Ecosystem impacts of three sequential hurricanes (Dennis, Floyd, and Irene) on the United States' largest lagoonal estuary, Pamlico Sound, NC

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Three sequential hurricanes, Dennis, Floyd, and Irene, affected coastal North Carolina in September and October 1999. These hurricanes inundated the region with up to 1 m of rainfall, causing 50- to 500-year flooding in the watershed of the Pamlico Sound, the largest lagoonal estuary in the United States and a key West Atlantic fisheries nursery. We investigated the ecosystem-level impacts on and responses of the Sound to the floodwater discharge. Floodwaters displaced three-fourths of the volume of the Sound, depressed salinity by a similar amount, and delivered at least half of the typical annual nitrogen load to this nitrogen-sensitive ecosystem. Organic carbon concentrations in floodwaters entering Pamlico Sound via a major tributary (the Neuse River Estuary) were at least 2-fold higher than concentrations under prefloodwater conditions. A cascading set of physical, chemical, and ecological impacts followed, including strong vertical stratification, bottom water hypoxia, a sustained increase in algal biomass, displacement of many marine organisms, and a rise in fish disease. Because of the Sound's long residence time (\approx 1 year), we hypothesize that the effects of the short-term nutrient enrichment could prove to be multiannual. A predicted increase in the frequency of hurricane activity over the next few decades may cause longer-term biogeochemical and trophic changes in this and other estuarine and coastal habitats.

Simpson scale, have made landfall in North Carolina between 1996 and 1999. Hurricanes Dennis (September 4–5) and Floyd (September 16), which passed through North Carolina during a 12-day period in September 1999, and Hurricane Irene, which passed near the North Carolina coast on October 17, 1999, led to unprecedented rainfall and prolonged record flooding in eastern North Carolina. The floodwaters inundated coastal rivers and impacted the hydrologic and chemical characteristics of Pamlico Sound (PS), the United States' second largest estuarine ecosystem (Fig. 1). PS is a major fish and shellfish nursery for the entire Atlantic coast. It supports more than 90% of North Carolina's commercial and 60% of recreational finfish and shellfish catches (1).

PS is a shallow lagoonal ecosystem (mean depth = 4.5 m, maximum depth = 7.3 m) with a vast surface area of 5,300 km (2) and limited water exchange with the Atlantic Ocean through four narrow inlets (2). The ratio of the volume of the sound (26 billion m^3) to the average annual inflow (910 $m^3 \text{ s}^{-1}$) yields a theoretical freshwater replacement time of about 11 months (3), far exceeding the replacement time of most temperate estuaries (4). Actual residence time is likely to be longer for much of the inflow because of restricted circulation in sheltered areas and the position of the tidal inlets relative to major tributaries (5).

During typical hydrologic conditions, elevated late winterearly spring water and nutrient inputs promote high springsummer primary productivity, especially in the Chowan River, Pamlico River, and Neuse River (Fig. 1), estuarine tributaries of PS (1, 6). These estuaries typically serve as effective traps for particulate and dissolved materials (7), retaining and processing a large portion of the nutrient inputs from upland areas (8–10), and acting as a filter for PS inflows. Reduced summer-fall inflows result in stable salinities in the estuaries and PS during critical life-history stages of the biota (1, 2). Together, the long residence times, low currents and tidal amplitudes (0.3–0.5 m), shallow depths, high primary productivity, and stable salinities provide an ideal nursery habitat for diverse finfish and shellfish populations. However, the long residence time of PS also ensures that elevated freshwater and nutrient loadings, resulting from high-flow events that move quickly through the estuarine "filter," likely remain in the open Sound for relatively long periods. These inputs could support continued elevated primary production that may overwhelm assimilation by grazers and higher fauna, enhancing the potential for bottom-water hypoxia (11).

Despite its ecological and economic importance, very little monitoring and research have been conducted in PS. This is likely related to the long-held assumption that the vast size of this system acts as a buffer against climatic, hydrologic, and biochemical perturbations. Fortunately, some environmental data were collected on several occasions during 1998 as part of university instructional activities and a water quality monitoring feasibility study (12). These data provided a critical baseline against which we tested the hypothesis that PS is susceptible to significant hydrologic, biogeochemical, and ecological alterations resulting from floods associated with hurricanes. In response to the unprecedented flooding in the fall of 1999, we initiated a collaborative study to examine and evaluate ecosystem-level responses to the floodwater inputs to PS. Here, we report on the magnitude of the flooding, and the short-term water quality and habitat effects and longer-term ramifications for the Sound.

