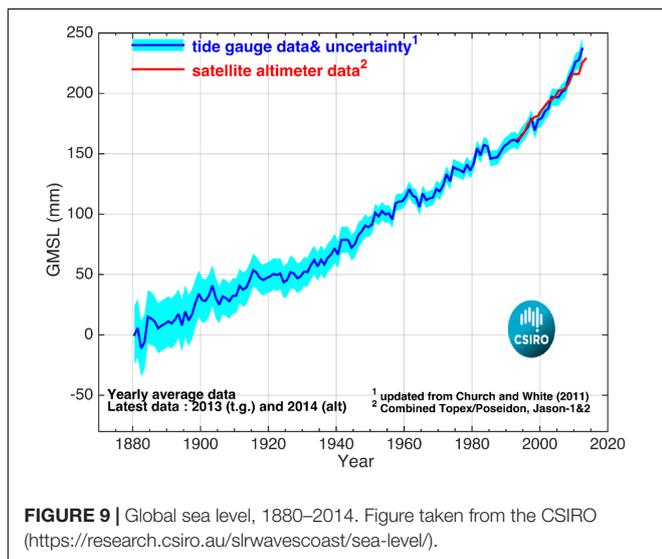


FIGURE 9 | Global sea level, 1880–2014. Figure taken from the CSIRO (<https://research.csiro.au/slrwavescoast/sea-level/>).

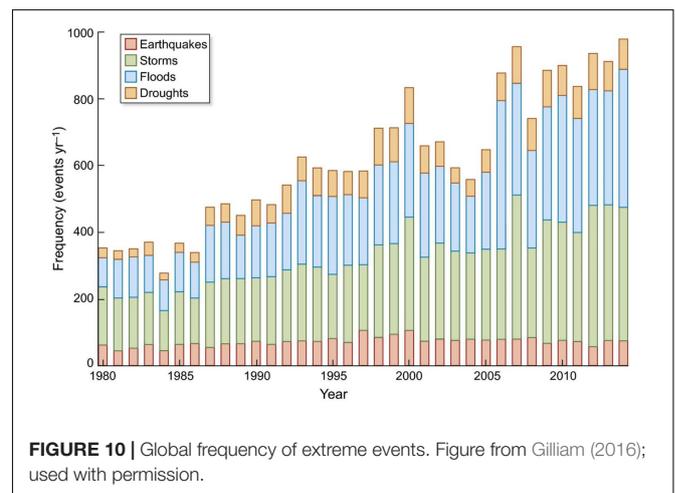


FIGURE 10 | Global frequency of extreme events. Figure from Gilliam (2016); used with permission.

Hosseini et al. (2018) found a strong correlation between SSTs and tropical cyclones, confining their analyses to hurricanes (i.e., excluding tropical storms) in the Atlantic Tropical Cyclogenesis Region (ATCR: 6–18° N, 20–60° W) from 1886 to 2017. The final section of this review summarizes analyses from the same data source, i.e., the National Oceanic and Atmospheric Administration (NOAA) [NOAA National Hurricane Center¹—Landsea et al., 2015], but expands spatial scale (all North Atlantic storms versus ATCR), temporal scale (1850–2019 versus 1886–2017), and types of tropical cyclones (tropical storms, hurricanes, and major hurricanes versus hurricanes). Two questions were addressed: (1) are frequencies/intensities of tropical cyclones increasing in the North Atlantic? and (2) do frequencies of tropical cyclone of all intensities vary significantly with measures of air and ocean temperature?

The first question was addressed in two ways. The first is via linear regression of frequencies of tropical cyclones versus time, separated by cyclone type/intensity—tropical storm, hurricane, and major hurricane—according to the Saffir-Simpson scale, with a major hurricane being of Category ≥ 3 (Landsea et al., 1999). The second is by examining temporal change in the mean annual number of cyclones by type. There has been increasing reference to a “new normal” in both meteorological events and biological processes brought on by anthropogenic climate warming (Lewis et al., 2017); this latter examination endeavors to place this into a context regarding tropical cyclones.

The number of tropical storms has increased significantly ($P < 0.00001$) from 1850 to the present (Figure 11). Understandably, given the numerous factors that contribute to tropical cyclogenesis as previously discussed, there is a considerable inter-annual variability in the number of tropical storms. A clearer pattern emerges from examining quarter-century means, i.e., 25-year running averages, exhibiting increases to 1910, followed by a slight decrease to 1930, a steep increase to 1955, another slight decrease to 1990, and finally

another steep increase to the present time. Other than in 2006 and 2014, since 1990, there have been no years with fewer than six tropical storms; prior to 1990, most years had fewer—often far fewer—than six storms (Figure 11).

Likely due to much lower frequencies than tropical storms, the magnitude of change through time is not as pronounced for hurricanes and major hurricanes. Nonetheless, both have increased significantly from 1850 to the present ($P < 0.002$ and $P < 0.0002$, respectively) (Figure 12). Notable on the X-axis is the asymmetrical distribution of points for major hurricanes, indicating years with no major hurricanes. To further examine this pattern, data were grouped by decade in two categories: number of years without major hurricanes (rarity) versus number years with major hurricanes (commonness) (Figure 13). These categories contrast sharply from the decades of the late 19th and early 20th centuries versus recent decades. That is, although years without major hurricanes were once quite common (> 3 year/decade from 1850 to 1920), there have only been 6 years

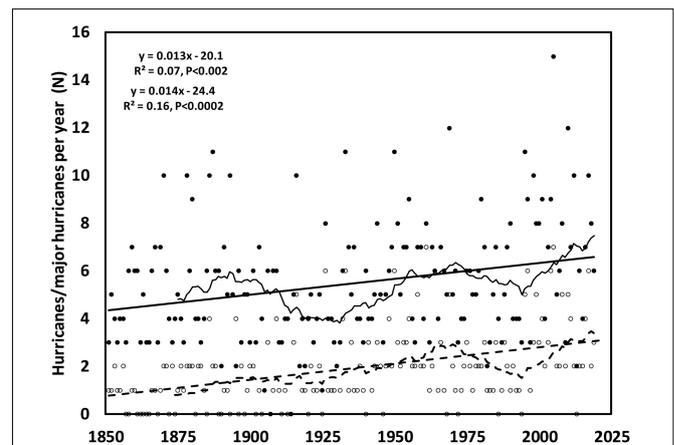


FIGURE 12 | Frequency of annual hurricanes and major hurricanes for North Atlantic Ocean, 1850–present. Thick straight lines are the results of linear regression; thin, varying lines are the 25-year moving averages.

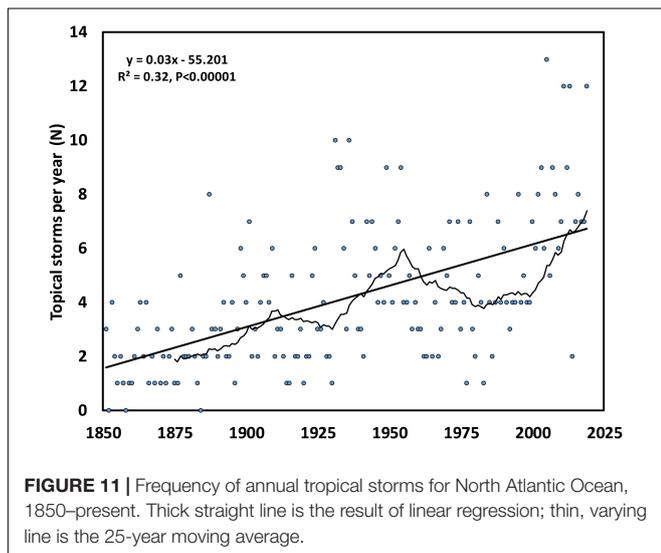


FIGURE 11 | Frequency of annual tropical storms for North Atlantic Ocean, 1850–present. Thick straight line is the result of linear regression; thin, varying line is the 25-year moving average.

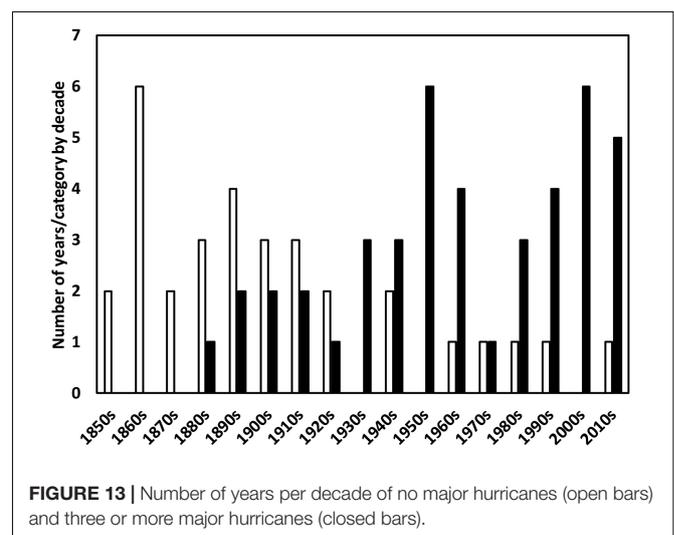
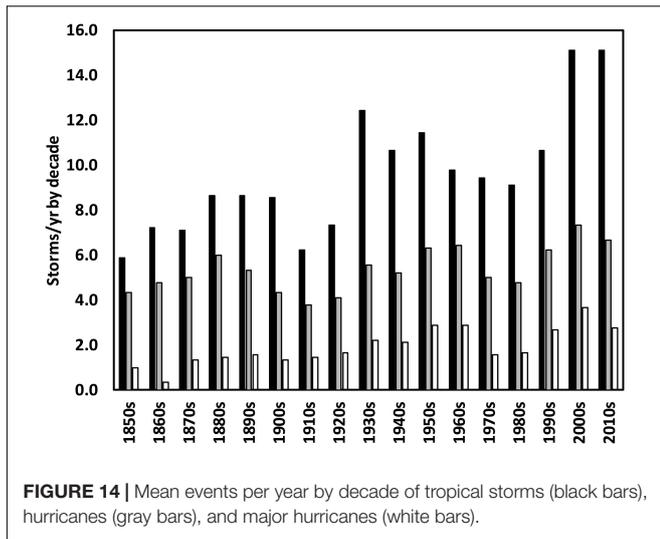


FIGURE 13 | Number of years per decade of no major hurricanes (open bars) and three or more major hurricanes (closed bars).



total without a major hurricane from 1950 to the present. Years with major hurricanes have become increasingly more common, averaging ~1 year/decade from 1850 to 1920, but > 4 year/decade from 1950 to the present (Figure 13).

Clearly, the number of tropical cyclones in the North Atlantic Ocean has increased over the period of record, and has done so across all types—tropical storms, hurricanes, and major hurricanes—suggesting that both frequency and intensity of cyclones are increasing. This indeed represents a “new normal,” as discussed by Lewis et al. (2017). In other words, what is currently considered an “average year” for tropical cyclones is far different from the past (Figure 14). From 1850 to 2000, the mean annual cyclones were 3.5, 3.0, and 2.0 for tropical storms, hurricanes,

and major hurricanes, respectively. In the first two decades of the new millennium, these increased to 8.1, 7.0, and 3.2. Thus, from a long-term mean of 6.5 tropical cyclones/year, the North Atlantic now averages 15.1/year.

The second question addresses the potential relationship between frequency/intensity of tropical cyclones and global warming, and does so using the Pearson product-moment correlation of cyclone number by type and three readily accessed indices of temperature²: global mean temperature, mean temperature of the Northern Hemisphere, and global mean SSTs. In addition, to address the possibility of a lag time in the response of cyclones to temperature, correlations were also run between cyclone types and the temperature indices of the previous year.

Among the types of tropical cyclones, tropical storms and hurricanes were correlated significantly ($P < 0.0001$) with all direct (i.e., same year) measures of global temperatures, whereas major hurricanes were correlated significantly with global SST and temperatures of the Northern Hemisphere (Table 2), supporting similar findings for an earlier time period (Gilliam and Platt, 2006). Using temperature anomalies from the previous year improved correlation for tropical storms and, to a lesser extent, major hurricanes. Surprisingly, this was not the case for hurricanes; correlation of hurricanes with current global temperatures was significant ($P < 0.003$), but not with the previous year’s global temperatures. Thus, there appears to be a lag effect for tropical storms, but less so for higher intensity cyclones. Of all temperature indices, the best correlation with any type of cyclone was the mean temperature for the Northern Hemisphere, which was further improved by using previous years’ data (Table 2).

²<https://www.ncdc.noaa.gov/>

TABLE 2 | Pearson product-moment correlations of annual frequencies of tropical cyclone types [tropical storms (TStorms), hurricanes, and major hurricanes (Majors)] with corresponding annual mean temperature anomalies: mean global temperature (GTemp), mean Northern Hemisphere temperature (NHemTemp), and mean ocean temperature (OTemp).

	TStorms	Hurricanes	Majors	GTemp	NHemTemp	OTemp	preGlobal	preNHem
Hurricanes	0.376							
	0.000							
Majors	0.335	0.660						
	0.000	0.000						
GTemp	0.420	0.247	0.196					
	0.000	0.003	0.021					
NHemTemp	0.531	0.313	0.324	0.719				
	0.000	0.000	0.000	0.000				
OTemp	0.409	0.284	0.268	0.587	0.929			
	0.000	0.001	0.002	0.000	0.000			
preGlobal	0.520	0.189	0.304	0.493	0.640	0.529		
	0.000	0.026	0.000	0.000	0.000	0.000		
preNHem	0.566	0.318	0.365	0.651	0.936	0.878	0.731	
	0.000							
preOcean	0.461	0.314	0.296	0.587	0.892	0.936	0.589	0.924
	0.000							

Correlated to assess a “lag effect” are temperature anomalies from the previous year (pre-). Correlations are for the period 1850–2019. For each correlation, top value is correlation coefficient (r), whereas lower value is P . Values in bold are significant at $P < 0.01$ (Zar, 2009).

SUMMARY AND CONCLUSIONS

Because of currently enhanced sophistication of methods of measurement and computer-driven models, increasingly more is known about tropical cyclogenesis. The essential factors comprise the following: (1) high SST, (2) high relative humidity in the mid-troposphere, (3) large surface-to-500 mb lapse rates of equivalent potential temperature, (4) small tropospheric vertical wind shear, (5) high low-level relative vorticity, and (6) sufficiently high Coriolis force. These vary on both spatial and temporal scales. For example, the Coriolis force is synoptic in scale, increasing with distance from the Equator and exhibiting essentially no diurnal variation; this explains the virtual absence of tropical cyclones along the Equator (Figure 4). By contrast, wind shear affects a much smaller area and can exhibit pronounced diurnal fluctuation. The combination of all factors often generates a considerable interannual variability in the frequency/intensity of tropical cyclones (Figures 11, 12).

Although landfall of tropical cyclones represents only a small percentage of their formation in the North Atlantic (Figure 6), landfall is far more common in the state of Florida than other states (Figure 7). This is largely the result of its location and peninsular shape which results in a great distance of shoreline with the Gulf of Mexico and the Atlantic Ocean. Not surprisingly, most landfall cyclones strike the southern-most tip of the state (Figure 8). Despite past debates on the potential relationship between tropical cyclones and anthropogenic climate warming (e.g., Emanuel, 2005b,c; Landsea, 2005; Pielke, 2005), it is clear that tropical cyclones are increasing in frequency and intensity over time in the North Atlantic Ocean (Figures 11, 12), an increase that appears to be driven, at least in part, by anthropogenic climate warming, consistent with more recent studies (Zhao and Held, 2010; Hosseini et al., 2018).

The degree to which the current scenario for tropical cyclones represents a future threat to longleaf pine ecosystems in general, and in Florida in particular, is unknown. Some models predict that global warming alone—with associated changes in ambient temperatures, growing seasons, and phenologies—may shift the distribution of longleaf pine out of its current extent in Florida (Hansen et al., 2001; Gilliam, 2016). Certainly, more frequent and more intense storms would exacerbate

this. As current empirical evidence indicates (e.g., Gang et al., 2020; Zampieri et al., 2020), tropical cyclones no longer occur within the constraints previously suggested by “natural disturbance” models that emphasize the historical role of cyclones in the natural physiognomy of longleaf pine ecosystems (Gilliam et al., 2006).

CODA—THE 2020 ATLANTIC HURRICANE SEASON

All told, including temporal patterns and cyclone/temperature correlations, these data support the contention that global warming has increased both the frequency and intensity of tropical cyclones in the North Atlantic. NOAA refers to the period of June 1 to November 30 of each year as the Atlantic hurricane season, and the 2020 hurricane season has been exceptional in several respects, breaking numerous records. As of the writing of the initial submission of this article, 13 named storms had formed before the end of August 2020, including four hurricanes (Hanna, Isaias, Laura, and Marco, with Laura making landfall as a Category 4 storm) and seven landfalls. This was the earliest on record to have at least 13 named storms in the North Atlantic. As of mid-November, 30 named storms had formed, the most in recorded history. Thus, in the ~10-week period of September 1 (Hurricane Marco) to November 13, 2020 (Hurricane Iota), an average of 1.7 named storms formed per week. Of the 30 named storms, 13 were hurricanes, including six major hurricanes (1, 4, and 1 each of Category 3, 4, and 5, respectively); 14 storms made landfall.

The toll of the 2020 hurricane season has been substantial, with more than \$40 billion in damage and, more tragically, nearly 400 fatalities. From a personal perspective, having experienced the eyewall of Hurricane Sally (Category 2, 165 km/h winds, >76 cm rainfall) for 12 h in Pensacola, Florida, I certainly hope that the 2020 hurricane will remain exceptional, in that we do not experience another like it. Regrettably, data presented in this article, along with those of other studies, suggest otherwise.

AUTHOR CONTRIBUTIONS

FG conceived of and wrote this review manuscript.

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Coastal Ecosystem Vulnerability and Sea Level Rise (SLR) in South Florida: A Mangrove Transition Projection

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We used static, elevation and land cover data to estimate sea level rise impacts (SLR) to urban, developed lands and coastal wetland systems in Everglades National Park and the East and West coastal regions in South Florida. Maps and data tables estimating potential state change to open water were compiled through overlay analysis of elevation, land cover, and SLR masks with future land cover projected using a land cover transition threshold model. Analysis was based on a 2–5-km-wide longitudinal band along the SW and SE coasts of Florida where sea-level rise has no surface impediments to inundation and will likely cause coastline transgression and wetland migration. Analysis used three different projections; 0.27 m (0.9 ft), 0.76 m (2.5 ft) and 1.13 m (3.7 ft) greater than current sea level by 2070 estimated by NOAA and IPCC. Under a 0.27 m SLR projection 51% of the coastal land cover may be impacted. Under 0.76 and 1.13 m projected SLR, coastal land cover areas were impacted by 56.5 and 59.1%, respectively. Migration of coastal wetlands from their current location into more inland areas in response to increased water depths and as a function of empirically derived marsh and mangrove accretion rates were also evaluated. With a SLR of 0.76 m by 2070, without accretion, 1,160 sq km of wetland became open estuarine water. However, with accretion values of 0.211 m (4.1 mm yr⁻¹) and 0.55 m (11 mm yr⁻¹) by 2070, there was a transition of wetland cover to open estuarine water of only 349 and 41 sq km, respectively. Under a low SLR of 0.27 m by 2070 scenario with accretion, the coastal mangroves were able to migrate inland while maintaining the current coastline. It was only under the more extreme scenario of 1.13 m SLR by 2070 that accretion was not able to compensate for inundation and there was a loss of wetland coastline everywhere.

Keywords: Everglades, wetland, restoration, mangrove, sea level, inundation, vulnerability

INTRODUCTION

Sea-level rise is expected to affect natural and urban areas by shifting habitats and inundating coastal developments. To plan for a sustainable South Florida ecosystem, it is important to identify ecological vulnerabilities to sea-level rise and ask how we might direct Everglades restoration and water management to minimize saltwater intrusion, peat collapse (Sklar et al., 2019) and land

loss. Sea-level rise (SLR) projections for the next 50 years will threaten the structure and function of coastal wetlands in South Florida and there is agreement among coastal scientists that sea level is rising at rates that will inundate most lowlands distributed along the coasts (Ross et al., 2000; Sweet et al., 2017; Sklar et al., 2019).

The Southeast Florida Regional Climate Change Compact's Sea Level Rise Ad Hoc Work Group (Compact) (2019) has established a set of climate indicators, including SLR, flooding, high tide events, groundwater elevation, saltwater intrusion, temperature, rainfall and severe storms. Analysis of observed and projected data from the four counties within the Compact (Palm Beach, Broward, Miami-Dade, and Monroe) include best available data and associated trends. One of the most important contributions of the Compact has been its regional unified SLR projections. When used in conjunction with vulnerability assessments, these projections inform the user of the potential magnitude and extent of SLR impact at a general timeframe in the future. Here we use the Compacts Median, Intermediate and the High projections at the 2070 timestep to analyze a qualitative, conceptual raster-based "bathtub" model of wetland response to SLR.

Sea level rise and inundation pose a substantial risk to many South Florida coastal communities, and the risk is likely to increase with continued development, changes in storm intensity and frequency (Wanless, 1989; Nungesser et al., 2014; Malone et al., 2015). The Southeast Florida Regional Climate Change Compact's Sea Level Rise Ad Hoc Work Group (Compact) (2019), IPCC and NOAA SLR scenarios project 40 cm by 2040 and 100 cm by 2070 (IPCC, 2014). These SLR projections will likely lead to more sustained extreme storm surges, increased coastal erosion, inundation of coastal wetlands, saline intrusion of coastal aquifers, and upward migration of estuarine salt fronts into formerly freshwater areas (Meeder et al., 2017; Park et al., 2019). Thus, there is an increasing urgency for federal and state governments to (1) focus on SLR adaptation at the local and regional levels and (2) consistently provide the information, tools, and methods necessary for adaptation to climate change.

Mangrove forests within the Everglades ecosystem rely on external inorganic sediment input and autochthonous organic matter generated to maintain a vertical soil elevation that have allowed them to keep pace with a relatively stable SLR (Parkinson et al., 1994; McKee et al., 2007). Over the last century, SLR rates have been estimated to be approximately 2.1 mm yr^{-1} based on long-term tide gauge data from South Florida (Maul and Douglas, 1993; Iz et al., 2012). Over the last 50 years, there is evidence of SLR acceleration (2.9 mm yr^{-1} , Obeysekera et al., 2011; $2\text{--}4 \text{ mm yr}^{-1}$, Wanless et al., 1994). The global rates of SLR for the last 50 years was approximately 2.6 mm yr^{-1} , adding up to about 21–24 cm since 1880, and about a third occurring in the past 25 years. Future rates are estimated to be somewhere between 3 mm yr^{-1} and 15 mm yr^{-1} depending on the selected emissions pathway and up to the NOAA intermedia high projections (Lindsey, 2021). Based on the geologic record 5,500 years before present, SLR rates were $\sim 5 \text{ mm yr}^{-1}$ and south Florida shorelines were still transgressive, moving marine waters inland, as evidenced by

thin, narrow and ephemeral sedimentary deposits (Wanless et al., 1994; Meeder and Parkinson, 2018). The resilience of the coastal mangrove ecosystems to continue to keep pace with SLR, and especially a rapid 2070 scenario rise, will be discussed herein in terms of Everglades' mangrove ability to balance this rise with soil accretion. Mangroves are currently distributed close to their lower thermal limits in Florida (Cavanaugh et al., 2019). However, with a projected 1.5°C temperature increase and with projected salt water intrusion, we assume that their ability to keep up with accelerated rates of SLR will improve with time (McKee et al., 2007; Doyle et al., 2010).

For coastal wetlands to persist in the face of SLR, the soil surface must accrete vertically at a rate equal to the rate of SLR (Cahoon et al., 1995). A number of studies have shown that coastal wetlands are indeed able to accrete at a rate equal to recent rates of SLR ($1\text{--}2 \text{ mm yr}^{-1}$, Church and White, 2006) and survive for thousands of years at these modest rates (McKee et al., 2007; Willard and Bernhardt, 2011). However, given current projections of SLR of $3\text{--}4 \text{ mm yr}^{-1}$, the forest floor will have to build sediments at a rate 4.5–9 times that observed over the last century. Wetland accretion rates are a function of the combination of inorganic and organic material inputs to the soil. Inorganic material is mostly supplied in the form of sediments that come from either the sea or freshwater sources, particularly in riverine and tidal mangrove systems. Organic material is mostly derived from the growth of plant roots, which provide a biological source to which other soil material can adhere and contribute to soil formation directly upon decomposition. Mangrove forests are considered excellent land builders due to the soil-binding capacity of their roots (McKee et al., 2007; Friess and McKee, 2020) as well as organic soil formation by high rates of belowground production (Castaneda-Moya et al., 2011). In carbonate environments where there is little mineral sediment input from riverine systems, such as South Florida, belowground production of mangrove peat is considered the primarily soil-building mechanism (Parkinson et al., 1994; Chen and Twilley, 1999; McKee et al., 2007) subsidized by marl deposition in some location near the shoreline.

For coastal wetland in South Florida, where elevations gradients are minimal, this study will explore if small changes in soil elevation relative to projected sea-level rise scenarios can lead to large spatial changes in ecosystem structure. We ask: Can coastal wetland systems adapt to the mean water depth changes specified in the SLR predictions over the next 50 years? Here we present a coast-wide overview based on a functional paradigm for forecasting potential retreat and migration of tidal forests (mangroves) along the northeast and southwest Everglades (South Florida) based on known expanse of mangrove ecosystems at the regional level. Our objective is to evaluate, on a broad, holistic scale, coastal wetland migration as a function of topography, peat collapse, and SLR. We assume that wetland loss due to SLR is a net reduction in ecosystem services, such as nutrient and carbon sequestration and that despite the ecological value of an estuary, a transition to an open water estuarine habitat is a significant decline in biodiversity, resilience and coastal zone functionality.

STUDY AREA

SLR Projections

The Southeast Florida Regional Climate Change Compact's Sea Level Rise Ad Hoc Work Group (Compact) (2019) projections for 2070 SLR (**Figure 1**) represents the consensus from the technical working group and includes projections developed by the Intergovernmental Panel on Climate Change (IPCC) Fifth Assessment Report (IPCC, 2014) and the National Oceanic and Atmospheric Administration (NOAA) (Sweet et al., 2017). The included projections account for regional effects that produce regional differences in Southeast Florida's rate of SLR compared to global projections. All projection curves assume a growing greenhouse gas emission concentration scenario. This study used the NAVD88 elevation associated with each 2070 projection to create sea level masks corresponding to the IPCC Median projection of 0.9 feet (0.27 m) NAVD, the NOAA Intermediate High projection of 2.5 feet (0.762 m) NAVD, and the NOAA High projection of 3.7 feet (1.12776 m) NAVD.

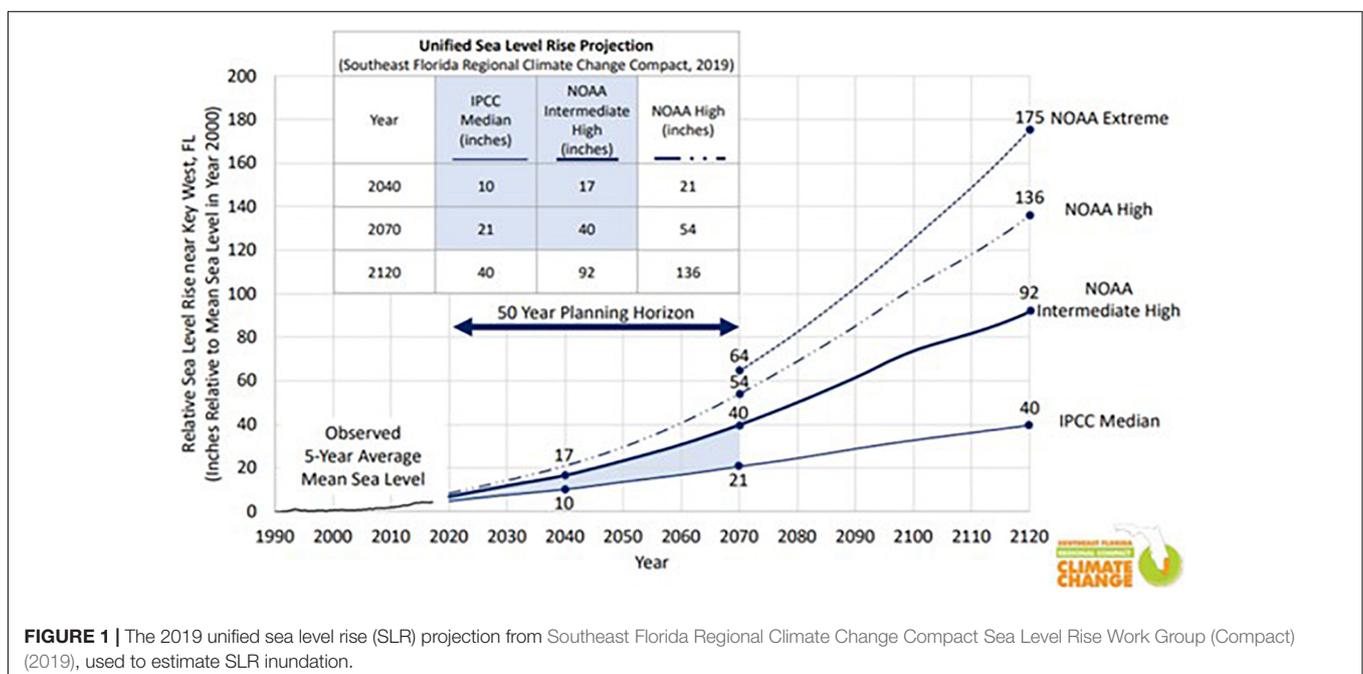
Current Conditions

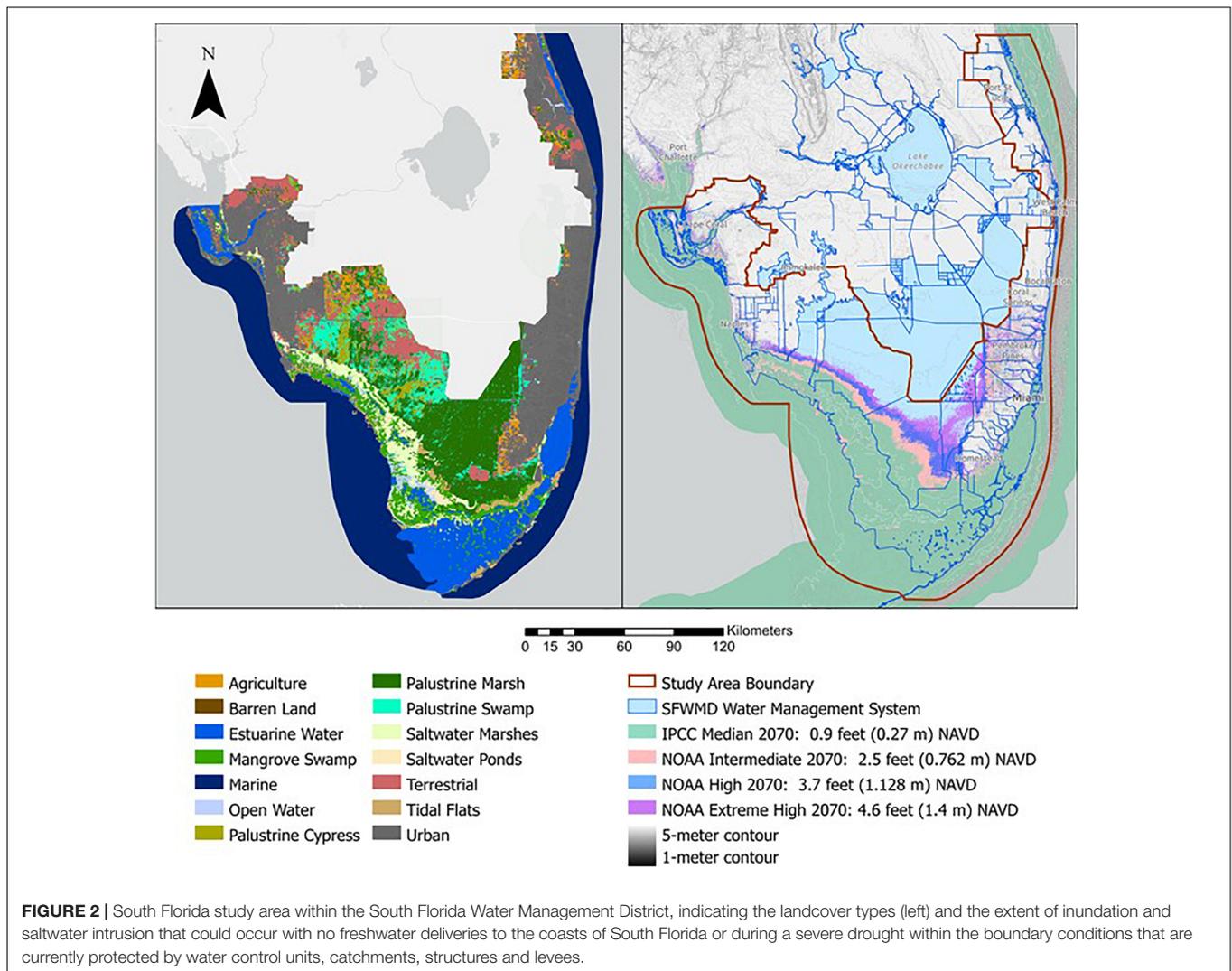
The South Florida Water Management District is a regional governmental agency that operates and maintains the regional water management system for the southern half of Florida. That regional system is divided into water control catchments that include drainage areas, waterbodies, and control structures. It also includes a coastal catchment comprised of bays, lagoons, rivers and other tidally influenced coastal waterbodies. The upstream divides for the coastal catchment include coastal structures that mitigate the flow of tidal waters upstream into freshwater areas. Our study area includes the coastal catchment along with a few inland areas that are expected to experience impacts from SLR (**Figure 2**).

Current condition land cover data (**Figure 2**) were derived from land cover mapped by the SFWMD from 2014, 2015, and 2016 aerial photography (South Florida Water Management District [SFWMD], 2014a). The SFWMD uses the Florida Land Use, Cover, and Forms Classification System (FLUCS) Handbook (Florida Department of Transportation [FDOT], 1999) as the basis for land use and land cover mapping (**Table 1**). They maintain classification updates and clarifications in Photointerpretation Keys (South Florida Water Management District [SFWMD], 2014b). Land Cover data were reclassified into 14 study categories shown in **Figure 2**.

Elevations

The elevation collections described and listed in **Table 2** and shown in **Supplemental Material** were the sources for elevation and depth data used in this analysis. These were used to derive a high resolution topo-bathymetric elevation mosaic (South Florida Water Management District [SFWMD], 2020; **Supplementary Figure 2**). This elevation mosaic used the Web Mercator spherical projection. Elevations values in the source mosaics were NAVD88 units of feet. The mosaic was used to derive sea level elevation masks and was resampled and recalculated to a 3-m Digital Elevation Model (DEM) with elevation values in NAVD88 units of meters for use in calculating depth. Elevation masks for the 2070 SLR predictions were derived from the South Florida elevation mosaic using conditional statements that resampled the elevation mosaic into pixels with elevation values equal to or less than the specified elevation and those not meeting those conditions. The resulting raster was converted to an SLR mask by eliminating pixels not meeting the specified conditions and calculating the remaining pixels to the SLR prediction elevation.





Mean elevations for the land cover classes within the study area ranged from a high of 4.79 m (Sd Dev 2.29 m) for the Terrestrial habitats to a low of -9.87 m (Sd Dev 11.3 m) for the Marine classification (Table 3). The high standard deviation for the Marine cover was due to the high bathymetric variance found in the study area. Standard Deviations were calculated as a check on the quality of the land cover classification protocol and to identify and correct land cover elevation outliers. Depth was calculated by subtracting the Study Area DEM from the SLR Masks. The resolution and pixel alignment of the 3-m land surface DEM was specified to be maintained in the resulting depth raster.

METHODS

Sediment Elevation Table (SET)

Changes in the elevation of the soil surface over time was measured using the surface elevation table–marker horizon (SET–MH) methodology (Figure 3), which has been widely used

and recommended for monitoring intertidal surface-elevation trajectories in coastal wetlands (Cahoon et al., 1999; Cahoon, 2015; McKee et al., 2020). Tide gauges record a relative sea level-rise (RSLR) associated benchmarks attached to the Earth's crust. We estimated the mangrove elevation change relative to the closest tidal gauge by subtracting the mangrove soil elevation change measured with the SET from nearest-neighbor tide gauge SLR calculations. This calculation is possible because the SET and tide gauge independently measure vertical elevation change in different portions of the substrate (Cahoon, 2015). The SET is attached to a benchmark pipe driven into the soil surface 2–3 m and it is assumed to be a stable datum over the period of study. Nine pins are lowered to the soil surface to measure elevation with an accuracy of around each SET platform in the fringe and basin zones of each study site. Vertical accretion was measured, to the nearest millimeter, using pressurized liquid nitrogen coring technology (Cahoon, 2015) and measuring the depth of the marker horizon below the surface.

Surface Elevation Table and marker horizons (SET–MH) sites were established along a East–West transect within the Mangrove

TABLE 1 | Cover type descriptions and class, based on the Florida land use, cover, and forms classification system (FLUCS) Handbook (Florida Department of Transportation [FDOT], 1999) and used in this conceptualization of sea level rise impacts.

General class	Land cover	Cover type description
Agriculture	Agriculture	FLUCS 2000 (Agriculture) All classes
Barren land	Barren land	FLUCS 7000 (Barren Land) Classes include sand other than beaches, exposed rock, borrow areas, spoil areas, dikes and levees and other disturbed land
Terrestrial	Terrestrial	FLUCS 3000 (Upland Non-forested), and 4000 (Upland Forest) classes
Urban	Urban	FLUCS 1000 (Urban and Built Up) and 8000 (Transportation, Communications, and Utilities) classes
Water	Estuarine water	FLUCS 5410 (Embankments opening directly to the Gulf or Ocean), 5420 (Embankments not opening directly to the Gulf or Ocean), 5710 (Atlantic Ocean), and 5720 (Gulf of Mexico)
Water	Marine	Marine habitat starting at coastal breakline and extending into the Atlantic Ocean and Gulf of Mexico to the Study Area extent
Water	Open water	FLUCS 5100 (Streams and Waterways), 5200 (Lakes), and 5300 (Reservoirs)
Palustrine	Palustrine cypress	FLUCS 6210 (Cypress Domes/Heads, Cypress Mixed Hardwoods) and 6240 (Cypress, Pine, Cabbage Palm)
Palustrine	Palustrine marsh	FLUCS 6410 (Freshwater Marshes/Graminoid Prairie), 6411 (Freshwater Sawgrass Marsh), 6430 (Wet Prairie), 6440 (Emergent Aquatic Vegetation)
Palustrine	Palustrine swamp	FLUCS 6110 (Bay Swamps), 6170 (Mixed Wetland Hardwoods), 6180 (Cabbage Palm Wetland including 6191 Wet Malealeuca), 6250 (Wet Pinelands Hydric Pine), and 6260 (Pine Savannah)
Estuarine	Mangrove forest	FLUCS 6120 (Mangrove Forest)
Estuarine	Saltwater marsh	FLUCS 6420 (Saltwater Marshes/Halophytic Herbaceous Prairie)
Estuarine	Saltwater ponds	FLUCS 5430 (Saltwater Ponds)
Estuarine	Tidal flats	FLUCS 6510 (tidal flats)

Salinity Zone between the Buttonwood Ridge and the C111 canal. Elevation change, and vertical accretion have been measured every year since 1997. Transects were designed to evaluate not only the effect of hydrology input but also the vulnerability of scrub mangroves to current trends in sea level-rise. Here we used a network of 10 SET-MH sites distributed within the Northeastern Florida Bay landscape gradient (**Figure 4**) with records of 20 years in length to determine the potential for mangrove submergence due to increasing sea levels.

