

Impacts of Hurricanes on Wetland Phytoplankton Communities in the Gulf of Mexico

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Research Article

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ABSTRACT

Measurements were made of inorganic nutrient and chlorophyll a (chl a) concentrations over a period of 7 months during the spring and summer of 2012 at coastal wetland sites along the northern coastline of the Gulf of Mexico. Tropical Storm Debby and Hurricane Isaac passed near several of the sampling sites during the study. Samples collected before and within a few days after passages of these storms allowed us to assess the impact of the storms on the wetland phytoplankton communities. Passages of the storms were associated with significant increases of chl a concentrations and reductions of nitrate, ammonium, and phosphate concentrations, but there were no significant changes of salinity or silicate concentrations. Much of the increase of the chl a concentrations could be explained by the reduction of dissolved inorganic nitrogen. The phytoplankton populations did not appear to be nutrient limited prior to passage of the storms, and the increases of chl a following passage of the storms appeared to reflect a reduction of zooplankton grazing pressure. Introduction of H₂S into the water column via resuspension of bottom sediments may have been the cause of the reduction of zooplankton grazing activity..

INTRODUCTION

Hurricanes and episodic storm events are common occurrences in wetland, estuarine, and coastal environments in the tropics and subtropics^[1-5]. Because there is no barrier between coastal wetlands and the ocean, the potential impact of these storms on coastal wetlands is great. Previous studies concerning the impacts of hurricanes on coastal wetlands have focused on storm-induced sedimentation changes of elevation and enhancement of wetland productivity^[6-10]. Although macrophytes such as *Spartina alterniflora* and *Juncus roemerianus* are important determinants of the physical stability and resilience of coastal marine ecosystems and account for much of the resilience of salt marshes to perturbations such as hurricane storm surges carbon and sulfur stable isotope studies have shown that the organic carbon in primary consumers in the Great Sippewissett marsh in Massachusetts and the Sapelo Island marsh in Georgia are derived about equally from *Spartina* and phytoplankton^[11-14]. Assessment of the impact of hurricanes on coastal marine and wetland food chains therefore requires consideration of hurricane effects on phytoplankton communities. Previous studies have shown that the impacts of hurricanes on resource availability and the microbial communities in wetland ecotones are quite variable. The impacts are influenced by the environmental conditions preceding the hurricane, the intensity of the hurricane (i.e., duration, wind strength, amount of precipitation, and proximity of the hurricane path to the wetland), and post-storm climatic and environmental conditions^[1,2,5,15,16]. During 2004, for example, three successive hurricanes made landfall over south Florida; phytoplankton biomass increased significantly in Florida Bay as a result of storm-related freshwater discharge but declined at the same time in the nearby wetland mangrove ecotone^[16]. Likewise, passages of hurricanes Gustav and Ike over the Louisiana coast within a period of two weeks in September of 2008 resulted in a decrease of the chlorophyll a (chl a) concentrations in the water column of a coastal lagoon but no significant change in sediment chl a^[17]. The effects of hurricanes on wetland phytoplankton communities are therefore variable, and the mechanisms responsible for observed effects are unclear.

The present study was undertaken with the goal of collecting sufficient data prior to and shortly after the passage of one or more hurricanes to enable an informed analysis of the response of wetland phytoplankton communities. The study was conducted during seven consecutive months during the spring and summer of 2012, which fortuitously was the third most active Atlantic hurricane season on record. The two storms that were the focus of this study were Tropical Storm Debby, which brought extensive flooding to North Florida and the Florida Panhandle in late June, and Hurricane Isaac, which made landfall on August 28 near the

mouth of the Mississippi River and caused severe flooding of coastal Louisiana and Alabama.

