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Biological and isotopic changes in coastal waters induced by Hurricane Gordon

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Abstract

The effects of a major storm event (Hurricane Gordon) on the biogeochemistry of Atlantic coastal and Gulf Stream waters were investigated during a research cruise in November 1994. Prestorm, NH_4^+ , NO_3^- , and PO_4^{3-} concentrations were consistently well below $1 \mu\text{M}$, whereas after the storm, nutrient concentrations were higher in the surface-water samples: $>2 \mu\text{M}$, in some instances. Primary and secondary (bacterial) production were stimulated by factors of 5 and 2, respectively, up to 4 d following the storm. Bioassay experiments showed that additions of inorganic N stimulated chlorophyll *a* (Chl *a*) concentrations, $^{14}\text{CO}_2$ fixation, and stable isotope fractionations both before and after the storm, but the addition of phosphate had a greater impact in post-storm experiments. The $\delta^{15}\text{N}$ of particulate nitrogen (PN) varied from +5 to +1.5‰ before Gordon, then afterward attained a consistent value of +3.0‰. Sedimentary organic $\delta^{15}\text{N}$ values were similar to water-column organic N, and the $\delta^{15}\text{N}$ of dissolved NH_4^+ from surface sediments (+4.0‰) almost matched the $\delta^{15}\text{N}$ of water-column particulates. These results indicate that storm-generated winds mixed sediments along with dissolved nutrients into surface waters, which supported a rapid increase in water-column primary production.

Interactions between atmospheric processes and primary production in the world's oceans are striking during and after major storm events over continental shelf regions. N, a lim-

iting nutrient in many oceanic environments, can enter the photic zone directly as dissolved species in rainfall (Paerl 1985; Willey and Paerl 1993; Paerl and Fogel 1994). Alternatively, strong and sustained winds mix the water column and advect nutrients (Walsh et al. 1978; Pant and Desai 1992; Malone et al. 1993). On continental shelves where depths are <100 m, winds from hurricanes can readily disturb the uppermost sediments. Resuspension of surface sediments and the nutrients results in initially turbid, yet productive, waters, as well as a redistribution of benthic microorganisms throughout the water column.

Acknowledgments

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The redistribution of benthic microbes and nutrients is marked by changes in biomass and productivity (Zeeman 1985; Pant and Desai 1992). In N-limited coastal shelf waters, benthic biomass can often be the principal reservoir of photosynthetic material (Cahoon et al. 1990; Cahoon and Cooke 1992). Diatoms in particular thrive on surface sediments, where nutrients from decomposing organic matter can support their growth. Following sediment resuspension by storm-generated wave action, large diatoms may be transported to surface waters and become dominant species.

Although major storms occurring in the coastal region of the world's oceans typically have a duration of only a couple of days, the physical and biological effects of the perturbation can last for up to 10 d (cf. Walsh et al. 1978; Dagg 1988; Furnas et al. 1989; Gagan et al. 1990). Ordinarily, continental shelves in midlatitude regions are affected by large storm events with an average frequency of five times per year (Dagg 1988), and worldwide, an average of 84 tropical cyclones per year have been recorded for the period 1973–1992 (Tsutsui and Kasahara 1996). The integrated effect from these storm events has the potential to account for a significant portion of ocean primary productivity, especially in situations where light or nutrients are limited (DiTullio and Laws 1991). Elevated rates of organic matter export from shelf regions can account for enhanced organic C burial on continental slopes and rises today and possibly were the cause for greater accumulation observed in the geologic past (Berger and Wefer 1990).

Storm-induced effects on phytoplankton biomass have been tracked by correlated changes in the stable N isotope compositions in the Chesapeake Bay, a eutrophic estuary (Montoya et al. 1991). In this study, $\delta^{15}\text{N}$ values of PN decreased by 3–4‰ after the passage of a major storm, owing to elevated nutrient levels in many areas of the bay. Chl *a* concentrations displayed a less obvious trend, increasing in half of the stations while decreasing in the remainder. Because the Chesapeake Bay ecosystem is eutrophic, alleviation of nutrient limitation had a less obvious effect on primary productivity, which was inferred from Chl *a* measurements.

Our work extends biogeochemical studies of storm-induced effects to N-limited coastal waters where phytoplankton are poised to take greater advantage of pulsed nutrient additions (Willey and Paerl 1993). Starting in 1993, we began a series of cruises to the Sargasso Sea to search for the influence of atmospherically derived N on coastal plankton production. Fortuitously, the November 1994 cruise coincided with Hurricane Gordon and provided the opportunity to test the relative importance of N deposition from rain vs. nutrient resuspension by wind for stimulating coastal primary production.

We report a comprehensive set of measurements on the changes in (1) biological (Chl *a*, primary production, bacterial production, and nutrient stimulation), (2) chemical (seawater and rainwater nutrients and dissolved inorganic carbon [DIC] analyses), and (3) isotopic (particulate and dissolved C and N in the water column and sediments) parameters of North Carolina coastal waters before and after the passage of Hurricane Gordon. Increases in primary and bacterial productivity were coupled with inputs of nutrients and

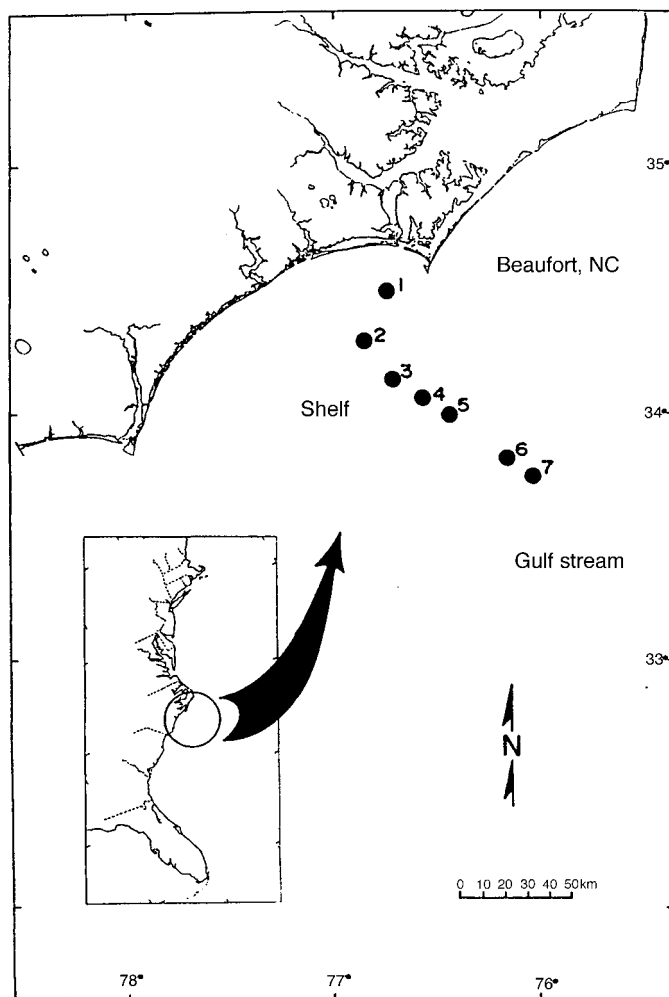


Fig. 1. Map of the North Carolina Coast showing the transects of the RV *Cape Hatteras* before and after Hurricane Gordon. Sta. 1–7 were occupied before the storm. On leg 2 of the transit offshore, Sta. 1–7 were reoccupied and are given numbers 11–17 in the text and certain figures. On the shoreward transit of leg 2, these same stations were occupied a third time and are given station numbers 11-2 through 17-2.

benthic microorganisms from disturbed sediments into the water column by wind mixing. Changes in the stable isotopic compositions of particulate organic matter and dissolved inorganic nutrients confirmed these processes.

