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

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

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 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). 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 is the negative effects of combined HAB-hypoxia event 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 (Rojas de Mendiola 1979, Pitcher & Probyn, 2011, Siedlecki et al. 2015, Watson et al. 2016), it is unclear to what extent this occurs during HABs that impact the West Florida Shelf. The toxin-producing dinoflagellate *Karenia brevis* is the main causative species for HABs occurring annually on the West Florida Shelf (Walsh et al. 2006). 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). Monitoring of *K. brevis* cell counts in Florida dates to the 1950s and provides information on several notable events in the past 20 years. 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 (Vaquer and Duarte, 2008). 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. 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, maximum and minimum values recommended by Garcia et al. (2018) for the variables in the coastal North Atlantic were used to flag data that were outside the range boundaries. 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. 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). 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).

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.

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. 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. 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), Suwanee (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). 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).

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 S1). 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). 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 2011demonstrating 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 7). 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 times 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 Suwanee 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 17 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. Whereas in years with blooms but without hypoxia, there was an absence of HAB activity in the summer months. There was one year 2006 in which there was a summer HAB that continued into the fall, and there was no hypoxia detected. The reason for 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, but there was data collected in September. So, either reduced sampling coverage precluded detection of hypoxia and it dissipated quickly, or, alternatively, there was no hypoxia in 2006. While sampling coverage may be invoked, the alternative that there was no hypoxia was supported by the other observational evidence. 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 are 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 contribute 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 of which 2005 and 2018 were the most significant HABs to occur in the past 20 years

(Figures 1, 4 and 5; Turley et al. 2021). Moreover, CTD profiles with observed hypoxia in 2014 and 2018 suggest a surface freshening consistent with riverine discharge driving the density stratification. 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). However, this relationship has been characterized as inconsistent (Dixon et al. 2014) and, more recently, non-linear (Medina et al. 2020). The more 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 Suwanee 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 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. 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 (also referred to as the 2018 bloom). 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 was neither direct nor consistent because there were several HABs in which river discharge was lower than average (i.e., 2006, 2007, and 2017) consistent with the results of previous studies (Vargo et al. 2008, Dixon et al. 2014, Medina et al. 2020). 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 HABs and the formation of hypoxic regions, particularly when HABs persist through the summer months. But chlorophyll and river discharge were not individually good indicators of either HABs or hypoxia. There are likely multiple pathways leading to HAB-hypoxic events that are not easily described in a singular conceptual model.

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 considered to be the worst events in the past 20 years (Hu et al 2006, Weisberg et al. 2019, Turley et al. 2021), while, 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 S1 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 southeastern Florida coast, 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 2005 and 2014, hypoxia in 2018 was not observed in the same location but was instead 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 indicating a lingering progression of high biological oxygen demand associated with the HAB (see Supplementary materials 2, Figure S2 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 is 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 marine life 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 HAB, 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 stock assessments incorporate data on age structure, abundance indices, and other biological information and are routinely used to track population status used in fisheries management. Population assessments for both red grouper and gag grouper show 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). This notion is corroborated by direct evidence of HAB induced mortality; for example, Driggers et al. (2016) documented mass grouper kills during fishery surveys that transected the major area impacted by the 2014 HAB-hypoxia. Additionally, a research effort 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. Multiple lines of evidence thus suggest 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. In addition, multiple long-term perturbations to these habitats likely results in cascading effects as habitat degradation is unlikely to be immediately manifested in population and community dynamics signals (i.e., impacts possibly lag in time).

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; modeling studies suggest that temperature has been a factor in driving intensification of some HABs (Gobler et al. 2017) and meta-analysis suggests an increase in some HABs which is partly attributable to improved monitoring over time (Anderson et al. 2021). However, *K. brevis* does not seem to favor warmer temperatures. In fact, it 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 (Magana and Villareal 2006, Hitchcock 1976, Eng-Wilmot et al. 1977). This suggests increasing temperatures from climate change may reduce the frequency and magnitude of HAB on the West Florida Shelf. However, HABs develop through unique combinations of physical and biological factors, but few studies have been carried out on co-stressor effects (Griffith and Gobler 2020), and unexpected patterns in future HAB activity may emerge (Wells et al. 2020). The West Florida Shelf is predicted to undergo dramatic warming in the future (Liu et al. 2015), which will increase stratification, but generally disfavor the formation of HABs (though the ability of *K. brevis* to vertically migrate and outcompete other phytoplankton species may change this). 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 (Philips et al. 2020). 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 low DO 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 was also thought to have 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 as the source of low DO on the shelf requires not just upwelling onto the West Florida Shelf, but also requires that 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 S3) 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 S3), 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 HAB 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. The low DO events 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 aggregated into monthly bins 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 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 since the maximum depth of any cast may not represent the true sea floor. There may have been cryptic bottom hypoxia that went unobserved 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 these events on the West Florida Shelf. 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 illuminating some 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. 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.