Wetland Habitat Transition Projections

A bathtub raster analysis method was used to evaluate how the potential for habitat transitions, mangrove mitigation and enhanced accretion rates might affect SLR (SLR) impacts. This approach is not intended to predict absolute extents and depths of inundation associated with the Southeast Compact's sea

level elevation projections but is instead intended to look at potential benefits accretion and habitat adaptations can have on preserving coastal ecosystems. Best available elevation data (see **Supplementary Material**) were used to calculate land surface elevation masks representing NAVD88 elevations for each of the 2070 SLR predictions to generate and calculate depth rasters. Water depth and salinity tolerance principles were applied to define transition thresholds within and between land cover categories. Depth rasters were classified into categories representing community transition thresholds (**Table 4**). For example, when water depths exceeded 1.0 ft for palustrine habitats, it was assumed that the environment would not be consumed by peat collapse, as a result of saltwater intrusion associated with SLR (Servais et al., 2019), and that it would instead transition to a mangrove forest (Krauss et al., 2011) and would remain a mangrove forest until water depths exceeded 2.5 ft, at which time a transition to estuarine open water was assumed. These transition thresholds were applied to the land cover data to predict community transition from their existing condition to a future 2070 condition under each SLR prediction, except for habitats not capable of transitioning due legacy effects (e.g., tidal flats) or social pressures (e.g., urban). Future conditions with accretion were developed by modifying depth rasters with sediment accretion rates as a surrogate for: (1) low TP (5–10 ppb) and moderate deliveries of freshwater (i.e., 4.1 mm yr⁻¹) and (2) high TP (11–20 ppb) and high deliveries of freshwater (i.e., 11 mm yr⁻¹) to the coastlines of South Florida. Accretion rates were based on SET measurements in the mangroves of Florida Bay (see “Results”) and on maximum accretion possible in an ecosystem not limited by nutrients or sediment inputs (i.e., 11 mm yr⁻¹; Krauss et al., 2010).

The raster-based habitat transition steps were as follows:

1. An elevation mosaic of best available digital elevation models (DEM) was assembled from the data described in **Table 2** to represent the bare earth elevation of the study area coastal bathymetry and terrestrial topography. This elevation mosaic was resampled to 3 m to create a study area bare earth DEM.
2. SLR masks were generated by querying the elevation mosaic with conditional statements that identified elevations within South Florida that were less than or equal to the NAVD88 elevation of the SLR prediction. These results were then converted to 32-bit floating point raster equal to the SLR prediction NAVD elevation. The resulting raster extent is the “bathtub” extent of inundation associated with that SLR prediction.
3. SLR prediction depth rasters were calculated by subtracting the study area bare earth DEM from the SLR masks.
4. Land cover data were reclassified into study land cover classes.
5. Zonal elevation statistics were calculated for each study land cover class from the 3-m study area bare earth DEM and used to check land cover classification delineations and identify and correct land cover elevation outliers.
6. Land cover polygons were assigned gridcodes and converted to 3-m rasters.

TABLE 2 | Vertical accuracy, resolution and source agencies for the SFWMD elevation collections used to create the topo-bathymetric DEM for South Florida (South Florida Water Management District [SFWMD], 2020; <https://sfwmd.maps.arcgis.com/home/item.html?id=ca44a6a0714d4d3daa43eba592e8b11b>).

Collection name	Acquisition year	ASPRS vertical accuracy	Resolution	Non-vegetated accuracy	Vegetated accuracy	Source agency
Broward 2018	2018	5–10 cm or ~2–4 in	1.6	≤0.08	≤0.209	USGS
C24 2018	2018	5–10 cm or ~2–4 in	2.5	≤0.156	≤0.65	USACE
Eastern Charlotte 2011	2011	Unknown	5.0	≤0.054	≤0.292	USGS
ENP 2017	2017	5–10 cm or ~2–4 in	1.6	≤0.068	≤0.253	USGS
Florida Keys 2007	2008	Unknown	5.0	≤0.094	≤0.186	FDEM
USGS HAED 2007	2007	Unknown	100.0	Unknown	Unknown	USGS
Martin 2016	2016	10 cm or ~4 in	4.0	≤0.08	≤0.196	USGS
Martin/St Lucie 2007	2007	Unknown	5.0	Unknown	Unknown	FDEM
Miami-Dade 2015	2015	Unknown	5.0	≤0.125	Unknown	Miami-Dade County
Miami-Dade 2018	2018	20 cm or ~8 in	5.0	≤0.204	Unknown	Miami-Dade County
Palm Beach 2017	2017	10 cm or ~4 in	2.5	≤0.091	≤0.219	USGS
Southwest Florida 2018	2018	5–10 cm or ~2–4 in	1.6	≤0.179	≤0.229	USACE
USACE WERP 2017	2017	Unknown	5.0	≤0.119	≤0.296	USACE
Yucca Pens 2016	2016	Unknown	2.5	≤0.196	≤0.271	SFWFMD
NOAA 1/9 Arc-Second Bathymetry	2014	Unknown	11.0	Unknown	Unknown	NOAA

7. SLR prediction depth rasters (Step #3) were reclassified into three categories: depths greater than 2.5 feet, depths between 1 foot and 2.5 feet and depths less than 1 foot and assigned an integer gridcode.
8. Reclassified SLR prediction depth rasters were added to land cover rasters to calculate new gridcode values representing the combination of depth category and land cover class.
9. Transition rules were applied to gridcode values resulting from Step #8. Rasters were converted back to polygons and joined with a transition rule table derived from the thresholds defined in **Table 4**. Based on gridcode value, the resulting polygons were assigned an original land cover, land cover with transition, and a transition status (maintained, converted to Estuarine Estuarine Water or converted to mangrove forest).
10. Area statistics were calculated for original land cover and land cover with transition from the polygons resulting from Step #9. These statistics were used to quantify the areal differences between the original land cover state and the state after transition rules were applied.
11. To estimate land cover transition with accretion, two accretion rasters (0.211 and 0.55 m) were generated from the land cover data. This was accomplished by assigning two accretion attributes to each land cover class and then converting the land cover data from vector to polygon using the accretion attribute for raster generation. Areas classified as Palustrine Cypress, Palustrine Marsh, Palustrine Swamp, Mangrove Forest, Saltwater Marsh, and Saltwater Pond were assigned a value of 0.211 m NAVD for the first attribute and 0.55 m NAVD for the second attribute. All other classes were assigned a 0 value. The accretion rasters resulting from the vector to raster transition were subtracted from the SLR prediction depth rasters to produce new SLR prediction

depth rasters corresponding to the 0.211 and 0.55 m accretion magnitudes.

12. Steps #7 through #10 were repeated using the SLR prediction accretion depth rasters.

RESULTS

Inundation Extent

The distribution of SLR Inundation across space, highlighted in **Figure 2**, is the total inundation expected up to 2070. The actual areal extent of this inundation is summarized in **Table 5**, where the total area impacted was over 50% no matter the rate of SLR. As expected, due to the extreme flatness: of southern Florida, all the

TABLE 3 | Areal extent, mean elevations and standard deviations for land cover classes within the study area.

Land cover class	Area (Sq. kilometers)	Mean elevation NAVD (meters)	Standard deviation
Agriculture	1,644.50	4.79	2.15
Barren land	74.39	3.17	2.61
Estuarine water	4,805.24	-1.94	1.09
Mangrove forest	2,555.19	0.16	0.32
Marine	9,347.02	-9.87	11.31
Open water	511.57	1.47	2.27
Palustrine cypress	1,524.05	2.76	1.61
Palustrine marsh	4,471.82	1.45	1.57
Palustrine forest	2,287.07	2.54	1.71
Saltwater Marshes/Halophytic Herbaceous Prairie	395.04	0.21	0.30
Saltwater ponds	42.04	-0.60	0.66
Terrestrial	1,329.63	4.29	2.29
Tidal flats	150.60	-0.57	0.66
Urban	5,725.03	3.45	2.20

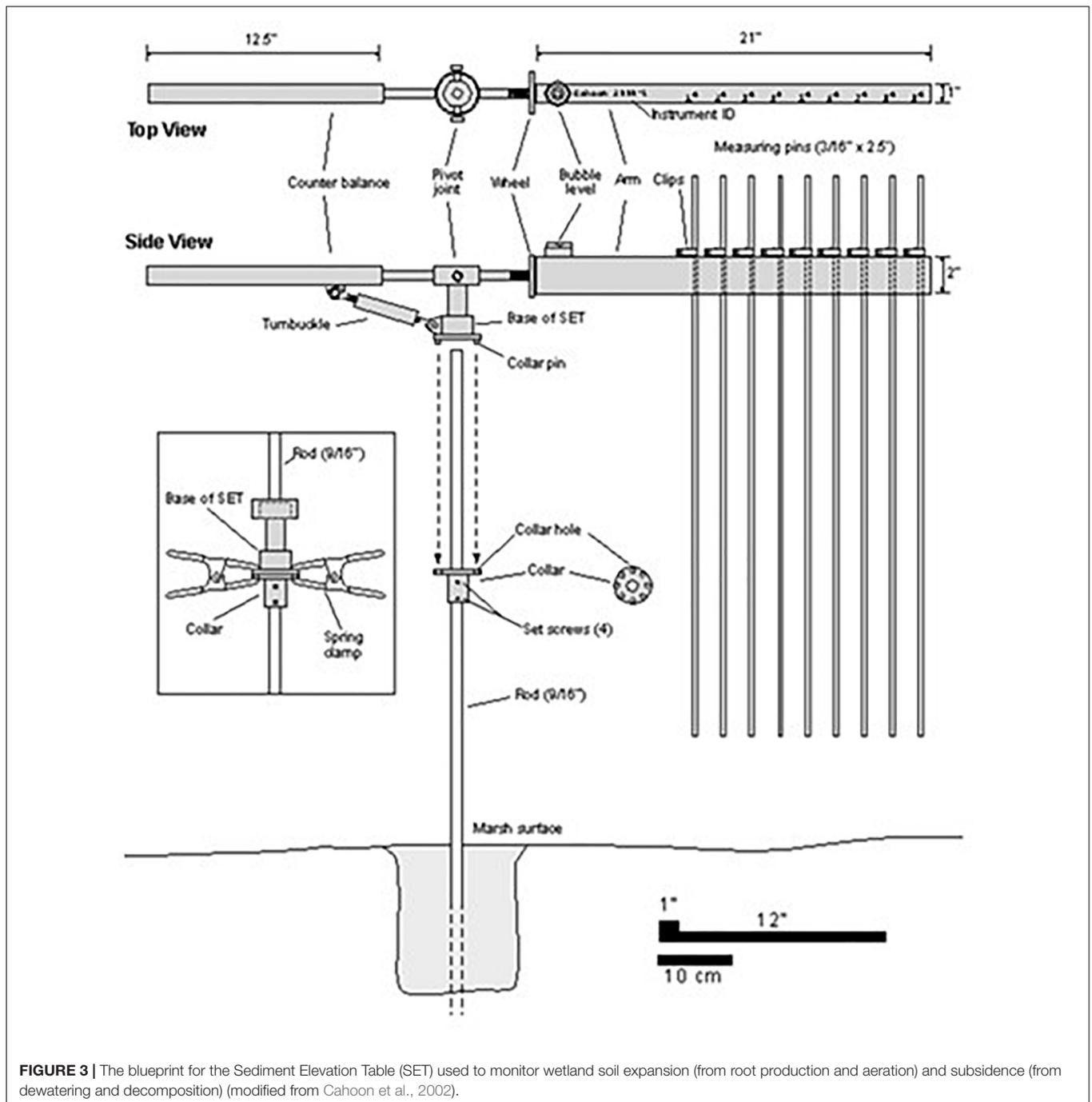


FIGURE 3 | The blueprint for the Sediment Elevation Table (SET) used to monitor wetland soil expansion (from root production and aeration) and subsidence (from dewatering and decomposition) (modified from Cahoon et al., 2002).

wetland habitats are inundated, At the coastline, 2,130 sq. km of mangrove forest were inundated (i.e., impacted) by a SLR of only 0.9 m by year 2070. This is 83% of the total mangrove landscape. With a SLR of 1.1 m, 99.8% of the current mangrove landscape was impacted. This same degree of inundation was found for the saltwater marsh habitats. The Palustrine habitats showed a higher degree of variability than the coastal habitats. The highest extent of palustrine inundation was found for marsh habitats, where 937 sq. km (21%), 1,578 sq. km (35%), and 1,978 sq. km (44%) of the current aerial extent of 4,472 sq. km was inundated by 0.27,

0.76, and 1.1 m of SLR by 2070, respectively. In general, the high elevations for most of the agriculture, barren land, terrestrial and urban categories prevented them from being inundated in the areas around the Caloosahatchee estuary along the west coast, along the urban lower east coast areas and the St. Lucie estuary along the east coast (see **Supplementary Materials**).

Sediment Elevation Trends

Organic matter accretion and shallow subsidence dominate the belowground processes of soil formation in the Florida Bay

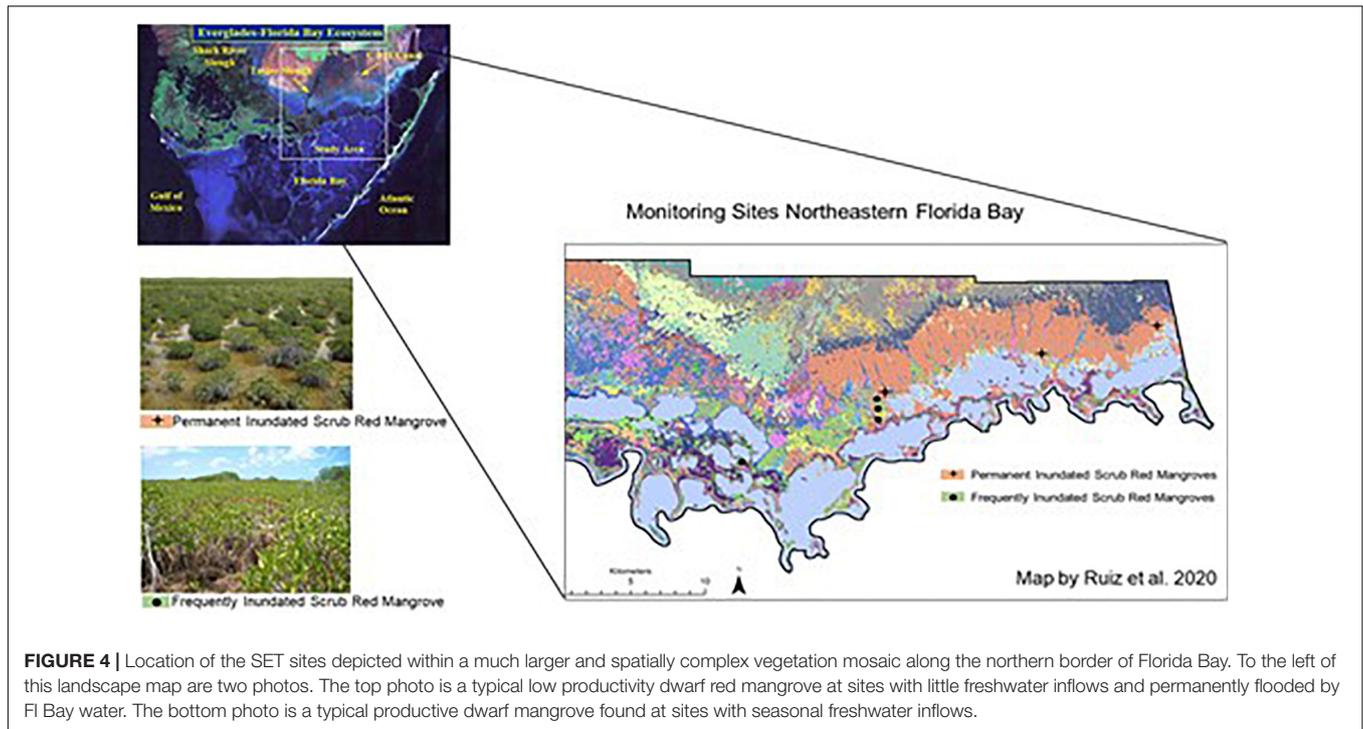


FIGURE 4 | Location of the SET sites depicted within a much larger and spatially complex vegetation mosaic along the northern border of Florida Bay. To the left of this landscape map are two photos. The top photo is a typical low productivity dwarf red mangrove at sites with little freshwater inflows and permanently flooded by FI Bay water. The bottom photo is a typical productive dwarf mangrove found at sites with seasonal freshwater inflows.

coastal mangrove forests. Soil subsidence or expansion is the result of elevation change minus accretion rate, incorporating both surface and subsurface processes. **Figure 5** illustrates

TABLE 4 | Raster-based habitat transition depth thresholds assume that increasing depths are the result of saltwater intrusion and SLR.

Land cover classification	Transition #1 water depth change (ft)	Transition #1 wetland type	Transition #2 water depth change (ft)	Transition #2 wetland type
Agriculture	1.0	Estuarine water		
Barren land	1.0	Estuarine water		
Mangrove forest	2.5	Estuarine water		
Saltwater marshes	2.5	Estuarine water		
Estuarine water		No change		
Saltwater ponds		No change		
Tidal flats		No change		
Marine		No change		
Open water		No change		
Palustrine cypress	1.0	Mangrove forest	2.5	Estuarine water
Palustrine marsh	1.0	Mangrove forest	2.5	Estuarine water
Palustrine swamp	1.0	Mangrove forest	2.5	Estuarine water
Terrestrial	1.0	Estuarine water		
Urban		No change		

Wetland habitats can transition to mangroves before transitioning to estuarine open water.

elevation changes and soil accretion rates in two hydrological mangrove environments in South Florida, showing a higher elevation change rate (3.9 mm yr^{-1}) at frequently flooded sites compared to permanently flooded sites (1.7 mm yr^{-1}). We used an accretion rate of 4.1 mm yr^{-1} , calculated from one of our permanently flooded SET sites in Taylor Slough, as a potential maximum elevation change rate for all marshes receiving some freshwater inputs, for calculating habitat transition trends (see below). Surface elevation table-marker horizon (SET-MH) data indicate mangrove sites with no or little freshwater inputs are not keeping pace with SLR rates, underlying the importance of microtopography and hydrology as environmental factors that needs to be more fully investigated to more precisely determine the vulnerability of mangrove forests in surviving future projections of SLR in south Florida.

Habitat Transition Trends

With a Sea Level Rise of 0.27 m by 2070 and without accretion there was a transition of total wetland cover to estuarine water of 46 sq km (**Table 6**). However, with an accretion value of 0.21 m by 2070, there was a transition of wetland cover to estuarine water of only 18 sq km and with an accretion of 0.55 m by 2070, there is transition to estuarine water of only 11 sq km. Analysis also showed that without accretion, mangrove forests gained at the expense of palustrine wetlands, which lost more than 200 sq km of habitat. With accretion at either 0.211 or 0.55 m by 2070, mangrove forests and all palustrine wetlands maintained, approximately, their original inundated land cover. These results emphasize the importance of managing for soil accretion if coastal wetlands are to keep up with a SLR projection of 0.27 m by 2070.

TABLE 5 | Areal extent of inundation within the study area.

Land cover	Current condition (sq km)	% of Study Area	Land cover impacted by SLR 0.27 m NAVD88 (sq km)	Land cover impacted by SLR 0.76 m NAVD88 (sq km)	Land cover impacted by SLR 1.13 m NAVD88 (sq km)
Agriculture	1,644	5%	3	40	77
Barren land	74	0%	4	12	16
Estuarine water	4,805	14%	4,763	4,796	4,800
Mangrove forest	2,555	7%	2,130	2,544	2,551
Marine	9,347	27%	9,039	9,063	9,067
Open water	512	1%	187	253	276
Palustrine cypress	1,524	4%	53	139	233
Palustrine marsh	4,472	13%	937	1,578	1,978
Palustrine swamp	2,287	7%	116	365	510
Saltwater marshes	395	1%	333	393	395
Saltwater ponds	42	0%	42	42	42
Terrestrial	1,330	4%	16	75	129
Tidal flats	151	0%	149	150	151
Urban	5,725	16%	92	237	398
Total area	34,864	100%	17,863	19,687	20,621
Degree of impact			51.2%	56.5%	59.1%

With a Sea Level Rise of 0.76 m by 2070 and without accretion there was a transition of total wetland cover to estuarine water of 1,160 sq km (Table 7). However, with accretion values of 0.211 and 0.55 m by 2070, there was a transition of wetland cover to estuarine water of 349 and 41 sq km, respectively. Further analysis indicated that without accretion, mangrove forests gained land cover (3,052 sq km) at the expense of the three palustrine wetlands, with palustrine marsh losing about 1,200 sq km and palustrine swamp losing about 290 sq km of land cover. With an accretion of 0.211 or 0.55 m, the transition of wetland cover to open estuarine water decreased to 349 and 41 sq km, respectively. Also, with an accretion of 0.55, all three palustrine environments generally maintained their original inundated land cover.

With a Sea Level Rise of 1.13 m by 2070 and without accretion there was a transition of wetland cover to estuarine water of 3656 sq km (Table 8). However, with accretion values of 0.211 and 0.55 m by 2070, the transition of wetland cover to estuarine water was 2,060 and 422 sq km, respectively. Analysis also indicated that without accretion, all coastal communities, particularly mangrove forest and palustrine marsh, lost significant land cover to estuarine water, which in-turn increased to 8,455 sq km from the current condition of 4,800 sq km; a 176% increase. With an accretion of 0.211 m by 2070, most of the land cover transition was from palustrine marsh and palustrine swamp to mangrove forest, which in-turn increased its cover by 168% relative to mangrove forest cover without accretion (i.e., 2,492 vs. 1,478 sq km). With an accretion 0.55 m, there was an increase of land cover for most coastal communities, particularly for palustrine marsh. Higher accretion rates allowed coastal communities to transition from one coastal community to another instead of losing wetland to estuarine waters.

Spatially explicit representation of the data summarized in Tables 6–8, shown in Figures 6, 7, indicated that wetland transitions to open estuarine water is greatly diminished when palustrine marsh and mangrove forests can build peat. When

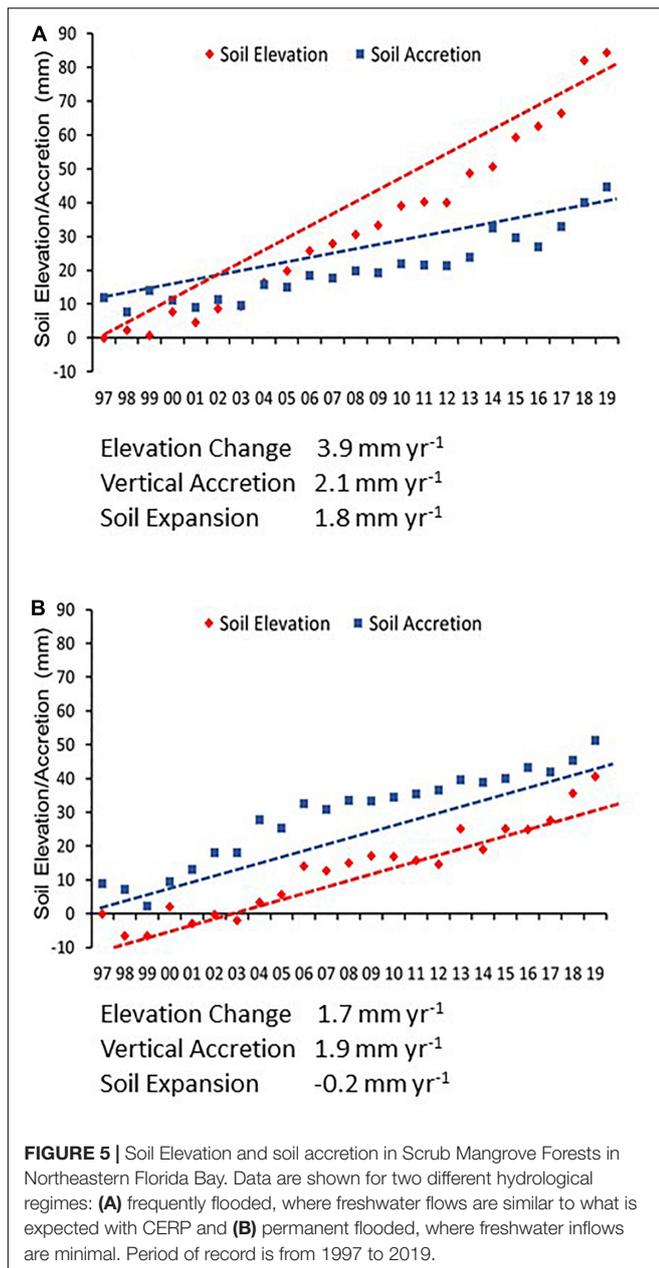
accretion accumulated to 0.211 m by 2070 (this study) and SLR was only 0.27 m by 2070, the landscape of marshes and mangroves was more extensive and more broadly distributed than the current condition (compare Figures 6A,B). However, with sea levels of 0.76 m higher than current conditions by 2070 (Figure 6C) or 1.13 m higher than current conditions by 2070 (Figure 6D) there was a significant loss of mangrove forest and palustrine marshes all along Florida Bay and the southwestern region of Florida in an area known as the Ten Thousand Islands region.

When accretion across the palustrine and coastal communities totaled 0.55 m by 2070 (Krauss et al., 2010; Fu et al., 2018) and SLR was only 0.27 m by 2070, the landscape distribution of mangrove forest was much more extensive than the current condition (compare Figures 7A,B). Under this low SLR scenario the mangroves were able to migrate inland while maintaining the current coastline. Even under a more significant SLR of 0.76 m by 2070, the mangrove forest community had the potential to maintain most of the current coastline. It was only under the more extreme scenario of 1.13 m increase in sea level by 2070 that we saw the loss of the wetland coastline everywhere. Yet even here there was significant evidence of mangrove migration into the freshwater wetlands upstream. Figures 6D, 7D indicated a dramatic increase of open estuarine waters at the expense of the coastal plant communities, particularly when accretion was 4.1 mm yr^{-1} (0.211 m by 2070). With a SLR of 1.13 m by 2070, most of the coastal communities and palustrine habitats were not able to transition to anything other than open estuarine water.

DISCUSSION

Peat Collapse

This evaluation of SLR with a raster-based habitat transition model has an implicit assumption that inundation with saline



waters will eventually lead to the peat collapse of the coastal marshes if inundation is too high to be mitigated by above and belowground soil accretion. The term “peat collapse” has been used to describe a shift in soil C balance, leading to a net loss of organic C and soil elevation, culminating in a transition of vegetated freshwater marshes to open water (Chambers et al., 2019). Peat collapse is a unique physical and biological process of shallow subsidence in highly organic soils characterized by a loss of soil strength and structural integrity that leads to elevation loss below the threshold for emergent plant growth and natural recovery (Chambers et al., 2019). The process of peat loss has been documented in various coastal wetlands (e.g., De Laune et al., 1994; Cahoon et al., 2003;

Day et al., 2011; Voss et al., 2013) and has been attributed to a number of factors including changes in microbial processes, increased sulfate reduction, inadequate plant production, root death, and vegetation damage (Stagg et al., 2017; Chambers et al., 2019). While recent research is beginning to develop a mechanistic understanding of peat collapse in the Everglades (e.g., Wilson et al., 2018; Servais et al., 2019; Wilson et al., 2019), uncertainties remain particularly in regards to how freshwater and oligohaline peat soils respond to salinization and the relevance of salinity-induced pore dilation for matrix deformation in peat soils.

A critical concern for the management of freshwater and coastal mangrove ecosystems is the potential for inland freshwater marshes, exposed to increasing sea-level rise, to collapse (National Academies of Sciences Engineering and Medicine, 2018) due to soil salinization and root death (Chambers et al., 2013; Kirwan and Megonigal, 2013; Stagg et al., 2017). If mangrove forests cannot maintain wetland functionality by expanding into regions unable to adapt to the salinity changes associated with increasing sea levels, then significant coastal wetland loss may occur, dramatically altering and increasing the vulnerability of the south Florida coastline.

Soil Elevation and Accretion

In South Florida long-term rates of elevation change and accretion have a strong reliance on belowground biomass and autochthonous processes to maintain elevation. Storm surges can deposit 10–80 mm in southwest mangrove forests and ~5 mm in Florida Bay coastal forests (Koch et al., 2014; Feher et al., 2019). Storms can also destabilize sediments especially when they cause high forest mortality and peat collapse, usually taking 3-years to recover (Cahoon et al., 2003). To put these data in a regional perspective, mangroves in the wider Caribbean typically kept pace with SLR rates of 2–4 mm yr⁻¹, but not at 5 mm yr⁻¹ during the Holocene period (McKee et al., 2007). While McKee et al. (2007) found fringe forests in Belize could gain elevation at an average rate of 4.1 mm yr⁻¹ (1.6 mm from accretion and 2.5 mm from subsurface expansion), Wanless et al. (1994) argue based on the past geologic record that any sustained SLR rates at or faster than 2.3 mm yr⁻¹ will ultimately cause complete coastal erosion in South Florida. The coastal Everglades mangrove forests would move inland as the coastal zone they currently occupy converts to open water and mudbanks.

Another important point to consider when looking at habitat transitions is the increase in forest floor elevations with hurricanes. For example, the Wilma storm surge in 2005 deposited ~5 to 10 mm of sediment at the Florida Bay sites highlighting the importance of hurricane tide surge for transporting sediment to microtidal mangrove forests (Castaneda-Moya et al., 2010). Elevation changes in the larger stature southwestern Florida peninsular coastal mangrove forests (Feher et al., 2019; Howard et al., 2020) showed that these forests had a high increase in soil elevation right after Hurricane Irma but the long-term elevation change rates of ~1–3.9 mm yr⁻¹ were similar to that of the smaller microtidal forests of Florida Bay (Table 9). These data from south Florida mangrove

TABLE 6 | Land cover changes in the coastal study area as a function of no accretion and total accretion elevations of 0.21 and 0.55 m, and a SLR of 0.27 m by the year 2070.

Land cover	No accretion		Accretion 0.211 m		Accretion 0.55 m	
	SLR 0.27 m NAVD		SLR 0.27 m NAVD		SLR 0.27 m NAVD	
	Original inundated land cover		Land cover with transition		Land cover with transition	
	Area (sq km)		Area (sq km)		Area (sq km)	
Estuarine water	4,763	4,809	4,809	4,809	4,809	4,809
Mangrove forest	2,130	2,321	2,138	2,138	2,119	2,119
Palustrine cypress	53	45	53	53	53	53
Palustrine marsh	937	727	913	913	937	937
Palustrine swamp	116	104	114	114	116	116
Saltwater marshes	333	328	332	332	333	333
Saltwater ponds	42	42	42	42	42	42
Total wetlands	3,610	3,568	3,591	3,591	3,599	3,599
Transition of wetland cover types to estuarine water	NA	46	18	18	11	11

TABLE 7 | Land cover changes in the coastal study area as a function of no accretion and total accretion elevations of 0.21 and 0.55 m, and a SLR of 0.76 m by the year 2070.

Land cover	No accretion		Accretion 0.211 m		Accretion 0.55 m	
	SLR 0.76 m NAVD		SLR 0.76 m NAVD		SLR 0.76 m NAVD	
	Original inundated land cover		Land cover with transition		Land cover with transition	
	Area (sq km)		Area (sq km)		Area (sq km)	
Estuarine water	4,796	5,956	5,956	5,956	5,956	5,956
Mangrove forest	2,544	3,052	3,194	3,194	2,651	2,651
Palustrine cypress	139	58	96	96	136	136
Palustrine marsh	1,578	311	725	725	1,445	1,445
Palustrine swamp	365	173	290	290	358	358
Saltwater marshes	393	312	364	364	388	388
Saltwater ponds	42	42	42	42	42	42
Total wetlands	5,061	3,948	4,712	4,712	5,019	5,019
Transition of wetland cover types to estuarine water	NA	1,160	349	349	41	41

TABLE 8 | Land cover changes in the coastal study area as a function of no accretion and total accretion elevations of 0.21 and 0.55 m by 2070, and a SLR of 1.13 m by the year 2070.

Land Cover	No Accretion		Accretion 0.211 m		Accretion 0.55 m	
	SLR 1.13 m		SLR 1.13 m		SLR 1.13 m	
	Original inundated land cover		Land cover with transition		Land cover with transition	
	Area (sq km)		Area (sq km)		Area (sq km)	
Estuarine water	4,800	8,455	8,455	8,455	8,455	8,455
Mangrove forest	2,551	1,478	2,492	2,492	3,213	3,213
Palustrine cypress	233	80	122	122	186	186
Palustrine marsh	1,978	348	533	533	1,060	1,060
Palustrine swamp	510	133	231	231	422	422
Saltwater marshes	395	107	227	227	361	361
Saltwater ponds	42	42	42	42	42	42
Total wetlands	5,708	2,188	3,647	3,647	5,285	5,285
Transition of wetland cover types to estuarine water	NA	3,656	2,060	2,060	422	422

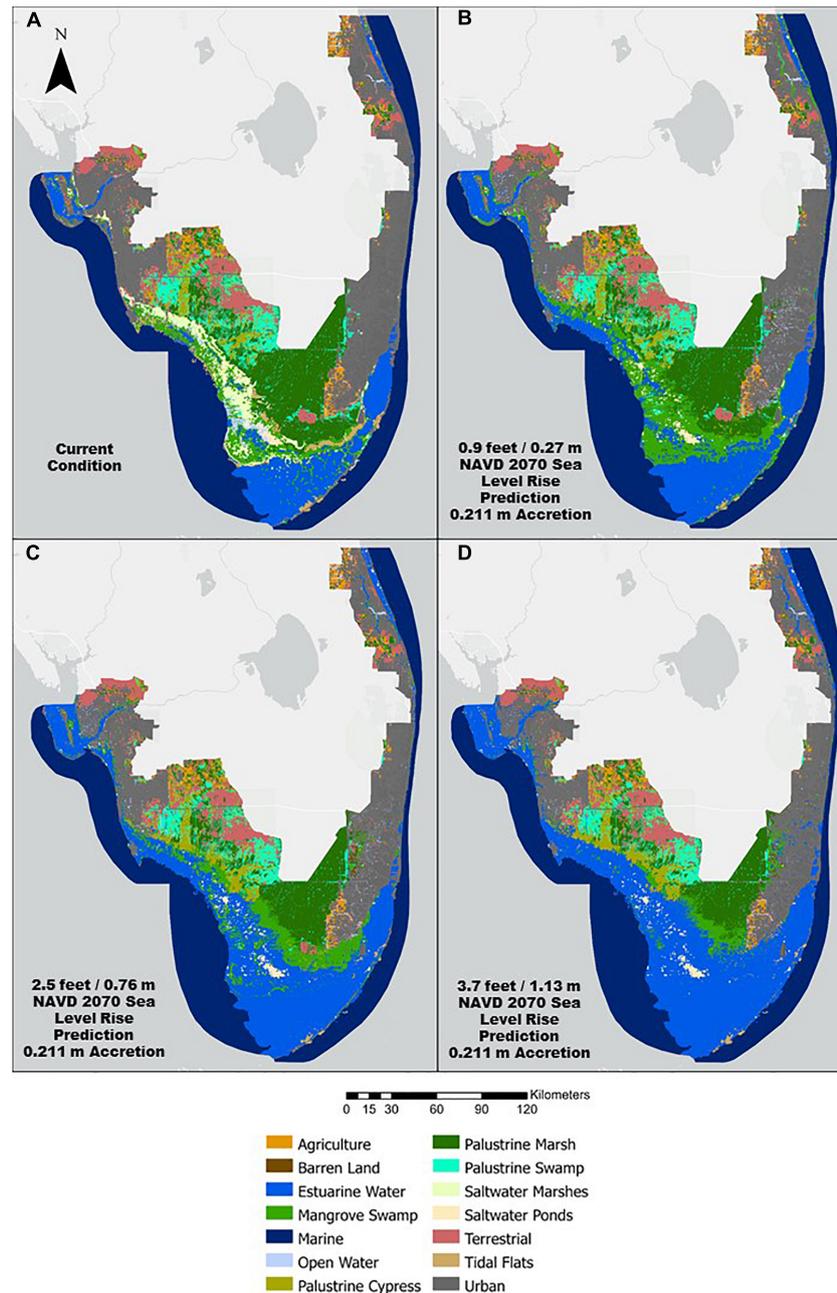


FIGURE 6 | Results of the habitat transition model and a wetland annual accretion rate of 4.2 mm yr^{-1} . **(A)** Current habitat distribution; **(B)** Projected habitat distribution by 2070 with a SLR of 0.27 m (0.9 ft); **(C)** Projected habitat distribution by 2070 with a SLR of 0.76 m (2.5 ft); **(D)** Projected habitat distribution by 2070 with a SLR of 1.1 m (3.7 ft).

forests indicate that on average mangrove forests can keep pace with current SLR but would have difficulty at rates projected for 2070. Although our habitat transition projections cannot be used to direct restoration it does indicate that we should expect significant shoreline transgression and ecosystem degradation without restoration and that we can preserve a high degree of ecological function, shoreline protection and habitat quality with restoration.

Transition Thresholds and Mangrove Migration

There is empirical evidence of mangrove movement into upstream freshwater marsh in the Everglades. During the mid-1940s, the marshes in the southeastern saline Everglades were arranged in well-defined plant communities running parallel to the coast, with shrub mangroves dominating along the coast and graminoid-mangrove communities and *Cladium* dominating

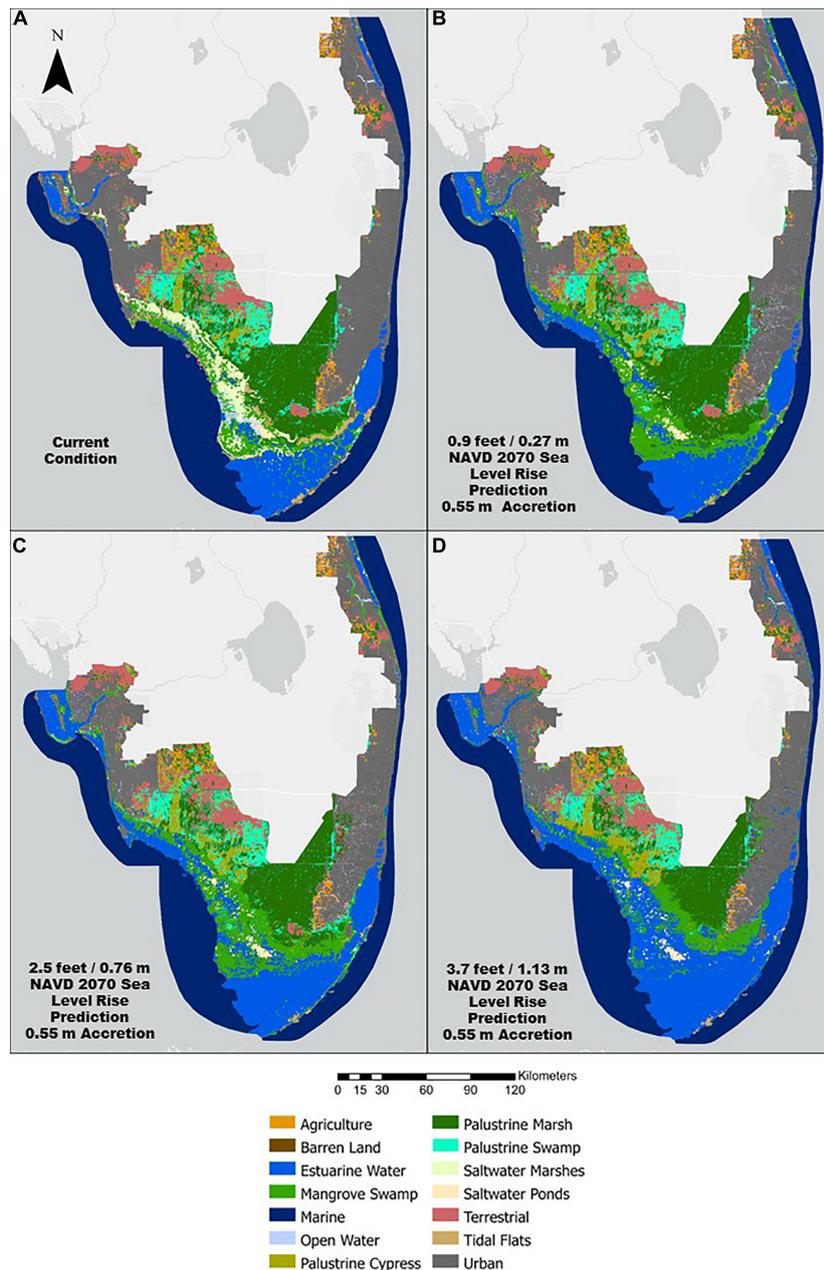


FIGURE 7 | Results of the habitat transition model and a wetland annual accretion rate of 11 mm yr^{-1} . **(A)** Current habitat distribution; **(B)** Projected habitat distribution by 2070 with a SLR of 0.27 m (0.9 ft); **(C)** Projected habitat distribution by 2070 with a SLR of 0.76 m (2.5 ft); **(D)** Projected habitat distribution by 2070 with a SLR of 1.1 m (3.7 ft).

farther inland (Meeder et al., 2017; Ross et al., 2000). However, by 1994, the boundary of the mixed graminoid-mangrove and *Cladium* communities had shifted inland by 3.3 km (Ross et al., 2000). The interior boundary of this low-productivity zone moved inland by some 1.5 km. A smaller shift in this “white zone” was observed in an area receiving freshwater overflow through gaps in the southeastern Everglades C-111 canal. These large-scale vegetation dynamics appear to be the combined result of SLR (approximately 10 cm since 1940) and water management

practices in the southeastern saline Everglades (Meeder and Parkinson, 2018; Sklar et al., 2019).

