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Impact of Hurricane Ian (2022) on *Karenia brevis* Bloom on the West Florida Shelf

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Key Points:

- Tropical storms with high winds and heavy precipitation provide a favorable condition for *Karenia brevis* blooms on the West Florida Shelf
- Storm-induced upwelling-favorable winds transport subsurface *K. brevis* cells toward the shore
- Heavy precipitation in tropical storms discharges a huge pulse of riverine nutrients to fuel *K. brevis* growth

Supporting Information:

Supporting Information may be found in the online version of this article.

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Abstract Blooms of toxigenic *Karenia brevis* are a major concern to public health and marine ecosystems on the West Florida Shelf. Hurricanes and tropical storms can discharge huge amounts of terrestrial nutrients into coastal oceans over a short time and have been linked to large plankton blooms, but the underlying mechanisms for the bloom generation are not well understood. In 2022, Hurricane Ian generated extensive river plumes laden with nutrients, followed by a large *K. brevis* bloom that lasted for six months. Analysis using a coupled hydrodynamic-biogeochemical model showed that Hurricane Ian drove the bloom in two ways. First, northerly winds on the western half of Ian generated coastal upwelling and onshore bottom currents that transported subsurface *K. brevis* cells toward the coast. Second, a substantial amount of the riverine nutrients remained after the initial diatom bloom and were dispersed widely, creating a favorable condition for the slow-growing *K. brevis*.

Plain Language Summary On the West Florida Shelf (WFS), *Karenia brevis* is a highly concerning toxicogenic species, posing threats to human health and marine ecosystems. Hurricanes and tropical storms, which can bring large amounts of nutrient input, were thought to be an important factor in driving harmful algal blooms (HABs) in coastal regions, but the connection is not well understood, particularly for HAB species that originate offshore. A large *K. brevis* bloom developed 3 weeks after the passage of Hurricane Ian in September 2022 and lasted for six months. Using a numerical model, we showed that Hurricane Ian affected the HABs in two ways. First, the northerly winds produced by Hurricane Ian generated onshore currents in the bottom layers and transported offshore subsurface *K. brevis* cells toward the coast. Second, a short bloom of fast-growing diatoms developed rapidly after the passage of Hurricane Ian, but this diatom bloom was terminated within a month and left a sufficient amount of nutrients for *K. brevis* cells to grow in the following months. Although Hurricane Ian moved across the WFS in a matter of days, it doubled the size of the *K. brevis* bloom and its impact lasted for several months.

1. Introduction

Blooms of the toxic dinoflagellate *Karenia brevis* occur almost annually on the West Florida Shelf (WFS), typically initiating in the fall and terminating in the spring. Blooms vary widely in intensity and duration from year to year, however, from brief and localized, to temporally and spatially expansive and ecologically devastating (Stumpf et al., 2022). The brevetoxins produced by *K. brevis* blooms are a major concern. Ingesting or inhaling the toxins can pose significant risks to human health and may lead to mass mortality of fish and marine mammals (Flewelling et al., 2005; Gannon et al., 2009; Hoagland et al., 2009; Steidinger, 1993).

Before developing into a coastal bloom, *K. brevis* cells reside offshore in subsurface waters and need to be transported onshore in order to utilize the nutrients near the coast (Steidinger, 1975; Walsh et al., 2002; Weisberg et al., 2019). The seasonal circulation pattern on the WFS is mainly driven by wind forcing (Liu et al., 2016; Weisberg & Liu, 2022). The prevailing wind direction switches from southeasterly during summer to northeasterly from fall to spring. Correspondingly, the shelf circulation switched from coastal downwelling to coastal upwelling during the fall (Liu & Weisberg, 2012). Coastal upwelling can transport the subsurface *K. brevis* cells toward the shore (Li & Weisberg, 1999; Stumpf et al., 1998). While upwelling and circulation are key to bloom initiation, variations in external nutrient sources also influence *K. brevis* blooms.

