

Advection of *Karenia brevis* blooms from the Florida Panhandle towards Mississippi coastal waters



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ABSTRACT

Harmful Algal Blooms (HABs) of *Karenia brevis* have been documented along coastal waters of every state bordering the Gulf of Mexico (GoM). Some Gulf Coast locations, such as Florida and Texas, suffer from recurrent intense and spatially large blooms, while others such as Mississippi seem to rarely observe them. The main objective of this work is to understand the dynamics that led to the *K. brevis* bloom in Mississippi coastal waters in fall 2015. Blooms of *K. brevis* from the Florida Panhandle region are often advected westward towards the Mississippi–Alabama coast; however there is interannual variability in their presence and intensity in Mississippi coastal waters. The 2015 *K. brevis* bloom was compared to the 2007 Florida Panhandle *K. brevis* bloom, which showed a westward advection pattern, but did not intensify along the Mississippi coast. Cell counts and flow cytometry were obtained from the Mississippi Department of Marine Resources, Alabama Department of Public Health, Florida Fish and Wildlife Conservation Commission and The University of Southern Mississippi. Ocean color satellite imagery from the Moderate Resolution Imaging Spectroradiometer onboard the Aqua satellite was used to detect and delineate the blooms in 2007 and 2015. Two different regional applications of NCOM–Navy Coastal Ocean Model (1-km resolution NCOM–GoM/Gulf of Mexico and 6-km resolution NCOM–IASNFS/Intra Americas Sea Nowcast Forecast System) were used to understand the circulation and transport pathways. A Lagrangian particle tracking software was used to track the passive movement of particles released at different locations for both bloom events. Ancillary data (e.g., nutrients, wind, salinity, river discharge) from local buoys, monitoring stations and coincident oceanographic cruises were also included in the analysis. The blooms of *K. brevis* reached the Mississippi coast both years; however, the bloom in 2007 lasted only a few days and there is no evidence that it entered the Mississippi Sound. Two major differences were observed between both years. First, circulation patterns in 2015 resulting from an intense westward–northwestward that persisted until December allowed for continuous advection, whereas this pattern was not evident in 2007. Second, local river discharge was elevated throughout late fall 2015 while 2007 was below the average. Thus, elevated discharge may have provided sufficient nutrients for bloom intensification. These results illustrate the complex, but important interactions in coastal zones. Further, they emphasize the importance in establishing comprehensive HAB monitoring programs, which facilitate our understanding of nutrient and phytoplankton dynamics, and stress the importance for multi-agency cooperation across state boundaries.

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1. Introduction

Harmful Algal Blooms (HABs) of the toxic dinoflagellate *Karenia brevis* (formerly: *Gymnodinium breve* (Davis, 1948) and *Ptychodiscus brevis*) pose a threat to coastal communities in the Gulf of Mexico (Baker, 2009; Heil and Steidinger, 2009). Brevetoxins produced by *K. brevis* cause Neurotoxic Shellfish Poisoning (NSP; Steidinger and Joyce, 1973; Poli et al., 2000). Additionally, wave action can easily break the cells, causing the toxins to aerosolize and travel inland up to 6 miles from the coast (Kirkpatrick et al., 2004; Kirkpatrick et al., 2011; Fleming et al., 2011). Therefore, public health concerns include NSP, respiratory irritation and illness. Blooms of *K. brevis* also are responsible for massive fish kills, mortality in higher vertebrates (e.g., turtles, dolphins, manatees and birds) and toxin bio-accumulation in filter-feeders such as oysters (Landsberg et al., 2009). Shellfish harvesting areas are closed when cell concentrations are above 5000 cells L⁻¹ and remain closed until toxin levels are 20 mouse units or less (Reich et al., 2015). In addition to the economic impact to local fisheries, HABs in Florida can lead to losses between 2.7 and 3.7 million USD per month for the lodging and restaurant industry alone (Larkin and Adams, 2007).

Blooms of *K. brevis* are quite common throughout the Gulf of Mexico (GoM). These HABs are often called “Florida red tides” because they occur almost every year in Florida waters, and can last months and extend thousands of kilometers along the West Florida Shelf. Although Florida is the GoM state that most frequently experiences *K. brevis* blooms, all other coastal states of the GoM have been affected by them to a lesser extent. Blooms of *K. brevis* are not limited by regional boundaries. For example, blooms in the Florida Panhandle can be advected west towards the Alabama and Mississippi coast (Dortch et al., 1998; Maier-Brown et al., 2006), and blooms in the West Florida Shelf can be advected by the Loop Current into the Florida Straits and then into the Gulf Stream current along the East Coast of the United States (Steidinger and Haddad, 1981; Tester et al., 1991). This manuscript focuses on blooms along the northern GoM (nGoM) from the Florida Panhandle to the western Mississippi Bight.

Blooms of *K. brevis* have rarely been observed along the Mississippi coast. The first official report of a *K. brevis* bloom along the Mississippi coast was November of 1996 by Dortch et al. (1998). Cell counts above 50,000 cells L⁻¹ were observed in 2005 after the passage of Hurricane Katrina (Holiday et al., 2008), although no major bloom was reported during that year. A short-term bloom (<10 days) was observed in November 2007 in the western Mississippi Bight. So after 1996, major *K. brevis* blooms were not reported until 19 years later in 2015 when a major bloom arrived in coastal Mississippi, generating notable news headlines (e.g., Clark, 2015) and causing widespread shellfish bed closures.

The bloom of 1996 was observed initially in the Florida Panhandle in mid-October and reached the Mississippi coast by 1 November 1996 and the Louisiana coast by 9 November 1996, giving the appearance of westward transport (Dortch et al., 1998; Maier-Brown et al., 2006). Although, circulation patterns favoring westward transport have been observed during the fall season in the nGoM (Weisberg et al., 1996; He and Weisberg, 2003; Morey et al., 2003), Maier-Brown et al. (2006) reported that drifter data (Sturges et al., 2002) showed no favorable westward currents from Pensacola, Florida to the Mississippi Sound during that time frame, except for a short time (3–10 October 1996) after the passage of Tropical Storm Josephine. As will be shown below, a similar westward transport event was observed during the bloom of 2015, which was initially observed in the Florida Panhandle in mid-September and later along the Alabama and Mississippi coast by mid-November. Also, remnants of tropical cyclone (TC) Patricia moved through the study area between 25 and 27 October 2015.

Seasonal winds in the nGoM shift from easterly to northerly throughout the autumn season (September–December) with a consistent westward/southward coastal current; however, winds may be more variable due to the passage of cold fronts (Morey et al., 2003). Using measurements and circulation models, He and Weisberg (2003) showed a strong mean westward flow from Cape San Blas, Florida towards the Mississippi River delta from October to December of 1998 and Weisberg et al. (1996) observed strong northward current in October 1993 and September 1994. Morey et al. (2003) also showed similar patterns during the fall seasons of 1993 to 1999 using satellite-tracked surface drifters. Given this persistent westward transport during the fall season, why are Florida Panhandle *K. brevis* blooms not more frequent events in Mississippi coastal waters? The Florida Fish and Wildlife Conservation Commission's Fish and Wildlife Research Institute (FWC-FWRI) reported *K. brevis* blooms in the Florida Panhandle during the fall of 1996, 2000–2003, 2005, 2007 and 2015. While *K. brevis* blooms reached the western edge of Florida in all of those years, major blooms were also reported in coastal Alabama in 1996, 2007, and 2015 and coastal Mississippi during 1996 and 2015. Additionally, a couple of short-lived blooms were reported in 2000 and 2005 in Alabama and 2005 and 2007 in Mississippi. It is possible that blooms were still advected westward toward the Mississippi River delta during those other years, but either remained offshore the Mississippi coast and were quickly transported out of the region, or local environmental conditions were not favorable for bloom maintenance.

The focus of this manuscript is to compare biophysical oceanographic conditions during two *K. brevis* blooms in the Florida Panhandle: one that preceded a major bloom in the western Mississippi Bight and Mississippi Sound (i.e., fall of 2015) and one that did not (i.e., fall of 2007). The objective is to identify mechanisms that may have led to a major bloom in Mississippi coastal waters in 2015 and not in 2007. These last two events were analyzed using *in situ* measurements, buoy data, circulation models, and satellite imagery. Cell counts and satellite ocean color imagery (e.g., normalized Fluoresce Line Height and Remote sensing reflectance) were used to describe the extension, duration and movement of the blooms. Circulation model output and Lagrangian tracking were used to determine possible transport pathways and were compared with the satellite-based observations of the bloom movement. Oceanographic (e.g., salinity and currents), meteorological (e.g., winds) and hydrologic (e.g., river discharge) data from local buoys, monitoring stations and coincident oceanographic cruises were also analyzed for both events. Nutrient data were gathered in an effort to analyze all possible contributing conditions for bloom development. The results of this work aim to (1) identify data gaps (e.g., nutrients, oceanographic or hydrological conditions), which may allow for a better understanding of the dynamics of these blooms in the nGoM, and (2) assist with the development of an integrated HAB forecast system for the river-dominated western Mississippi Bight region that couples ocean color satellite remote sensing with circulation models.

2. Methods

2.1. *Karenia brevis* field observations

A comprehensive database of *K. brevis* cell counts was assembled by taking advantage of the multiple institutions that continuously monitor the nGoM, as well as contemporaneous oceanographic cruises that were sampling during the 2015 bloom. For the State of Florida, the FWC-FWRI historical dataset was used. This database contains data from different programs, such as the Ecology and Oceanography of Harmful Algal Blooms (ECO HAB; Heil

et al., 2014). This data is available online in map format at <http://myfwc.com/research/redtide/statewide/> and most recently at <http://optics.marine.usf.edu/> in the forms of Google Earth layers. The Alabama Department of Public Health (ADPH) provided *K. brevis* cell counts for the State of Alabama for both years and the State of Mississippi for 2007. The Mississippi Department of Marine Resources (MDMR), in collaboration with The University of Southern Mississippi (USM), collected field data during the 2015 *K. brevis* bloom. Prior to the HAB event in Mississippi waters, additional samples were collected during the first research cruise of the Consortium for oil spill exposure pathways in Coastal River Dominated Ecosystems (CONCORDE) from 28 October to 7 November 2015. The cruise was immediately after the passage of TC Patricia's remnants (Dzwonkowski et al., 2017) and transited close to the Florida-Alabama coast (Fig. 1; circles) in time to capture some of the first advected *K. brevis* cells. The sampling methods for cell counts varied across the different institutions. Some samples were counted live, while others were preserved in Lugol iodine solution for later counting using an inverted phase or light microscope. Samples from MDMR used the Sedgewick rafter cell counting method and an inverted microscope, whereas samples collected by CONCORDE were analyzed using a Flow-CAM[®] Benchtop B3 Series and following methods outlined by Bushey and Hyatt (2006).

2.2. Ocean color imagery and satellite detection

Ocean color satellite imagery from the Moderate Resolution Imaging Spectroradiometer (MODIS) onboard the Aqua satellite were downloaded from the NASA Goddard Space Flight Center, Distributed Active Archive Center for fall (September to December) of 2007 and 2015. The satellite imagery covered the region from 85.0° to 90.0°W and 29.0° to 30.5°N (Fig. 1). Data were downloaded at Level-1 and processed to Level-2 using the SeaWiFS Data Analysis System (SeaDAS, version 7.3.2). Daily image composites were mapped to a rectangular projection at 1 km pixel resolution and level-2 flags were applied to discard low-quality data.

Ocean color satellite imagery has been used to successfully detect, track, and monitor *K. brevis* blooms in the West Florida Shelf (Steidinger and Haddad, 1981; Stumpf, 2001; Stumpf et al., 2003; Tomlinson et al., 2004; Hu et al., 2005; Wynne et al., 2005; Hu et al., 2008; Cannizzaro et al., 2008; Amin et al., 2009; Tomlinson et al., 2009; Carvalho et al., 2011a, 2011b; Soto et al., 2015, Hu et al., 2015, Soto et al., 2016). Satellite detection techniques have been

improved substantially for the West Florida Shelf thanks to the large historical *K. brevis* cell counts database, which allows for technique validation and optimization. Unfortunately, there is not enough *in situ* data for a comprehensive technique validation in Mississippi coastal waters. Most of the data collected in Mississippi and Alabama were very close to the coast or inside the estuarine system which makes it very difficult to find reliable match-ups to validate satellite techniques. Usually satellite data pixels within 1 to 2 km from the coast are discarded by quality flags, contaminated by land or bottom reflectance, and/or have high sediment content. For this work, the R_{rs} -nFLH (Soto et al., 2015) satellite detection technique was used, which is less susceptible to contamination from colored dissolved organic matter (CDOM) in near river-dominated regions. The detection technique was not used inside the Mississippi Sound or Mobile Bay where shallow waters and high sediment loads can contaminate the satellite signal. Only *in situ* data was used to characterize the spatial and temporal distribution of the bloom inside the Mississippi Sound where satellite data is not reliable.