Paleoecology studies confirm (Ross et al., 2000) the transgressive encroachment of coastal mangroves into historically freshwater marshes. Cores from Upper Joe Bay, approximately 5 km north of the Florida Bay coastline, display a transgressive stratigraphic sequence of sawgrass peat-marl to marl to mangrove peat-marl and documenting saltwater encroachment in the southeastern saline Everglades. The date

TABLE 9 | Comparison mangrove forests elevation change in mm yr⁻¹ from scrub, riverine, fringe and basin mangrove forests in South Florida.

Location	Forest type	Soil elevation change (mm yr ⁻¹)	Soil accretion (mm yr ⁻¹)	Shallow subsidence (mm yr ⁻¹)
Florida Bay ^a	Scrub (FF)	3.9	2.1	-1.8
	Scrub (PF)	1.7	1.9	0.2
Lostmans River ^b	Riverine	3.5	4.6	1.1
Rookery Bay	Basin	3.9	2.0	-1.9
Twin Cays ^c	Fringe	4.1	1.6	-2.5
Twin Cays ^c	Scrub	-3.7	0.7	4.4
Kosrae ^d	Riverine	-3.0	11.0	14.0
Hainan ^e	Riverine	8.6	13.2	4.6
Hainan ^e	Riverine	7.8	7.4	-0.4

Negative values for shallow subsidence indicate soil expansion. Data from 1997 to 2019 in fringe and scrub forests in Florida Bay (Taylor Creek Basin) under frequently flooded (FF) and permanently flooded (PF) sites, Lostmans River Florida, Rookery Bay Florida, Twin Cays Belize, Kosrae, Micronesia, Hainan, China. Data from ^aThis study; ^bFeher et al. (2019), ^cMcKee et al. (2007), ^dKrauss et al. (2010), ^eFu et al. (2018).

is based on 210Pb dating of these mangrove peat-marl cores indicate an average accretion rate of 3.2 mm per year (Willard and Bernhardt, 2011).

Management Implications

Although this was a very coarse representation of the dynamics of accretion, mangrove migration and palustrine marsh transition in the face of SLR, it served to demonstrate the principle of RAD resource management (Lynch, in press). Ecosystem transformations around the world are occurring at unprecedented rates and spatial extents due to pollution, invasive species, land cover changes, and now, climate change and SLR. Transformations are defined by Beever (2006) and Lynch (in press) as the emergence of a self-organizing ecological system, like an open waters estuary, that diverges significantly and irreversibly from prior historical ecosystem structure and function. Lynch (in press) argued that new thoughtful, holistic resource management and restoration requires iterative learning (e.g., adaptive management) and a strategy tailored to consider the need to *Resist*, *Accept* or *Direct* (RAD) ecosystem transformations. To *Resist* ecosystem transformations, actions focus on maintaining current or historical ecosystem composition and function. To *Accept* transformations, by not intervening, society yields to the emergence of the structure and function of the transformed ecosystem. To *Direct* a transformation, resource management accepts change is inevitable, but decides to intervene to steer the ecosystem toward a particular structure and function. According to this RAD approach there are three feasibility criteria to consider when deciding which RAD strategy is appropriate and practical: ecological, societal, and financial. Our mangrove transition analysis suggests that scenarios that increase freshwater flows to the coastal wetlands and thus enhance both above and belowground processes of accretion can *Direct* rising sea levels toward less peat collapse, less land loss and expanded mangroves forests via migration into palustrine habitats.

Building a Better Model

The model presented here is of limited utility for testing specific resource management options because it is based on a very broad conceptualization of habitat specific transition thresholds and accretion rates, and because a bathtub approach like ours does not capture the true hydrological dynamics and complexities of South Florida. Future empirical and experimental research is needed to reduce the uncertainties associated with: (1) saltwater intrusion impacts to soils, sediments and plants; (2) habitat-specific inundation and water quality transition thresholds; and (3) mechanisms of enhanced mangrove productivity and inland migration. Directed coastal zone management, focused upon minimizing land loss in the face of SLR, will need a dynamic ecosystem succession model that integrates the impacts of extreme water levels due to upstream events and storm surge, especially if the goal is to preserve coastal wetland ecosystem services such as, flood control, aquifer protection, fisheries productivity and landscape biodiversity. Future analytical and modeling research is needed to do a better job of reducing the uncertainties associated with: (1) SLR and climate change; (2) landscape evolution, transformation and change and (3) the integration of bio-geomorphic changes (i.e., subsidence and accretion) with hydrodynamics flow patterns, stage and extreme events.

CONCLUSION

To be clear, this spatial analysis does not suggest a “Pollyanna” solution to SLR in South Florida. Marine transgression with SLR will cause saltwater intrusion (surficial and groundwater) and significant environmental impacts. The results also indicate that on average mangrove forests can keep pace with current SLR but would have difficulty at higher SLR scenarios projected for 2070. We are aware that a deeper unpacking of storm surges and other forms of extreme climatic events is needed. Yet, there was significant evidence of mangrove migration into the freshwater wetlands upstream. The movement of the mangrove community into the freshwater marsh habitat, facilitated by increased freshwater inflows, tidal surge salt wedge incursion and propagule recruitment (Cahoon et al., 2006; Doyle et al., 2010; Smoak et al., 2013; Raabe and Stumpf, 2016) is a *Directed* adaptation that shows a great deal of promise. Increased freshwater flows could stave off projected saltwater intrusion and facilitate mangrove inland migration under less salty water conditions (Raabe et al., 2012). Thus, maintaining lower salinities could make the mangrove community more resilient. In the end, forest soil vertical elevation must keep pace with current and projected accelerated SLR to reserve the vital ecosystem services provided by this unique wetland.

The extent of inundation depicted in this analysis does not include upstream headwaters effects or specific habitat mechanisms that build peat. This bathtub modeling approach of ours, compared to more sophisticated hydrodynamic and ecological modeling approaches has been found to over-estimate inundation because it does not take friction and other hydrodynamic forces into consideration

(Neumann and Ahrendt, 2013). However, our approach allowed us to conceptualize the issue and the impact. Next steps are to apply more complex models, build understanding of the role each cover type has in generating the friction that would reduce the inland migration of coastal waters and to design studies to look at community response and transitions due to SLR.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

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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Viable Putative *Vibrio vulnificus* and *parahaemolyticus* in the Pensacola and Perdido Bays: Water Column, Sediments, and Invertebrate Biofilms

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Vibriosis is the general term for human illnesses caused by infection of pathogenic *Vibrio* species. *Vibrio vulnificus* (*Vv*) and *parahaemolyticus* (*Vp*) are two problematic waterborne pathogens that have yet to be enumerated in northwest Florida coastal Gulf of Mexico estuaries. In this regionally novel study, we surveyed 43 locations in two subtropical estuarine systems, Perdido Bay and Pensacola Bay, over seven dates in winter 2020. Sampling included three substrate types: surface waters, sediments, and invertebrate biofilms. We determined baseline abundances of presumptive viable *Vv* and *Vp* appearing as colonies on CHROMagar (*Vv*, blue; *Vp*, purple). *Vv* was detected in 37 out of 43 water samples, with maximum levels of 3,556 CFU/mL. *Vp* was only detected in 15 water samples, with a maximum concentration of 8,919 CFU/mL. Sediments contained *Vv* in all but one sample, with concentrations ranging from 121 to 607,222 CFU/mL. In contrast, *Vp* were only detected in 33 sediment samples, where concentrations ranged from 28 to 77,333 CFU/mL. Opportunistically-sampled surface swabs (biofilms), collected from shells (either oyster or barnacle) and polychaete worms found in sediment samples, contained on average 7,735 and 1,490 CFU/mL of *Vv* and *Vp*, respectively. Surface water *Vv* abundances covaried with bottom water pH, maximum prior cumulative wind speeds, and tidal coefficient on the day of sampling. *Vp* surface water abundances negatively correlated with surface water salinity, surface water pH, and bottom water pH and positively correlated with total surface dissolved inorganic and total Kjeldahl nitrogen concentrations, and wind. Spatially, there was large variation in *Vibrio* densities in surface waters; abundances of both species were strongly correlated with wind, suggesting resuspension was important. Sedimentary abundances of both putative *Vv* and *Vp* shared a correlation with one parameter: salinity stratification. Due to the length of this study, temperature was not considered a major factor. This short-term (1 month) study was designed not to enumerate pathogenic *Vv* or *Vp*, but rather to establish the first winter baseline of *Vibrio* abundances for this region. Determination of these baseline winter cultivable putative *Vibrio* abundances will be valuable in predicting relative risk factors in each waterbody of interest.

Keywords: *Vibrio parahaemolyticus*, *Vibrio vulnificus*, estuary, water column, sediment, viable, resuspension, stratification

INTRODUCTION

Warm and salty or brackish waters in Florida and other nearby coastal states are currently subject to increased temperatures and frequency of storm events, changing heterotrophic bacterial communities (Lønborg et al., 2019). The success of specific groups of bacteria in subtropical estuaries and coasts are affected by many factors including eutrophication, sea-level rise, warming temperatures, and changes in trophic states (Montánchez et al., 2019; Krishna et al., 2020; Li et al., 2020). One major concern associated with these factors is increased *Vibrio* abundances: in the water column, in and on invertebrates, and in the sediments (Hughes et al., 2013). *Vibrio vulnificus* (*Vv*) and *V. parahaemolyticus* (*Vp*) are two species that are potentially harmful to humans and the marine life on which local economies depend. *Vibrio* infections in the USA account for approximately 8,000 deaths annually (Pruzzo et al., 2005). *Vv* mostly causes human disease via entrance of open cuts or wounds, with a case fatality rate as high as 50% (Johnson et al., 2012). Pathogenesis of *Vp*, on the other hand, occurs through the consumption of raw or undercooked shellfish (especially oysters) and is the leading cause of reported fatalities through gastroenteritis and septicemia due to foodborne illness (Panicker et al., 2004; Johnson et al., 2012). Both species possess specialized genes that contribute to pathogen virulence by promoting phenotypes such as increased epithelial (intestinal) cell adhesion or erythrocyte (red blood cell) lysis (i.e., hemolysis) (Zhang and Austin, 2005).

Although *Vp* infections are more common in recent years (Lovell, 2017), serious *Vv* infections are concurrently increasing in frequency (Baker-Austin and Oliver, 2018). These increased pathogenic loads can be attributed to a variety of factors. Temperature is considered to be a driving factor of *Vibrio* abundances (Johnson, 2013; Wetz et al., 2014) and may even affect the relative severity of vibriosis (Hernández-Cabanyero et al., 2020). However, temperature was not a major factor in this study. In fact, our findings suggest other factors may also be responsible for higher abundances of culturable *Vibrio*. Water column *Vibrio* abundances may increase after storm events, possibly from sediment bacteria resuspension (Fries et al., 2008). Increased nutrient loads, often associated with anthropogenic and climatic-influenced eutrophication, will likely promote higher concentrations of human pathogens such as *Vibrio* species (Malham et al., 2014). Higher turbidity has been previously related to *Vp* in subtropical estuaries near coastal northern Gulf of Mexico (GoM) (Zimmerman et al., 2007). Because *Vibrio* may be associated with diatoms and zooplankton, their abundances are likely positively related to increased turbidity, typically measured as concentrations of total suspended solids (TSS). Similarly, a positive relationship is often observed between *Vibrio* abundance and phytoplankton biomass, typically measured by chlorophyll *a* (chl *a*) (Martinez-Urtaza et al., 2012). Therefore, the combination of terrestrial inputs of nutrients from rain and storm events, sediment resuspension from high wind speeds, and the quite evident rise in global water temperatures may provide optimal environmental conditions for the success of human pathogens such as *Vv* and *Vp* (Davis et al., 2017; Froelich et al., 2019).

Invertebrate filter-feeders (such as oysters or barnacles) are also susceptible to minor changes in water and sediment quality, making them common carriers of pathogenic *Vp* (Aagesen et al., 2013). Oysters in the Pensacola Bay System (PBS), including in polluted waterbodies within, such as Bayou Chico, are common (Caffrey et al., 2016). Barnacles were abundant invertebrates settling on artificial reefs in the nearby GoM shelf in a recent study (Babcock et al., 2020). Often, biofilms on invertebrate shells are considered anoxic, a key consideration in our evaluation of *Vibrio* on invertebrates. *Vv* and *Vp* are aerobes, with most strains functioning as facultative anaerobes (Drake et al., 2007). Biofilms on oyster or barnacle shells are often oxic (Ray et al., 2019), which could promote success of *Vv*, *Vp*, and other aerobes in shell biofilms. For example, desiccation or regular air exposure of oysters from nearby northern GoM bays promotes *Vibrio* growth (Grodeska et al., 2019; Prunte et al., 2020).

In water and sediments or on invertebrates of Florida subtropical estuaries, there is currently little data with respect to *Vv* or *Vp* abundances, except in Apalachicola Bay, FL (Williams and LaRock, 1985; Lipp et al., 2001), formerly home to one of the largest oyster fisheries in the United States. It is estimated that warming water temperatures due to climate change may have a more significant effect in temperate waters (Froelich and Daines, 2020). However, abundances in subtropical estuaries are important to assess, not only considering the potentially pathogenic nature of *Vv* and *Vp*, but also because of increasing water and sediment temperatures anticipated with climate change (Thomas, 2016). Furthermore, estuaries may be fragile ecosystems, especially so in the current threat of climate change in subtropical regimes. Extreme climate events (droughts, floods, tropical cyclones, heat waves, etc.) have increased in frequency and intensity, coinciding with climate model predictions due to anthropogenic causes. Consequences of warming waters combined with increased intensity or frequency of such extreme events impact a wide range of trophic levels. Terrestrial-derived nutrient influxes into fresh and estuarine systems promote a chain of succession in both primary and secondary producers, leading to changes in the types of heterotrophs. Warming waters expected with global climate change combined with increased terrestrial organic matter inputs exacerbates these changes, in both temperate (Paczkowska et al., 2019) and subtropical (Williams and Quigg, 2019) regions. Clearly, there is cause for investigating the effects of these changes locally in relation to potentially pathogenic *Vibrio* loads.

Study site. To determine baseline presumptive *Vv* and *Vp* loads in winter, we surveyed seven major basins in the Pensacola, FL area. Locations for this survey were chosen within the PBS and the Perdido Bay, located in northwest Florida. The PBS is an excellent model system to examine the responses of subtropical microbial responses to anthropogenically-driven changes in temperature, freshwater flow, and other parameters (Murrell et al., 2018). The PBS is the fourth largest estuary in Florida and is unique in that it is microtidal, nutrient inputs are relatively low (Caffrey and Murrell, 2016), and heterotrophs are substrate-limited (Murrell, 2003). Flow from the Escambia River provides approximately 70% of the freshwater to Escambia Bay, which is part of the PBS (Caffrey and Murrell, 2016).

While light availability, nutrient fluxes, primary productivity, and chl *a* are influenced by riverine nutrient inputs (Caffrey and Murrell, 2016), the impact of freshwater flow on the distribution of *Vibrio* in the estuary and adjacent basins is unknown. Chl *a* concentrations range from 1 to 26 $\mu\text{g}/\text{mL}$ and are highest in mesohaline portions of the Bay (Murrell and Lores, 2004; Murrell et al., 2007; Caffrey and Murrell, 2016). Bacterial abundances and production are also influenced by freshwater inputs from the Escambia River (Murrell, 2003). Cyanobacteria abundances in these systems are low at the marine ends and undetectable in freshwaters, but dominate in mesohaline zones (Murrell and Caffrey, 2005).

In the PBS, chl *a* and phytoplankton productivity peak about a month following seasonal maximum freshwater flow from the Escambia River (Murrell et al., 2007). Summer benthic hypoxia occurs during periods of stratification (Hagy and Murrell, 2007), but is moderated by light that supports sub-pycnocline phytoplankton and benthic primary production (Murrell et al., 2009). However, regional strong storm events do result in high particle loads ($> 6,000$ particles/mL), particularly in the summer. In winter (February 2014 and 2015), total particle abundances ranged from 500 to $> 3,500$ particles/mL, as determined by FlowCam analysis (Sieracki et al., 1998) of Lugols-preserved whole water samples from the Escambia Bay (Michael Murrell, personal communication). Interestingly, the detrital contribution to total particulate matter composition is low (Murrell, 2003), suggesting the majority of particulate matter in the estuary is comprised of zooplankton and phytoplankton. The phytoplankton are diverse, with picocyanobacteria ($< 5 \mu\text{m}$) dominating during summer months, representing 70 to 100% of total chl *a* (Murrell and Lores, 2004), a pattern found in other GoM estuaries (Murrell and Caffrey, 2005).

Perdido Bay is another shallow estuarine system whose watershed includes southeast Alabama. Waters in this system are generally more turbid than in the PBS as a whole, and major sources of freshwater input include the Perdido River and Elevenmile Creek (Macauley et al., 1995). While Escambia Bay/Pensacola Bay and Perdido Bay are major river-dominated systems with freshwater inflow, Big Lagoon is a mesohaline system connecting the PBS and Perdido Bay, where sediments are more sandy than muddy, light attenuation is generally low, and seagrasses are more abundant than in the Escambia or Perdido Bays (Hester et al., 2016; Murrell et al., 2018). Creeks provide freshwater inputs into the three urban bayous in this study: Bayou Grande, Bayou Texar, and Bayou Chico. All three bayous, adjacent to the city of Pensacola, are the largest bayous in the PBS that are impacted by stormwater runoff (Lewis et al., 2016). Other inputs of freshwater to the bayous include adjacent creeks, but runoff contributes greatly to eutrophication and sedimentation, as well as contamination with heavy metals and pesticides (Lewis et al., 2002; Nature Conservancy, 2014). Septic tank systems within the Bayou Chico and Grande watersheds contribute to eutrophication, and Bayou Chico fails to meet total maximum daily load goals of US and FL standards (Nature Conservancy, 2014). We hypothesized that abundances of *Vibrio* species in the Perdido and Pensacola Bay Systems would be higher in water column samples with high turbidity. We also expected *Vibrio*

species to thrive where dissolved or total nutrient concentrations were high, especially when salinity and temperature fell within optimal ranges as described by previously-published studies (Kaspar and Tamplin, 1993; Motes et al., 1998; Hsieh et al., 2008). Temperature was not considered a major factor in this short-term study, as all sampling was done within one winter month (February 2020).

MATERIALS AND METHODS

Field Sampling

Forty-three stations were chosen, representing a wide range of salinities, stratification, eutrophication, and freshwater influence. We surveyed surface waters and sediments on seven dates between 02/03/20 and 03/02/20 (**Supplementary Figure 1**). All sampling and *in situ* measurements were performed from small vessels. Hydrographic data (surface water and bottom water) were measured with a YSI multimeter (Xylem, Yellow Springs, OH). Parameters measured *in situ* at all stations included surface and bottom water column readings of salinity (PSU), temperature ($^{\circ}\text{C}$), and dissolved oxygen (mg/L). Surface and bottom water pH were determined with a ProDSS pH sensor, which became available on 02/21/20; thus, surface and bottom pH were reported only for Bayou Grande (02/21/20), Big Lagoon (02/28/20), and Perdido Bay (03/02/20). Statistical analyses (**Supplementary Table 4**) for pH data reflect the correct sample size ($n = 20$). Light attenuation coefficient (K_d , m^{-1}) was calculated from the slope of attenuation of photosynthetic photon flux fluence rate (PPFFR) at 0.5-meter intervals measured with a LiCor 4II spherical underwater quantum sensor. Total water column depth (meters) was measured with the line on a Secchi disk and with the vessel's on-board instrumentation. Total precipitation and cumulative maximum wind speeds were recorded in the three days leading up to sampling, including the mornings of sampling events in which windy conditions delayed the start of sampling. Precipitation and maximum wind speed data were obtained from the NOAA Climate Online Data station ID: GHCND:USW00013899, 30.47° N, 87.2° W located at Pensacola Regional Airport (WUnderground, 2020; **Supplementary Table 4**). Tidal coefficient (m) at Lora Point (Escambia Bay, 30.5178° N, 87.1700° W), also within our sampling area and in one of the seven basins, was also recorded for each sampling date (TidalCoefficient, 2020). Since precipitation, wind speed, and tidal coefficient were the same within basins, values for each were considered reflective of the entire basin. Therefore, sample size for these parameters was $n = 7$.

Forty-three surface water samples were collected *via* bucket cast and held in an acid-washed 1-L Nalgene bottle (one for each site) in coolers maintained at *in situ* temperature. Sediment samples were collected using a PONAR grab sampler. Forty-two sediment samples (0.5 to 2.0 mL of superficial sediment) were collected from the top 0 to 30 cm with sterile, single-use plastic spatulas and resuspended in 0.5 mL of phosphate-buffered saline (1X solution contains 0.137M NaCl, 0.0027M KCl, 0.0119M phosphates, pH 7.4) (Fisher BioReagents, Pittsburgh, PA), and

held in sterile 50-mL centrifuge tubes in coolers maintained at *in situ* temperature. An additional 50 mL of sediment was collected for analysis of sediment water content, organic matter content (loss on ignition), sediment chl *a* and phaeopigment concentrations. Surface water was filtered on-site through Whatman GF/F filters to collect filtrates which were deposited into acid-washed bottles and immediately preserved in coolers on ice and later stored at the laboratory at -20°C for subsequent dissolved nutrient analyses. Filters were also immediately cooled on site and preserved at -20°C for subsequent chl *a* analyses. Whole water was preserved with H_2SO_4 as per EPA method 351.2 and held at 4°C for total Kjeldahl nitrogen (TKN) analyses. Where invertebrates were present (on marker poles or in sediment grabs), we collected invertebrate surface (presumptive biofilm) samples *via* surface-swab, henceforth referred to as biofilm or biofilm swab samples. A total of 13 samples of these biofilms, approximately 1 cm^2 surface area each, were collected with sterile cotton swabs, resuspended in 0.1 mL of sterile phosphate-buffered saline in centrifuge tubes and held at *in situ* temperature until processed.

All surface water samples were analyzed using the following methods: dissolved inorganic phosphate (DIP) as in (Parsons et al., 1984), NH_4^+ as in (Holmes et al., 1999), and $\text{NO}_3^- + \text{NO}_2^-$ as in (Schnetger and Lehnert, 2014). Dissolved inorganic nitrogen (DIN) is the sum of NH_4^+ , NO_3^- , and NO_2^- . Whole water was preserved with acid and analyzed for TKN with EPA method 351.2 on a Lachat Quikchem FIA Model autoanalyzer. Samples for chl *a* were extracted in 90% acetone for 24 hours and analyzed as in (Welschmeyer, 1994). Sediment samples were evaluated for biomass of benthic microalgae using the acidified chl method to determine concentrations ($\mu\text{g/g}$) of sediment chl *a* and phaeopigment as in (Parsons et al., 1984). Sediment aliquots were also processed for water content and organic carbon (ash content) percentages. Ash-free dry weight combustion was at 500°C . Surface water concentrations of TSS were determined using EPA method 160.2.

Viable Putative *Vibrio* Abundances

To determine abundances of presumptive viable *Vv* and *Vp*, all samples (surface water, sediment suspension, and biofilm surface-swab suspension) were plated on CHROMagarTM-*Vibrio* (DRG International, Inc., Springfield, NJ), an agar medium with chromogenic substrates (15.0 g/L agar, 8.0 g/L peptone and yeast extract, 51.4 g/L salts, 0.3 g/L chromogenic mix, pH 9.0). In winter (January) and summer (June) of 2019, we had performed preliminary end-point PCR testing to narrow color ranges of presumptive *Vv* (bright blue, with early color development before 24 h) and *Vp* (bright mauve, again with early color development). To assess accuracy of presumptive *Vv* colored colonies on CHROMagar, *vvhA* was assayed using primer pair F-vvh785/R-vvh990 as previously described (Panicker et al., 2004; Panicker and Bej, 2005). Presumptive *Vp*, appearing as bright pink, not purple, were confirmed as *Vp* with either *tdh*- or *trh*-positive end-point PCR, employing primer pairs *tdh*-F/R and *trh*-F/R as previously described (Nordstrom et al., 2007). All samples of colony biomass were also tested by end-point PCR for prokaryotic 16S rRNA (BACT1369 + PROK1541R), to

verify there were no false-negatives. None of the 2019 preliminary data (abundances based on colony counts or end-point PCR results) are presented here, since data collection in 2019 did not include environmental data. In the preliminary work, depending on the body of water sampled, the percent of bright blue colonies scoring *vvhA*-positive ranged from ~ 50 to 85%, with an average of 75% among all summer and winter 2019 samples for *Vv* (bright blue colony, *vvhA*-positive) and *Vp* (bright pink colony, *tdh*- or *tlh*-positive.) The same person (L. Waidner) who observed *vvhA*-positive and *trh*- or *tdh*-positive colonies was also the one who counted colonies in the winter 2020 data presented in this study.

In this study, to assess presumptive *Vv* and *Vp* abundances, water samples were plated undiluted on CHROMagarTM-*Vibrio*; fresh sediment samples were diluted 2-, 3-, and 4-log-fold with phosphate-buffered saline before plating, and biofilm surface-swab samples were similarly diluted 1- and 2-log-fold. Subsequent to dilutions and plating, exact volumes of each sediment sample were determined. Each abundance calculation accounted for the variability in volume of sediments collected in the field. Presumptive biofilm, sediment, and undiluted surface water samples were vigorously shaken (water) or mixed *via* vortex (sediment and biofilm) prior to plating. Three aliquots (0.15 mL each) of each dilution of each sample, in triplicate, were plated on Petri plates as previously described (Oliver, 2003; Huq et al., 2012; Thomas et al., 2014; Yeung and Thorsen, 2016). Plating was followed by incubation in the dark at room temperature (24°C , chosen since this was most similar to *in situ* temperature) for 24, 48, and 72 h. At each 24-hour interval, the number of each of the colored colony types was recorded and reported as CFU of presumptive *Vv* or *Vp*. The abundances of each type of *Vibrio* were calculated in the same manner for all sample types and included all abundances of dilutions that could be accurately assessed (between 3 and 300 CFU/plate). Abundances lower than the limit of detection (15 CFU/mL) were recorded as zero. For presumptive abundance determination across all samples, abundances at 48 hours were used, and average cell abundances were normalized to milliliters (mL), since abundances per cm^3 are equivalent to abundances per volume (mL). We did not use molecular methods to confirm *Vv* and *Vp* (i.e., bright blue and bright pink colonies, respectively) in this study.

Statistical Analyses

Mathematical relationships and each corresponding significance were performed using the “Analyze” function of the Statistical Package for the Social Sciences (SPSS). All surface water and sedimentary *Vibrio* abundances were log-transformed to accommodate normality for Pearson (parametric) correlation analysis. SPSS was used to generate one-way analysis of variance (ANOVA) tests to determine differences between log-transformed *Vibrio* abundances and environmental parameters among all seven basins. Parameters that showed relatively strong evidence ($r \geq 0.30$) for a difference among basins were followed with multiple comparison procedures (Tukey’s *Post Hoc*) to determine wherein the seven basins lies the difference. In addition to basin-by-basin comparisons, one-way ANOVAs

were also generated to determine differences between open and enclosed basins. Pearson correlation coefficients were calculated in the statistical package Plymouth Routines in Multivariate Ecological Research (PRIMER) version 7. Box- and surface-plots showing the distribution of measured abundances and ecological parameters across all basins were also generated using PRIMER.

RESULTS

Overview of Bodies of Water Sampled

In all stations of all basins surveyed, the minimum depth was approximately 0.4 m, with a maximum depth at any station of 6.1 m. The average surface water temperature of all stations was 15.4°C, and temperatures ranged from 12.3 to 22.2°C (Table 1A). Surface water salinities ranged from 0.9 to 18.2 PSU. Among all seven basins, Bayou Chico had the greatest average water chl *a* (8.6 ± 5.4 µg/L), TKN (53.5 ± 16.7 µM), and DIN (39.0 ± 38.7 µM) concentrations. Of all basins examined, the surface waters' temperature and salinity in Bayou Chico were overall the highest and lowest, respectively (Figure 1). Additionally, salinity stratification was high at two of the five locations sampled within Bayou Chico, V-20 and V-23, with surface and bottom values of 9.4 and 21, respectively (Supplementary Table 4). Perdido Bay had the lowest average water chl *a* concentration (1.9 ± 1.0 µg/L), and Big Lagoon had the lowest average TKN (24.2 ± 3.0 µM) and DIN (1.7 ± 0.5 µM) concentrations. DIP concentrations were negligible or undetectable in surface water samples (Table 1A and Figure 2).

Bottom water temperatures and salinities ranged from 13.0 to 22.0°C and 1.9 to 28 PSU, respectively (Table 1B). Bayou Texar had the greatest average sediment chl *a* concentration (3.7 ± 2.4 µg/g). Escambia Bay had the greatest average concentration of sediment phaeopigment (4.7 ± 1.5 µg/g) and average sediment water content ($58.0 \pm 22.7\%$). Perdido Bay had the greatest average sediment organic content ($8.3 \pm 6.0\%$), with Pensacola Bay as the lower bound ($1.8 \pm 2.8\%$).

Overview of Putative *Vibrio* in Surface Waters

Overall, in surface waters, *Vv* was more ubiquitous than *Vp*. In seven of the 43 surface water samples, putative *Vv* was below detection limits of the chromogenic agar assay (Table 2). In the remaining 36 locations, *Vv* concentrations ranged from 15 to 3,556 CFU/mL, with a median concentration of 44 CFU/mL. In contrast, putative *Vp* abundance was below the limit of detection at 28 of the 43 stations (Table 3). In the 15 surface water samples where it was detected, *Vp* concentrations ranged from 15 to 8,919 CFU/mL, with a median concentration of 104 CFU/mL. Bayou Texar greatly outnumbered the other basins with regards to *Vp* abundances, with Pensacola Bay and Perdido Bay having the lowest surface water *Vp* abundances (Table 3). Conversely, Bayou Chico had the greatest abundance of surface water *Vv* of the seven basins, as well as the largest range in *Vv* surface water abundance at the sites within the basin (Figure 3).

Overview of Putative *Vibrio* in Sediment Samples

Basin-wide analyses indicated there was no body of water with low concentrations of *Vibrio* in sediments. At the 43 locations sampled, 42 sediment samples were obtained. Sediment types ranged from sand to sand-mud mix to mud. When *Vv* was detected, concentrations ranged from 169 to 607,222 CFU/mL, with a median concentration of 18,160 CFU/mL (Table 2). In three of the seven major basins, there were exceptionally high *Vv* concentrations in at least one location each. In Bayous Chico and Texar, *Vv* was found in some locations at concentrations > 300,000 CFU/mL, and in one location of Big Lagoon at > 600,000 CFU/mL (Table 2). In contrast, *Vp* was generally less concentrated in the sediments and was below detection limits in nine of the sediment samples (Table 3). In the remaining 33 stations, *Vp* concentrations ranged from 28 to 77,333 CFU/mL, with a median concentration of 652 CFU/mL. The highest densities of *Vp* were observed in the sediments of Bayou Chico (77,333 CFU/mL) and in

TABLE 1A | Means and ranges of physical and chemical parameters of surface water.

Basin	Range of depths (m)	Surface water ^a						
		K_d^b	Temp. (°C)	Salinity (PSU)	Chl <i>a</i> (µg/L) ^c	TKN (µM) ^d	DIN (µM) ^e	DIP (µM) ^f
Pensacola Bay	0.9–3.5	0.9 ± 0.1	12.9 ± 0.4	14.7 ± 1.6	2.8 ± 1.1	27.1 ± 1.4	3.0 ± 2.4	0.0 ± 0.0
Escambia Bay	1.5–3.4	1.1 ± 0.2	13.9 ± 0.3	9.6 ± 4.0	4.1 ± 0.9	32.7 ± 3.7	2.8 ± 3.1	0.0 ± 0.0
Bayou Texar	1–2.7	1.3 ± 0.4	15.1 ± 0.6	8.5 ± 1.0	2.9 ± 1.1	40.6 ± 3.7	20.7 ± 4.8	0.1 ± 0.1
Bayou Chico	0.4–4.3	1.8 ± 0.8	20.7 ± 0.9	4.1 ± 2.1	8.6 ± 5.4	53.5 ± 16.7	39.0 ± 38.7	0.0 ± 0.0
Bayou Grande	0.9–2.9	1.2 ± 0.3	16.5 ± 0.7	8.8 ± 3.3	3.4 ± 1.5	38.1 ± 6.5	5.7 ± 1.5	0.1 ± 0.1
Big Lagoon	1.1–6.1	0.7 ± 0.1	13.8 ± 0.5	16.7 ± 1.2	2.3 ± 0.8	24.2 ± 3.0	1.7 ± 0.5	0.1 ± 0.1
Perdido Bay (FL)	1.1–3	1.0 ± 0.3	16.1 ± 0.4	9.8 ± 3.0	1.9 ± 1.0	41.1 ± 5.6	4.7 ± 2.2	0.1 ± 0.1

^aMean ± SD.

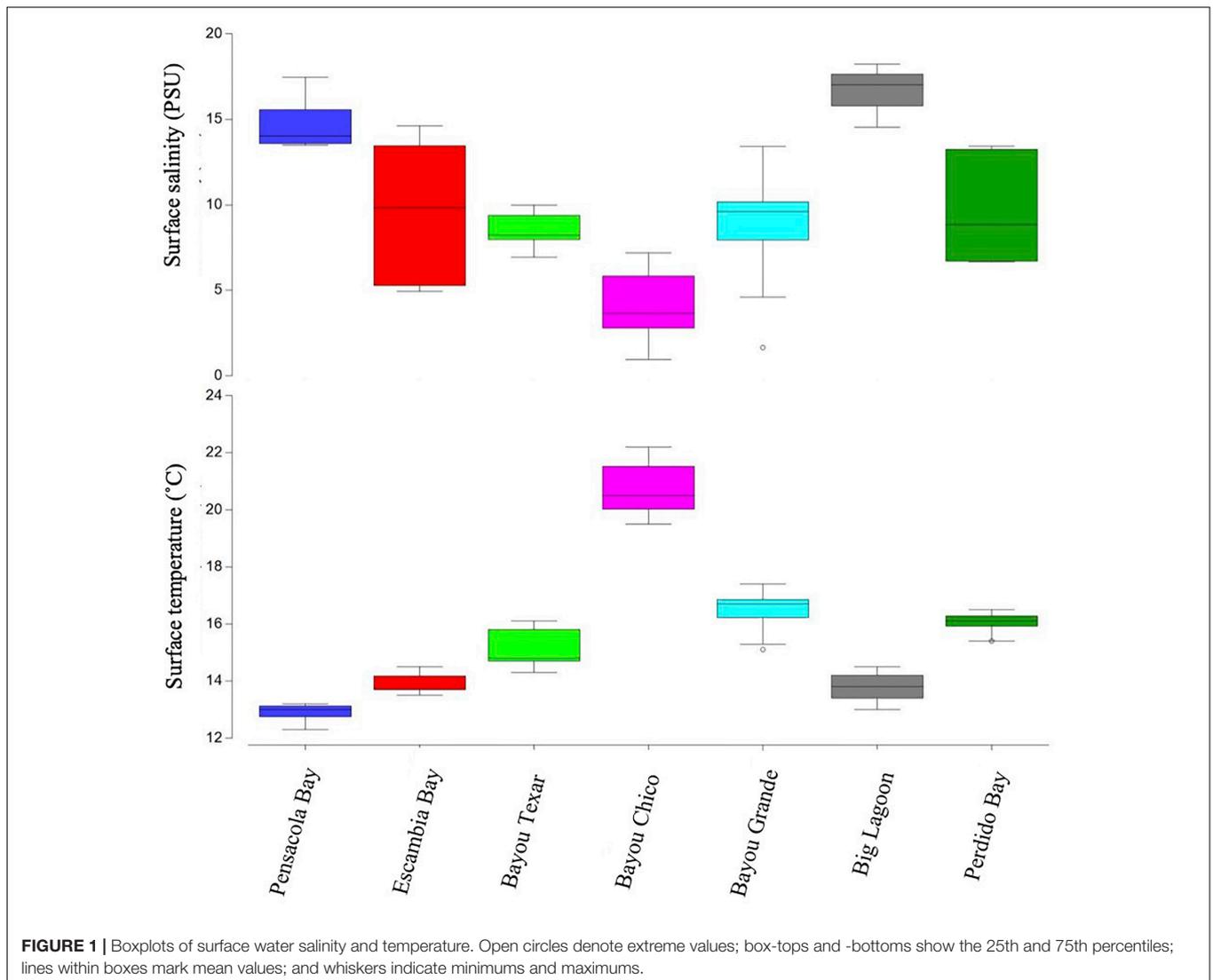
^b K_d , light attenuation coefficient.

^cchl *a*, chlorophyll *a*.

^dTKN, total Kjeldahl nitrogen.

^eTotal dissolved inorganic nitrogen (DIN), sum of NH_4^+ , NO_3^- , and NO_2^- .

^fDIP, dissolved inorganic phosphate.



Big Lagoon (19,185 CFU/mL). In four of the five Perdido Bay sites, *Vp* was undetectable. In Bayou Grande, *Vp* was undetectable in two of the seven locations. In the Pensacola Bay basin (Pensacola Bay and Escambia Bay), we collected 11 sediment samples. Of those, three contained undetectable levels of *Vp*, one site had 1,649 CFU/mL, and the remaining eight sites contained fewer than 655 CFU/mL in the sediments (Table 3).