MATERIALS AND METHODS

Site Descriptions

Three main sampling sites were chosen along the Gulf Coast, the objective being to cover a large enough area to maximize the probability of intercepting the path of a hurricane or tropical storm. Water depths at the sampling sites were no more than 2–3 m. The three sites were Vermillion Bay (VB) in Louisiana, Mobile Bay (MB) in Alabama, and Apalachicola Bay (AB) in Florida (**Figure 1**). The Vermillion Bay wetland was sampled at only one site because the site was difficult to access. The site was located adjacent to the Intracoastal Waterway near the Leland Bowman Lock (29° 45'58"N, 92° 10'14"W). The Mobile Bay wetlands were sampled at two sites, MB1 and MB2, located about 3 km apart along the Interstate-10 Bridge that crosses MB at 30° 40'17"N, 87° 58'9"W. The Apalachicola Bay wetlands were also sampled at two sites, which were located about 3 km apart and centered at 29° 42'49"N, 85° 1'22"W.

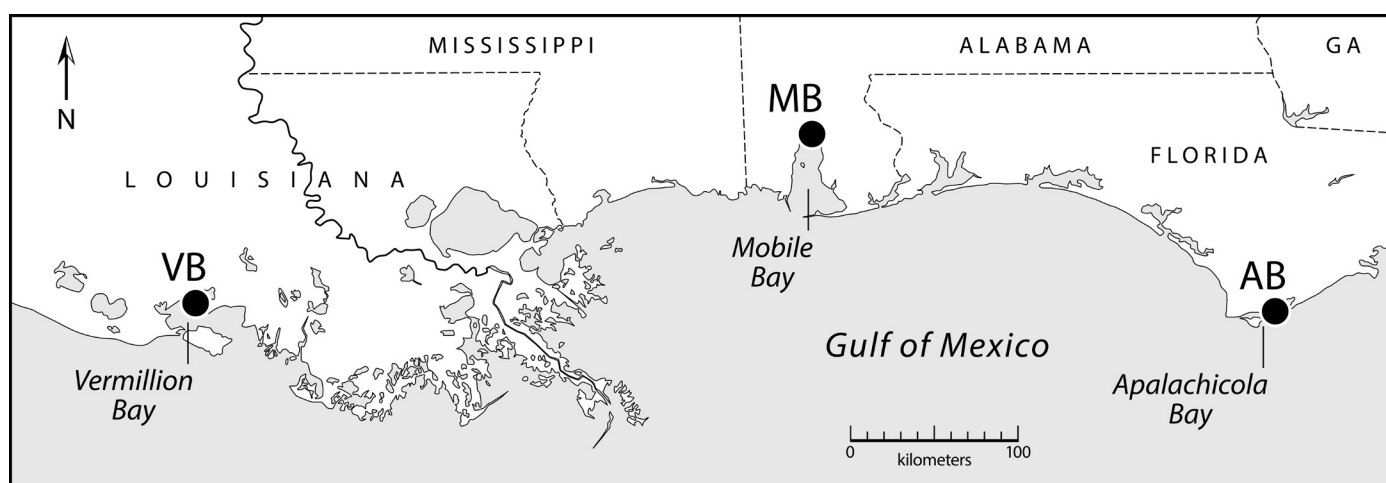


Figure 1. Locations of sampling sites in Vermillion Bay (VB), Mobile Bay (MB), and Apalachicola Bay (AB).

Sample Collection and Initial Processing

Water samples to be assayed for inorganic nutrients were collected with a 36-cc hand-operated vacuum pump that was used to filter 1–2 liters of water into a 1000-mL Erlenmeyer flask. The filter was a Whatman 47-mm glass fiber GF/C filter (nominal porosity: 1.6 microns). The filtrate was then immediately transferred to a 1-liter, opaque, polypropylene bottle, which was kept refrigerated prior to analysis in the laboratory. Samples to be assayed for chl *a* concentrations were filtered through Whatman 25-mm glass fiber GF/F filters (nominal porosity: 0.7 microns) to retain phytoplankton. These filters were then wrapped in foil and kept frozen prior to analysis in the laboratory. Six to nine 1-liter bottles were filled with unfiltered sample water for nutrient enrichment experiments. These bottles were kept in a refrigerator prior to initiation of the nutrient enrichment experiments.