Blooms of *K. brevis* manifest high chlorophyll-*a* and low backscattering per unit chlorophyll-*a*, which could lead to 3 to 4 times lower remote sensing reflectance [$R_{rs}(\lambda)$] (Carder and Steward, 1985; Mahoney, 2003; Cannizzaro et al., 2008). Nonetheless, satellite-derived chlorophyll-*a* near areas with high river discharge often is contaminated by CDOM, which exhibits similar bio-optical properties as chlorophyll-*a* (see example in Fig. 2a). To overcome this issue, Hu et al. (2005) suggested the use of normalized Fluorescence Line Height (nFLH; Letelier and Abbott, 1996) as a good indicator of chlorophyll-*a* in river-dominated regions (see example in Fig. 2b). Blooms of *K. brevis* were detected using the R_{rs} -nFLH technique (Soto et al., 2015), which uses two thresholds: nFLH above $0.33 \text{ W m}^{-2} \mu\text{m}^{-1} \text{ sr}^{-1}$ and R_{rs} at 555 nm below 0.007 sr^{-1} . The former threshold takes advantage of the high chlorophyll-*a* properties, while reducing the errors associated with CDOM. The R_{rs} threshold takes advantage of the low backscattering properties and eliminates pixels with high sediment concentrations which could also saturate the satellite signal. It also avoids errors associated with calculations of more complex bio-optical algorithms (such as backscattering) or regional relationships (Fig. 2c–d).

Soto et al. (2015) evaluated the R_{rs} -nFLH technique and six other detection techniques using a statistical test known as F-measure (FM), which accounts for the number of correct matches and number of misclassifications to calculate method accuracy. The FM

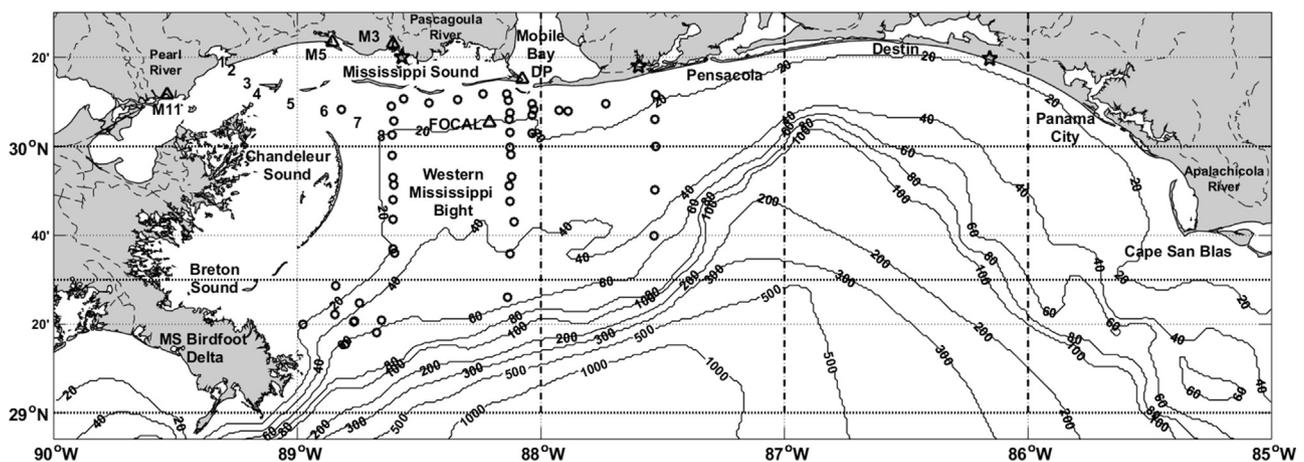


Fig. 1. Study area map showing the NGI stations (1–8), MDMR stations (M3, M5, M11), FOCAL station and NDBC Dauphin Island (DP) location which include stations DPIA and DPHA. The circles represent the stations during the CONCORDE cruise. The three star symbols represent the High Frequency Radar stations. Rivers are represented by the dash line inside the land mask. USGS river discharge stations were outside of the map boundaries however the names for the rivers are included in the map. The dotted lines represent the East-West transects and the dashed lines the North-South transects.

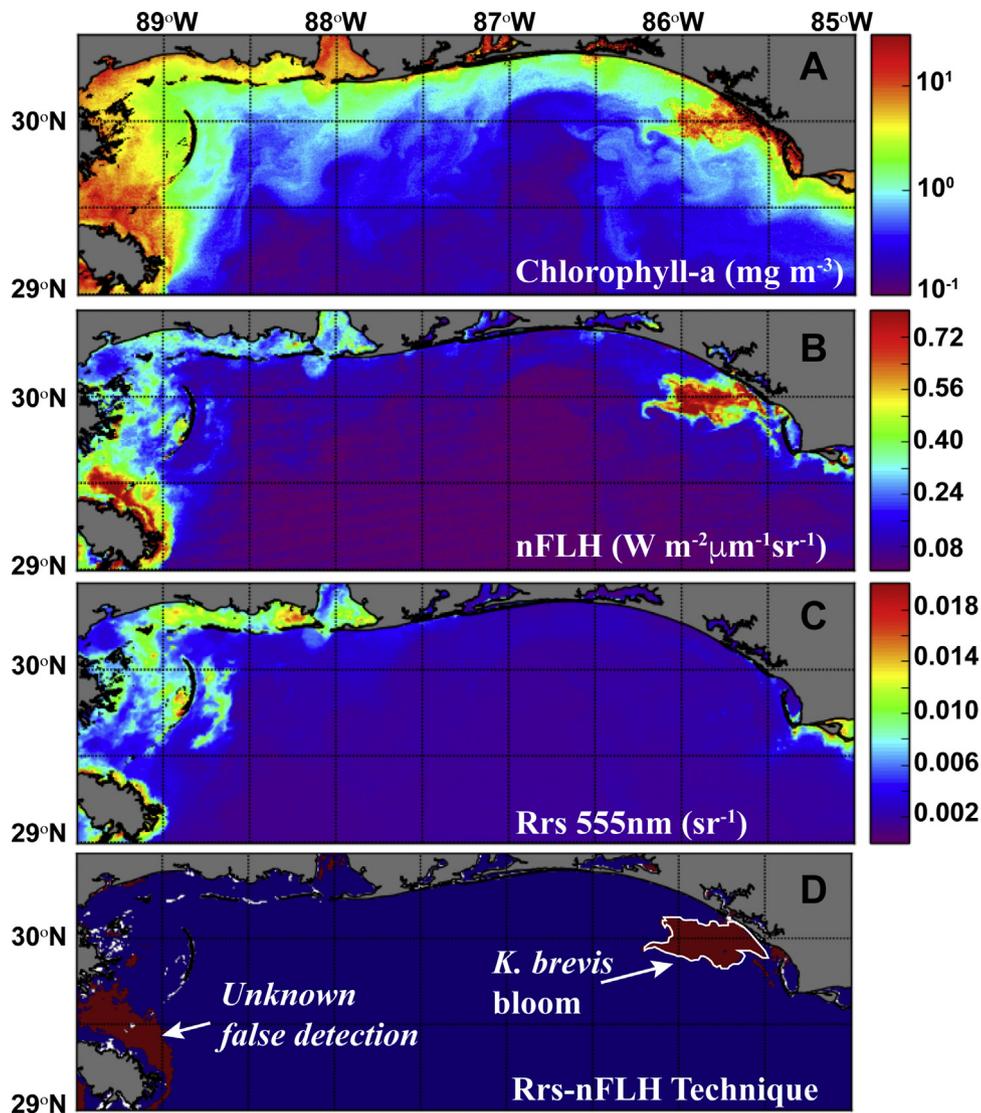


Fig. 2. Example of the detection and delineation of a *K. brevis* bloom. 14 October 2015 MODIS-Aqua products: a) chlorophyll-*a*, b) nFLH, c) R_{rs} at 555 nm. d) Detection and manual delineation of *K. brevis* bloom using the R_{rs} -FLH technique. Red colors mean the algorithm detected a bloom. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

values range from 0 to 1, and higher values indicate a better technique performance. The R_{rs} -nFLH technique showed a FM = 0.62 compared to an average FM = 0.47 (min = 0.34, max = 0.62) for all the other detection techniques (e.g., chlorophyll anomaly (Stumpf et al., 2003), backscattering or water leaving radiance ratio (Cannizzaro et al., 2008; Carvalho et al., 2011a, 2011b), Red Band Ratio (Amin et al., 2009), and spectral slope (Tomlinson et al., 2009)) in the entire West Florida Shelf. Overall for the north West Florida Shelf, which is similar to the western Mississippi Bight and is a river dominated region with major discharge from the Suwannee River, the R_{rs} -nFLH technique had a FM = 0.57, showed a 62% sensitivity and 95% specificity, which are equivalent to 38% false negatives and 5% false positives. Other HAB algorithms (i.e., Stumpf et al., 2003; Cannizzaro et al., 2008; Amin et al., 2009; Tomlinson et al., 2009; Carvalho et al., 2011a, 2011b) had a mean FM = 0.37 (min = 0.18, max = 0.60) and mean percentage of false positive of 17% for the same region. Only the Red Band Ratio technique (Amin et al., 2009) performed similar to the R_{rs} -nFLH technique.

Overall, the R_{rs} -nFLH technique performed well for a river-dominated region in northern Florida as demonstrated by Soto et al. (2015). Nevertheless, it is important to emphasize that these

techniques could be greatly improved and optimized for different regions. Future work, and monitoring programs should consider data collection for detection techniques validation, which will require data from at least 2-km from the coast. Another possible weakness of satellite detection techniques is that blooms of other dinoflagellates could exhibit similar optical properties, leading the algorithm to detect a bloom, when it is not necessarily *K. brevis* (Soto et al., 2015). For example, Breton Sound south of the Chandeleur Islands was flagged as a potential bloom region in October 2015 (Fig. 2d). No field data was available to determine the accuracy of this detection, but it is highly unlikely that a *K. brevis* bloom could reach Breton Sound because based on *in situ* sampling it had only reached the Florida panhandle at that time, so this detected area was discarded. Blooms of *K. brevis* are generally monospecific, with the exception of other *Karenia* spp. Therefore, other dinoflagellates blooms do not pose a concern for satellite detection techniques once we have some *in situ* data indicating that the bloom in the region is *K. brevis* or other *Karenia* species.

Once *K. brevis* blooms were detected, the method outlined in Soto et al. (2016) to delineate the extent of the bloom was followed. This method confirms the bloom patch detected by the R_{rs} -FLH technique by comparing with other detection techniques and

ancillary imagery. Bloom delineations were compared with field data and only cloud and glint-free images were used in this method (Fig. 2d). The best delineations were put together in one graph to describe bloom dynamics. Pixels such as the ones in Fig. 2d that shows an unknown possible bloom, pixels inside the estuaries or that could represent high uncertainty were manually discarded by the person delineating the bloom (first author).