The variation in sediment *Vibrio* abundance, both among the seven basins and within each of them, was high. The upper bound of *Vv* was similar across all basins, with Pensacola Bay and Perdido Bay having the largest range (Figure 4). *Vp*, however, was more abundant in Bayou Chico, with Bayou Texar and Big Lagoon following closely behind. Sites within basins Pensacola Bay and Bayou Grande generally had the lowest abundance of *Vp* in sediments. Given that the average concentration of total active aerobic bacterial cells present per mL of estuarine, riverine, or coastal marine sediments is 1 to 500×10^6 (Glavin et al., 2004; Kirchman, 2018; Luna et al., 2002; Proctor and Souza, 2001),

the data suggest *Vv* make up from 0.2 to 60% of total sediment bacteria; whereas *Vp* could comprise 0.003 to 0.2% of all bacteria in sediments. On average, *Vv* outnumbered *Vp* by approximately 18-fold in all sediments. Notably, very high abundances of *Vv* and *Vp* in sediments were found in stations V-24 and V-25, two sites in Bayou Grande. In these locations, bottom pH and stratification were closely tied and showed the greatest variation among all sites (Figure 5).

Putative *Vibrio* in Biofilm Samples

The median concentrations of *Vv* and *Vp* in all presumptive biofilms were 2,281 and 163 CFU/mL, respectively (Table 4). Only two invertebrate biofilm samples resulted in undetectable *Vibrio* – one from a polychaete worm in Pensacola Bay, and the other from an oyster located at Bayou Grande. In the remaining 11 samples, mostly from swabbed oyster or barnacle shells, putative *Vv* abundances ranged from 81 to 28,844 CFU/mL, and putative *Vp* from 81 to 14,422 CFU/mL. There was not a statistical difference between oysters ($n = 5$) and barnacles

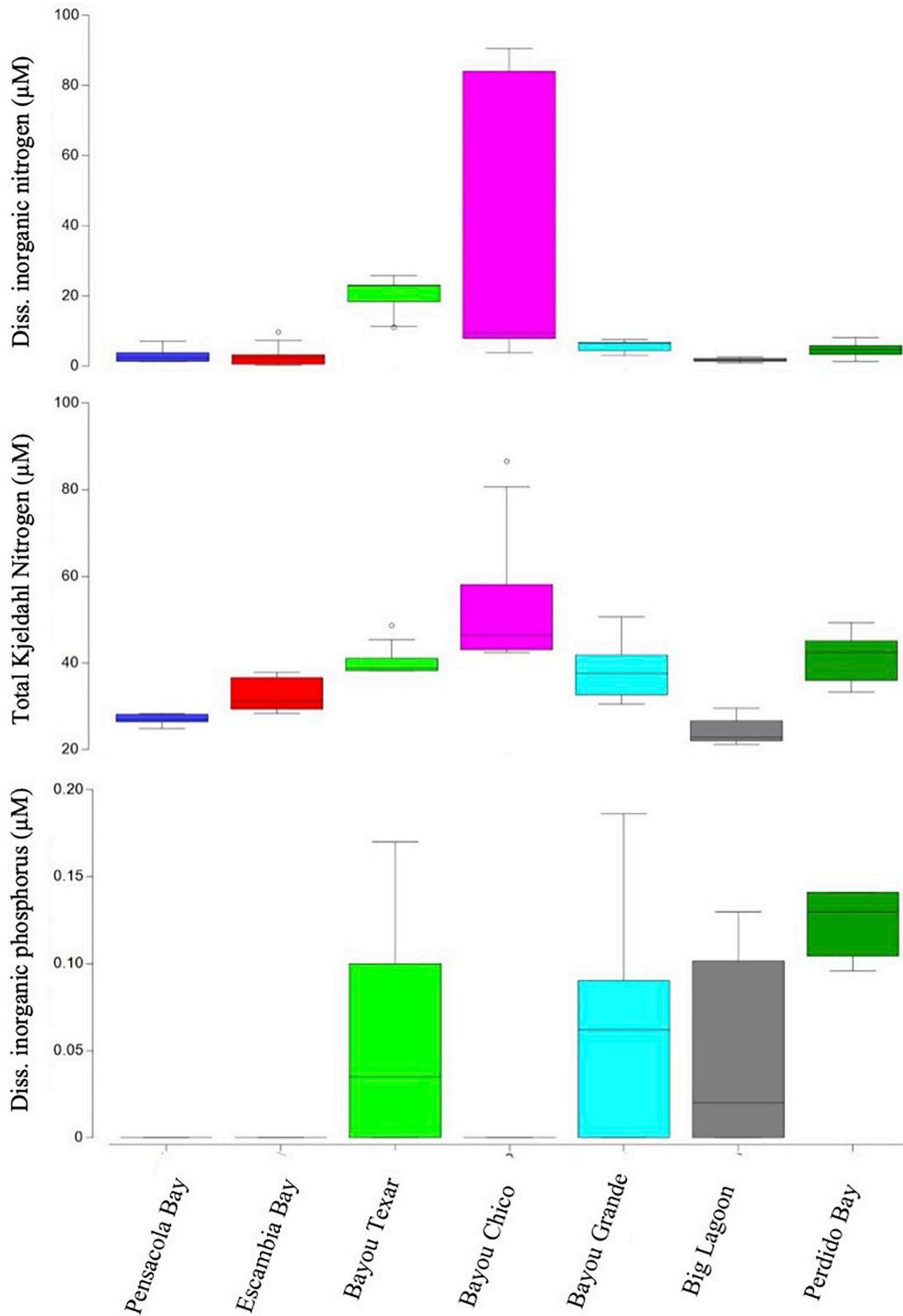


FIGURE 2 | Boxplots of dissolved inorganic nitrogen and phosphorus (DIN, DIP) and total Kjeldahl nitrogen (TKN) concentrations. Open circles denote extreme values; box-tops and -bottoms show the 25th and 75th percentiles; lines within boxes mark mean values; and whiskers indicate minimums and maximums.

TABLE 1B | Means and ranges of physical and chemical parameters of bottom water and sediment.

Basin	Range of depths (m)	Bottom water and sediment ^a					
		Temp. (°C)	Salinity (PSU)	Chl <i>a</i> (μg/g) ^b	Phaeopigments (μg/g) ^b	OC content (%) ^b	Water content (%) ^b
Pensacola Bay	0.9–3.5	13.4 ± 0.3	18.0 ± 2.8	3.3 ± 1.0	3.4 ± 1.3	1.8 ± 2.8	35.1 ± 20.3
Escambia Bay	1.5–3.4	13.4 ± 0.1	11.3 ± 3.8	2.1 ± 2.1	4.7 ± 1.5	7.0 ± 5.6	58.0 ± 22.7
Bayou Texar	1–2.7	15.8 ± 0.6	12.1 ± 3.4	3.7 ± 2.4	4.1 ± 1.0	6.0 ± 6.1	49.8 ± 29.0
Bayou Chico	0.4–4.3	19.7 ± 1.9	11.6 ± 7.0	2.9 ± 1.7	4.0 ± 1.4	6.8 ± 8.0	41.2 ± 23.7
Bayou Grande	0.9–2.9	17.1 ± 0.5	10.5 ± 3.9	1.9 ± 1.0	3.5 ± 1.2	5.1 ± 5.1	45.8 ± 22.5
Big Lagoon	1.1–6.1	15.3 ± 0.9	22.4 ± 3.3	3.4 ± 1.4	3.9 ± 1.9	3.4 ± 5.0	40.5 ± 25.7
Perdido Bay	1.1–3	16.0 ± 0.3	10.5 ± 3.0	1.5 ± 0.6	4.2 ± 1.7	8.3 ± 6.0	56.8 ± 22.1

^aMean ± SD.^bSediment parameter.**TABLE 2** | Abundances of culturable *Vv* in sediments and surface waters.

Basin	Sediment (CFU/mL)					Surface water (CFU/mL)				
	n ^a	# samples undetect. ^b	Min. > 0 ^c	Max.	Basin Median	n ^d	# samples undetect. ^b	Min. > 0 ^c	Max.	Basin Median
Pensacola Bay	4	0	762	21,055	7,590	5	2	15	89	15
Escambia Bay	7	0	1,653	42,218	14,926	7	2	15	44	15
Bayou Texar	6	0	169	388,338	10,499	6	0	89	207	126
Bayou Chico	5	0	188	314,667	51,839	5	1	15	3,556	15
Bayou Grande	7	0	475	17,333	8,757	7	1	15	222	44
Big Lagoon	8	0	36,681	607,222	70,274	8	0	15	148	51
Perdido Bay	5	1	4,665	164,273	20,993	5	1	15	59	15

Medians and ranges in each basin are provided. ^aNumber of sediment samples obtained in each basin; ^bNumber of samples in which *Vibrio* species was below detection limit;

^cMinimum CFU/mL in which *Vibrio* species was above detection limit; ^dNumber of surface water samples obtained from each basin.

TABLE 3 | Abundances of culturable *Vp* in sediments and surface waters. Medians and ranges in each basin are provided.

Basin	Sediment (CFU/mL)					Surface water (CFU/mL)				
	n ^a	# samples undetect. ^b	Min. > 0 ^c	Max.	Basin Median	n ^d	# samples undetect. ^b	Min > 0 ^c	Max.	Basin Median
Pensacola Bay	4	2	73	655	36	5	5	0	0	0
Escambia Bay	7	1	92	1,649	187	7	6	193	193	0
Bayou Texar	6	0	132	3,124	1,445	6	0	1,096	8,919	2,066
Bayou Chico	5	0	586	77,333	2,689	5	3	15	89	0
Bayou Grande	7	2	28	392	30	7	3	15	104	15
Big Lagoon	8	0	227	19,185	1,444	8	6	15	30	0
Perdido Bay	5	4	130	130	0	5	5	0	0	0

^aNumber of sediment samples obtained in each basin; ^bNumber of samples in which *Vibrio* species was below detection limit;

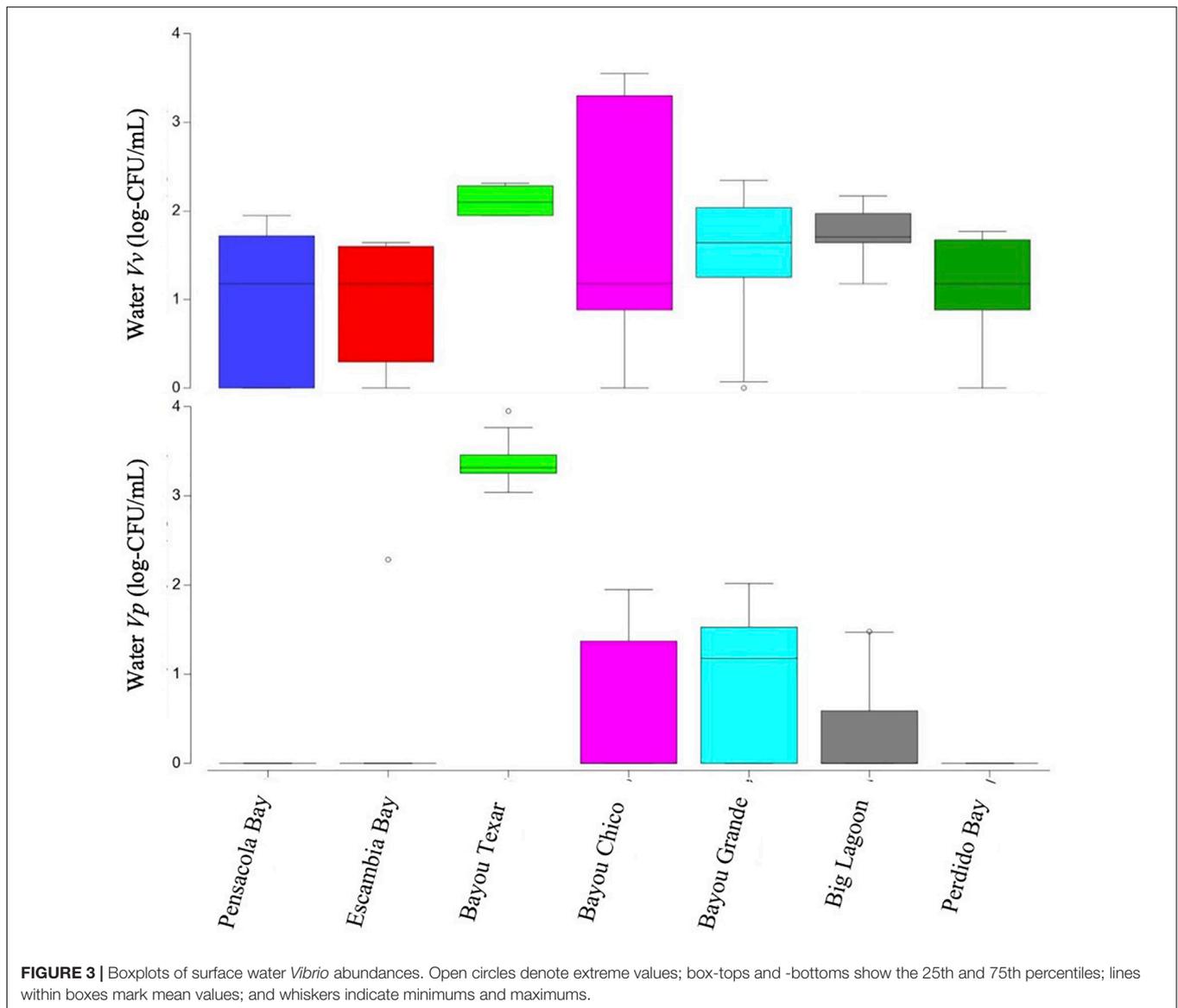
^cMinimum CFU/mL in which *Vibrio* species was above detection limit; ^dNumber of surface water samples obtained from each basin.

($n = 6$) for *Vv* (t -test, $p = 0.750$) nor *Vp* (t -test, $p = 0.560$) (Table 4).

Correlation of Abundances With Abiotic Environmental Parameters

Vibrios were generally most abundant in Bayou Chico (with the exception of *Vp* water abundances, which were greatest in Bayou Texar) (Tables 2, 3 and Figure 3). Prior wind speeds showed strong evidence for a positive correlation between surface water abundances of both *Vv* ($r = 0.84$, $p < 0.05$) and *Vp*

($r = 0.83$, $p < 0.05$), but not with sedimentary *Vibrio* abundances (Table 5). Water *Vv* abundances were also positively correlated with bottom water pH ($r = 0.46$, $p < 0.05$) and tidal coefficient ($r = 0.86$, $p < 0.01$) and moderately correlated with average sediment chl *a* concentrations ($r = 0.29$, $p = 0.057$) (Table 5). Surface water *Vv* did not covary strongly with salinity. Surface water *Vp* abundances correlated with seven parameters, the greatest number of correlations among the four calculated species abundances. Parameters that showed negative correlations with surface water *Vp* included surface salinity ($r = -0.36$, $p < 0.05$), surface pH ($r = -0.45$, $p < 0.05$), and bottom pH ($r = -0.47$,

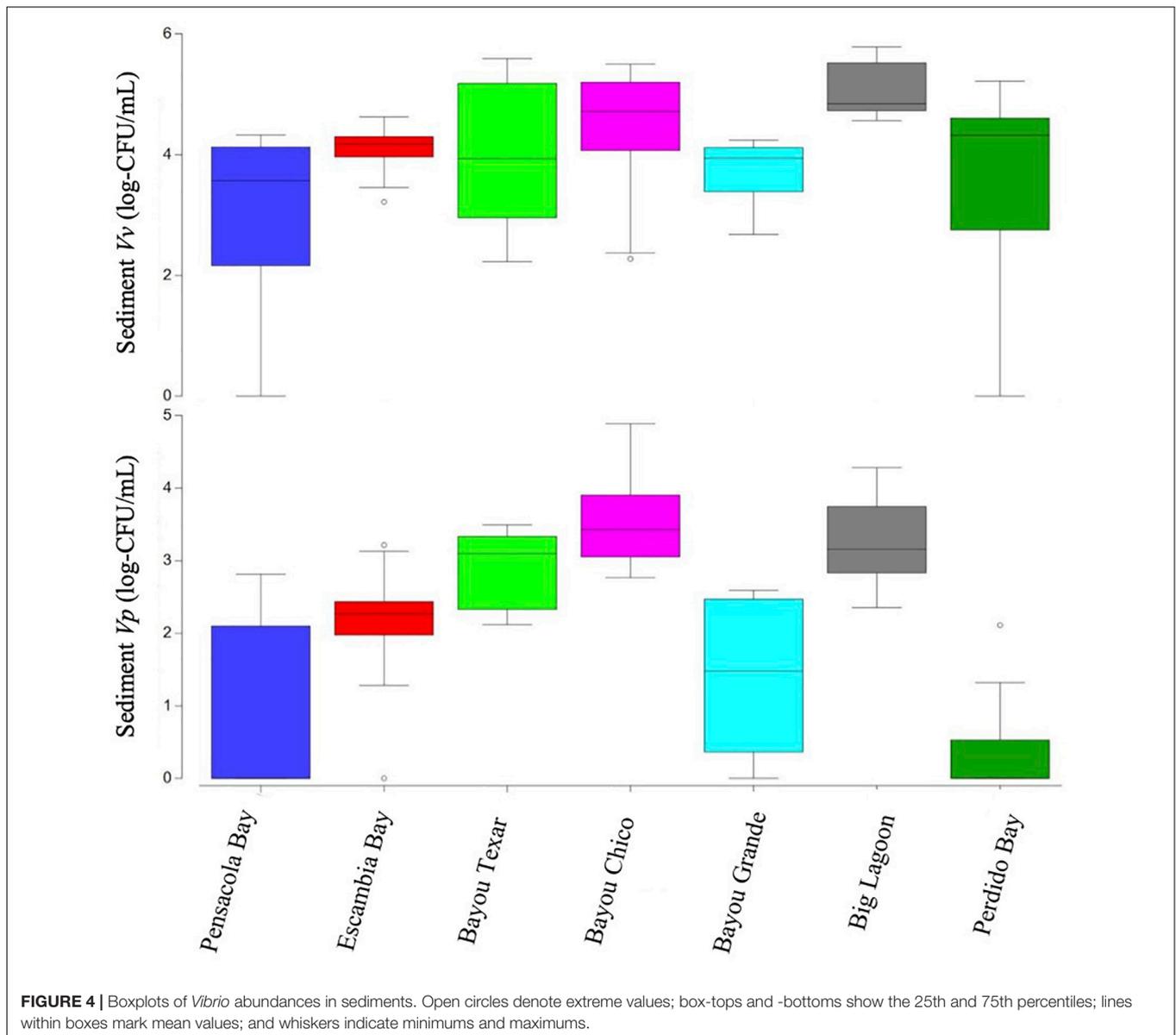


$p < 0.05$). Positive correlations with surface Vp included total DIN ($r = 0.32$, $p < 0.05$) and TKN ($r = 0.36$, $p < 0.05$) concentrations. Maximum cumulative wind speed ($r = 0.83$, $p < 0.05$) also showed evidence for a positive correlation with water Vp (Table 5).

In sediments, putative Vv abundances positively correlated with both surface ($r = 0.50$, $p < 0.05$) and bottom ($r = 0.52$, $p < 0.05$) pH (Table 5). Sedimentary Vp was correlated with average sediment chl *a* concentrations ($r = 0.31$, $p < 0.05$) and tidal coefficient ($r = 0.77$, $p < 0.05$). Interestingly, both Vv and Vp sediment abundances shared a correlation with one parameter: salinity stratification. Although winter levels of salinity stratification among all basins were generally low, stratification positively correlated with sedimentary abundances of both Vv ($r = 0.31$, $p < 0.05$) and Vp ($r = 0.33$, $p < 0.05$). Within the salinity values measured at different locations in this study, there was no optimal salinity range where Vv or Vp

was found to be more abundant (Supplementary Figure 3 and Supplementary Table 4). To further examine the relationship of salinity with these presumed Vv and Vp abundances, we also examined *Vibrio* abundances within a subset of stations that had salinities only between 5-25 PSU. Five stations (V-7, V-19, V-20, V-23, V-27) with surface or bottom water salinities outside this range were excluded from this additional correlation analysis. Even when salinity did fall within the optimal range, there still was no significant relationship with abundance, whether in the water column (Vv ; $r = -0.0089$, $p = 0.958$, $n = 38$) or in the sediments (Vv ; $r = 0.0875$, $p = 0.596$, $n = 39$ and Vp ; $r = 0.1107$, $p = 0.542$, $n = 39$). Only surface Vp showed a strong relationship with optimal salinity conditions, but it did so negatively ($r = -0.435$, $p < 0.01$, $n = 38$) (Supplementary Table 4).

Water column *Vibrio* abundances were not correlated with concentrations of TSS, dissolved oxygen, DIP, chl *a*, or K_d .



Sedimentary *Vibrio* abundances were not correlated with the following sediment characteristics: percent water, percent organic content, and sediment phaeophyte pigments. Additionally, neither presumptive *Vv* nor *Vp* abundances were correlated with water column K_d .

Analysis of Variance (ANOVA) Among Basins

ANOVA tables were generated for each environmental parameter and subsequently used to determine factors that indicated strong evidence for a difference among basins (**Supplementary Table 1**). Bottom pH ($F = 16.548$), bottom salinity ($F = 7.771$), bottom water temperature ($F = 33.328$), log-DIN concentrations ($F = 10.684$), log-*Vp* sediment abundances ($F = 9.421$), log-*Vp* water abundances ($F = 19.735$), surface pH ($F = 21.012$), surface

salinity ($F = 13.750$), surface water temperature ($F = 96.284$), and TKN concentrations ($F = 9.732$) were different at $\alpha < 0.001$. Additionally, TSS ($F = 3.225$, $p = 0.01$), water chl *a* ($F = 4.791$, $p = 0.001$), DIP ($F = 5.210$, $p = 0.001$), and K_d ($F = 4.817$, $p = 0.001$) showed strong evidence for a difference among basins.

ANOVA Between Open and Enclosed Waterbodies

Statistical analysis was also performed to determine evidence of a difference between open estuaries (Pensacola Bay, Escambia Bay, and Perdido Bay) and enclosed estuaries (Bayou Texar, Bayou Chico, Bayou Grande, and Big Lagoon). Log-*Vv* water abundance ($F = 9.973$, $p = 0.003$), log-*Vp* water abundance ($F = 9.662$, $p = 0.003$), log-*Vp* sediment abundance ($F = 17.271$, $p < 0.001$), surface temperature ($F = 7.838$, $p = 0.008$), bottom temperature

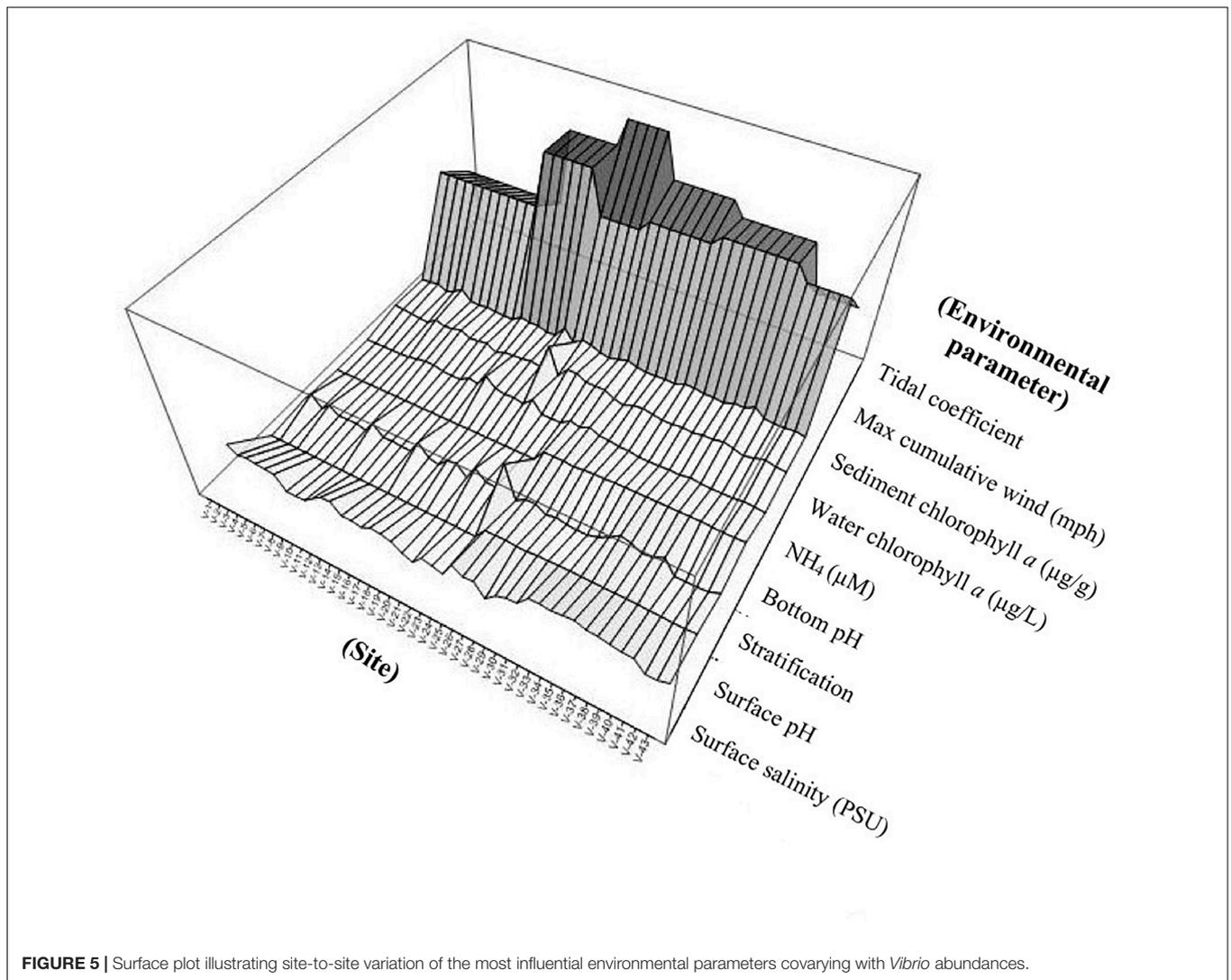


FIGURE 5 | Surface plot illustrating site-to-site variation of the most influential environmental parameters covarying with *Vibrio* abundances.

TABLE 4 | Numbers of Vv and Vp present in biofilms on invertebrates.

Waterbody	Organism type ^d	Vv (CFU/mL)	Vp (CFU/mL)	Ratio Vv:Vp	Total DIN ^a (µM)	TKN ^b (µM)	DIP ^c (µM)	Chl a (µg/L)
Pensacola Bay	Barnacle	7,822	489	16	2.74	27.00	0.00	3.55
	Barnacle	2,281	326	7	1.42	28.14	0.00	2.81
	Oyster	28,844	0	n/a	2.28	26.93	0.00	1.83
	Worm	0	0	n/a	7.11	28.36	0.00	1.57
Escambia Bay	Worm	27,215	0	n/a	3.48	29.14	0.00	5.30
Bayou Texar	Oyster	1,630	4,726	0.34	22.73	38.64	0.00	2.88
	Oyster shell	1,548	163	9.5	25.78	39.00	0.00	3.09
Bayou Chico	Barnacle	17,519	14,422	1.2	3.82	42.43	0.00	8.57
	Barnacle	244	163	1.5	9.21	46.43	0.00	8.46
	Oyster shell	9,289	81	114	9.39	43.29	0.00	5.60
Bayou Grande	Barnacle	10,267	163	63	6.45	33.36	0.06	5.41
	Oyster	0	0	n/a	7.66	42.57	0.19	5.36
	Barnacle	81	326	0.25	4.30	50.64	0.00	0.86

^aDissolved inorganic nitrogen.

^bTotal Kjeldahl nitrogen.

^cDissolved inorganic phosphorus.

^dExact taxonomic identification was not determined for sampled invertebrates. Worm, polychaete worm.

TABLE 5 | Correlations between *Vibrio* abundances and environmental parameters.

Water, meteorological, or sediment parameter	Surface water				Bottom water/sediment			
	<i>Vv</i> (log)		<i>Vp</i> (log)		<i>Vv</i> (log)		<i>Vp</i> (log)	
	<i>r</i> ^b	<i>p</i> ^a	<i>r</i> ^b	<i>p</i> ^a	<i>r</i> ^b	<i>p</i> ^a	<i>r</i> ^b	<i>p</i> ^a
Surface water salinity (PSU)	N.S.	0.22	-0.36	**(<i>p</i> = 0.018)	N.S.	0.57	N.S.	0.48
Surface water pH	N.S.	0.080	-0.45	**(<i>p</i> = 0.044)	0.50	**(<i>p</i> = 0.025)	N.S.	0.065
Bottom water pH	0.46	**(<i>p</i> = 0.040)	-0.47	**(<i>p</i> = 0.035)	0.52	**(<i>p</i> = 0.018)	N.S.	0.17
Salinity stratification	N.S.	0.66	N.S.	0.75	0.31	**(<i>p</i> = 0.040)	0.33	**(<i>p</i> = 0.029)
Total surfaceDIN (μM)	N.S.	0.52	0.32	**(<i>p</i> = 0.037)	N.S.	0.57	N.S.	0.092
Total KjeldahlNitrogen (μM)	N.S.	0.57	0.36	**(<i>p</i> = 0.017)	N.S.	0.85	N.S.	0.37
Avg. sediment chl <i>a</i> (μg/g)	0.29	*(<i>p</i> = 0.057)	N.S.	0.21	N.S.	0.29	0.31	**(<i>p</i> = 0.043)
Max cumulative wind (mph)	0.84 ^c	**(<i>p</i> = 0.018)	0.83 ^c	**(<i>p</i> = 0.022)	N.S.	0.70	N.S.	0.46
Tidal coefficient (m)	0.86 ^c	***(<i>p</i> = 0.008)	N.S.	0.28	N.S.	0.64	0.77 ^c	**(<i>p</i> = 0.045)

^aSignificance levels indicated: **p* ≈ 0.05; ***p* < 0.05; ****p* < 0.01; N.S., not significant.

^bBacterial abundances, Pearson correlation coefficient (*r*) of log(CFU/mL) with parameter. D.F. for these analyses was 42 (surface water abundances) and 41 (sediment abundances). Bottom and surface water pH *n* = 20.

^cD.F. for these analyses was 6, and basin-wide means of *Vv* or *Vp* were used.

Values in bold to indicate strong evidence (*p* ≥ 0.05) for a significant correlation between parameters.

($F = 24.197$, $p < 0.0001$), salinity stratification ($F = 4.257$, $p = 0.045$), log-DIN concentrations ($F = 8.305$, $p = 0.006$), and tidal coefficient ($F = 25.809$, $p = 0.004$) were different between open and enclosed estuaries (Supplementary Table 2). In surface waters, *Vv* median abundance was approximately 2-fold greater in open basins than in the enclosed basins. The difference was more striking for *Vp*; in only three of the 25 stations, *Vp* abundances were at levels above the minimum detection limit in open basins (12% of samples), whereas this species was found in surface waters in 12 of the 18 locations in enclosed waterbodies (67% of samples). Median *Vv* and *Vp* in sediments, however, did not follow the same pattern of surface water *Vibrio* abundances. In open basins, the median *Vv* sediment abundance exceeded that of enclosed waterbodies by approximately 1.8-fold, while median sediment *Vp* was approximately 2-fold greater in enclosed systems than in open systems.

DISCUSSION

Salinity, among others, is often considered a predictive variable for *Vibrio* in the water column, with optimal conditions ranging from 5 to 25 PSU (Kaspar and Tamplin, 1993; Motes et al., 1998; Hsieh et al., 2008). However, this was not the case in this study. In the seven basins examined, locations chosen for the survey represented waterbodies with a wide range of salinities and stratification (Figure 5). Within the salinity values measured at these different locations, there was no optimal salinity range where presumptive *Vv* or *Vp* was found to be more abundant (Supplementary Figure 3 and Supplementary Table 4). Moreover, bottom pH and stratification also correlated with one another, though not as dramatically ($r = 0.4541$, $p = 0.044$). This could have been attributed to the lower sample size ($n = 20$), as pH measurements were only taken for approximately half of all basins (Bayou Grande, Big Lagoon, and Perdido Bay). *Vv*

abundances can increase with depth, particularly in bottom waters within shallow estuaries (Wetz et al., 2014). This trend may be attributed to variation in salinity and/or temperature at different depths, suggesting covariation between temperature and salinity in regards to estimating *Vibrio* abundance. However, in our study, putative abundances of *Vv* and *Vp* did not significantly vary with total water column depth, and there was no consistent pattern of depth, salinity, and *Vibrio* abundances. In some basins, surface water *Vibrio* abundances may have been greater than usual due to high wind speeds, which likely promoted mixing in the water column and resuspension of sediments. Therefore, it would have been unlikely to see a relationship between *Vibrio* abundances and depth. However, we did notice a strong relationship between *Vibrio* abundances and salinity stratification, which does in fact align with findings in previous studies, especially for shallow estuaries (Wetz et al., 2014). We also chose to sample from a diverse group of waterbodies, varying greatly in salinity, stratification, eutrophication, and freshwater influence. Although the method employed here assesses only abundances based on viable CFU, this broad range of data is useful in determining baseline abundances in the region.

Correlations of *Vibrio* abundance with temperature are often linked to seasons (Hsieh et al., 2008; Wetz et al., 2014). For example (Wetz et al., 2014), reported seasonal data over a four-year period for environmental parameters that may influence surface and bottom water abundances of *Vv* within the Neuse River Estuary (NRE). Certainly, the length of this survey capacitates the reporting of seasonal data. Although the NRE and the PBS are both shallow, river-dominated estuarine systems, and despite the contrast in duration of the study, actual relationships between water or sedimentary *Vibrio* abundances and environmental parameters differ depending on the influence of physicochemical factors (i.e., runoff, mixing, resuspension). Evidently, seasonal data reported for temperature, salinity, turbidity, and chl *a* all showed strong correlations to

Vv abundances, whereas none of the four covaried with *Vibrio* abundances in our study (Wetz et al., 2014). In fact, surface water temperatures in this winter survey were less than optimal for maximum concentrations of *Vv* or *Vp*, presumed to fall within the range of 20 and 37°C (Tantillo et al., 2004; Johnson et al., 2012; Johnson, 2013). Maximum abundances of surface water putative *Vv* were in Bayou Chico, the one basin with the highest overall *Vv* surface water abundances. In this basin, surface water salinities were lowest of all, but temperatures (Figure 1) and salinity stratification (Supplementary Table 3) were the highest. It was surprising to see very high winter abundances in surface waters, sediments, or both, in particular basins of this study.

Surface water presumptive *Vp* were maximal in Bayou Texar where total DIN concentrations were high, and sedimentary presumptive *Vp* was greatest in Bayou Chico where chl *a* concentrations were high – factors that are both associated with eutrophication suspected to promote *Vibrio* success (Wetz et al., 2008; Turner et al., 2009; Froelich et al., 2019; Han et al., 2020). It is feared that eutrophication will promote higher concentrations of pathogens such as *Vibrio* species (Malham et al., 2014). Estuarine eutrophication alone, often measured by chl *a* concentrations, does not necessarily assess the number of higher trophic levels (Van Meerssche and Pinckney, 2019). Genomic evaluation of *Vv* and *Vp* suggests most are chitinolytic (Grimes et al., 2009), and *Vibrio* may be attached to zooplankton or eukaryotic phytoplankton (Takemura et al., 2014). Abundances of particle-associated estuarine *Vibrio* may be strongly correlated with chl *a*, but this relationship may vary seasonally or from year to year (Main et al., 2015). These data suggest much of the particulate material in these estuaries, terrestrial-derived and autochthonous, drives and is associated with primary production. If *Vibrios* in subtropical estuaries are largely associated with diatoms or zooplankton (Martinez-Urtaza et al., 2012), one might expect a positive relationship of *Vibrio* abundances with increased turbidity and phytoplankton biomass (chl *a*). However, surface water *Vibrio* abundances were not significantly correlated with TSS or chl *a* in this study. A lack of, or negative, correlation of abundance with chl *a* and/or TSS is consistent with findings of previous temperate estuarine studies (Wetz et al., 2014; Deeb et al., 2018). However, culture-dependent methods of total *Vibrio* counts do suggest their abundances are strongly and positively correlated with turbidity and DIN (Froelich et al., 2019). Here, we observed culturable presumptive *Vp* positively correlating with DIN and TKN, similar to the findings of (Froelich et al., 2019) in a temperate estuary. However, neither surface water putative *Vv* nor sedimentary putative *Vp* or *Vv* significantly covaried with nitrogen. Additionally, an earlier study (Wetz et al., 2008) of culture-dependent enumeration of total *Vibrio* found abundances strongly correlated with temperature during two significant storms, but abundances were correlated with salinity and TSS in only one of the two events. These findings were explained by the different wind directions and levels of sediment resuspension. Therefore, in addition to nutrients, turbidity, and phytoplankton biomass, estuarine dynamics such as tidal influence, salinity stratification, and wind-driven mixing may also be important considerations.

Salinity and stratification, both affected by wind and/or rain events, can affect *Vibrio* concentrations (Fries et al., 2008). Therefore, we evaluated the effect of maximum cumulative wind speeds recorded in the Pensacola metropolitan area in the three days leading up to and on the mornings of our sampling events. Wind mixing introduces sediment-dwelling bacteria into surface waters and may partly explain increased *Vibrio* concentrations in surface waters, particularly in Bayou Texar (02/07/20), the basin with the highest cumulative wind speeds (84 MPH). While wind-driven resuspension could explain the very high numbers of presumptive *Vp* in all stations sampled there, corresponding water abundances of *Vv* do not support wind as the sole cause for high *Vp* numbers on that sampling date. For example, in Bayou Texar, *Vv* water levels were between 89 and 207 CFU/mL, while *Vp* concentrations ranged from ~1,000 to 9,000 CFU/mL. In contrast, concentrations of both species in sediments showed the opposite trend. In two of the six locations sampled, putative *Vv* in sediments roughly equaled those of putative *Vp*. At the remaining four stations, *Vv* exceeded *Vp* by at least eight-fold. It is clear that other factors, in addition to wind, are likely responsible for high *Vibrio* concentrations in the water column and within the sediments.

In sediments of subtropical coasts or temperate estuaries, *Vp* are generally more prevalent than *Vv* (Pfeffer et al., 2003; Vezzulli et al., 2009), but this overall pattern was not seen in this study. The relative abundances of these two species in sediments varied widely, with an approximate 1500:1 ratio of presumptive *Vv*:*Vp* in Perdido Bay, but approximately 50:1 in all other basins, except Bayou Chico, where *Vv*:*Vp* was only 6:1 (Figure 4 and Tables 2, 3). Multiple comparison procedures (Tukey's *Post Hoc*) determined *Vp* sedimentary abundances in Pensacola and Perdido Bays were significantly lower than in the other basins. Interestingly, *Vibrio* abundances covaried with tidal coefficient and maximum wind speeds, indicating the influence of sediment resuspension. In this study, bottom water oxygen concentrations and putative *Vibrio* abundances in the sediments were not correlated. Generally, there is a lack of hypoxia in bottom waters of these basins in winter (Caffrey and Murrell, 2016), which was also found in winter 2020 (Supplementary Table 3). Since all types of putative *Vibrio* we enumerated except sediment *Vv* were significantly correlated with prior cumulative wind speeds, resuspension may be a contributing factor in explaining *Vibrio* in the surface waters of the Pensacola and Perdido Bay water basins.

