Hurricane-driven alteration in plankton community size structure in the Gulf of Mexico: A modeling study

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[1] This was the first study to analyze phytoplankton and zooplankton community size structure during hurricane passage. A three-dimensional biophysical model was used to assess ecosystem dynamics, plankton biomass, and plankton distribution in the Gulf of Mexico during Hurricane Katrina (2005). Model simulations revealed that large phytoplankton were most responsive to hurricane-induced turbulent mixing and nutrient injection, with increases in biomass along the hurricane track. Small phytoplankton, microzooplankton, and mesozooplankton biomass primarily shifted in location and increased in spatial extent as a result of Hurricane Katrina. Hurricane passage disrupted the distribution of plankton biomass associated with mesoscale eddies. Biomass minimums and maximums that resided in the center of warm- and cold-core eddies and along eddy peripheries prior to hurricane passage were displaced during Hurricane Katrina. **Citation:** Gierach, M. M., B. Subrahmanyam, A. Samuelsen, and K. Ueyoshi (2009), Hurricane-driven alteration in plankton community size structure in the Gulf of Mexico: A modeling study, *Geophys. Res. Lett.*, *36*, L07604, doi:10.1029/2009GL037414.

1. Introduction

[2] Open ocean regions like the Gulf of Mexico (GoM) are characterized by low nutrient concentrations in surface waters and a food web based on regenerated production. These oligotrophic environments are dominated by small phytoplankton, which can grow at low nutrient concentrations due to high surface area to volume ratios. Ecosystem disturbances, such as frontal activity and hurricane passage, can perturb phytoplankton community composition and result in temporary dominance of opportunistic species over equilibrium species [*Platt et al.*, 2005]. Alterations at the food web base impact secondary production and change zooplankton community composition and biomass.

[3] Currently, no studies exist that analyze phytoplankton and zooplankton community composition during hurricane passage due to extreme weather conditions. Past studies have assessed diatom abundance before and after hurricanes using ocean color data and bio-optical algorithms [*Platt et al.*, 2005; *Son et al.*, 2007]. The disadvantages of these studies are their assessment of one particular phytoplankton group and coarse temporal resolution of 9–14 days pre- and post-storm. As a result, these studies speculate, but render it impossible to observe and understand changes in ecosystem dynamics during hurricane periods.

[4] Hurricane passage is characterized by strong Ekman pumping and vertical mixing. Combination of these processes causes nutrient enrichment in the euphotic zone by mixed layer deepening and nitracline shoaling, as well as resuspension of plankton from the mixed layer base. The conventional view is that as nutrient availability and mesoscale vertical motion increase, the abundance of large phytoplankton also increases due to high growth rates and nutrient requirements of larger cells [*Chisholm*, 1992; *Rodriguez et al.*, 2001]. Physical events enhance phytoplankton production and increase zooplankton biomass, wherein zooplankton can respond to greater prey availability on relatively brief timescales (<10 days) [*Cowles et al.*, 1987].

[5] Oceanic processes can have an additional influence on plankton distribution and community composition during hurricane passage. In the GoM, these processes include the Loop Current (LC), warm-core eddies (WCEs), and cold-core eddies (CCEs). CCEs have elevated plankton biomass and nutrient concentrations near the ocean surface, whereas WCEs have maximum concentrations displaced deeper in the water column. Phytoplankton biomass is generally enhanced at the center of mesoscale eddies, whereas elevated zooplankton biomass occurs at mesoscale eddy centers and peripheries [*Goldthwait and Steinberg*, 2008; *Yebra et al.*, 2005]. During hurricane passage, Ekman pumping and vertical mixing mediate the transport of nutrients and plankton biomass to the surface in CCEs and near-surface in WCEs/LC. Such transport likely increases plankton biomass in mesoscale eddies; however, biomass is expected to be greatest in CCEs.

[6] The focus of this paper is to analyze plankton community size structure in the GoM during Hurricane Katrina (2005) using a three-dimensional biophysical model. Ecosystem dynamics, plankton biomass, and plankton distribution in association with eddies are examined during the hurricane period. The benefits of using a model are greater spatial and temporal resolutions, and the ability to recreate scenarios that are generally impossible to observe.