Inorganic Nutrients

Soluble reactive phosphorous (SRP), reactive silicate, nitrate + nitrite (hereafter nitrate), and ammonium + ammonia (hereafter ammonium) were measured in sample filtrate via the methods described by Strickland and Parsons^[18]. Assays for ammonium were made only at sites VB, MB1, and MB2. Absorptions were measured at wavelengths of 810, 885, 543, and 640 nm, for silicate, phosphate, nitrate, and ammonium, respectively, using a spectrophotometer (Varian Cary 50 WinUV, Agilent Technologies, Santa Clara, CA, USA).

Chlorophyll *a*

The filters for chl *a* analysis were removed from their foil wrappers and placed in glass centrifuge tubes with enough 90% acetone to submerge the filters. The pigments were allowed to extract overnight in a freezer. The filters were then placed in test tubes and ground using a Teflon tissue grinder. The solution of acetone and filter debris was then filtered through a GF/F filter to remove the filter debris. The concentrations of chl *a* in the acetone were then determined by measuring the absorptions at 750 nm (turbidity correction) and 665 nm with the Cary model 50 WinUV spectrophotometer.

Nutrient Enrichment Experiments

The unfiltered water samples were brought to room temperature (22°C) in the laboratory, and the salinity was measured with a refractometer (RF20, Mettler Toledo, Greifensee, Switzerland). To determine the limiting nutrient at each site and to better

understand the response of the phytoplankton to the perturbations caused by the storms, nutrient enrichment experiments were conducted on sample water collected in June and July. For each experiment, 100 mL of sample water from each site was filtered through a 47-mm GF/C glass fiber filter to remove zooplankton and then transferred to 16-mL test tubes. Each tube was then inoculated with a 1-mL aliquot of the unfiltered sample water. There were four treatments for each site: a control that received no added nutrients, a P-enriched treatment, an N-enriched treatment, and a treatment that received additions of both N and P. All treatments were run in triplicate. The N and P were added at concentrations specified for f/2 medium 882 μM for nitrate and 36 μM for phosphate^[19,20]. The tubes were incubated at room temperature ($\sim 20^\circ\text{C}$) with illumination of approximately 200 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ of 400–700 nm radiation provided from a bank of daylight fluorescent lights. The optical density (OD) of each tube was then read on the Cary model 50 WinUV spectrophotometer at a wavelength of 750 nm each day for 12 days at the same time each day. The asymptotic value of the OD readings was determined by fitting a logistic growth model to the data. The asymptote was taken to be a measure of the yield in each treatment.

Statistical Analyses

We compared pre-hurricane and post-hurricane chl a and nutrient concentrations using paired t-tests after log-transforming the data to stabilize variances. Effects were judged to be significant if the associated type I error rate (p) was less than 0.05. We also examined graphs of concentrations at each site versus day of the year to determine whether differences between pre-hurricane and post-hurricane concentrations merely reflected seasonal trends as opposed to being the result of an episodic event. Results of nutrient enrichment experiments were considered to be significant if the yields in the enriched treatments were more than twice the yields in controls. Nitrogen and phosphorus were judged to be simultaneously limiting if yields in the N+P treatments were more than twice the yields in the N-enriched and P-enriched treatments.

RESULTS

Pre-hurricane salinities at all sampling sites were no more than 10 (**Table 1**) and concentrations of nitrate and silicate were well above concentrations that would be expected to limit phytoplankton growth^[21-23]. Pre-hurricane phosphate concentrations were less than 0.7 μM and at most stations less than 0.2 μM . However, because phosphate concentrations that are limiting to phytoplankton growth are on the order of 10 nM and because many phytoplankton can exploit dissolved organic phosphorus via enzymes such as alkaline phosphatase it seems unlikely that phytoplankton growth was limited by concentrations of inorganic nutrients at any site during pre-hurricane conditions^[24-26]. The paired t-tests revealed that post-hurricane concentrations of nitrate, phosphate, and ammonium were significantly lower ($p < 0.04$) than pre-hurricane concentrations, whereas post-hurricane concentrations of chl a were significantly higher ($p < 0.001$) than pre-hurricane concentrations. There was no significant difference in silicate concentrations ($p = 0.93$) or salinity ($p = 0.37$).