To determine the effects of rain events prior to our sampling dates, we evaluated precipitation with respect to *Vibrio* abundances and environmental parameters. In all basins, total precipitation did not positively covary with turbidity as expected (Supplementary Figure 2 and Supplementary Table 4). K_d , not unexpectedly, was positively correlated with TSS ($r = 0.30$, $p = 0.05$) and chl *a* ($r = 0.73$, $p < 0.0001$). Pensacola Bay cyanobacterial abundances in these waters are lowest in winter (Murrell and Loes, 2004; Murrell and Caffrey, 2005), and while we did observe different chl *a* concentrations among the basins examined, there was no significant relationship with surface or sedimentary *Vibrio* abundances (Supplementary Table 4). Although we anticipated increased *Vibrio* densities in waters with

higher turbidity, as observed previously with *Vp* in subtropical waters of coastal northern GoM (Zimmerman et al., 2007), abundances of *Vv* and *Vp* may not consistently covary with turbidity, where patterns are either site- or season-specific (Zimmerman et al., 2007; Blackwell and Oliver, 2008; Johnson et al., 2012). Our findings suggest terrestrial inputs of nutrients concomitant with mixing and increased turbidity are alone not sufficient to explain *Vibrio* success, as previously suggested for temperate estuaries (Davis et al., 2017; Froelich et al., 2019).

For the purposes of initial surveys to determine baseline levels, culture-dependent methods can provide notable ecological insights, yet also be limited in scope. For example, the false-positive rate of identifying *Vv* on CHROMagar as a bright blue colony was previously tested from a low-salinity body of water (Lake Ponchartrain) in the same approximate latitude as the waterbodies surveyed here (Nigro and Steward, 2015). In this typically oligohaline environment, with a salinity in the range of our study sites Bayous Texar and Chico (**Supplementary Table 3**), winter abundances of *Vv* and *Vp* may be overestimated by 50% (Nigro and Steward, 2015). Additionally, enumeration of *Vv* and *Vp* using the colony method likely underestimates the count, as a single particle may contain numerous *Vibrio* cells but still appear as a single colony (Joux et al., 2015).

False-positives may also be due to cross-reactivity of the substrate, such as blue colonies presenting as putative *Vv* confirmed by other methods to be *V. cholerae* or *V. mimicus* (Hara-Kudo et al., 2001). In our preliminary testing (winter and summer of 2019) of similar bodies of water, molecular method verification indicated that *Vv* presented not only as bright blue on this solid medium, but also *vvhA*-positive in end-point colony PCR, using established primers for the *vvhA* gene, a species-marker for *Vv*. Similarly, bright pink (not purple, which may be *Aeromonas* species) were determined to be either *tdh*- or *trh*-positive (data not shown). Molecular analyses (either end-point PCR of colonies or qPCR on DNA extracted directly from the sample) may also provide over- or underestimates of *Vv* abundance data, due to possible cross-reactivity of *vvhA* PCR primers with related *Vibrio* species (Canizalez-Roman et al., 2011; Klein et al., 2014). However, this is not the case for *Vp*-specific PCR primers, such that they do not cross-react with other species of *Vibrio* (e.g., *V. mimivus*, *V. fluvialis*, *V. cholerae*).

Another limitation of the plating method may be a potential underestimate of the *Vibrio* abundance due to incubation temperatures or other factors affecting bacterial growth on solid agar. Conversely, there is a possibility that not all putative *Vv* and *Vp* detected on plates may contain the established marker genes (e.g., *tdh*, *trh* for *Vp* or *vvhA* for *Vv*). Therefore, a combination of plating and molecular methods is ideal for enumerating putative *Vibrio* species in the water column or sediments. For example, in a study of *Vibrio* abundances responding to hurricanes, low percentages of the colonies detected on plates of water or sediment samples contained genes associated with virulence (*vcgC* and *tdh*), and none of the sediment or water colonies were positive for *trh*. Notably, in that study, abundances of sedimentary and water column *Vv* and *Vp*, detected with culture methods, were not significantly impacted

by wind or freshening due to the storm (Shaw et al., 2014). In contrast, in our study, putative *Vibrio*, based on only the culture method employed here, did significantly covary with prior wind speeds. Cultivable *Vv* and *Vp* abundance determination is dependent on culture substrate, time and temperature of incubation, among other factors. In a GoM estuary near our study site, for instance, *Vibrio* abundances associated with finfish or shellfish were previously determined using simultaneous culture-dependent and -independent methods (Givens et al., 2014). The abundances determined by both approaches were similar, but it should be noted that molecular methods may be more sensitive when attempting to enumerate all *Vibrio*, culturable and non-culturable, or when enumerating only pathogenic species (Gutierrez West et al., 2013).

Additionally, both *Vv* and *Vp* can be underestimated by culture-dependent techniques as compared to molecular methods (Kirchman et al., 1982; Froelich et al., 2012; Williams et al., 2017). There was variability of putative *Vibrio* abundances among the few surface swab samples collected (**Table 4**), but this could be explained by the diversity of strains enumerated, some of which may have missed being counted due to slow recovery after plating. Recovery of *Vv*, *Vp*, or other *Vibrio* on various types of culture media is variable (Nordstrom and DePaola, 2003; Warner and Oliver, 2007) and possibly dependent on the nutrient state of the environment from which the sample was derived (Warner and Oliver, 2007). In this study, low abundances from swab samples may have been rectified by a longer period of incubation on agar plates or use of a different medium (Nordstrom and DePaola, 2003; Warner and Oliver, 2007). We enumerated colonies after 24, 48, and 72 h, but there were no significant increases in numbers of *Vv* nor *Vp* colonies after 48 h. Therefore, the variability of *Vibrio* in the opportunistically-sampled biofilms in this study may be more dependent on the abundances of *Vv* and *Vp* in the surrounding water column, but this was not seen in oysters and water samples in Tampa Bay, FL (Chase et al., 2015).

Consistent with other studies that examined subtropical water column and sediments, *Vv* and *Vp* in sediments outnumbered those in surface waters by at least 10-fold. In surface waters of temperate or subtropical estuaries, *Vv* distributions are highly variable (Heidelberg et al., 2002; Franco et al., 2012; Givens et al., 2014), but this may be explained by underestimates in the culture method, due to overwintering, in which *Vv* enter a “viable but not culturable” (VBNC) state when conditions are not optimal, such as in cooler months (Oliver and Bockian, 1995; Foster, 2004; Franco et al., 2012). In temperate systems, culture-dependent abundances in winter sediments are low compared to those in surface waters, also suggesting overwintering (Pfeffer et al., 2003), but bottom water temperatures in systems such as those examined here are generally warmer. Evaluation of subtropical Mediterranean coastal lagoon sediments did not yield cultivable *Vv*, but incubations were performed at higher temperatures (41°C) (Cantet et al., 2013) than in this study.

The design of this study was not to enumerate pathogenic *Vv* and *Vp*, but rather to determine baseline bacterial loads in winter for a set of waterbodies yet to be examined for *Vibrio*. Although the method employed here assesses only “presumptive”

V_v and V_p abundances based on viable CFU, this broad range of data is useful in determining baseline abundances in the region. Cultivable abundance estimates, previously shown to be representative of consistent sample-to-sample comparison (Zimmerman et al., 2007), are valuable in and of themselves for determining relative risk factors in each waterbody of interest. Pathogenic strains' abundances vary extensively – within samples, between sampling dates in the same location, among samples with different source salinities, among seasons, or after significant storm events (Kaufman et al., 2003; Zimmerman et al., 2007; Nigro et al., 2011; Liu et al., 2016). Therefore, to confirm estimated loads of pathogenic strains of either species measured with culture-dependent analyses, future efforts will be directed toward species-specific enumeration, with additional methods using culture-independent analyses of *Vibrio* species abundances.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

LW and JC conceptualized the research design, executed or oversaw the laboratory assays, and analyzed the data. LW, JC, and WJ acquired the funding. LW and TP wrote the manuscript. JC donated lab resources in collaboration with the efforts of MS and MR for water quality lab analyses. WJ created the map figures. LW, JC, WJ, and BA each provided efforts in their areas of expertise. TP, JC, MS, CD, BA, and LW all assisted with field

sampling and processing. All authors contributed to the article and approved the final version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2021.645755/full#supplementary-material>

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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 O₂ in the atmosphere. Their role in sequestering atmospheric CO₂ 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., O₂ 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	<i>Karenia brevis</i>	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	<i>Pyrodinium bahamense</i> var. <i>bahamense</i>	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	<i>Pseudo-nitzschia</i> spp.	Fish, shellfish, crustaceans	≥ 20 mg/kg domoic acid	Glutamate receptors
Saxitoxin puffer fish poisoning (SPFP)	Saxitoxin and derivatives	<i>Pyrodinium bahamense</i> var. <i>bahamense</i>	Fish	≥ 0.8 mg/kg saxitoxin equivalents (80 mg/100 gm)	Voltage dependent Na channel, Site 1
Ciguatera fish poisoning (CFP)	Ciguatoxins	<i>Gambierdiscus toxicus</i>	Reef fish	Caribbean ciguatoxins: > 0.1 mg/kg Caribbean Ciguatoxins-1 (C-CTX-1) equivalents	Voltage dependent Na channel, Site 5
Diarrhetic shellfish poisoning (DSP)	Okadaic acid and derivatives	<i>Dinophysis</i> spp. <i>Prorocentrum</i> 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 intoxication 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 Scatista (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 Scatista, 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 \$775,000 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 symptomatology (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 symptomatology 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 NO₃⁻ 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 Pollinger, 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* N₂ fixation. Lenos 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 NH₄⁺ and dissolved organic N (Capone et al., 1994; Glibert and Bronk, 1994). This N, in turn, is taken up by *K. brevis* (e.g., Lenos 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 >10⁶ 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 N₂ fixation and release and decay of seasonal *Trichodesmium* bloom biomass are sufficient to provide for the N needs of larger blooms (Lenos 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 Okechobee water through the Caloosahatchee and St. Lucie Rivers. Both a δ¹⁵N_{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. Lenos 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 (Kubaneck 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 mortalities, 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. brevis* 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 Lehan 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
<i>Gambierdiscus</i> sp.	Florida Bay	Parsons et al., 2012
<i>Gambierdiscus toxicus</i> 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
<i>G. caribaeus</i> Vandersea, Litaker, Faust, Kibler, Holland & Tester		Litaker et al., 2010; Accoroni et al., 2020
<i>G. carolinianus</i> Vandersea, Litaker, Faust, Kibler, Holland & Tester		Litaker et al., 2010; Rains, 2015
<i>G. carpenteri</i> Kibler, Litaker, Faust, Holland, Vandersea & Tester		Litaker et al., 2010; Rains, 2015
<i>G. yasumotoi</i> Holmes		Rains, 2015
<i>G. belizeanus</i> Faust	Florida Keys	Litaker et al., 2017
<i>Fukuyoa</i> sp.	Florida Keys	Accoroni et al., 2020
<i>Coolia</i> sp.	Florida Keys	Besada and Loeblich, 1982; Accoroni et al., 2020
<i>Coolia monotis</i> Meunier	Florida Keys	Morton et al., 1992
<i>Coolia santacroce</i> Karafas, Tomas & York	Florida Keys	Accoroni et al., 2020
<i>Ostreopsis</i> sp.	Florida Keys	Besada and Loeblich, 1982; Babinchak et al., 1986; Bomber et al., 1988a; Accoroni et al., 2020
<i>Ostreopsis heptagona</i> Schmidt Norris, Bomber & Balech	Florida Keys	Bomber, 1987; Bomber et al., 1988a; Morton et al., 1992
<i>Ostreopsis siamensis</i>	Florida Keys	Morton et al., 1992
<i>Prorocentrum</i> spp.	Florida Keys	de Sylva, 1982; Accoroni et al., 2020
<i>Prorocentrum lima</i> (Ehrenberg) Stein	Florida Keys	Bomber et al., 1985, 1988a; Morton et al., 1992; Accoroni et al., 2020
<i>Prorocentrum hoffmanianum</i> Faust	Florida Keys	Accoroni et al., 2020
<i>P. concavum</i> Fukuyo	Florida Keys	Bomber et al., 1988a; Morton et al., 1992
<i>P. emarginatum</i> Fukuyo	Florida Keys	Bomber et al., 1988a; Accoroni et al., 2020
<i>Prorocentrum rhathymum</i> Loeblich III, Sherley & Schmidt	Florida Bay	Accoroni et al., 2020
<i>Sinophysis</i> sp.	Florida Bay	Accoroni et al., 2020
<i>Amphidinium</i> 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 Bruslé, 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 $>29^{\circ}\text{C}$, and that the number of days with temperatures $>29^{\circ}\text{C}$ 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 (~ 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 adsorb 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
<i>Pseudo-nitzschia brasiliiana</i> Lundholm, Hasle & Fryxell	Parsons et al., 2012
<i>Pseudo-nitzschia calliantha</i> Lundholm, Moestrup & Hasle	Phlips et al., 2011; O'Dea, 2012; Parsons et al., 2012
<i>Pseudo-nitzschia cuspidata</i> (Hasle) Hasle	O'Dea, 2012; Parsons et al., 2012; Hubbard et al., 2014, 2015
<i>Pseudo-nitzschia delicatissima</i> (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
<i>Pseudo-nitzschia granii</i> (Hasle) Hasle	O'Dea, 2012
<i>Pseudo-nitzschia linea</i> Lundholm, Hasle and G.A.Fryxell	Lundholm et al., 2002
<i>Pseudo-nitzschia micropore</i> Priisholm, Moestrup & Lundholm	O'Dea, 2012
<i>Pseudo-nitzschia multiseris</i> (Hasle) Hasle	O'Dea, 2012
<i>Pseudo-nitzschia obtusa</i> (Hasle) Hasle & Lundholm	Sullivan, 1978; Krayesky et al., 2009
<i>Pseudo-nitzschia pungens</i> (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
<i>Pseudo-nitzschia</i> <i>pseudodelicatissima</i> 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; Barga et al., 2016
<i>Pseudo-nitzschia turgidula</i> (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 $\mu\text{g gm}^{-1}$ 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 $\mu\text{g g}^{-1}$ 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 (Spàeil 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 m³ to 50 + 20 ng m³. 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 $\sim 1.5 \text{ m}$), $2,200 \text{ km}^2$ 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 ($\sim 2 \mu\text{m}$ 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; Philips 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 Philips, 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 N₂ gas into NH₄⁺. The scale of N₂ 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*, *Euclidean*, *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 μm), non-descript (Koch et al., 2014) phytoplankton that contains the accessory pigment fucoxanthin (DeYoe et al., 1997) and reaches sufficiently high concentrations (200 $\mu\text{g L}^{-1}$ 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 $\delta^{15}\text{N}$ 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 CO₂ 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 Woessik, 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 N₂ 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 $p\text{CO}_2$ concentrations rise in the atmosphere, increasing CO_2 concentrations dissolve in seawater. 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 $p\text{CO}_2$ concentrations, *Pseudo-nitzschia multiseriata* (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 $p\text{CO}_2$ on *K. brevis* are somewhat contradictory. Errera et al. (2014) reported higher growth rates at higher $p\text{CO}_2$ concentrations, but did not find any relationship between toxin concentrations and either temperature or $p\text{CO}_2$ concentrations. In contrast, Hardison et al. (2014) reported reduced growth and enhanced toxicity under reduced $p\text{CO}_2$ 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 $p\text{CO}_2$ concentration range from 150 to 780 μatm . They reported no statistically significant correlation between $p\text{CO}_2$ and brevetoxin content, but a strong effect on *K. brevis* acquisition of inorganic carbon, with an

increase in half saturation values for CO_2 (from 1.5 to 3.3 μM), a switch in inorganic carbon preference from HCO_3^- to 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 $p\text{CO}_2$ levels. Although Bercel and Kranz (2019) conclude that net photosynthesis of *K. brevis* is not impacted by $p\text{CO}_2$, 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 $p\text{CO}_2$ concentrations which require further study before a reasonably assured prediction can be made of the impacts of changing $p\text{CO}_2$ 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 nanoseconds 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 disciplines [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.

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Ranking 67 Florida Reefs for Survival of *Acropora cervicornis* Outplants

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Over the past three decades, coral populations have declined across the tropical and subtropical oceans because of thermal stress, coral diseases, and pollution. Restoration programs are currently attempting to re-establish depauperate coral populations along the Florida reef tract. We took an integrated Bayesian approach to determine which Florida reefs ranked highest based on the survival of outplanted colonies of *Acropora cervicornis* from 2012 to 2018. Survival of *A. cervicornis* outplants was highly variable in the upper Florida Keys with some reefs showing the highest likelihood of survival (e.g., North Dry Rocks, Carysfort, Key Largo Dry Rocks, and Conch Reef), whereas some adjacent reefs showed the lowest likelihood of survival (e.g., an Unnamed Reef, Pickles Reef, and U47 Patch Reef). Similarly, survival was highly variable in the middle and lower Florida Keys and in the Broward-Miami subregions. Survival was high and less variable in Biscayne Bay and low and less variable in the Marquesas subregions. The reefs that ranked lowest for outplant survival were exposed to high wave energy. Partitioning out the spatial effects of reefs and subregions from the model, we detected spatial latent effects of low survival that were most evident in the middle and the upper Florida Keys, particularly between 2015 and 2017. The overall high spatial and temporal variability in survival among adjacent reefs highlights a need to outplant nursery-reared colonies strategically, in order to optimize coral-population recovery efforts in Florida.

Keywords: coral, restoration, outplants, survival, *Acropora cervicornis*, Florida reef tract

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INTRODUCTION

Coral populations have declined globally in the past three decades (Hoegh-Guldberg et al., 2007; Edwards and Gomez, 2007; Hughes et al., 2018; Lough et al., 2018). Two acroporid species, *Acropora cervicornis* and *Acropora palmata*, which previously dominated the Caribbean, and were major reef builders through millennia (Agassiz, 1885; Vaughan, 1919; Goldberg, 1973; Marszalek et al., 1977; Precht and Miller, 2007), have experienced some of the largest declines. Diseases and thermal anomalies have been the main causes of coral population declines in the Caribbean (Porter and Meier, 1992; Aronson and Precht, 2001; Toth et al., 2014; Precht et al., 2016; Walton et al., 2018). A major outbreak of white-band disease in the 1970s caused a 95% decline in Caribbean acroporids (Aronson and Precht, 2001; Miller et al., 2002; Gardner et al., 2003). Since then, *A. cervicornis* and *A. palmata* have been listed as “threatened” under the US Endangered Species Act in 2006 (National Marine Fisheries Service, 2006) and “critically endangered” on the World Conservation Union (IUCN) Red List in 2008 (Aronson et al., 2008). Coral restoration efforts are now attempting to restore acroporid populations along the Florida reef tract.

Reef-restoration programs first appeared in Florida and the wider Caribbean in the 1990s. *Acropora* species have been targeted in recent restoration efforts because of their: (i) threatened status (National Marine Fisheries Service, 2006), (ii) low recruitment rates (van Woesik et al., 2014), (iii) rapid growth rates (Tunncliffe, 1981), (iv) importance in reef-building framework (Jackson, 1992), and (v) reproductive strategies through fragmentation (Highsmith, 1982). These factors make acroporids ideal candidates for coral restoration programs. However, restoration through propagation and outplanting techniques alone will not be enough if the benchmarks set by the Paris Agreement are not met (Hoegh-Guldberg et al., 2014).

Restoration techniques primarily rely on either securing corals that have been naturally fragmented (Bruckner and Bruckner, 2001), rescuing and relocating colonies from habitats threatened by local stressors (Gayle et al., 2005; Seguin et al., 2010; Young et al., 2012), or outplanting nursery-based corals (Ware et al., 2020). Most recent efforts have focused on outplanting nursery-reared corals and these methods are evolving rapidly (Edwards and Gomez, 2007; Rinkevich, 2014; Forsman, 2015; Page et al., 2015) and include both land-based and marine programs (Rinkevich, 1995; Oren and Benayahu, 1997; van Treeck and Schuhmacher, 1999). Coral-restoration practitioners are also attempting to identify coral genotypes that are most tolerant to disease and thermal stress (Baums et al., 2019), essentially accelerating natural selection, with the goal of using those robust individuals to repopulate reefs (van Oppen and Gates, 2006; Baums, 2008; van Oppen et al., 2015; Pausch et al., 2018).

One of the more difficult hurdles of coral restoration, however, is developing models that can accurately predict optimal localities for coral outplanting at a variety of spatial scales (Wirt et al., 2013; van Woesik et al., 2020a). Such models aim to determine which subregions (at the 100-km scale), reefs (at the 10-km scale), or habitats (at the 0.1–1-km scale) are most favorable for *Acropora* survival along the Florida reef tract. Indeed, there is an urgent need for hierarchical models that inform restoration practitioners and managers which coral species to outplant, and where to outplant them, at a range of spatial scales along the Florida reef tract.

There are, however, some analytical barriers preventing accurate predictions, primarily because acroporids along the Florida reef tract are scarce. Most models that estimate the spatial distribution of *Acropora* species in Florida have had high specificity (i.e., skilled at predicting true negatives) but low sensitivity (i.e., not skilled at predicting true positives) (van Woesik et al., 2020b). In other words, regional models have a low accuracy of predicting where an acroporid species is likely to occur because the frequency and intensity of recent disturbances makes that niche space highly dynamic and unpredictable. Therefore, developing models that can perform with limited presence data, incorporate environmental predictors, and accurately predict optimal restoration sites are urgently needed at all spatial scales along the Florida reef tract.

At the local, habitat scale, several studies have recently made considerable progress at predicting the presence of *A. cervicornis*. For example, *A. cervicornis* colonies are most commonly found growing close to reef edges, where water-flow rates are high

(D'Antonio et al., 2016), and in habitats with moderate wave energy, between 0.5 and 1.5 kJ/m² (van Woesik et al., 2020b). In addition, *A. cervicornis* outplant survival appears highest in back-reef and fore-reef habitats (van Woesik et al., 2020a). There is, however, little information on the survival of acroporids at the reef scale, even though the reef scale has been identified as the scale of highest variability in Florida (Murdoch and Aronson, 1999). To optimize restoration efforts and improve *A. cervicornis* outplant survival we developed a spatio-temporal Integrated Nested Laplace Approximation (INLA) survival model, within a Bayesian framework, which used survival data from *A. cervicornis* outplants along the Florida reef tract from 2012 to 2018. The objectives of this study were to: (i) rank 67 reefs in terms of survival of outplanted colonies of the coral *A. cervicornis* along the Florida reef tract, and (ii) determine whether outplant survival was geographically consistent through time.

MATERIALS AND METHODS

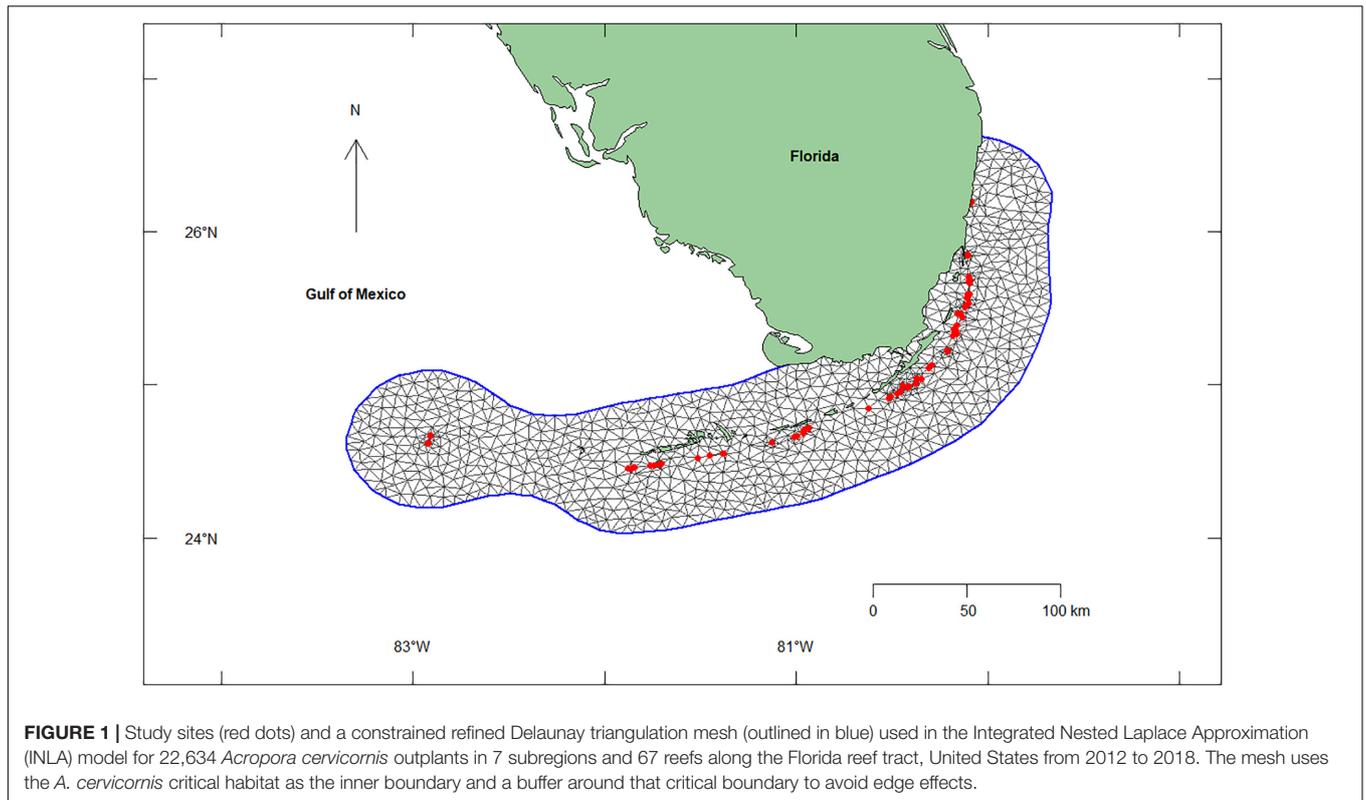
The data were a compilation of work conducted by six different coral restoration programs that examined the survival of a total of 22,634 *A. cervicornis* colonies raised in nurseries and outplanted to reef habitats along the Florida reef tract between 2012 and 2018 (van Woesik et al., 2020a). The restoration programs were conducted by: (1) The Nature Conservancy, (2) the Mote Marine Laboratory, (3) the Florida Fish and Wildlife Conservation Commission, (4) the Coral Restoration Foundation, (5) the University of Miami, and (6) Nova Southeastern University (**Supplementary Document**). All six coral restoration programs monitored the survival of *A. cervicornis* outplants after 1-month and 1-year, and several programs continued to monitor colony survival annually for 4 years (i.e., The Nature Conservancy, the Mote Marine Laboratory, the Florida Fish and Wildlife Conservation Commission, and the University of Miami). Each outplanted colony was visually assessed to determine whether it was alive or dead at each monitoring interval. An *A. cervicornis* colony was considered censored when the colony was still alive at the last monitoring interval. For analysis purposes, censored individuals were given a value of 0. By contrast, individuals that died within the timeframe of the study were given a value of 1, at the time of death. All outplanted *A. cervicornis* colonies analyzed in this study were considered as shallow (<8 m) outplants. All the data are available at: https://github.com/rvanwoesik/Acropora_survival.

Data Analysis

We used Integrated Nested Laplace Approximation (INLA) (Rue et al., 2009) within a Bayesian framework to examine spatial differences in coral survival (η) at a given site on a reef, i , expressed as:

$$\eta_i = \gamma + \sum \beta_j Z_j(s_i) + \zeta(s_i) + \varepsilon(s_i) \quad (1)$$

where γ is an intercept coefficient, β is the fixed-effect coefficient vector, Z is a matrix of covariates at the location of the data points s_i , $\zeta(s_i)$ is the spatial random effect in a spatial Gaussian



Markov Random Field (GMRF), and $\varepsilon(s_i)$ is the measurement error defined by a Gaussian white-noise process [$\sim N(0, \sigma^2_\varepsilon)$]. The GMRF combines the Gaussian field with Matérn covariance functions using stochastic partial differential equations, which in turn use a finite element representation to define the Matérn field by triangulation of the spatial domain (Lindgren et al., 2011; **Figure 1**). The GMRF computational properties have been recently enhanced by using INLA (Rue et al., 2009) for Bayesian inference, which is a computationally effective algorithm that produces fast and accurate approximations of posterior distributions (Blangiardo and Cameletti, 2015). Here we are particularly interested in the coefficients of the covariates, to determine how much of the variance is explained by the covariates reef and subregion, and the variation in the spatial latent effect explained by the variance-covariance matrix calculated using the Matérn correlation function. Model selection was based on the lowest Deviance Information Criterion (DIC) and the lowest Watanabe-Akaike Information Criterion (WAIC). To validate the model, we used spatial leave-one-out cross validation, to assess the root mean squared error (Le Rest et al., 2014). All the models were coded in R (R Core Team, 2018) and are available at: https://github.com/rvanwoesik/INLA_Florida.

In conjunction with the INLA coral survival model, we used a binary logistic regression model to examine the relationship between the probability of survival of *A. cervicornis* outplants along the Florida reef tract and wave energy. Mean wave energy was derived from site location and fetch, at a 1-km resolution (from van Woesik et al., 2020b; **Supplementary Document**) and used as the predictive covariate. For the response covariates, we

assigned 33 reefs (ranked 1–33) that had the highest likelihood of outplant survival (**Table 1**), based on the INLA results, a value of 1, and 34 reefs (ranked 34–67) that had the lowest likelihood of outplant survival (**Table 1**), based on the INLA results, a value of 0.

RESULTS

The INLA coral survival model examining “reefs” as fixed effects showed considerable variability in outplant survival across the study region. Indeed, the top ranked reefs, where the likelihood of survival of outplants was highest, were widely distributed along the Florida reef tract (**Figure 2**). There was also considerable variability in outplant survival within each of the seven subregions (**Table 1**). Survival of *Acropora cervicornis* outplants was highly variable in the upper Florida Keys with some reefs showing high survival (e.g., North Dry Rocks, Carysfort, Key Largo Dry Rocks, and Conch Reef), whereas some adjacent or nearby reefs showed low survival (e.g., an Unnamed Reef, Pickles Reef, and U47 Patch Reef) (**Figure 2**). Similarly, survival of *A. cervicornis* was highly variable in the middle and lower Florida Keys and in the Broward-Miami subregions, with some reefs showing high survival, whereas some adjacent or nearby reefs in the same subregion showed low survival (**Table 1**). By contrast, survival of *A. cervicornis* outplants in the Biscayne subregion showed low variability, but survival was consistently high (**Table 1**). Similarly, survival of *A. cervicornis* outplants was consistent within the Marquesas and the Dry Tortugas

TABLE 1 | Posteriori mean (Mean); standard deviation (SD); 0.025, and 0.975% Quantile values; and Mode of the posteriori mean values using 67 reefs as the fixed effect in the Integrated Nested Laplace Approximation (INLA) model for 22,634 *Acropora cervicornis* outplants in 7 subregions along the Florida reef tract, United States from 2012 to 2018. The 7 subregions (from north east to south west) include: 1) Broward-Miami, 2) Biscayne, 3) Upper Keys, 4) Middle Keys, 5) Lower Keys, 6) Marquesas, and 7) Dry Tortugas. The reefs are listed from highest to lowest likelihood of survival of *A. cervicornis* outplants. Carysfort Reef, ranked # 4 and marked in bold, is included in the “Iconic Reefs” initiative.

Rank	Reef	Subregion	Mean	SD	0.025% Quantile	0.975% Quantile	Mode
1	North Dry Rocks	Upper Keys	-0.0442	7.6775	-15.1176	15.0167	-0.0442
2	Davis Ledge	Upper Keys	-0.0372	7.6774	-15.1106	15.0236	-0.0372
3	CNC2	Upper Keys	-0.0346	7.6774	-15.1080	15.0262	-0.0346
4	Carysfort	Upper Keys	-0.0320	7.6774	-15.1053	15.0288	-0.0320
5	MBNOAA1	Broward-Miami	-0.0270	11.9816	-23.5509	23.4773	-0.0270
6	Key Largo Dry Rocks	Upper Keys	-0.0264	7.6774	-15.0997	15.0344	-0.0264
7	Conch	Upper Keys	-0.0255	7.6774	-15.0988	15.0354	-0.0255
8	Coffins Patch	Middle Keys	-0.0240	10.5610	-20.7589	20.6936	-0.0240
9	MBPOM1	Broward-Miami	-0.0204	11.9816	-23.5443	23.4839	-0.0204
10	Tropical Rocks	Middle Keys	-0.0172	10.5610	-20.7521	20.7004	-0.0172
11	U	Lower Keys	-0.0171	11.2043	-22.0150	21.9625	-0.0171
12	Grecian Rocks	Upper Keys	-0.0166	7.6774	-15.0900	15.0442	-0.0166
13	M9	Middle Keys	-0.0163	10.5611	-20.7513	20.7013	-0.0163
14	DPNOAA1	Biscayne	-0.0163	5.8609	-11.5232	11.4811	-0.0163
15	Q	Lower Keys	-0.0161	11.2043	-22.0139	21.9635	-0.0161
16	Fowey	Biscayne	-0.0136	5.8609	-11.5205	11.4838	-0.0136
17	White Banks	Upper Keys	-0.0123	7.6774	-15.0857	15.0485	-0.0123
18	Western Sambo	Lower Keys	-0.0111	11.2043	-22.0090	21.9684	-0.0111
19	DP Dan	Biscayne	-0.0109	5.8609	-11.5178	11.4865	-0.0109
20	Barge	Biscayne	-0.0109	5.8609	-11.5178	11.4865	-0.0109
21	Safety Valve	Biscayne	-0.0109	5.8609	-11.5178	11.4865	-0.0109
22	KBCF2	Biscayne	-0.0109	5.8609	-11.5178	11.4865	-0.0109
23	Kpeebs	Biscayne	-0.0109	5.8609	-11.5179	11.4865	-0.0109
24	Bertha	Biscayne	-0.0108	5.8609	-11.5177	11.4867	-0.0108
25	South Inshore	Biscayne	-0.0104	5.8609	-11.5174	11.4869	-0.0104
26	Molasses	Upper Keys	-0.0098	7.6774	-15.0832	15.0509	-0.0098
27	KBPOM	Biscayne	-0.0097	5.8609	-11.5166	11.4876	-0.0097
28	Flamingo	Biscayne	-0.0097	5.8609	-11.5167	11.4877	-0.0097
29	Emerald	Biscayne	-0.0088	5.8609	-11.5157	11.4886	-0.0088
30	North Emerald	Biscayne	-0.0075	5.8609	-11.5144	11.4899	-0.0075
31	CVFD	Biscayne	-0.0070	5.8609	-11.5139	11.4904	-0.0070
32	North Midchannel	Biscayne	-0.0062	5.8609	-11.5131	11.4912	-0.0062
33	Snapper Ledge	Upper Keys	-0.0059	7.6774	-15.0793	15.0549	-0.0059
34	P	Lower Keys	-0.0047	11.2043	-22.0026	21.9748	-0.0047
35	1196	Biscayne	-0.0042	5.8609	-11.5112	11.4931	-0.0042
36	Miami Beach	Broward- Miami	-0.0027	11.9816	-23.5266	23.5016	-0.0027
37	Reef 1	Dry Tortugas	-0.0011	14.1906	-27.8621	27.8366	-0.0011
38	Reef 2	Dry Tortugas	-0.0006	14.1906	-27.8616	27.8372	-0.0006
39	Cooper	Biscayne	-0.0003	5.8609	-11.5072	11.4971	-0.0003
40	Alligator	Middle Keys	0.0005	10.5611	-20.7344	20.7181	0.0005
41	Stag Acres	Middle Keys	0.0007	10.5610	-20.7342	20.7183	0.0007
42	Reef 4	Dry Tortugas	0.0049	14.1906	-27.8562	27.8426	0.0049
43	Reef T	Marquesas	0.0051	15.8791	-31.1710	31.1552	0.0051
44	Steph's	Biscayne	0.0056	5.8609	-11.5013	11.5029	0.0056
45	Nearshore Patch	Middle Keys	0.0079	10.5610	-20.7270	20.7255	0.0079
46	Struggle Bus	Biscayne	0.0085	5.8609	-11.4985	11.5058	0.0085
47	Reef S	Marquesas	0.0097	15.8791	-31.1664	31.1598	0.0097
48	Crocker	Upper Keys	0.0097	7.6774	-15.0637	15.0705	0.0097
49	Grounding	Biscayne	0.0112	5.8609	-11.4957	11.5086	0.0112
50	CWW	Lower Keys	0.0115	11.2043	-21.9864	21.9911	0.0115
51	South Midchannel	Biscayne	0.0133	5.8609	-11.4936	11.5106	0.0133
52	Reef R	Marquesas	0.0136	15.8791	-31.1625	31.1637	0.0136

(Continued)

TABLE 1 | Continued

Rank	Reef	Subregion	Mean	SD	0.025% Quantile	0.975% Quantile	Mode
53	North Inshore	Biscayne	0.0139	5.8609	-11.4931	11.5112	0.0139
54	French	Upper Keys	0.0140	7.6774	-15.0594	15.0748	0.0140
55	Staghorn City	Broward-Miami	0.0161	11.9816	-23.5078	23.5204	0.0161
56	Aruba's	Broward-Miami	0.0188	11.9816	-23.5051	23.5230	0.0188
57	M8	Middle Keys	0.0194	10.5611	-20.7155	20.7370	0.0194
58	Little Conch Ledge	Upper Keys	0.0199	7.6774	-15.0535	15.0807	0.0199
59	Reef 3	Dry Tortugas	0.0199	14.1906	-27.8411	27.8577	0.0199
60	Jons	Biscayne	0.0256	5.8609	-11.4813	11.5230	0.0256
61	South Commercial	Broward-Miami	0.0259	11.9816	-23.4980	23.5301	0.0259
62	9 Foot Stake	Lower Keys	0.0326	11.2044	-21.9654	22.0122	0.0326
63	Horseshoe Low	Middle Keys	0.0347	10.5610	-20.7002	20.7523	0.0347
64	Marker 32	Lower Keys	0.0373	11.2043	-21.9606	22.0168	0.0373
65	Unnamed Reef	Upper Keys	0.0613	7.6775	-15.0122	15.1222	0.0613
66	Pickles	Upper Keys	0.0849	7.6774	-14.9884	15.1457	0.0849
67	U47 Patch	Upper Keys	0.0886	7.6774	-14.9847	15.1494	0.0886

subregions, although survival was moderate to low (Table 1). Notably, the Marquesas and the Dry Tortugas had comparably fewer outplanting sites (3 and 4, respectively) than the other subregions.

Outplant survival on reefs was significantly ($p = 0.0124$) related to mean wave energy. Reefs exposed to moderate levels of mean wave energy ($2-4 \text{ kJ m}^{-2}$) had a high probability of outplant survival. Conversely, reefs exposed to high levels of mean wave energy ($>4 \text{ kJ m}^{-2}$) had a relatively low probability of outplant survival (Figure 3).

After removing the effects of “reefs” and “subregions” from the spatio-temporal model, spatial latent effects were evident for each sampling period (Figure 4). These spatial latent effects showed consistently low survival of *A. cervicornis* outplants in the middle Florida Keys, which were consistent through time (Figure 4). There were also spatial latent effects from 2015 through to 2017 in the upper Florida Keys, suggesting lower survival of *A. cervicornis* outplants in these years. There were no obvious spatial latent effects northeast of the upper Florida Keys and west of the lower Florida Keys, although survival of *A. cervicornis* outplants was lower between 2015 and 2017 than for 2012 and 2014 in both of those subregions (Figure 2).