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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.

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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
Suwanee	249	30	1368	181
Peace	26	0	614	41
Caloosahatchee	54	0	716	74

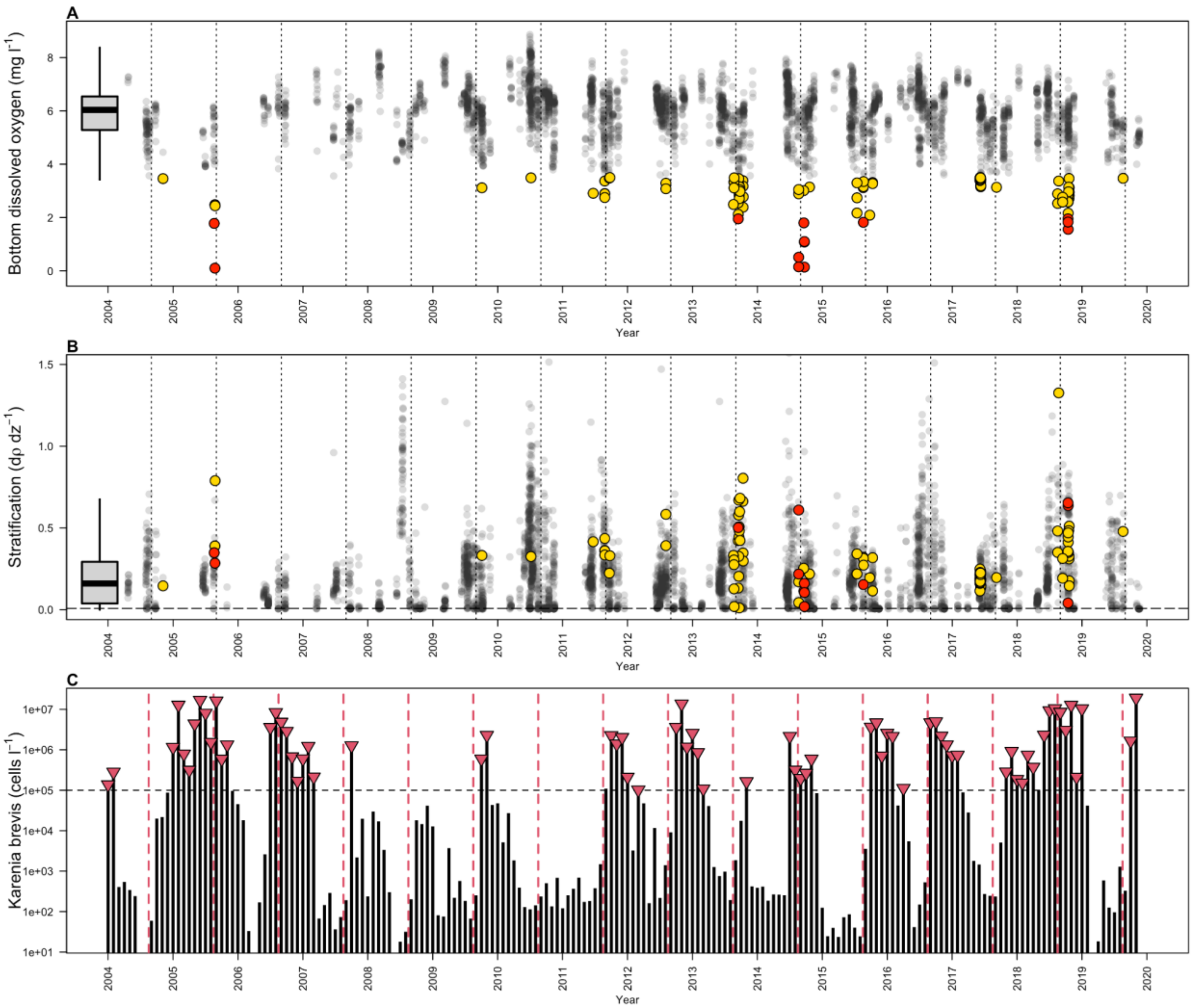

Figure 1. (A) Time series of all near bottom dissolved oxygen concentrations (DO) from CTD casts on the West Florida Shelf. (B) Time series of stratification defined as the density gradient with depth. The no-stratification cutoff (0.0081) is indicated by a horizontal dashed line. (C) Time series of monthly 99th percentile of K. 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. 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. The vertical dotted lines reference the approximate peak of HAB season on September 1st of every year. Boxplots demonstrating the distribution of all the data are added (subplots A and B).