Methods

The environmental data used in this study were collected before and after the three 1999 hurricanes through ongoing cooperative watershed and estuarine-based monitoring programs in the tributaries of PS. The Neuse and Pamlico River estuaries, the two largest tributaries of PS, are sampled at weekly to biweekly intervals (see http://www.marine.unc.edu/neuse/modmon) and monitored continuously via instrumentation (see http://nc.water.usgs.gov).

Three continuous monitoring platforms are located in both the Pamlico River estuary and in the Neuse River estuary; an additional platform is located near the mouth of the Roanoke River. Near-surface and near-bottom pH, water temperature, salinity, and dissolved-oxygen concentration are measured at

Abbreviations: DIN, dissolved inorganic nitrogen; DOC, dissolved organic carbon; PS, Pamlico Sound; psu, practical salinity unit(s); R/V, research vessel; USGS, U.S. Geological Survey.

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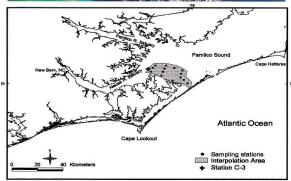


Fig. 1. SeaWiFS satellite-based image of PS, before (*Top*) and after (*Middle*) hurricane Floyd. For comparative purposes, mid-September 1998 (Top) and 23 September 1999 (Middle) images are shown. Note the brown-stained floodwaters entering PS following Floyd. Large turbidity plumes can also be seen escaping PS and advected into the coastal Atlantic Ocean waters by the Gulf Stream (Middle). The area within the yellow rectangle contains the grid of sampling stations (Bottom) for examining hydrological and ecological impacts of Hurricanes Dennis, Floyd, and Irene in western PS. This grid includes station C-3, a reference location (35° 7.22′ N, 76° 28.66′ W) that has been monitored since September 1998.

15-min intervals by using in situ sensors. Instruments are serviced and calibrated at 1- to 2-week intervals. Some of these platforms were removed in advance of Hurricane Dennis, but they were reinstalled in early October 1999.

PS proper has not been routinely monitored. However, during 1998 and in 1999, before the hurricanes, Duke University researchers conducted nine instructional cruises in western PS. They collected data along a series of four transects including a site termed "C-3" (35° 7.22' N, 76° 28.66' W), which is near the mouth of the Neuse River estuary and which has been sampled since September 1998 (Fig. 1). Shortly after the passage of Hurricane Floyd on September 16, 1999, an additional grid of 15 sampling locations, including C-3, was established by University of North Carolina at Chapel Hill researchers (Fig. 1). This grid, which was based on the remotely sensed mixing plume of Neuse River estuary water into PS (Fig. 1), was sampled monthly since early October 1999.

Sampling approaches and analytical methods were as follows.

Freshwater Inflows. Freshwater inflows to the estuaries and to PS were determined from data collected at the U.S. Geological Survey (USGS) network of stream gauges in North Carolina and Virginia, and from estimates of flow in ungauged areas. Streamflow from 67.7% of the land area draining to PS is gauged. Rainfall on the surface of Albemarle Sound and PS was estimated from rain gauge and Doppler radar measurements. Average inflow to PS was computed from long-term monthly mean streamflow records. The period of streamflow record at the various stream gauges used in the analysis ranged from about 15 years to more than 100 years (13).

Flood Recurrence Intervals. Flood recurrence intervals for Hurricane Floyd flooding at stream gauges in the PS watershed were computed by using established procedures (14). Recorded peak flows from this event and associated flood recurrence intervals are available on the USGS web site (http://water.usgs.gov/ pubs/wri/wri004093/)and in ref. 14.