Riverine nutrient input is one nutrient source for *K. brevis* growth but was thought to be insufficient (Heil et al., 2014; Vargo, 2009). It was estimated that the combined external nutrients from deeper Gulf of Mexico (GoM) and river discharge only account for 17% and 69% of the N and P needs of *K. brevis* blooms, while regenerated nutrients and pelagic N_2 fixation were thought to be more important in supporting large coastal blooms

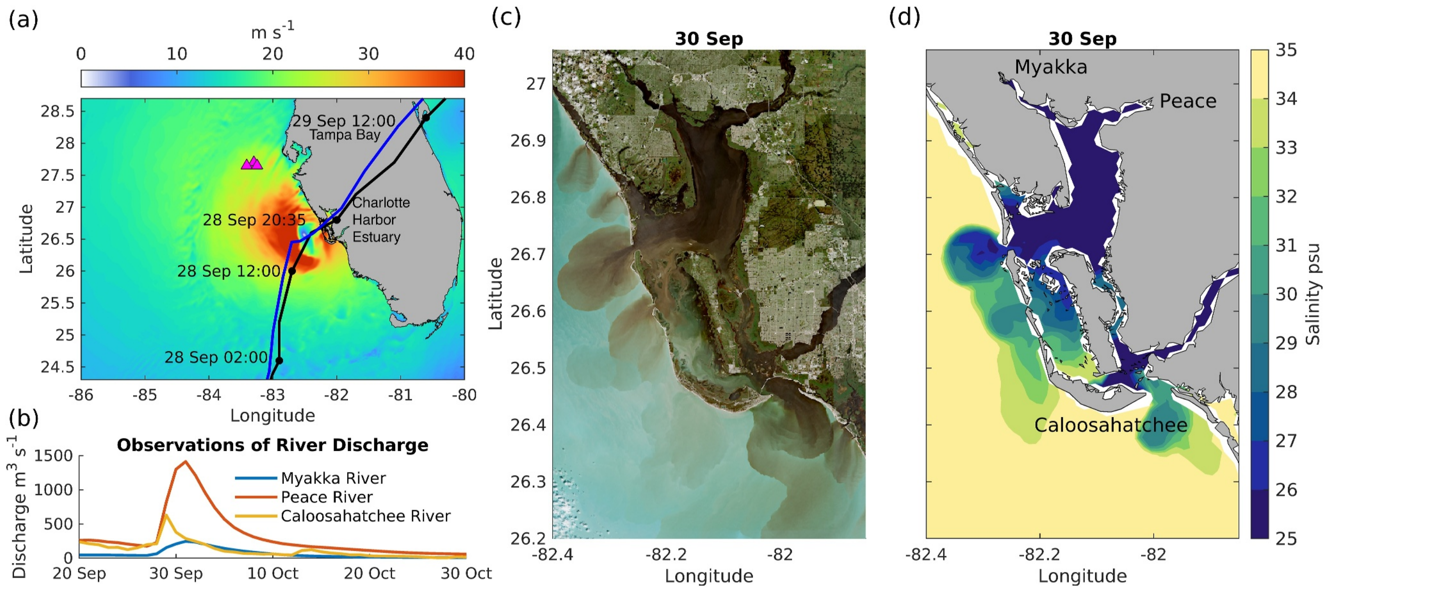

Figure 1. (a) Snapshot of the modeled-predicted wind speed magnitude (color) at 20:00 (UTC) on 28 September 2022. The solid lines represent the predicted (blue) and observed (black) track of Hurricane Ian with time stamps. The red triangles showed the offshore locations of the initial *K. brevis* cells. (b) Time series of the observed flows from three major rivers discharging into the Charlotte Harbor Estuary. (c) True color image of the coastal region captured by Sentinel-2 satellite and (d) the distribution of modeled surface salinity on 30 September.

(Dixon, Murphy, et al., 2014; Glibert et al., 2009; Heil et al., 2014). However, eutrophication has been found to be a major factor in driving long-term increases in *K. brevis* blooms (Brand & Compton, 2007; Medina et al., 2020, 2022).