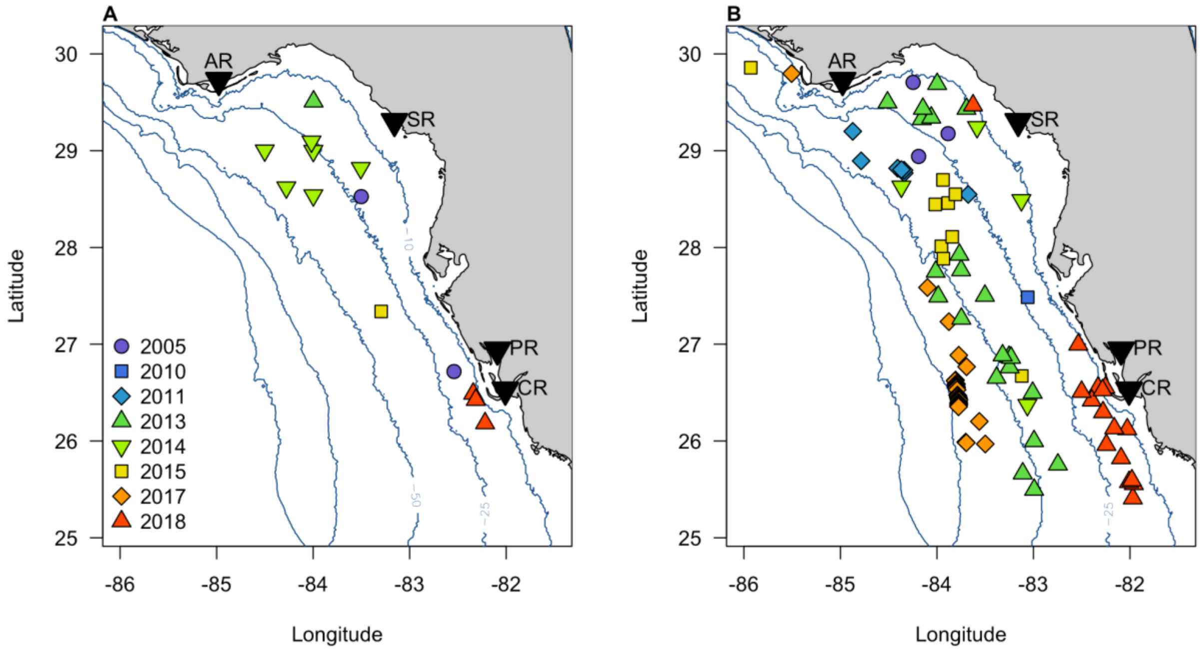

Figure 2. (A) Spatial distribution of all CTD casts with near bottom dissolved oxygen concentrations that were hypoxic (DO ≤ 2 mg l^{-1}). (B) Spatial distribution of all CTD casts with near bottom dissolved oxygen concentrations that were near hypoxic (2 < DO ≤ 3.5 mg l^{-1}). Bathymetric contours at 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.

