Relationships between blooms of *Karenia brevis* and hypoxia across the West Florida Shelf

Brendan D. Turley[a,b], b.turley@miami.edu, *corresponding author*
Mandy Karnauskas[b], mandy.karnauskas@noaa.gov
Matthew D. Campbell[c], matthew.d.campbell@noaa.gov
David S. Hanisko[c], david.s.hanisko@noaa.gov
Christopher R. Kelble[d], chris.kelble@noaa.gov

[a]Cooperative Institute for Marine and Atmospheric Studies
Rosenstiel School for Marine and Atmospheric Science
University of Miami
4600 Rickenbacker Causeway
Miami, FL, USA 33149

[b]NOAA Southeast Fisheries Science Center
75 Virginia Beach Drive
Miami, FL, USA 33149

[c]NOAA Southeast Fisheries Science Center
Mississippi Laboratories
P.O. Drawer 1207
Pascagoula, MS, USA 39567

[d]NOAA Atlantic Oceanographic and Meteorological Laboratory
4301 Rickenbacker Causeway
Miami, FL, USA 33149

ABSTRACT

Harmful algal blooms (HABs) caused by the dinoflagellate *Karenia brevis* on the West Florida Shelf have become a nearly annual occurrence causing widespread ecological and economic harm. Effects range from minor respiratory irritation and localized fish kills to large-scale and long-term events causing massive mortalities to marine organisms. Reports of hypoxia on the shelf have been infrequent; however, there have been some indications that some HABs have been associated with localized hypoxia. We examined oceanographic data from 2004 to 2019 across the West Florida Shelf to determine the frequency of hypoxia and to assess its association with known HABs. Hypoxia was present in 5 of the 16 years examined and was always found shoreward of the 50-meter bathymetry line. There were 2 clusters of recurrent hypoxia: midshelf off the Big Bend coast and near the southwest Florida coast. We identified 3 hypoxic events that were characterized by multiple conductivity, temperature, and depth (CTD) casts and occurred concurrently with extreme HABs in 2005, 2014, and 2018. These HAB-hypoxia events occurred when *K. brevis* blooms initiated in early summer months and persisted into the fall likely driven by increased biological oxygen demand from decaying algal biomass and reduced water column ventilation due to stratification. There were also four years, 2011, 2013, 2015, and 2017, with low dissolved oxygen located near the shelf break that were likely associated with upwelling of deeper Gulf of Mexico water onto the shelf. We had difficulty in assessing the spatiotemporal extent of these events due to limited data availability and potentially unobserved hypoxia due to the inconsistent difference between the bottom of the CTD cast and the seafloor. While we cannot unequivocally explain the association between extreme HABs and hypoxia on the West Florida Shelf, there is sufficient evidence to suggest a causal linkage between them.

Keywords: ecosystem-based fisheries management; normoxic; remote sensing; river discharge; stratification; upwelling

HIGHLIGHTS

- Three years (2005, 2014, 2018) had both hypoxia and notable K. brevis blooms
- Blooms with hypoxia initiated early in summer and persisted into fall
- Similar bloom activity occurred in 2006, but no hypoxia was detected

- Hypoxia co-occurred with stratification, high surface temperature and reduced surface salinity
- Several low oxygen events were likely associated with upwelling onto the shelf

INTRODUCTION

Harmful algal blooms (HABs) can have wide-ranging ecological effects and are a major concern for coastal communities. The main hazards of these events include respiratory irritation in mammals, including humans (Backer 2009), bioaccumulation through the food chain causing delayed mortality in higher trophic levels (Landsberg et al. 2009), shutdown of shellfish aquaculture harvest to avoid human consumption of the toxin (Backer 2009), and development of ecosystem-disrupting hypoxia (Pitcher & Probyn 2011). Harmful algal blooms can cause significant fish kills that have downstream negative impacts on coastal communities including fisheries resources as key components of their cultures and economies (Backer 2009). As algal biomass accumulates in the surface water during a HAB, the sinking and decomposition of dead cells near the bottom increases respiratory demand and depletes dissolved oxygen, a condition generally referred to as hypoxia. Hypoxia is typically defined as dissolved oxygen concentrations of 2 mg l^{-1} or less (Vaquer and Duarte, 2008). The term hypoxia has been used to define low oxygen conditions that elicit observed stress to demersal and benthic fauna (Hofmann et al. 2011). The 2 mg l^{-1} value used in this paper for delineating hypoxia is a reasonable threshold in which most organisms display a negative response, but each species' threshold lies on a spectrum between 0 and 4 mg l^{-1} (Vaquer and Duarte, 2008). Without mixing between surface and bottom layers, a hypoxic layer will form and persist near the seafloor (Watson et al. 2016). Of particular concern from an ecosystem-based fisheries management perspective are the negative effects of combined HAB-hypoxia events on demersal and benthic organisms (Diaz & Rosenberg 2008, Vaquer and Duarte 2008, Gravinese et al. 2020). While the HAB-hypoxia sequence has been observed in other regions (e.g., Peruvian coast, Rojas de Mendiola 1979; Saint Helena Bay, South Africa, Pitcher & Probyn, 2011; Washington and Oregon continental shelf, Siedlecki et al. 2015; Lake Erie, USA, Watson et al. 2016), it is unclear to what extent this occurs during HABs that impact the West Florida Shelf. HABs are disruptive events that have long lasting effects on marine ecosystems and human communities.

Hypoxia can have negative ecosystem effects depending upon the spatiotemporal scale and the species that are affected by the event (Diaz and Rosenberg, 1995; Diaz and Rosenberg, 2008; Vaquer and Duarte, 2008; Hofmann et al. 2011). On an individual level, organisms experiencing hypoxia undergo an acute stress response leading to reduced activity, decreased growth, and possible death (Wu 2002). In addition to a physiological response, a range of behavioral responses can also occur including avoidance of hypoxia and increased movement to find higher dissolved oxygen concentrations (Wannamaker and Rice 2000), decreased predator avoidance (Domenici et al. 2007), reduced feeding (Wu 2002), and changes in dietary composition (Glaspie et al. 2019). Thus, diverse individual responses to hypoxia combine into a complex ecosystem response. Recovery from hypoxic events is dependent upon the ecosystem's capacity to respond to the disturbance and the magnitude of loss of benthic habitats and sessile organisms (Wu 2002, Steckbauer et al. 2011). The causes of hypoxic zone formation depend upon local conditions and are typically due to a combination of several factors. Eutrophication from terrestrial sources such as river discharge or coastal runoff can stimulate algal blooms which increases respiratory demand during decomposition of excess algal biomass (Turner and Rabalais 1994, Hagy et al. 2003). Warm surface temperatures and anomalous freshwater discharge can increase stratification of the water column and reduced wind speeds can decrease water column ventilation and increase the likelihood of forming hypoxia (Wiseman et al. 1997). Hypoxic events can be devastating by themselves but may be more ecologically disruptive if they occur in conjunction with HABs (Driggers et al. 2016, Pitcher and Probyn 2011).

The motivation for this study was to examine the connection between stratification, hypoxia, and HABs on the continental shelf off the gulf coast of Florida, referred to as the West Florida Shelf. Reports of HABs affecting the coastal waters of the Gulf of Mexico from Florida to Texas date back to the arrival of Europeans with the first well documented bloom in 1844 (Magaña et al. 2003). The toxin-producing dinoflagellate *Karenia brevis* is the main causative species for HABs occurring annually on the West Florida Shelf (Walsh et al. 2006). Monitoring of *K. brevis* cell counts in Florida dates to the 1950s and provides information on several notable events in the past 20 years. The West Florida Shelf is a relatively wide and shallow continental shelf with ample wind energy to mix the water column for much of the year (Yang and Weisberg, 1999). However, during the summer and early fall, warm sea surface temperatures and increased runoff during the Florida wet season leads to increased stratification, and in conjunction with HABs may contribute to an increased likelihood of hypoxia on the West Florida Shelf. For example, in 2014, a National Marine Fisheries Service (NMFS) longline survey observed a fish kill near sampling stations in which bottom oxygen levels were hypoxic and close to the edge of a shoreward-extending HAB (Driggers et al. 2016). For this study, we wanted to assess the prevalence of hypoxia across the West Florida Shelf and determine if these events were associated with annually occurring HABs in the region. We asked several questions to assess potential regional drivers of HAB-hypoxia events. First, how common was hypoxia in the region? Did hypoxia only occur when there were HABs and stratification? And as a corollary, were there periods where strong stratification occurred but there was neither HAB nor hypoxia? Additionally, what other processes, like increased primary production not associated with HABs or increased stratification due to runoff or river discharge, were associated with presence of hypoxia? To answer these questions, we examined conductivity, temperature, and depth (CTD) and dissolved oxygen concentration data from oceanographic surveys (2004 to 2019) in conjunction with HAB monitoring data (2004 to 2019) and other environmental data.

METHODS

CTD DATA

Oceanographic survey data collected on the West Florida Shelf from 2004 through 2019 were aggregated from multiple sources into a singular dataset for analyses. The data were obtained from the Southeast Area Monitoring and Assessment Program (SEAMAP), NOAA-NMFS surveys, NOAA AOML South Florida Ecosystem Restoration Research surveys, NOAA National Centers for Environmental Information (NCEI), World Ocean Database (WOD), and the Rolling Deck to Repository (R2R) databases. Survey data consisted of cruises with multiple stations where environmental and water column data were collected from the surface to near seabed (further information about data sources and surveys can be found in Supplementary materials 1). The water column data were acquired by either Seabird SBE-911 or SBE-25 profilers (CTD) outfitted to record conductivity (converted to practical salinity units), temperature (degrees Celsius), depth (meters), and dissolved oxygen (data collected by SBE43 oxygen sensors, converted to mg l^{-1}). The data were filtered to retain only CTD casts that had a maximum depth of 100 m or less and which were located within a bounding box that covered the West Florida Shelf (25°N 86°W, 30.5°N 80.6°W). Duplicated CTD data were a concern because of the aggregated nature of the databases used for this study. For example, some of the NMFS survey data are regularly added to the SEAMAP, NCEI, and WOD databases. Additionally, the NCEI, WOD, and R2R databases are a collection of data from various sources, which can also include SEAMAP data and NMFS survey data. Duplicated data were filtered and eliminated by CTD casts that had the same cruise and station number (if available) or by filtering for casts that were on the same date and time and were within 1 kilometer of each other to account for some differences in reporting location data by database managers.

The aggregated CTD data were quality controlled to produce a consistent dataset for downstream analyses. The quality control methods followed some of the guidelines outlined by the WOD (Garcia et al. 2018). Briefly, depth specific maximum and minimum values recommended by the WOD for temperature, salinity, and dissolved oxygen in the coastal North Atlantic were used to flag data that were outside the range boundaries (see Garcia et al. 2018; Fig. 1 for geographic scope and Appendix 11 for min-max values therein). These min-max values are broad ranges used to flag values that were conspicuously different than expected values for the region. The values for coastal North Atlantic within the WOD are the most reasonable reference for QA/QC because the WOD is the most comprehensive database of oceanographic data available to the authors. Gradient checks were used to flag data in consecutive depth bins that exceeded values determined by the WOD quality control group. Additionally, individual data points were removed if it was greater or less than five standard deviations of the overall mean value, except salinity and oxygen were allowed to have a lower tail that extended to zero. Particular attention was focused on dissolved oxygen (DO) data: data were discarded if calibration dates were greater than one year from reported data, and CTD casts with low DO (DO $\leq$ 3.5 mg l^{-1}) were examined by eye. If DO percent saturation at the surface was below 90, the DO data for that cast, and in some cases the whole cruise, were discarded. Data that were flagged by these methods or that already had QA/QC flags produced by the original source were removed to ensure analyses were based upon high quality data.

It was necessary to determine the altitude off seafloor of each CTD cast to assess the presence of bottom hypoxia. However, the maximum depth of each profile was not necessarily near the seabed because shipboard echosounders were not always calibrated per station to adjust for speed of sound variation, the CTD operating procedures have changed over the past 20 years, and CTD operators have varying levels of comfort during different sea conditions affecting operational proximity of the CTD to the seafloor. Thus, each cast was not necessarily within acceptable limits to determine if hypoxic conditions were present near the seafloor. As a result, the NOAA Coastal Relief Model (CRM, NOAA National Geophysical Data Center, 2001) was used to assess the proximity of the CTD cast to the seafloor and the appropriateness of the data collected. If either the max depth bin of the CTD cast or the reported station depth were within 15 m of the CRM bathymetry the CTD cast was assumed to be close enough to the seafloor to have detected hypoxia otherwise the bottom DO was removed. The 15 m depth cutoff was a tradeoff between the accuracy of the CRM (0.5 - 4.7m), CTD depth binning where the bottom data can include data shallower and deeper than the reported depth, and our inclination for data retention.