Extreme weather events such as hurricanes can also supply a large pulse of nutrients and drive coastal circulation through strong winds. Previous studies showed that hurricanes and tropical storms stimulated phytoplankton blooms in different ways. In the open ocean, satellite observations showed that plankton blooms developed after the passage of a hurricane as wind-driven vertical mixing injected deep-ocean nutrients into the euphotic layer, fueling phytoplankton growth that lasted days to 1–2 weeks (Davis & Yan, 2004; Zheng & Tang, 2007). The same mechanism was responsible for generating a fall bloom in Chesapeake Bay following Hurricane Isabel (Miller et al., 2006; Roman et al., 2005). In estuarine and coastal environments where rivers are the main conduit of terrestrial nutrients, tropical storms carrying heavy precipitation can stimulate phytoplankton blooms by discharging a large amount of nutrients (Loftus & Seliger, 1976). However, different phytoplankton species may respond differently (Fiorendino et al., 2023; Thompson et al., 2023), resulting in changes in phytoplankton community composition (Paerl et al., 2006; Peierls et al., 2003; Tester et al., 2003). In particular, Paerl et al. (2018) found that plankton response depends on riverine nutrient loading, the flushing rate [defined as "water replacement rate, relative to the volume of that water body" in Paerl et al. (2014)], and algal growth rate. High freshwater discharge and nutrient loads favored fast-growing species such as chlorophytes and cryptophytes, while moderately wet storms stimulated blooms of vertically migrating dinoflagellates, such as *Karlodinium veneficum* (Hall et al., 2008).

On the WFS, hurricanes have also been associated with large *K. brevis* blooms. For example, Hurricanes Irma (2017), Tropical Storm Gordon (2018), and Hurricane Michael (2018) have been suspected of contributing to the severity of the 2017–2019 *K. brevis* bloom that lasted for 17 months (Heil & Muni-Morgan, 2021). The large bloom in 2005 was also thought to be related to nutrient inputs from a series of hurricanes that hit southwest Florida (Hu et al., 2006). It was suggested that terrestrial nutrients discharged during the storms may have contributed to the *K. brevis* blooms. However, the underlying mechanisms are not well understood, particularly whether a hurricane can facilitate the onshore transport of the offshore *K. brevis* cells and whether a large pulse of riverine nutrients discharged during a hurricane could be sufficient to support *K. brevis* blooms.

On 28 September 2022, Hurricane Ian, a category 4 hurricane with winds exceeding 50 m s^{-1} (Figure 1a), made landfall in southwest Florida (Heidarzadeh et al., 2023). It produced >530 mm of rainfall over 24 hr (Bucci et al., 2023), and caused extensive flooding, with flows in the Peace River and the Caloosahatchee River exceeding 40 and 12 times of their annual averages, respectively (Figure 1b). On October 17, 2 weeks after the hurricane's landfall, *K. brevis* cells with a concentration of $\sim 10^4$ cells L^{-1} were detected by the Florida Fish and Wildlife Research Institute (FWRI) along the coast between the Tampa Bay and Charlotte Harbor Estuary. This initial population developed into a dense coastal bloom exceeding 10^5 cells L^{-1}, a threshold commonly used as an alert level for red tide conditions and fish kills (Flaherty & Landsberg, 2011; Gannon et al., 2009). The bloom peaked in November and persisted into the next spring.

Here we use the Coupled Ocean-Atmosphere-Wave-Sediment Transport (COAWST) modeling system (Warner et al., 2010) to simulate waves, currents, and sediment dynamics during and following Hurricane Ian (Chen et al., 2019; Warner et al., 2010, 2017; Zang et al., 2018). COAWST is coupled to a biogeochemical model which was used to simulate the *K. brevis* bloom after the Piney Point event in Tampa Bay in 2021 (Chen et al., 2023). The same biogeochemical model was also used in several studies in Chesapeake Bay (Li et al., 2021, 2022; Testa et al., 2014; Zhang et al., 2021). We use this coupled modeling system to investigate how Hurricane Ian affected the *K. brevis* bloom on WFS.

2. Methods

COAWST contains four components: the Regional Ocean Modeling System (ROMS) (Haidvogel et al., 2008; Shchepetkin & McWilliams, 2005); the Weather and Research Forecasting (WRF) model (Skamarock et al., 2019); the Simulating Waves Nearshore model (Booij et al., 1999; Zang et al., 2018); and the Community Sediment Transport Modeling System (Warner et al., 2017; Xie et al., 2018; Zang et al., 2018).

ROMS was configured to cover the WFS and adjacent estuaries using a curvilinear coordinate system with 456 by 186 grid points, with a resolution ranging from 800 m inside estuaries to 3 km at the offshore boundary (Figure S1 in Supporting Information S1). In the vertical direction, 21 terrain-following sigma layers were used. A WRF model with double-nested domains was configured to hindcast Hurricane Ian's wind field and other atmospheric variables over the WFS. Its outer domain covers the GoM at 6 km resolution while the inner domain covers the WFS at 2 km resolution. A detailed model description can be found in Text S1 in Supporting Information S1.