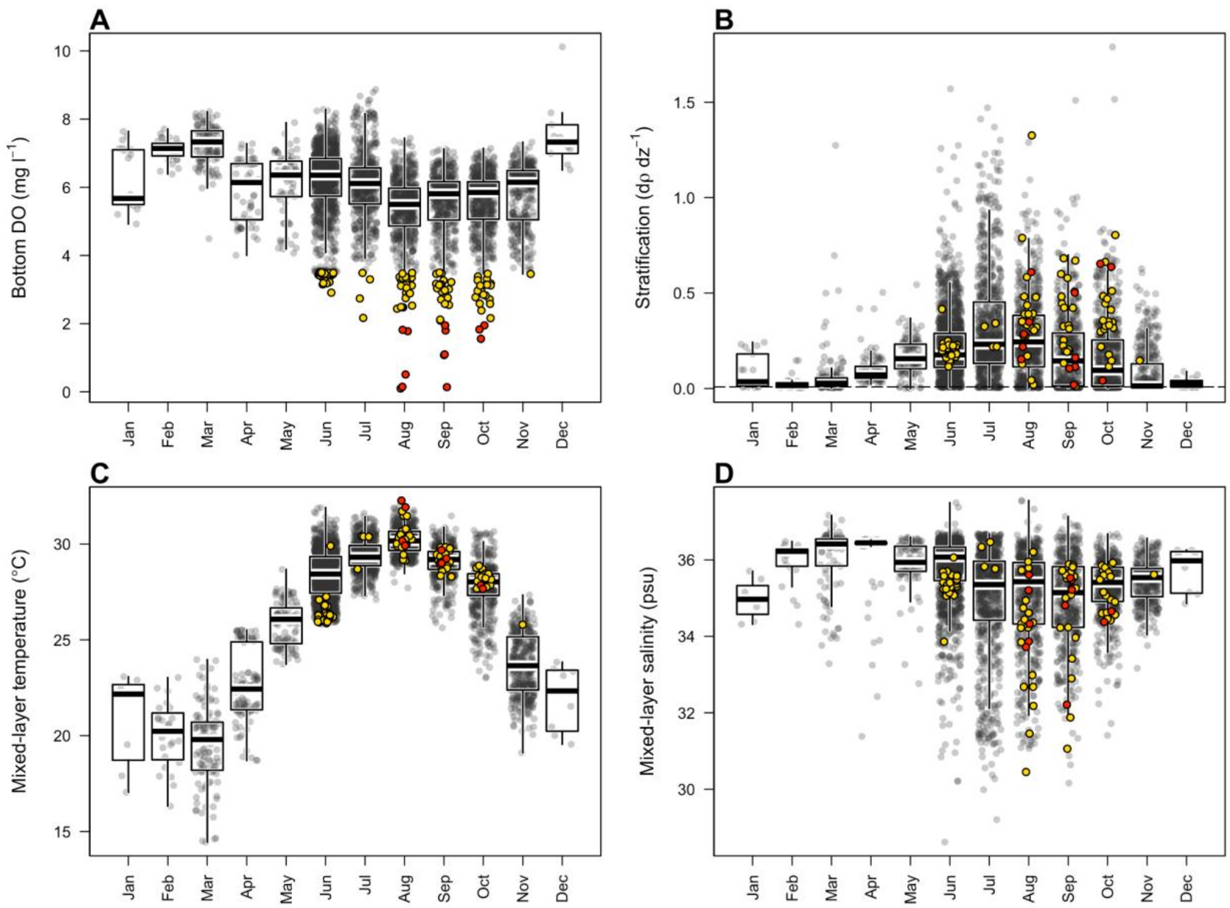

Figure 3. Boxplots displaying the climatology per month of bottom dissolved oxygen (A), stratification (B), mixed-layer temperature (C), and mixed-layer salinity (D). The no-stratification cutoff (0.0081) is indicated by a horizontal dashed line (subplot B). Data points that were hypoxic (DO ≤ 2 mg l^{-1})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

