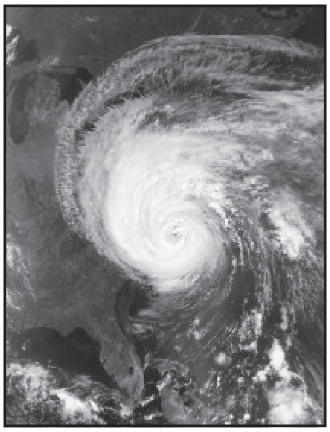

Hurricane Isabel in Perspective: Keynote Address

ECOLOGICAL EFFECTS OF A RECENT RISE IN ATLANTIC HURRICANE ACTIVITY ON NORTH CAROLINA'S PAMLICO SOUND SYSTEM: PUTTING HURRICANE ISABEL IN PERSPECTIVE

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ABSTRACT

The intensity and frequency of hurricanes have varied historically in the Mid-Atlantic region. Since the mid-1990's, this region has witnessed a sudden rise in hurricane landfalls. During this period, eastern North Carolina has experienced seven Category 2 or higher hurricanes: Fran and Bertha in 1996, Bonnie in 1998, Dennis, Floyd, and Irene in 1999, and Isabel in 2003. These storms have had distinctive hydrologic and nutrient loading effects on the Pamlico Sound and its tributaries, including large changes in nutrient enrichment that led to variable phytoplankton biomass and compositional responses. These contrasting effects were accompanied by biogeochemical (hypoxia, nutrient cycling) and habitat alterations. Food web changes may also have occurred.

While floodwaters from the two largest hurricanes, Fran and Floyd, exhibited long-term (months) effects on hydrology, nutrient loads, and algal production, windy but relatively low rainfall hurricanes such as Isabel led to strong vertical mixing, storm surges, but relatively little flushing. Each storm type influenced algal growth and compositional dynamics; however, their respective ecological impacts differed substantially. Isabel made landfall near Drum Inlet on the Outer Banks of North Carolina, transected Pamlico Sound, and tracked onto the Virginia-Maryland tidewater region west of Chesapeake Bay. In the sound, strong vertical mixing and sediment resuspension caused injection of nutrients into the water column, which affected phytoplankton composition and growth. This effect was minor and short-lived (< 2 weeks), however, compared to the larger, lengthy (>6 months) effects of Floyd. The effects of Hurricane Isabel on phytoplankton production and composition in the relatively shallow (~ 5 m), well-mixed Pamlico Sound proved marginal compared to the deeper, stratified mainstem Chesapeake Bay (>15 m), where a large amount of hypolimnetic water was introduced into near-surface waters. Hydrological and wind forcing are important factors and must be integrated with nutrient loading effects when assessing the ecological effects of hurricanes on large estuarine ecosystems.

INTRODUCTION

Hurricane Isabel struck the Mid-Atlantic coastline near Drum Inlet on the Outer Banks of North Carolina on 18 September 2003. After making landfall, Isabel traveled northward across Pamlico Sound and then west of the Chesapeake Bay. This storm is among the most recent of a spate of hurricanes that reflects a projected 10- to 40-year increase in North Atlantic hurricanes that began in the mid-1990's [1]. In Eastern North Carolina, seven major hurricanes (Category 2 or higher) have made landfall since 1996: Bertha and Fran in 1996; Bonnie in 1998; four visits from three hurricanes (Dennis, Floyd, and Irene) in 6 weeks from September to October 1999; and Hurricane Isabel in 2003 (Figure 1). Hurricanes Fran and Floyd led to unprecedented 100- to 500-year flood events [2], inundating coastal rivers and estuaries and impacting the Pamlico Sound system—the second largest estuary in the United States and the country's largest lagoonal ecosystem [2, 3, 4, 5] (Table 1). Prior to 1996, coastal North Carolina had not been seriously affected by a large hurricane