Materials and methods

Location—The cruise took place on the RV *Cape Hatteras* from 15 to 21 November 1994. The cruise transect (Fig. 1) was from Beaufort, North Carolina (34°7'N, 76°65'W), southeast across the continental shelf to the main axis of the Gulf Stream (33°6'N, 75°9'W). As the hurricane approached the Gulf Stream and conditions for working were untenable, we retreated to Beaufort for 2 d. Immediately after the storm's passage, we resampled along the same transect into the Gulf Stream.

Rain collection—During the cruise, rain was collected on the flying bridge of the RV *Cape Hatteras*, approximately 10 m above the sea surface, ahead of the stacks. Rain was collected in three separate precleaned bottles with funnels. Rain amounts were estimated from a rain gauge in combination with amounts in the sample collectors.

Biological and chemical parameters—Chl *a*: Samples were filtered onto 25-mm Whatman GF/F filters, extracted in dimethyl sulfoxide (DMSO):90% acetone (1:1, v:v) (Shoaf and Lium 1976), and assayed using a Turner model 10 fluorometer.

Nitrate: Concentrations of nitrate plus nitrite ($\text{NO}_3^- + \text{NO}_2^-$) were determined by flow injection analysis using the sulfanilamide reaction and cadmium reduction of nitrate (APHA 1992). Discernible peaks were observed at 0.5 μM ; the lower limit of observable detection was ca. 0.3 μM .

Ammonium and phosphate: Seawater samples filtered with muffled GF/F filters (500°C, 8 h) and rainwater samples were frozen and then analyzed by the colorimetric technique described by Solorzano (1969). Phosphate concentrations were determined on these same water samples by the method of Strickland and Parsons (1972).

Radioassays for photosynthesis and bacterial production measurements: Radioisotope studies of photosynthetic $^{14}\text{CO}_2$ incorporation and ^3H -leucine-based bacterial production were conducted in clean, acid-washed liquid scintillation vials (LSV) in 10-ml aliquots. A constant temperature block (the photosynthetron, Back et al. 1991) connected to a circulating water bath was used for all incubations (shelf stations, 16°C; Gulf Stream stations, 25°C).

Photosynthesis: Water samples (200 ml) were inoculated with $\text{NaH}^{14}\text{CO}_3$ to a final activity of 0.5 $\mu\text{Ci ml}^{-1}$ under dim red light. Incubation was terminated and unincorporated $^{14}\text{CO}_2$ removed by the addition of 0.25 ml 2N H_2SO_4 to the LSV, and the light intensity was measured with a flat-plate sensor (LiCor) inserted into each well. Acidified samples were mixed with 10 ml scintillation cocktail (Scintiverse, Fisher Scientific) and counted onboard ship using a Packard 1600 liquid scintillation counter (Lewis and Smith 1983).

Leucine uptake studies: Immediately prior to water sample addition, ^3H -leucine was added to vials along with any supplements. A typical addition of 108 nM consisted of 1 $\mu\text{Ci L}$ -[4,5- ^3H]-leucine ml^{-1} (final activity; 130 Ci mmol^{-1} undiluted specific activity) with 50 μl of 20 μM carrier L-leucine per 10 ml. At various time intervals, proteins from subsamples were precipitated with 100% (w/v) trichloroacetic acid. The precipitate was pelleted by centrifugation, resuspended in 1 ml of liquid scintillation cocktail (Ecolume), and counted with a Packard Tricarb 200 liquid scintillation counter. In all of the leucine uptake studies, time-course sampling at about 0.5, 1, and 2 h was used. Uptake was typically linear ($r > 0.98$) for at least 3 h, and no initial rapid uptake was indicated by y-intercepts of regressions (Kirchman et al. 1985; Smith and Azam 1992).

Calculations for leucine uptake conversion to microbial biomass were similar to those described by Simon and Azam (1989). An average intracellular isotope dilution factor of 2 was used in consideration of the degree of saturation achieved based on the kinetics results (Simon and Azam 1989; Pace and Cole 1994). A conversion factor of 2.94 $\mu\text{g protein (nmol leu)}^{-1}$ was adopted, a value slightly lower than the 3.092 employed by Pace and Cole (1994).

Bioassays: Rainwater was collected during specific storm events in receptacles on the roof of the Institute of Marine Sciences, Morehead City, North Carolina. Subsamples (60 ml) were analyzed for nutrients as described above. The remaining samples were frozen (-20°C) in precleaned polypropylene bottles for bioassay experiments.

Nutrient and rainwater addition bioassays were performed in triplicate for each treatment in 1- and 4-liter precleaned polyethylene Cubitainers (Rudek et al. 1991; Willey and Paerl 1993). Near-surface seawater (~ 2.5 m), freshly collected with a low-velocity, nondisruptive pump, was dispensed in Cubitainers at each site. Rainwater addition volumes of 1–3% (v/v) mimicked actual dilutions following rainfall events. Synchronous NO_3^- (5- μM final concentration), NH_4^+ (5 μM), and PO_4^{3-} (2 μM) additions were also made. A 10- μCi aliquot of $\text{NaH}^{14}\text{CO}_3$ (58 $\mu\text{Ci } \mu\text{mol}^{-1}$; ICN) was added to each Cubitainer to determine photosynthetic $^{14}\text{CO}_2$ assimilation as a measure of microalgal growth. The other growth parameter was Chl *a*.