In addition to the data acquired in-situ, mixed-layer depth and stratification were derived from profile data. The mixed-layer depth (MLD) was calculated as the depth at which the density was 0.125 kg m^{-3} greater than the near surface density (Brainerd and Gregg, 1995). The mixed-layer temperatures and salinities were determined by estimating the mean of the values from depths down to the MLD. Stratification was defined as the greatest slope of a 5-meter moving linear regression of depth versus density which is intended to remove spikes in density that do not represent the true pycnocline. Bottom DO concentrations were plotted by year per month to visualize the spatial distribution. The bottom DO was defined as the deepest DO data point from each CTD cast. We defined hypoxia as DO concentrations that were at or below 2 mg l^{-1}, near hypoxia was defined as DO greater than 2 and less than or equal to 3.5 mg l^{-1}, and low DO was defined as DO less than 3.5 mg l^{-1}, encompassing both hypoxia and near hypoxia, to serve as a summary for reporting results and discussion. We included a broader range of DO concentrations than the traditional definition of hypoxia to capture low DO events that may be associated with hypoxia or may otherwise be potentially impactful to ecosystems in the region (Vaquer and Duarte, 2008; Hofmann et al. 2011).

HARMFUL ALGAL BLOOM DATA

Karenia brevis cell count data (2004 to 2019) were obtained from the Florida Fish and Wildlife Research Institute (FWRI) HAB monitoring database, which maintains a repository that is available upon request. This data was collected by a collaboration of research institutions and citizen scientists for quantification of *K. brevis* cell concentrations. Historical HAB sampling in

Florida has been collected opportunistically, limiting the use of the data for robust statistical analyses (Christman and Young 2006), but more recently there have been efforts to conduct routine monitoring. The monitoring data can be used to identify extreme events, examine the geographic extent, and determine approximate temporal limits of an event. To overcome some of the data limitations, we aggregated the *K. brevis* cell concentrations data by year and month into 0.5° latitudinal bins from 24.5° N (near Key West, FL) to 29.5° N (near Steinhatchee, FL) and we calculated the 99-percentile cutoff per year-month-latitude bin. The latitudinal bins cover the full range of latitude on the west coast of Florida, and we therefore consider it to be spatially representative of the region. Water samples used to quantify *K. brevis* cell concentrations have been collected across the continental shelf, but we only included samples out to 84°W to capture some of the bloom dynamics mid shelf. This aggregation removes some of the known observational bias due to the irregular spatiotemporal sampling and can describe the general characteristics in which HABs occur. This, however, assumes that major events don't go completely undetected, which is not likely for nearshore events but could occur in the case of offshore blooms. The use of the term HABs in this paper refers to blooms of *K. brevis* in sufficient cell densities (>100,000 cells l^{-1}) to cause respiratory distress in mammals and associated with mass mortalities of marine life. This threshold is more conservative than FWRI's definition (i.e., respiratory irritation possible at 1,000 cells l^{-1} and fish kills possible at 10,000 cells l^{-1}).

REMOTE SENSING DATA

In addition to *in-situ* oceanographic data, satellite-derived chlorophyll was used to examine synoptic-scale variability as a proxy for primary production relevant to HABs and hypoxia along the West Florida Shelf. We examined monthly surface chlorophyll-a anomalies using the Aqua MODIS level-3 data at a 4km spatial resolution from January 2004 to December 2019, which amounts to 192 months or 16 years. While there may be a bias in satellite-based estimates of chlorophyll-a especially in deeper waters (Smith 1980), the data are useful to examine synoptic-scale variability especially in shallow, coastal waters where this study was focused. Chlorophyll-a (dataset ID: erdMH1chlamday) data was downloaded from the NOAA NMFS Southwest Fisheries Science Center Environmental Research Division ERDDAP server. The data were logarithm base 10 transformed and then the standardized anomaly was calculated.

The anomaly was calculated by aggregating data into monthly bins then subtracting the monthly climatological mean and dividing by the monthly climatological standard deviation using all 16 years of data. Two anomalies were calculated by estimating the mean of the anomalies in the Big Bend (28°N 84.5°W, 29.5°N 82.5°W) and Southwest Florida (25.5°N 83°W, 27.5°N 81.5°W) regions, which are the locations for recurrent HABs and hypoxia identified in this study.

RIVER DISCHARGE DATA

River discharge was considered as a proxy for runoff contributing to salinity-driven stratification along the West Florida Shelf. Only the major rivers in the region were included in the analyses based upon mean annual discharge (Table 1). The rivers examined, moving west to southeast, were the Apalachicola (USGS ID: 02359170), Suwannee (USGS ID: 02323500), Peace (USGS ID: 02296750), and Caloosahatchee Rivers (USGS ID: 02292900). Other rivers were considered, but the Choctawhatchee River discharge typically stays close to shore and disperses westward toward Alabama. The Mississippi River was also considered because it has been known to impact the West Florida Shelf; however, the effects tend to remain near the shelf break and are dependent on the Gulf Loop current dynamics and the regional wind field (Le Hénaff & Kourafalou, 2016). Daily discharge data for each river were downloaded from the USGS National Water Information System, aggregated into monthly mean values, and the standardized anomalies were calculated per river using the same method as the chlorophyll data except that the discharge data were not logarithm transformed.

DATA ANALYSES

Data manipulations, transformations, and analyses were conducted in the R Statistical Computing Environment (ver. 4.0.2, R Core Team 2020) and in the RStudio integrated development environment (ver. 1.4.1106, RStudio Team 2021). The following R packages were used: ncdf4 (Pierce 2019) and rgdal (Bivand et al. 2021) for spatial data handling and mapping; gsw (Kelley et al. 2017) and oce (Kelley and Richards 2021) for oceanographic data handling and conversion functions; lubridate (Grolemund and Wickham 2011) for handling date-times; scales (Wickham and Seidel 2020) for plotting and visualization; fields (Nychka et al. 2017) for kriging; and rerddap (Chamberlain 2021) was used to download MODIS chlorophyll-a data.

RESULTS

HYPOXIC AREAS IDENTIFICATION

In total, 4930 out of 17935 CTD casts were retained within the spatial and temporal domain of interest for further analyses (for details on cruises see Supplementary materials 1). Out of the 17935 CTD casts, there were 5925 duplicates; 6417 were in waters deeper than 100 meters; 236 had quality issues; 393 outside spatial domain; and 34 outside temporal domain. There was an uneven distribution of seasonal sampling on the West Florida Shelf with most of the sampling occurring in the summer months June (n = 1424), July (n = 779), and August (n = 664). While the least sampled time of year was the winter months December (n = 17), January (n = 22), and February (n = 35). The mean number of CTD casts per year was 308, and, before 2009, the number of casts per year was lower, ranging from 84 in 2005 to 188 in 2008. The most sampled year was 2010 (n = 627), followed by 2014 (n = 446) and 2016 (n = 411). The majority of the CTD casts used in this study were collected as part of regular monitoring conducted by NMFS, which includes the bottom longline surveys, and SEAMAP trawl and plankton cruises. These cruises occur in the summer and fall months except for the winter SEAMAP plankton cruises. In addition, the other regular cruises used in this study were the South Florida Ecosystem Restoration cruises conducted by NOAA's Atlantic Ocean and Meteorological Laboratory since at least 2006; however, only cruises conducted quarterly since 2010 were included in our dataset due to availability.

There were 4008 CTD casts with reported bottom DO after removing readings that were 15 m greater than the CRM depth. Between 2004 and 2019, hypoxia was present in 13 CTD casts over 5 years (Figure 1), in 2005 (n = 2), 2013 (n = 1), 2014 (n = 6), 2015 (n = 1), and 2018 (n = 3). Seasonally, hypoxia was observed in the months of August (n = 5), September (n = 5), and October (n = 3). Near-hypoxic conditions were present in 96 CTD casts over 12 years (Figure 1A). Seasonally, June (n = 29), August (n = 23) and September (n = 20) were the months near hypoxia most frequently occurred. Annually, near hypoxia was most prevalent in 2017 (n = 29), 2013 (n = 22), and 2018 (n = 16). Generally, low DO events were found throughout the latitudinal range of the West Florida Shelf study area. Hypoxia was found shallower than the 50-meter isobath and generally clustered in 2 areas (Figure 2). A northern cluster was identified midshelf (10 to 50 m depth) in the Big Bend region that includes data from 2005 (n = 1), 2013 (n = 1), and 2014 (n = 6). A southern cluster found primarily midshelf (10 to 25 m) near Charlotte

Harbor composed of data from 2005 (n = 1) and 2018 (n = 3). There was one CTD cast with hypoxia from 2015 that was between the two hypoxic clusters and midshelf (25 to 50 m; Figure 2A). Near-hypoxic conditions were more homogeneously spread across the West Florida Shelf compared to hypoxic conditions (Figure 2B). In addition to the clusters mentioned above, near hypoxia was detected midshelf (25 to 50 m) and near the shelf break at approximately 100 m depth across multiple years (Figure 2B). Sampling coverage on the shelf between June 1st and October 31st, which accounts for about 80% of the CTD casts, was sparse before 2009 and regular coverage increased thereafter (Figure S1).

There were several notable low DO events observed in multiple CTD casts on the West Florida Shelf, and, in many cases, the low DO was observed across multiple months (Figures 1 and 2). In August 2005, hypoxia was observed in two CTD casts, in the Big Bend region and near Boca Grande, and three casts were near hypoxic in the Big Bend region (Figure 2). Near hypoxia was detected in 7 CTD casts during 2011 in June (n = 1), August (n = 4), and September (n = 2). These data were located south and southeast of the Apalachicola River mouth (Figure 2) between the 25 and 50 m isobaths. In 2013, low DO occurred in August (n = 5), September (n = 14), and October (n = 4) with hypoxia observed in only one CTD cast in September in the Big Bend region (Figure 1 and 2). The near hypoxia in 2013 was observed in the Big Bend and formed a line extending roughly along the 50 m isobath from 28°N to 25.5°N (Figure 1 and 2). Low DO in 2014 was observed in the Big Bend area in 15 CTD casts taken in August (n = 6) and September (n = 9). Hypoxia was observed in 2 CTD casts midshelf (10 to 25 m, Figure 2) in August and 4 casts in September further away from shore (25 to 50 m, Supplementary Materials 2; Figure S2). The low DO in 2015 was observed in July through October primarily midshelf (25 to 50 m, Figure 2) with hypoxia only observed in one cast in September. There was one near-hypoxic event in June of 2017 that was not associated with hypoxia and encompassed 28 CTD casts restricted to an area near the shelf break at 100 m depth and from 27.5°N to 26°N (Figure 2). In 2018, low DO was observed in 22 CTD casts off Sanibel Island and further south (Figure 2, Supplementary Materials 2; Figure S3). Near hypoxia was observed in August (n = 2), September (n = 2), and October (n = 14), and hypoxia was observed in 3 casts in October.

The observed low DO events occurred primarily in summer and early fall (Figure 3A) coinciding with the seasonally lowest median bottom DO observed. This time of year was also associated with the highest stratification (Figure 3B), warmest mixed-layer temperatures (Figure

3C), and a reduction of mixed-layer salinity (Figure 3D). Nearly all instances of low DO occurred with some level of stratification (Figure 1B). We estimated the median value of density gradient to be 0.0081 $d\rho\ dz^{-1}$ (25^{th} percentile = 0.0056; 75^{th} percentile = 0.016) when there was failure to detect MLD, which we call the no stratification cutoff. There were 5 CTD casts that the estimated stratification was near the no-stratification cutoff. These CTD casts were either midshelf (August 2013 and 2014) or later in the year (September 2014 or October 2018). The low DO in 2017 is notable because mixed-layer temperature was low relative to expected values, while stratification was typical for that time of year (Figures 1 and 3).

HARMFUL ALGAL BLOOM

Analysis of the aggregated *K. brevis* cell counts provided a synoptic scale overview of HABs along the west coast of Florida. Generally, HABs tend to be absent in the early summer months and initially occur in the late summer then dissipate late fall or early winter; however, they can last into the winter and disappear by spring (Figure 1C). However, in 2005, 2006, 2014, and 2018 K brevis cell concentrations above the bloom threshold (>100,000 cells l^{-1} as defined by FWRI) appeared in the summer and persisted into the fall and the 2006-7 bloom lasted into the winter (Figure 1C). The HAB in 2018 had the greatest spatiotemporal extent during the period of interest for this study lasting 16 months from November 2017 to February 2019 and at its largest spatial extent ranged across nearly 4° of latitude (Figure 4B). On the southern extent of the *K. brevis* bloom, low DO was observed in multiple CTD casts (Figure 5F). The 2005 event was also extensive, lasting at least 13 months from February 2005 to January 2006 and encompassed nearly 4° of latitude (Figure 4A). Cell counts increased in a northward progression, and bloom conditions did not abate until February 2006. In August 2005, there were two CTD casts with hypoxia that bracketed most of the K. brevis concentrations for that month (Figure 5A). The year 2004, and a stretch of years starting in 2008 and ending in 2010 were notable for unusually low cell counts and no bloom level events (>100,000 cells l^{-1}, Figure 1C and 4A). There were several years with unusual patterns; in 2013 there was an early HAB that was a continuation of the 2012 event followed by anomalously low cell counts in summer and fall of 2013 (Figures 1C and 4B). Then in 2014, much of the year there were low cell counts but in August and September there was an intense, localized bloom in the Big Bend region (Figure 4B) concurrent with observed hypoxia (Figure 5C). The sampling effort on this spatiotemporal scale of aggregation was lacking north of Saint Petersburg, but sampling became more consistent after 2011 demonstrating some of the dataset limitations even at this coarse resolution. These results serve as qualitative descriptions of major HAB events and years without major HAB events due to the limitations of HAB monitoring data. The HAB monitoring data provided by FWRI are valuable contributions to our understanding of HAB dynamics on the west coast of Florida.