2.3. Circulation models and Lagrangian particles

Ocean current components (u , v) from a regional application of the Navy Coastal Ocean Model (NCOM; Barron et al., 2006; Martin

et al., 2009) for the GoM at 1-km resolution and from the Intra-Americas Sea Nowcast Forecast System (IASNFS) at 6-km resolution were used to understand circulation and transport pathways during the blooms of 2015 and 2007, respectively. Both model domains covered the entire GoM, with IASNFS additionally covering the Florida Straits, the Caribbean Sea, and parts of the Western North Atlantic Ocean (Ko et al., 2003; Ko, 2009). A higher temporal and spatial model resolution for 2007 is not available for the study region. Regardless of the lower resolution of the NCOM-IASNFS, this is still a reliable source to approximate the major circulation patterns in the GoM during this time frame. Model

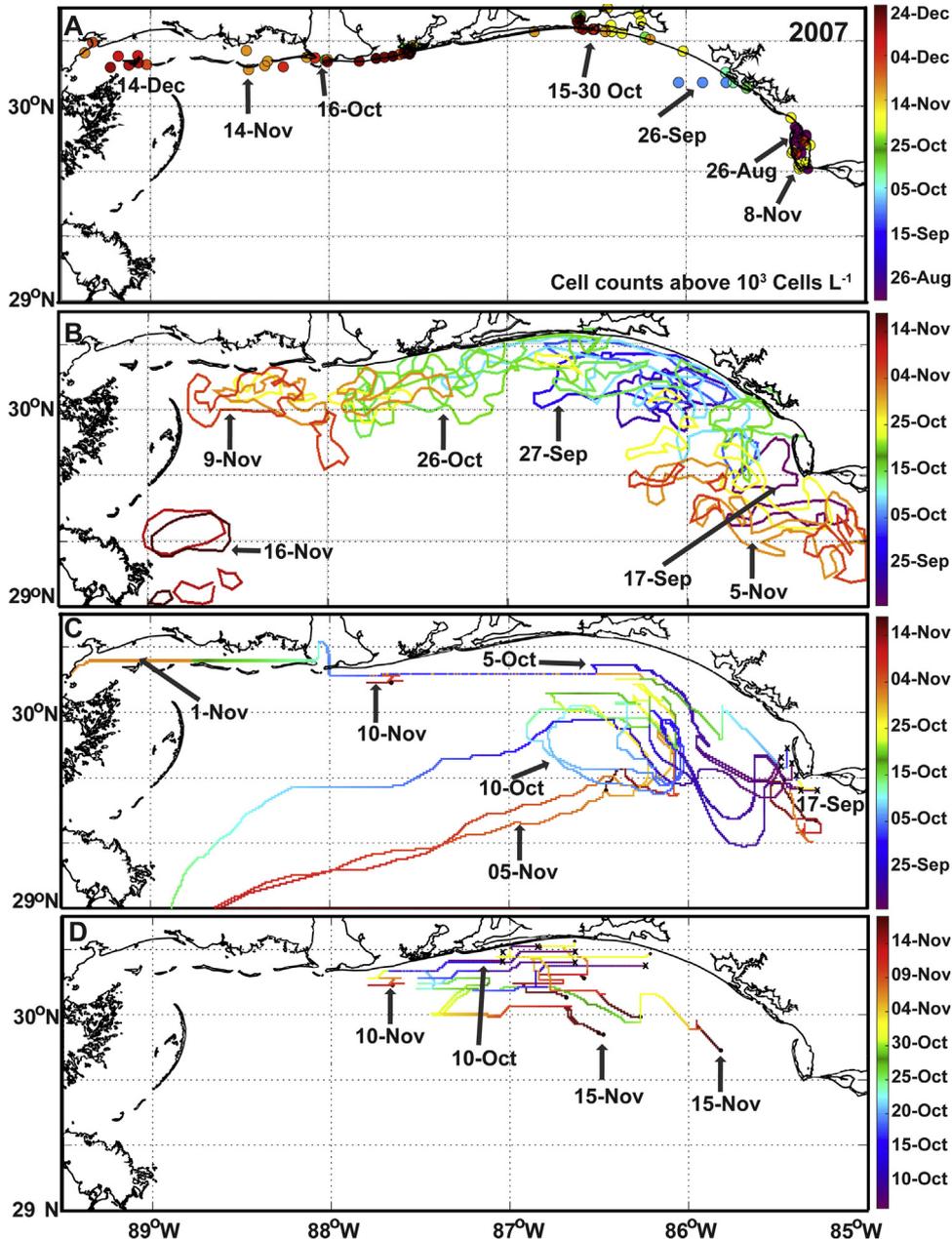


Fig. 3. a) Map of *Karenia brevis* samples taken by FWC, ADPH, MDMR and USM during fall of 2007. The color represents the date and only samples with cell counts above 10^3 cells L^{-1} were plotted. b) MODIS-Aqua *K. brevis* delineations for fall 2007. The color represents the date. c) First set of Lagrangian particles released 17 September 2007 inside the first bloom delineation. The color scale is the same as Fig. 3a. Particles were allowed to move until 17 November 2007. d) Second set of Lagrangian particles released 8 October 2007 inside the first bloom delineation. The color scale is the same only for subfigures b and c. Particles were allowed to move until 17 November 2007. The circulation model NCOM-IASNFS was used for both Lagrangian scenarios. Note that a detailed panel for the cell counts and delineations per month has been added to the Appendix A and B in Supplementary file. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

predictions were 24-h moving averaged to eliminate the tidal signal and these daily averages were used for the analysis.

A built-in particle trace function in IDL™ (Interactive Data Language) was used to track the passive movement of particles released inside the delineation of the first satellite bloom observation of each year (17 September 2007, 23 September 2015). Particles were allowed to move until the last satellite observation of the bloom (17 November 2007, 19 December 2015). A second set of particles was released when the bloom was near Alabama (6 October 2007, 12 November 2015). All particles were released at 2-m depth to avoid instability in surface current vectors. The particles were tracked in two-dimensions without vertical advection or diffusion. The IDL particle trace function delineated the path of massless particles through a vector field at given locations (seed points). The integration parameter in IDL was set to a 4th order Runge-Kutta scheme, and the step size was three hours for NCOM-GoM and six hours for NCOM-IANSFS.

Oceanographic data from buoys and moorings were limited spatially for the region, especially historical data from 2007. Therefore, sea surface currents from circulation models offer a large spatial and temporal coverage and probably the only option to study the flow and transport mechanisms during both events for the entire region. Similar to the Lagrangian particles exercise, two different models were used for each year: the NCOM-GoM for 2015 and the IANSFS for 2007. In this case, the spatial resolution of the NCOM-GoM was interpolated to the same spatial grid as the NCOM-IANSFS at 6-km resolution to allow for direct comparison of the transport. Hovmöller diagrams of daily averaged u-velocity component (i.e., east-west component) from both models were created at three different north-south (29.0°N to 30.6°N) transects (Fig. 1, dash lines) at 86.0°W, 87.0°W and 88.0°W from 1 September to 31 December 2015. Hovmöller diagrams of daily averaged v-velocity component (i.e., north-south component) three east-west (90.0°W to 85.0°W) transects (Fig. 1, dotted lines) at 29.0°N, 29.5°N, and 30.0°N from 1 September to 31 December 2015. The difference between the daily averaged u-velocity component from the NCOM-GoM model (2015) and the NCOM-IANSFS model (2007) for the same time period was also calculated.

2.4. Ancillary data

Surface currents over much of the Mississippi Bight were obtained from High Frequency Radar (HFR) data obtained from three 5-MHz long-range CODAR SeaSonde stations (Station Singing River Island, 30.334°N, 88.569°W; Station Gulf State Park, 30.300°N, 87.600°W; Station Henderson Beach State Park, 30.329°N, 86.157°W; Fig. 1, star symbols) operated by the USM Central Gulf of Mexico Ocean Observing System (cengoos.org) at Singing River Island, Mississippi; Orange Beach, Alabama; and Destin, Florida (Howden et al., 2011). Please note that not all HFR stations were operating for the entire period; some months had more spatial coverage than others. The data for the month of October 2007 was limited to the last two days of the month. In addition to the monthly means, a fall (September–November) average surface current data from HFR was created using all the data available for those months from 2010 to 2016.

Wind magnitude and direction data was obtained from the National Oceanic and Atmospheric Administration's (NOAA) National Data Buoy Center (NDBC) station at Dauphin Island, Alabama (Station DPIA, 30.250°N, 88.075°W; Fig. 1).

River discharge data was obtained from four U.S. Geological Survey (USGS) stations from the Mobile (Station 02470629, 31.016°N, 88.021°W), Apalachicola (Station 02359170, 29.949°N, 85.016°W), Pascagoula (Station 02479310, 30.611°N, 88.641°W), and Pearl (Station 02489500, 30.793°N, 89.821°W) rivers.

Salinity data was obtained from five stations in the Mississippi Sound and Mobile Bay. Three of those are from real-time hydrological monitoring stations operated by MDMR in partnership with USGS. While MDMR-USGS have more stations within the Mississippi Sound, only M3 (30.382°N, 88.608°W), M5 (30.388°N, 88.857°W), and M11 (30.195°N, 89.534°W) were selected for this study because they have data available back to 2007 (Fig. 1). The instruments measuring conductivity, from which the salinity is calculated, are mounted near the sea-floor. Salinity data were collected from the Fisheries Oceanography in Coastal Alabama (Fig. 1, FOCAL, 30.090°N, 88.212°W) mooring at the 20 m isobath on the inner-shelf and from the Alabama Real-time Coastal Observing System (ARCOS) Dauphin Island Station (Fig. 1, DPHA, 30.251°N, 88.078°W). MDMR collected salinity data along with the cell counts using a handheld YSI Pro2030 instrument.

Nutrient data was obtained from two different sources. Historical data for October–November 2007 to 2011 was collected during Northern Gulf Institute (NGI)-sponsored cruises at eight stations (Fig. 1; numbers 1–8). Surface samples were collected using a pole sampler, affixed with a 1 L brown, acid-washed Nalgene polyethylene bottle and kept cold until filtration. Samples were filtered through pre-rinsed glass fiber filters (GF/F) into 125 mL acid-washed brown polyethylene bottles and stored in a freezer until analysis. All nutrients were measured using fluorometric (N species) and spectrophotometric (Phosphate (PO₄) and Silica (SiO₃)) methods on the Astoria-Pacific A2+2 nutrient auto-analyzer (Method #A179, A027, A205, and A221; Astoria-Pacific International, Oregon USA). Nutrient samples for October and November 2015 were collected during the Fall CONCORDE cruise from October 28–November 7, 2015 (Fig. 1, circles). Surface samples were analyzed by the Dauphin Island Sea Lab (DISL) using similar collection methods to the NGI data, except the filtrates were analyzed colorimetrically using a Skalar Sans 10 autoanalyzer (Liefer et al., 2013; Liefer et al., 2014). The molar nitrogen/phosphate (N/P) ratio was calculated for every year, with and without ammonium (NH₄), to determine how much NH₄ could be contributing using the NGI data. Data for NH₄ was not available for most of the CONCORDE cruise, so the N/P ratio was calculated without NH₄ for 2015.

3. Results

3.1. Bloom dynamics (field cell counts, satellite delineations and Lagrangian particles)

Cell counts of *K. brevis* were gathered from multiple institutions along the nGoM from Florida to Mississippi. Fig. 3a shows the spatial and temporal distribution of the *in situ* *K. brevis* cell counts in 2007. In this case, only samples with cell counts above 10³ cells L⁻¹ were plotted, the colors represent the sampling date. Fig. Appendix A in Supplementary file shows the spatial distribution and concentration ranges of the cell counts for each month. This bloom was first observed along the Florida Panhandle near Cape San Blas and Panama City by mid-August (concentrations less than 10⁴ cells L⁻¹) and was not observed in the Mobile Bay area until 16 October 2007 (Fig. 3a). *K. brevis* samples were observed outside the Mississippi Sound near the barrier islands from Dauphin Island to West Ship Island. Maximum cell concentrations in this area did not exceed 7 × 10⁴ cells L⁻¹ and were observed from 14 to 20 November 2007. It is important to mention that sampling in Mississippi coastal waters did not begin until approximately 14 November 2007. Additional samples were collected after 20 November 2007, but the concentrations ranged from zero to below 10⁴ cells L⁻¹ (See Appendix A in Supplementary file).

A similar pattern was observed in the ocean color satellite imagery. Fig. 3b summarizes the delineations of the *K. brevis* bloom

observations in the MODIS-Aqua imagery in 2007. Fig. Appendix B in Supplementary file shows the same delineations, however they were separated for each month to show the monthly progress of the delineations derived from satellite imagery. The initial observations from ocean color of the 2007 bloom were on 17 September 2007 near Cape San Blas (Fig. 3b, purple delineations). The bloom moved westward and reached Mobile Bay by 20 October 2007 (See Fig. Appendix B in Supplementary file). The bloom was observed outside the Mississippi barrier islands for several days at the beginning of November. Subsequently, a bloom patch moved southwards near the Mississippi Birdfoot Delta. After 16 November 2007, bloom patches were no longer observed in the ocean color

imagery in the western Mississippi Bight or Mississippi Sound. However, the bloom was still active near the Cape San Blas region.