Table 1. Ranges of pre-hurricane concentrations of inorganic nutrients (μM), salinity, and chl a ($\mu\text{g L}^{-1}$) at sampling sites.

Sites	Parameter					
	PO ₄	NO ₃	NH ₄	Si	Salinity	Chl a
AB1	0.15–0.17	24–35	–	170	5–6	4.6–8.0
AB2	0.106–0.111	25–33	–	150–188	8	3.9–5.8
VB	0.01–0.04	14–28	3.5–4.7	168–220	0–5	20–27
MB1	0.07–0.11	7–16	0.8–1.9	69–164	3–7	5.4–6.9
MB2	0.6–0.7	7–8	0.6–1.7	63–101	5–10	5.7–7.0

Examination of time series of nutrient and chl a concentrations at each site revealed that in some cases the differences between pre-hurricane and post-hurricane values could logically be attributed to seasonal trends (**Figure 2a**) rather than to episodic effects. However, in most (67%) cases, the differences appeared to reflect storm effects (**Figures 2b–2d**). This was especially true of chl a concentrations, which increased by roughly a factor of 2 at VB and MB (e.g., **Figure 2c** between a few days before and a few days after Hurricane Isaac).

Site AB was sampled on April 29 and May 24, but no samples were collected at AB immediately before Tropical Storm Debby (June 26). However, samples were collected 2–3 days prior to Hurricane Isaac at MB and VB. To determine whether the increase of chl a concentrations between a few days before and a few days after Hurricane Isaac could be attributed to uptake of dissolved inorganic nitrogen (DIN) by the phytoplankton, we plotted the predicted changes of chl a concentrations based on the decreases of NH₄ and NO₃ concentrations, an assumed carbon-to-chl a ratio of 50 gg^{-1} and a molar carbon-to-nitrogen (C:N) ratio of 106:16^[18,27]. The observed changes of chl a were closely correlated ($r = 0.995$) with the predicted changes but higher by about 1.7 $\mu\text{g L}^{-1}$ (**Figure 3**).