REMOTE SENSING

Satellite derived chlorophyll anomalies on the West Florida Shelf demonstrate synoptic-scale variability between months across 16 years of data. The chlorophyll anomalies displayed some coherence between the two regions, Big Bend and Southwest Florida, bounded by the black boxes (Figure 6). For example, positive anomalies in 2005 were coherent between regions, and mostly negative anomalies between 2007 and 2013 were also coherent between regions. There were positive chlorophyll anomalies in 2005, 2014, and 2018 (black boxes, Figure 6 A-C) at similar locations and at the same time there were instances of hypoxia observed in the CTD casts (Figures 1A and 5). When examining the time series of anomalies for regions bounded by those black boxes, the chlorophyll anomalies before August 2005, August 2013, August 2014, and October 2018 were elevated relative to the other months (Figure 6D) for the Big Bend (2005, 2013, 2014) and SWFL region (2018).

RIVER DISCHARGE

River discharge in the region was dominated by the Apalachicola and Suwannee Rivers (Table 1). There was some coherence of river discharge amongst rivers (Figure 7). For example, there was anomalously high discharge for all rivers starting late 2004 and continuing to nearly the end of 2005. Then there was a period of anomalously low discharge starting mid-2006 and continuing to the end of 2012 with brief reprieve in 2010. There was also some coherence in positive anomalies amongst rivers in 2013, 2016, 2017, and 2018 (Figure 7). When we consider the timing and location of hypoxic events identified from the CTD data, some general patterns emerge. In 2005, there were large positive river discharge anomalies from all rivers several months preceding the detection of hypoxia in August (Figure 7). Riverine discharge was anomalously high from the Suwannee River preceding both the 2013 and 2014 hypoxia.

Similarly, the Peace and Caloosahatchee Rivers had positive anomalies preceding the hypoxia observed in 2018 (Figure 7).

DISCUSSION

Examining 16 years of CTD data collected over the West Florida Shelf, we identified three hypoxic events in 2005, 2014, and 2018, that co-occurred with major HABs. Other studies have identified hypoxia associated with HABs on the West Florida Shelf in 2005 (Hu et al. 2006), 2014 (Driggers et al. 2016), and 2018 (Milbrandt et al. 2021); however, no study has examined this relationship across longer time scales and on a larger geographic scope in this region. We hypothesize that HAB-hypoxia events were driven by the temporal coincidence of HABs and associated climatological factors. During HAB-hypoxia events, *K. brevis* cell concentrations reached bloom levels (>100,000 cells l^{-1}) during the summer months (June-August) and then continued into the fall. In contrast to years with HAB-hypoxia events, there was an absence of HAB activity in early to mid-summer months in years with blooms without hypoxia. The year 2006 was an outlier in which there were summer HABs that continued into the fall, but there was no concurrent hypoxia detected. The absence of hypoxia may be due to the lack of CTD casts in the Big Bend region and sparse sampling south of Tampa Bay during August 2006. Either reduced sampling coverage precluded detection of hypoxia and it dissipated quickly because there was data from September in the region, or, alternatively, there was no hypoxia in 2006. While sampling coverage may be invoked, the alternative that there was no hypoxia was supported by other observational evidence. Specifically, stratification, chlorophyll anomalies, and river discharge anomalies were all lower during the summer of 2006, whereas these properties were elevated during the HAB-hypoxia events identified in this study.

Our results indicate that there were several factors that contributed to the timing and creation of hypoxia on the West Florida Shelf. Considering that during summer on the West Florida Shelf wind speeds are low, surface heat content is high, and the south Florida rainy season provides ideal conditions for strongly stratified conditions (Liu and Weisberg 2012), we hypothesized that stratification would be an important driver of decreased bottom DO levels. We found that hypoxia and low DO, more generally, occurred across the range of stratification and mixed-layer temperatures and salinities indicating that there is a partial decoupling of local water column properties from bottom DO. We take this evidence to suggest that the presence of hypoxia was also influenced by remote conditions such as advection of algal bloom biomass and riverine discharge, which contributes to both nutrient enrichment and water column stratification. For example, the hypoxia in 2005, 2014, and 2018 co-occurred both in space and time with HABs (Figure 1, 4, and 5), and CTD profiles with observed hypoxia in 2014 and 2018 indicate a surface freshening consistent with riverine discharge driving the density stratification (See Supplementary Materials 2; Figures S4). Consistent with this explanation, stratification observed with hypoxic CTDs casts were predominantly driven by changes in salinity (See Supplementary Materials 2; Figures S5 and S6); however, there are no examples of exclusively thermal and haline driven stratification. Furthermore, there was little stratification in 2006 in which the water column in both the Big Bend and off Sanibel Island were well mixed compared to either 2005 or 2014 (Figure S3). Despite the connection between HABs and hypoxia observed in 2005, 2014, and 2018, hypoxia was not an outcome of all HABs on the West Florida Shelf (e.g., 2006, 2012, and 2016, Figures 1 and 4). This disjunction in the HAB-hypoxia relationship might be due to gaps in the spatiotemporal coverage of surveys that conduct CTD operations or perhaps the relationship only arises in years with extreme HABs that initiate in the summer and persist into the fall.

River discharge and chlorophyll anomalies for the years with extreme blooms, combined with salinity-driven stratification above hypoxia, appear to be important conditions that contribute to the formation of HAB-hypoxia events. Riverine discharge has typically been considered a source of nutrients adequate for sustaining a bloom, but not sufficient to initiate a bloom (Vargo et al. 2008). Earlier work failed to establish a linear relationship between Caloosahatchee River discharge and K. brevis blooms (Dixon et al. 2014); however, more recently it has been shown that there is a non-linear relationship between Caloosahatchee discharge, nutrients, and K. brevis blooms in SWFL (Medina et al. 2020). The relationship established by Medina et al. (2020) is dynamic and the outcome is dependent upon the state of other variables in the system. Given the evidence presented in this study for HAB-hypoxic events, a similarly dynamic, state-dependent relationship likely exists between algal blooms, river discharge, stratification, and hypoxia formation. The likely influence of riverine discharge is not supplying nutrients to fuel blooms but rather creating conditions conducive for the formation of hypoxia. River discharge, and runoff more generally, reduces nearshore surface salinity driving stratification and concomitant reduction of water column ventilation. In the

HAB-hypoxia years (2005, 2014, and 2018), there were large river discharge and chlorophyll anomalies that were spatially and temporally coherent with the observed hypoxic events. During the 2014 event, there were positive discharge anomalies from the rivers closest to the HAB (i.e., Apalachicola and Suwannee Rivers) and regions of hypoxia. Additionally, Mississippi River discharge was near average in the summer of 2014; however, surface circulation in the GOM transported the river plume onto the West Florida Shelf and southwards toward the Florida Keys creating a midshelf salinity front (Le Hénaff et al. 2016). Restricted cross-shelf transport due to the front, referred to as "nutrient trapping", would support the sinking of excess biomass, and intensify local biological oxygen demand through increased benthic metabolic activity amplifying the likelihood of hypoxia formation (Flynn et al. 2020). The relationships between riverine discharges and the HAB that was initiated in late 2017 and persisted until early 2019 are less clear (also referred to as the 2018 bloom). There was anomalously high discharge from both the Caloosahatchee and Peace Rivers during the period from August to November 2017 that preceded initiation of the long-lasting bloom in 2017-9. A second period of higher-than-normal Caloosahatchee and Peace discharge from April to June 2018 preceded an intensification of the HAB and the formation of hypoxic conditions offshore of Sanibel Island (Figures 4-7). The connection between HABs and river discharge is not direct nor consistent highlighted by several HABs in which river discharge was lower than average (i.e., 2006, 2007, and 2017). Chlorophyll anomalies may be indicative of HABs, which could create hypoxic conditions; however, satellite derived chlorophyll is known to be positively biased by CDOM in regions dominated by coastal runoff and thereby limits inferences exclusively using satellite data (Hu et al. 2006). Taken together, chlorophyll and river discharge likely contribute to the formation of hypoxic regions, particularly when HABs persist through the summer months. Overall, chlorophyll and river discharge were not individually good indicators of either HABs or hypoxia and there are likely multiple pathways leading to HAB-hypoxic events.

Despite the limitations of the data, we were able to characterize multiple hypoxia events, and examine similarities and differences in their expression and relation to HABs. The 2005 and 2018 HABs were the worst events in the past 20 years based upon spatiotemporal extent (Hu et al 2006, Weisberg et al. 2019) and local ecological knowledge (Turley et al. 2021). In contrast, the 2014 event had major socio-ecological impacts but a minor coastal expression (Driggers et al. 2016, Turley et al. 2021). During the 2005 event, hypoxia was detected in August at two locations and coincided with the northwest expansion of the nearshore HAB (Figures 4A and 5A). Seasonal surface circulation moves northwest along the Florida coast and winds tend to be favorable for downwelling, which in turn facilitates the retention of algal bloom biomass in the area where hypoxia was observed (Yang and Weisberg 1999). Similarly in 2014, hypoxia was observed off the Big Bend coast of Florida (Figure 5C; see Supplementary materials 2, Figure S2 for September 2014), which coincided with the bloom level *K. brevis* cell concentrations collected by FWRI that expanded and moved northward (Figure 4B). The localized hypoxia and expansion of the bloom support the coastal circulation transport mechanism (Yang and Weisberg 1999). Moreover, *K. brevis* cell concentrations were not anomalously high on the Florida coast south of the Big Bend, consistent with expectations that a cyclonic (counterclockwise) surface circulation pattern in the Big Bend region would prevent the bloom from spreading southeastward into shallow coastal waters. In contrast to 2014, hypoxia in 2018 was found southwest of Sanibel Island (Figure 5F) in an area near where hypoxia was also observed during 2005. Near-hypoxic conditions were observed in several CTD casts in the same general area during surveys in August and September associated with HABs (see Supplementary Materials 2; Figure S3 for August and September plots). We suggest that coincident HAB conditions and hypoxia in 2005, 2014 and 2018 are evidence of a sustained accumulation of biomass from the bloom depleting local bottom oxygen and forming near-bottom hypoxia due to favorable physical conditions. Despite the evidence presented in this study, the exact linkage between HABs and hypoxia is not clear. The toxins produced by *K. brevis* are known to cause mortality in many marine organisms (Landsberg et al. 2009) and their decomposition may lead to hypoxia, however, there is also evidence that decaying organic matter due to hypoxia may release nutrients vital to sustaining HABs forming a positive feedback loop (Vargo et al. 2008).

An open question is whether the most deleterious impacts on the ecosystem result from HABs, hypoxia, or a combination of both stressors–and how these impacts may vary by species. A laboratory study focused on the stone crab *Menippe mercenaria*, which occurs on the West Florida Shelf in areas frequently impacted by HABs and target in an important regional commercial fishery, indicated that lethal and sublethal impacts were more sensitive to oxygen concentrations than *K. brevis* concentrations (Gravinese et al. 2020). Fish population assessments incorporating data on age structure, abundance, and other biological information are routinely used to track population status used in fisheries management. Population assessments for both red grouper and gag grouper have shown major declines in abundance in the years 2005, 2014, and 2018, suggesting that HABs associated with hypoxia cause significant increases in natural mortality for these species (SEDAR 2019, SEDAR 2021, Sagarese et al. 2021). This notion is corroborated by direct observed evidence of HAB induced mortality; for example, Driggers et al. (2016) documented mass grouper kills during fishery surveys that transected an area impacted by the 2014 HAB-hypoxia. Additionally, research efforts conducted to quantify severe HABs over time using fishermen's local knowledge, identified 2005, 2014 and 2018 as extreme HAB years, with grouper, drum and crab species perceived to be the most significantly affected species (Turley et al. 2021). Hypoxia may also impact benthic organisms such as sponges and corals which make up habitat for other species (Smith 1974), leading to limitations in recruitment and delayed recovery of populations that have undergone increased mortality from HABs. Taken together, multiple lines of evidence thus demonstrate that HABs associated with hypoxia have been particularly damaging and can have immediate impacts on some of the major economically important fishery species in the region. Additionally, there is likely a lag between HAB-hypoxia events and population or community level responses because multiple long-term perturbations to these habitats result in cascading effects that take time to manifest.