2. Storm History

[7] Hurricane Katrina (23–30 August 2005) was the costliest and one of the deadliest hurricanes to date in United States history. During its lifespan, Hurricane Katrina made landfall three times (Figure 1). Landfall took place in southeastern Florida at 2230 UTC 25 August as a category 1 hurricane, near Buras, Louisiana at 1110 UTC 29 August as a category 3 hurricane, and at the Louisiana/Mississippi

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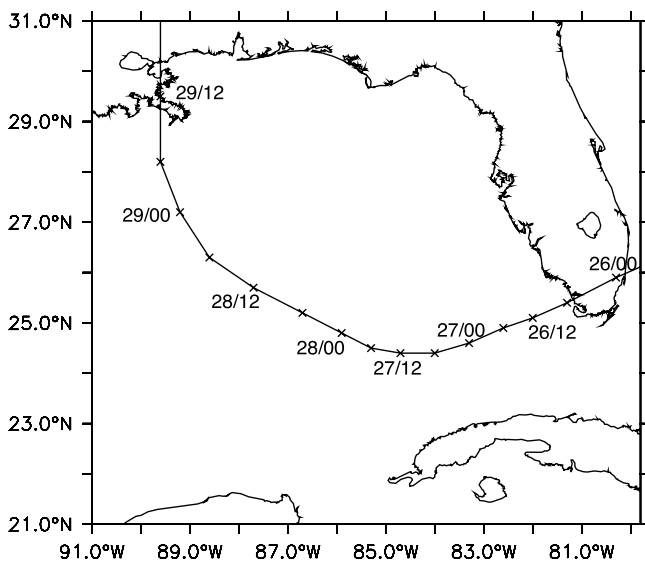
Figure 1. Track of Hurricane Katrina through the GoM, with associated dates and times.

border as a category 3 hurricane [*Knabb et al.*, 2005]. Hurricane Katrina attained peak intensity at 1800 UTC 28 August in the GoM, with wind speeds of 150 kt, an atmospheric pressure of 902 mb, and a width of 92.6–166.68 km. The average translation speed of Hurricane Katrina through the GoM was ∼5.2 m s^{-1}.

3. Methods

3.1. Physical Model

[8] The Navy Coastal Ocean Model (NCOM) was configured for the GoM with an algorithm implemented to calculate surface heat and momentum fluxes as described by *Morey et al.* [2006]. The regional NCOM has a horizontal resolution of 1/20° and 60 vertical layers (20 sigma levels above 100 m, and 40 z-levels below 100 m). The model domain encompasses the GoM and Caribbean Sea in a region from 15.55°N–31.5°N, 80.5°W–98.15°W, with an open eastern boundary.

[9] The model assimilates Modular Ocean Data Assimilation System (MODAS) [*Fox et al.*, 2002] temperature and salinity profiles and is forced by surface heat and momentum fluxes from the Bourassa-Vincent-Wood boundary layer model [*Bourassa et al.*, 1999]. Different from *Morey et al.* [2006], the model was forced by wind fields constructed using NOAA AOML Hurricane Research Division Wind Analyses (H*Wind fields) and National Centers for Environmental Prediction Reanalysis II (NCEPR2) winds. H*Wind fields have a spatial resolution of 6 km, covering a 960 km by 960 km area. Due to this confined spatial resolution, NCEPR2 winds were used to complete the wind field with an objective gridding method derived from that described by *Morey et al.* [2005].

[10] The GoM NCOM model was initialized with data assimilation and surface fluxes included from 8–26 August 2005 and ran from 26 August–1 September 2005 for Hurricane Katrina. Output variables of temperature, salinity, sea surface height (SSH), and vertical, meridional, and zonal velocities were provided with 2-hour temporal reso-

lutions. Temperature and vertical velocity were used directly by the ecosystem model, whereas zonal and meridional velocities were needed to calculate flow trajectories for the ecosystem model's semi-Lagrangian advection scheme (for more details see *Samuelsen and O'Brien* [2008]; hereinafter referred to as SO08).

3.2. Ecosystem Model

[11] The GoM ecosystem model was based upon the work of SO08, who created an ecosystem model for the northeast tropical Pacific. The model is a seven-component, nitrogen-based model that consists of nitrate, ammonium, two size classes of phytoplankton (small and large) and zooplankton (micro- and meso-), and detritus. Trophic dynamics within the model are as follows: small phytoplankton are grazed upon by microzooplankton, and mesozooplankton feed upon large phytoplankton, micro-zooplankton, and detritus, but have a strong preference for large phytoplankton (SO08). SO08 provided extensive details of the model setup, such that only a brief description is provided here with emphasis on model differences.