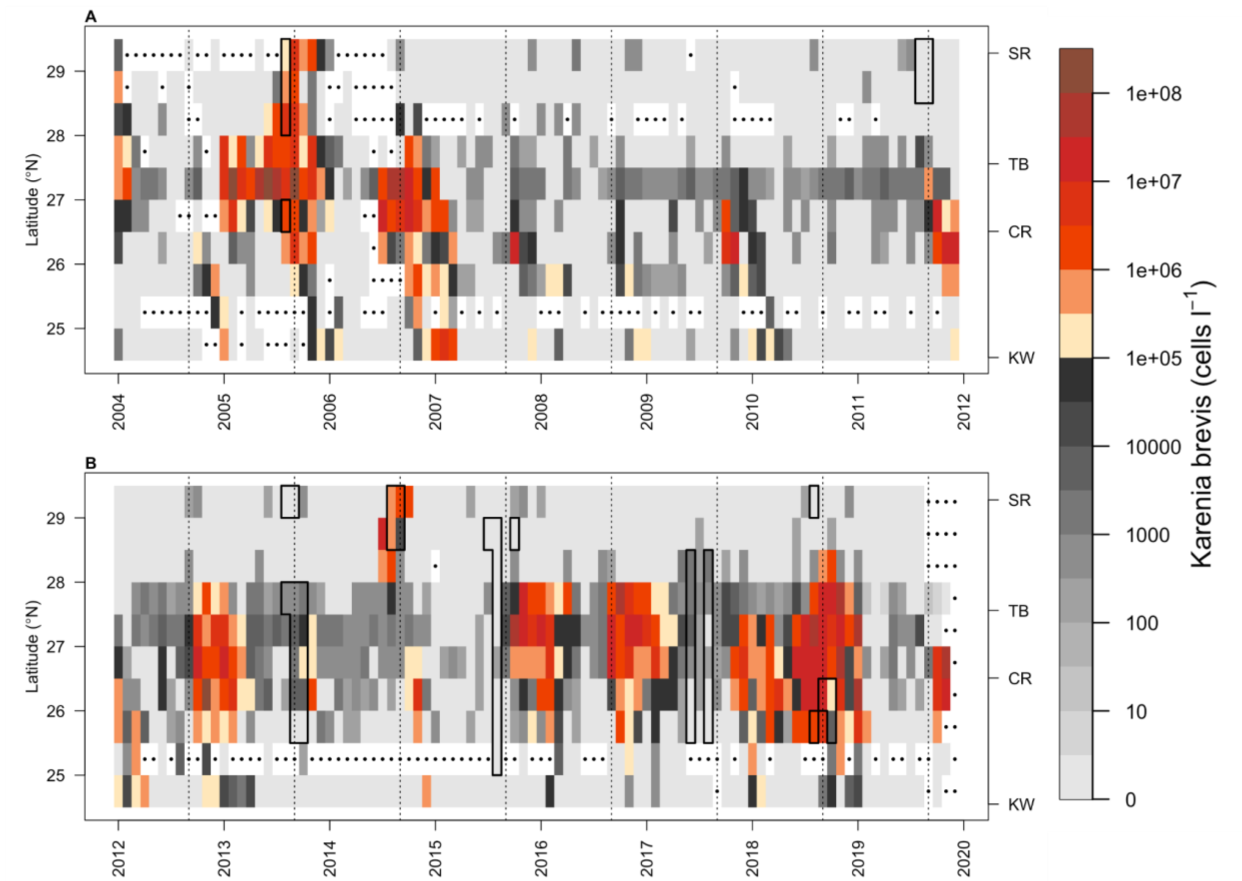

Figure 4. *Karenia brevis* (cells l^{-1}) Hovmöller diagram. Each box was aggregated as the 99% percentile of K brevis cell counts per 0.5° latitude per month. Missing data are indicated by black dots. (A) Data from 2004 through 2011 and (B) bottom plot is data from 2011 through 2019. On the right side of the plots Suwannee River (SR), month 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-September 2014, 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.