Given that these HAB-hypoxic events have significant impacts on marine ecosystems, another concern is whether we can expect to see increases in the number of HABs and associated hypoxia events under changing climate and associated environmental conditions. There is some evidence that HAB activity is already expanding; some modeling studies indicate that temperature has been a factor in driving intensification of some HABs (Gobler et al. 2017) but meta-analysis also indicates an observed increase in some HABs is partly attributable to improved monitoring over time (Anderson et al. 2021). Overall, it is unclear how *K. brevis* blooms will respond to changing climate conditions. For example, several studies have found that *K. brevis* does not survive in culture at temperatures greater than 30-33°C and a rapid decline in viability has been observed at temperatures above 31°C (Eng-Wilmot et al. 1977, Hitchcock 1976, Magana and Villareal 2006, Errera et. al 2014). This suggests increasing temperatures from climate change may reduce the frequency and magnitude of HABs on the West Florida Shelf. However, more recent studies have found that K. brevis growth rates increase with increasing pCO2 concentrations (Bercel and Kranz 2019) and that higher growth rates were observed despite increased temperatures (Errera et. al 2014). Taken together, it is likely that unexpected patterns in future HABs activity may emerge (Wells et al. 2020) especially considering that HABs develop through unique combinations of physical and biological factors. More research is needed to understand the combined effect of multiple stressors since few studies have been carried out examining these interactions (Griffith and Gobler 2020). The West Florida Shelf is predicted to undergo dramatic warming in the future (Liu et al. 2015) increasing stratification, which will tend to favor the formation of HABs on the West Florida Shelf due to the ability of dinoflagellates like *K. brevis* to vertically migrate and outcompete other phytoplankton species. Tropical storm activity is also expected to increase under future climate conditions (Emanuel 2021), and associated precipitation causes increased runoff as well as discharges to the Caloosahatchee River for flood control purposes (Phlips et al. 2020). Generally, precipitation is expected to decrease over the Florida Peninsula and increase over the West Florida shelf in the latter part of the 21st century (Misra et al. 2019). Thus, overall freshwater input will likely decrease in favor of extreme pulses due to storm activity. If land-derived nutrients do intensify already active HABs (sensu Medina et al. 2020), these pulses and resulting prolonged HABs may become more common similar to events in 2018 and more recently 2021. In addition to temperature and precipitation, hypoxia is triggered by a host of other factors including ocean circulation and wind patterns (Altieri and Gedan 2015), but it is unclear how these regimes may change in the future to impact hypoxia formation in this region.

While we found evidence that several hypoxic events on the West Florida Shelf were connected to HABs, our analyses also found four years, 2011, 2013, 2015, and 2017, with low DO events that were not associated with HABs. Due to the spatial distribution of the CTD casts with low DO, we hypothesize that these events were likely a result of upwelling of deeper Gulf of Mexico waters onto the West Florida Shelf. During all four years, most of the low DO, which was primarily near hypoxic, was observed between the shelf break at 100 m and about the 50 m isobath (Figure 2). The distribution of low DO is consistent with the expected path that an upwelled parcel of water would take on the West Florida Shelf (Weisberg et al. 2014, Weisberg et al. 2016b). In a series of modeling experiments, Weisberg et al. (2016b) demonstrated that water upwelled on the eastern edge of the Desoto Canyon at the northwestern corner of the West Florida Shelf would be advected along the shelf bottom in a roughly southwestward direction. In fact, Weisberg et al. (2016a) hypothesized that HABs in 2013 were nearly absent on the West Florida Shelf because upwelling injected deeper, offshore Gulf of Mexico waters onto the shelf.

The upwelled nutrients were believed to be more rapidly taken up by diatoms outcompeting dinoflagellates like *K. brevis*. It is difficult to assess how unusual this upwelling event may have been and the role upwelling at the shelf break plays in the suppression of HABs because the relative amount of upwelling in 2013 was not compared to an expected annual climatology (Weisberg et al. 2014).

Invoking upwelling of low DO involves not just movement of deeper Gulf of Mexico water onto the West Florida Shelf, but also requires that the source of the upwelled water has a reduced DO signature. We found low DO in 2005, 2011, 2014, 2015 and 2017 in CTD casts at locations in depths greater than 100 m near the Desoto Canyon on the northwest edge of the shelf (Figure 8). We propose that this low DO observed offshore was likely an important initial condition for some of the low DO events found on the shelf in this study. Of all the potential upwelling-caused, low-DO events in this study, 2017 has the most support from the data. The low DO was found along the shelf break (Figures 2B and 5E), both mixed-layer temperatures (Figure 3C) and bottom temperatures (Supplementary materials 2, Figure S7) were lower than expected, and CTD casts in deeper waters just offshore also had low DO (Figure 8). Taken together, it seems like deeper, colder waters were upwelled onto the shelf edge that had a characteristic low DO signature. Bottom temperatures were also quite low in 2013 (Supplementary materials 2, Figure S7), which may be an indication that upwelling was a factor in the low DO that was observed midshelf in 2013 (Weisberg et al. 2014), but hypoxia and near hypoxia was also detected on Florida Panhandle (Figures 2 and 5). There were no HABs detected at that time of the year (Figures 1C and 4B), there were slightly elevated chlorophyll anomalies in the months before (Figure 6C), and river discharge was elevated (Figure 7). From these data, it is not clear what caused the low DO near the Panhandle in 2013. If upwelling occurred in 2013 as suggested by Weisburg et al. (2016a), there was an absence of low DO in the 2013 CTD casts further offshore (Figure 8). A more likely explanation of the low DO in 2013 near the shelf break was that nutrients upwelled onto the shelf increased biological oxygen demand through plankton productivity, stratification (Figures 1 and 3), and restricted cross-shelf advection leading to localized oxygen depletion. Thus, there are multiple mechanisms by which upwelling could lead to low DO on the West Florida Shelf. The low DO events located midshelf to shelf break in 2013 and 2017 were not due to HABs but rather they are likely a result of upwelled low DO water on the West Florida Shelf.

There are several caveats and limitations to this study. The CTD data were collated from a variety of sources and thus needed to be quality controlled and standardized. Additionally, much of the data were not available in regular spatiotemporal intervals and as a result the data were frequently analyzed by month to allow a synoptic scale analysis. The lack of comprehensive *K. brevis* sampling and oceanographic survey data hampers a robust spatiotemporal description of HAB-hypoxic events identified in this paper. The current spatiotemporal coverage of surveys in the region makes it difficult to determine the persistence of hypoxia and its association with HABs. For example, given the large spatial distribution of the HAB in August 2005 identified by FWRI sampling, it is likely that the hypoxic region was much larger than could be reasonably inferred from the CTD data. Unfortunately, the available CTD data for 2005 does not extend into the nearshore area nor into the month of September. Therefore, limiting any estimate of the shoreward extent of hypoxic conditions in 2005 and the ability to determine if hypoxia persisted into September as it did in 2014. The survey data in 2005 is limited because sampling schedules were truncated in August and canceled for September due to an active hurricane season in the Gulf of Mexico. While the collated data were likely useful for analyses for their original purpose, the inherent coarse spatiotemporal scales at which they were collected likely explains lack of coherence across time and space in the HAB-hypoxia relationship we have posited. We recommend that priority be given to increasing survey coverage in the case of the Big Bend region to include more locations closer to shore in August and September where recurrent hypoxia has been identified in this study. This would better prepare regional stakeholders to identify and adapt to future HAB-hypoxic events that are more likely under future climate change scenarios. Data limitations may also have obscured a comprehensive identification of hypoxia because the maximum depth sampled by the CTD casts were rarely close (within 1 m) to the seafloor thereby hypoxic zones were unavailable to the instruments. As a result, the hypoxia identified here is likely an underestimate of the number of hypoxic events and likely underestimate the spatiotemporal scope of the events on the West Florida Shelf that were identified. There was an inherent limitation in the analyses because all bottom DO data were treated similarly regardless of depth. It is generally true of oceanographic data, including this dataset, that DO is negatively correlated with depth; however, we were not trying to quantitatively predict DO and including bottom depth does not affect our interpretation of the data. Broadly, there was a depth dependence in our analyses in which low DO less than 50 meters depth appears to be HAB related and low DO greater than 50 m appears to be upwelling related. Any effort to conclusively link HABs to hypoxia on the West Florida Shelf is also hampered by the lack of a consistent spatiotemporal index of HAB severity. Previous indices have attempted to create a synoptic view of offshore HAB activity over time (Walter et al. 2013), but discontinuation of satellite platforms with changing sensors has presented challenges for creating a complete time series. Incomplete survey coverage across the shelf in addition to uncertainty surrounding true near-bottom sampling is evidence that the hypoxia identified in this study is underestimated.

The broader implication for this study includes an initial assessment of parameters that could be used for seasonal prediction of HABs and hypoxia. Given the complexity of hypoxia formation, time-varying, 3-dimensional circulation models incorporating algal bloom biomass transport are needed to better understand the mechanisms of HAB driven hypoxic conditions (for examples, see Bouffard et al. 2013, Siedlecki et al. 2014**)**. Such a model would be able to capture the dynamics in which algal bloom biomass is transported into an area of convergence, sinks, and increases local biological oxygen demand creating a localized region of low DO. Such predictions could be useful for helping the fishing industry to plan their operations around these impacted areas and could improve current nearshore forecast systems to benefit coastal economies and human health. However, additional work is needed to assess in a robust statistical manner the possible relationships described here. The main limitation to a more robust study is a lack of a spatiotemporally consistent metric of HAB and hypoxia. Some work has been completed which shows promise for a satellite-based, red-tide index that could be used in a hierarchical model (Walter et al. 2013). However, at the present time, there are no robust satellite-based indices of hypoxia or other synoptic data sources that could be used in similar analyses as HAB. The present study also suggests that HABs with associated hypoxia are particularly damaging to at least some components of marine ecosystems. When considering the spectrum of HABs in the period considered for this study, the events that have been recognized as damaging the ecosystems and fishery resources were also associated with hypoxia. Other HABs with large spatiotemporal expressions (e.g., 2006, 2015, 2016), which were not associated with hypoxia, have not been identified in the literature or during local ecological knowledge interviews as having as great of impacts on ecosystems or fishery resources. For management of economically important species as well as endangered and protected species on the West Florida

Shelf, further work needs to be done to understand the immediate and lagged impacts of these HAB-hypoxia events, versus HABs that are not associated with hypoxia. Should these events become more frequent and severe in the future, it would likely impact overall ecosystem productivity and would need to be accounted for in management plans of many ocean users and interest groups including fisheries, protected resources, tourism, and aquaculture industry.

ACKNOWLEDGEMENTS

The scientific results and conclusions, as well as any views or opinions expressed herein, are those of the author(s) and do not necessarily reflect those of NOAA or the Department of Commerce. We are greatly appreciative of all the efforts by the crew, scientists, and volunteers who collected data and processed samples for the HAB database provided by FWRI, the SEAMAP CTD data, the NMFS CTD data, and other cruises that were used in this manuscript. Thank you to Dr. Katherine Hubbard (FWRI) for her HAB expertise on the West Florida Shelf and Laura Markley (FWRI) for responding to our HAB data requests and for her tireless efforts at *K. brevis* ID for the HAB database. We are grateful for the HAB-hypoxia discussions and efforts by fishermen associated with the Florida Commercial Waterman's Conservation non-profit based in Matlacha, Florida. We are also greatly appreciative of Dr. Rick Stumpf (NOAA-NCCOS) and three anonymous reviewers for their helpful comments and suggestions. This research was conducted as part of NOAA's Gulf of Mexico Integrated Ecosystem Assessment program. This research was also carried out [in part] under the auspices of the Cooperative Institute for Marine and Atmospheric Studies (CIMAS), a Cooperative Institute of the University of Miami and the National Oceanic and Atmospheric Administration, cooperative agreement # NA20OAR4320472.

AUTHOR CONTRIBUTIONS

BT, MK, MC, and CK collaborated on the original idea for the study and manuscript. BT, MK, MC, DH, and CK contributed to compiling data from various databases. BT harmonized and quality controlled the data, performed the analyses, and created the plots. BT, MK, MC, DH, and CK contributed to writing and editing the manuscript.