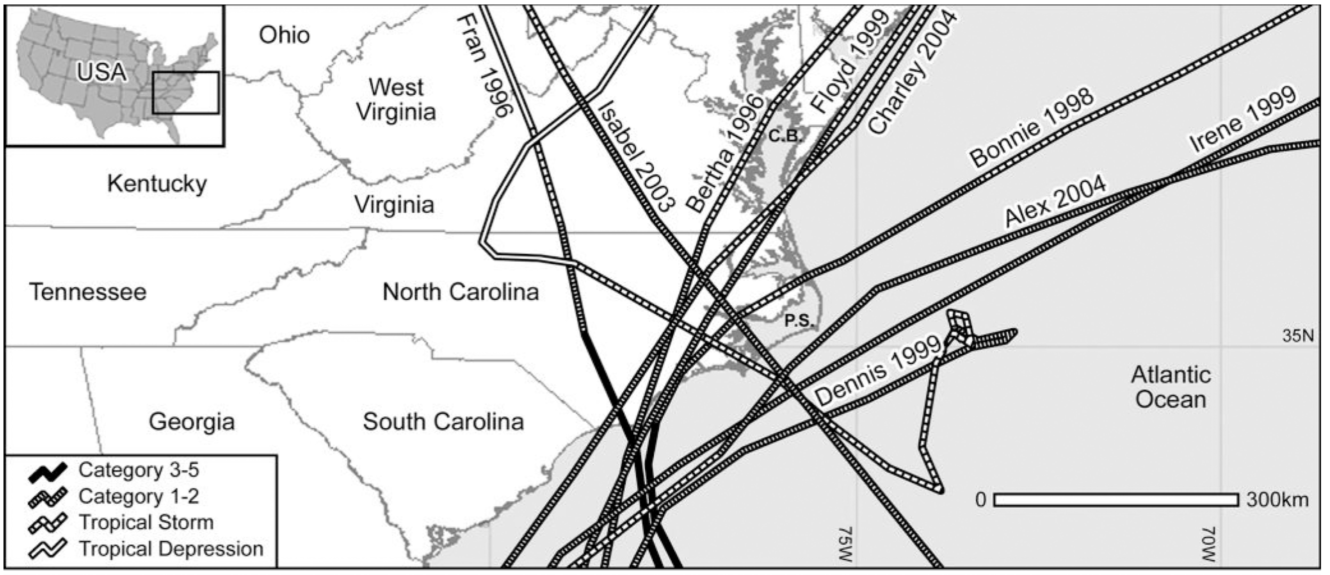

Figure 1. Tracks and intensities of hurricanes that have struck eastern North Carolina since 1996.

since mid-October 1954, when Hurricane Hazel made landfall in South Carolina.

Hurricane Hazel was followed by a 40-year hiatus in major hurricane impacts on eastern North Carolina. This lull was suddenly broken in 1996 with the arrival of hurricanes Bertha and Fran. This lengthy gap in hurricane landfalls is not unusual however. Analysis of weather records for coastal North Carolina indicates that this region has experienced repeatable 10 to 40-year periods of elevated Atlantic hurricane activity. For example, the late 1800's (1880's–1900) and early to mid-1900's (1930's–1950's) were particularly active periods interspersed with calm. During the 1890's, there were several years when multiple Category 2 or higher hurricanes struck the North Carolina coast (Figure 2). The 1940's and 1950's were also very active years, with hurricane landfall frequencies matching those of the late 1990's (Figure 3).