Lagrangian particles were released at the location where the bloom was observed initially in the imagery and a second set of particles was released when the bloom was between Destin and Pensacola, Florida (Fig. 3b, cyan delineation). Fig. 3c shows the trajectory of the first set of particles released on 17 September 2007. Note that the colors for dates match those of the delineations (Fig. 3b). Most of the particles released on 17 September 2007 were entrained by an offshore mesoscale feature south of Destin, Florida (location in Fig. 1) and eventually moved westward along the 200–500 m isobaths. However, one particle made it all the way to the

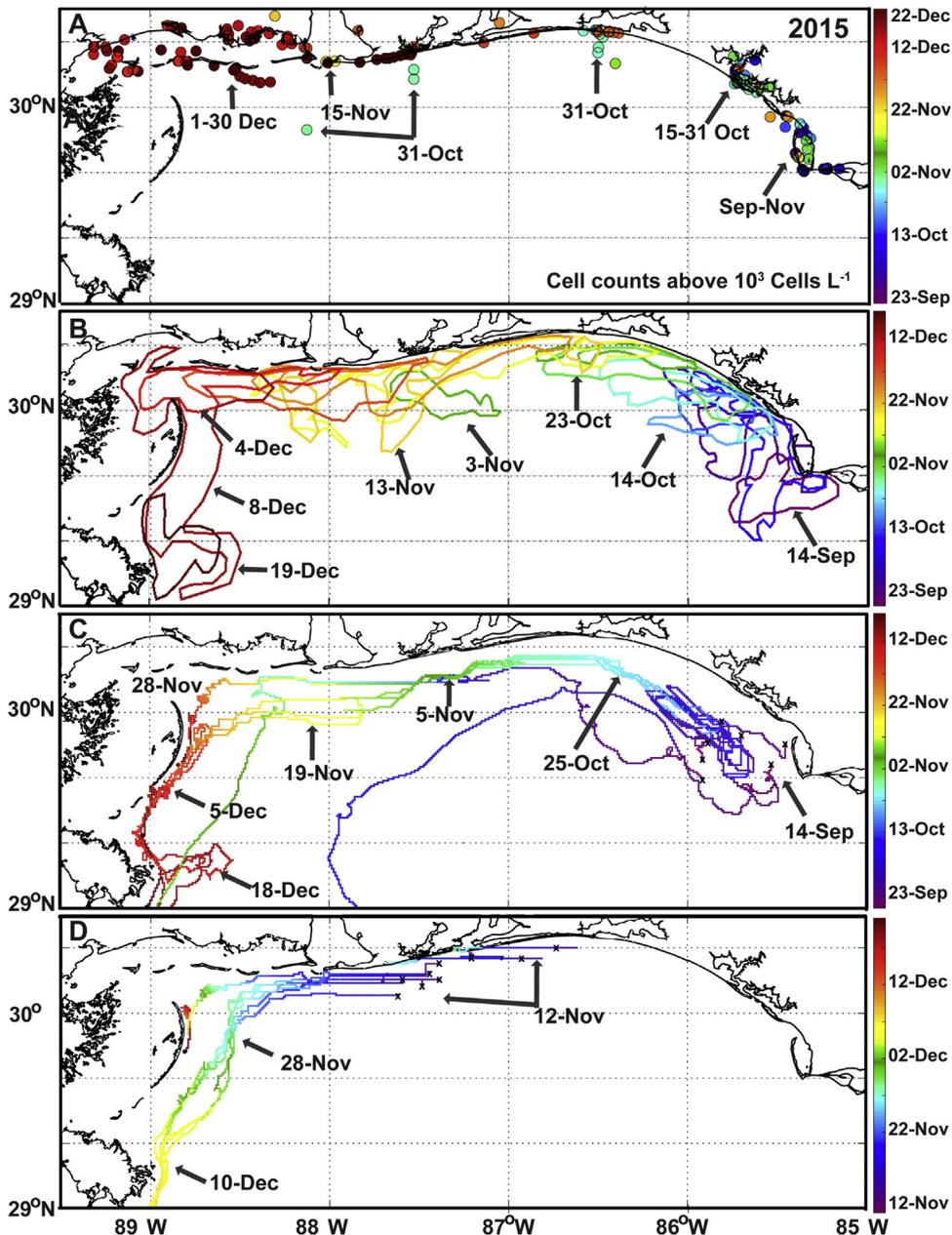


Fig. 4. a) Map of *Karenia brevis* samples taken by FWC, ADPH, MDMR and USM during fall of 2015. The color represents the date and only samples with cell counts above 10^3 cells L^{-1} were plotted. b) MODIS-Aqua *K. brevis* delineations for fall 2015. The color represents the date. c) First set of Lagrangian particles released 23 September 2015 inside the first bloom delineation. The color scale is the same as Fig. 4a. Particles were allowed to move until 19 December 2015. d) Second set of Lagrangian particles released 12 November 2015 inside the first bloom delineation. The color scale is the same only for subfigures b and c. Particles were allowed to move until 19 December 2015. The circulation model NCOM-GoM was used for both Lagrangian scenarios. Note that a detailed panel for the cell counts and delineations per month has been added to the Appendix C and D in Supplementary file. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Mississippi Sound by mid-October. The second release of particles was on 6 October 2007 between Destin and Pensacola, Florida (Fig. 3d). This time the particles moved westward for less than 2 weeks, but before reaching Mobile Bay, the particles began to move eastward until the end of the period of interest (17 November 2007). A third set of particles (not shown) were released on 15 October 2007 near Pensacola and similar to Fig. 3d, particles moved westward for a few days but then drastically shifted towards the east.

In 2015, the bloom was observed initially near Cape San Blas in early September, but by mid-November was observed near Mobile Bay, Alabama (Fig. 4a, Fig. Appendix C in Supplementary file). In contrast to 2007, the 2015 bloom intensified in Mississippi coastal waters during the month of December with concentrations exceeding 2×10^6 cells L^{-1} . The bloom inside the Mississippi Sound lasted approximately one month and samples collected in January found no to low presence of *K. brevis*. The MODIS-Aqua delineations showed similar patterns as observed in the field data (Fig. 4b, Fig. Appendix D in Supplementary file). The bloom was first observed on 23 September 2015 and it reached Mobile Bay and Mississippi coastal waters by mid-November. The bloom moved southward along the Chandeleur Islands and reached the Mississippi Birdfoot Delta by 19 December 2015; however, cloud cover limited satellite data after that date. The first set of Lagrangian particles were released on 23 September 2015, and the trajectory of most of the particles mimicked both the temporal and spatial delineations by the MODIS-Aqua imagery (Fig. 4c). A second set of particles was released on 12 November 2015 (Fig. 4d). The particle trajectories were initially westward and became southward after reaching the Chandeleur Islands.

3.2. Sea surface currents and winds

Sea surface currents from circulation models and HFR stations were used to understand the transport patterns and intensity during fall of both years and to validate and understand the Lagrangian particles' behavior. Fig. 5a–f shows Hovmöller diagrams of daily averaged u-velocity component from both models (2015–left column and 2007–middle column) across three different north-south transects at 86.0°W, 87.0°W and 88.0°W from 1 September to 31 December 2015. The difference between the daily averaged u-velocity component from the NCOM-GoM model (2015) and the NCOM-IANSFS model (2007) for the same time period and averaged over each transect is shown in Fig. 5g–i. The Hovmöller diagrams of differences for each transect are shown in Fig. Appendix E in Supplementary file. In 2015, westward currents were predominant after 1 October 2015 with stronger westward currents before and after the passage of the remnants of TC Patricia (18–30 October 2015) and these continued for the month of November (Fig. 5a–c). Weaker currents were observed in the northern section of the transect along 88.0°W (Fig. 5c) and a slight shift towards eastward currents was observed in December at the 86.0°W and 87.0°W transects (Fig. 5a–b). In 2007, westward currents were observed until the first week of November on all transects; after that, a shift toward weaker and predominantly eastward currents was observed until January (Fig. 5d–f). The difference of the current pattern between 2015 and 2007 averaged over each transect shows the distinctive periods of time with intense westward currents during 2015 (Fig. 5g–i). Two main events of stronger westward currents were observed from 17 to 28

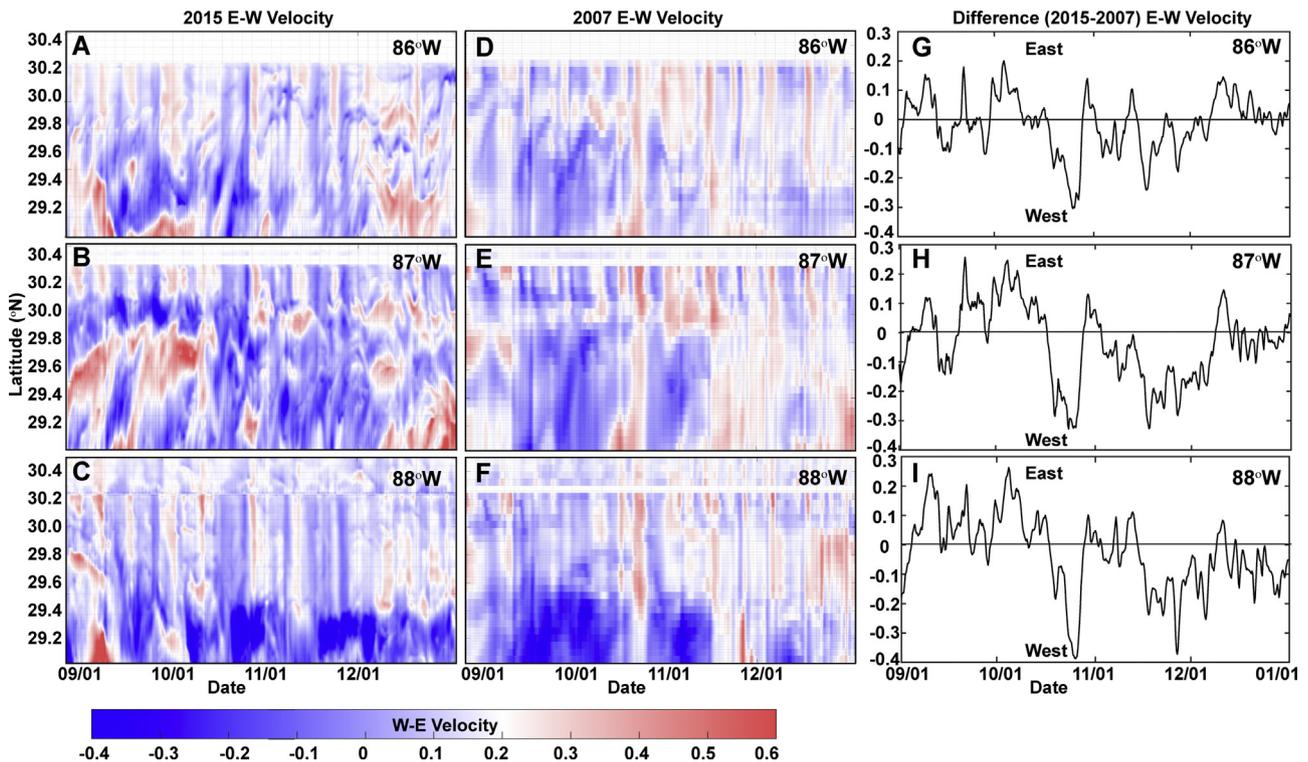


Fig. 5. a–c) Hovmöller diagram of daily mean u-velocity component ($m s^{-1}$) from the NCOM-GoM model at three different North-South (29.0°N to 30.6°N) transects at 86.0°W (a), 87.0°W(b) and 88.0°W(c) from 1 September to 31 December 2015. d–f) Hovmöller diagram of daily mean u-velocity component from the NCOM-IANSFS model at three different North-South (29.0°N to 30.6°N) transects at 86.0°W (d), 87.0°W(e) and 88.0°W(f) from 1 September to 31 December 2007. g–i) Plot of mean daily difference between the u-velocity component from the NCOM-GoM model (2015) and the NCOM-IANSFS model (2007) at three different North-South (mean from 29.0°N to 30.6°N) transects at 86.0°W (g), 87.0°W(h) and 88.0°W(i) from 1 September to 31 December. The difference u-velocity magnitude is relative to the magnitude from NCOM-GoM 2015. The red colors represent the east velocity component and the blue colors the west component. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