LITERATURE CITED

Anderson, D. M., Fensin, E., Gobler, C. J., Hoeglund, A. E., Hubbard, K. A., Kulis, D. M., … Trainer, V. L. (2021). Marine harmful algal blooms (HABs) in the United States: History, current status and future trends. *Harmful Algae*, *102*, 101975. https://doi.org/10.1016/j.hal.2021.101975

Backer, L.C. (2009). Impacts of Florida red tides on coastal communities. Harmful Algae 8(4): 618–622. doi:https://doi.org/10.1016/j.hal.2008.11.008.

Bercel, T. L., & Kranz, S. A. (2019). Insights into carbon acquisition and photosynthesis in Karenia brevis under a range of CO2 concentrations. Progress in Oceanography, 172, 65–76. https://doi.org/10.1016/j.pocean.2019.01.011

Bivand, R., Keitt, T., Rowlingson, B. (2021). rgdal: Bindings for the 'Geospatial' Data Abstraction Library. R package version 1.5-23. https://CRAN.R-project.org/package=rgdal

Bouffard, D., Ackerman, J. D., & Boegman, L. (2013). Factors affecting the development and dynamics of hypoxia in a large shallow stratified lake: Hourly to seasonal patterns. *Water Resources Research*, *49*(5), 2380–2394. https://doi.org/10.1002/wrcr.20241

Brainerd, K.E., and Gregg, M.C. (1995). Surface mixed and mixing layer depths. Deep. Res. Part I 42(9): 1521–1543. doi:10.1016/0967-0637(95)00068-H.

Chamberlain, S. (2021). rerddap: General Purpose Client for 'ERDDAP' Servers. R package version 0.7.4. https://CRAN.R-project.org/package=rerddap

Christman, M, Young L. (2006). Analysis of Karenia brevis Gulf Data. Final project report to Florida Wildlife Research Institute, from University of Florida, Gainsville, FL, June 2006

Diaz, R., & Rosenberg, R. (1995). Marine benthic hypoxia: A review of its ecological effects and the behavioural response of benthic macrofauna. *Oceanography and Marine Biology. An Annual Review [Oceanogr. Mar. Biol. Annu. Rev.]*, *33*, 245–303.

Diaz, R., & Rosenberg, R. (2008). Spreading Dead Zones and Consequences for Marine Ecosystems. *Science*, *321*(5891), 926–929. https://doi.org/10.1126/science.1156401

Dixon, L.K., Kirkpatrick, G.J., Hall, E.R., and Nissanka, A. (2014). Nitrogen, phosphorus and silica on the West Florida Shelf: Patterns and relationships with Karenia spp. occurrence. Harmful Algae 38: 8–19. https://doi.org/10.1016/j.hal.2014.07.001.

Domenici, P., Lefrançois, C., and Shingles, A. (2007). Hypoxia and the antipredator behaviours of fishes. Philos. Trans. R. Soc. B Biol. Sci. 362(1487): 2105–2121. Royal Society. doi:10.1098/rstb.2007.2103.

Driggers, W.B., M.D. Campbell, A.J. Debose, K.M. Hannan, M.D. Hendon, T.L. Martin, and C.C. Nichols. (2016). Environmental conditions and catch rates of predatory fishes associated with a mass mortality on the West Florida Shelf. Estuarine, Coastal and Shelf Science 168: 40-

49.

Emanuel, K. (2021). Response of Global Tropical Cyclone Activity to Increasing CO2: Results from Downscaling CMIP6 Models. *Journal of Climate*, *34*(1), 57–70. https://doi.org/10.1175/JCLI-D-20-0367.1

Eng-Wilmot, D. L., & Martin, D. F. (1977). Large-Scale Mass Culture of the Marine Blue-Green Alga, *Gomphosphaeria Aponina*. Florida Scientist, 40(2), 193–197.

Errera, R. M., Yvon-Lewis, S., Kessler, J. D., & Campbell, L. (2014). Responses of the dinoflagellate Karenia brevis to climate change: pCO2 and sea surface temperatures. Harmful Algae, 37, 110–116.https://doi.org/10.1016/j.hal.2014.05.012

Flynn, R.F., Granger, J., Veitch, J.A., Siedlecki, S., Burger, J.M., Pillay, K., and Fawcett, S.E. (2020). On-Shelf Nutrient Trapping Enhances the Fertility of the Southern Benguela Upwelling System. J. Geophys. Res. Ocean. 125(6): e2019JC015948. https://doi.org/10.1029/2019JC015948.

Garcia, H. E., T. P. Boyer, R. A. Locarnini, O. K. Baranova, M. M. Zweng. (2018). World Ocean Database 2018: User's Manual (prerelease). A.V. Mishonov, Technical Ed., NOAA, Silver Spring, MD (Available at https://www.ncei.noaa.gov/sites/default/files/2020-04/wodreadme_0.pdf).

Glaspie, C.N., Clouse, M., Huebert, K., Ludsin, S.A., Mason, D.M., Pierson, J.J., Roman, M.R., and Brandt, S.B. (2019). Fish Diet Shifts Associated with the Northern Gulf of Mexico Hypoxic Zone. Estuaries and Coasts 42(8): 2170–2183. doi:10.1007/s12237-019-00626-x.

Gobler, C. J., Doherty, O. M., Hattenrath-Lehmann, T. K., Griffith, A. W., Kang, Y., & Litaker, R. W. (2017). Ocean warming since 1982 has expanded the niche of toxic algal blooms in the North Atlantic and North Pacific oceans. *Proceedings of the National Academy of Sciences*, *114*(19), 4975 LP – 4980. https://doi.org/10.1073/pnas.1619575114

Gravinese, P.M., Munley, M.K., Kahmann, G., Cole, C., Lovko, V., Blum, P., and Pierce, R. (2020). The effects of prolonged exposure to hypoxia and Florida red tide (*Karenia brevis*) on the survival and activity of stone crabs. Harmful Algae 98: 101897. https://doi.org/10.1016/j.hal.2020.101897.

Griffith, A. W., & Gobler, C. J. (2020). Harmful algal blooms: A climate change co-stressor in marine and freshwater ecosystems. Harmful Algae, 91, 101590. https://doi.org/10.1016/j.hal.2019.03.008

Grolemund, G., Wickham, H. (2011). Dates and Times Made Easy with lubridate. Journal of Statistical Software, 40(3), 1-25. https://www.jstatsoft.org/v40/i03/.

Hagy, J.D., Boynton, W.R., Keefe, C.W., and Wood, K. V. (2004). Hypoxia in Chesapeake Bay, 1950-2001: Long-term change in relation to nutrient loading and river flow. Estuaries 27(4): 634–658. doi:10.1007/BF02907650.

Hitchcock, G.L., Vargo, G.A., and Dickson, M.-L. (2000). Plankton community composition, production, and respiration in relation to dissolved inorganic carbon on the West Florida Shelf, April 1996. J. Geophys. Res. Ocean. 105(C3): 6579–6589. https://doi.org/10.1029/1998JC000293.

Hofmann, A. F., Peltzer, E. T., Walz, P. M., & Brewer, P. G. (2011). Hypoxia by degrees: Establishing definitions for a changing ocean. Deep Sea Research Part I: Oceanographic Research Papers, 58(12), 1212-1226.

Hu, C., Muller-Karger, F.E., and Swarzenski, P.W. (2006). Hurricanes, submarine groundwater discharge, and Florida's red tides. Geophys. Res. Lett. 33(11). John Wiley & Sons, Ltd. doi:https://doi.org/10.1029/2005GL025449.

Karnauskas, M., M. McPherson, S. Sagarese, A. Rios, M. Jepson, A. Stoltz and S. Blake. 2019. Timeline of severe red tide events on the West Florida Shelf: insights from oral histories. SEDAR61-WP-20. SEDAR, North Charleston, SC. 16 pp.

Kelley, D., Richards, C., and WG127 SCOR/IAPSO (2017). gsw: Gibbs Sea Water Functions. R package version 1.0-5. https://CRAN.R-project.org/package=gsw

Kelley, D., Richards, C. (2021). oce: Analysis of Oceanographic Data. R package version 1.4-0. https://CRAN.R-project.org/package=oce

Landsberg, J.H., Flewelling, L.J., and Naar, J. (2009). Karenia brevis red tides, brevetoxins in the food web, and impacts on natural resources: Decadal advancements. Harmful Algae 8(4): 598–607. doi:https://doi.org/10.1016/j.hal.2008.11.010.

Le Hénaff, M., and Kourafalou, V.H. (2016). Mississippi waters reaching South Florida reefs under no flood conditions: synthesis of observing and modeling system findings. Ocean Dyn. 66(3): 435–459. doi:10.1007/s10236-016-0932-4.

Liu, Y., and Weisberg, R.H. (2012). Seasonal variability on the West Florida Shelf. Prog. Oceanogr. 104: 80–98. Elsevier Ltd. doi:10.1016/j.pocean.2012.06.001.

Liu, Y., Lee, S.-K., Enfield, D. B., Muhling, B. A., Lamkin, J. T., Muller-Karger, F. E., & Roffer, M. A. (2015). Potential impact of climate change on the Intra-Americas Sea: Part-1. A dynamic downscaling of the CMIP5 model projections. *Journal of Marine Systems*, *148*, 56–69. https://doi.org/https://doi.org/10.1016/j.jmarsys.2015.01.007

Magaña, H.A., Contreras, C. and Villareal, T.A. (2003). A historical assessment of Karenia brevis in the western Gulf of Mexico. *Harmful Algae*, *2*(3), pp.163-171.

Magaña, H. A., & Villareal, T. A. (2006). The effect of environmental factors on the growth rate of Karenia brevis (Davis) G. Hansen and Moestrup. *Harmful Algae*, *5*(2), 192–198. https://doi.org/https://doi.org/10.1016/j.hal.2005.07.003

Medina, M., Huffaker, R., Jawitz, J.W., and Muñoz-Carpena, R. (2020). Seasonal dynamics of terrestrially sourced nitrogen influenced Karenia brevis blooms off Florida's southern Gulf Coast. Harmful Algae 98: 101900. https://doi.org/10.1016/j.hal.2020.101900.

Milbrandt, E. C., Martignette, A. J., Thompson, M. A., Bartleson, R. D., Phlips, E. J., Badylak, S., & Nelson, N. G. (2021). Geospatial distribution of hypoxia associated with a Karenia brevis bloom. *Estuarine, Coastal and Shelf Science*, *259*, 107446. https://doi.org/10.1016/j.ecss.2021.107446

Misra, V., Mishra, A., & Bhardwaj, A. (2019). A coupled ocean-atmosphere downscaled climate projection for the peninsular Florida region. Journal of Marine Systems, 194, 25–40. https://doi.org/10.1016/j.jmarsys.2019.02.010

NOAA National Geophysical Data Center. (2001). U.S. Coastal Relief Model Vol.3 - Florida and East Gulf of Mexico. https://doi.org/10.7289/V5W66HPP. Accessed [2020/02/24].

Nychka, D., Furrer, R., Paige, J., Sain, S. (2017). "fields: Tools for spatial data." doi:10.5065/D6W957CT (URL: https://doi.org/10.5065/D6W957CT), R package version 12.5, https://github.com/NCAR/Fields.

Phlips, E. J., Badylak, S., Nelson, N. G., & Havens, K. E. (2020). Hurricanes, El Niño and harmful algal blooms in two sub-tropical Florida estuaries: Direct and indirect impacts. *Scientific Reports*, *10*(1), 1910. https://doi.org/10.1038/s41598-020-58771-4

Pierce, D. (2019). ncdf4: Interface to Unidata netCDF (Version 4 or Earlier) Format Data Files. R package version 1.17. https://CRAN.R-project.org/package=ncdf4

Pitcher, G. C., & Probyn, T. A. (2011). Anoxia in southern Benguela during the autumn of 2009 and its linkage to a bloom of the dinoflagellate Ceratium balechii. *Harmful Algae*, *11*, 23–32. https://doi.org/10.1016/j.hal.2011.07.001

R Core Team (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL: https://www.R-project.org/.

Rojas de Mendiola, B. (1979). Red tide along the Peruvian coast. In D.L. Taylor, & H.H. Seliger (Eds.), *Toxic Dinoflagellate Blooms*. Elsevier, Amsterdam, pp. 183-190.

RStudio Team (2021). RStudio: Integrated Development Environment for R. RStudio, PBC, Boston, MA URL http://www.rstudio.com/.

Sagarese, S. R., Vaughan, N. R., Walter III, J. F., & Karnauskas, M. (2021). Enhancing single-species stock assessments with diverse ecosystem perspectives: a case study for Gulf of Mexico Red Grouper (Epinephelus morio) and red tides. *Canadian Journal of Fisheries and Aquatic Sciences*, *78*(8), 1168–1180. https://doi.org/10.1139/cjfas-2020-0257

SEDAR. (2019). SEDAR 61 - Gulf of Mexico Red grouper Stock Assessment Report. SEDAR, North Charleston, SC.

SEDAR. (2021). SEDAR 72 - Gulf of Mexico Gag grouper Stock Assessment Report. SEDAR, North Charleston, SC.