Even as a Category 2 (40–45 $m \cdot s^{-1}$) hurricane, Isabel is considered one of the most significant hurricanes to affect portions of coastal North Carolina and the Virginia-Maryland tidewater region since hurricanes Dennis and Floyd in 1999 [3], Hurricane Hazel in 1954, and the Chesapeake-Potomac Hurricane of 1933 [6]. In North Carolina, Hurricane Isabel's most notable physical effects were storm surges on the Outer Banks and throughout the Albemarle-Pamlico Sound system, including its estuarine tributaries (Neuse, Tar-Pamlico, and Chowan-Roanoke). Perhaps most notable, this storm caused a breach at Hatteras Island between Hatteras Village and Frisco, North Carolina, creating a new 518-m-wide inlet with depths ranging to 6 m (Figure 4). This breach persisted for approximately two months, at which time the U.S. Army Corps of Engineers and the North Carolina Department of Transportation (DOT) filled the inlet. During its brief lifetime, the inlet had a significant impact on water exchange

Table 1. Water residence time (in days) calculated from monthly mean flow for two key tributaries (Neuse and Pamlico) and the Pamlico Sound proper. Values are shown for September and October, 1999, during the hurricane flood period. Average residence time is based on mean flow data obtained from the 1989–1999 USGS upstream river gauging records.

Waterbody	September		October	
	1999	Ave.	1999	Ave.
Neuse River Estuary	7	69	11	81
Pamlico River Estuary	7	133	19	175
Pamlico Sound	36	219	79	313