Stable isotope bioassays: Samples were taken at 5-m depth from Sta. 2 ($34^\circ 17' \text{N}$, $76^\circ 48' \text{W}$) on 15 November 1994 and at the corresponding Sta. 12 on 20 November following the storm. For stable isotope measurements, 20-liter water samples were incubated in polypropylene Cubitainers on the deck of the ship. Water temperature was 23.2°C. Parallel 1-liter incubations with $^{14}\text{HCO}_3^-$ were made for productivity measurements. Additions were as follows: (1) control—no additions; (2) rain (final concentrations: $\text{NO}_3^- = 1.6 \mu\text{M}$; $\text{NH}_4^+ = 0.15 \mu\text{M}$); (3) rain + phosphate (N as in No. 2; $\text{PO}_4 = 2 \mu\text{M}$); (4) nitrate (7.5 μM); (5) ammonium (5.7 μM); and (6) ammonium plus phosphate ($\text{NH}_4^+ = 5.7 \mu\text{M}$; phosphate = 2 μM). Chl *a* and nutrient concentrations were measured on subsamples from the 20-liter volumes by the methods described above. The isotopic composition for the $\text{NO}_3^- + \text{NO}_2^-$ in rain was +1.2‰, whereas that of the ammonium was +1.8. The $\delta^{15}\text{N}$ of the added nitrate was +0.6‰, and for the ammonium, it was -0.7‰. For isotopic analysis, the remaining water was filtered through a 1- μm Nuclepore filter and processed as described below.

Stable isotopes: The particulate fraction from the water was sampled from 30-liter Niskin bottles at discrete depths on the leg of the cruise prior to Hurricane Gordon. Particulates from approximately 8 liters were filtered onto muffled GF/F filters. After Hurricane Gordon, owing to high sea state, surface seawater from 2.5 m was taken from the ship's pumping system and filtered either on GF/F filters or on a 1- μm Nuclepore filter (147 mm) under 1 atm of N. Particles from the 1- μm filters were centrifuged, washed once with distilled water, and then freeze dried. All samples were re-

Table 1. Nutrient concentrations in surface waters (0–5 m) from the continental shelf and Gulf Stream before and after Hurricane Gordon. On leg 2 (poststorm), values above detection limits are given for outbound and return visits to the same station locations. All values are in μM . ND, not determined.

Location	Leg 1 (before)				Leg 2 (after)			
	Station	NO_3^-	NH_4^+	HPO_4^{2-}	Station	NO_3^-	NH_4^+	HPO_4^{2-}
Inner shelf	1	<0.3	0.2	<0.1	11/11-2	1.0/0.91	1.1/1.4	<0.1/0.27
Shelf	2	<0.3	trace	<0.1	12/12-2	trace/<0.3	0.4/0.3	<0.1
Shelf	3	<0.3	<0.2	<0.1	13/13-2	<0.3	<0.2	<0.1
Shelf	4	<0.3	trace	<0.1	14/14-2	<0.3	<0.2	<0.1
Outer shelf	5	<0.3	ND	ND	15/15-2	<0.3	<0.2	<0.1
West Gulf Stream	6	<0.3	<0.2	<0.1	16	<0.9	<0.2	<0.1
East Gulf Stream	7	<0.3	trace	<0.1	17	<0.9	ND	<0.1

acted with 200–1,000 μl of 1 N HCl to remove carbonates then were rinsed with distilled water before analysis. C isotopes were analyzed on a Finnigan 252 mass spectrometer, whereas N_2 was measured on a double-focusing Nier–Johnson-type mass spectrometer. The reproducibility of both measurements on filter samples is about $\pm 0.3\%$. Samples of unfiltered seawater were collected in 500-ml glass bottles fitted with ground-glass Rodaviss joints for DIC analysis. Isotopic compositions of total DIC were determined on CO_2 gas released in vacuo by the addition of concentrated phosphoric acid.

Sediments: Concentrations and isotopic compositions of extractable NH_4^+ and organic N and C isotopic compositions were measured in surface sediment samples taken by box core from $34^\circ 17' \text{N}$, $76^\circ 48' \text{W}$ at 29-m depth. For the NH_4^+ measurements, about 10–15 g (wet weight) sediment was extracted with 80 ml distilled water. Preheated zeolite (W-85, Union Carbide) was added to adsorb dissolved NH_4^+ (Velinsky et al. 1989). Extractable nitrate concentrations were determined by reduction of NO_3^- using cadmium powder mixed with dye in an acidified solution (LaMotte nitrate reagent). Limits of detection from this nitrate method were about 0.5 μM . The N and C isotopic compositions were measured on sediments that were reacted with an acetic acid/acetate buffer to remove carbonates at pH 5.5. The shelf sediments consisted primarily of sand with some finer particles, including shell fragments.

Results

Nutrients and Chl *a* concentrations—Prior to the storm, nutrients were at or below limits of detection in continental shelf waters and in the mixed layer of the Gulf Stream (Table 1). Nitrate and phosphate were first detected at 125–150 m in Gulf Stream profiles (Fig. 2), with western edge samples (Sta. 6) showing a steeper gradient between 150 and 250 m but reaching similar deep-water maxima. Ammonium was not detected at any depth.

Following the hurricane, NH_4^+ appeared at the innermost continental shelf Sta. 11, depth = 23 m, with a uniform vertical distribution of $1.1 \pm 0.1 \mu\text{M}$ ($n = 6$), while $\text{NO}_3^- + \text{NO}_2^-$ and PO_4^{3-} remained below detection. With the exception of an occasional NH_4^+ sample of $<1 \mu\text{M}$, no other continental shelf samples contained detectable levels of these

nutrients following the hurricane. Although surface waters of the Gulf Stream were enriched to 0.9 μM nitrate at both stations, PO_4^{3-} was undetectable (Table 1).

Samples of rain collected just before, during, and after the hurricane contained a wide range of $\text{NO}_3^- + \text{NO}_2^-$ concentrations between 1 and 100 μM (Table 2). On leg 1, the first light rain event had 13 μM , whereas the second event was $>90 \mu\text{M}$ initially but dropped to 17 μM after several hours. Subsequent collections contained $<10 \mu\text{M}$. Even though we were under the influence of winds circulating around Hurricane Gordon, little rainfall ($<4 \text{ cm}$) on the shelf regions was associated with this storm. On leg 2 of the cruise, rain from one event contained 25 μM NO_3^- . All of these concentrations fall within the range of rain events observed along the North Carolina coast (Willey and Kiefer 1993; Paerl and Fogel 1994). Dissolved inorganic nitrogen (DIN) input via rainfall during Hurricane Gordon was 760 $\mu\text{mol m}^{-2}$ over the 2-d storm time (Table 2). The concentration change that this addition would cause, assuming total and uniform mixing to 30 m, is 0.025 $\mu\text{mol DIN liter}^{-1}$ seawater. Conversely, if initial rainwater inputs were dispersed in only the surface 3 m of the water column, concentrations would be roughly doubled from typical seawater values.

Surface Chl *a* in continental shelf and Gulf Stream waters averaged 0.56 $\mu\text{g liter}^{-1} \pm 0.16$ ($n = \text{seven stations}$), with little apparent relation to location or hydrography prior to the hurricane. Posthurricane Chl *a* was elevated up to sixfold over prestorm values (Fig. 3). The degree of enhancement was greatest inshore and decreased toward the outer shelf (Sta. 5). Surface Chl *a* concentrations were doubled at the western edge of the Gulf Stream (Sta. 6). A slight but consistent increase in surface Chl *a* was observed for mid- and innershelf stations on the homeward transect (21 November 1994). In the continental shelf stations, increased Chl *a* concentrations were inversely related ($r^2 = 0.83$ and 0.85) to water-column depth (Fig. 3).