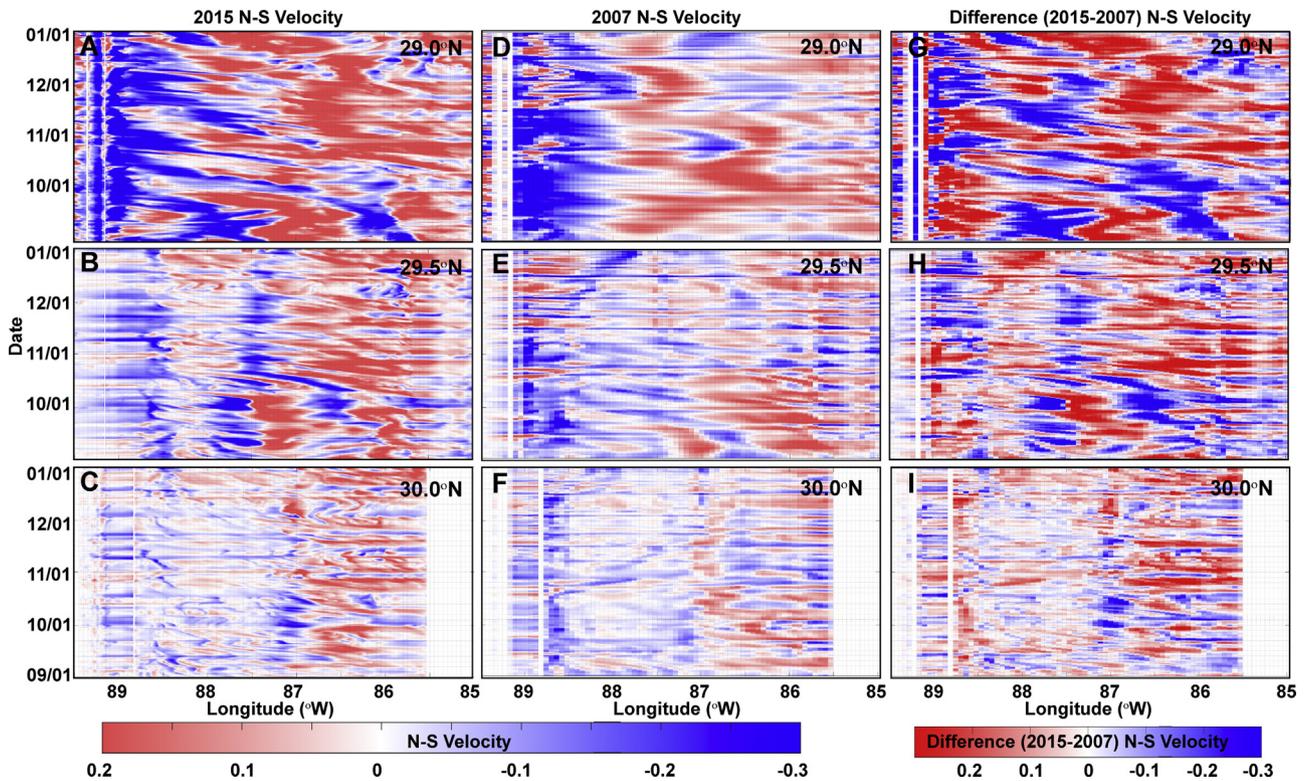


Fig. 6. a–c) Hovmöller diagram of daily mean v -velocity component (m s^{-1}) from the NCOM-GoM model at three different East-West (90.0°W to 85.0°W) transects at 29.0°N (a), 29.5°N (b) and 30.0°N (c) from 1 September to 31 December 2015. d–f) Hovmöller diagram of daily mean v -velocity component from the NCOM-IASNFS model at three different East-West (90.0°W to 85.0°W) transects at 29.0°N (d), 29.5°N (e) and 30.0°N (f) from 1 September to 31 December 2007. g–i) Hovmöller diagram of daily difference between the mean v -velocity component from the NCOM-GoM model (2015) and the NCOM-IASNFS model (2007) at three different East-West (90.0°W to 85.0°W) transects at 29.0°N (g), 29.5°N (h) and 30.0°N (i) from 1 September to 31 December. The difference v -velocity magnitude is relative to the magnitude from NCOM-GoM 2015. The red colors represent the north velocity component and the blue colors the south component. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

October 2015 before the passage of TC Patricia's remnants and 14 November to 8 December 2015 especially west of Pensacola.

A similar analysis was performed for the daily averaged v -velocity using three east-west transects at 29.0°N , 29.5°N , and 30.0°N (Fig. 6). Northward currents (red colors) were dominant from 88.0°W to 85.0°W from September to December 2015 at the 29.0°N transect (Fig. 6a). Currents were similar along the 29.5°N transect, except they were weaker east of 87.5°W than along the 29.0°N transect (Fig. 6b). Weak N-S currents (near 0) were observed along the 30.0°N transect with some stronger northward currents towards the east (87.0°W to 85.5°W , Fig. 6c). A similar pattern was observed for 2007 (Fig. 6d–f), except the magnitude was weaker ($\sim 0.1 \text{ m s}^{-1}$) than in 2015. The difference plots showed that currents were overall stronger ($>0.2 \text{ m s}^{-1}$ difference) in the north direction in 2015 than 2007 for the 29.0°N and 29.5°N transects, especially from 89.0°W to 85.0°W (Fig. 6g–h). Near the barrier islands (transect 30.0°N , Fig. 6i) the currents were much weaker and the difference in north-south velocity was minimal between 2015 and 2007, except for the eastern side (87.0°W to 85.5°W) that showed stronger northward currents ($\sim 0.2 \text{ m s}^{-1}$ difference).

Monthly mean surface currents were obtained from HFR data for October to December of 2007 and 2015. Although the October 2007 mean was temporally limited, sea surface currents were mainly westward, with stronger currents ($>25 \text{ cm s}^{-1}$) south of Pensacola near the 30 to 50 m isobath (Fig. 7a). Monthly currents for November 2007 were mainly southward and weak ($<15 \text{ cm s}^{-1}$; Fig. 7b), while December 2007 did not show a

definitive direction pattern and velocities were below 20 cm s^{-1} (Fig. 7c). Monthly currents from October to December 2015 were predominantly westward and stronger ($>30 \text{ cm s}^{-1}$) than in 2007, especially during October and November (Fig. 7d–f). Current velocities were slower ($<15 \text{ cm s}^{-1}$) in December 2015 than the previous two months, however the direction is predominantly westward and northward towards the Mississippi Sound. Fig. 7g represents the average sea surface circulation patterns during fall (September–November, 2010–2016) for the nGoM. Sea surface currents were predominately west-southwestward in the northern Mississippi Bight west of Mobile Bay and westward from the Florida Panhandle towards Mobile Bay.

Cambazoglu et al. (2017) studied a strong inflow event of saltier offshore waters advected into the Mississippi Sound in October 2015. Using a cross correlation analysis between wind, adjusted water level (i.e., corrected for inversed barometer effects) and salinity, they found that wind forcing was the primary driver of the low frequency salinity variability during the fall season, and southeast winds [45° – 180°] were favorable for forcing the transport of saline offshore waters into the Mississippi and Chandeleur Sounds. Based on the favorable wind direction range identified by Cambazoglu et al. (2017), the difference between the number of consecutive hours of winds favorable to onshore transport of saltier offshore waters was compared in fall 2007 and 2015. Fig. 8 shows wind rose plots describing the longest consecutive time frame of favorable winds for each fall month (October–December) in 2007 and 2015. In 2007, the total number of consecutive hours for which the wind was favorable ranged from 122 h in October

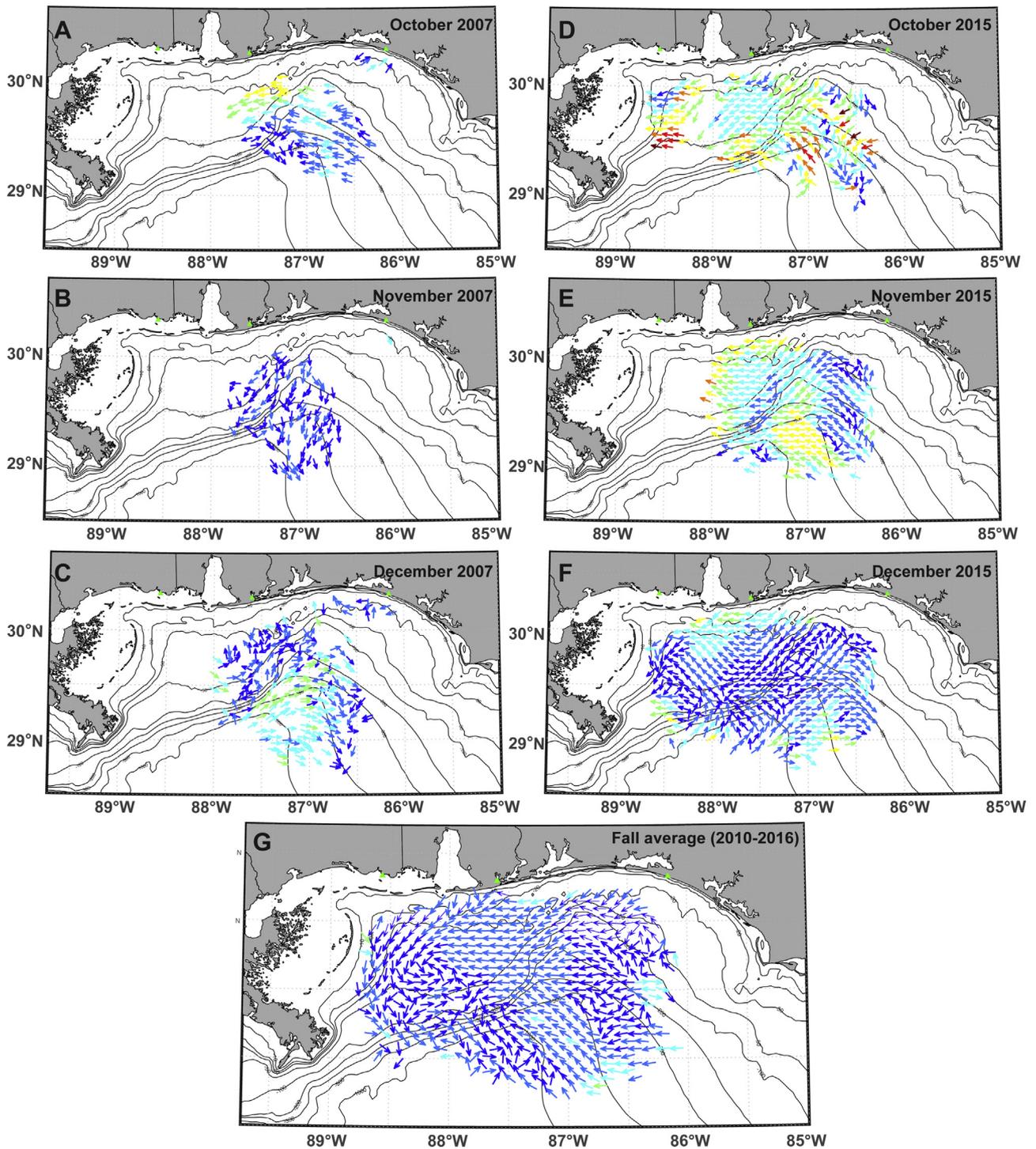


Fig. 7. Monthly mean surface currents from HFR on a) October 2007, b) November 2007, c) December 2007, d) October 2015, e) November 2015, and f) December 2015. g) Average sea surface circulation during fall (September–November 2010–2016). Color indicates the current speed. The green triangles represent the HFR stations. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(Fig. 8a) to 87 h in both November and December (Fig. 8b–c). The wind speed for fall 2007 ranged from 0 to 9 m s^{-1} with weaker winds predominantly from the east (Fig. 8a–c). In 2015, the duration of consecutive hours of favorable winds lasted much longer, especially in October with 204 h (Fig. 8d) as well as 160 and 150 h for November and December, respectively (Fig. 8e–f). The wind speed for fall 2015 ranged from 0 to 15 m s^{-1} with stronger winds in October, probably due to remnants of TC Patricia (Fig. 8a–c).