Hydrological, Oxygen, Salinity, and Nutrient Dynamics. The 15 sampling stations in western PS (Fig. 1) were surveyed at monthly intervals by both the R/V (research vessel) Susan Hudson and the R/V Capricorn. Hydrocasts were made at each station with a Sea-Bird Electronics (Bellevue, WA) 25-03 Sealogger CTD (conductivity, temperature, depth) equipped with a Sea Tech (Wet Labs, Inc., Philomath, OR) in situ fluorometer, a Sea Tech transmissometer (0.5 m), a Biospherical Instruments (San Diego) QSP-200PD 4π photosynthetically active radiation (PAR; 400–700 nm) sensor, and a Yellow Springs Instruments 5739 DO (dissolved oxygen) probe. The diffuse attenuation coefficient (k_d) and the depth limit of the photic zone ($z_{eu} = z$ at 1% I_o , surface irradiance) were determined from PAR profiles by using the Beer-Lambert Law. Surface-water samples were taken with a cast bucket, and bottom-water samples were taken with General Oceanics (Miami) 5-liter Niskin bottles attached to the CTD.

Dissolved nutrient samples were prepared by filtering freshly collected PS water through precombusted Whatman GF/F filters. If not analyzed immediately, samples were frozen at -20° C until analysis. Dissolved inorganic nitrogen (DIN) concentrations were determined by colorimetric methods by using a Lachat Instruments (Milwaukee) Quickchem QC 8000 autoanalyzer. The following methods were used: ammonium, nos. 31-107-06-1-A and 31-107-06-1-C; nitrate/nitrite, no. 31-107-04-1-C (Lachat Instruments). DIN concentrations were measured at weekly or biweekly intervals; linear interpolation was used to calculate concentrations for days not sampled. Daily DIN loading to the Neuse River estuary was calculated as the product of DIN concentrations and daily mean discharge. Daily loading values were summed to obtain monthly or yearly loading. The 1999 loading estimates used concentration data from a station near the head of the Neuse River estuary at New Bern and the sum of daily discharge data from three streamflow gauging stations that together measure streamflow from 97% of the Neuse River basin upstream from New Bern. Floodwater loading was calculated for the period 1 September to 25 October 1999. The 1994-1997 loading was derived from concentration data collected 15 km upstream from New Bern, and from discharge data measured at Kinston, and prorated to the nutrient sampling site (11).

Dissolved organic carbon (DOC) and particulate organic carbon measurements were made by using high-temperature combustion techniques (15) using a Shimadzu 5000A total organic carbon analyzer (DOC) and a Perkin-Elmer 2400 Series II CHN analyzer (particulate organic carbon).

Chlorophyll a Measurements. Fifty-milliliter water samples were gently filtered through 25-mm Whatman GF/F filters while a few drops of aqueous MgCO₃ (1%) were added (six samples per station, three surface and three bottom). The filters were extracted 90% acetone overnight at -10° C. Fluorescence was measured on a Turner Designs (Sunnyvale, CA) 10AU fluorometer ($F_{\rm o}$), and then two drops of 10% HCl were added to the acetone extract and fluorescence was measured again ($F_{\rm a}$). The fluorometer was calibrated with a chlorophyll a standard, the concentration of which was determined with a Perkin-Elmer Lambda 3B spectrophotometer and the trichromatic equation of Jeffrey and Humphrey (16).

Fish Surveys. Fish surveys accompanied the hydrological, chemical, and chlorophyll time series measurements. We sampled fish at station C-3 with short trawls (5 min, 2–3 knots) using a 9-m headrope mongoose trawl (4.8-cm inch bar mesh wings and body with a 1.2-cm tail bag mesh). After each trawl, all fish were identified to species and counted, measured (total length, in mm), and examined for external signs of disease (i.e., lesions or bloating caused by bacterial infection). Fish catch was standardized by calculating a catch per unit effort as the number of fish per 100 m trawled. Distance towed was estimated from the speed of the boat and trawl time and checked with positions taken at the start and end of each trawl with a Garmin (Olathe, KS) GPS.

Results and Discussion

Hydrology. Hurricanes Dennis, Floyd, and Irene occurred within a 6-week period between September 4 and October 17, 1999, and brought heavy rains to the PS watershed, which includes the Neuse, Tar-Pamlico, Roanoke, and Chowan River basins, as well as coastal drainage located primarily to the north and south of Albemarle Sound (see Fig. 6, which is published as supplementary material on the PNAS web site, www.pnas.org). The central part of the Tar-Pamlico River basin received 96 cm of rain during September and October, or about 85% of the average annual rainfall. The central and lower Neuse River basin received about 75 cm of rain during September and October, and more than half of the average annual rainfall fell during September alone (see Fig. 7, which is published as supplementary material on the PNAS web site). Most of the rainfall reporting stations in eastern North Carolina received at least half of the average annual rainfall during September and October (13).