Primary and bacterial production—Photosynthesis measurements: Photosynthesis at Sta. 4 was enhanced by addition of rain (10% v/v) in 3-h photosynthesis–irradiance (*P-I*) incubations prior to Hurricane Gordon (Fig. 4; open symbols). Productivity and assimilation efficiency at optimum light both increased by a factor of 1.5 in rain-enriched samples relative to controls. Using the constants alpha and P_m^B derived by the Fee programs (1990), a photosynthetically

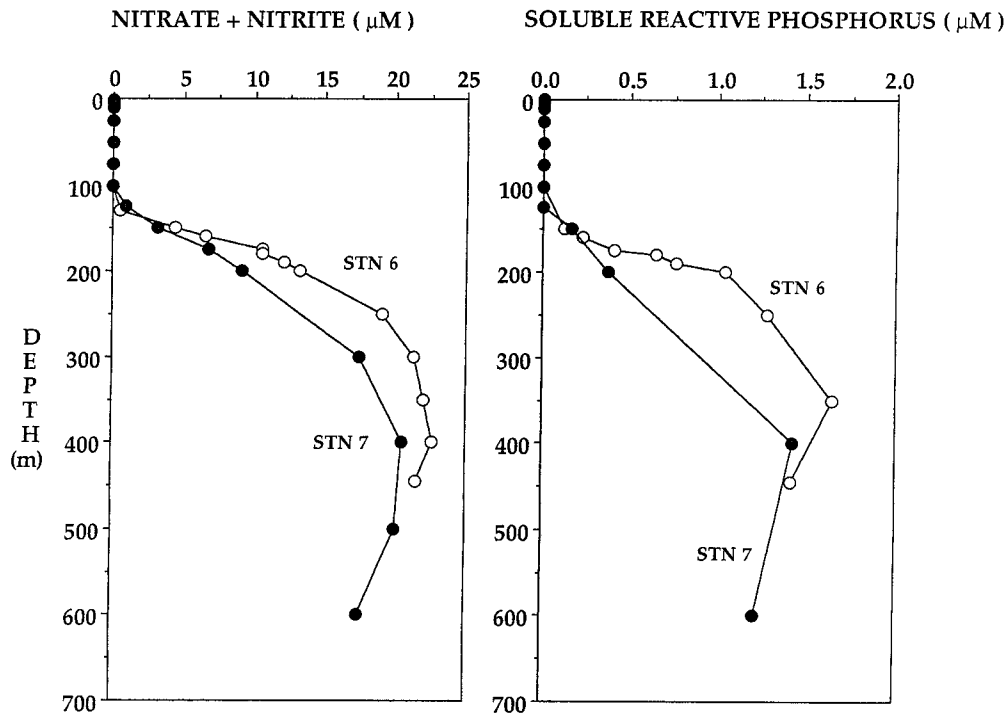


Fig. 2. Vertical profiles of concentrations of nitrate plus nitrite ($\text{NO}_3^- + \text{NO}_2^-$) and phosphate at Gulf Stream Sta. 6 and 7 prior to the storm.

available radiation (PAR) extinction coefficient of -0.11 m^{-1} (1% light depth, 41.9 m; Woodruff unpubl. data), an average 30% cloud cover, and the water-column Chl *a* profile, areal productivity was estimated to be 210 and 290 $\text{mg C m}^{-2} \text{ d}^{-1}$ for control and rain-supplemented conditions, respectively. Rain enrichment therefore could have stimulated productivity by 38% in the short term.

Following Hurricane Gordon, photosynthesis in control and rainwater-enriched incubations was enhanced over three-fold (Fig. 4; filled symbols) from those conducted prior to the storm. Rainwater-enriched samples were only slightly higher (8%) than the control, and assimilation efficiency was increased only 20% (Fig. 4). In fact, rain-supplemented pre-

storm assimilation efficiency (4.01) was only slightly higher than control (3.11) and enriched (3.74) poststorm results. The significantly greater variability on the second leg could have resulted from the introduction of large cells, clumps of normally benthic algae, and resuspended sediments, which may promote shade adaptation (Cahoon and Cooke 1992). In fact, photosynthetic efficiency (α) was 84% greater than on leg 1, and the light-saturation parameter decreased from 194 on leg 1 to 133 $\mu\text{mol PAR photons m}^{-2} \text{ s}^{-1}$ on leg 2.

Table 2. Nutrient concentrations in rainwater sampled on the RV *Cape Hatteras* in November 1994. Rain samples were collected on the upper deck of the ship in precleaned vessels. ND, not determined.

Rain event	Amounts (mm)	pH	NH_4^+ (μM)	NO_3^- (μM)
Leg 1				
1630 h, 16 Nov	2	ND	ND	13.0
1715 16 Nov	2.5	ND	ND	93.2
1900 16 Nov	3.8	6.67	7.0	17.0
0730 17 Nov	8.4	6.59	3.1	2–11.0
1330 17 Nov	12	6.52	1.1	1.9
0700 18 Nov	6	6.61	2.1	1.4
1330 18 Nov	2.5	4.99	4.3	8.9
Leg 2				
20 Nov	ND	ND	ND	25.2

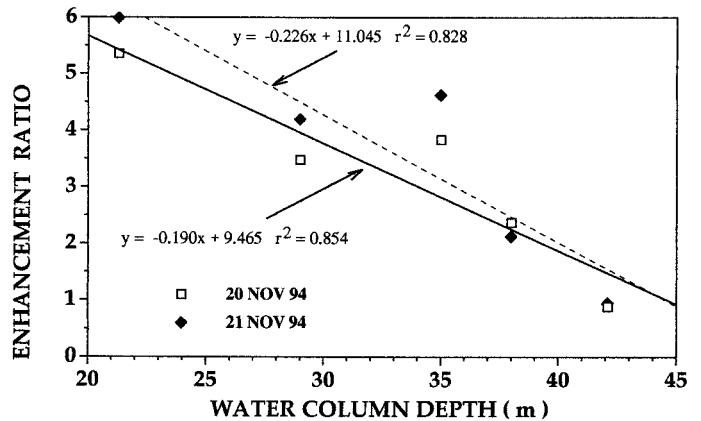


Fig. 3. Inverse relationship between Chl *a* enhancement factor (Fig. 4) and water-column depth observed at the continental shelf stations. Enhancement at shallower depths attests to greater mixing of surficial sediments into the water column.