3.3. River discharge and salinity

Fig. 9 shows a comparison of the river discharge between fall 2007 and 2015. The dashed lines represent the mean daily discharge from 2007 to 2015. River discharge for fall 2007 (blue line) was mostly below the mean for all the stations during fall months (October–December). In 2015, river discharge was above the mean for all the rivers after October. In the case of the

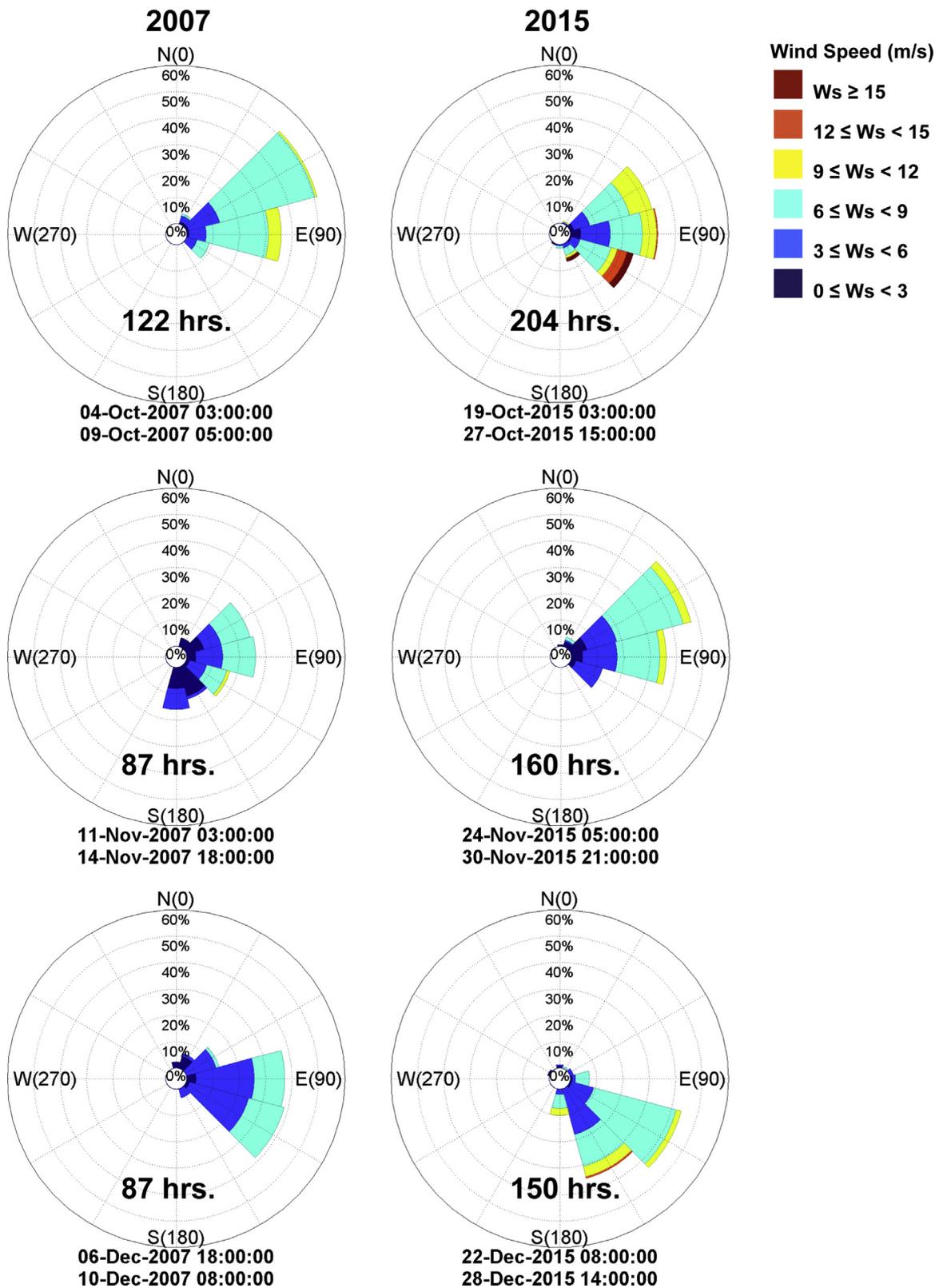


Fig. 8. Wind roses at Dauphin Island when the wind had consecutive hours from the $[45\text{--}180^\circ]$ direction interval during a) October 2007, b) November 2007, c) December 2007, d) October 2015, e) November 2015, and f) December 2015. The total number of hours that each event lasted is written inside each wind rose. The colors represent wind speed. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

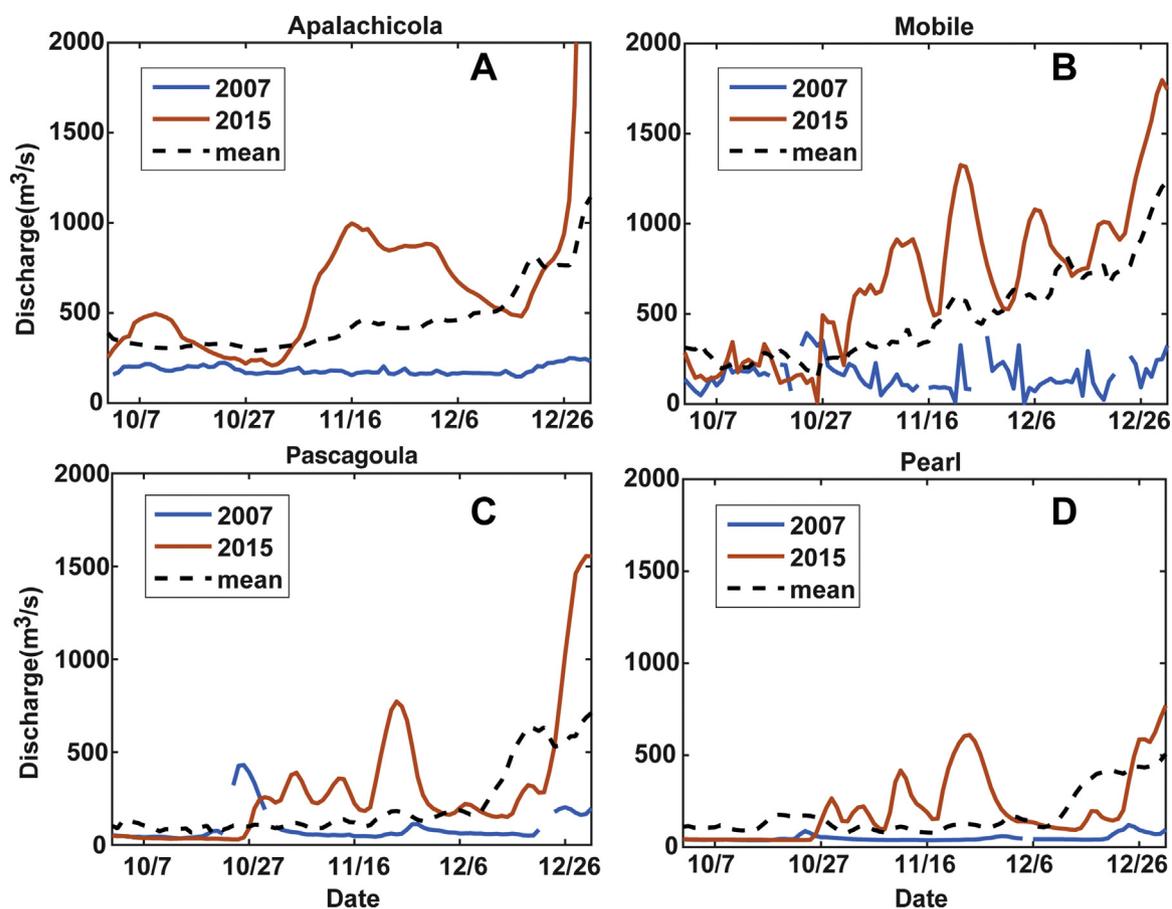


Fig. 9. River discharge from a) Apalachicola River, b) Mobile River and c) Pascagoula River and d) Pearl River during 1 October to 31 December 2007 (blue line) and 2015 (orange line). The river discharge mean for that time period from 2007 to 2016 was plotted as the dash line. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Apalachicola River (Fig. 9a), discharge peaked the second week of November, while for the Mobile (Fig. 9b) and Pearl Rivers (Fig. 9c) the increase in river discharge began earlier, right after the passage of TC Patricia's remnants (27 October 2015). River discharge increased dramatically at the end of 2015 for all rivers.

Differences in river discharge are reflected in the regional salinity data with drastic differences between fall of 2007 and 2015. For example, the effect of the high river discharge after the passage of TC Patricia's remnants (27 October 2015) is clearly observed in the salinity, which decreased drastically at stations M3 (salinity dropped from ~ 24 to 3; Fig. 10a), M5 (salinity dropped from ~ 28 to 15; Fig. 10b), M11 (salinity dropped from ~ 25 to 3; Fig. 10c) and Dauphin Island (salinity dropped from ~ 33 to 17; Fig. 10d). Overall, the stations within the Mississippi Sound (Fig. 10a–c; MDMR stations 3, 5, 11) showed salinities above the mean in October 2007 and 2015. Salinities after November remained below the mean in 2015 for most of the stations, while in 2007 they remained above the mean. For the FOCAL station, the data was limited; however, salinity at the surface (~ 4 m) was lower (~ 2) in October 2015 than 2007 (Fig. 10e). After October, the salinity was lower in 2015 but very variable (Fig. 10e). Salinity at the bottom (Fig. 10f; ~ 20 m) was between 2 and 3 lower in 2015 than 2007 in October and no difference was observed in December, although data was very limited after November for both years.

This interannual difference in fall salinities might be expected to have a significant role in the *K. brevis* bloom dynamics as this species is not typically associated with lower salinity values, although exceptions to the environmental expectation have been

observed (Maier-Brown et al., 2006). Fig. 11 shows a plot of *K. brevis* cell counts versus salinity for 2007 and 2015. In 2007, 85% ($n = 76$) of *K. brevis* cell counts (above 100 cells L^{-1}) were found at salinities above 25, while only 28% ($n = 75$) was found at similar salinities in 2015. In 2015, *K. brevis* was found at salinities from 7 to 25, even at areas of high cell count concentrations ($>10^5 \text{ cells L}^{-1}$). The samples collected at lower salinities (<25) had a wide range of cell count concentration (10^2 – $10^6 \text{ cells L}^{-1}$) and they were observed during the entire sampling period.

3.4. Nutrients

The first step was to provide a baseline for fall nutrient concentrations in the Mississippi Bight and Sound. Historical data for October–November 2007 to 2011 was collected during Northern Gulf Institute (NGI)-sponsored cruises at eight stations (Fig. 1). For the purposes of this work, stations were organized and spatially averaged into inside (Stations 1–4) and outside (Stations 5–8) the Mississippi Sound. Nitrate and Nitrite ($\text{NO}_3 + \text{NO}_2$) ranged from 0.02 to $0.26 \mu\text{M}$ for October and November 2007–2011 at the stations inside the Mississippi Sound, while it ranged from 0.04 to $0.57 \mu\text{M}$ at the stations outside the Mississippi Sound (Fig. 12a). Ammonium ranged from 0.10 to $1.28 \mu\text{M}$ for October and November inside the Mississippi Sound, and 0.09 to $1.97 \mu\text{M}$ outside the Mississippi Sound (Fig. 12b). Phosphate ranged from 0.43 to $1.55 \mu\text{M}$ for October and November inside the Mississippi Sound, and 0.08 to $0.50 \mu\text{M}$ outside the Mississippi Sound (Fig. 12c). Silica ranged from 5.04 to $88.41 \mu\text{M}$ for October and

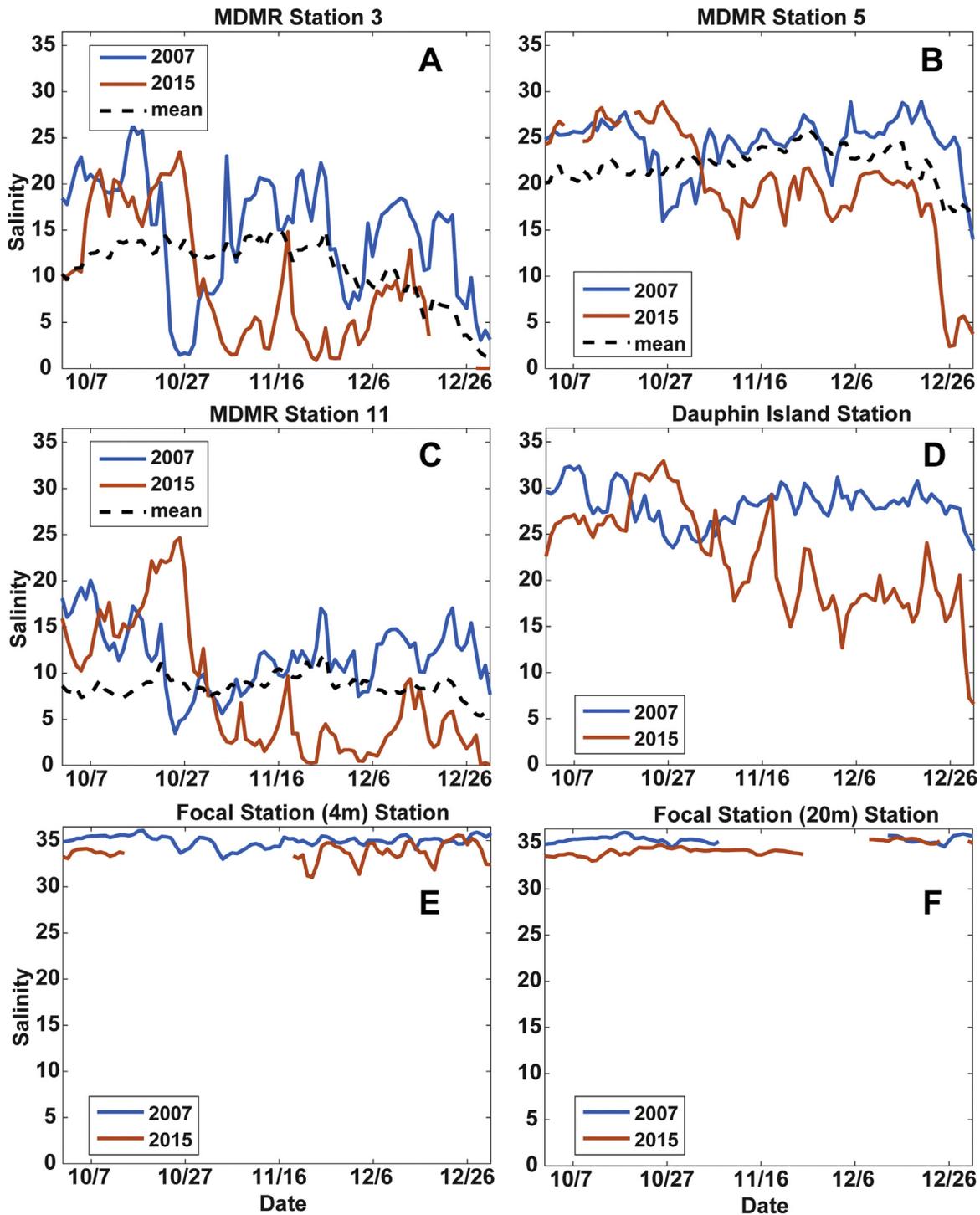


Fig. 10. Field salinity measurements at (a) MDMR station M3, (b) MDMR station M5, (c) MDMR station M11, (d) Dauphin Island station, (e) Focal station at 4 m depth and (f) Focal station at 20 m depth during 1 October to 31 December 2007 (blue line) and 2015 (orange line). The salinity mean for that time period from 2007 to 2016 was plotted as the dash line for the MDMR stations. The location of the stations is plotted in Fig. 1. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