All of the river basins draining to PS experienced flooding in at least one location at the 500-year recurrence interval (Fig. 6). Record high water levels were measured at 11 of the 12 USGS stream gauging stations in the Tar-Pamlico River basin, including Tarboro, where the recorded level was about 3 m higher than previously recorded in more than 100 years of records and the peak flood flow was about double the previous maximum flow (13). The most prolonged flooding occurred in the Neuse River basin. Water levels were above the National Weather Service flood stage at Kinston continuously from September 10 through October.

Freshwater inflow to PS during September and October 1999 was equivalent to about 83% of the total volume of the Sound. Typically, mean inflow volume for these two months is $\approx 13\%$ of the Sound volume (Table 1). The Neuse and Tar-Pamlico River basins, which together comprise about 31% of the drainage area to PS, contributed about 44% of the inflow to the Sound in September, and more than half of the inflow in October. Inflow volume to the head of the Pamlico River estuary during September was more than 90% of the mean annual flow volume (13). Inflow to the Neuse River estuary was slightly less than to

Table 1. Freshwater inflow to PS during September and October 1999

		Expressed a		Expressed as % of PS volume		
Basin	Drainage area, km²	Sep-Oct 1999	Normal	Sep-Oct 1999	Normal	
Roanoke	25,400	2.49	0.93	9.6	3.6	
Chowan	12,820	3.32	0.33	12.8	1.3	
Neuse	14,560	5.58	0.54	21.4	2.1	
Tar-Pamlico	11,190	4.61	0.31	17.7	1.2	
All others	16,320	5.63	1.30	21.6	5.0	
Total	80,290	21.63	3.41	83.1	13.2	

Freshwater input to PS

"All others" refers to drainage other drainage to Albemarle S and PS, as well as direct rainfall to the surface of Albemarle S and PS. "Normal" values are based on data from Giese et al. (3).

the Pamlico River, with September inflow volume equivalent to 55–60% of average annual inflow (13). In response to the exceedingly high discharge associated with floodwaters, estimated water residence times were only about 7 days for the Pamlico and Neuse River estuaries during September, compared with a more typical mean value of about 70 days (17, 18).

During normal hydrologic years, more than 60% of the annual rainfall and river basin discharge occurs during the November–March rainy season. The high spring water and nutrient loading accompanying this discharge supports large winter–spring phytoplankton blooms (11). This pattern was drastically altered during the fall of 1999, when approximately half of the annual water discharge occurred during a 6-week period in early fall instead.

Salinity. Weekly monitoring along the axis of both the Neuse and Pamlico estuaries following Floyd and Dennis floodwater discharge (late September 1999) revealed freshwater conditions [salinity < 0.2 practical salinity units (psu)] stretching from the headwaters to the mouths of these major tributaries. A comparison of pre- and posthurricane salinity regimes throughout these estuaries can be found on the Neuse River Modeling and Monitoring (ModMon; http://www.marine.unc.edu/neuse/modmon) and USGS (http://nc.water.usgs.gov) web sites.

Historic late summer salinities are typically at their maximum of 10–13 psu near the mouths of the two systems (17, 18), whereas surface salinities in southwestern PS also reach maximum values from 15 to 20 psu in September (19) (Fig. 2). The week before Hurricane Floyd, surface salinities at stations in the western PS ranged from 18 to 20 psu. Two weeks after the

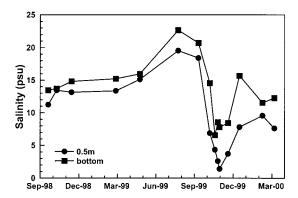


Fig. 2. Surface and bottom water salinities (in psu) at station C-3 in the western PS.

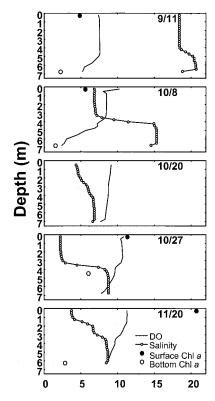


Fig. 3. Vertical distribution of salinity (psu) and dissolved oxygen (mg liter⁻¹) profiles, and surface- and bottom-water chlorophyll a concentrations (mg m⁻³) from station C-3 for 11 September (pre-Floyd), 8 October (post-Floyd), 20 and 27 October (post-Irene), and 20 November 1999. Chlorophyll a samples were not obtained on 20 October.

passage of Hurricane Floyd, surface salinity in PS averaged 8.9 ± 1.4 psu, or less than half of typical values, with the lowest salinities reported at the shallower locations.