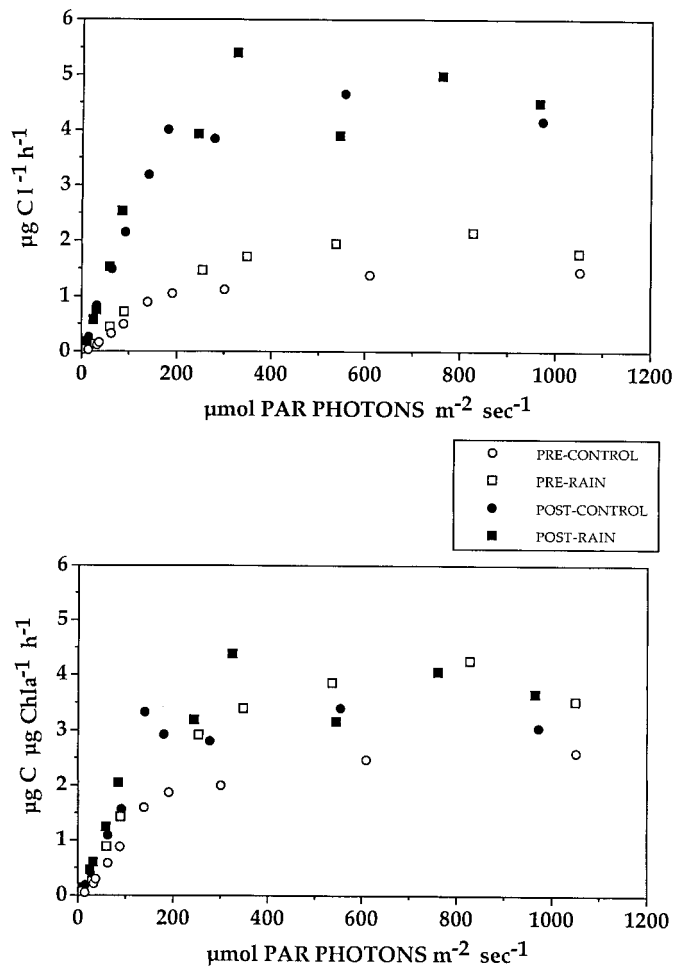


Fig. 4. *P-I* curves for 5-m samples from continental shelf Sta. 4 before (open symbols) and after (filled symbols) Hurricane Gordon. Absolute productivity (upper panel) and chlorophyll-specific productivity (lower panel) are shown for control (circles) and 10% rain-amended samples (squares).

Bacterial production: Bacterial production was relatively uniform across the continental shelf prior to Hurricane Gordon and was at least doubled by the passage of the storm. Vertical profiles at midshelf Sta. 2 and 3 were similar, with consistent increases in bacterial production near the bottom of the water column prior to the storm (Fig. 5). Assuming constant rates, areal protein production by bacteria was 40.5 (Sta. 2) and 76.0 (Sta. 3) $\text{mg m}^{-2} \text{d}^{-1}$, or about 20% of primary productivity prior to the storm. Posthurricane bacterial production rates were significantly higher. Then, areal heterotrophic production increased 2.4-fold to 98.5 $\text{mg m}^{-2} \text{d}^{-1}$ at Sta. 12 and was similar (103 $\text{mg m}^{-2} \text{d}^{-1}$) at innershelf Sta. 11.

Bioassays—Prior to Hurricane Gordon, additions of different N compounds or phosphate had little effect on Chl *a* concentrations, although primary production increased in response to all of the N additions (Fig. 6). Chl *a* concentrations and $^{14}\text{CO}_2$ uptake in control and treated bioassay experiments increased by almost one order of magnitude following Hur-

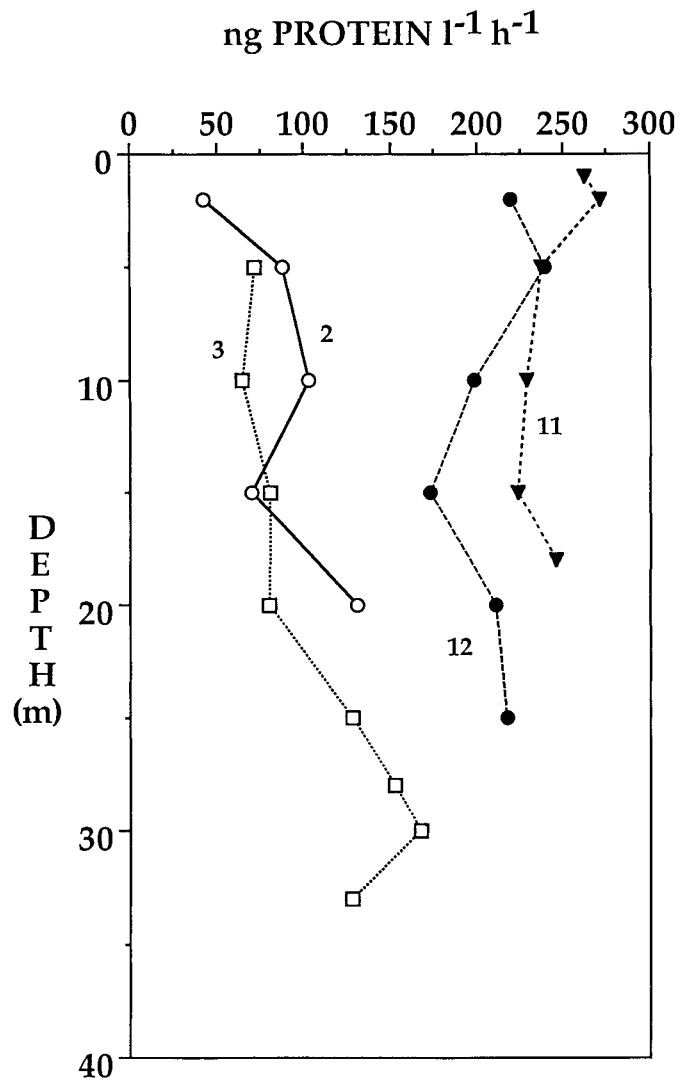


Fig. 5. Vertical profiles of heterotrophic bacterial protein synthesis at continental shelf stations before (open symbols) and after (filled symbols) the storm. Stations are identified by number.

ricane Gordon. Furthermore, in these after-storm incubations, nitrate, ammonium, and rainwater additions stimulated Chl *a* synthesis relative to controls. Only bioassays receiving individual N compounds, rather than rain, however, exhibited higher production. Phosphate additions elicited an increased response in primary production after the storm but not before. Using ^{14}C uptake as an indicator of primary productivity, coastal North Carolina waters appeared to be N limited both before and after the storm.