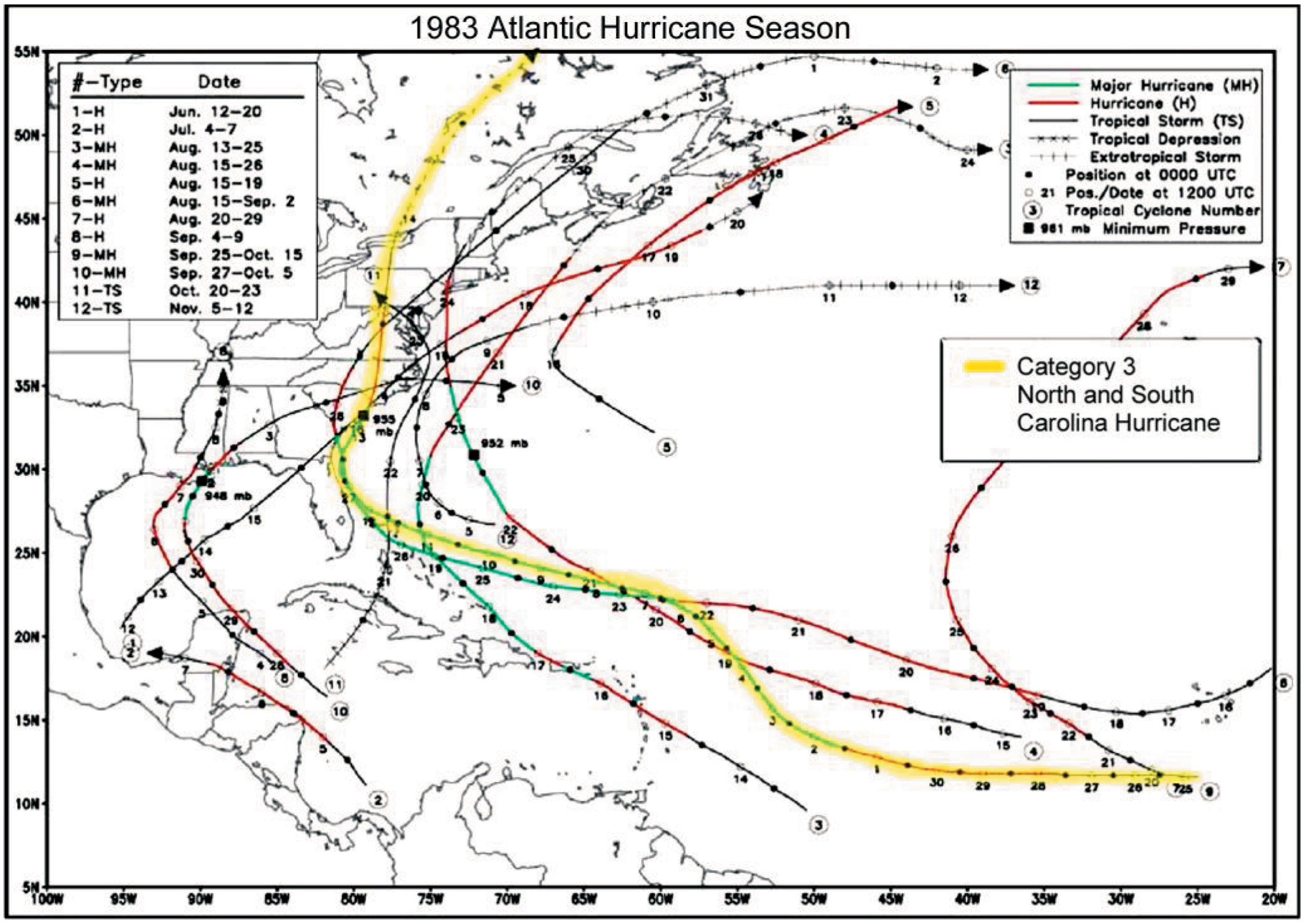

Figure 2. The 1983 North Atlantic hurricane season when four hurricanes co-existed in September. All four hurricanes eventually made landfall in eastern North Carolina (courtesy of NOAA).

between the Atlantic Ocean and the lagoonal Pamlico Sound system, as witnessed by altered salinity regimes in the sound. These hydrologic and chemical changes were documented by the North Carolina Ferry-Based Water Quality Monitoring Program, FerryMon *(www.ferrymon. org)*.

The purpose of this paper is to place the ecological effects of Isabel on North Carolina estuaries in perspective with regard to the effects of recently preceding hurricanes, most notably Hurricane Frances in 1996 and hurricanes Dennis, Floyd, and Irene in 1999. Specific emphasis will be on the phytoplankton community, forming the base of the food web. We used data from temporally and spatially intensive water quality monitoring programs that have been in place since the early 1990's on a key tributary of the Pamlico Sound, the Neuse River Estuary. In addition, ferry- and small-vessel-based water quality monitoring programs on the sound proper have been used to examine hydrologic and water quality impacts of these storms. In recent years, these programs have proven timely and essential for assessing the combined ecosystem-level effects of growing anthropogenic nutrient loads and what appears to be a new era of elevated hurricane frequency and intensity.

METHODS AND MATERIALS

The Pamlico Sound System

North Carolina's Pamlico Sound system is comprised of five major watersheds—the Tar-Pamlico, Neuse, Roanoke, Chowan, and Pasquotank—covering an area of approximately 80,000 km^2 (Figure 5). The sound has a surface area of 4,350 km^2 and estimated volume of about 21 km^3. Together, these basins drain approximately 40% of North Carolina and about 10% of Virginia.