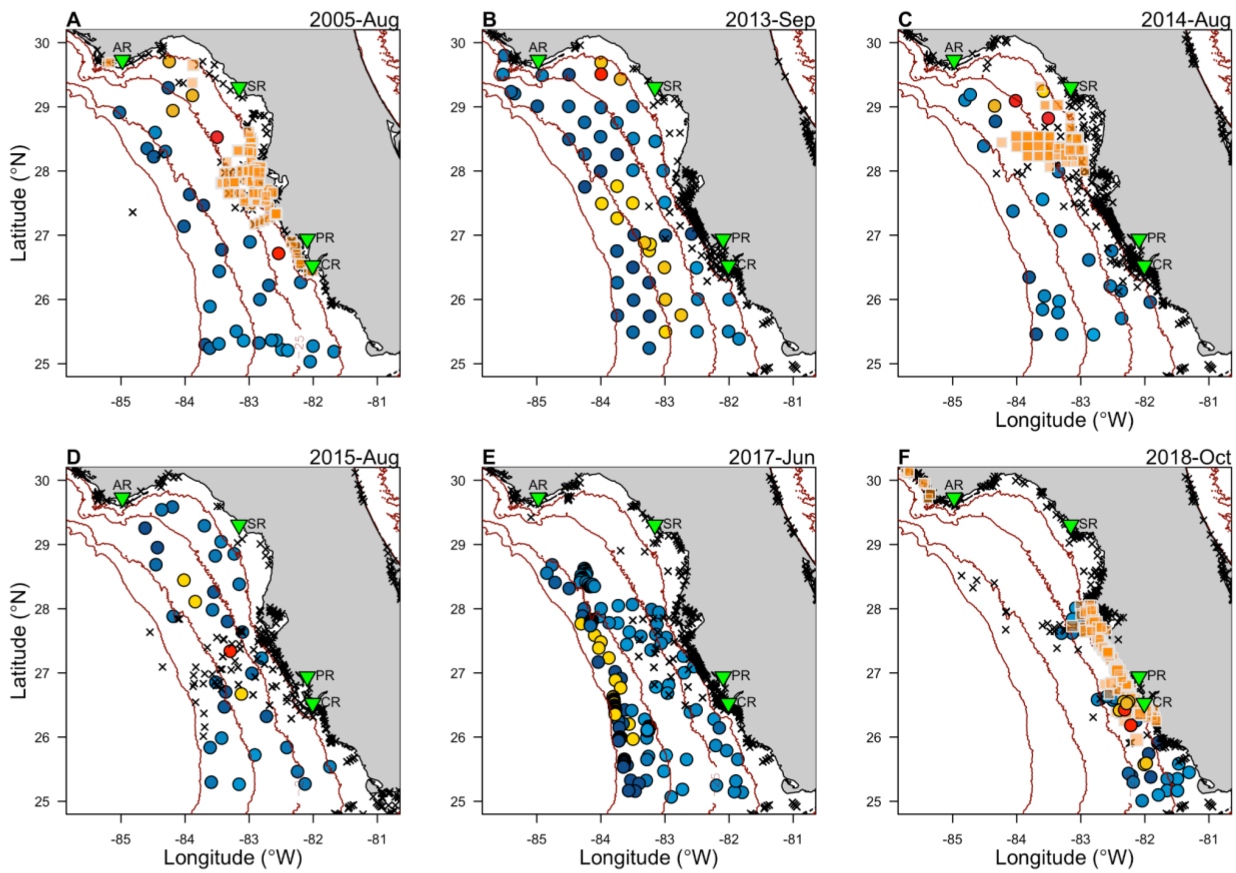

Figure 5. Sampled near bottom dissolved oxygen (DO) concentrations for months with hypoxia (DO ≤ 2 mg l^{-1}) or near hypoxia ($2 \leq$ DO ≤ 3.5 mg l^{-1}) present. Bathymetric contours at 10, 25, 50, and 100 meters are included as reference. Orange squares are proportional to the logarithm base 10 of *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 circles are normoxic (DO > 3.5 mg l^{-1}), yellow circles are near hypoxia ($2 \leq$ DO ≤ 3.5 mg l^{-1}), and red circles are hypoxic (DO ≤ 2 mg l^{-1}).