The mass and momentum of the inflow created vertical stratification and a well defined pycnocline at a depth of ≈5 m by early October (Fig. 3). Strong stratification was accompanied by development of bottom water hypoxia (<4 mg liter $^{-1}$ O₂). The difference between surface and bottom salinity (stratification) for southwestern PS averaged 6 psu in October 1999, which is 2-3 times greater than normally encountered at that time of the year (12). Stratification greater than 3 psu is usually sufficient to stimulate hypoxia and anoxia below the pycnocline in this system (11).

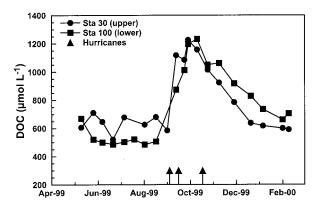


Fig. 4. Surface water DOC concentrations measured biweekly at two locations in the lower Neuse River estuary near its juncture with PS. Dates of landfall for Hurricanes Dennis, Floyd, and Irene are shown.

Reduced salinity and vertical stratification, combined with a high organic matter content and resulting hypoxia existed in PS for ≈3 weeks, beginning after floodwaters reached the Sound in late September. The stratification and hypoxia persisted until Hurricane Irene (16 October) destratified, re-aerated, and further freshened the Sound to ≈6 psu. The Sound subsequently restratified (Fig. 3), demonstrating the continued strong influence of freshwater inflows.

A comparison of 1998–1999 salinity data before landfall of the hurricanes with posthurricane data at station C-3 shows the initial and sustained depression of salinity imposed by "freshening" of this long residence time system (Fig. 2).

Biogeochemical and Ecological Considerations. The DIN load at the head of the Neuse River estuary in September and October 1999 amounted to over 800 Mt of nitrogen, which was 71% of the 1994–1997 average annual DIN loading. This high load translated into elevated concentrations of ammonium and nitrate throughout the estuaries and PS. DIN concentrations are usually less than $1 \mu M$ at the Neuse River estuary mouth in late summer (6, 8, 10, 11), but ammonium and nitrate concentrations at this location were greater than 10 μ M and 2 μ M, respectively, in early October. DIN concentrations in the open Sound were elevated (0.71–11.06 µM nitrogen) and atypically similar to Neuse River estuary concentrations (6.64-15.56 μM nitrogen). In contrast, DIN in the Chesapeake Bay, after flooding associated with Hurricane Agnes, increased only at the head of the Bay, not throughout the Bay (20).

The hurricane floodwater was greatly enriched in organic matter. The DOC concentration in the Neuse River estuary near its entrance to PS rose from prehurricane values of 500–700 μ M C to more than 1,200 μ M C after the storms (Fig. 4), whereas particulate organic carbon concentrations rose from 80 to $>200 \mu M$ C (data not shown). The highly colored (brown) organic material influenced water column irradiance and potentially phytoplankton photosynthetic rates in PS. This was evident as a substantial increase in the diffuse attenuation coefficient (K_d) from 0.5-0.8 m⁻¹ in August (prestorm), to $>1.6 \text{ m}^{-1}$ after the storms.

Phytoplankton biomass, as chlorophyll a, increased 3- to 5-fold relative to prehurricane conditions (Fig. 5). Chlorophyll a concentrations were several times higher in the surface water than in the bottom water, most likely a consequence of strong vertical stratification that accompanied the huge amount of freshwater inflow (Fig. 3, Table 2). Interpolation of surface chlorophyll a values in the transect area during early October 1999 indicated that highest concentrations existed near the center of the western basin of the Sound (Fig. 5). Chlorophyll a concentrations remained elevated in the Sound well into 2000 (Fig. 5), indicative of protracted enhancement of primary production in this highly retentive system. Previous nutrient-productivity studies throughout this system have shown consistent stimulation of productivity in response to nitrogen additions (21–23). Therefore, we believe that the upsurge in phytoplankton production in the surface water reflects the large infusion of nitrogen into a shallowerthan-normal near-surface mixed layer.