[12] The biological model has the same horizontal, vertical, and temporal resolutions as the physical model. The biological model domain was reduced to extend from 18°N–31.5°N and 80.65°W–98.15°W because of large vertical velocities close to the physical models' open boundaries that caused the biological model to perform poorly. The model was spun-up for a year, and then ran from 26 August–1 September 2005 for Hurricane Katrina. The ecosystem model was applied to the upper 441 m (i.e., 40 levels) of the physical model. Open boundary conditions were applied below 441 m and at the bottom in regions where the water column was shallower than 441 m, constituting sinks in the model. Therefore, the GoM continental shelf was a sink of organic sediments to the seafloor.

[13] Initial values for model variables were set to 0.01 mmol N m^{-3}, except for nitrate. Nitrate was calculated using a linear temperature-nitrate relationship that was derived from objectively analyzed 1° monthly climatologies of nitrate and temperature from the World Ocean Atlas 2005. The equation for the relationship was nitrate = 42.63−1.515*temperature (r^2 = 0.976, p < 0.05). To avoid negative nitrate concentrations at high temperatures, a minimum nitrate concentration of 0.01 mmol N m^{-3} was set. At depth, nitrate was relaxed back to the observed linear temperature-nitrate relationship to avoid nitrate loss in the model. Nutrient input from river discharge was excluded in the model.

[14] Denitrification and iron limitation were not included in the model like that of SO08, since oxygen is not depleted nor iron a limiting nutrient in the open GoM. Iron-limitation was parameterized by SO08 through the ammonium preference coefficient for large phytoplankton ($K_{p,P2}$). In the GoM model, ammonium preference was weakened by increasing $K_{p,P2}$ from 0.3 to 0.5 mmol N m^{-3}. Furthermore, the assumed ratio of chlorophyll-a (chl-a) to nitrate in phytoplankton was changed from 1.2 g chl-a/mol N (SO08) to 1 g chl-a/mol N [*Marra et al.*, 1990].

[15] A sensitivity analysis was performed at 24.4°N, 84°W using the same approach as SO08. The GoM model was sensitive to 3 out of 25 parameters, including maximum growth rate, assimilation coefficient, and mortality of mes-
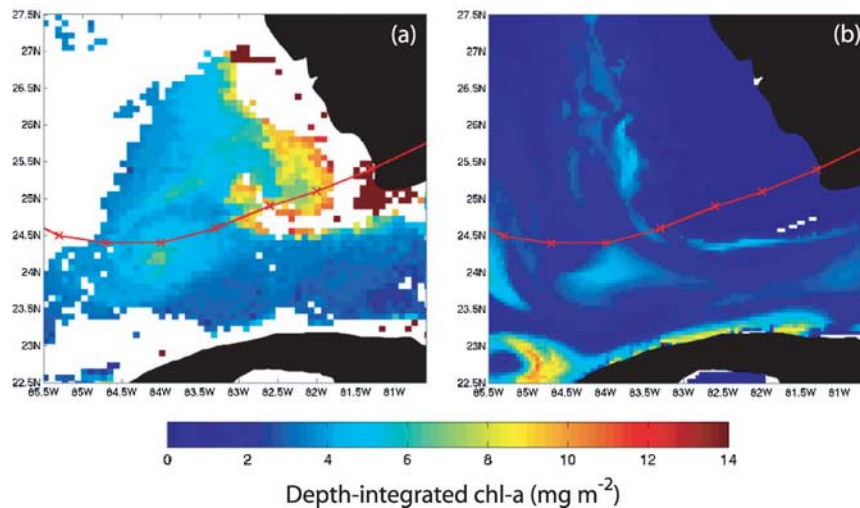
Figure 2. Time-averaged (30–31 August) comparison of (a) SeaWiFS and (b) model depth-integrated chl-a concentrations. The red line represents Hurricane Katrina's track. White pixels in Figure 2a are due to clouds.

ozooplankton. Ecosystem models are generally sensitive to the highest trophic level parameters [*Steele and Henderson*, 1992], explaining model sensitivity to mesozooplankton parameters.

3.3. Model Validation

[16] There was a lack of *in situ* data during Hurricane Katrina in the GoM. Therefore, the model was validated against Level 3 SeaWiFS chl-a data from NASA Goddard Space Flight Center's Ocean Biology Processing Group, with daily temporal and 9 km spatial resolutions. Satellite data was problematic during Hurricane Katrina, wherein only two days of data (30 and 31 August) were acquired in association with the model period. Data obtained was plagued with cloud interference, such that only a region from 22.5°N–27.5°N, 80.6°W–85.5°W was visible (Figure 2).