The biogeochemical model, based on the Row-Column Advanced Ecological Systems Modeling Program (RCA) (HydroQual, 2004), has a water-column component (Isleib et al., 2007) and a two-layer sediment diagenesis model (Di Toro, 2001). The state variables include nitrate (NO_3^-), ammonium (NH_4^+), phosphate (PO_4^{3-}), dissolved and particulate organic forms of nitrogen and phosphorus of various levels of reactivity, dissolved O_2 (DO), and 3 groups of phytoplankton. Besides phytoplankton nutrient uptake, the model considers several important processes that can affect nutrient cycling (e.g., N cycling), including remineralization, nitrification, and denitrification. The sediment diagenesis model has one aerobic layer and one anaerobic layer. Following previous modeling studies (e.g., Chen et al., 2023; Walsh et al., 2001; Walsh et al., 2003), three major phytoplankton groups are simulated: diatoms, *K. brevis*, and cyanobacteria *Synechococcus sp*.

River flows were obtained from daily measurements at the United States Geological Survey (USGS) gauging stations (https://waterdata.usgs.gov/nwis). Water quality data from the Coastal and Heartland National Estuary Partnership (CHNEP), including NO_3^-, NH_4^+, PO_4^{3-}, and organic forms of N and P, were used to prescribe nutrient concentrations at the river boundaries (https://chnep.wateratlas.usf.edu/). More details about the RCA configuration can be found in Text S1 in Supporting Information S1.

ROMS ran for a spin-up period of one year, and its output was used to set the initial condition for the ROMS-RCA which ran from 1 September 2022–31 May 2023 (Chen & Li, 2025). A comparison between the true color satellite image and the modeled surface salinity field showed that the river plumes generated by Hurricane Ian are well captured in the model (Figures 1c and 1d). The model-predicted water levels, current velocities, salinity, temperature, nutrient concentrations, and chlorophyll *a* (Chl *a*) concentration are also in good agreement with the observational data collected at National Oceanic and Atmospheric Administration (NOAA) tidal stations, offshore mooring stations, and CHNEP water atlas (Figures S2–S7 in Supporting Information S1). In addition, the model captured the temporal and spatial variations in *K. brevis* bloom intensity, with a correlation coefficient of 0.53 (Figure S8 in Supporting Information S1). Detailed validation for the hydrodynamic and biogeochemical models is shown in Text S2 in Supporting Information S1.