Stable isotope bioassays—Before the storm: The distributions of N isotopes in the particulate material were almost identical to previous experiments using North Carolina coastal waters (Aguilar et al. 1995). Rain decreased the value by 1‰, but the addition of nitrate had no effect on the isotopic composition. A 9.8‰ decrease in $\delta^{15}\text{N}$ was measured in the PN from the ammonium-amended Cubitainer, however, and $\delta^{15}\text{N}$ values were more negative (−5.9‰) than the

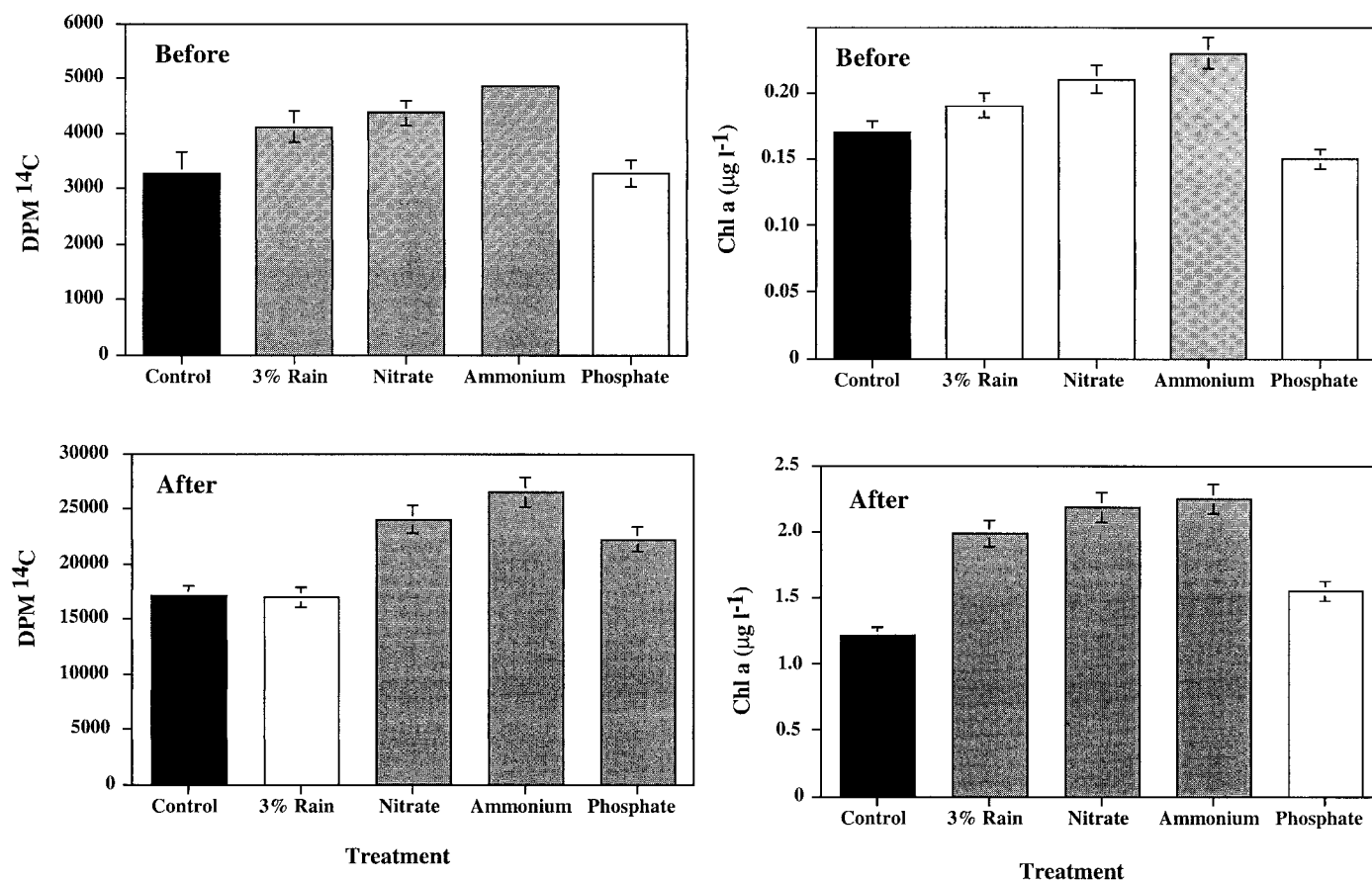


Fig. 6. Bioassay experiments from incubations before and after the hurricane using Chl *a* concentrations (A) and uptake of ^{14}C (B) as response indicators. The 3% rain addition gave a final concentration of nitrate of $0.5\ \mu\text{M}$ and $0.05\ \mu\text{M}$ ammonium. Final concentrations of both nitrate and ammonium after single nutrient additions were $5\ \mu\text{M}$. Final phosphate concentrations were $2\ \mu\text{M}$. For example, prior to the storm, ^{14}C counts were about one order of magnitude less than afterward. Black bars indicate controls (with six replicates), gray bars indicate different from control (three replicates, *t*-test, $P < 0.05$), and clear bars are not different from controls (three replicates). Note the difference in scales before and after the storm.

added NH_4^+ (-0.7‰), indicating significant isotope fractionation. C isotopic compositions of the particulate material in the control were 1.7‰ more negative after incubation. With the addition of either form of N, $\delta^{13}\text{C}$ values were from 0.6 (plus NO_3^-) to 2.0‰ (plus NH_4^+) more positive.

After the storm: At the termination of these experiments, about 30–40% of the added ammonium was taken up,

Table 3. Stable isotope bioassay experiments incubated with water taken after the passage of the storm. Bacterial productivity (% control) is based on leucine incorporation.

Treatments	Chl <i>a</i> ($\mu\text{g liter}^{-1}$)	Bacterial production (% control)	$\delta^{15}\text{N}$ (‰)	$\delta^{13}\text{C}$ (‰)
Control	1.23	100	3.64	-22.77
+ Rain	2.25	236	4.12	-22.24
+ Rain + P	3.08	207	2.90	-22.06
+ NO_3^-	2.85	246	3.93	-22.38
+ NH_4^+	3.5	193	-0.08	-21.77
+ NH_4^+ + P	3.97	223	-1.44	-21.81

whereas $\text{NO}_3^- + \text{NO}_2^-$ uptake was undetectable. The addition of either form of N, including rain, resulted in a large increase in Chl *a* concentrations after an 18-h incubation relative to the control (Table 3). Per amount of N, ammonium produced a greater stimulation than nitrate. The greatest stimulation occurred with the addition of ammonium plus phosphate.

Primary production was greatest in the treatments in which both phosphate and NH_4^+ were added (data not shown). Nitrogenous compounds alone did not stimulate production, although biomass, as determined by Chl *a* concentrations, did increase (Table 3). On the basis of this evidence, phytoplankton in continental shelf waters appeared to be N and P limited after the storm. In bacterial productivity measurements performed on these same incubations, the addition of nutrients approximately doubled heterotrophic production (Table 3).