November inside the Mississippi Sound, and 0.71 to 9.42 μM outside the Mississippi Sound (Fig. 12d). The N/P ratio not considering NH_4 never exceeded 2 in October and November inside the Sound (Fig. 12e). Outside the Sound, N/P ratios generally were below 5, and only in 2011 did this ratio exceed the Redfield value of 16 (Fig. 12e). If NH_4 is considered in the N/P ratio, the values would be below 2 for every year inside and outside the

Mississippi Sound, except 2011 when the N/P values reached 8 (Fig. 12f).

Nutrient data for 2015 was collected during the CONCORDE cruise from 29 October to 5 November 2015. Although this is a small time frame compared with the entire bloom period of 2015, it provides some information for comparison with the baseline data from the NGI dataset. The data was divided into two time frames: 29–31 October 2015 and 1–5 November 2016. Nitrate and Nitrite

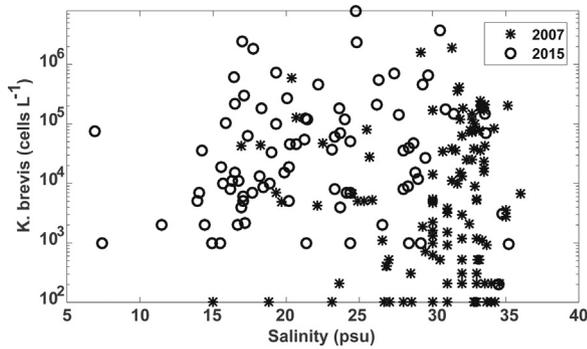


Fig. 11. Salinity versus *K. brevis* cell counts for all the field measurements taken by the ADPH, MDMR and USM. Salinity was measured in the field at the same time the phytoplankton samples were collected. Samples from 2007 are plotted using a star symbol and 2015 using an empty circle.

were mainly below 0.5 μM in October (Fig. 13a) and drastically increased in November up to 1.4 μM (Fig. 13b). PO₄ ranged from 0.2 to 0.4 μM during October and November (Fig. 13c–d); however, lower values were observed near the Chandeleur Islands in November (Fig. 13d). Silica values ranged from 1 to 14 μM, with lower values (<9 μM) in October (Fig. 13e) and one station in the western Mississippi Bight reached 14 μM in November (Fig. 13f). N/P ratios were below 4 in October (Fig. 13g) and slightly increased (2–6) in November for all the stations in the proximity of the Chandeleur Islands (Fig. 13h).

4. Discussion

The 2015 *K. brevis* bloom raised concerns within the local public and scientific communities because of its impact on the valuable recreation and commercial fisheries activities within the region. The Mississippi Sound produces nearly 10% of the Gulf-wide oyster

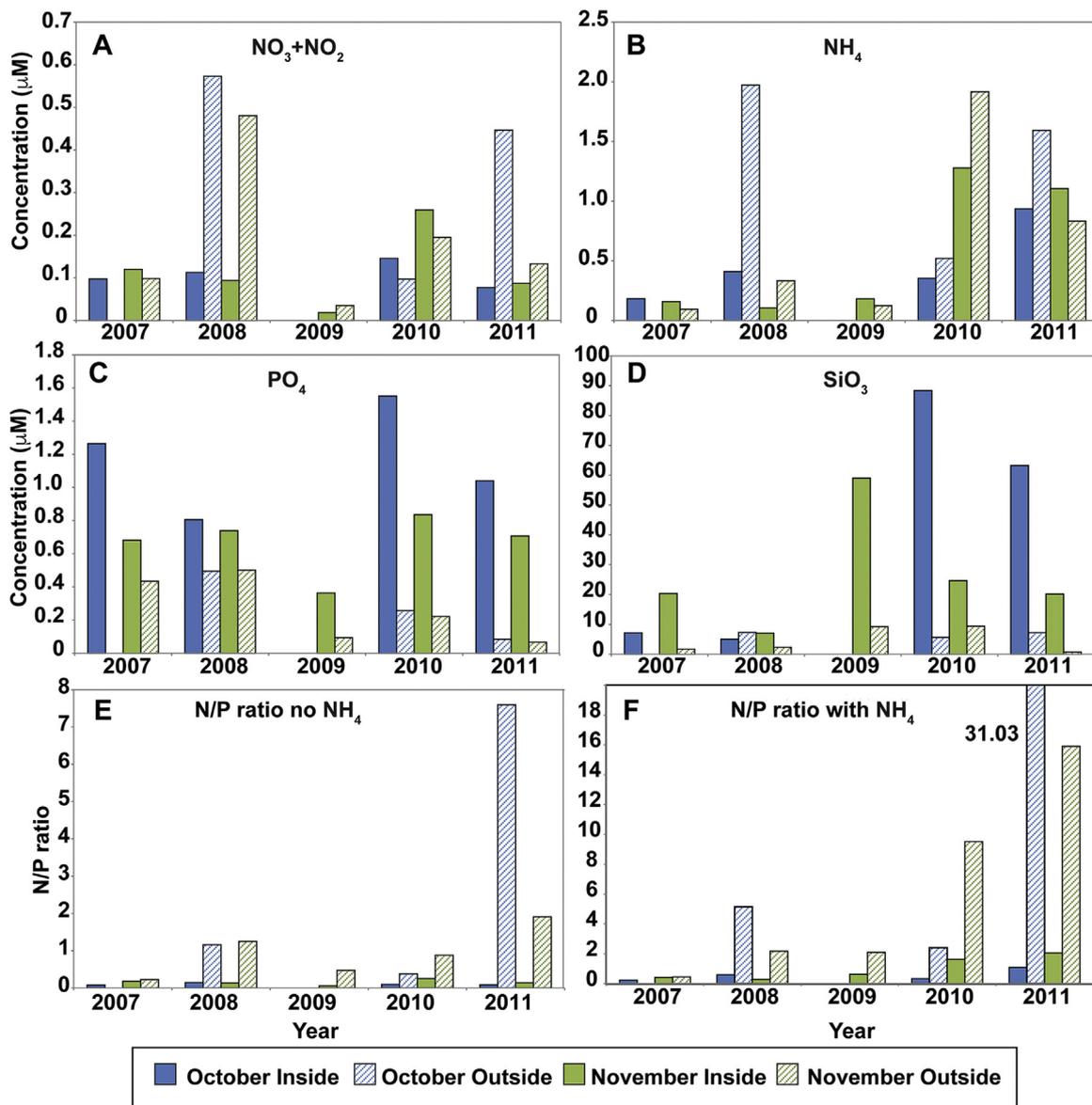


Fig. 12. Historical nutrient data at 8 stations from the NGI cruises during October and November 2007–2011. Stations 1–4 were average in a group called “inside” the Mississippi Sound and stations 5–8 were average in a group called “outside” the Mississippi Sound. The blue and green color bars represent the inside stations for the month of October and November, respectively. The side line blue and green bars represent the outside stations for October and November. a) NO₃ + NO₂, b) NH₄, c) PO₄, d) SiO₃, e) N/P ratio not considering NH₄, and f) N/P ratio considering NH₄. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

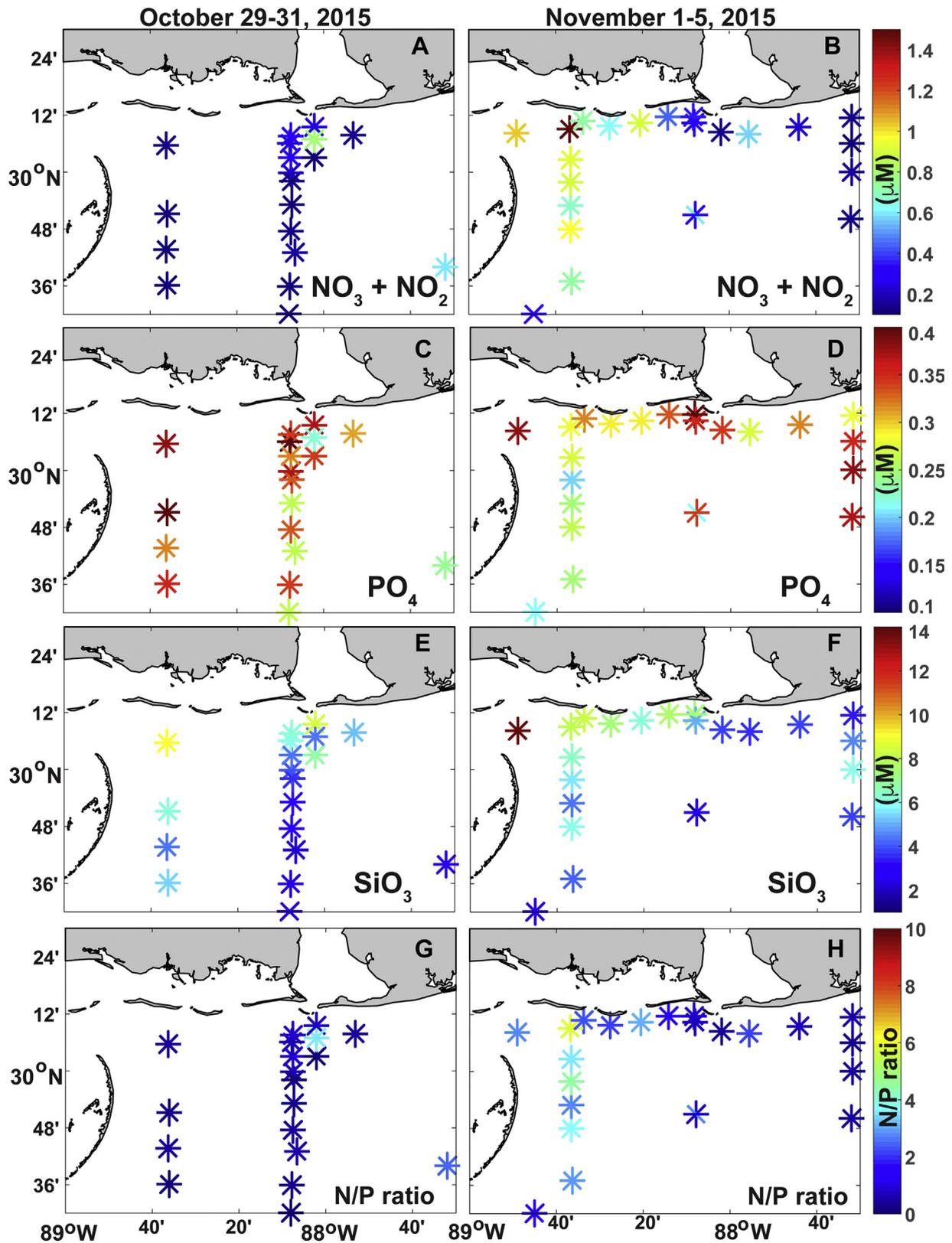


Fig. 13. Nutrient samples collected during the fall CONCORDE cruise. The left column has the nutrient data from 29 to 31 October 2015, right before the heavy river discharge associated to the passage of TC Patricia's remnants. The right column has the data for 1–5 November 2015. a–b) $\text{NO}_3 + \text{NO}_2$, c–d) PO_4 , e–f) SiO_3 and g–h) N/P ratiion calculated without NH_4 . NH_4 measurements were not available for most of the cruise. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

harvest (VanderKooij, 2012). HAB monitoring programs are required and should be adequately supported with trained personnel and equipment. The Harmful Algal Bloom Integrated

Observing System (HABIOS) plan of the Gulf of Mexico Coastal Ocean Observing System (Nowlin et al., 2008) could be used to implement enhanced HAB monitoring, modeling and prediction in

the western Mississippi Bight, that could feed into the NOAA Harmful Algal BloomS Observing System (HABSOS) site (<https://habsos.noaa.gov/>) and be directly utilized by marine resource managers.