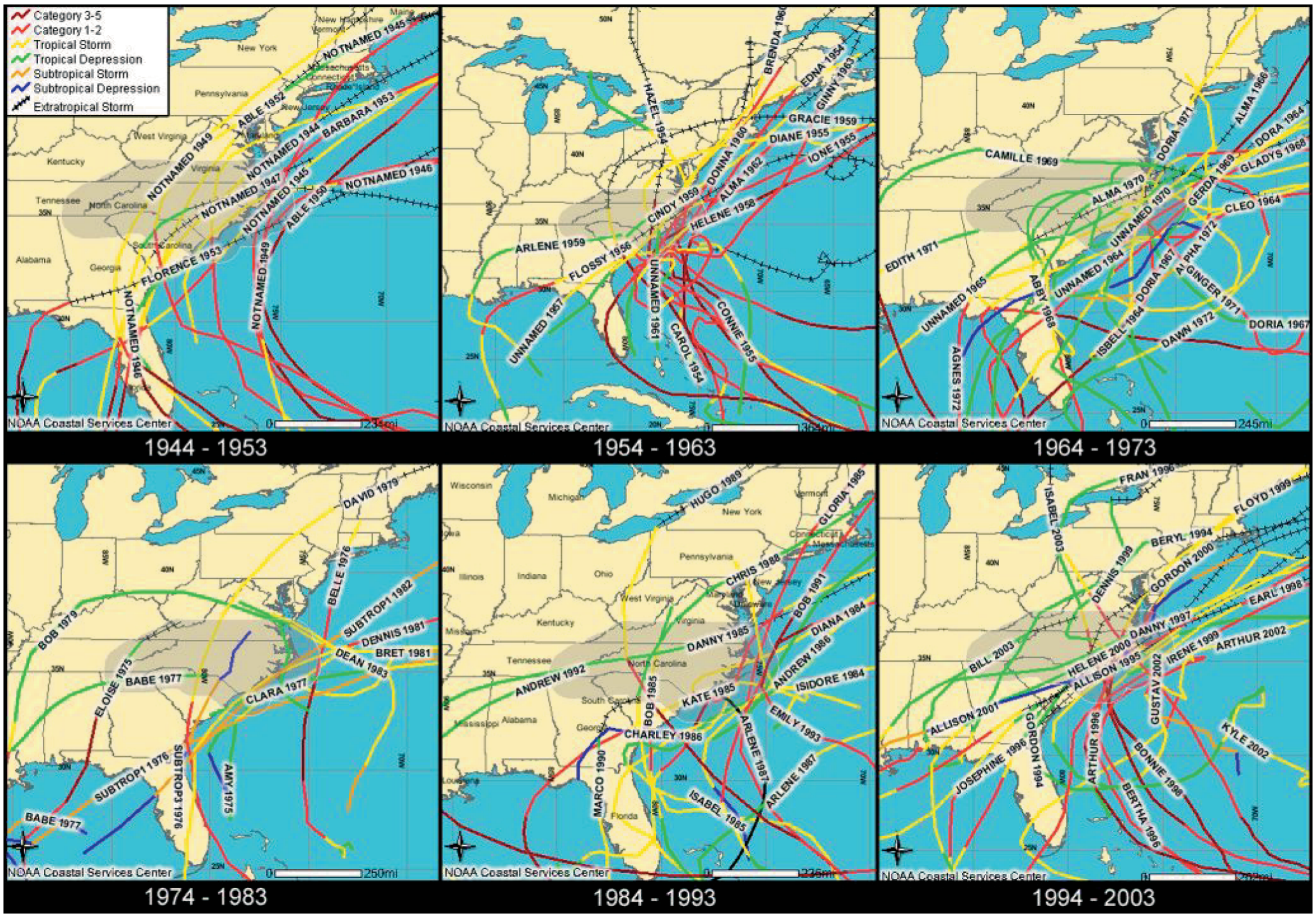

Figure 3. Decadal records for tracks of major Atlantic storms from 1944 to 2003.

A geologically and ecologically important feature of the sound is its lagoonal nature, attributable to the surrounding barrier islands, the Outer Banks. Water exchange with the coastal Atlantic Ocean and nearby Gulf Stream is restricted to three narrow, shallow inlets, leaving the sound with a relatively long residence time (~1 yr) during average years [7]. This provides ample time for resident phytoplankton and vascular plants to assimilate nutrient inputs and is a critical ingredient for the sound's high productivity per unit nutrient input and fertility. However, the long residence time also makes the sound sensitive to excessive nutrient loading and eutrophication [3]. The Pamlico Sound is an important fishing ground and provides critical nursery and foraging habitats for the surrounding Mid-Atlantic fishery [8].

Development in the sound's watershed came later than in some other major estuaries, such as the Chesapeake Bay. Recent (since the early 60's) conversion of watersheds to agricultural crops, intensive livestock, silviculture, and urbanization has greatly increased nutrient loading to the river estuaries of the sound [9, 10, 11].