DISCUSSION

This study showed considerable variability in *A. cervicornis* outplant survival across the Florida reef tract from 2012 to 2018. Reefs within the upper and middle Florida Keys had high variability in survival of *A. cervicornis* outplants, supporting some of the best, but also some of the worst, reefs for outplant survival. For example, North Dry Rocks, Carysfort, Key Largo Dry Rocks, and Conch Reef, in the upper Florida Keys, and Coffins Patch and Tropical Rocks, in the middle Florida Keys were among the best reefs for outplant survival. Yet, some reefs that were immediately adjacent to or nearby these high-survival reefs were among the

worst reefs for outplant survival (Figure 2). Such results suggest that although the environmental conditions within a subregion influence outplant survival (Toth et al., 2018; van Woelik et al., 2020a), variation among reefs within a given subregion, and variation of habitats within reefs also play major roles in the probability of outplant survival.

High variability among reefs within subregions agrees with Murdoch and Aronson (1999), who examined variation in coral cover across the Florida reef tract. They suggested that coral cover on a given reef did not predict coral cover on the adjacent or nearby reefs, because reefs are disproportionately exposed to stressors and disturbances. Some of the stressors include differential exposure to the inclement waters from Florida Bay that have long been variable in temperature, salinity, nutrients, and sediment loads (Ginsburg and Shinn, 1994). Murdoch and Aronson (1999) found that most variation along the Florida reef tract occurred among reefs at the 10–20-km scale. These results from Florida contrast with a study along the Great Barrier Reef, in Australia, by Hughes et al. (1999) who showed that the highest variation in coral cover occurred among habitats at the 0.5–3-km scale. Understanding variation in coral cover and outplant survival is critical for restoration practitioners, because such variation reflects differences in key processes, such as differential recruitment and post-settlement mortality, that can influence restoration success. In addition, outplant survival does not always suggest an increase in coral cover as growth can be independent of survival. Similarly, outplant mortality does not necessarily result in a decline in coral cover as coral colonies can fragment, move, and fuse. Monitoring outplant survival is the cornerstone of monitoring restoration success, but to improve the overall understanding of restoration success, colony growth and fragmentation records should be also examined.

Coral reef restoration and monitoring is performed by various agencies throughout the Florida Keys, with each agency generally self-restricted to a particular subregion for outplanting and monitoring. Therefore, intra-regional variation in survival is

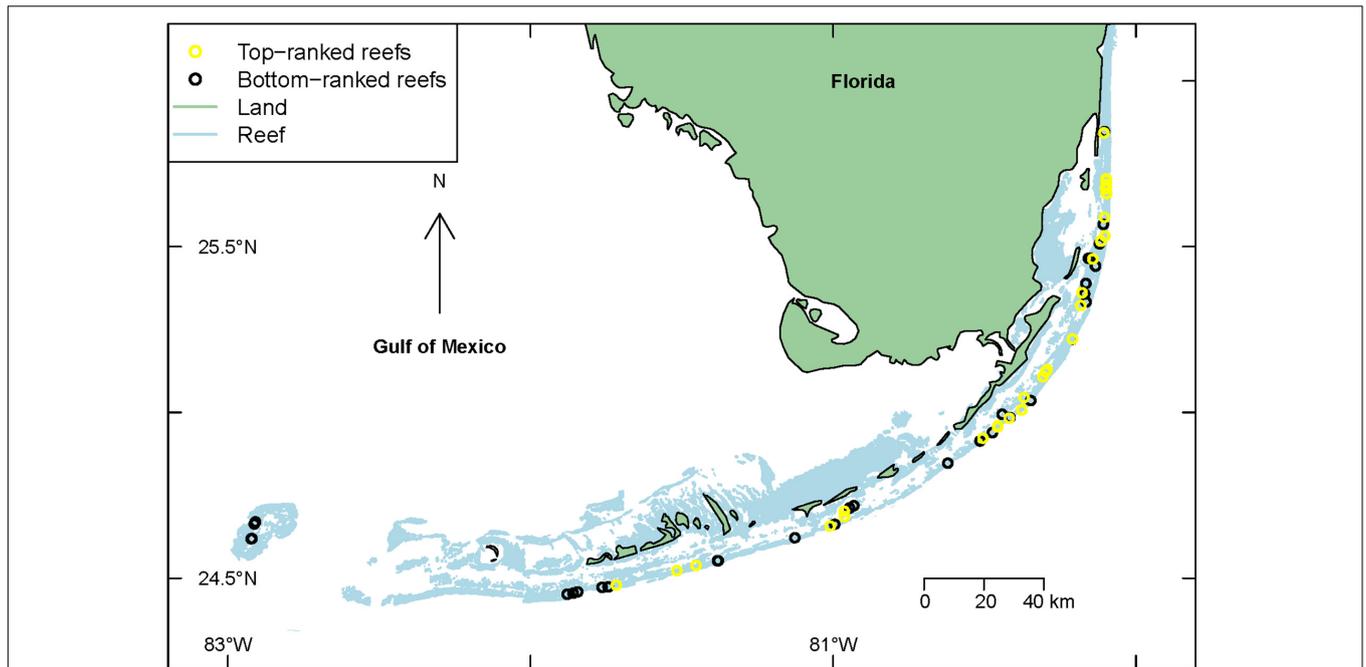


FIGURE 2 | Location of the top-ranked 33 reefs (depicted by yellow circles) with the highest likelihood of survival of *Acropora cervicornis* outplants, and the bottom-ranked 34 reefs (depicted by black circles) with the lowest likelihood of survival for *A. cervicornis* outplants in 7 subregions along the Florida reef tract, United States from 2012 to 2018—based on the *posteriori* mean values using “reef” as the fixed effect in the Integrated Nested Laplace Approximation (INLA) model.

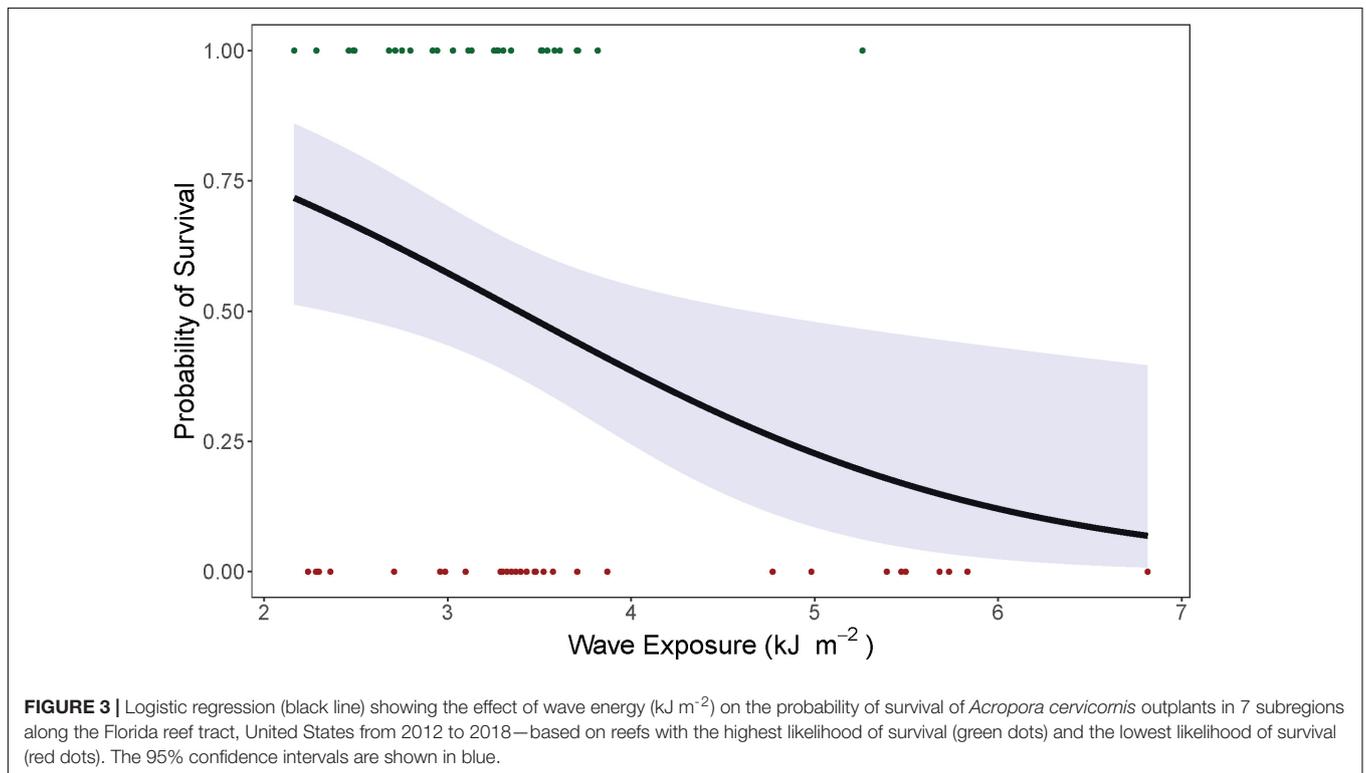
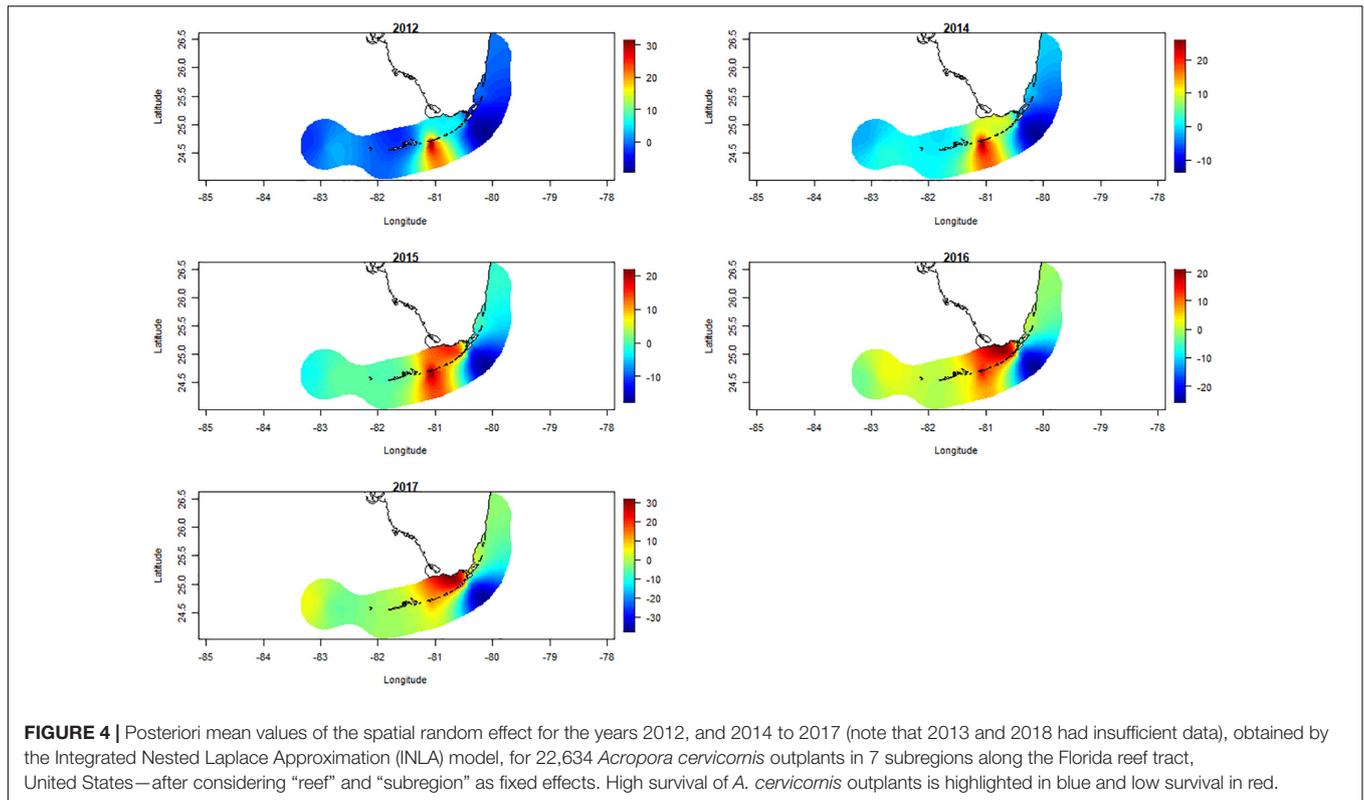


FIGURE 3 | Logistic regression (black line) showing the effect of wave energy (kJ m^{-2}) on the probability of survival of *Acropora cervicornis* outplants in 7 subregions along the Florida reef tract, United States from 2012 to 2018—based on reefs with the highest likelihood of survival (green dots) and the lowest likelihood of survival (red dots). The 95% confidence intervals are shown in blue.

likely not a consequence of outplanting technique, as the same agency uses the same technique across each subregion. We did find that differences in reef exposure to water flow and

wave energy influenced outplant survival, which warrants further investigation. Based on previous findings (D’Antonio et al., 2016; van Woelik et al., 2020b) *A. cervicornis* seems to prefer reef



substrate that is exposed to moderate levels of water flow and wave energy—a finding which is supported in the present study. For example, the reefs that ranked highest for outplant survival were exposed to moderate wave energy, whereas nearby reefs that ranked lowest for outplant survival were exposed to moderate to high wave energy (Figure 3). These results point to a potential wave-energy threshold, where high wave energy is not conducive to *A. cervicornis* survival. No outplants were positioned on reefs with low wave-energy exposure, and therefore we do not know the wave-energy threshold where waters may become stagnant and thus harmful for *A. cervicornis* outplant survival.

Since suitable habitat for *A. cervicornis* outplant survival is limited throughout the Florida reef tract (van Woësik et al., 2020b), reefs showing high survival of outplants, in subregions with low overall survival, deserve special attention. Such bright spots, within subregions that are less conducive to survival, have been referred to as microrefugia and have played major roles in genetic preservation and population recovery during glacial-interglacial cycles in the past (Mosblech et al., 2011). With the continuation of climate change and ocean warming, protecting such microrefugia should be prioritized in the hope of sustaining coral populations. For example, microrefugia in the middle Florida Keys could be vital stepping-stones in maintaining connectivity among coral populations between the lower and upper Florida Keys (Frys et al., 2020). Additionally, with *A. cervicornis* and *A. palmata* listed as “threatened” and “critically endangered,” microrefuges throughout the Florida reef tract are of great importance in protecting and restoring the acroporids. Unfortunately, the genetic identity for all of the

22,634 outplants in this study were not available and prevented the assessment of individual genotypes as a confounding variable. However, we encourage the inclusion of individual genotypes as a variable in further analyses because it could reveal valuable insights into the performance of coral outplants under current and future stressors.

While the present study highlights reefs where *A. cervicornis* had the highest and lowest likelihood of survival, other coral species may have broader or narrower tolerances. Therefore, this study does not suggest abandoning coral-restoration practices in the middle Florida Keys, nor does it serve as a conduit for judging the success of other coral species. Conservation initiatives and restoration programs are only in their infancy in Florida. One such recent 2020 initiative, called “Iconic Reefs” (NOAA Fisheries, 2019), was designed to conserve and restore seven reefs along the Florida reef tract. The “Iconic Reefs” mission is an emergency restoration plan focused on providing rapid restoration efforts to seven reefs in the Florida Keys (i.e., Carysfort Reef, Horseshoe Reef, Cheeca Rocks, Sombrero Reef, Newfound Harbor, Looe Key Reef, and Eastern Dry Rocks). Carysfort Reef (north and south) is scheduled to receive 36,554 *A. cervicornis* outplants during phases 1 and 2—a notable amount of outplants, and higher than the number of outplants scheduled for the other “Iconic Reefs” (NOAA Fisheries, 2019). Carysfort Reef was ranked fourth among the highest-ranking reefs in the present study (Table 1). While we cannot comment on whether all seven reefs of the “Iconic Reefs” program will support *A. cervicornis* populations (because we did not have any outplant data on 6 of the 7 chosen reefs), the variability within our

study suggests that the seven “Iconic Reefs” will also show variable responses in outplant success, and future studies may reveal that the seven reefs vary in which coral populations they can best support.

Contemporary restoration efforts take place in a dynamic backdrop of global, regional, and local stressors (van Hooidonk et al., 2017). Coral populations in Florida have been heavily impacted by diseases and thermal-stress events (Porter and Meier, 1992; Toth et al., 2014; Precht et al., 2016; Walton et al., 2018). For example, the Stony Coral Tissue Loss Disease (SCTLD)—a particularly aggressive disease affecting more than 19 coral species throughout the Florida reef tract and wider Caribbean (Muller et al., 2020)—recently changed the composition of reefs in Florida (Muller et al., 2020). Similarly, the effects of thermal stress was evident in our study in the years 2015–2017 (Figure 4), which coincided with a global El Niño event. *A. cervicornis* outplant survival was, in general, lower between 2015 and 2017 than it was for 2012 and 2014 in the upper and lower Florida Keys. Therefore, we suggest that *A. cervicornis* restoration efforts along the Florida reef tract should: (i) continue to strive for breeding diverse yet thermally tolerant and disease resistant colonies (Baums et al., 2013; van Oppen et al., 2015), and (ii) evaluate outplant success and the dynamics of that success on a reef-by-reef basis.

The INLA approach helped us examine temporal consistency in *A. cervicornis* outplant survival, but it also helped us detect spatially latent effects that were not explicit variables in our analysis. In particular, spatially latent effects were observed in the middle Florida Keys that were independent of reef, subregion, and year of monitoring. We also noticed lower survival of *A. cervicornis* outplants in the upper Florida Keys from 2015 through to 2017 than in the other years of the study—that was most likely associated with thermal-stress related effects. In addition, the effects of Hurricane Irma may have had an effect on the survival of colonies outplanted immediately prior to its overpass in 2017 (van Woesik et al., 2020a).

In conclusion, *A. cervicornis* outplant survival was highly variable in the middle and lower Florida Keys and Broward-Miami subregions. By contrast, *A. cervicornis* outplant survival was relatively high and less variable in Biscayne Bay, and low and less variable in the Marquesas subregions. The highest variability in *A. cervicornis* outplant survival, in general, was evident among adjacent or nearby reefs, as reefs appear disproportionately exposed to stressors. Such spatial and temporal differences in survival of *A. cervicornis* outplants at a “reef” scale highlight

a need for strategic research to enhance our understanding of processes that influence growth and survival of *A. cervicornis* outplants in order to optimize population recovery along the Florida reef tract.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/Supplementary Material, further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

RBB and RvW analyzed the data and wrote the manuscript. RvW conceptualized the study and provided funding. Both authors contributed to the article and approved the submitted version.

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Impact of Extreme Disturbances on Suspended Sediment in Western Florida Bay: Implications for Seagrass Resilience

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Seagrasses are threatened worldwide due to anthropogenic and natural disturbances disrupting the multiple feedbacks needed to maintain these ecosystems. If the disturbance is severe enough, seagrass systems may undergo a regime shift to a degraded system state that is resistant to recovery. In Florida Bay, Florida, United States, two recent, large-scale disturbances (a drought-induced seagrass die-off in 2015 and Hurricane Irma in 2017) have caused 8,777 ha of seagrass beds to degrade into a turbid, unvegetated state, causing a large sediment plume. Using satellite imagery digitization and long-term seagrass cover data, we investigate the expansion of this sediment plume between 2008 and 2020 and the potential interaction of this sediment plume with seagrass recovery in two focal basins in Florida Bay affected by the die-off, Johnson and Rankin. The average size of the sediment plume increased by 37% due to the die-off and Hurricane Irma, increasing from an average of 163.5 km² before the disturbances to an average of 223.5 km². The expansion of the plume was basin-specific, expanding into Johnson after the 2015 seagrass die-off with expansive and long-lasting effects, but only expanding into Rankin after Hurricane Irma with less severe and short-term effects. Furthermore, the sediment plume was negatively correlated with seagrass cover in Johnson, but held no relationship with seagrass cover in Rankin. Thus, different disturbances can act upon seagrass ecosystems at varying scales with varying consequences. This study illustrates the advantage of combining satellite imagery with field data to monitor disturbances as well as highlights the importance of investigating disturbances of seagrass ecosystems at various scales to comprehend seagrass resilience in the context of future extreme events.

Keywords: seagrass, suspended sediment, disturbance, resilience, Florida Bay, Everglades, seagrass die-off, Hurricane Irma

INTRODUCTION

Seagrass communities are a vital part of coastal ecosystems worldwide, providing many ecosystem services such as carbon storage (McLeod et al., 2011; Fourqurean et al., 2012; Duarte et al., 2013), habitat for fish and other fauna (Gillanders, 2006; Unsworth et al., 2019), sediment stabilization (Bos et al., 2007), and primary production (Duarte and Chiscano, 1999). However, seagrasses around the world are declining due to anthropogenic and natural disturbances, threatening the balance of these shallow water ecosystems (Orth et al., 2006; Waycott et al., 2009). One of the main causes of seagrass decline is the disruption of natural feedbacks that promote seagrass growth and sustenance (Duarte, 2002; Orth et al., 2006). Stabilizing feedbacks (i.e., negative feedback loops) control seagrass ecosystems at multiple scales (Maxwell et al., 2017; O'Brien et al., 2017), from supporting mesograzers populations at the meter scale (Valentine and Duffy, 2006; Duffy et al., 2015) to genetic diversity at the ecosystem scale (Procaccini et al., 2007; Reynolds et al., 2013). For example, grazing by sea urchins results in the reduction of aboveground seagrass biomass, which increases the predation pressure on sea urchins. The predation pressure leads to a decrease in urchin population, thus allowing for the seagrass to recover (Heck and Valentine, 1995). External disturbances can result in the disruption of one or more of these stabilizing feedbacks, creating destabilizing feedbacks (i.e., positive feedback loops) that drive seagrass decline (Nyström et al., 2012; Maxwell et al., 2017; O'Brien et al., 2017). An example of a destabilizing feedback is the decline of seagrass, which increases sediment resuspension events. The water column becomes more turbid, which in turn lowers the light available for photosynthesis and leads to further seagrass loss and further sediment resuspension (Nyström et al., 2012; Maxwell et al., 2017; O'Brien et al., 2017; **Figure 1**).

How seagrass ecosystems respond to these external disturbances is dependent upon the frequency and severity of the disturbance (O'Brien et al., 2017). Strong, or frequent disturbances can result in regime shifts, or a change from one ecosystem state to another, at the spatial scale of the disturbance (Nyström et al., 2012; O'Brien et al., 2017). For example, removal of seagrass due to propeller scarring changes the ecosystem state within the width of the scar (often <1 m) from vegetated to unvegetated. Without further disturbance, the seagrass recovers within a year and reaches the original ecosystem state within 6 years (Dawes et al., 1997; Kenworthy et al., 2002). However, if the disturbance is severe or frequent enough, ecosystems can become locked into a degraded state through the creation of new stabilizing feedbacks. If the destabilizing feedback loops are strong enough, the system will experience a lag in recovery (i.e., hysteresis) and may enter an alternative stable state (Scheffer et al., 2001; Beisner et al., 2003; Petraitis et al., 2009; Nyström et al., 2012).

Seagrass ecosystems are particularly vulnerable to changes into alternative stable states due to the number and strength of feedbacks within these systems (Maxwell et al., 2017). One example of the long-term impact that hysteresis can have on a seagrass ecosystem is the Dutch Wadden Sea (Scheffer et al., 2001; van der Heide et al., 2007). The construction of a large

dam and a seagrass wasting disease in the 1930s resulted in the collapse of large eelgrass (*Zostera marina*) meadows, which led to an unvegetated, turbid alternative stable state that still persists despite restoration efforts (van Katwijk and Hermus, 2000; van Katwijk et al., 2000; van der Heide et al., 2007). Unfortunately, the number of coastal ecosystems experiencing shifts to degraded alternative stable states has risen since the mid 20th century (Duarte et al., 2009; Carstensen et al., 2011; Maxwell et al., 2017). Proper management of coastal ecosystems, specifically seagrass ecosystems, requires more information on the causes and impacts of such regime shifts.

Florida Bay, the estuary between the Florida mainland and the Florida Keys, has a long history of anthropogenic and natural disturbances, including the reduction of freshwater inputs from water management practices, altered water circulation associated with the completion of the Flagler Over-Sea Railroad in 1912, and a number of hurricanes and tropical storms (Fourqurean and Robblee, 1999). Such disturbances have resulted in a reduced exchange between Florida Bay and the Atlantic Ocean, increased water residence time, changes in water circulation patterns, higher salinities, more frequent algal blooms, and decreased seagrass diversity (i.e., an increase in *Thalassia testudinum*-dominated communities, Rudnick et al., 2005; Madden et al., 2009). A combination of high bottom water temperatures, hypersalinity and prolonged bottom water anoxia caused a large-scale seagrass die-off between 1987 and 1991 that affected 27,000 ha of *T. testudinum*, and led to loss of submerged aquatic vegetation (SAV) coverage, increased water column production and turbidity, and trophic shifts (Robblee et al., 1991; Fourqurean and Robblee, 1999). After nearly a decade of persistent algal blooms, the system required an additional 6–10 years to return to pre-die-off levels of *T. testudinum* coverage (Hall et al., 2016). However, a second drought-induced seagrass die-off occurred in 2015, leading to another potential regime shift (Hall et al., 2016; **Figure 2**). The region was disturbed again in 2017, when Hurricane Irma passed through Florida Bay as a category 4 hurricane, impacting areas of Florida Bay and the Florida Keys (Wilson et al., 2020; **Figure 2**). Large and frequent disturbance events such as these could induce a state of turbidity that influences the growth and stability of seagrass habitats (**Figure 1**).

In this article, we describe the expansion of a heretofore undocumented sediment plume in the western region of Florida Bay in relation to these two recent disturbances: the 2015 seagrass die-off and Hurricane Irma in 2017. Furthermore, we investigate the potential interaction of the sediment plume with seagrass recovery. Using a remote sensing approach, we addressed the following questions: (a) To what extent did the sediment plume expand after each of the two disturbances (pre vs. post comparisons)? (b) Which disturbance had a greater effect on the expanse of the plume? and (c) Is there an interaction between sediment plume coverage and changes in seagrass cover? We addressed these questions by delineating changes in plume extent over 2008–2020 and in relation to the timing of the two disturbances using satellite imagery. We then compared changes in plume extent relative to long term seagrass cover data across two focal basins of interest, Johnson and Rankin, both affected and undergoing recovery from the 2015 seagrass event. Based

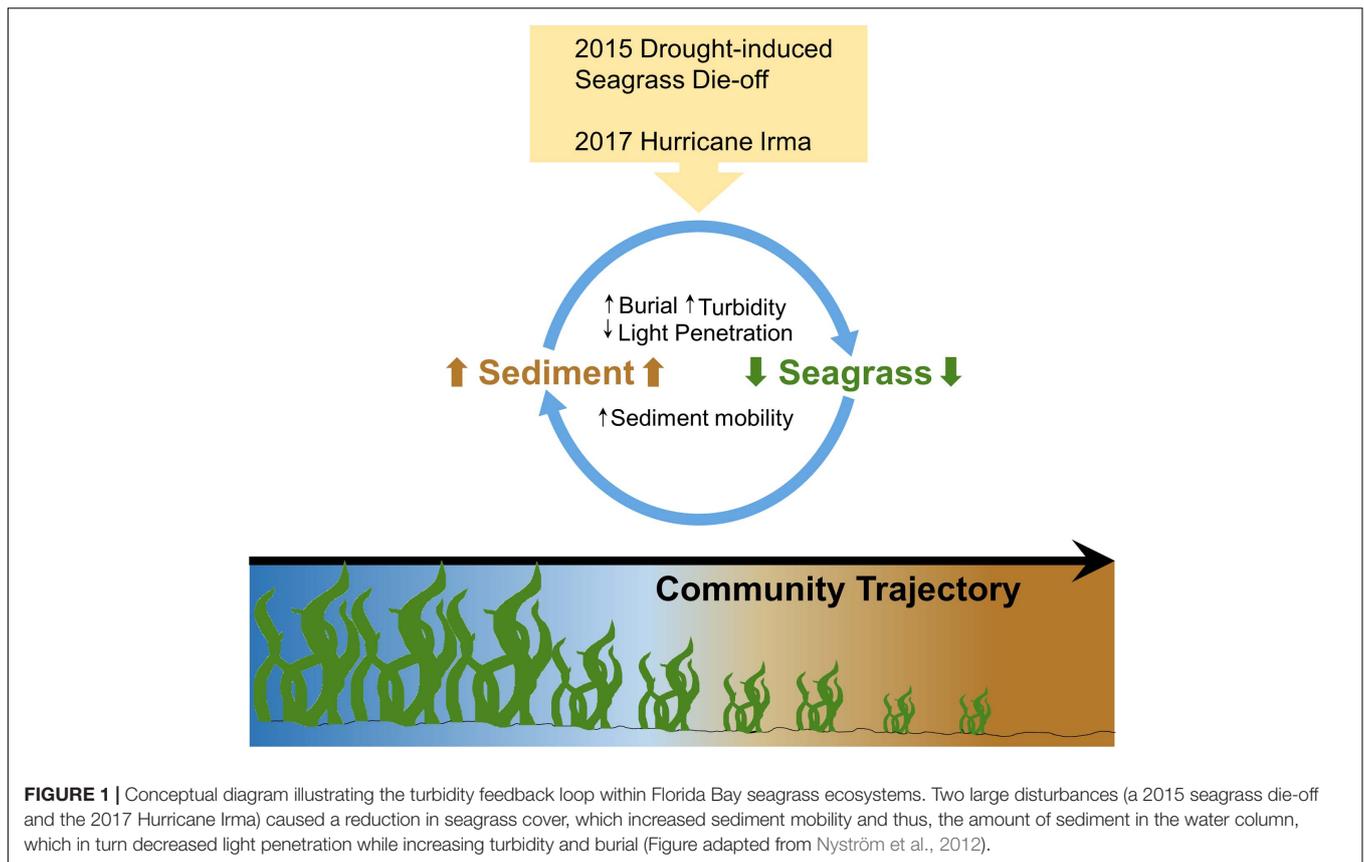


FIGURE 1 | Conceptual diagram illustrating the turbidity feedback loop within Florida Bay seagrass ecosystems. Two large disturbances (a 2015 seagrass die-off and the 2017 Hurricane Irma) caused a reduction in seagrass cover, which increased sediment mobility and thus, the amount of sediment in the water column, which in turn decreased light penetration while increasing turbidity and burial (Figure adapted from Nyström et al., 2012).

on these data, we discuss the potential impact of this expanding sediment plume on seagrass communities throughout Florida Bay and what to expect in the future.

MATERIALS AND METHODS

Study Site

Florida Bay is the largest estuary in Florida (2,200 km²), located at the southern end of the Florida peninsula and of Everglades National Park (ENP, **Figure 2**). The bay consists of a patchwork of shallow interconnected basins (1–2 m depth), mud banks (<0.5 m depth), seagrass meadows, mangrove islands, and narrow tidal channels. Florida Bay has restricted water exchange and high residence time, which can make regions of the bay prone to hypersalinity (Nuttle et al., 2000; Rudnick et al., 2005). Importantly, Florida Bay has undergone major changes over the past century as a result of anthropogenic impacts associated with the construction of the railroad across the Florida Keys and drainage and impoundment of freshwater wetlands upstream (Fourqurean and Robblee, 1999), resulting in increased salinity, decreased water exchange, and changes in benthic macrophyte communities (Rudnick et al., 2005; Madden et al., 2009).

Today, a large portion of Florida Bay functions as a reverse estuary with chronic hypersalinity conditions prevailing in the north-central part of the bay during the low precipitation and freshwater inflow periods of the dry season (December–May;

Kelble et al., 2007). Relative to historical conditions, freshwater flows have been reduced by 60%, with nearshore present-day salinities being 5–20 ppt higher than pre-drainage (Marshall et al., 2009). These conditions make the bay vulnerable to drought events, which in 1987 and 2015 resulted in massive seagrass die-off events, affecting approximately 30% of the bay (Zieman et al., 1999; Hall et al., 2016). Two basins, Johnson and Rankin, were chosen as focal basins for this study because they are located in the north-central part of the bay affected by the 2015 die-off, and because long long-term seagrass cover monitoring data exists, which are useful to examine recovery trends (Hall et al., 2016; **Figure 2**). Additionally, the basins were affected by Hurricane Irma, which passed through Florida Bay as a category 4 hurricane in September 2017, disturbing benthic communities and significantly altering the circulation of water in the bay (Liu et al., 2020).

Satellite Imagery Processing

LandSat imagery from three LandSat missions (LandSat 5, LandSat 7, and LandSat 8)¹ were used to map the sediment plume. LandSat satellites are a very popular tool in coastal mapping due to a relatively short revisit rate (2 weeks), high resolution (30 m), long time series (LandSat 5 was launched in 1985), and availability. LandSat satellites collect data in 7 bands across the visible and infrared spectrums. Two LandSat images per year

¹<https://landsat.gsfc.nasa.gov>

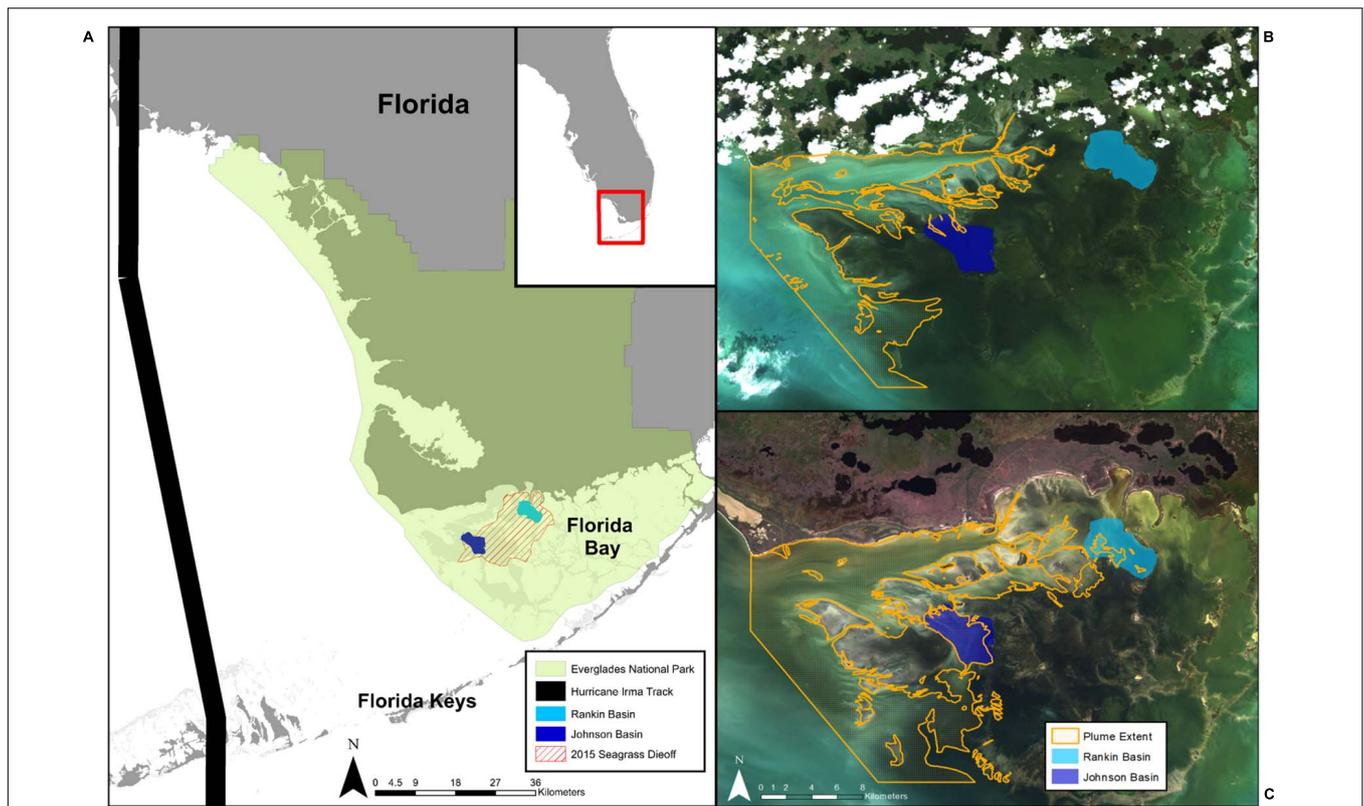


FIGURE 2 | (A) Map of Florida Bay showing the location of our two study basins (Rankin and Johnson), the extent of the 2015 seagrass die-off, and the track of Hurricane Irma in 2017. Everglades National Park is denoted by green shading. Extent of the sediment plume overlaid over satellite imagery shows the **(B)** smallest (119.6 km²; 10/03/2009), and **(C)** largest plume areas (249.2 km²; 11/29/2018) observed in the study.

from 2008 to 2020 were used to map the plume expansion for a total of 24 images. 2008 was chosen as the early cutoff since it matches the time series of total seagrass cover data provided by the Florida Fish and Wildlife Commission Fish and Wildlife Research Institute (FWC-FWRI). Google Earth Engine, an online coding platform, was used to process each satellite image (Gorelick et al., 2017). Google Earth Engine is a popular tool for seagrass mapping at regional scales due to its availability, ease of use, and batch processing that allows multiple satellite images to be analyzed at once (Lyons et al., 2012; Zhang et al., 2019; Wang et al., 2020).

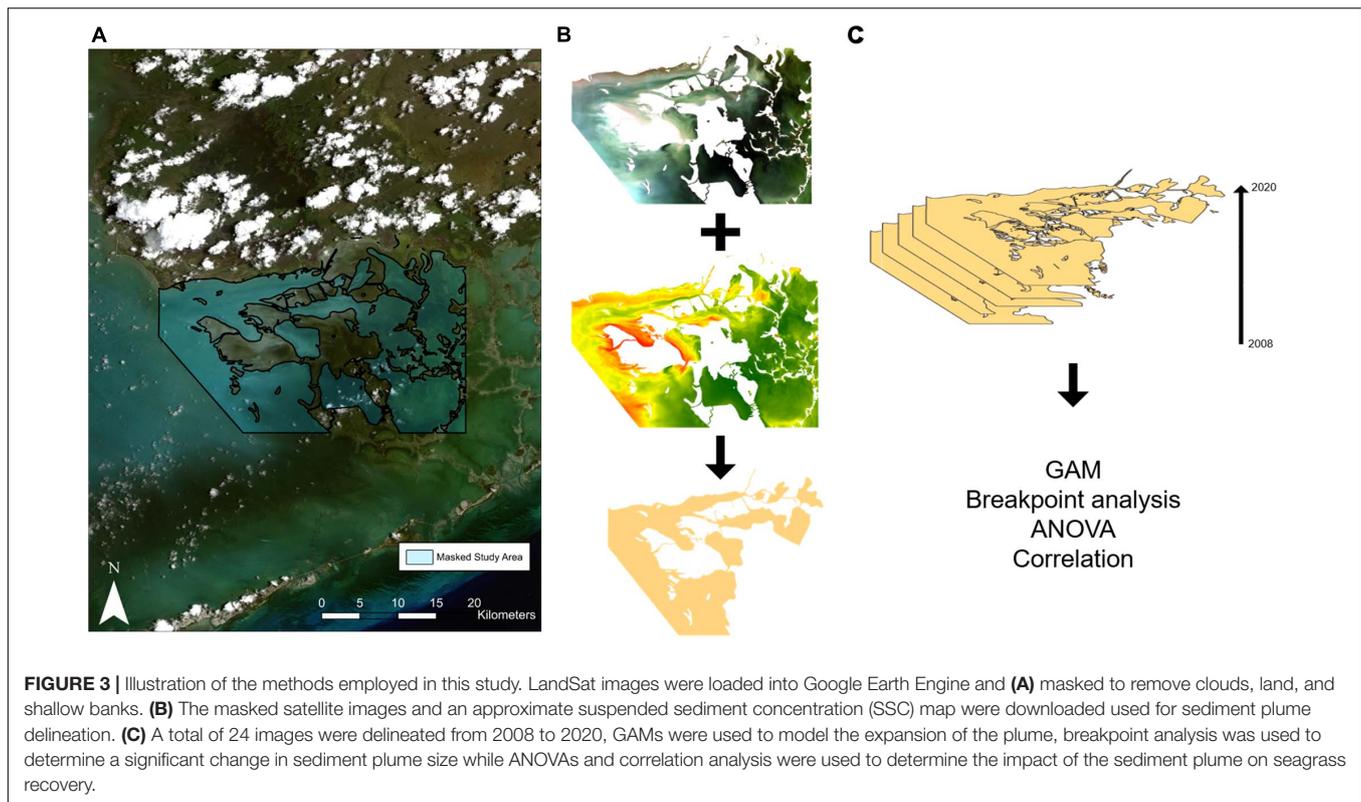
Atmospherically and geometrically corrected Landsat images (courtesy of the U.S. Geological Survey) were loaded into Google Earth Engine to mask clouds, land, and shallow banks. Masking each image removes the areas of the satellite image that are not the focus of the study. Images were chosen based on a visual inspection of cloud cover, where images needed to have less than 10% cloud cover to be considered. Clouds were masked via the U.S. Geological Survey (USGS) quality assessment algorithm, which uses the CFMask algorithm (Foga et al., 2017) to calculate pixels with cloud cover and shadow. Land and shallow banks were masked using a Florida Bay Basin shapefile provided by FWC-FWRI (Figure 3A). Banks were masked due to the lack of seagrass data and difficulty of differentiating sediment plume from bottom. Masked Landsat images were downloaded from

Google Earth Engine, keeping the bands in the visible and near-infrared spectrums.