Rapid declines in salinity and oxygen have been shown to have direct short-term physiological effects on estuarine macrofauna and greatly reduce the habitable area for resident fish and shellfish species in this system (24, 25). Dissolved oxygen concentrations less than 2 mg O₂ liter⁻¹ are stressful to most motile finfish and shellfish species and fatal to sessile biota (26–28). On 8 October, after Floyd and before Irene, dead and dying shrimp and blue crabs were collected from below the pycnocline where dissolved oxygen was consistently less than 4 mg O₂ liter⁻¹ (hypoxia) and in places reached less than 2 mg O_2 liter⁻¹ (anoxia). In contrast, blue crabs apparently were unaffected by floods following Hurricane Agnes in Chesapeake Bay (20).

Catches of many species (e.g., croaker, spot, bay anchovy, and shrimp) declined by 50% or more in the Neuse River estuary

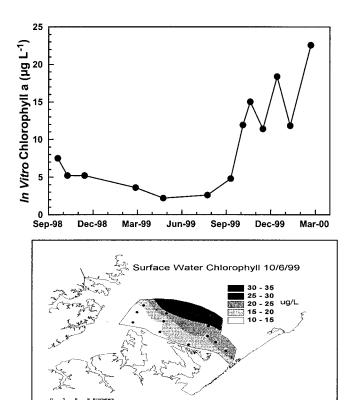


Fig. 5. (*Upper*) Continuous record of surface-water chlorophyll *a* concentrations at station C-3. (*Lower*) Interpolated surface chlorophyll *a* values for the western basin of the PS. Data were derived from the transect stations shown in Fig. 6.

compared with samples taken before the flooding. Catches were also reduced substantially relative to fall catches in 1998. In PS, the number of live finfish and crabs caught during each of three trawls in the western Sound was about 3-fold higher than the number caught before the flooding, although species richness was lower (Table 2). Peak catches in October 1999 were more than 5 times higher than peak catches at the same time in 1998. Thus, it appeared that many of the motile species moved out of the estuaries with the influx of freshwater, but sessile benthic invertebrates were stressed or killed by exposure to low-salinity, hypoxic water. Diseased fish were first noted in the Neuse River and propagated downstream; by 27 October, disease increased substantially in the PS, when about 10-20% of three common species (pinfish, 17%; spot, 20%; and croaker, 14%) had lesions, sores, or sloughing skin; 50-70% showed signs of systemic bacterial infections (E. Noga, North Carolina State University, personal communication). During the same period in a nonhurricane year (October 1998), the incidences of external sores in the Neuse River estuary were 0.18% in spot (n=566) and 0.14% in croaker (n=718); there is no data for pinfish.

The shallow depths and long residence time of PS suggest that a large proportion of the allochthonous and autochthonous organic input during 1999 was deposited in the sediments. Preliminary examinations of the Sound's surface sediments indicate organic matter enrichment from both nutrient-enhanced primary production and sediments transported to the Sound from the riverine tributaries by flood flows. Increased rates of oxygen consumption and inorganic nutrient release from sediment diagenesis have been observed in the Neuse and Pamlico estuaries in response to organic matter enrichment (8, 10, 29). The inorganic nutrient release should further stimulate primary production, as occurred in Chesapeake Bay after Hurricane Agnes (20). Spring and summer of 2000 proved to be very windy, preventing strong vertical stratification and persistent bottom-water hypoxia in the open Sound; however, high rates of primary production were maintained, and hypoxic bottomwater conditions were observed in portions of western PS from June to October 2000. During the same period, increased aerial extent and frequencies of hypoxia and elevated (relative to 1994–1999) rates of primary production were observed in the more sheltered (from wind mixing) lower Neuse River estuary (6, 11, 25, 30). These findings suggest lingering effects of nutrient and organic matter enrichment to the system. This, combined with long water residence time, represents a mechanism that could extend the short-term nutrient enrichment effects of the floodwaters to multiannual enhancement of primary production and nutrient cycling of PS. We conclude that the sustained elevated chlorophyll a levels thus far observed are indicative of longer-term nutrient (specifically nitrogen) retention and recycling within this system.

On the multiannual time scale, microbial denitrification may help purge the system of the large nitrogen load associated with the floodwaters. However, denitrification measurements thus far completed in the Neuse River estuary indicate that annually, this process may remove only about 20% of its external nitrogen load (S. Thompson *et al.*, unpublished results). Therefore, we do not expect denitrification to be a mechanism capable of rapidly "cleansing" the Sound of elevated nitrogen loading associated with floodwater discharge.