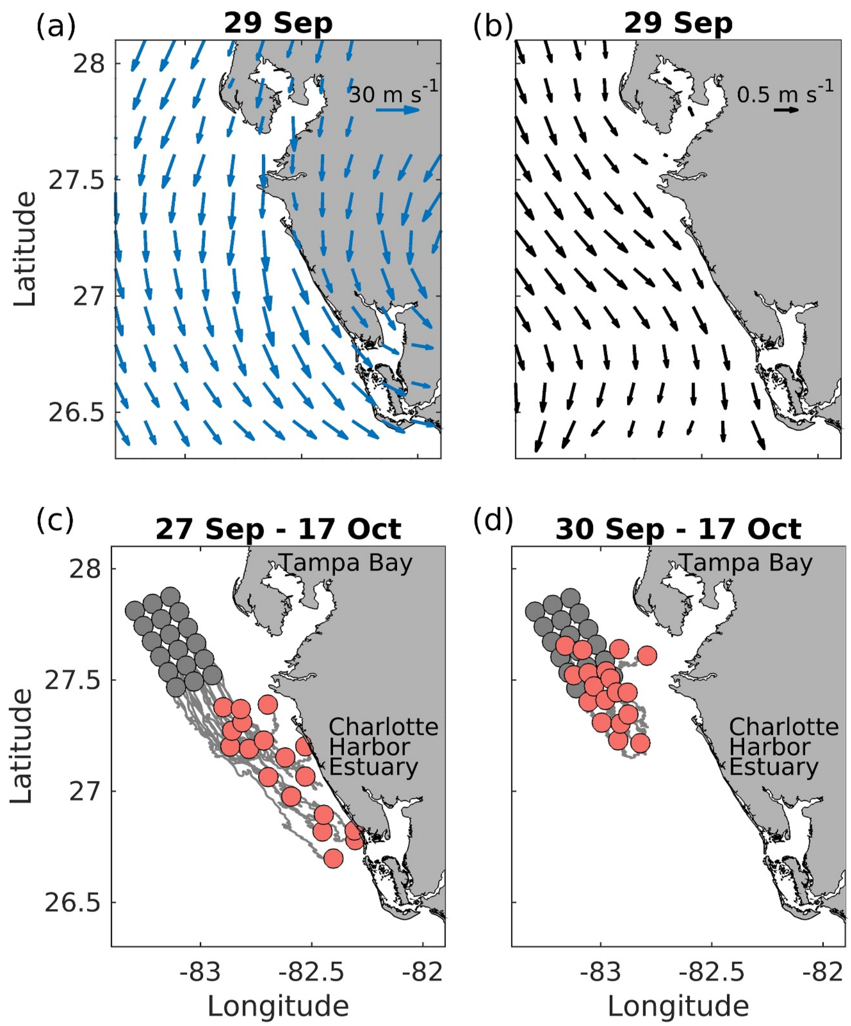

Figure 2. Snapshots of the modeled wind speed vector (a) and bottom current vector (b) on 29 September 2022. (c) and (d) Trajectories of the particles released before (c) and after (d) Hurricane Ian, respectively. The Gray circles mark the initial particle positions while the red circles denote their positions on 17 October.

To discern the impact of Hurricane Ian on the *K. brevis* bloom, we conducted a hypothetic scenario model run in which the effects of hurricane winds and precipitation were removed. Specifically, the wind speeds during the storm passage were reduced by 90% and the river flows were linearly interpolated between the flow observations before and after the storm, as described in Text S3 and shown in Figures S9–S12 in Supporting Information S1.

3. Results

An initial population of *K. brevis* with a concentration of 600 cells L^{-1} was observed at 30 m isobath, about 50 km to the southwest of Tampa Bay (Figure 1a). As Hurricane Ian approached the shore, strong northerly winds drove coastal upwelling and produced strong onshore currents in the bottom layer (Figures 2a and 2b; Figure S4 in Supporting Information S1). Two particle-tracking numerical experiments were conducted in which particles were released into the bottom layer at the offshore locations on September 27 (before the storm) and September 30 (after the storm). The particles released before the storm reached the coast on October 17 (Figure 2c), whereas those released after the storm failed to reach it (Figure 2d). Hence, storm-induced coastal upwelling transported the subsurface *K. brevis* cells toward the coast, where they could take advantage of the nutrients discharged during Hurricane Ian.