Sediment Plume Delineation

The areal extent of the sediment plume was delineated using manual digitalization. Manual digitalization, also known as photo interpretation, has been used in coastal mapping for many decades (Roelfsema et al., 2009) and continues to be a popular method of coastal ecosystem mapping (Sherwood et al., 2017). Manual delineation was used in this study due to a lack of field training data as well as the presence of optically similar areas (i.e., sandy bottom vs. sediment plume). Two image interpreters were trained to delineate two classes: sediment plume with no light penetration (i.e., the bottom was not visible) and sediment plume with some light penetration (i.e., the bottom was visible; Figure 3B). Algal blooms within our area of study were not delineated. Accuracy assessment was performed by comparing delineations from 2017 to 2020 with turbidity measured from grab samples taken within the area of the plume by ENP. A turbidity measurement of >8 NTU was considered turbid, corresponding to an average Secchi depth of less than 1 m (Effler, 1988).

To aid in delineation, approximate suspended sediment concentration (SSC) was mapped using the algorithm developed in Islam et al. (2001). This algorithm assumes a linear relationship



between the red band and the sediment concentration and was chosen because it best visually represented the sediment plume in Florida Bay out of several algorithms considered by Pereira et al. (2019). This study utilized delineation instead of an algorithm derived from satellite data to map the sediment plume because the goal of this study was to map the extent of the plume, not SSC. Furthermore, the shallow waters and algal blooms within Florida Bay make isolating a sediment plume difficult and require an algorithm to be derived from extensive field sampling, which was not available for this study. Future work will focus on building upon the work done by Hajjgholizadeh and Melesse (2017) to create an algorithm and threshold that maps the sediment plume within Florida Bay.

Seagrass Cover

Seagrass data was obtained from the Fish Habitat Assessment Program (FHAP), established through the Comprehensive Everglades Restoration Plan's (CERP) Restoration, Coordination and Verification (RECOVER) program to “provide information for the spatial assessment and resolution of inter-annual variability in seagrass communities, and to establish a baseline to monitor responses of seagrass communities to water management alterations associated with CERP activities” (Hall et al., 2016; Hall and Durako, 2019). Monitoring for FHAP is conducted once a year in May–June (with the exception of 2015 when monitoring occurred after the die-off in November) at 30 sites within 17 basins across Florida Bay. At each site, eight 0.5×0.5 m quadrats are deployed and benthic macrophyte cover is quantified using the Braun-Blanquet (BB) method (Hall et al.,

2016). The BB method is a rapid and highly repeatable visual assessment technique that has been employed in Florida Bay for over two decades (Fourqurean et al., 2001; Furman et al., 2018). The scoring system is as follows: 0 = no presence, 0.1 = 1 shoot, 0.5 = less than 5 shoots, 1 = many shoots but <5% cover, 2 = 5–25% cover, 3 = 25–50% cover, 4 = 50–75% cover, 5 = 75–100% cover. The BB score for total seagrass is then averaged for each site. Our study utilized 30 sites in Johnson Basin and 30 sites in Rankin Basin surveyed each year for a total of 720 seagrass measurements. To determine the relationship between seagrass cover and sediment plume extent, the total seagrass cover from the 30 sites within each basin was averaged to create one BB score per year for each basin.

Data Analyses

To determine the extent of the sediment plume and how it changed over time, the two classes were combined and the area of the plume was calculated for each time step (Figure 3C). A Generalized Additive Model (GAM) was used to model plume size across years using the R package “mgcv” (Wood, 2017). Two models were run in preliminary analyses: one with seasonality and one without seasonality to determine whether seasonality was a significant driver of plume size. A breakpoint analysis was run to determine years in which plume size significantly changed over the 12 years.

In order to relate plume extent to changes in seagrass cover, plume expansion and contraction within Johnson and Rankin Basins were investigated. Shapefiles of Rankin and Johnson were used to determine the proportion of each basin the plume covered

within each image. A breakpoint analysis was also run on the Rankin and Johnson Basin time series individually to identify the years in which the plume coverage within each basin significantly changed. For all of the breakpoint analyses, the optimal number of breakpoints in the data was determined by the minimum Bayesian Information Criterion (BIC; Bai and Perron, 2003). Breakpoint analyses were done with the R package “strucchange” (Zeileis et al., 2002, 2003).

In order to examine the interaction of plume expansion and seagrass cover, an analysis of variance (ANOVA) was used to test for differences in the proportion of each basin covered by the sediment plume and seagrass cover before and after the breakpoints between each basin. A Tukey’s HSD was run to identify which time periods significantly differed. Pearson’s correlation tests were run to test the relationship between the proportion of each basin covered by the sediment plume and seagrass cover. Only spring images ($n = 12$, includes the November measurement after the seagrass die-off) were included in the seagrass ANOVA and correlation analyses since seagrass cover was only monitored once a year in May–June. ANOVA and correlation analyses were done in R v 4.0.3 (R Core Team, 2020).

RESULTS

Accuracy of Sediment Plume Delineation

The areal extent of the sediment plume in western Florida Bay increased over the period of the study (2008–2020). At its largest, the sediment plume covered an area of 249.2 km², increasing 108% from a minimum of 119.6 km² during the period of observation (Supplementary Table 1). The overall accuracy of satellite imagery plume delineations tested with grab samples over 2017–2020 was 80.5% (Table 1). However, the majority (69.2%) of that error was due to lower turbidity measurements in the deeper, southern portion of our study area (around Rabbit Key Basin), where the bottom can be obscured by lighter sediment loads due to depth. The overall accuracy increased to 93.1% when the deeper, southern area was excluded from the accuracy assessment.

Sediment Plume Expansion Across the Study Area

When considering the full spatial extent of the study, we observed a significant, non-linear increase of the plume over the period examined. The GAM results found that yearly variation

significantly affected the size of the plume, explaining 63% of the deviance, and found no evidence of variation as a function of season (e.g., fall vs. spring satellite images; Figure 4 and Table 2). We detected a breakpoint in the sediment plume coverage of the region in November 2016 (95% CI: September 2015–February 2018; Table 3). This date straddled the Fall 2015 seagrass die-off and the Fall 2017 hurricane Irma. The average size of the sediment plume before the breakpoint was 163.5 km² (± 26.8 km²), which increased to 223.5 km² (± 19.9 km²) post-breakpoint—a 37% increase in area.

Basin Specific Responses to Disturbances and Sediment Plume Coverage

When considering our focal basins, Johnson and Rankin, we found differences in the magnitude, timing and duration of effects of the sediment plume. Both basins exhibited breakpoints, but the breakpoint was earlier, and resulted in more severe and longer lasting effects in the western basin, Johnson (Figure 5). An ANOVA conducted on the proportion of the basins covered by the plume, showed a significant basin and breakpoint interaction, with both Johnson and Rankin having a significantly higher proportion of basin covered by the plume after the change point compared to before (Tukey’s HSD < 0.05 ; Figure 6A and Table 4). In Johnson, there was a breakpoint in March 2015 (95% CI: October 2014–September 2015; Figure 5 and Table 3), and sustained high sediment coverage through the last data point in the time series. Before the breakpoint, an average of 11.6% ($\pm 10.8\%$) of Johnson was covered by the sediment plume while 78.6% ($\pm 13.4\%$) of Johnson was covered by the plume after the breakpoint (Figure 6A). In contrast, for Rankin, there were two breakpoints. The first breakpoint was February 2017 (95% CI September 2015–November 2017), and the second was November 2018 (95% CI February 2018–February 2020; Figure 5 and Table 4). Here, 0% of Rankin was covered by the plume before the first breakpoint, while 22% ($\pm 21\%$) was covered by the plume after the first breakpoint (Figure 6A). The second breakpoint in Rankin represents a sediment contraction, indicating the short term effects in this basin, and thus, was not considered in further analyses.

Interaction Between Sediment Plume Coverage and Changes in Seagrass Cover

Along with differences in the extent of the sediment plume, we also found differences in seagrass cover between basins, and a basin-specific interaction between plume extent and seagrass cover. For seagrass cover, the interaction between basin and before and after the change point was significant (Table 4). Seagrass cover in Johnson basin decreased significantly after its March 2015 breakpoint (Tukey’s HSD < 0.05 ; Figure 6B and Table 4). The average BB score in Johnson dropped from 3.6 (± 0.34 ; approximately 60% cover) to 2.5 (± 0.38 ; approximately 35% cover) after the breakpoint. In contrast, we found no change in seagrass cover as a function of its February 2017 breakpoint in Rankin. The average BB score of Rankin before

TABLE 1 | Summary of accuracy assessment of images from 2017 until 2020 using grab sample data provided by ENP.

Date	Correct	Total	Accuracy
11/26/2017	13	15	86.6%
2/14/2018	10	13	76.9%
2/17/2019	11	13	84.6%
6/25/2019	11	13	84.6%
2/4/2020	9	13	69.2%
Total	54	67	80.6%

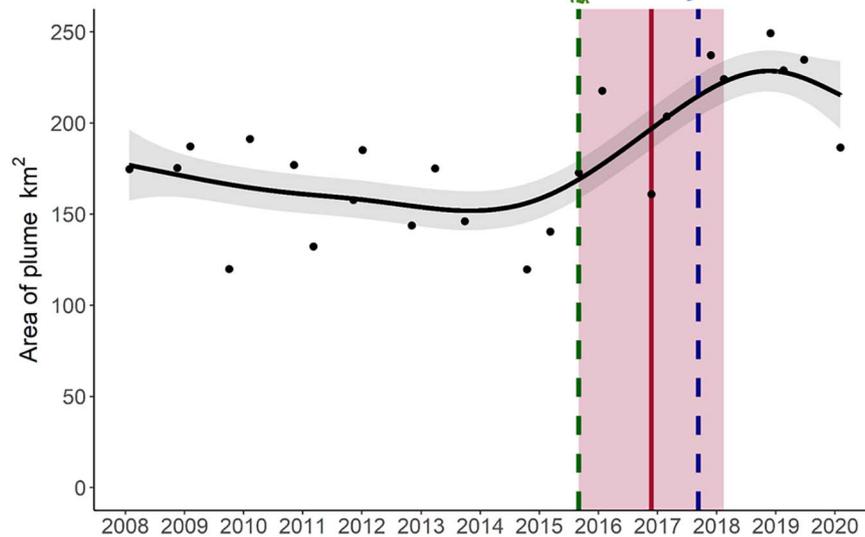


FIGURE 4 | Temporal trend in the sediment plume size in Florida Bay between 2008 and 2020. The black line shows the fitted GAM model and 95% confidence interval (gray shaded area). The vertical red line shows the breakpoint in sediment plume size, with its 95% confidence interval (red shaded area). The vertical green line represents the 2015 seagrass die-off and the vertical blue line represents Hurricane Irma.

the breakpoint was 2.7 (± 0.61 ; approximately 40% cover) and was 2.8 (± 0.05 ; approximately 45% cover) after the breakpoint. Further, in Johnson, there was a negative correlation between the proportion of basin covered by the sediment plume and seagrass cover ($r = -0.75$, $p = 0.005$; **Figure 6C**). There was no correlation between the proportion of basin covered by the sediment plume and seagrass cover in Rankin ($r = 0.05$, $p = 0.88$; **Figure 6C**).

DISCUSSION

Anthropogenic and natural disturbances have jointly contributed to the degradation of seagrass habitats worldwide, including in Florida Bay, which have resulted in two drought-induced seagrass die-offs (Fourqurean and Robblee, 1999; Hall et al.,

2016). The most recent seagrass die-off occurred in 2015, causing a potential localized regime shift from a densely vegetated state to a turbid, non-vegetated state (Hall et al., 2016; Hall and Durako, 2019). The system was further perturbed when Hurricane Irma passed over Florida Bay in 2017. In this paper, we describe evidence based on remote sensing and field data of how an expansion of a sediment plume in the western region of Florida Bay resulted from these two disturbances. Overall, we saw a 37% average increase in sediment plume area as the plume expanded eastward post the 2015 die-off (time series breakpoint is November 2016), with peak sediment values reached post Hurricane Irma. The expansion of the plume into individual basins was dependent on the scale and location of the disturbance, expanding in Johnson soon after the die-off but only expanding into Rankin after Hurricane Irma. Further, the effect of the plume in Rankin was smaller and shorter lasting than the more expansive and persistent effects in Johnson. We also investigate the potential interaction of this sediment plume expansion with seagrass, which we found to be basin specific. The sediment plume was negatively related to seagrass cover in the more and earlier impacted Johnson basin while had no relationship in Rankin due to the recovery of seagrass before the sediment plume reached Rankin.

How a system responds to a disturbance is spatially explicit, dependent on the spatial scale (Norkko et al., 2006; Dumbrell et al., 2008) and intensity of a disturbance event (Platt and Connell, 2003; Miller et al., 2011). This is especially true in coastal ecosystems, where different levels of exposure to a disturbance result in a spatial gradient of effects on community composition and function (Fonseca and Bell, 1998; Fonseca et al., 2008; Santos and Lirman, 2012). For example, Stipek et al. (2020) found that seagrass beds closer to pulses of freshwater experienced

TABLE 2 | Generalized additive models (GAM) used for the temporal assessment of sediment plume size.

	Term	edf	Ref.df	F	p	Deviance explained	AIC
(a) Date	Date	4.3	5.3	5.8	0.002*	62.8	229.8
(b) Date and Season	Date*Fall	2.2	2.8	7.3	0.002*	59.5	230.5
	Date*Spring	1.4	1.7	3.5	0.04*		

Two models were fitted: (a) without seasonality and (b) with seasonality. Models were based on a log link function. Shown are the smooth term effective degrees of freedom (edf), the test statistic of the model smooth terms (F), and the p-values for the null hypotheses that each smooth term is zero (p). Percentage deviance explained and Akaike information criterion (AIC) of the GAMS were used to determine the best model.

Significant values are denoted with *.

TABLE 3 | Breakpoint analysis used to determine significant changes in sediment plume size.

	<i>F</i>	<i>p</i>	1st breakpoint (95% CI)	2nd breakpoint (95% CI)	BIC 1 break	BIC 2 breaks	BIC 3 breaks
(a) Sediment plume area	27.7	<0.001*	11/2016 (09/2015–02/2018)	NA	60.2	63.2	65.5
(b) Proportion of Johnson covered	161.55	<0.001*	03/2015 (10/2014–09/2015)	NA	28.9	33.4	38.2
(c) Proportion of Rankin covered	17.1	<0.001*	02/2017 (09/2015–11/2017)	02/2017 (09/2015–11/2017)	66.0	54.6	60.1

Three analyses were run: (a) the whole sediment plume area, (b) the proportion of Johnson Basin covered by the sediment plume, and (c) the proportion of Rankin Basin covered by the sediment plume. Shown are the test statistic of the significance of the breakpoint (*F*), the approximate *p*-values for the null hypothesis that there is no breakpoint (*p*), and the location of the breakpoint(s). Bayesian information criterion (BIC) was used to determine the number of significant breakpoints. Significant values are denoted with *.

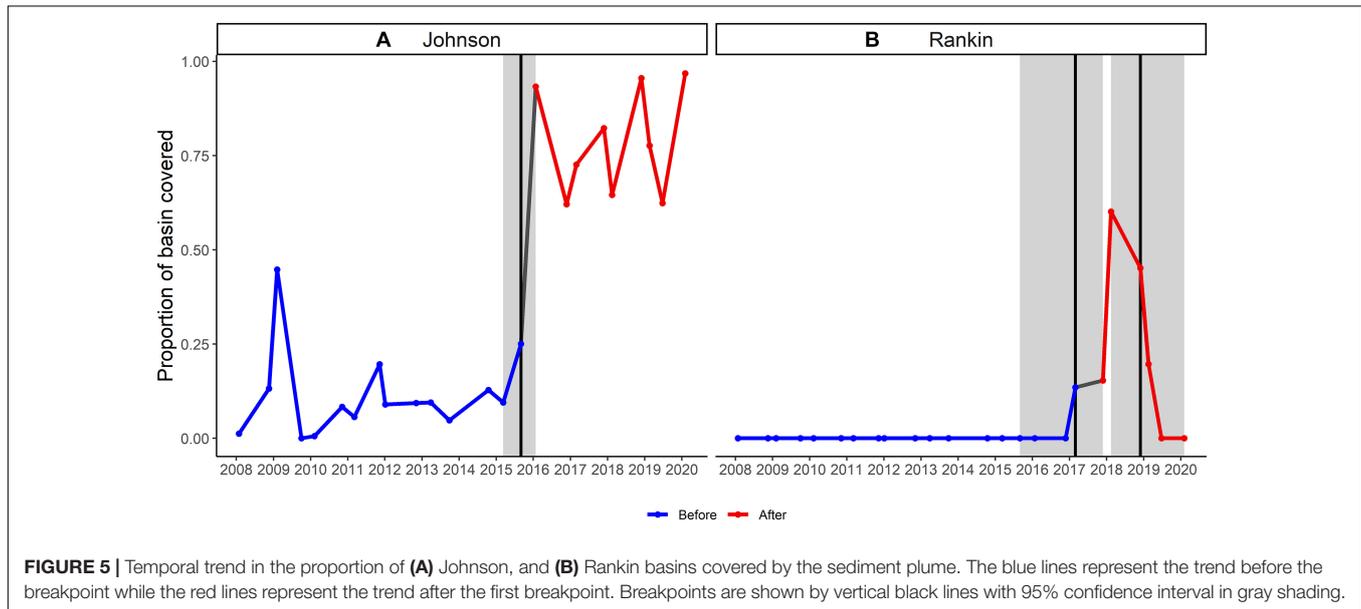


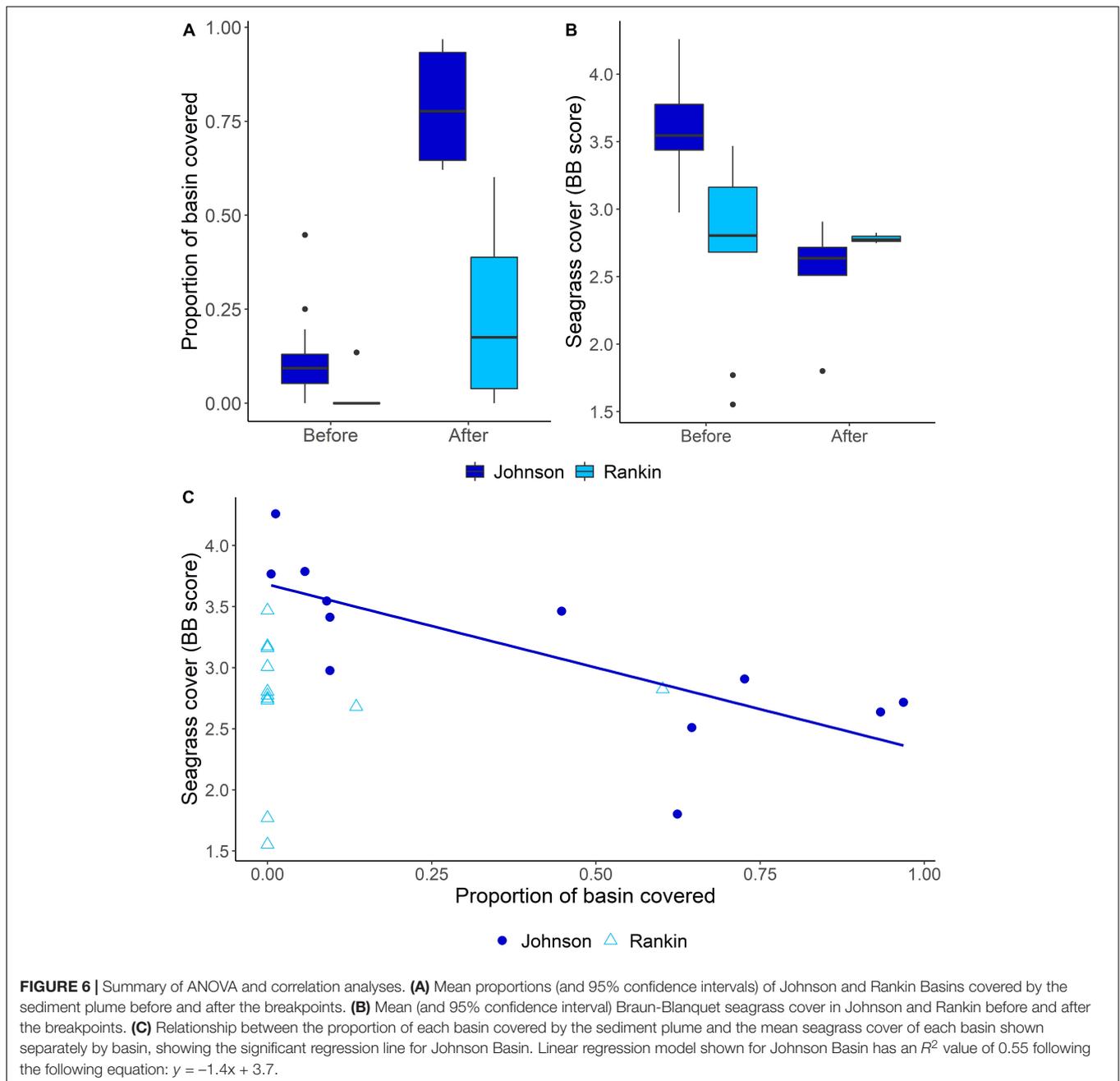
FIGURE 5 | Temporal trend in the proportion of (A) Johnson, and (B) Rankin basins covered by the sediment plume. The blue lines represent the trend before the breakpoint while the red lines represent the trend after the first breakpoint. Breakpoints are shown by vertical black lines with 95% confidence interval in gray shading.

higher fragmentation rates and higher mortality of small seagrass patches. In our study, the expansion of the sediment plume in response to the seagrass die-off and Hurricane Irma was also spatially explicit due to the unique hydrological dynamics of Florida Bay. Both disturbances contributed to the expansion of the sediment plume, but at different spatial scales. We expected high sediment mobilization after the seagrass die-off due to the loss of the mechanisms that promote sediment stabilization in densely covered SAV habitats (Fonseca and Fisher, 1986; Nyström et al., 2012). Even though the sediment was more easily mobilized after the seagrass die-off, the low water movement within the system, due to restricted water exchange and high residence time (Nuttall et al., 2000; Rudnick et al., 2005), may explain why the plume did not expand immediately after the die-off into certain areas of the Bay, such as in Rankin.

Hurricane Irma was a bay-scale disturbance that drastically moved water throughout the estuary, and the combination of the water movement and increased sediment mobility likely led to the expansion of the sediment plume to its largest extent (Liu et al., 2020). The different spatial extent and location at which the two disturbances acted created a spatially explicit gradient in their effects, as seen by the differences in the timing of breakpoints between basins. Early during the study period, Johnson was on

the eastern border of the sediment plume (Figure 2). There was a breakpoint in the proportion of Johnson covered with the sediment plume that corresponded with the seagrass die-off. This was not the case for Rankin, which is located east of Johnson, where the sediment concentration before the disturbances was zero. The sediment plume in Rankin was ephemeral, increasing in size after Hurricane Irma in 2017 but exiting Rankin in 2019.

The timing of disturbances also plays a role in determining effects on an ecosystem (Miller et al., 2011; Santillan et al., 2019). In Florida Bay, Johnson Basin became turbid due to the sediment plume right after the 2015 seagrass die-off while the sediment plume did not migrate to Rankin Basin until 2017. The difference in timing between when each basin experienced the sediment plume may have affected seagrass recovery. Both Johnson and Rankin lost most of their *T. testudinum* cover in the drought-induced seagrass die-off in 2015 (Hall et al., 2016; Hall and Durako, 2019). Since both systems were *T. testudinum*-dominated before the die-off, the loss of this species resulted in a severe reduction to the total seagrass cover as well. However, recovery trajectories differ between the two basins (Hall and Durako, 2019; McDonald et al., 2020). Total seagrass cover, dominated by *Halodule wrightii* (a pioneer species), recovered to near pre-die-off levels in Rankin within 2 years, whereas



Johnson continues to lose *T. testudinum* and was not being recolonized by *H. wrightii* until 2020 (McDonald et al., 2020). This difference in seagrass recovery may be due to the high proportion of the Johnson covered by the sediment plume that occurred immediately after the die-off.

Several factors acting at various spatial and temporal scales influence seagrass recovery after a disturbance. In Tampa Bay, water clarity was the main driver preventing seagrass recovery (Greening et al., 2011), while genetic material was the limiting factor in the recovery of seagrass in Shark Bay, Australia (Nowicki et al., 2017). The sequence of events (die-off > plume extent > lack of SAV recovery) in Johnson suggests that the

seagrass seascape in Johnson entered into a feedback cycle of degradation between seagrass cover and turbidity, preventing recovery (Figure 1). This cycle is common within degraded seagrass habitats and does not allow for seagrass to recover, which is evident in Johnson. A similar pattern occurred in seagrass beds near the Great Barrier Reef, where sediment plumes from dredging prevented the establishment of seagrass (York et al., 2015).

Persistent algal blooms and proximity to freshwater inflows may also play a factor in reducing light penetration and preventing seagrass recovery in Florida Bay. Central Florida Bay experiences seasonal algal blooms originating

from anthropogenically altered freshwater deliveries (Boyer et al., 2009; Briceño and Boyer, 2010) and large-scale algal blooms brought on by tropical storms and hurricanes (Glibert et al., 2009; Wahl, 2019). The seagrass die-off in the late 1980's exacerbated algal blooms in this region, leading to negative effects on seagrass recovery (Robblee et al., 1991; Fourqurean and Robblee, 1999). However, Hall et al. (2021) found no evidence of algal blooms depleting sources of seagrass recruits after the 1980's die-off. Furthermore, freshwater inflows may be affecting the recovery of seagrass within Florida Bay. *H. wrightii*, the pioneer seagrass species, is favored over *T. testudinum* in lower salinity conditions (Herbert et al., 2011). Rankin Basin is located closer to freshwater inflows than Johnson Basin. Therefore, higher freshwater inflows and lower salinities in Rankin Basin may have contributed to a more rapid recovery. Further research is needed to determine the variables affecting seagrass recovery within Florida Bay, especially considering the hydrodynamics drivers that interactively influenced seagrass physiology, productivity and patch formation.

While Johnson Basin experienced high turbidity from the sediment plume right after the die-off, suspended sediment associated with the sediment plume did not reach Rankin until 2 years later. This delay in disturbance may have allowed Rankin to begin recolonizing the benthos as illustrated by the recovery of seagrass cover (by mostly *H. wrightii*) to a BB score of 2.5 before the sediment plume entered Rankin. Recolonization followed traditional models of SAV succession, wherein macroalgae colonize the bare sediment and then *H. wrightii* replaces the macroalgae (Den Hartog, 1979; Zieman, 1982). Due to the known function of seagrass habitats for sediment stabilization and deposition in coastal environments (Bos et al., 2007), we hypothesize that the establishment of *H. wrightii* within Rankin helped stabilize the sediment. Therefore, when Hurricane Irma expanded the plume into Rankin, the system exhibited resistance to the increase in turbidity and prevented the shift into the degrading feedback loop shown in **Figure 1**. Furthermore, the wind may have played a role in reducing the impact of the sediment plume in Rankin. Southern Florida experiences strong easterly winds in fall and winter (Klink, 1999), which may have aided in removing the plume from Rankin after a couple of years.

Western Florida Bay, including Johnson, faces a more difficult road to recovery. The sediment plume expanded into this region

right after the 2015 die-off, preventing any SAV recovery and driving the system into a turbid alternative state that persisted through 2020 in our study. Recovery of seagrass after the die-off in the late 1980's might present a solution that includes light availability and time. Stumpf et al. (1999) mapped albedo throughout Florida Bay before and after the first seagrass die-off. They found that sediment expanded into the western region starting in 1988 and persisted through 1997 (the duration of their time series), but lost intensity beginning in 1996. Once this loss in intensity (reduction in turbidity) reaches a certain threshold, benthic macroalgae can start recolonizing an area. Benthic macroalgae only need approximately 8–10% of surface irradiance to grow (Choice et al., 2014). Therefore, time may be the only factor required for sediment settlement to occur, reducing turbidity and increasing benthic light intensity to the 8–10% threshold needed for macroalgae recolonization. Macroalgae recolonization then has the potential to create a beneficial feedback loop, leading to increased sediment stabilization. If there is a source of seagrass genetic material available (seed reserve or connectivity to clonal sources), the sediment stabilization may result in seagrass recovery in Johnson and the rest of western Florida Bay (Austin et al., 2017). Florida Bay returned to pre-die-off conditions by 2012 (Hall et al., 2016), illustrating that the system can undergo the lengthy (15 years) recovery process. But it is unknown whether there are enough sources of seagrass, and instead active restoration techniques may be required.

Climate change presents seagrass meadows with an additional set of disturbances, which have various impacts on seagrass distribution and productivity (Short and Neckles, 1999; Duarte et al., 2018). Increased temperature will lead to species distribution changes (Carlson et al., 2018; Duarte et al., 2018), ocean acidification will impact seagrass metabolism (Apostolaki et al., 2014; Zimmerman, 2020), and sea level rise will cause dynamic changes in seagrass areal extent (Albert et al., 2017). How these factors will interact with the current conditions within Florida Bay and the impact climate change will have on seagrass ecosystems is unknown (but see Browder et al., 2002; Carlson et al., 2018; Peñalver et al., 2020). Therefore, it is vital to focus on the resilience (the ability to persist after external disturbances; Holling, 1973; Côté and Darling, 2010) of seagrass within Florida Bay. A healthy ecosystem requires conditions that build resilience in order to withstand multiple disturbances at different spatial scales (Costanza and Mageau, 1999; Standish et al., 2014; Gladstone-Gallagher et al., 2019). Considering recent events, increased resilience of Florida Bay seagrasses is vital to maintain the various ecosystems services that they provide. However, increasing resilience within seagrass systems requires knowledge of parameters, such as genetic and species diversity, trophic interactions, water quality, and connectivity with other coastal systems that drive habitat stability and the ability to recover from compounded disturbance effects (Unsworth et al., 2015). Therefore, further monitoring of how extreme disturbances impact the structure and function of seagrass ecosystems is needed.

Seagrasses around the world are declining due to anthropogenic and natural disturbances disrupting natural feedbacks that promote seagrass growth and sustenance. Our

TABLE 4 | Analysis of variance (ANOVA) used to determine significant differences in (a) proportion of basin covered and (b) seagrass cover between basin and before and after the breakpoint.

	Variable	$F_{1,44}$	p
(a) Proportion of basin covered	Basin	73.2	<0.001*
	Break	150.8	<0.001*
	Basin*Break	32.8	<0.001*
(b) Seagrass cover	Basin	4.3	0.051
	Break	6.7	0.018*
	Basin*Break	7.2	0.014*

Shown are the variable tested (Variable), test statistic of the significance (F), the approximate p -values for the null hypotheses that there is no difference (p). Significant values are denoted with *.

study demonstrates the usage of long-term seagrass monitoring and remote sensing to investigate how two disturbances may interact to impact seagrass ecosystems at multiple scales. We found that a sediment plume may be a contributing factor in preventing seagrass recovery in Florida Bay after a large-scale seagrass die-off and a hurricane. Given that seagrass beds provide many ecosystem services such as carbon sequestration, habitat for fish and other fauna, and sediment stabilization (Bos et al., 2007; Fourqurean et al., 2012; Unsworth et al., 2019), more information is needed to increase seagrass resilience against impacts of future extreme events such as hurricanes and droughts.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

JRR, WJ, RS, JSR, BF, CRK, ZF, and CK conceptualized the project. JRR, VB, and JL delineated sediment plumes. BF and MH provided long-term seagrass data. ZF and CK provided turbidity grab sample data. JRR, WJ, and RS ran statistical analyses. JRR, WJ, NV, JOL, and LL prepared first draft. All authors contributed to the manuscript preparation and revision, and read and approved the submitted version.

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SUPPLEMENTARY MATERIAL

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Microplastics in Florida, United States: A Case Study of Quantification and Characterization With Intertidal Snails

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Concentrations of microplastics are increasing within the oceans, including waters surrounding Florida, United States. Miles of sandy beaches make the sunshine state a prime tourist destination leading to an increased amount of pollution along Florida coasts. Microplastics can cause damage to intertidal organisms, as well as causing issues up the food chain with biomagnification and seafood consumers, such as humans. Florida is also subject to hurricanes which often distribute sediments, filling the water column with previously settled microplastics. These factors make Florida a special case to review considering the state is affected heavily by hurricanes and tourism, which can contribute to microplastic concentrations in the Gulf of Mexico. The focus of this study was to quantify, characterize, and compare microplastics contamination in two predatory marine snail species from intertidal habitats in Florida, United States. Ingestion results were also compared to microplastics contamination of water samples collected from the same locations. Red-mouth rock shell (*Stramonita haemastoma*, $n = 30$) and Crown conch (*Melongena corona*, $n = 30$) snails were collected from intertidal habitats in Florida and digested for microplastics quantification. Water samples were filtered and microplastics were quantified. 256 microplastics, of which 93% were microfibers and 7% were microfragments were isolated from snails ($n = 60$). Additionally, 67 microplastics were isolated from 8 L of seawater (8.375 microplastics/L), of which 97% were microfibers and 3% were microfragments. This is the first known study to demonstrate microplastics contamination of tissues in predatory marine intertidal snails. Marine intertidal snails may be good organisms for biomonitoring of microplastics in intertidal sandy habitats.

Keywords: marine pollution, *Stramonita haemastoma*, *Melongena corona*, Gulf of Mexico, microfibers, microfragments

INTRODUCTION

Marine pollution, in particular plastic pollution, is widely recognized as a global issue (Shim and Thomposon, 2015). Plastic pollution is ubiquitous in the ocean and accounts for upwards of 60–80% of marine debris (Derraik, 2002). As a result of great durability, plastic persists in marine ecosystems from hundreds to thousands of years (Barnes et al., 2009). Of particular focus

for this study, microplastics are defined as small pieces of plastic debris that measure 5 mm or less in size (Von Moos et al., 2012). Microplastics originate from direct manufacturing of small plastics for beauty products or other manufactured goods such as (primary microplastics), or from the degradation and breakdown of larger plastic debris (secondary microplastics) (Hale et al., 2020). Globally, estimates of total microplastics in the ocean range from 5.25 to 125 trillion pieces (Cozar et al., 2014; Lindeque et al., 2020).

Though microplastics are found in water bodies all over the world (Rezania et al., 2018), microplastic debris is most prevalent within the ocean (Ivar do Sul et al., 2013). Microplastics in aquatic ecosystems originate from both land-based and sea-based sources and can make their way to marine ecosystems through runoff, industrial activity, human activities such as tourism and textile industries, and from sewage treatment plants (Rezania et al., 2018). Primary microplastics originate from spillage during the production or recycling or as micro-cleansing beads in personal care products such as facial scrubs and toothpastes are washed into aquatic ecosystems (Anderson et al., 2017). Secondary microplastics most commonly originate from marine litter, laundry discharge, discharge from landfills, and industrial or agricultural sources (Rezania et al., 2018; Hale et al., 2020).

Microplastics in aquatic environments are considered to be a serious issue and threat to aquatic ecosystems and the organisms that inhabit these ecosystems. Many studies have been conducted in the marine environment, from tropical to polar ecosystems, to characterize and quantify microplastics contamination in marine systems (Barnes et al., 2009; Wessel et al., 2016; Waller et al., 2017). Further, due to their small size, microplastics are bioavailable to many organisms across trophic levels. Microplastics have been documented negatively affecting the fecundity, growth, and feeding rates of zooplankton. Though the documented effects on zooplankton are categorized as sublethal, the microplastics can prompt transgenerational mortality effects (Yu et al., 2020; Yu and Chan, 2020). Several studies have demonstrated contamination of microplastics in marine organisms with various feeding strategies such as marine invertebrates, fishes, mammals, and birds (Brilliant and MacDonald, 2000; Besseling et al., 2012, 2015; Browne et al., 2013; Cole et al., 2013; Romeo et al., 2015; Carlin et al., 2020). Although it is not clear yet how microplastics might affect human health, evidence from aquatic organisms shows that microplastics cause negative effects on organism growth, metabolism, reproduction, and lead to weakened immune systems (Wright et al., 2013; Costa et al., 2015; Lu et al., 2016; Sussarellu et al., 2016). Humans rely heavily on aquatic biodiversity and ecosystems, both of which are greatly impacted by microplastics.

Microplastics in Florida

Peninsular Florida (United States), is surrounded by the Gulf of Mexico on the west side and the Atlantic Ocean on the east side. Waters surrounding Florida are polluted with a variety of debris, including microplastics, resulting from anthropogenic activity. Specifically, several studies have quantified microplastics from both seawater and sediment samples from Florida. For example, McEachern et al. (2019) quantified microplastic contamination

from surface seawater and sediment samples from Tampa Bay, Florida, with seawater samples ranging from 0.25 to 7.0 particles/L and sediment samples ranging from 30 to 790 particles/kg. In a study by Yu et al. (2018), occurrence and distribution of microplastics was determined from sand samples in Florida from Dry Tortugas National Park, Everglades National Park, Biscayne National Park, Canaveral National Seashore, Fort Matanzas National Monument, and Timucuan Ecological and Historical Reserve. Counts of microplastics from these locations ranged from 43 to 253 pieces/kg of sand (Yu et al., 2018). Further, citizen scientists have been employed throughout the Gulf Coast of the United States to quantify nurdles, or plastic pellets that are manufactured to melt down to make plastic products, along shorelines. Approximately 12% of the sampling sites of this citizen science project were along the Gulf Coast of Florida. Interestingly, very few nurdles were collected along the coast of Florida, while 20 of the highest standardized counts were collected in Texas, close to the location where the majority of nurdles are manufactured in the United States (Tunnell et al., 2020).