Stable C and N isotope ratios of particulates support colimitation by N and P (Table 3). The $\delta^{15}\text{N}$ of the PN generally decreases with the addition of the "new" N (Paerl and Fogel 1994; Aguilar et al. 1995). Surprisingly, the $\delta^{15}\text{N}$ of PN increased by 1‰ with addition of rain, and the $\delta^{15}\text{N}$ of PN

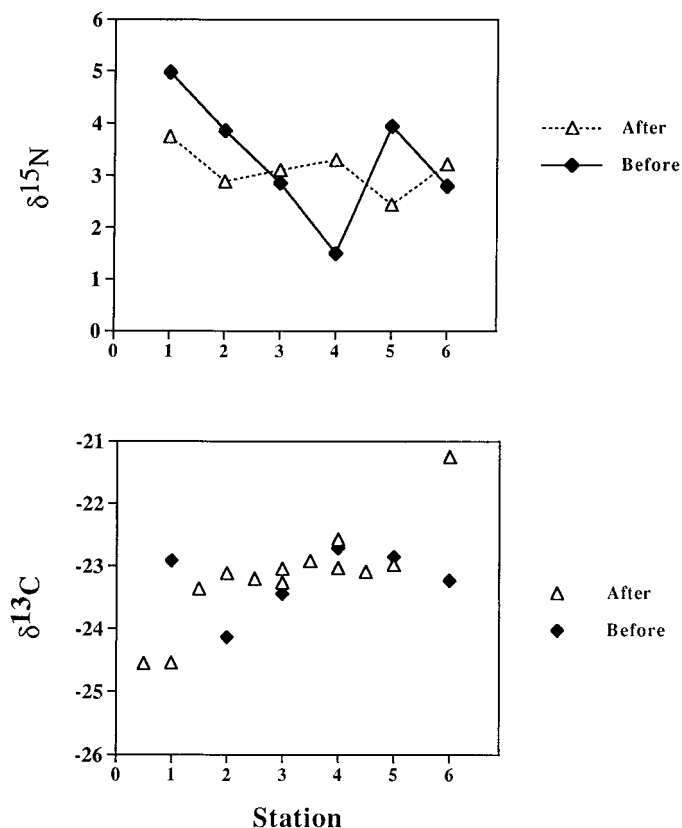


Fig. 7. Isotopic composition of particulate material sampled in the upper 2–5 m of the water column before and after the passage of Hurricane Gordon. On leg 2 on the transit offshore, Sta. 1–7 were reoccupied. On the shoreward transit of leg 2, these same stations were occupied a third time. In addition, stations located exactly between the basic set of seven were sampled on the shoreward track after Hurricane Gordon.

with added ammonium decreased by only 3–4‰, which is about half the shift measured in the experiment conducted before Hurricane Gordon. Only when phosphate was added with ammonium did $\delta^{15}\text{N}$ decrease as expected. The $\delta^{13}\text{C}$ of the initial particulate carbon (PC) was -22.8 and thus was 1.2‰ more positive than just prior to the passage of Hurricane Gordon (Fig. 7). Added N compounds increased the $\delta^{13}\text{C}$ even further, showing that as nutrient limitations on growth were relieved, reduced C availability became even more pronounced.

Stable isotopes of the water column and sediments—Isotopic compositions of total particulate material from the water column at most stations differed before and after the storm (Fig. 7; Table 4). Before the storm, N isotope ratios were highest nearshore, possibly reflecting more terrestrial input, and decreased with distance offshore. The observed variability of 3.5‰ among samples collected before the hurricane is not atypical for PN measured in this region (Aguilar et al. 1995). After Hurricane Gordon, $\delta^{15}\text{N}$ values were more uniform: between 3 and 4‰ in the shelf region.

The $\delta^{13}\text{C}$ of PC along the transect changed after the storm

Table 4. Isotope systematics for coastal waters off North Carolina.

Source	$\delta^{15}\text{N}$ range	$\delta^{13}\text{C}$ range
Suspended particulates		
Shelf and Gulf Stream*	+1 to +10‰	-22 to -25‰
Pre-Gordon	+1.5 to +5.0‰	-23 to -24‰
Post-Gordon	+2.8 to +3.9‰	-21 to -25‰
Sediments		
Self surface sediments	+4.3‰	-23‰
Gulf Stream surface sediments	+4.0‰	-21 to -21.5‰
Dissolved inorganic N and C*		
Atmospheric N-NH ₄ ⁺	-13 to +2‰	
Atmospheric N-NO ₃ ⁻	-5 to +2‰	
Shelf pore-water NH ₄ ⁺	+4.4‰	
G.S. Pore water NH ₄ ⁺	+0.7‰	
Total DIC		+0.9 to 1.6‰

* From Paerl and Fogel 1994; Aguilar et al. 1995.

at both ends (Sta. 1, 6) but remained constant at Sta. 2–5 (Fig. 7). At Sta. 1, nearest the coast, $\delta^{13}\text{C}$ values decreased from -23 to -24.5 ‰, possibly reflecting a greater contribution of resuspended, terrestrial-derived organic C. At Sta. 6 in the Gulf Stream, $\delta^{13}\text{C}$ in PC increased from -23 to -21.2 ‰. The $\delta^{13}\text{C}$ of DIC became more positive by 0.4–0.6‰ after Hurricane Gordon, both in the shelf and Gulf Stream waters.

The shifts in $\delta^{15}\text{N}$ of water-column material could be related isotopically to the insoluble and soluble nitrogenous compounds in surface sediment from the continental shelf (Table 4). The $\delta^{15}\text{N}$ of sedimentary material before and after dissolution of carbonates was +4.3‰ from the surface to 6-mm depth. Dissolved sedimentary ammonium from the same layers had almost identical values of +4.4‰. Extractable NH₄⁺ concentrations from this core were highest near the surface and decreased with depth, a pattern typical of oxic marine sediments (Fig. 8). Nitrate concentrations were low throughout the core. The $\delta^{13}\text{C}$ of surface sediment after treatment to remove carbonates was -23 ‰, which was almost identical to that of suspended particles.