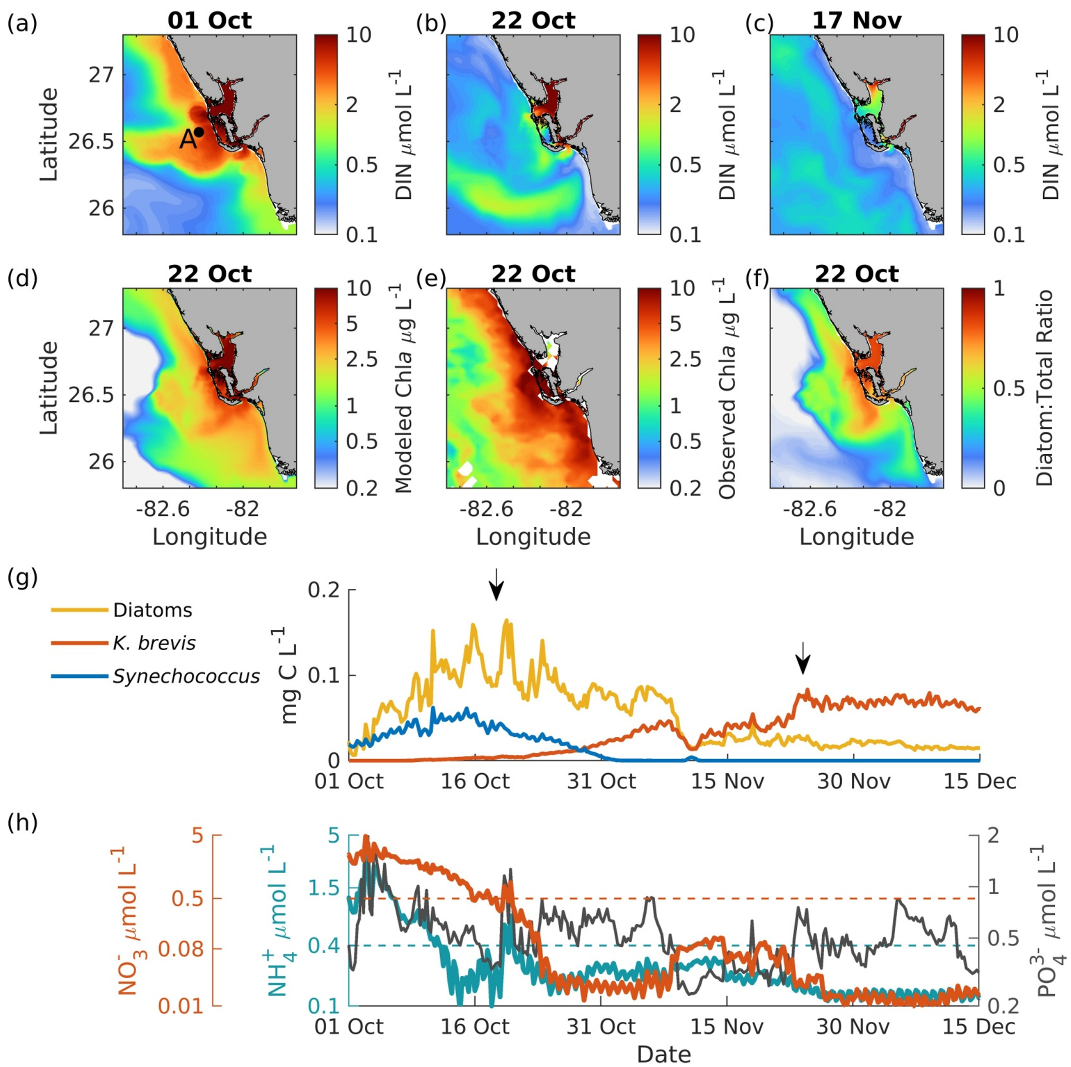

Figure 3. (a)–(c) The daily averaged surface dissolved inorganic nitrogen concentration predicted by the model. Station A in the center of the *K. brevis* bloom is marked by a black dot in (a). A comparison of Chl *a* concentration between the model results (d) and the National Oceanic and Atmospheric Administration MSL12 Ocean Color data set (e) on 22 October. (f) The ratio of diatom-bounded Chl *a* to the total Chl a. (g) Model-predicted time series of diatoms, *K. brevis*, and *Synechococcus* biomass at Station A (panel (a)). The two black arrows indicate the timing of diatom and *K. brevis* bloom peaks. (h) Model-predicted time series of NO_3^-, NH_4^+, and PO_4^{3-} at Station A in which the dashed lines mark the half-saturation levels for *K. brevis* uptake of NO_3^- and NH_4^+, respectively.

The growth of *K. brevis* cells was closely related to nutrient availability. In the two weeks following Hurricane Ian, our model estimated that about 2,500 metric tons of nitrogen (*N*) and 1,000 metric tons of phosphorus (*P*) were discharged into the Charlotte Harbor Estuary, which was comparable to the annual average loading of 3,700 metric tons of *N* and 700 metric tons of *P* according to historical data. The river plumes transported the nutrient-rich freshwater to the coastal ocean (Figure 1c), where *K. brevis* growth was *N*-limited. The dissolved inorganic nitrogen (DIN) was dominated by the terrestrial input after Ian's passage and exceeded 10 μmol L^{-1} near the coast (Figure 3a). The nutrient-rich patches subsequently extended offshore, and DIN concentration in coastal regions remained above 0.4 μmol L^{-1} in the next couple of months (Figures 3b and 3c). The elevated nutrient concentrations stimulated phytoplankton growth. The modeled Chl *a* exceeded 8 μg L^{-1} near the estuary mouth on October 22 (Figure 3d), in agreement with the ocean color observations from the NOAA's MSL12 data set (Figure 3e). This initial bloom was composed primarily of diatoms (Figure 3f). Time series of the three phytoplankton groups in the model results at Station A in the bloom center (marked in Figure 3a) showed rapid