Microplastics have also been documented in a variety of organisms that live in or associated with waters surrounding Florida, such as osprey, fishes, jellyfish, oysters, mud crabs, sand dollars, and sea cucumbers (Phillips and Bonner, 2015; Waite et al., 2018; Carlin et al., 2020; Iliff et al., 2020; Plee and Pomory, 2020). For example, Carlin et al. (2020) quantified the abundance of microplastic accumulation in gastrointestinal tracts of birds of prey in central Florida and found that all birds examined contained microplastics. Further, Waite et al. (2018) digested oysters (*Crassostrea virginica*) and mud crabs (*Panopeus herbstii*) from an estuary along the east coast of central Florida and discovered 1,482 microplastics from 90 oysters and 1,979 microplastics from mud crabs, with microfibers being the most common type of microplastics. Microplastic contamination can have negative impacts, such as false satiation, reproductive complications (Auta et al., 2017), and toxicological impacts (Ogunola et al., 2018) on marine organisms.

Subject to tourism and hurricanes, the state of Florida, may also be particularly vulnerable to marine pollution. Both tourism and storms can increase microplastic pollution in marine ecosystems. Florida has been subject to some of the most catastrophic storms and hurricanes that have been recorded in the United States (Malmstadt et al., 2009). Hurricanes can increase the amount of microplastics transferred from land to water, thus expediting the process of the pollutants entering the ocean (Barnes et al., 2009). Further, storms that disturb sediments can also move and resuspend once settled microplastics throughout the water column (Von Moos et al., 2012). Hurricanes and other natural phenomena can also transfer more personal products, and potentially microplastics into the ocean (Duis and Coors, 2016). Florida has been named the “tourism capital of the world” in reference to the vast number of theme parks and tourist destinations (Carlin et al., 2020). In South Florida during the winter months, Wightman (2020) observed an increase of microplastics in the water column. This observation correlated with the increased tourism during the wintertime which left a higher amount of litter on the beaches,

and a higher amount of microplastics being washed down drains (Wightman, 2020). With increased tourism and the frequent occurrence of hurricanes, the waters surrounding Florida and the organisms that inhabit these waters become a special case to study microplastics.

Case Study With Snails in Florida

The species *Stramonita haemastoma* (Red-mouth rock shell) and *Melongena corona* (Crown conch) are both predatory gastropod molluscs that can be found in coastal intertidal areas and are the focus of species of this case study in microplastics contamination. Both species of snails are commonly seen clinging to rocks and marine vegetation, as well as on other organisms such as crustaceans. Red-mouth rock shells feed primarily on filter feeding organisms such as bivalves, gastropods and barnacles (Watanabe and Young, 2005). Crown conchs prey upon bivalves and gastropods, including the Marsh periwinkle (*Littorina irrotata*) (Randall, 2013). Crown conchs are also known to be opportunistic scavengers preying upon horseshoe crabs and other dead organisms (Hayes, 2003). In general, marine snails serve as a food source for other organisms in the ecosystem, such as whelks, murex (O'Connor, 2018) and stone crabs (Richardson and Brown, 1992; Whitenack and Herbert, 2015), which creates the potential for transfer of microplastics to other organisms, as well as impacts on overall ecosystem health (Walkinshaw et al., 2020). Additionally, neither species of snail migrates great distances, thus any microplastic contamination should be from the localized areas of collection.

The objective of this study was to quantify and compare the amount and type of microplastics present in two predatory species of snails collected from Florida, United States. Ingestion results were also compared to microplastics contamination of water samples collected from the same locations. Red-mouth rock shells from the panhandle of Florida and Crown conchs from Central Florida were examined for microplastics to determine the abundance, type, and size ranges of microplastics ingested by each species. Though Red-mouth rock shells and Crown conchs are both predatory snails and have similar prey items, they are different in size, thus microplastic contamination will be compared between the two.

MATERIALS AND METHODS

Seawater and Snail Collection

Both seawater and snails were collected from intertidal beach habitats in Florida, United States. Two major locations of Northwest Panhandle Florida and Central Florida were selected for this study. At each of the two major locations, two sampling sites were selected for seawater and snail collection. Prior to snail collection, at each site, two replicates of 1 L of seawater were collected in sterile and rinsed 1 L Nalgene bottles. Immediately before collection of seawater samples, Nalgene bottles were dipped in the seawater and rinsed three times before a final dip for collection. Nalgene bottles were immediately sealed in order to prevent contamination. *Stramonita haemastoma* samples ($n = 30$) were collected haphazardly by hand from

Shoreline Park (30.3540883 N, 87.1752466 W), 3-Mile Bridge (30.3741196 N, 87.1795937 W), in Pensacola Florida (Northwest Panhandle Florida). Additionally, *Melongena corona* samples ($n = 30$) were collected haphazardly by hand from Sand Key Park (27.960541 N, 82.824362 W), and Shell Point Park (27.916478 N, -82.840774 W), in Clearwater Florida (Central Florida) (Figure 1). Snails were placed into sealable plastic bags, and then placed into the cooler with ice. Upon returning from the field, snails were immediately placed in the freezer still contained in their plastic bags until tissue digestion.

Each of the sites in this study have varying levels of anthropogenic impacts, though not explicitly measured. For instance, Shoreline Park has many daily visitors that use the location for recreational activities such as boating, fishing, and swimming (Shoreline Park South, 2020). The 3-Mile Bridge site has been subject to ongoing construction and many people fish within the area for tourism and fishing. Both Sand Key Park and Shell Point Park are impacted by beach development along with recreational activities (boating, fishing, and swimming). Additionally, the Gulf of Mexico is subject to a long history of tropical storms and hurricanes dating back to the Holocene period (Conner et al., 1989). Over the last 30 years, the Atlantic Ocean averages 14 named storms, of which seven become hurricanes (NOAA, 2021).

Tissue Digestion and Sample Filtration

Before tissue digestion, individual snails were measured using Neiko 12" calipers to gather measurements on individual shell height, width, thickness, lip height, and lip width. Following shell measurements, soft tissue was removed from the shell using sterile and rinsed forceps. Snails were prepared for tissue digestion according to Claessens et al. (2013). All glassware was thoroughly rinsed with milliQ water prior to digestion to help eliminate microplastics contamination. Frozen individual snails were then transferred to a sterile separate 250 mL Erlenmeyer flask and 20 mL of nitric acid was added. Flasks containing individual snails were left overnight at room temperature in a semi-enclosed chemical hood. The nitric acid and snail tissue mixture was then diluted with 200 ml of warm (~80°C) filtered deionized water. After the addition of warm milliQ water, flasks containing *Stramonita haemastoma* were completely digested, while flasks containing *Melongena corona* were boiled for 5 min for complete tissue digestion. Following tissue digestion, the remaining liquid was filtered using a vacuum hand pump through a 0.45 μ gridded cellulose filter (Whatman). To avoid contamination the filtering apparatus, a magnetic 500 mL filter cup and magnetic filter base were flushed using milliQ water in between each sample and were covered during filtration to help prevent contamination. Each filter was then stored in a sterile Petrislide™ (MilleporeSigma™) for drying and quantification. To control for microplastics contamination from the air during digestion, a control flask only containing nitric acid (no tissue) was placed alongside flasks during tissue digestion. After digestion, the control flask was also diluted with milliQ water and filtered in the same way. Seawater samples were filtered following the same protocol as the tissue samples. A 1-L sample of milliQ water was also filtered to be used as a

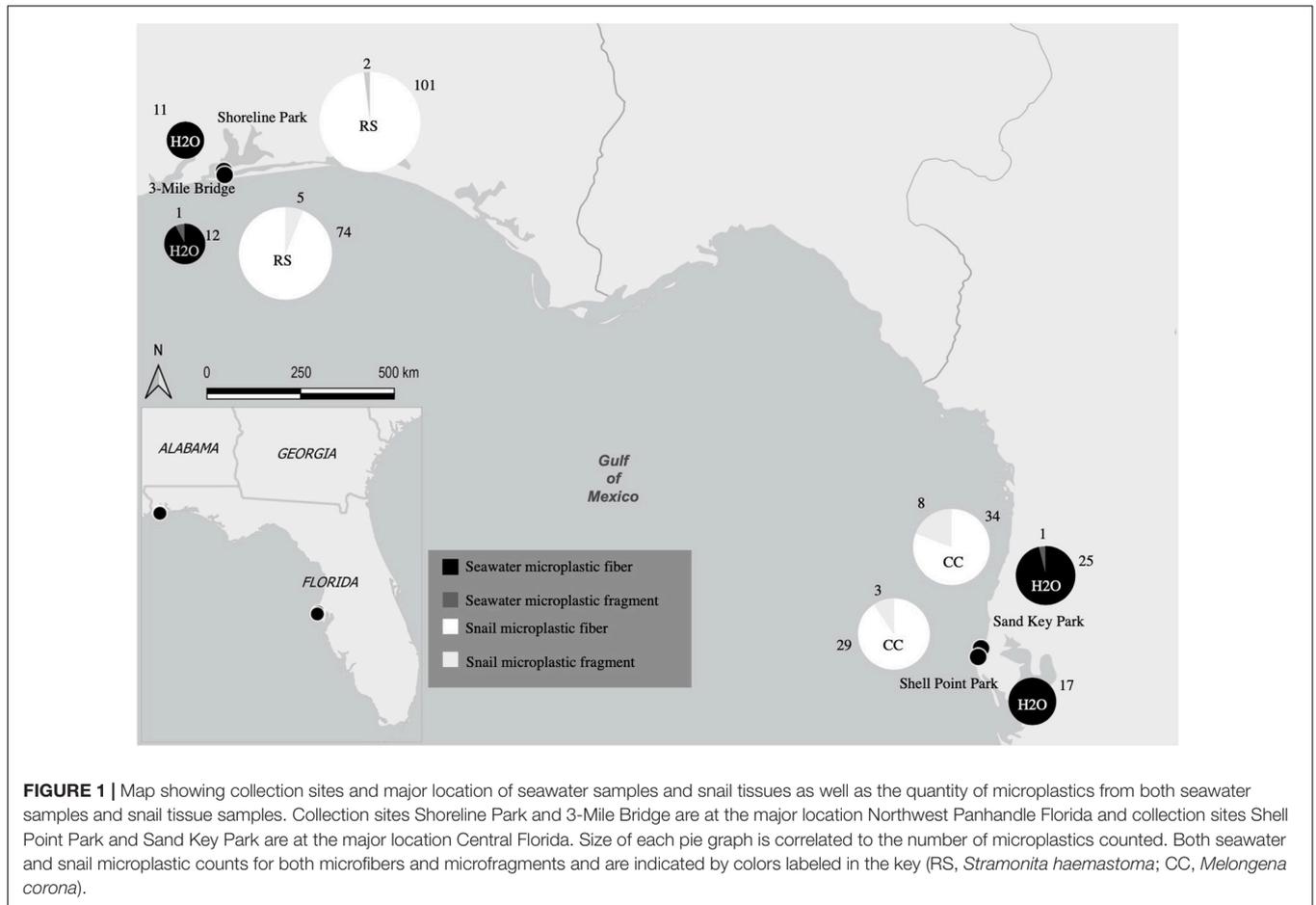


TABLE 1 | Microplastics identified for seawater samples for 2 L of water.

Site name	Date time	Latitude	Longitude	Fibers	Fragments	Total
3-Mile Bridge	6/15/2020	30.3741196	-87.1795937	11	0	11
Shoreline Park	6/15/2020	27.952523	-87.8295337	12	1	13
Sand Key Park	6/20/2020	27.960541	-82.824362	17	0	17
Shell Point Park	6/20/2020	27.916478	-82.840774	25	1	26
Total				65	2	67

Location and abundance of microfbers and microfragments for seawater samples are provided. Bold values indicate totals of fibers, fragments and total overall.

control for microplastics contamination during the seawater filtration process.

Quantification of Microplastics

Using a compound microscope (4X and 10X), microplastics on filters from tissue and seawater samples were directly quantified and characterized according to abundance and diversity. Visual identification was employed to differentiate plastics from other natural organic debris (algae, sediment, invertebrates, and plant material). To help ensure proper identification, each suspected microplastic was examined following methods of Whitaker et al. (2019). Specifically, suspected microplastics were examined for cellular and organic structures, for even thickness of fibers, and homogenous color, according to Hidalgo-Ruz et al. (2012).

To further distinguish between organic and plastic material, a metal probe was heated and placed next to the putative plastic. According to Hendrickson et al. (2018), employing a “melt test” will cause plastic fibers to melt, while cotton and wool fibers will burn. Thus, in this study, if an item melted, it was classified as microplastic. Microplastics were categorized by type (microbeads, microfragments, and microfibers), size, and color. Measurements of microplastics were made using ImageJ¹ v 1.52a bundled with Java 1.8.0_172 for Windows. Photographs of each filter were taken prior to the “melt test” with a Nikon DS-Fi2 microscope and the corresponding soft-ware, NIS-Elements, was used to burn the set scale of 100 μm for every photograph. Measuring required the scale to be set on each individual photo,

¹<https://imagej.nih.gov/ij/>

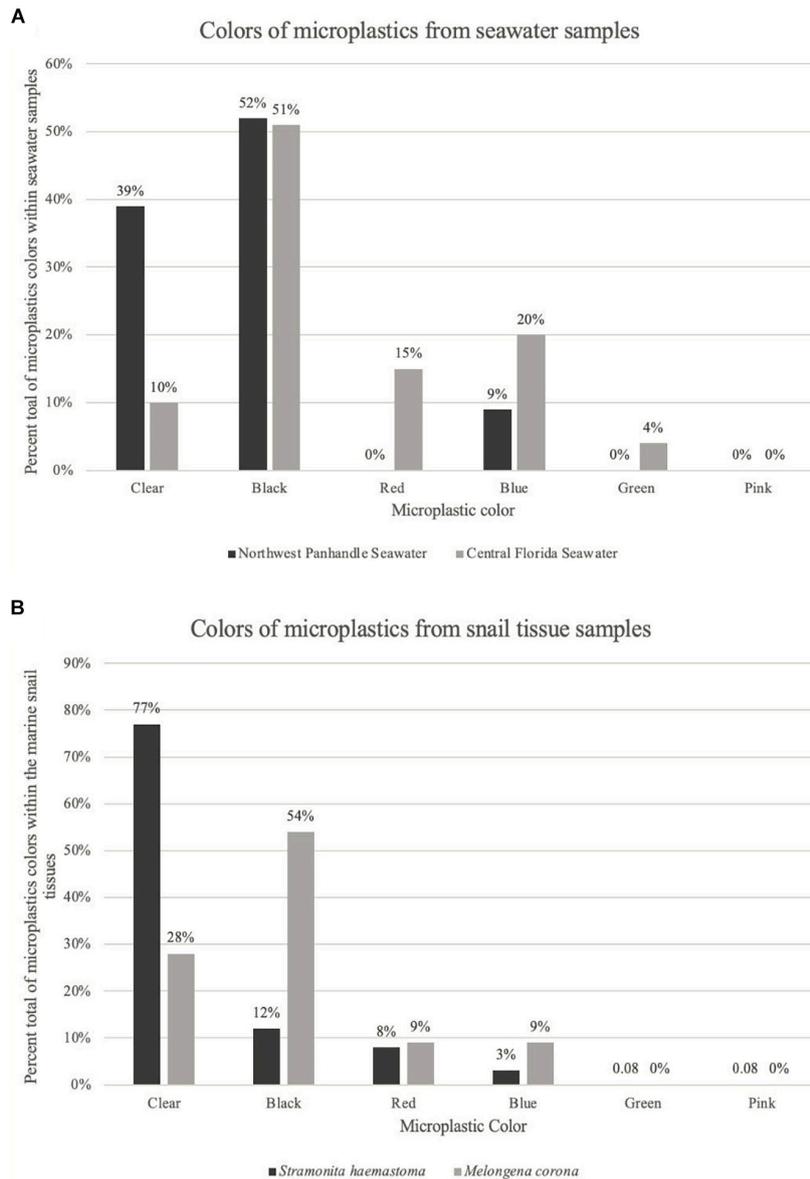


FIGURE 2 | Graph of color distribution of microplastics from seawater samples and snail tissue samples. **(A)** Shows the percent of each color of microplastics from seawater samples. Dark gray bars correspond to seawater microplastics from Northwest Panhandle Florida and light gray bars correspond to seawater microplastics from Central Florida. **(B)** Shows the percent of each color of microplastics from snail tissue samples. Dark gray bars correspond to snail tissue microplastics from Northwest Panhandle Florida and light gray bars correspond to snail tissue microplastics from Central Florida.

as each filter had multiple photos to capture all plastic debris. Using the straight-line tool in ImageJ, the scale line was traced and set before beginning measurements. All fibers and fragments were traced using the freehand tool to accommodate twisting and bending of fibers and irregular edges of fragments. Thus, length of fibers and surface area of microfragments were estimated.

Analyses

Statistical analyses were conducted in R (R Core Team, 2014) and boxplots were produced using the package ggplot2 (Wickham, 2009). A Welch two sample *t*-test was also used

to determine if there was a significant difference in shell height between the species of snails (*Stramonita haemastoma* and *Melongena corona*) to demonstrate if size differences were apparent of collected specimens between species. To determine if there was a difference in the number of microplastics from filtered seawater samples from the two major locations of this study (Northwest Panhandle Florida and Central Florida) a Wilcoxon rank-sum test with continuity correction was employed (Wilcoxon, 1945). Further, to determine if there was a difference in the number of microplastics from digested tissues between species of snails (*Stramonita haemastoma* and

TABLE 2 | Microplastics identified for snail tissue samples.

Site Name	Species Name	Number of Snails	Date Time	Latitude	Longitude	Snail Fibers	Snail Fragments	Snail Total	Mean \pm microplastics per snail
3-Mile Bridge	<i>Stramonita haemastoma</i>	15	6/15/2020	30.3741196	-87.1795937	101	2	103	6.86 (\pm 3.41)
Shoreline Park	<i>Stramonita haemastoma</i>	15	6/15/2020	30.3540883	-87.1752466	74	5	79	5.26 (\pm 4.44)
Sand Key Park	<i>Melongena corona</i>	15	6/19/2020	27.960541	-82.824362	29	3	32	2.13 (\pm 1.82)
Shell Point Park	<i>Melongena corona</i>	15	6/20/2020	27.916478	-82.840774	34	8	42	2.8 (\pm 1.79)
Total		60				238	18	256	

Location and abundance of microfibers and microfragments for snail and seawater samples are provided.

For mean microplastics per snail, standard deviation is represented in parentheses.

Bold values indicate totals of snail fibers, snail fragments and snail total overall.

Melongena corona) a Wilcoxon rank-sum test with continuity correction was also used.

One-way Analysis of Variance (ANOVA) with Tukey's multiple comparison adjustment was employed to determine if there was a significant difference in size and color of microfibers between seawater samples collected from two major locations in this study (Northwest Panhandle Florida and Central Florida). Additionally, an ANOVA with Tukey's multiple comparison adjustment was also employed to determine if there was a significant difference between species (*Stramonita haemastoma* and *Melongena corona*) by size and color of microfibers contamination in terms of fiber length. Microfragment sizes and colors were not compared between species due to low sample size of recovered microfragments.

To validate that seawater samples were statistically different from filtration milliQ water blanks (control), a Welch two sample *t*-test was employed. Further to validate that snail tissue samples were statistically different from digestion blanks (control), a Welch two sample *t*-test was used.

RESULTS

In total 8 L of seawater were collected. Specifically, 2 L of seawater were collected at each of the following sites: Northwest Florida: Shoreline Park, 3-Mile Bridge; Central Florida: Shell Point Park, and Sand Key Park. Seawater filtration for microplastics revealed a total of 67 microplastics from 8 L of seawater (8.375 microplastics/L), of which 97% were microfibers and 3% were microfragments. Specifically, seawater filtration of Northwest Panhandle Florida samples revealed 24 microplastics from 4 L of seawater (6 microplastics/L), of which 95% were microfibers and 5% were microfragments (Table 1 and Figure 1). Seawater filtration of Central Florida samples revealed 43 microplastics from 4 L of seawater (10.75 microplastics/L), of which 98% were microfibers and 2% were microfragments (Table 1 and Figure 1). No microbeads were identified from seawater samples. Microfibers from seawater samples were primarily red, black, translucent, and blue, varying in length ranging from 14 to

886 μ m. The majority of microfragments from seawater samples were black with one clear fragment and varied in surface area from 169 to 275 μ m. Color distribution of both microfibers and microfragments from seawater samples can be seen in Figure 2.

Tissue digestion for microplastics of 60 snails (Northwest Florida Panhandle: *Stramonita haemastoma*, $n = 30$; Central Florida: *Melongena corona*, $n = 30$) showed a total of 256 microplastics, of which 93% were microfibers and 7% were microfragments. Specifically, tissue digestion of *Stramonita haemastoma* ($n = 30$) from Northwest Panhandle Florida revealed 182 microplastics, of which 96% were microfibers and 4% were microfragments (3-mile Bridge mean 6.86 (\pm 3.41), Shoreline Park mean 5.26 (\pm 4.44); Table 2 and Figure 1). Tissue digestion of *Melongena corona* ($n = 30$) from Central Florida showed 74 microplastics, of which 85% were microfibers and 15% were microfragments (Sand Key Park mean 2.13 (\pm 1.82), Shell Point Park mean 2.8 (\pm 3.41.79); Table 2 and Figure 1). The majority of microfibers from snail tissue samples were clear, while others were blue, green, black, red, and pink, with length ranging from 21 to 1492 μ m. Microfragments from snail tissue samples were mostly commonly clear, while others were black, red, and blue and varied in surface area from 48 to 220 μ m. A graph of color distribution of both microfibers and microfragments from snail tissue samples can be seen in Figure 2. A composition of representative microfibers and microfragments for both seawater and snail tissue samples can be seen in Figure 3.

There was no significant difference in the number of microplastics from seawater samples collected from Northwest Panhandle Florida and Central Florida (Wilcoxon rank-sum test: $p = 0.3719$). There was, however, a statistical difference in the number of microplastics from digested tissues between species *Stramonita haemastoma* (Northwest Panhandle Florida) and *Melongena corona* (Central Florida) as seen in Figure 4 (Wilcoxon rank-sum test: $p = 1.927e-05$).

Further, there was a significant difference in the size of microplastic fibers comparing the two major locations, Northwest Panhandle Florida and Central Florida seawater samples (ANOVA: $p = 0.039$; $F = 4.706$; $df = 1$). There was also no significant difference between the size of microplastic

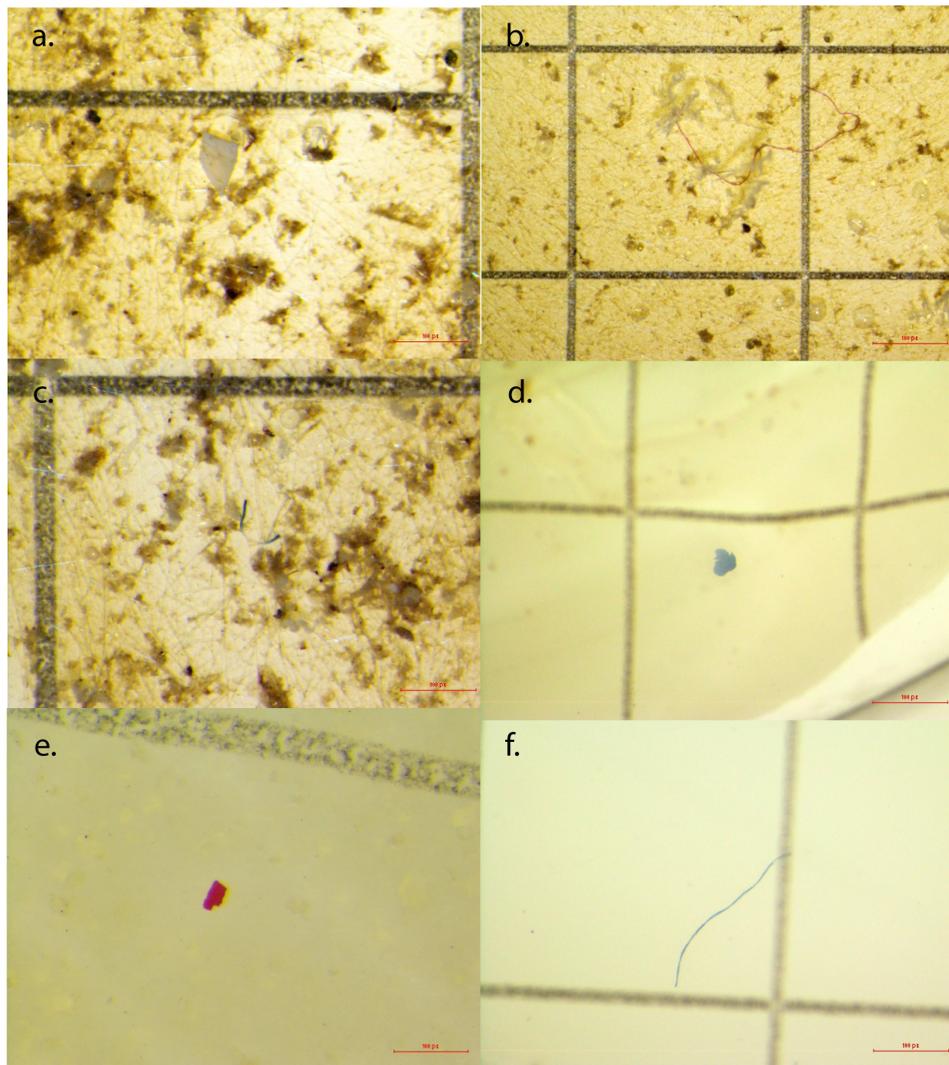


FIGURE 3 | Examples of microplastics from seawater samples and snail tissues. **(a)** Clear microfragment from Shell Point Park seawater sample; **(b)** red microfiber from Sand Key Park seawater sample; **(c)** blue and clear microfiber from Shell Point Park seawater sample; **(d)** blue microfragment from Crown conch snail tissue from Sand Key Park; **(e)** red microfragment from Crown conch snail tissue from Shell Point Park; **(f)** blue microfiber from Red-mouth rock shell tissue from 3-Mile Bridge.

fibers between the two snail species tissue samples, *Stramonita haemastoma* (Northwest Panhandle Florida) and *Melongena corona* (Central Florida) (ANOVA: $p = 0.53$; $F = 0.396$; $df = 1$). There was a significant difference in the color of microplastics in seawater samples from the two major sampling locations, Northwest Panhandle Florida and Central Florida (ANOVA: $p = 4.17e-4$; $F = 13.92$; $df = 1$). Black microfibers dominated the seawater from Northwest Panhandle Florida (52%) and Central Florida (51%), however, Northwest Florida had a greater number of clear microfibers, while Central Florida had a greater number of red and blue microfibers. There was also a significant difference in the color of microplastics from digested tissues between *Stramonita haemastoma* (Northwest Panhandle Florida) and to *Melongena corona* (Central Florida) (ANOVA: $p = 7.09e-6$; $F = 21.05$; $df = 1$). Clear microfibers dominated the tissues of

Stramonita haemastoma (Northwest Panhandle Florida), while black microfibers dominated the tissues of *Melongena corona* (Central Florida) (**Figure 2**). Given that there were so few microfragments from both seawater and tissue samples (**Table 3**), they were not included in statistical analyses.

Water filtration blanks had significantly fewer microplastics than seawater samples (Welch two sample t -test: $p = 2.238e-12$). Digestion blanks had significantly fewer microplastics than tissue samples (Welch two sample t -test: $p = 3.502e-09$).

DISCUSSION

The results from this study indicate that both seawater and snail tissue samples from Northwest Panhandle Florida and Central

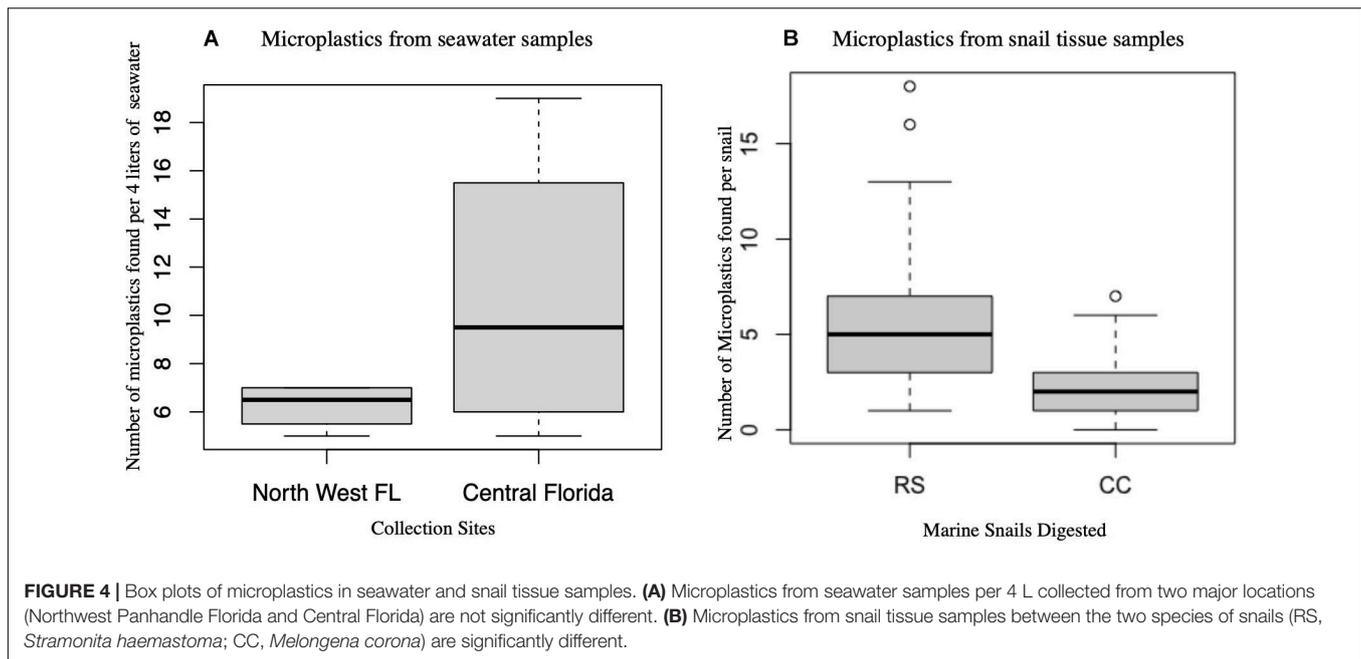


TABLE 3 | Body measurements of *Stramonita haemastoma* from Northwest Panhandle Florida sites (Shoreline Park, 3-Mile Bridge) and *Melongena corona* from Central Florida sites (Sand Key Park and Shell Point Park).

Site	Species	Height Avr. (mm)	Width Avr. (mm)	Shell Thickness Avr. (mm)	Lip Height Avr. (mm)	Lip Width Avr. (mm)
Shoreline Park	<i>Stramonita haemastoma</i>	27.71	14.89	0.301	16.42	5.276
3-Mile Bridge	<i>Stramonita haemastoma</i>	26.45	15.21	0.804	16.57	7.142
Sand Key Park	<i>Melongena corona</i>	45.77	27.49	0.589	31.02	11.27
Shell Point Park	<i>Melongena corona</i>	51.62	30.54	1.165	35.53	13.37

Florida were contaminated with microplastics. The number of microplastics in seawater samples from Northwest Panhandle Florida and Central Florida was not significantly different, though in general there were more microplastics in the seawater samples from Central Florida. There were, however, significantly more microplastics in Red-mouth rock shells (*Stramonita haemastoma*) that were collected from Northwest Panhandle Florida, when compared to Crown conchs (*Melongena corona*) that were collected from Central Florida. Possible reasons for this difference in microplastics quantity will be discussed below.

Microfibers were the dominant type of microplastic from both seawater samples (97% microfibers) and snail tissue samples (93% microfibers) from Northwest Panhandle Florida and Central Florida, respectively. These results are similar to findings in several other studies both in waters surrounding Florida and other locations around the globe (e.g., Waite et al., 2018; Akindele et al., 2019; Whitaker et al., 2019). Sizes of microfibers from both seawater and snail tissue samples were similar, indicating that fibers are likely being consumed from the environment,

transferred indirectly through trophic transfer from prey items of both Red-mouth rock shells and Crown conchs. Microfibers in marine samples originate from a variety of sources including wastewater, clothing, ropes and nets, cigarettes, and fishing activity (Wright et al., 2013; Wang et al., 2018; Hale et al., 2020). Microfragments in marine samples originate from the breakdown of larger pieces of plastic debris. Only a few microfragments (<3%) were isolated from snail and water samples, which is similar to findings of other studies (e.g., Waite et al., 2018; Akindele et al., 2019; Whitaker et al., 2019). Though it is not known how microplastics impact Red-mouth rock shells or Crown conchs, microplastic impacts have been demonstrated in several other organisms. For example, microplastic ingestion has been shown to clog and block feeding structures and the digestive tract, thus limiting food intake (Cole et al., 2013). Further, microplastics have been shown to cause a change in behavioral vigilance and predator avoidance in the Common periwinkle (Seuront, 2018). Ingested microplastics may also be transferred to the circulatory system (Browne et al., 2008),

causing a reduction of feeding activity (Besseling et al., 2012), and an increased immune response (Avio et al., 2015). Ultimately, microplastics may act as vectors for transferring novel bacterial assemblages (Barnes, 2002; Gregory, 2009) and may contain adsorbed chemical pollutants (Carpenter and Smith, 1972; Hale et al., 2020).

In general, feeding strategy and environmental prevalence have been shown to be the main drivers of microplastic consumption (Walkinshaw et al., 2020). As predatory snails, Red-mouth rock shells and Crown conchs are both likely consuming microplastics indirectly through trophic transfer from prey items from their marine environment, though unlikely, microplastic consumption may be occurring directly from the environment. Red-mouth rock shells are smaller bodied compared to Crown conchs. Specifically, Red-mouth rock shells typically reach 40 mm in length, while Crown conchs reach approximately 120 mm in length (Limaverde et al., 2007; Masterson, 2008). The snails used in this study are not full length, however, they were significantly different in shell length, with Crown conchs being the larger of the two species. Despite the overall size difference between snail species, the generally smaller bodied Red-mouth rock shells contained significantly more microplastics compared to the generally larger bodied Crown conchs. This difference in microplastic contamination could result from one or more of the following reasons.

Differences in contamination could result from differences in prey items and subsequent microplastic contamination of prey items of each snail. As such, Red-mouth rock shells and Crown conchs, have similar ecological roles, and feed mostly on bivalves, gastropods, and barnacles that are likely directly filtering/consuming microplastics as they feed in the benthos (Bowling, 1994; Watanabe and Young, 2005). In fact, filter feeders have been shown to more effectively consume microplastics from surrounding waters than non-filter feeding organisms (Van Cauwenberghe and Janssen, 2014; Setälä et al., 2016; Gonçalves et al., 2019). Thus, perhaps a difference in microplastic contamination of snails resulted from a difference in contamination of prey items. Further, trophic transfer from snails to other predators could potentially be occurring as the Red-mouth rock shells and Crown conchs consume contaminated prey items, and then are consumed by other predators such as crabs (Brown, 1997) and birds (Krueger, 2021). There is also some evidence to suggest that microplastic contamination of body tissues could also arise from filtration of water through the gills (Watts et al., 2014). Further, there is evidence to demonstrate that filter feeding bivalves such as *Crassostrea virginica* and *Mytilus edulis* selectively ingested microplastics preferentially, based on the physical characteristics of the plastic (Ward et al., 2019). A key factor in bioavailability of microplastics is their small size, making them more likely to be available to lower trophic levels (Wright et al., 2013). Thus, it is possible that the Red-mouth rock shells examined in this study consumed prey items that were more contaminated with microplastics, due to preferential selection or retention of microplastics, compared to the prey items of the Crown conchs. Another possible reason that Red-mouth

rock shells contained more microplastic contamination is that the snails themselves had microplastic retention or transfer of microplastics into tissues other than the digestive system (Walkinshaw et al., 2020).

Further, a lower concentration of microplastics in the Crown conchs may indicate that microplastics could be egested through the digestive system, instead of being retained or translocated to tissues. Fewer microplastics in predatory Crown conchs could also indicate that microplastics are commonly passed through the guts and released in the feces of prey items, rather than building up in the consumed organisms as was also seen in *Littorina littorea* (Gutow et al., 2016). Consequently, microplastic contamination likely poses a greater threat to certain species depending upon prey items consumed, retention or lack thereof of microplastics, and place in the food chain (Walkinshaw et al., 2020).

Although there was no significant difference in the number of microplastics in the seawater samples from the two major locations sampled in this study, there was a significant difference in terms of size of microplastics from the two major locations. As such, Northwest Florida Panhandle water samples showed significantly larger microplastics, though snail samples did not show a significant difference in size of microplastics consumed. This may indicate that prey items of both species of predatory snails are possibly selecting and consuming similar sizes of microplastics from the environment. Filter feeding organisms have been shown to show selection based on physical characteristics of microplastics (Ward et al., 2019). It is important to mention that microplastic contamination of seawater can fluctuate with storms and effluence and was only sampled at one place and time in this study. Fluctuations of microplastics in the water could also potentially account for the difference in contamination of snail tissues seen in this study.

There was a significant difference in terms of color of ingested microplastics between the two major locations of this study. Both Northwest Panhandle Florida and Central Florida seawater samples had similar numbers of black microfibers, however, Central Florida seawater samples had a greater number of red and blue microfibers, while Northwest Panhandle Florida had a greater number of clear microfibers. Interestingly, in the snail tissue samples, Red-mouth rock shells from Northwest Panhandle Florida, were contaminated with a greater number of clear microfibers (77%), while Crown conchs from Central Florida, were contaminated mostly with black microfibers (54%). Clear microfibers are commonly recovered as the dominant color of microplastics from tissues of organisms such as birds (Zhu et al., 2019; Carlin et al., 2020), fishes (Romeo et al., 2015; Peters et al., 2017) and invertebrates (Waite et al., 2018).

Microplastics have been documented to cause many deleterious effects in a variety of different organisms (see citations above). If microplastics cause deleterious effects (e.g., reduced feeding and reproduction) to the intertidal snails of this study, snail populations could decline. Likewise, a decline in snail populations could cause a trophic cascade impacting food

availability for other species and ecosystem health (Walkinshaw et al., 2020). In this study, both Red-mouth rock shells and Crown conchs were contaminated with microplastics, which is likely originating from indirect trophic transfer from prey items. It is still questionable if microplastics can be transferred to even higher trophic levels following predation. However, Red-mouth rock shells and Crown conch are commonly found in intertidal habitats and serve as prey items for several other organisms in these ecosystems, creating the potential for the trophic transfer of microplastics potentially having an effect on both ecosystem and human health (Carbery et al., 2018; Walkinshaw et al., 2020).

Overall, this is the first study on predatory marine intertidal snails to demonstrate microplastics contamination, indicating these snail species are likely consuming microplastics indirectly through trophic transfer from prey items from their environment. As such, Red-mouth rock shells may have greater contamination of microplastics as a result of increased microplastic contamination of prey items or from retention of microplastics. The results from this study raise substantial ecotoxicological concern for small invertebrate species which are often not the focus of ecological or conservation studies. Understanding the types and abundance of microplastics is necessary for future studies to understand how microplastics move through the food web and how microplastics directly and indirectly impact organisms. Further work is needed to determine the impacts of microplastics on these two benthic species and the overall impact on ecosystem health, particularly for Florida ecosystems.

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DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

JK and AJ identified the research question and study approach, carried out specimen collection, designed laboratory methods, and were responsible for manuscript data and writing. JK performed the laboratory methods and data analysis. AJ oversaw data analysis and interpretation. Both authors contributed to the article and approved the submitted version.

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