Siedlecki, S.A., Banas, N.S., Davis, K.A., Giddings, S., Hickey, B.M., MacCready, P., Connolly, T., and Geier, S. (2015). Seasonal and interannual oxygen variability on the Washington and Oregon continental shelves. J. Geophys. Res. Ocean. 120(2): 608–633. https://doi.org/10.1002/2014JC010254.

Smith, G. B. (1975). The 1971 Red Tide and its Impact on Certain Reef Communities in the Mid-Eastern Gulf of Mexico. Environmental Letters, 9(2), 141–152. https://doi.org/10.1080/00139307509435843

Smith, R. C. (1981). Remote Sensing and Depth Distribution of Ocean Chlorophyll. *Marine Ecology Progress Series*, *5*(3), 359–361.

Steckbauer, A., Duarte, C.M., Carstensen, J., Vaquer-Sunyer, R., and Conley, D.J. (2011). Ecosystem impacts of hypoxia: thresholds of hypoxia and pathways to recovery. Environ. Res. Lett. 6(2): 25003. doi:10.1088/1748-9326/6/2/025003.

Turley, B., M. Karnauskas, M. McPherson, S. Sagarese, A. Rios, M. Jepson, A. Stoltz and S. Blake. (2021). Local ecological knowledge outlining severe red tide events between 2000 – 2019 on the West Florida Shelf. SEDAR72-DW-09. SEDAR, North Charleston, SC. 19 pp.

Turner, R.E., and Rabalais, N.N. (1994). Coastal eutrophication near the Mississippi river delta. Nature 368(6472): 619–621. doi:10.1038/368619a0.

Vaquer-Sunyer, R., and Duarte, C.M. (2008). Thresholds of hypoxia for marine biodiversity. Proc. Natl. Acad. Sci. 105(40): 15452 LP – 15457. doi:10.1073/pnas.0803833105.

Vargo, G.A., Heil, C.A., Fanning, K.A., Dixon, L.K., Neely, M.B., Lester, K., Ault, D., Murasko, S., Havens, J., Walsh, J., and Bell, S. (2008). Nutrient availability in support of Karenia brevis blooms on the central West Florida Shelf: What keeps Karenia blooming? Cont. Shelf Res. 28(1): 73–98. https://doi.org/10.1016/j.csr.2007.04.008.

Walsh, J. J., Jolliff, J. K., Darrow, B. P., Lenes, J. M., Milroy, S. P., Remsen, A., … Bontempi, P. S. (2006). Red tides in the Gulf of Mexico: Where, when, and why? *Journal of Geophysical Research: Oceans*, *111*(C11). https://doi.org/https://doi.org/10.1029/2004JC002813

Walter, J.F., M.C. Christman, J. Landsberg, B. Linton, K. Steidinger, R. Stumpf, and J. Tustison. (2013). Satellite derived indices of red tide severity for input for Gulf of Mexico Gag grouper stock assessment. SEDAR33-DW08. SEDAR, North Charleston, SC. 43 pp.

Wannamaker, C.M., and Rice, J.A. (2000). Effects of hypoxia on movements and behavior of selected estuarine organisms from the southeastern United States. J. Exp. Mar. Bio. Ecol. 249(2): 145–163. doi:https://doi.org/10.1016/S0022-0981(00)00160-X.

Watson, S. B., Miller, C., Arhonditsis, G., Boyer, G. L., Carmichael, W., Charlton, M. N., … Wilhelm, S. W. (2016). The re-eutrophication of Lake Erie: Harmful algal blooms and hypoxia. *Harmful Algae*, *56*, 44–66. https://doi.org/https://doi.org/10.1016/j.hal.2016.04.010

Weisberg, R. H., Liu, Y., Lembke, C., Hu, C., Hubbard, K., & Garrett, M. (2019). The coastal ocean circulation influence on the 2018 West Florida Shelf *K. brevis* red tide bloom. *Journal of Geophysical Research: Oceans*, *124*, 2501–2512. https://doi.org/10.1029/ 2018JC014887

Weisberg, R.H., Zheng, L., Liu, Y., Lembke, C., Lenes, J.M., and Walsh, J.J. (2014). Why no red tide was observed on the West Florida Continental Shelf in 2010. Harmful Algae 38(C): 119–126. Elsevier B.V. doi:10.1016/j.hal.2014.04.010.

Weisberg, R.H., Zheng, L., and Liu, Y. (2016a). West Florida Shelf upwelling: Origins and pathways. J. Geophys. Res. Ocean. 121(8): 5672–5681. John Wiley & Sons, Ltd. doi:https://doi.org/10.1002/2015JC011384.

Weisberg, R.H., Zheng, L., Liu, Y., Corcoran, A.A., Lembke, C., Hu, C., Lenes, J.M., and Walsh, J.J. (2016b). Karenia brevis blooms on the West Florida Shelf: A comparative study of the robust 2012 bloom and the nearly null 2013 event. Cont. Shelf Res. 120: 106–121. Elsevier Ltd. doi:10.1016/j.csr.2016.03.011.

Wells, M. L., Karlson, B., Wulff, A., Kudela, R., Trick, C., Asnaghi, V., … Trainer, V. L. (2020). Future HAB science: Directions and challenges in a changing climate. *Harmful Algae*, *91*, 101632. https://doi.org/https://doi.org/10.1016/j.hal.2019.101632

Wickham, H., Seidel, D. (2020). scales: Scale Functions for Visualization. R package version 1.1.1. https://CRAN.R-project.org/package=scales

Wiseman, W.J., Rabalais, N.N., Turner, R.E., Dinnel, S.P., and MacNaughton, A. (1997). Seasonal and interannual variability within the Louisiana coastal current: stratification and hypoxia. J. Mar. Syst. 12(1): 237–248. https://doi.org/10.1016/S0924-7963(96)00100-5.

Wu, R.S.S. (2002). Hypoxia: from molecular responses to ecosystem responses. Mar. Pollut. Bull. 45(1): 35–45. doi:https://doi.org/10.1016/S0025-326X(02)00061-9.

Yang, H., and Weisberg, R. H. (1999). Response of the West Florida Shelf circulation to climatological wind stress forcing, *J. Geophys. Res.*, 104(C3), 5301– 5320, doi:10.1029/1998JC900101.

TABLES AND FIGURES

Table 1. Daily river discharge statistics for major rivers influencing the West Florida Shelf.

River name	Mean Daily Discharge (m^3 s^{-1})	Daily Minimum (m^3 s^{-1})	Daily Maximum (m^3 s^{-1})	Daily SD
Apalachicola	638	138	6173	486
Suwannee	249	30	1368	181
Peace	26	0	614	41
Caloosahatchee	54	0	716	74

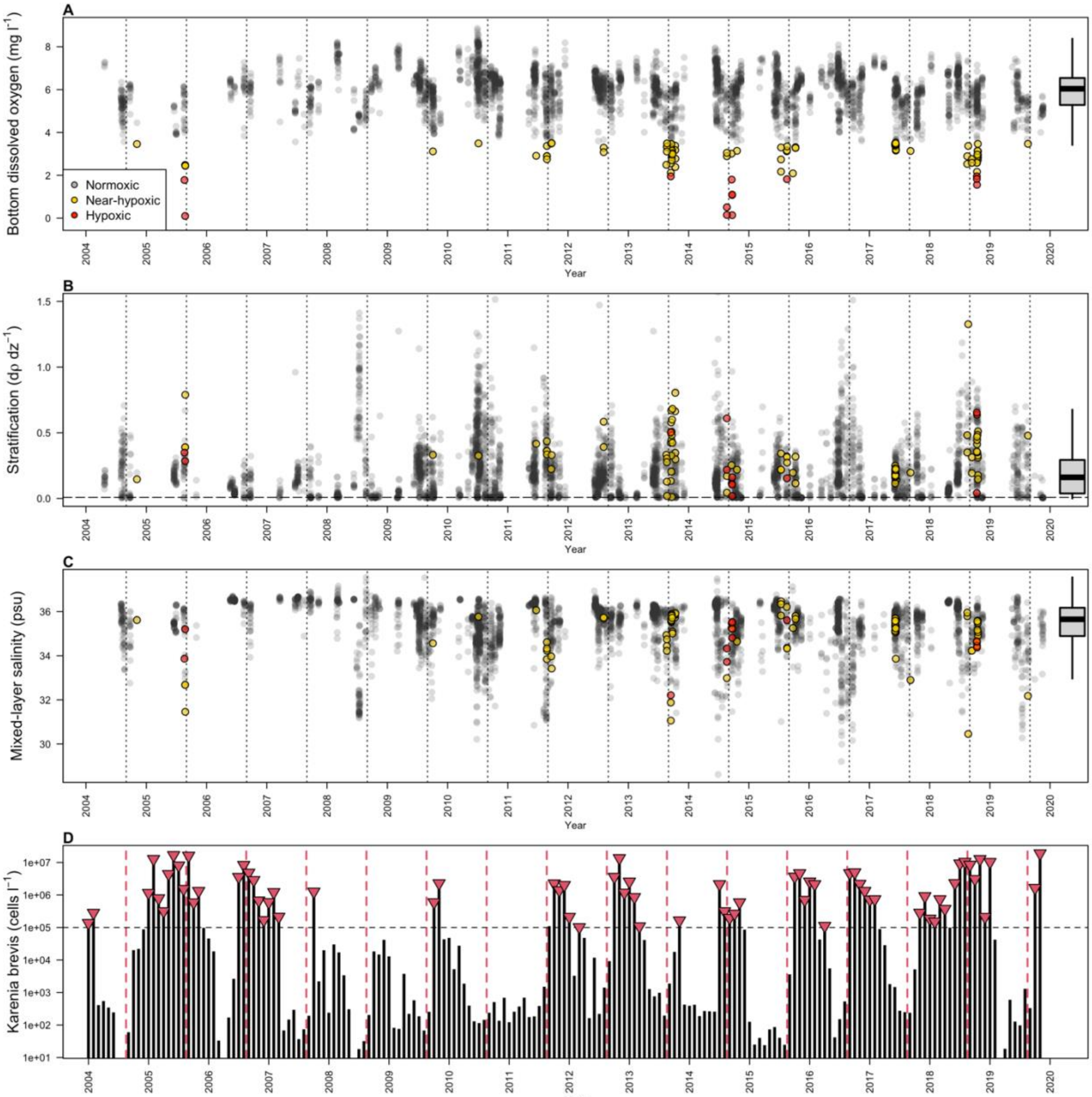

Figure 1. (A) Time series of all near bottom dissolved oxygen concentrations (DO, mg l^{-1}) from CTD casts on the West Florida Shelf. (B) Time series of stratification defined as the density (kg m^{-3}) gradient with depth. The no-stratification cutoff (0.0081) is indicated by a horizontal dashed line. (C) Time series of mixed-layer salinities from CTD data. Data points that were hypoxic (DO $\leq$ 2 mg l^{-1}) are red and near hypoxic (2 < DO $\leq$ 3.5 mg l^{-1}) are gold (subplots A and B). Boxplots demonstrating the distribution of all the data are added (subplots A – C). (D) Time series of monthly 99th percentile of *Karenia brevis* concentrations (cells liter $^{-1}$) on the West

Florida Shelf. Downward pointing red triangles indicate months above the bloom threshold (>100,000 cells l^{-1}) denoted by the horizontal dashed line. The vertical dotted lines reference the approximate peak of HAB season on September 1st of every year (subplots A – D).