[17] Validation was performed through a time-averaged comparison of depth-integrated chl-a concentrations from the model to those of SeaWiFS. This data was acquired from the ratio of observed chl-a to the diffuse attenuation coefficient at 490 nm for SeaWiFS, integration of chl-a from the surface down to one optical depth for the biological model, and then calculation of a two-day mean (30–31 August) for both model and satellite estimates. Model optical depth was calculated using SO08's formulation of light attenuation and modeled phytoplankton results.

[18] Synoptic comparison between simulation and satellite observations on 30–31 August revealed that the model reproduced high chl-a concentrations in a region from 23.5°N–25.5°N, 83°W–85°W (Figure 2). However, depth-integrated values were ~2 mg m^{-2} lower in the model (~4–6 mg m^{-2}) than SeaWiFS (~6–8 mg m^{-2}). It is possible that SeaWiFS overestimated chl-a concentrations in this region due to signal contamination by colored dissolved organic matter, or advection of resuspended sediments from the West Florida Shelf (WFS; Figure 2a). The model underestimated chl-a concentrations along the GoM continental shelf. This was a direct result of model setup, wherein the shelf was treated as an organic sediment sink

and riverine input was excluded, contributing to lower shelf production (section 3.2). High chl-a concentrations were depicted along the northern coast of Cuba in the model, but were not observed by satellite due to cloud interference (Figure 2).
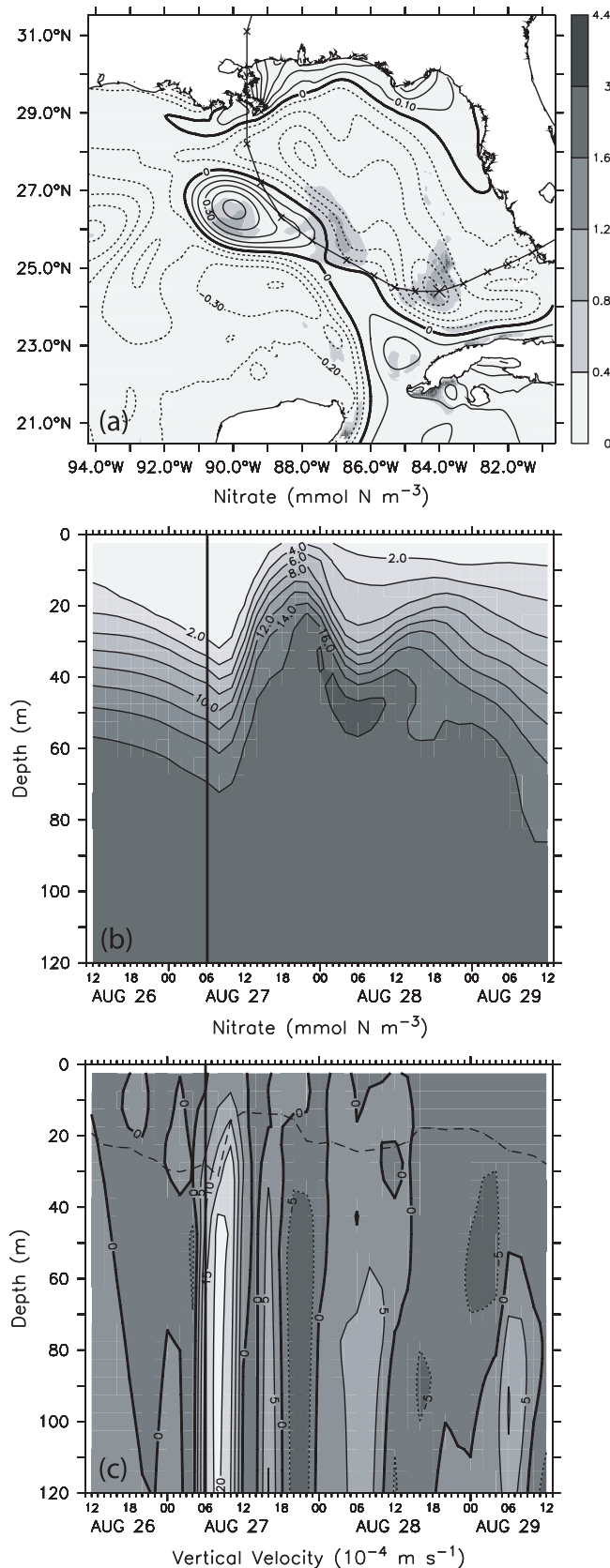
4. Results