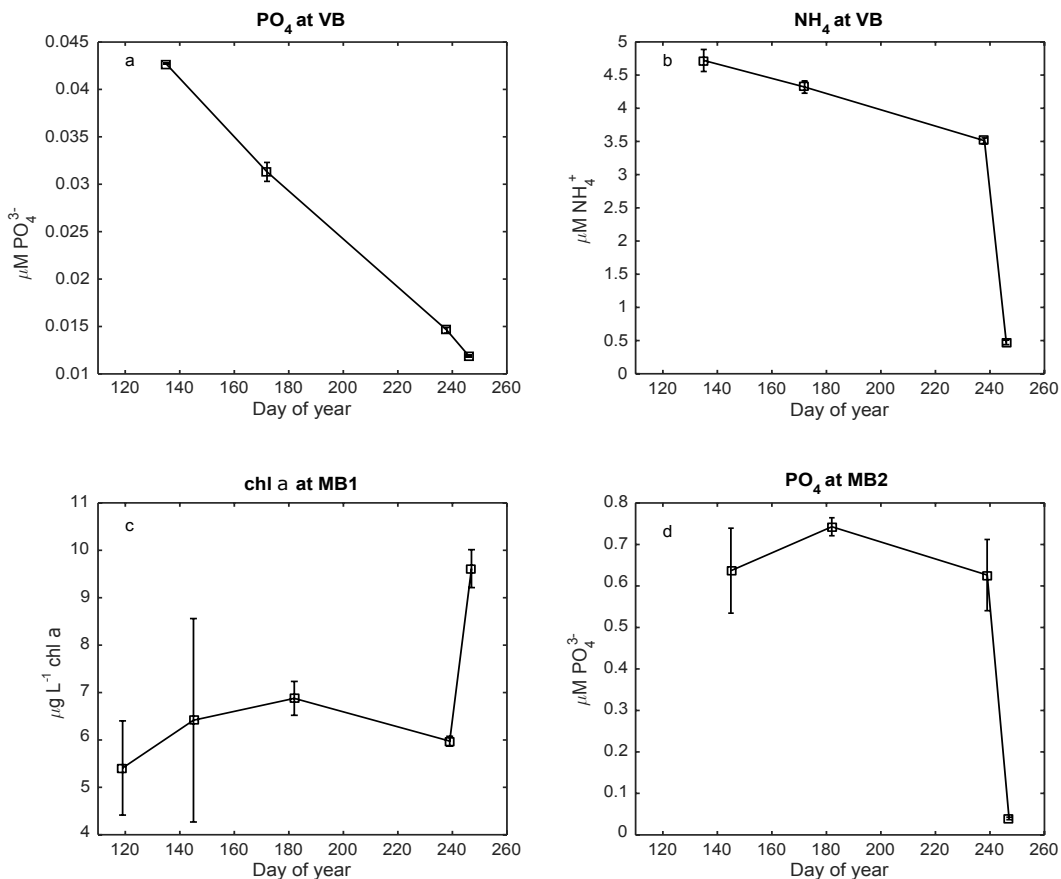


Figure 2. Inorganic nutrient and chl a concentrations at selected sites before and after passage of Hurricane Isaac. The low post-Isaac (day 246) phosphate concentration at VB (a) appeared to be part of a steady decline of phosphate concentrations from day 135 to day 246. However, the low post-Isaac ammonium concentration at VB (b), the high post-Isaac chl a concentration at MB1 (c), and the low post-Isaac phosphate concentration at MB2 (d) were all very different from the concentrations measured immediately before Isaac and did not appear to be part of a seasonal trend. Error bars are standard errors of mean values.

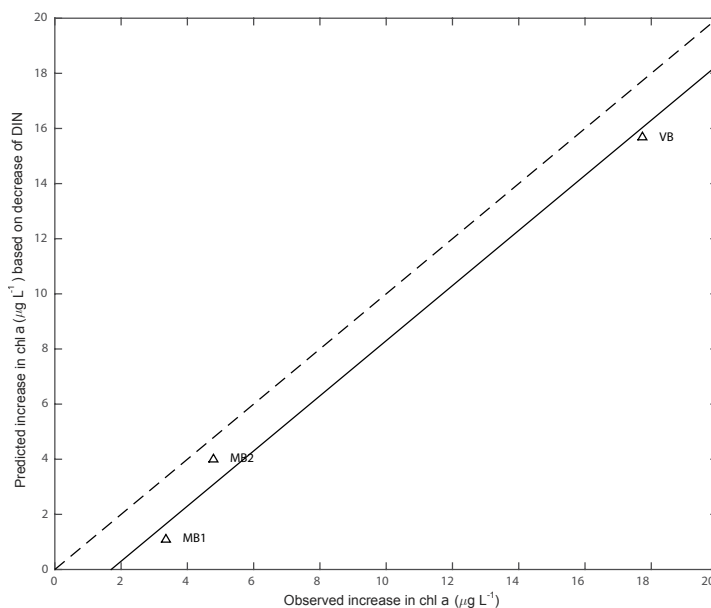


Figure 3. Observed and predicted increases in chl a concentrations between a few days before and a few days after Hurricane Isaac. Predicted changes were based on decreases in concentrations of dissolved inorganic nitrogen (DIN), the Redfield C:N ratio and an assumed C:chl a ratio in the phytoplankton of 50 g g⁻¹. The dashed line is the 1:1 line. The solid line is a parallel line with an intercept of 1.7 μg L⁻¹ on the abscissa.