The 2015 *K. brevis* bloom initially showed similar characteristics to the 1996 bloom documented by Dortch et al. (1998) and Maier-Brown et al. (2006). The 1996 bloom advected westward from the Florida Panhandle, which was attributed to the circulation pattern set up by TC Josephine. The passage of TC Patricia's remnants over the study area during the 2015 bloom signaled a similar pattern, although the time frame in which the bloom occurred in Mississippi waters was different. In 2015, *K. brevis* cells were observed offshore south of Mobile Bay (see green symbols in Fig. 4a) as early as 31 October during the CONCORDE cruise. However, the 2015 bloom did not intensify in Mississippi coastal waters until December, while in 1996 the bloom in Mississippi Sound and Bight was documented from 1 November to 11 December 1996 (Dortch et al., 1998). In other cases, such as fall 2007, a *K. brevis* bloom advected westward from the Florida Panhandle to the western Mississippi Bight between late October and early November, but the bloom did not enter or intensify in the Mississippi Sound and lasted only several days in the western Mississippi Bight before it dissipated.

In the nGoM, westward flow is common throughout fall (Weisberg et al., 1996; He and Weisberg, 2003; Morey et al., 2003; Dzwonkowski and Park, 2010), but that pose the question: why are *K. brevis* blooms in the Mississippi Sound not as recurrent as those in the Florida Panhandle? An average of fall (September–November) surface current data from HFR data over the period 2010–2016 (Fig. 7g) shows predominately west-southwestward flow in the northern Mississippi Bight west of Mobile Bay. This lack of mean advection to the Mississippi Sound indicates that pathways to the Sound are controlled either by the intra-seasonal time variable flow or inter-annual fall differences. To understand the mechanisms that bring blooms to the Mississippi Sound, we compared the bio-physical conditions during fall 2007 and 2015. Both years had *K. brevis* blooms near Cape San Blas; however, as documented above, the impact on Mississippi Sound was quite different. While no documentation or news reports exist of a bloom in the Mississippi Sound for 2007, the analysis here of historical cell counts databases and satellite imagery show that the *K. brevis* bloom did reach the western Mississippi Bight but probably not the Sound. The 2007 bloom in Mississippi coastal waters was short-lived and concentrations were not as elevated as in other years, such as in 2015 where cell counts exceeded 10^6 cells L^{-1} . This suggests that blooms may reach the western Mississippi Bight more often than previously thought, although they may not always intensify or enter the Mississippi Sound unless ideal oceanographic conditions are present.

The next question is why in some years, such as in 2015, do blooms intensify, while in other years they are short lived, such as 2007? Although the question is extremely ambitious and data is too limited to fully answer it, we investigated several factors (e.g., circulation, wind, river discharge, salinity and nutrients), which may have influenced differences in intensification and duration of blooms in 2007 and 2015. The near-surface Lagrangian particle releases revealed notable difference in the interannual connectivity between the bloom sources (i.e., Cape San Blas) and the Mississippi Sound. In 2015, the particles (Fig. 4c) followed the same westward pattern observed in the satellite imagery (Fig. 4b) and *in situ* data (Fig. 4a). Particles released a month later were still following a westward flow (Fig. 4d). In the case of 2007, Lagrangian particles did not fully capture the bloom reaching the Mississippi Bight in November, except for one particle that suggests the possibility of westward transport during the first Lagrangian release (Fig. 3c) moving westward towards the western Mississippi

Bight, while the other particles moved west-southwest offshore of the Mississippi Sound and eventually outside the Mississippi Bight (Fig. 3c). The second set of particles released later in October (Fig. 3d) transported westward for a few days, but a strong eastward shift of currents began in early November and none of the particles reached Mobile Bay, let alone the Mississippi Sound (Fig. 3d). Therefore, particle tracking suggests that *K. brevis* counts should have arrived to the Mobile Bay area and western Mississippi Bight before the currents shifted. Indeed, *K. brevis* cell counts were observed in Mobile Bay as early as 16 October 2007, and the satellite delineations (Fig. 3b, green color, and Figs. Appendix A and B in Supplementary file) reached Mobile Bay around the same time. The first satellite delineation in the Mississippi Bight was 2 November 2007 (Fig. 3b, yellow color, Fig. Appendix B in Supplementary file), whereas *in situ* samples for validation were not available until 14 November 2007.

Two distinctive events of strong westward currents were seen clearly in 2015: one from 18 to 28 October 2015, and a prolonged event from 15 November to 8 December (Fig. 5). In 2007, westward currents were stronger from September to mid-October and during the first week of November, but weaker after that (<0.1 $m s^{-1}$) especially in nearshore waters. Northward currents were also stronger in 2015 than 2007, especially between $87.0^{\circ}W$ and $85.0^{\circ}W$ (Fig. 6). Mean current fields from HFR confirmed the model predictions, suggesting strong mean westward-northwestward flow from October to December for 2015 and only in October for 2007 (Fig. 7). Wind data from the Dauphin Island station showed that the number of consecutive hours of winds favorable for offshore waters flowing into the Mississippi Sound was nearly twice as much for fall 2015 in comparison to 2007. It is important to mention that the *K. brevis* blooms near Cape San Blas and Panama City generally persisted until December. So, an intense westward-northwestward flow until December may increase the probability of advecting cells into the western Mississippi Bight and Mississippi Sound, allowing them plenty of time to adapt to regional environmental conditions (e.g., salinity) and/or settle in this region. A northward flow may also enhance the retention of blooms in the Mississippi Bight.

In addition to the sea surface currents and winds, other factors such as river discharge, salinity and nutrients were explored, which may have influenced the intensification of the 2015 bloom. River discharge increased drastically after the passage of TC Patricia's remnants on 27 October 2015 for all nGoM rivers, while river discharge for 2007 was below the 10-year mean (Fig. 9). The effect of such high river discharge and freshwater input into the Mississippi Sound and Mobile Bay estuarine systems in 2015 is clearly observed in the salinity, which decreased drastically after the passage of TC Patricia's remnants. For example, at station M3 (near the Pascagoula River) salinity decreased from 25 to 3, while river discharge increased from 50 to 300 $m^3 s^{-1}$ on 27 October 2015. Another peak in discharge was observed on 24 December 2015 at the Mobile River which resulted in a salinity drop from ~ 25 to 6 at the Dauphin Island station (Figs. 9 and 10). Salinities above 30 were observed in Mississippi Sound and Mobile Bay for almost the entire month of October 2015, as reported by Cambazoglu et al. (2017), due to an intense intrusion of shelf waters into the estuarine system. Although the currents and the wind after October were also favorable for intrusions, high river discharge dominated the region after the passage of TC Patricia's remnants. The salinity gradient between the Dauphin Island and FOCAL stations exceeded a salinity of 10 for most of the month of December. This could also generate a density-driven transport towards the coast, exacerbating the westward-northwestward wind-driven transport. This should enhance the transport of *K. brevis* bloom towards the Mississippi Sound.

Finucane (1960, 1964) suggested that *K. brevis* does not thrive well in salinities below 24. Further, Steidinger and Ingle (1972) and Landsberg and Steidinger (1998) suggest that salinity could be a barrier for *K. brevis* entering the estuaries such as Tampa Bay and Charlotte Harbor. In contrast, this has not been the case for the nGoM during the 1996 and 2015 *K. brevis* bloom events, where blooms thrived in salinities as low as 5. In an attempt to explain the occurrence of high concentrations of *K. brevis* at such low salinities, Maier-Brown et al. (2006) suggest the possibilities of 1) a seed population along the Florida Panhandle containing cells like the Mexico Beach clone, which can tolerate lower salinities and/or 2) sufficient time with optimal growth conditions to allow adaptation to occur. The bloom of *K. brevis* reported in 2015 was similar to 1996. Above 72% of the total *K. brevis* cell counts were found in salinities below 25, while in 2007 only 13% were in salinities below 25. These results emphasize that salinity is not always a physiological barrier for the inner sections of the Mississippi Sound estuary where oysters are harvested.

Historical nutrient data from the NGI cruises (Fig. 12) for the fall showed very low $\text{NO}_3 + \text{NO}_2$ concentrations ($<0.1 \mu\text{M}$), variable NH_4 concentrations (0.1 to $1.3 \mu\text{M}$), and elevated PO_4 concentrations ($>0.6 \mu\text{M}$) inside the Mississippi Sound throughout much of the 5-year study. Regardless, nutrient concentrations overall were greater and more variable at stations outside the Mississippi Sound. The molar nitrogen/phosphate ratios inside the Mississippi Sound were below 2. However, this is one of the main data gaps for this region that needs further investigation. The data collected during the CONCORDE cruise in 2015 (Fig. 13) allowed us to determine the nutrient response right after a heavy rain event. Relative to the historic NGI baseline data, $\text{NO}_3 + \text{NO}_2$ concentrations doubled after the event, but PO_4 did not change. The molar nitrogen/phosphate ratios were still very low even after the rain event, although a slight increase was observed towards the western side of the Mississippi Bight.

Research has shown that *K. brevis* is capable of efficient utilization of nitrogen (N) and phosphate (P) at low concentrations (Vargo, 2009 and references therein). It is also capable of optimizing organically-derived nutrients such as urea and amino acids (e.g., Wilson, 1966; Baden and Mende, 1979; Vargo and Shanley, 1985; Shimizu and Wrensford, 1993; Steidinger et al., 1998; Gomperts, 2002). Some possible nutrient sources include *Trichodesmium* nitrogen fixation, zooplankton excretion, anthropogenic nutrients, benthic nutrient fluxes, nutrients from decaying fish, submarine water discharge (SGD), atmospheric deposition and mixotrophic consumption of picoplankton (e.g., Hu et al., 2006; Mulholland et al., 2006; Lapointe and Bedford, 2007; Lester et al., 2008; Vargo et al., 2008; Yentsch et al., 2008; Glibert et al., 2009; Uhlenbrock, 2009; Dixon et al., 2014; Killberg-Thoreson et al., 2014; Mulholland et al., 2014).

Although *K. brevis* can thrive in low nutrient environments, the historical $\text{NO}_3 + \text{NO}_2$ concentrations observed inside the Mississippi Sound do not seem favorable for maintaining a large bloom. In 2015, river discharge increased throughout late fall, suggesting a possible source of nutrients and more favorable conditions for bloom maintenance than fall 2007, which was a dry year. Additionally, a large *Trichodesmium* aggregation, indicative of a bloom, was also observed near Mobile Bay in late October 2015 (Dzwonkowski et al., 2017). Although information about the size and duration of this bloom is lacking, this may have been a source of fixed nitrogen (Mulholland et al., 2006; 2014) and should be investigated further. SGD also has been suggested as a nutrient source for the Mississippi Sound and near the Barrier Islands (Joung et al., 2017), as well as a possible nutrient source for *K. brevis* (Hu et al., 2006). Unfortunately, nutrient data is limited for the Mississippi Sound and Bight, so further research and monitoring

programs should consider adding them into their routine sampling programs.

5. Conclusion

Two major differences were observed in the bio-physical conditions during fall 2007 and 2015 that may have favored the intensification of a *K. brevis* bloom in Mississippi coastal waters in 2015 but not in 2007. The first difference was an intense westward-northwestward flow in 2015 that persisted until the beginning of December. This allowed for continuous advection of a persistent bloom in the Florida Panhandle, which increased the time for possible adaptation of *K. brevis* to lower salinity environments. This persistent westward-northwestward flow is favorable for bringing Mississippi Bight waters into the Mississippi Sound. The second major difference was the elevated river discharge during fall 2015, which probably contributed a large nutrient flux to a region that generally seems to be nutrient-limited during this time of year. Blooms of *K. brevis* may reach the Mississippi Coast more often than was previously thought; however, conditions may not always be favorable for bloom intensification. Field monitoring, satellite imagery and circulation models may be sufficient to forecast future blooms in Mississippi coastal waters; other parameters such as nutrient data are necessary to understand the dynamics and duration of these blooms. Further validation and improvement of the satellite detection techniques for the Mississippi coastal waters should also be considered and coordinate with the local HAB monitoring programs.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.hal.2017.12.008>.

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