The Neuse River Estuary is the largest (in terms of water discharge) tributary of the sound. It drains a rapidly growing urban, industrial, and agricultural watershed and illustrates the plight of many coastal river systems under the influence of accelerating nutrient loading. This estuary is approximately 100 km long from its fresh headwaters to the mesohaline (15–25 psu) waters of Pamlico Sound (Figure 5). Its physical, chemical, and biological characteristics have been intensively monitored and are the focus of modeling studies [12, 13]. Primary production in the Neuse River Estuary is strongly controlled by nitrogen inputs [14, 15, 16], which have nearly doubled in the past three decades [9, 10, 11]. Within this time frame, the estuary has experienced multiple symptoms of

Figure 4. Hurricane Isabel struck the North Carolina coast on 18 September 2003. Upper frame: The new inlet that was cut by Isabel's storm surge and overwash of Hatteras Island. Shown are before and after images (courtesy of USGS). Lower left frame: NOAA rainfall intensity image showing Isabel making landfall near Drum Inlet on the Outer Banks. Lower right frame: Hurricane Isabel's northwesterly track across the Pamlico Sound after making landfall.

eutrophication, including nuisance (i.e., toxic and food-web-disrupting) dinoflagellate and cyanobacterial blooms, extensive bottom-water hypoxia, and periodic shellfish and finfish kills [14, 17, 18]. Nonpoint sources contribute about 75% of the external or "new" nitrogen loads, much of it from agricultural activities. Agricultural expansion—including creation of new farm land, widespread use of nitrogen fertilizers, proliferating livestock (swine, cattle) and poultry (chicken, turkey) operations, coastal urbanization, and increasing contributions from groundwater and atmospheric deposition—have led to unprecedented increases in nitrogen loading [19]. Industrial-style farms have increased the region's hog population from approximately 1 million to over 12 million between 1989 and 1999 alone. As a result, land-applied and atmospherically deposited nitrogen inputs to this estuary constitute a large and growing source of externally supplied "new" nitrogen [20].

Eutrophication and algal bloom formation have been linked to enhanced deposition of organic matter [21], leading to growing frequencies, magnitudes, and aerial coverage of large-scale, bottom-water hypoxia and anoxia (Figure 6) [24]. Relatively long water-residence times (from 30 to over 70 days) and persistent stratification