The results of the nutrient enrichment experiments proved revealing. There was growth in the control cultures in all cases. The control ODs increased from essentially zero at the start of the incubations to 0.03–0.07 after 12 days (**Table 2**). Addition

of phosphate produced little additional growth versus controls at AB and MB, and addition of nitrate produced little additional growth versus controls at AB. Thus the water at AB appeared to contain insufficient N and P to support much additional growth, and indeed the OD in the control cultures at AB was the lowest (0.03) among the three sites. Addition of both N and P to the AB water produced an OD 10 times that of the control cultures. Addition of nitrate at MB produced yields almost four times that of the control culture. Thus MB had much more surplus P than N. VB had the highest OD of the control cultures (0.07), and addition of either nitrate or phosphate to VB produced ODs that were 2–3 times the OD of the control cultures ^[18,27].

DISCUSSION

Table 2. Results of nutrient enrichment experiments. Yields are expressed as optical densities (ODs) after incubations lasting 12 days.

Site	Treatment			
	control	phosphate	nitrate	phosphate and nitrate
AB	0.03	0.05	0.04	0.3
MB	0.06	0.08	0.22	0.55
VB	0.07	0.22	0.13	0.4

The fact that salinities and silicate concentrations did not change significantly as a result of passage of the storms suggests that the effects we observed on concentrations of nitrate, ammonium, phosphate, and chl a were not due to rainfall, stormwater runoff, or storm surge. The fact that the observed increases of chl a concentrations following Hurricane Isaac were about 1.7 $\mu\text{g L}^{-1}$ higher than the increases predicted from the decreases of DIN suggests that there was an input of allochthonous DIN sufficient to raise the DIN concentration by about 1 μM , but at least 50% of the increases of chl a could be accounted for by uptake of DIN present in the water before Hurricane Isaac, and at VB 90% of the increase of the chl a concentration could be explained by uptake of autochthonous DIN (**Figure 3**). Why was the autochthonous DIN not utilized before passage of Hurricane Isaac, and why did the passage of Hurricane Isaac cause most of the DIN to be incorporated into phytoplankton biomass? The results of the nutrient enrichment experiments suggest an explanation. Phytoplankton grew in all the control cultures. It is therefore clear that the water at all sampling sites contained inorganic nutrients sufficient to support an increase of phytoplankton biomass. Furthermore, the much greater increases in phytoplankton biomass following addition of both nitrate and phosphate indicated that essential nutrients other than N and P were present in great excess. By passing the water through a filter with a nominal porosity of 1.6 microns, we removed most zooplankton predators. Although 1 mL of unfiltered water was then added to 15 mL of filtrate, the concentration of grazers would have been reduced by approximately a factor of 16, and the experimental design therefore corresponded to a dilution experiment in which the grazing rate of zooplankton was greatly reduced by diluting the raw water samples with sample filtrate ^[28,29].

Passage of the hurricanes would have stirred up sediments from the bottom of these shallow wetlands. The interstitial water in the sediments would have contained DIN and phosphate, which could account for the fact that the observed increases of chl a exceeded the increases estimated from the decreases of DIN concentrations. Because the water at our sampling sites was brackish (**Table 1**) the interstitial water would also very likely have contained H_2S , which is a very toxic gas. EC50 values for H_2S lie in the range 40–3000 μM for marine phytoplankton and 0.4–100 μM for marine crustaceans ^[30]. Thus marine crustaceans are roughly 30–100 times more sensitive to H_2S than marine phytoplankton. It is therefore possible that release of H_2S from the sediments greatly reduced the grazing pressure from herbivorous zooplankton in the days immediately following the hurricanes while having little effect on the phytoplankton. The reduction in grazing pressure would have allowed the phytoplankton to multiply until nutrient concentrations became truly limiting.

CONCLUSION

Phytoplankton communities at the sampling sites were apparently not nutrient limited prior to passage of the storms, but instead were controlled via zooplankton grazing. A logical explanation for the increase of chl a concentrations following passage of the storms is that storm-related winds stirred up bottom sediments that increased DIN concentrations by roughly 1 μM but more importantly introduced H_2S into the water column. Because of the much greater sensitivity of zooplankton than phytoplankton to H_2S , zooplankton grazing was inhibited, and the phytoplankton population rapidly increased.

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