[19] Time-averaged, near-surface nitrate concentrations during Hurricane Katrina revealed elevated nitrate values in a CCE and at eddy peripheries (Figure 3a). Nitrate concentrations of 0.4–1.6 mmol N m^{-3} were simulated along the track of Hurricane Katrina within these features, with highest concentrations of 1.2–1.6 mmol N m^{-3} occurring within a CCE at 24.4°N, 84°W. A time series of nitrate with depth within the CCE showed that subsurface nitrate of 2–4 mmol N m^{-3} concentration was brought to the near-surface at 2200 UTC 27 August via upwelling and entrainment from hurricane-force winds (Figures 3b and 3c).

[20] Depth-averaged spatial plots of the two-size classes of phytoplankton and zooplankton from 0–20 m depths are shown before and during Hurricane Katrina at 0000 UTC 26 August and 2200 UTC 27 August, respectively, as well as the difference between these times (Figure 4). Snapshots were chosen rather than time-averages since the biological responses associated with Hurricane Katrina occurred on hourly timescales. During Hurricane Katrina, positive SSH occurred along the WFS, depressed SSH associated with the CCE deepened, and the spatial pattern of the LC/WCE constricted (Figure 4). Common responses among the two-size classes of phytoplankton and zooplankton included a shift in CCE biomass to the east, WCE biomass to the west, southward displacement of biomass along the LC's eastern periphery, and either an increase in biomass spatial extent or concentration around 25.5°N, 86.5°W. Displaced CCE biomass was reduced for all size classes, except small phytoplankton, when compared to initial values within the eddy center (Figure 4). This is likely a result of entrainment of water below the plankton maximum, which has reduced plankton values [*Zimmerman and Biggs*, 1999]. Addition-

ally, plankton biomass that resided along the WFS prior to hurricane passage was displaced to the west during Hurricane Katrina (Figure 4). Displacement was caused by the counterclockwise rotation of the enhanced CCE, and/or

buildup of positive SSH along the WFS from hurricane-force winds.

[21] Small phytoplankton did not have much of a response to enhanced nitrate concentrations from Hurricane Katrina due to their low nutrient requirements, and as a result either did microzooplankton (Figures 4a–4c and 4g–4i). Primarily small phytoplankton and microzooplankton biomass shifted and increased in spatial extent in association with hurricane passage. In contrast, large phytoplankton responded well to hurricane-induced mixing and nitrate injection with increases in biomass along the track of Hurricane Katrina (Figures 4d–4f). Note that these concentrations were greater if snapshots were taken near the ocean surface, or if the maximum depth used in the depth-average was reduced. There was not an associated increase in mesozooplankton at 2200 UTC 27 August, contrary to what the difference image depicted (Figures 4j–4l). The increase in mesozooplankton biomass in the difference image was a result of biomass displacement due to Hurricane Katrina. The time period selected was not long enough after Hurricane Katrina for the mesozooplankton growth rate to show a response to greater prey availability of large phytoplankton.

5. Conclusions

[22] This was the first biophysical modeling study to assess ecosystem dynamics, plankton biomass, and plankton distribution during Hurricane Katrina (2005). Results revealed that phytoplankton and microzooplankton responded to hurricane passage on relatively short time scales. Large phytoplankton showed increases in biomass along the hurricane track, whereas small phytoplankton and microzooplankton biomass primarily shifted and increased in spatial extent. With increases in large phytoplankton, it was expected that there would be corresponding increases in mesozooplankton biomass; however, no such increases were observed. The time period selected was insufficient for a response to be observed with the mesozooplankton growth rate defined in the model.

[23] Hurricane passage disrupted the distribution of plankton biomass associated with mesoscale eddies. Plankton biomass was minimal in the center of WCEs, maximal along the WCE periphery, and maximal in the center of CCEs prior to hurricane passage. WCE biomass shifted to the west and CCE biomass to the east in association with the strong winds and track position of Hurricane Katrina, as well as the circulation patterns of the mesoscale eddies. Different from what was suggested during hurricanes, plankton biomass increased in WCEs as a result of biomass displacement and was likely reduced in CCEs due to entrainment of subsurface water with reduced plankton values.