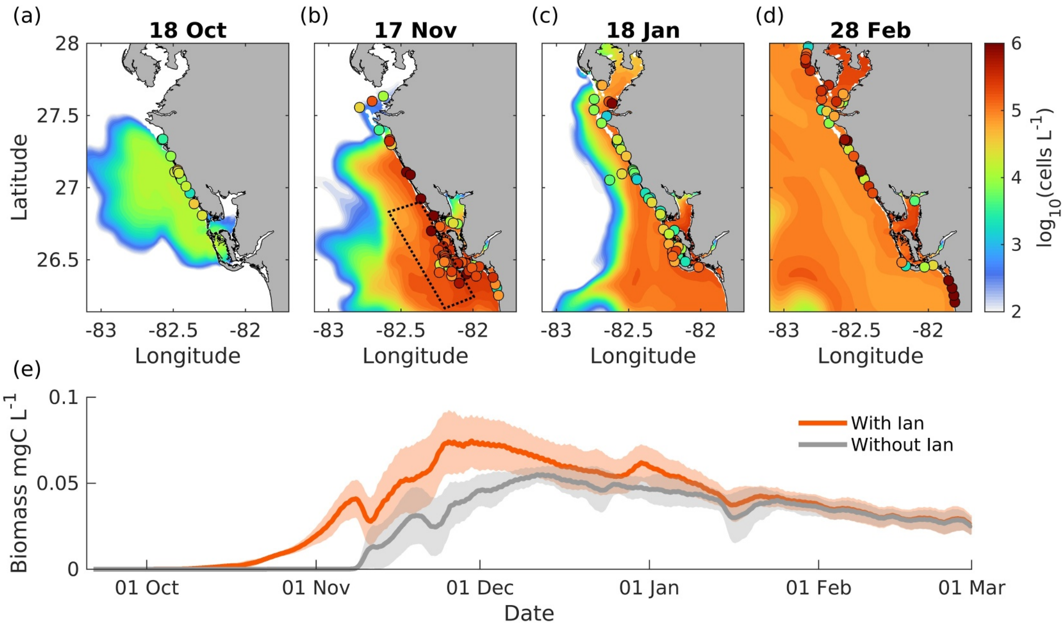

Figure 4. (a)–(d) Comparison between the modeled (color map) and observed (filled circles) surface *K. brevis* cell density; (e) Regional averaged *K. brevis* biomass in the model runs with and without hurricane Ian, with the shaded areas representing the standard deviation of the biomass across the region shown in panel (b).

increases in diatoms and *Synechococcus* biomass following the storm, with diatoms reaching a peak concentration of 0.16 mg C L^{-1} in mid-October (first arrow, Figure 3g). By early November, this diatom bloom disappeared.

The model showed that a weak bloom of *K. brevis* occurred in the west of Charlotte Harbor Estuary on 18 October (Figure 4a, Figure S13 in Supporting Information S1). It then spread northward toward Tampa Bay and southward along the coast, forming a widespread coastal bloom in November. The cell density remained around 10^5 cells L^{-1} through February (Figures 4b–4d). Unlike the short diatom bloom, the *K. brevis* bloom lasted for about 6 months before terminating in late spring (Figure S14 in Supporting Information S1). The modeled coastal *K. brevis* bloom agreed well with the observations in both bloom intensity and patterns (Figures 4a–4d).

The time series obtained from the model results at Station A shows how nutrients fueled *K. brevis* growth (Figures 3g and 3h). The initial diatom bloom in mid-October did not consume all inorganic nutrients. NO_3^- and NH_4^+ concentrations in November were comparable to the half-saturation coefficients for NO_3^- (0.5 μmol L^{-1}) and NH_4^+ (0.4 μmol L^{-1}) uptake by *K. brevis*. As a result, the *K. brevis* biomass showed a large increase and reached its peak (second arrow, Figure 3g) during November. Afterward, the nutrient concentrations declined and the cell density gradually decreased.

We compared the model results with and without Hurricane Ian. The time series of *K. brevis* biomass averaged across the bloom region (marked in Figure 4b) shows a large difference (Figure 4e). Without Hurricane Ian, the bloom did not develop until mid-November when seasonal upwelling transported the offshore population towards the coast. With Ian, the bloom initiated in late October and its peak biomass was twice as large as the one without Ian. The differences between the two model runs lasted for about 3 months (Figure 4e).