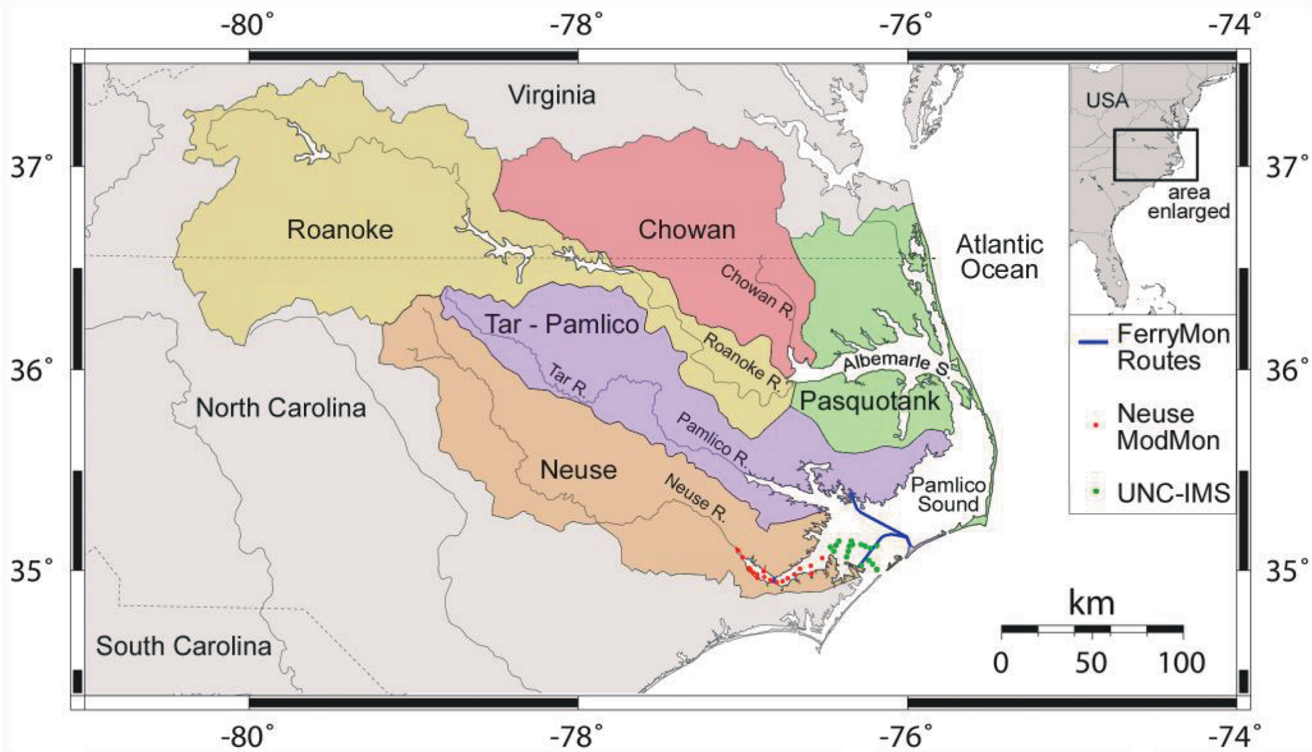

Figure 5. Map of the Pamlico Sound estuarine system showing the major river tributaries and sampling programs for the Neuse River estuary and sound proper.

exacerbate low dissolved oxygen conditions during summer, which can cover at least half the bottom of the estuary [12, 22]. Finfish and shellfish kills have been linked to these events [23, 24].

The water quality monitoring programs used to examine hydrologic and nutrient effects on the Pamlico Sound and Neuse River Estuary (Figure 5) are: 1) The Neuse River Estuary Monitoring and Modeling Program, ModMon (*www.marine.unc.edu/neuse/modmon)* and 2) the Ferry-Based Water Quality Program, FerryMon (*www.ferrymon.org)*. The ModMon program collects near-surface (upper 0.5 m) and near-bottom (0.5 m from the bottom) water quality samples at 19 locations (reduced to 13 in 2003) along the main stem of the estuary. Water quality parameters include: temperature, salinity, dissolved oxygen, turbidity, transparency (vertical attenuation of photosynthetically active radiation), dissolved inorganic nutrients (nitrate/nitrite and ammonium-N, orthophosphate-P, silicate), dissolved organic carbon (DOC) and nitrogen (DON), particulate C and N, chlorophyll *a* (*in situ* fluorescence and extracted), and diagnostic algal photopigments (chlorophylls and carotenoids).