Phytoplankton community compositional changes in response to freshwater discharge, depressed salinity, and nutrient enrichment could additionally influence primary production, nutrient cycling, and trophodynamics of this system. Preliminary evidence, based on microscopic observations and HPLC analyses of photopigments diagnostic for major phytoplankton functional groups, indicate that the enhanced stimulation of phytoplankton production was distributed among taxa normally dominant in this system (dinoflagellates, diatoms, cryptophytes, and cyanobacteria) (31). However, a noticeable upsurge in the relative dominance of cyanobacteria was observed in the lower Neuse River estuary and PS (L. Twomey et

Table 2. Summary of PS ecosystem responses to 1999 hurricanes at station C-3

Date (1999)	Salinity, psu		Chl a, mg m ^{−3}		Bottom O ₂ ,	No. of fish	Fish	Fish
	Surface	Bottom	Surface	Bottom	mg l ⁻¹	species	CPUE	disease
11 Sep	19.1	20.3	4.8	2.2	4.6	8	11.5	L
8 Oct	9.0	14.2	5.6	1.5	3.9	3	38.5	L
27 Oct	5.6	9.5	11.3	6.0	8.8	8	124.2	Н
31 Oct	4.0	8.3	NA	NA	9.6	7	218.2	VH
20 Nov	5.5	9.1	20.7	2.8	8.7	8	23.2	M
17 Dec	8.4	17.1	12.2	3.2	8.4	8	3.5	L

Salinity is reported as practical salinity units (psu). CPUE is catch per unit effort in number of fish per 100 m trawled. Number of fish species counted were at least 1% of the total catch. Fish disease categories are low, medium, high, and very high (L, M, H, and VH). Data not available are listed as NA.

al., unpublished results). A reduction in salinity accompanied by nutrient enrichment is known to stimulate cyanobacterial dominance in the upper Neuse River estuary (32). Furthermore, cyanobacterial dominance in this system can alter zooplankton grazer community structure and function (33), indicating the potential for trophic changes associated with shifts in phytoplankton community structure.

Phytoplankton community changes could affect both food web structure and nutrient flux. If, for example, zooplankton consumption of phytoplankton is reduced in response to an increase in cyanobacterial dominance (34), relatively less phytoplankton biomass will be transferred to higher trophic levels. As a result, relatively more phytoplankton-based organic matter will be transferred to the sediments, enhancing microbial decomposition, oxygen consumption, and nutrient regeneration. In long residence-time systems like the PS, this scenario would ensure a long-term response to episodic nutrient-loading events accompanying hurricanes.

As the PS ecosystem recovers from the flooding effects, its nursery function is also expected to recover. With sustained bottom salinities nearly fresh for months, we expect most of the sessile marine benthos in the Neuse River was killed. Indeed, in May 2000 we observed newly set clams that were killed by low oxygen in the mouth of the Neuse River estuary. Given the direct effects of depressed salinity and low oxygen on shellfish and finfish as well as indirect effects mediated through their benthic prey, one might expect reduced densities of these organisms with potentially detrimental effects on fisheries. The most profound fisheries effect was on blue crabs, for which Neuse fishermen reported reduced catches beginning in May 2000. Neuse River estuary sampling during summer 2000 shows blue crab abundances reduced by at least a

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factor of 10 relative to catches in the same period during 1997–1999. Fishermen also report reduced oyster and clam landings in the affected area. We expect time lags in the expression of these effects commensurate with the period before young-of-year fish and shellfish recruit to the fisheries.

Concluding Remarks

The hurricanes of 1999 have provided perspective on how intense meteorological events on the scale of multiple hurricanes can induce both short- and longer-term biogeochemical and ecological changes in a large coastal ecosystem. It is possible that the observed and hypothesized estuarine responses provide a glimpse into effects of future climatic trends on the structure and function of coastal ecosystems. Increased tropical storm and hurricane activity is predicted over the next few decades, and the hurricanes of 1999 may be indicative of this phenomenon (35, 36). Such a trend merits close scrutiny from both intensive monitoring and research perspectives, because it could be indicative of long-term disruption of ecosystems critical for fishery resources, economic development, and habitability of the coastal zone.

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