Discussion

Typically, hurricanes or tropical depressions, in addition to major winter storms, disturb continental shelf regions in the Northern Atlantic about nine times per year, with the perturbations lasting 4–5 d per storm event (average = 40 d yr⁻¹) (Tsutsumi and Kasahara 1996). Meteorological forcing associated with hurricanes can affect the biologically available N status of coastal North Atlantic waters in two major ways: (1) wet and dry deposition, and (2) wind mixing, which may result in the resuspension of sediments and nutrients (St. John et al. 1993). First, in this study, rainfall associated with Hurricane Gordon was relatively low (<4 cm in 3 d, Table 2). Hurricanes are commonly capable of delivering ≥ 10 cm of rain during their passage through a region (Zeeman 1985; Paerl and Fogel 1994), but these oce-

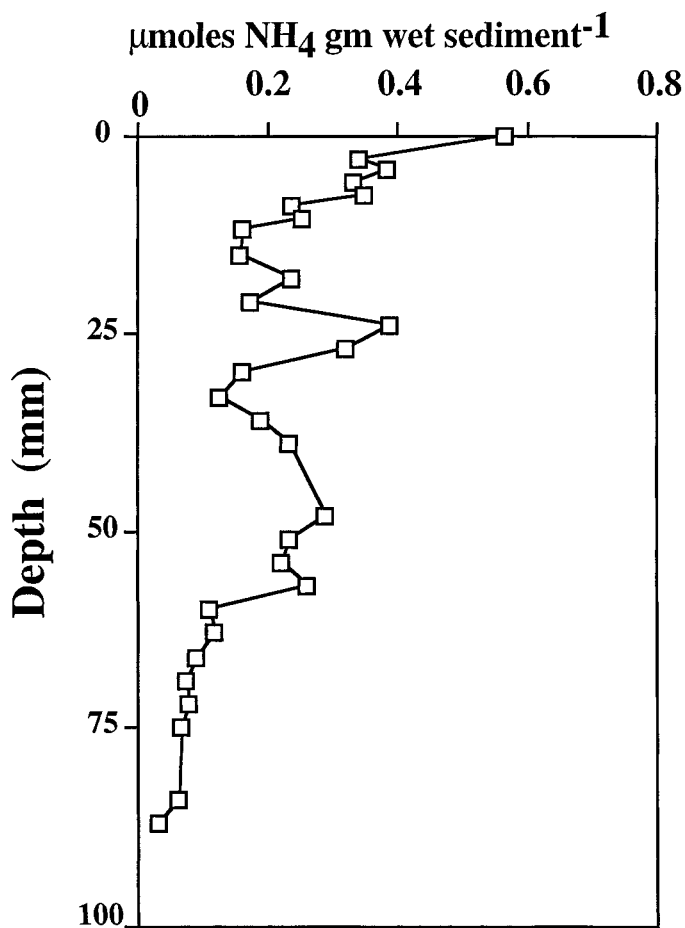


Fig. 8. Concentrations of extractable NH_4^+ from sediments, as a function of depth in the sediment.

anic rains typically have relatively low concentrations of DIN compared to continental rains (Willey and Kiefer 1993). In the rain collected onboard ship during this study, concentrations of dissolved N were significant, but owing to low rainfall amounts over the continental shelf region, direct N input from atmospheric deposition was not substantial.

The second forcing process of wind mixing was particularly strong in coastal shelf and Gulf Stream areas off North Carolina, where Hurricane Gordon produced 65-knot winds with gusts to 80 knots. After the passage of the main body of the storm on leg 2 of the cruise, we encountered wind speeds of 20 knots nearshore, increasing to 30 knots in the Gulf Stream. Storm-associated winds have the potential of completely mixing shallow continental shelf waters (20–50 m) down to the sediment surface in this region (Ridderinkhof et al. 1992). In deeper waters, where the nitracline develops at 125–150 m, wind erosion of deeper layers of water could deliver deep-water nitrate to the photic zone. Detectable nitrate concentrations measured in surface samples in the Gulf Stream serve as evidence that this process occurred.

High wind speeds associated with hurricanes often resuspend sediments and associated benthic organisms (Bothner et al. 1981; Cahoon and Cooke 1992). Bottom waters on the continental shelf become stratified during calm weather con-

ditions, and a chlorophyll-rich layer often resides 5–10 m above the sediment–water interface. Resuspension of sediments will bring phytoplankton that was previously light-limited to the photic zone (Zeeman 1985). At the same time, nutrients from sedimentary pore waters are transferred to surface waters (Pederson et al. 1995). Lastly, bacterial populations attached to sediment particles at the sediment–water interface are greater than those typically measured in the water column (Carlucci and Wolgast 1992). Therefore, resuspension should also result in increased heterotrophic biomass in the water column.

The effects of these physical processes on biological characteristics of coastal North Carolina are summarized as follows: (1) photosynthetic and heterotrophic bacterial production increased; (2) nutrient injections increased the production, and in certain instances, N limitation was ameliorated; and (3) as N and light levels increased due to algal resuspension, phytoplankton in the water column showed an increasing tendency toward P limitation and possibly reduced DIC availability. The resuspension of benthic biomass could explain the increased Chl *a* concentrations in the water column; however, the C fixation experiments in bioassays and in *P-I* experiments confirmed that de novo primary production occurred in the water column after the storm's passage. Absolute ^{14}C incorporation by phytoplankton in the light was about five times greater in bioassays incubated with water sampled on leg 2 of the cruise. Elevated bacterial production accompanied primary production increases (see Ritzrau and Graf 1992), and sediments were likely contributors of these organisms or dissolved organic matter.

Nutrient injections into the water column occurred simultaneously. For a brief period following high storm winds, nutrient concentrations were detectable in surface waters, even though productivity had increased by fivefold. Alleviation of N limitation was further supported by the *P-I* measurements performed during each leg. Photosynthetic capacity was enhanced by added N only before Hurricane Gordon (Fig. 4). In bioassay experiments following the hurricane, N had less of a stimulatory effect on isotopic shifts (Table 3) than did similar enrichments in incubations on leg 1 and from prior cruises (Aguilar et al. 1995). Together, detectable nutrients and a decreased ability to stimulate photosynthesis following N additions imply a substantial influence from sedimentary resuspension.

Amelioration of N limitation was detected by N isotopic measurements in the water column as well as by experimental incubations. The uniformity in $\delta^{15}\text{N}$ values following Hurricane Gordon can be directly linked with sedimentary particulate and dissolved N signals. Injection of surficial sediment, associated benthic organisms, and the ammonium in associated pore fluids into surface waters most likely influenced particles in the water column. A 1‰ shift in $\delta^{15}\text{N}$ relative to sedimentary N is indicative of isotopic fractionation resulting from kinetic isotope effects during ammonium uptake (Montoya et al. 1991; Pennock et al. 1996).

As N limitation was relieved, C isotopes indicated increased tendency toward P limitation and reduced C availability. Following the storm, Gulf Stream particulates were isotopically heavier and coincided with primary and bacterial production rates that were significantly higher after the

storm, which can significantly decrease C isotopic fractionation by phytoplankton (Bidigare et al. 1997). The $\delta^{13}\text{C}$ values of the stable isotope bioassay experiments increased as well, particularly with added P, which is consistent with water-column measurements.

In summary, meteorological forcing resulting from wind generated by this storm resulted in significant changes in primary production in the continental shelf photic zone. Resuspended sediments laden with microorganisms and dissolved, growth-limiting nutrients were mixed into the water column. Significant increases in Chl *a*, CO_2 fixation, and bacterial production were observed over relatively large areas. Stable isotopic compositions of suspended particulate material shifted quickly and recorded the biological perturbations to the water column. Increases in the rate of primary production in association with major storm events could therefore be important in the calculation of coastal and global ocean production and may influence the sedimentary organic C record in coastal areas.

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