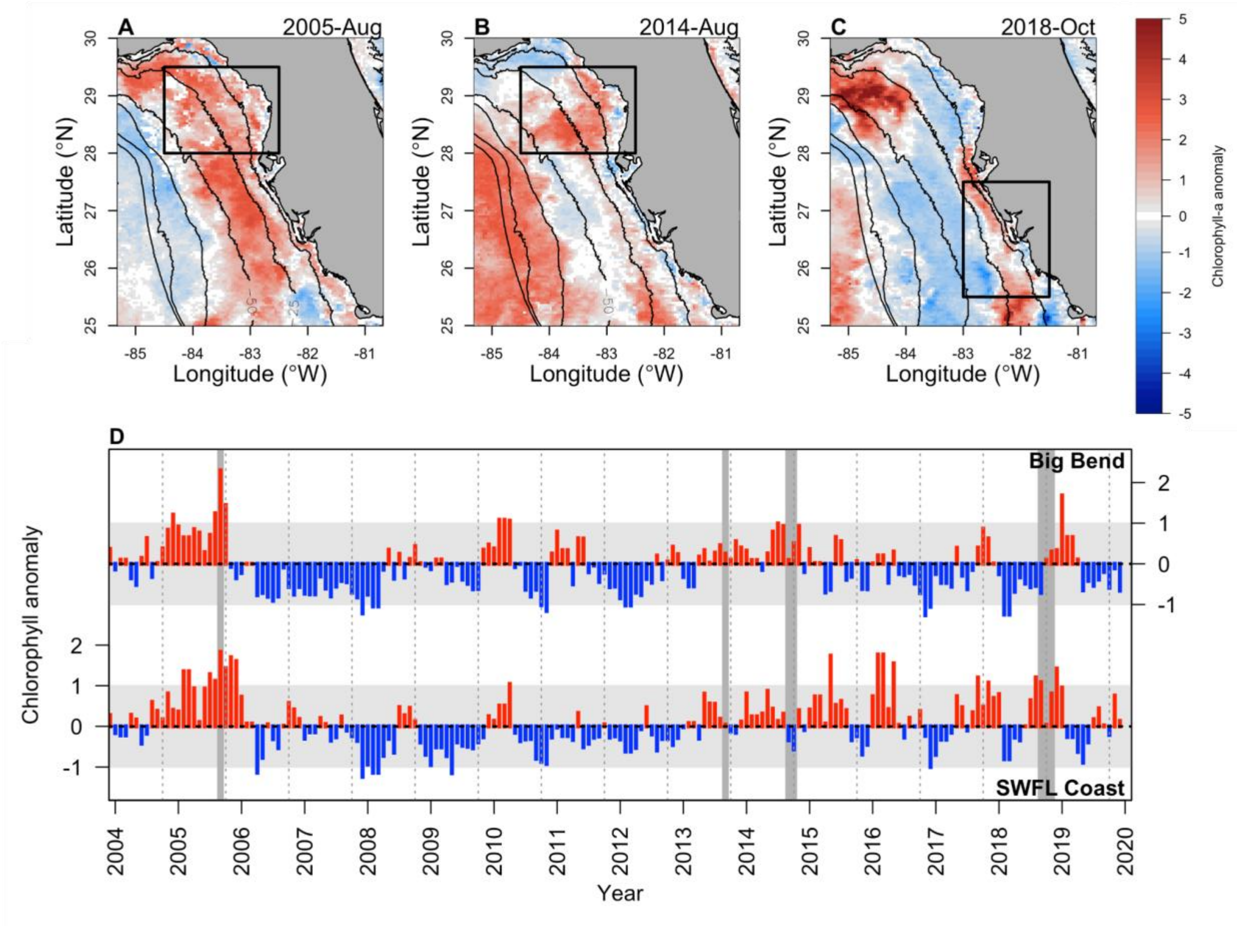

Figure 6. Chlorophyll-a anomalies calculated from MODIS imagery for (A) August 2005, (B) August 2014, and (C) October 2018. (D) Anomaly time series for the Big Bend region corresponding to box in plot B and southwest Florida (SWFL) coast corresponding to box in plot C. Bathymetric contours at 10, 25, 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.