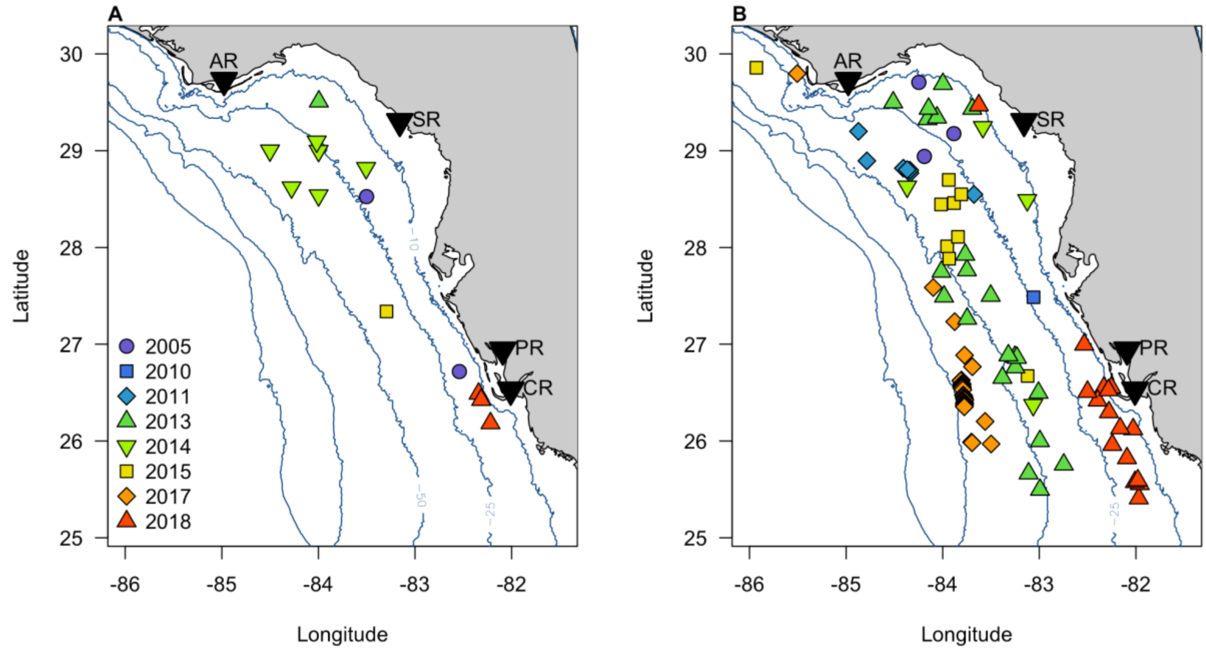

Figure 2. (A) Spatial distribution of all CTD casts with near bottom dissolved oxygen concentrations that were hypoxic (DO ≤ 2 mg l^{-1}). (B) Spatial distribution of all CTD casts with near bottom dissolved oxygen concentrations that were near hypoxic (2 < DO ≤ 3.5 mg l^{-1}). Bathymetric contours at 10, 25, 50, 100, and 200 meters are included as reference. The mouths of the three major rivers defined by highest discharge–Apalachicola River (AR), Suwannee River (SR), Peace River (PR) and the Caloosahatchee River (CR)–are indicated as upside-down, black triangles.

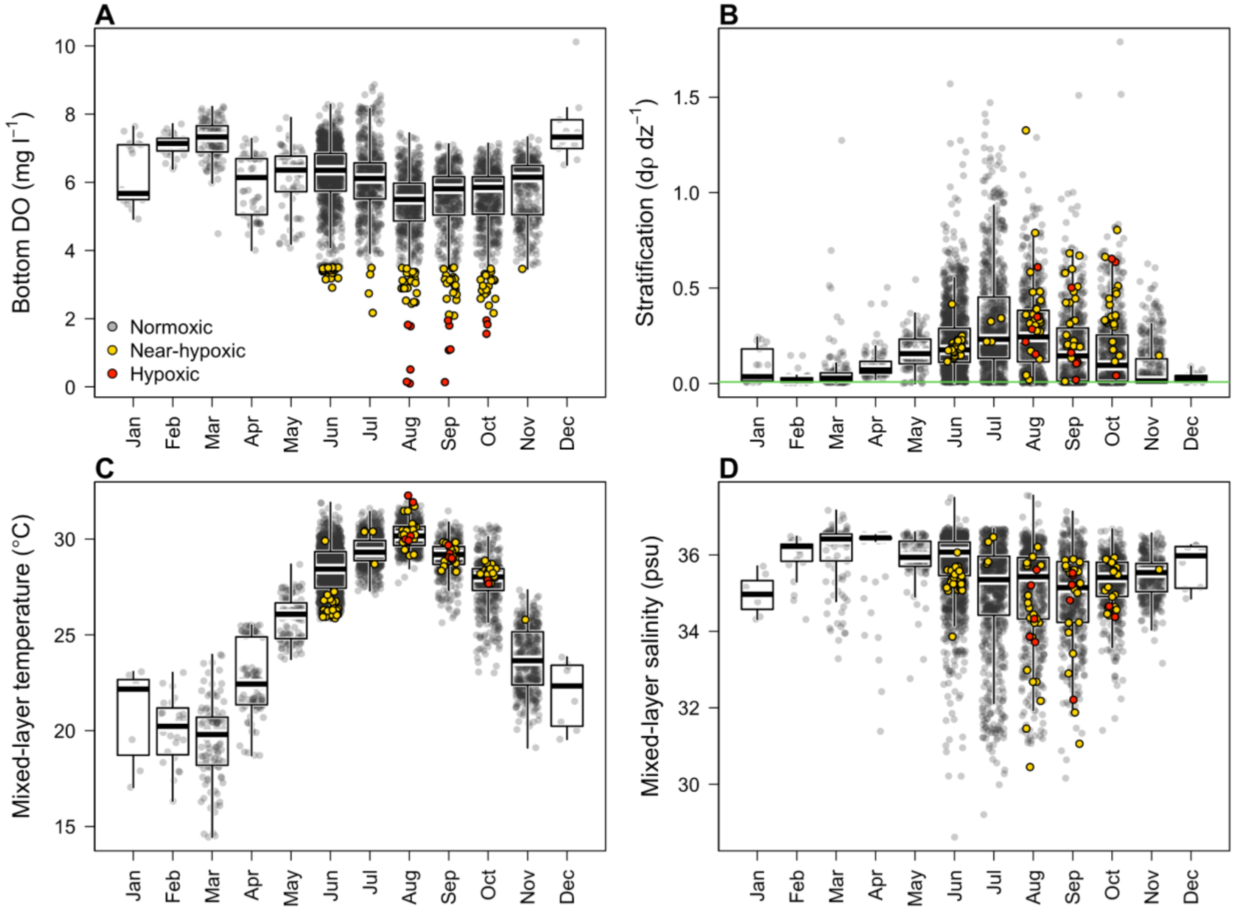

Figure 3. Boxplots displaying the climatology per month of bottom dissolved oxygen (A), stratification (B), mixed-layer temperature (C), and mixed-layer salinity (D). The no-stratification cutoff (0.0081) is indicated by a horizontal green line (subplot B). Data points that were hypoxic (DO $\leq$ 2 mg l^{-1}) are red and near hypoxic (2 < DO $\leq$ 3.5 mg l^{-1}) are gold. Boxplots are overlaid on top of all the data points.

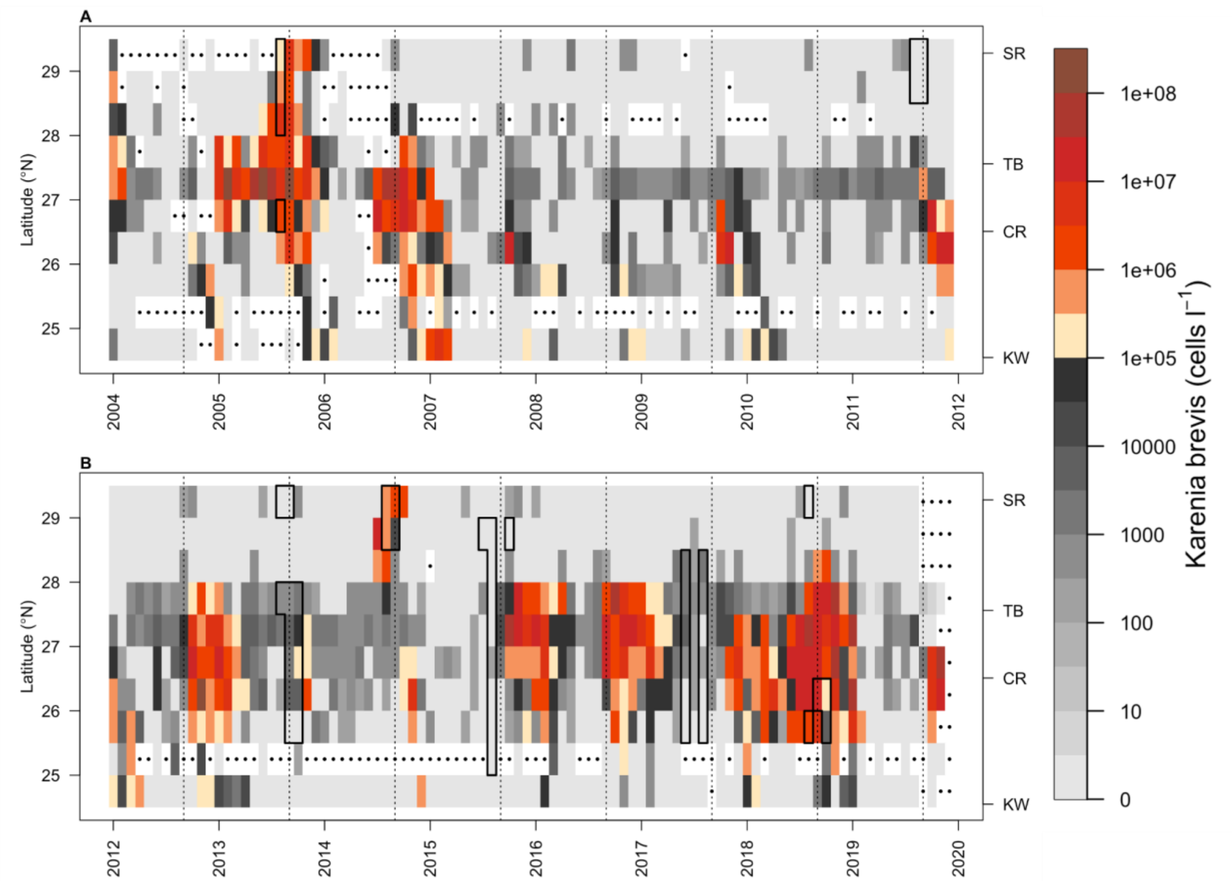

Figure 4. *Karenia brevis* (cells l^{-1}) Hovmöller diagram. Each box was aggregated as the 99% percentile of *K. brevis* cell counts per 0.5° latitude per month. Missing data are indicated by black dots. (A) Data from 2004 through 2011 and (B) bottom plot is data from 2011 through 2019. On the right side of the plots Suwannee River (SR), mouth of Tampa Bay (TB), Caloosahatchee River (CR), and Key West (KW) are indicated as reference. The vertical dotted lines reference the approximate peak of the HAB season in September of every year. Black boxes highlight observed hypoxia events in August 2005, August-October 2013, August-September 2014, June and August 2017, and August-October 2018. The colorbar has a break at 100,000 cells l^{-1}, which is defined by Florida Fish and Wildlife Institute as a medium level HAB with respiratory irritation, shellfish closures, fish kills and likely detection by satellite observations.

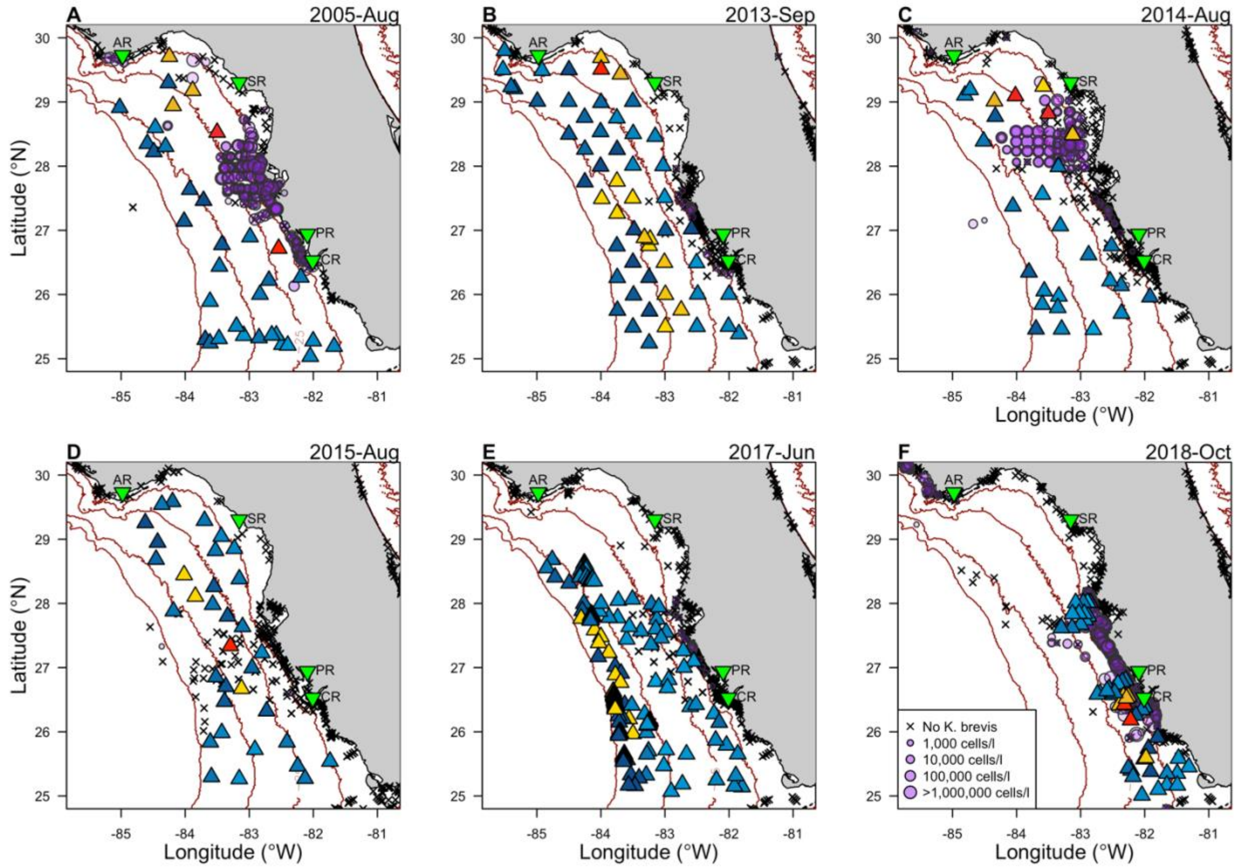

Figure 5. Sampled near bottom dissolved oxygen (DO) concentrations for months with hypoxia (DO ≤ 2 mg l^{-1}) or near hypoxia (2 ≤ DO ≤ 3.5 mg l^{-1}) present. Bathymetric contours at 10, 25, 50, and 100 meters are included as reference. The diameter of the purple circles is proportional to the logarithm base 10 of *Karenia brevis* cell counts for the same month the CTD data were obtained and black Xs indicate water samples without detectable *K. brevis* cells. The Apalachicola River (AR), Suwannee River (SR), Peace River (PR), and the Caloosahatchee River (CR) are indicated as upside-down, green triangles. Blue filled triangles are normoxic (DO > 3.5 mg l^{-1}), yellow triangles are near hypoxia (2 ≤ DO ≤ 3.5 mg l^{-1}), and red triangles are hypoxic (DO ≤ 2 mg l^{-1}).