Figure 3. (a) Time-averaged (1200 UTC 26–29 August) nitrate concentrations at 2.5 m depth during Hurricane Katrina. Black lines superimposed on Figure 3a represent SSH and the hurricane track, where the large "x" indicates 24.4°N, 84°W. Time series of (b) nitrate and (c) vertical velocity at 24.4°N, 84°W from 0–120 m, with hurricane passage denoted by a black line. The dashed black line in Figure 3c is mixed layer depth.
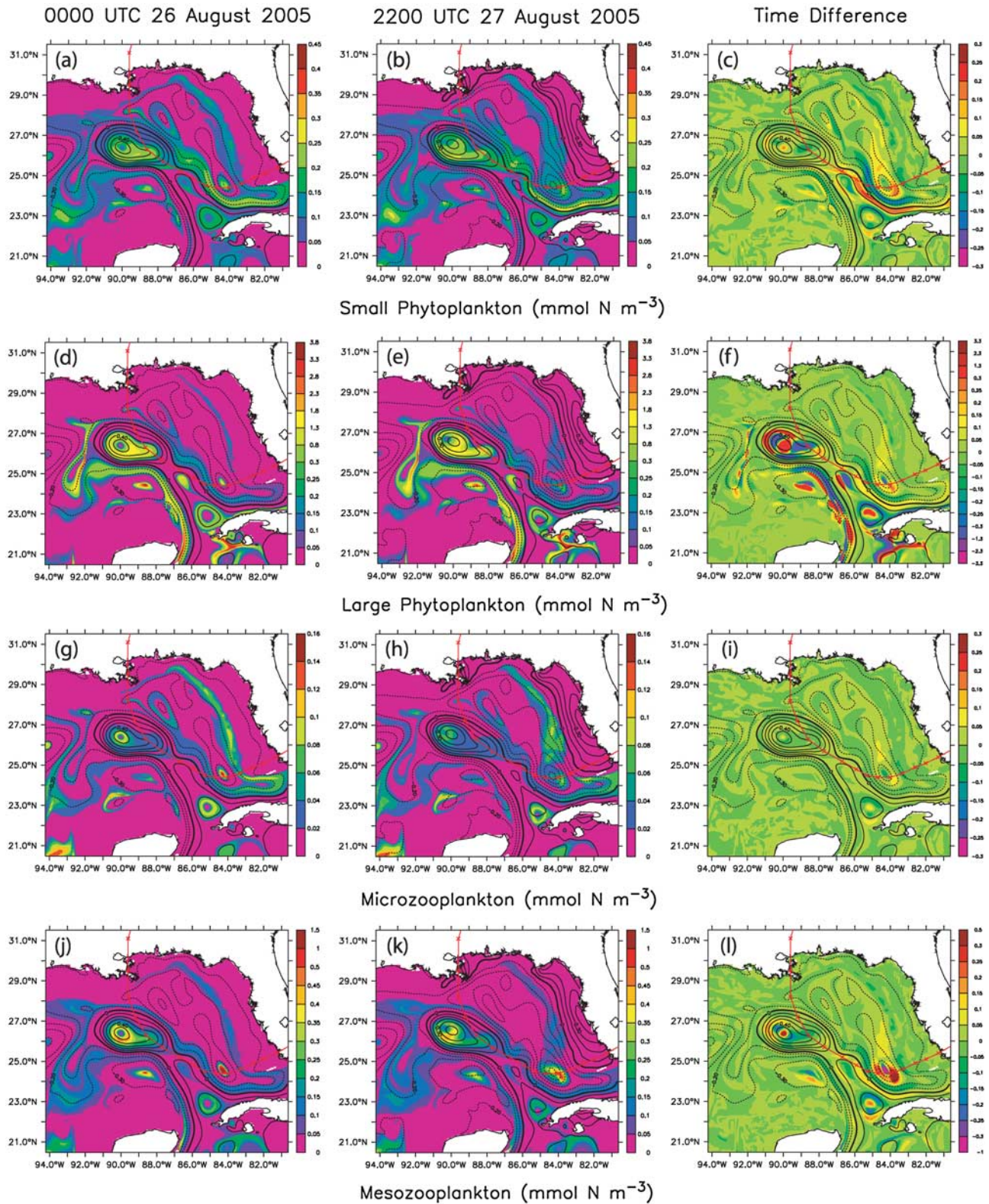
Figure 4. Depth-averaged (0–20 m) spatial plots of (a–c) small phytoplankton, (d–f) large phytoplankton, (g–i) microzooplankton, and (j–l) mesozooplankton at 0000 UTC 26 August (before Hurricane Katrina), 2200 UTC 27 August (during Hurricane Katrina), and the time difference. Black lines superimposed on Figures 4a–4l represent SSH and the red line depicts the hurricane track.

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