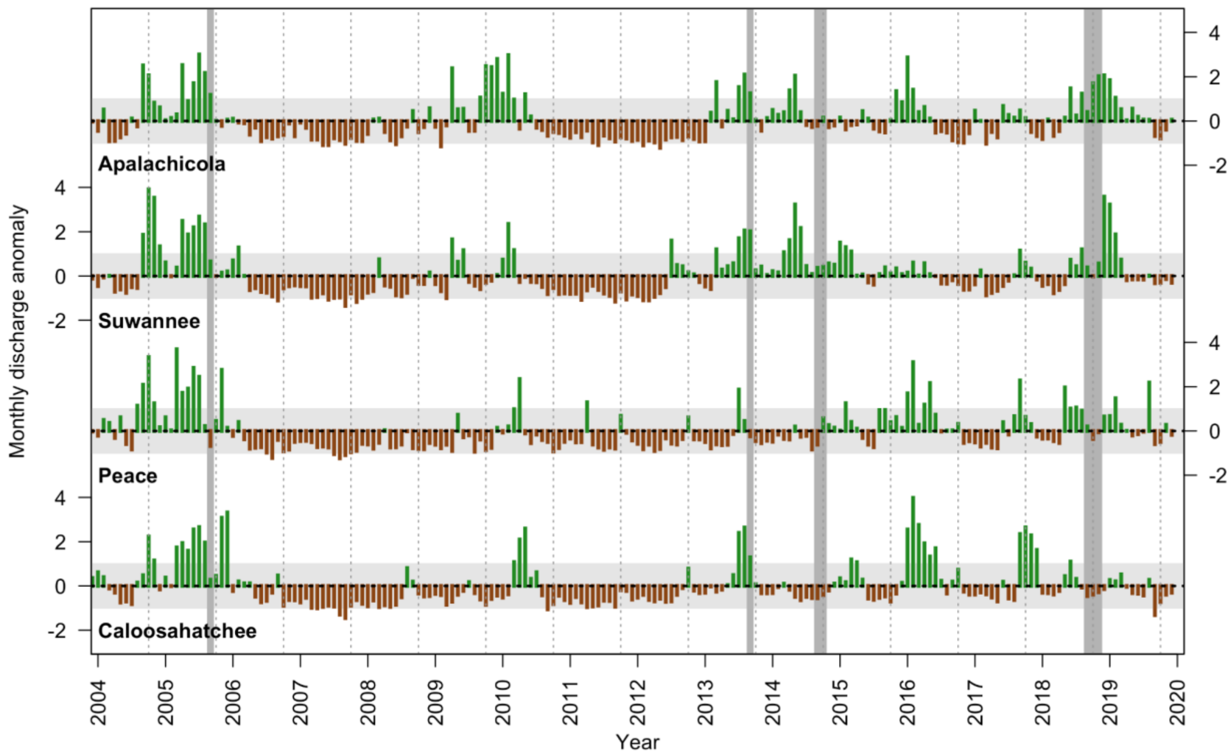

Figure 7. Daily river discharge anomalies for Apalachicola, Suwanee, Peace, and Caloosahatchee Rivers. Daily discharge data for each river were downloaded from the USGS National Water Information System website. Daily data were aggregated into monthly mean values and then the standardized anomalies were 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.

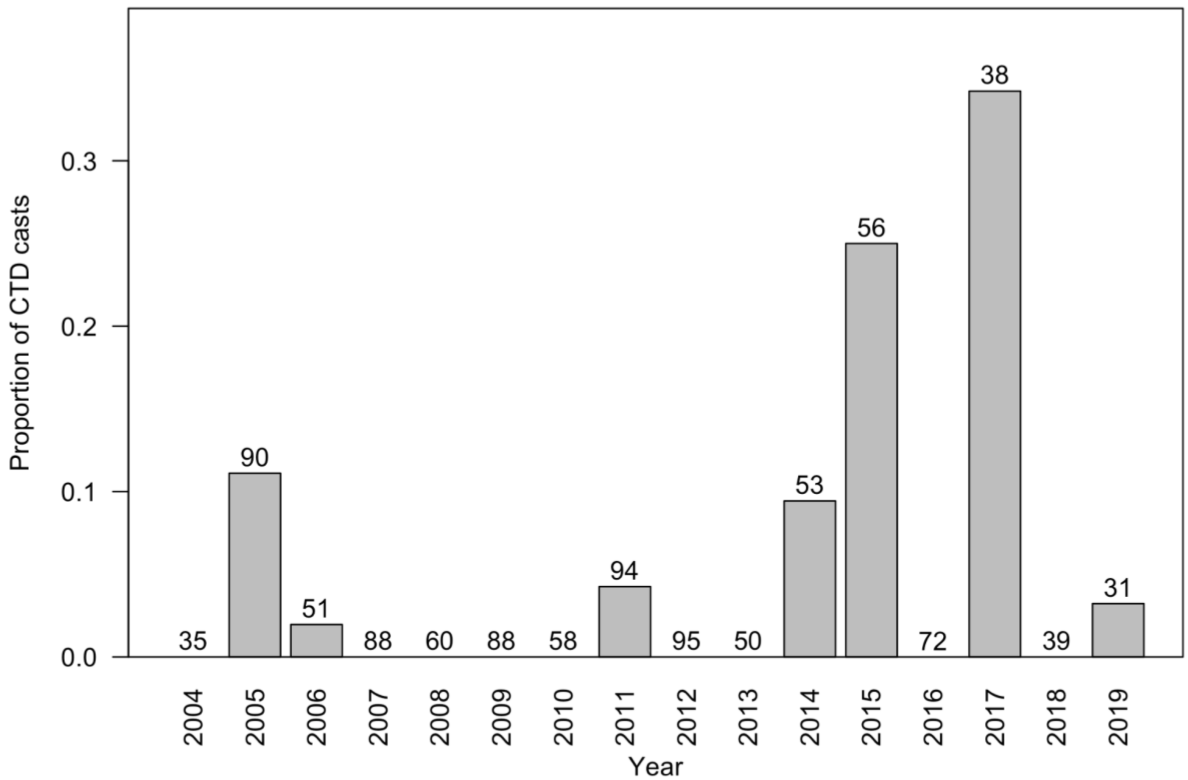

Figure 8. Bar chart displaying the proportion of CTD casts with low DO (DO $\leq$ 3.5 mg l^{-1}) sampled at depths greater than 100 m during May through September of each year. The total number of casts regardless of DO concentrations are displayed above bars as a reference.