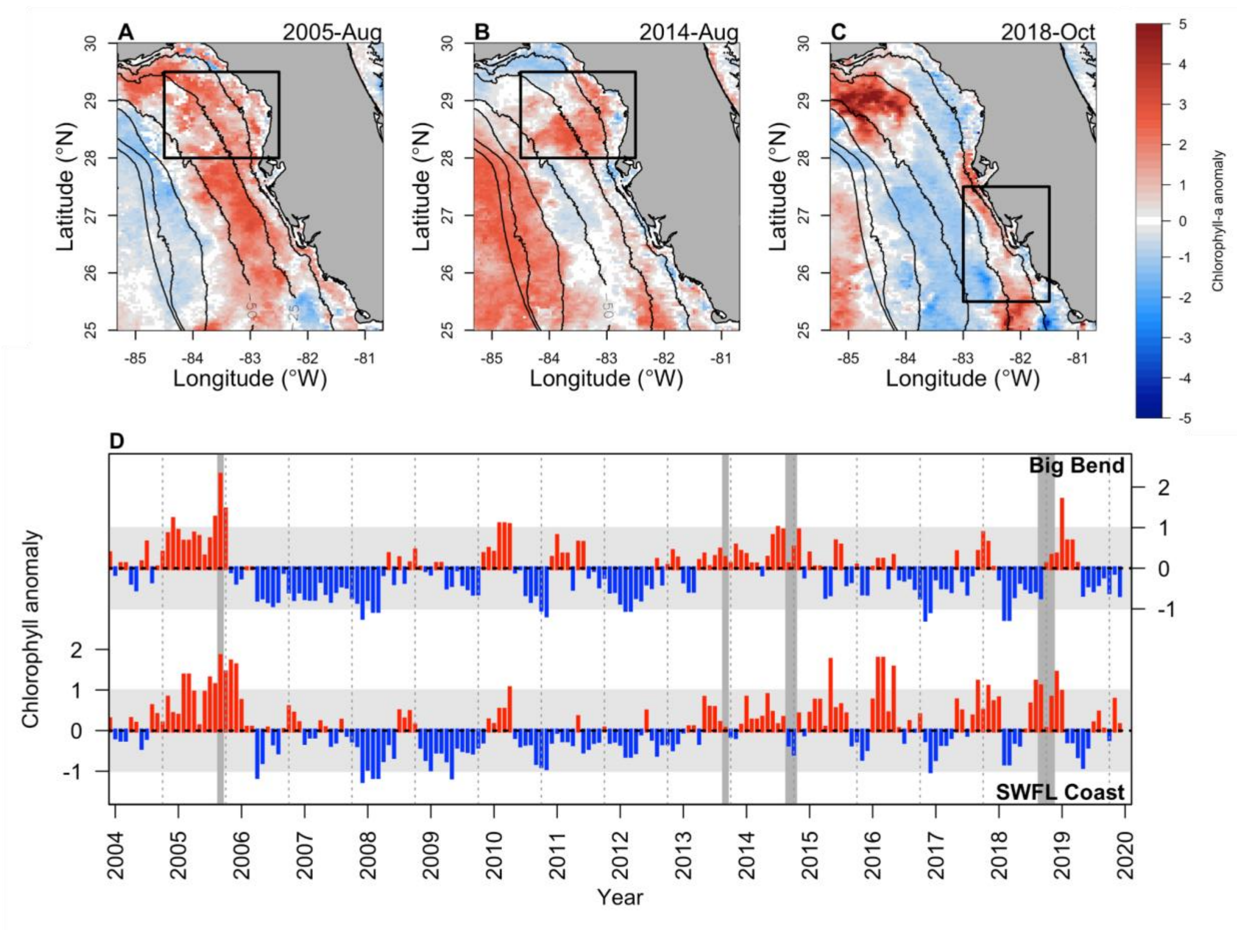

Figure 6. Chlorophyll-a anomalies calculated from MODIS imagery for (A) August 2005, (B) August 2014, and (C) October 2018. (D) Anomaly time series for the Big Bend region corresponding to box in plot B and southwest Florida (SWFL) coast corresponding to box in plot C. Bathymetric contours at 10, 25, 50, 100, 200, and 300 meters are included as reference. The dashed vertical lines in plot D are September of each year, which is the approximate peak of HAB season. Vertical gray bars indicate the observed hypoxia events in August 2005, August 2013, August-September 2014, and August-October 2018. Horizontal gray bars are the +/- 1 standard deviation anomaly.

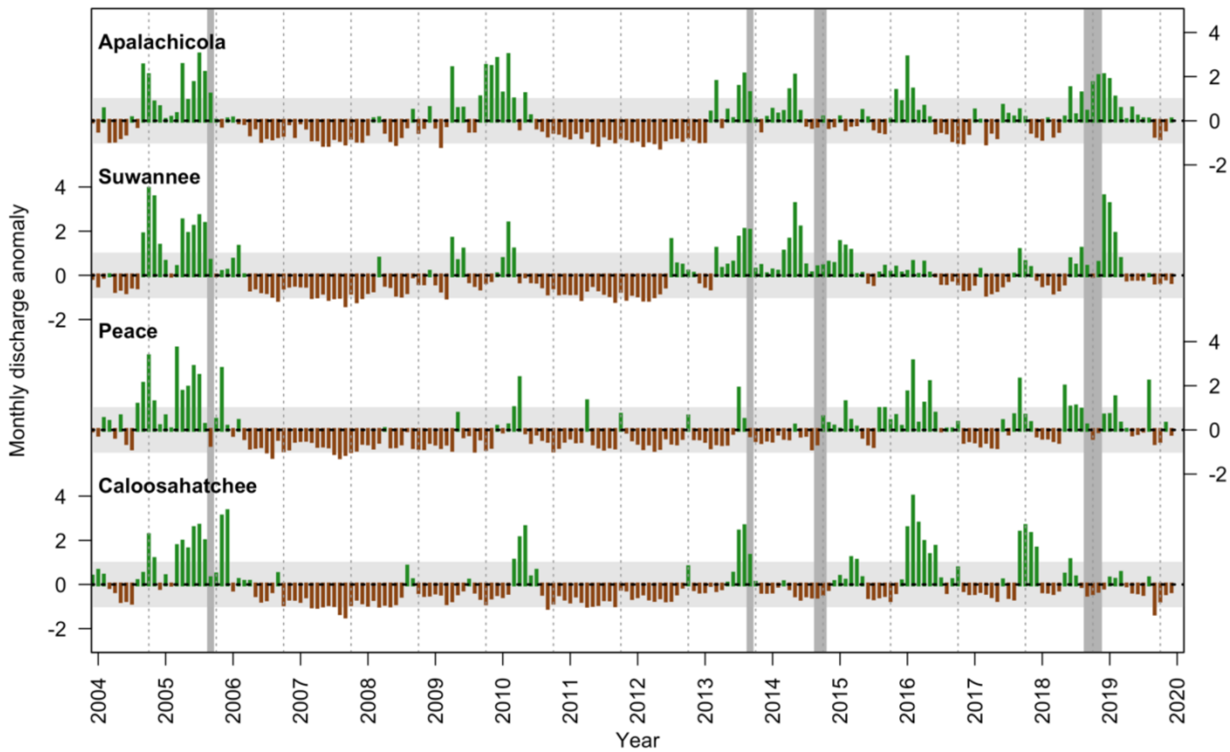

Figure 7. Daily river discharge anomalies for Apalachicola, Suwannee, Peace, and Caloosahatchee Rivers. Daily discharge data for each river were downloaded from the USGS National Water Information System website. Daily data were aggregated into monthly mean values and then the standardized anomalies were calculated per river. The vertical dashed lines denote September, which is approximately the peak HAB season. Vertical gray bars indicate the observed hypoxia events in August 2005, August 2013, August-September 2014, and August-October 2018. Horizontal gray bars are the +/- 1 standard deviation anomaly.

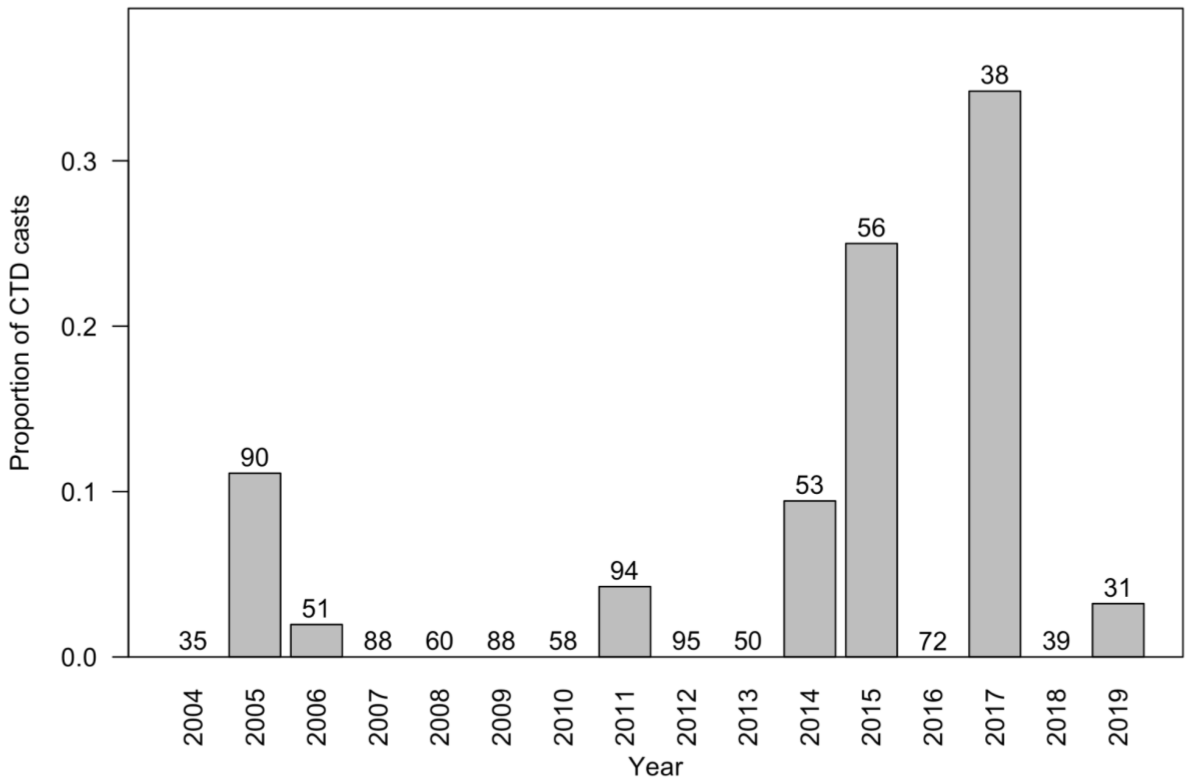

Figure 8. Bar chart displaying the proportion of CTD casts with low DO (DO ≤ 3.5 mg l^{-1}) sampled at depths greater than 100 m during May through September of each year. The total number of casts regardless of DO concentrations are displayed above bars as a reference.