4. Discussion and Conclusion

This study integrates the COAWST model commonly used to study hurricanes and tropical storms with the RCA biogeochemical model that can simulate the dynamics of major phytoplankton groups in a coastal ocean. We showed how the strong wind fields and heavy precipitation produced by Hurricane Ian created a favorable condition for the development of large phytoplankton blooms on the WFS, including a succession from an initial short diatom bloom to a prolonged bloom of the toxic *K. brevis*. Although previous observational studies have documented how plankton community structure responds to hurricanes and tropical storms (Fiorendino

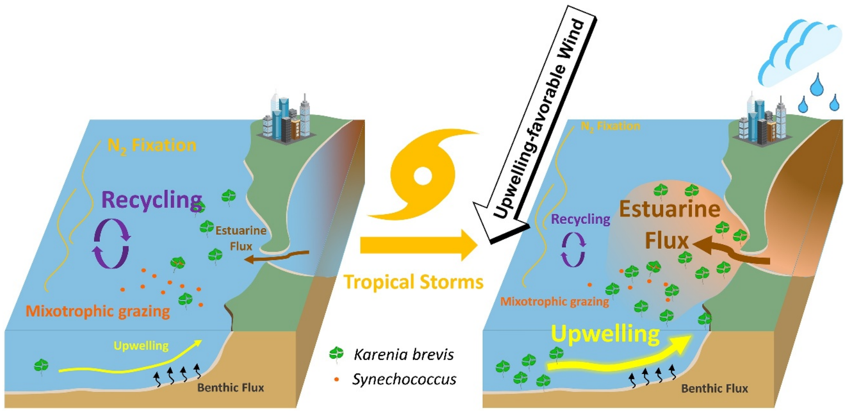

Figure 5. Schematic diagram of the storm impacts on harmful algal blooms in a coastal ocean. As a hurricane or tropical storm approaches the coast, wind-driven upwelling can advect subsurface *K. brevis* cells onshore, where they can utilize riverine nutrients discharged during the storm.

et al., 2023; H. Li et al., 2024; Paerl et al., 2018; Thompson et al., 2023), our modeling study explores the mechanism underlying the plankton response to hurricane forcing. Such a study is timely as stronger and wetter tropical storms are expected to hit coastal regions more frequently in a changing climate (Knutson et al., 2019, 2020).

We showed a positive effect of tropical storms in stimulating coastal phytoplankton blooms, but a few other studies showed variable and even negative storm effects. For example, only 43 out of 79 typhoon events in the South China Sea triggered phytoplankton blooms during 2000–2009 (Pan et al., 2017). A numerical modeling study by Zang et al. (2020) demonstrated that sediment resuspension during Hurricane Gustav (2008) in the northern GoM significantly depressed coastal primary production for more than a week. It indicates that storms may have suppressed phytoplankton blooms in the shallow coastal waters as strong sediment resuspension resulted in light limitation. Laboratory experiments have also shown that strong turbulence, which is common during storms, can cause increased cell death in various plankton species (Berdalet, 1992; Liu et al., 2024). Such a high level of mortality was thought to be sufficient to terminate *Karenia mikimotoi* blooms off the French coasts (Gentien et al., 2007).

Overall, our modeling analysis provides a quantitative validation of how hurricanes and tropical storms may drive *K. brevis* blooms on the WFS, as illustrated in the schematic diagram (Figure 5). First, the upwelling-favorable northerly winds generated by the storm create onshore bottom currents that transport offshore subsurface *K. brevis* cells toward the coast. Second, hurricanes and tropical storms with heavy precipitation deliver a large pulse of N and P loads that are comparable to the typical annual nutrient input. Following Hurricane Ian, coastal NO_3^-, NH_4^+, and PO_4^{3-} concentrations surged to over 10 times their typical levels of 0.1 μmol L^{-1}, 0.2 μmol L^{-1}, and 0.16 μmol L^{-1}, respectively (Dixon, Kirkpatrick, et al., 2014). Though some of the nutrients were utilized by fast-growing species like diatoms, a substantial amount was left on the shelf to support the growth of slow-growing *K. brevis* cells (Figures 3a–3c). With higher nutrient affinity (Magaña & Villareal, 2006; Vargo, 2009), *K. brevis* cells eventually developed into a large coastal bloom.

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Data Availability Statement

The Florida Fish and Wildlife Research Institute (FWRI) database provided the observations of *K. brevis* in this study, which can be found at https://myfwc.com/research/redtide/monitoring/database/.

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