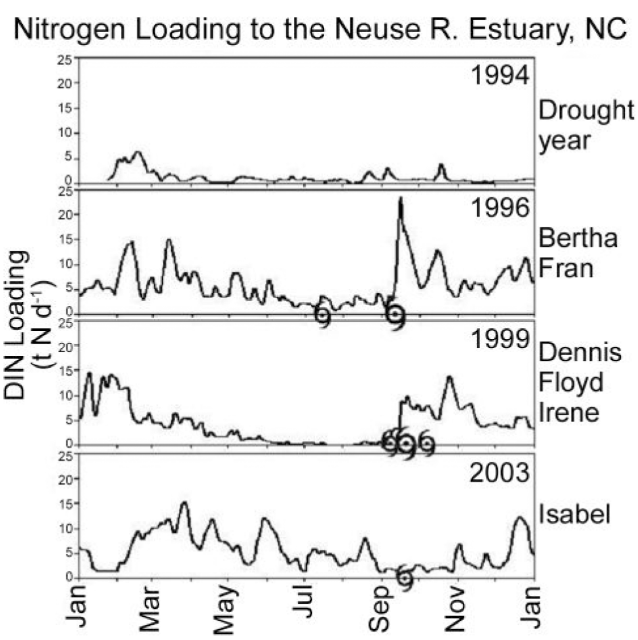

Figure 6. Dissolved inorganic nitrogen (DIN) loading to the Neuse River estuary during selected years reflecting different storm and hydrologic discharge conditions. Loading was calculated by multiplying water discharge at the Kinston gauging station by DIN concentrations at Streets Ferry, the most upstream Modmon sampling site. A relatively dry year (1994) was chosen for comparison. Hurricane landfalls and names are indicated.

Additional data were obtained from the Neuse River FerryMon route with 40 crossings per day (05:00–01:00) between Cherry Point and Minnesott Beach. This representative, mid-estuarine location has periodic algal blooms, low-oxygen bottom waters, and periodic fish kills. It is also a major water and nutrient input source for the Pamlico Sound. Near-surface water quality data were obtained from a continuous flow, automated system using a YSI 6600 multi-probe sensor, which monitored surface waters along the ferry route for temperature, salinity, pH, dissolved oxygen, turbidity, chlorophyll *a*, and geographic position.

ModMon and FerryMon also serve as platforms for collecting data on diagnostic photopigments as indicators of the major taxonomic groups comprising the phytoplankton community (i.e., diatoms, dinoflagellates, chlorophytes, cyanobacteria, and cryptomonads). High-performance liquid chromatography (HPLC), coupled to photodiode array spectrophotometry (PDAS), was used to determine phytoplankton group composition based on the diagnostic photopigments [25]. Pigments include specific chlorophylls (*a, b, c*), carotenoids, and phycobilins. A statistical procedure, ChemTax [26], partitions chlorophyll *a* (i.e., total microalgal biomass) into the major algal groups, to determine the relative and absolute contributions of each group. In the Neuse River Estuary, key photopigment markers include chlorophyll *b* and lutein (chlorophytes); zeaxanthin, myxoxanthophyll, and echinenone (cyanobacteria); fucoxanthin (diatoms); peridinin (dinoflagellates); and alloxanthin (cryptomonads) [27]. The HPLC measurements were also used to calibrate remotely sensed (aircraft, satellite) phytoplankton distributions on the ecosystem and regional scale [13].

RESULTS AND DISCUSSION

The recent period of elevated hurricane landfalls started in 1996 with the arrival of hurricanes Bertha and Fran. Hurricane Bertha made landfall near Wilmington, North Carolina on 14 July 1996, then rapidly moved north just inside the coastline. While its high winds caused significant storm surges, beach erosion, and structural damage, Bertha was a relatively low rainfall storm. The Neuse River freshwater discharge record at Kinston (USGS Station No. 02089500), located approximately 25 km upstream from the entrance to the estuary, showed little impact on hydrologic or nutrient loading to the estuary (Figure 6). In contrast, Hurricane Fran, which struck the coast near Wilmington on 5 September 1996, moved inland and stalled over the Piedmont region. This large, Category 2 hurricane delivered up to 50 cm of rainfall in areas of the Pamlico Sound watershed, causing extensive, long-lasting (4 weeks) flooding in the Neuse River Estuary drainage basin. Discharge from Hurricane Fran contained high levels of nutrients, as reflected in nitrogen loading (Figure 6), and low dissolved oxygen concentrations, with stressful (to finfish and shellfish) hypoxic (<2 mg $O_2 \cdot L^{-1}$) conditions persisting throughout the water column of the estuary for nearly 3 weeks [24] *(www.marine.unc.edu/neuse/modmon).* During this period, fish kills were reported along the entire length of the estuary [24] (Figure 7). Two months after the event, the estuary returned to pre-Fran oxic (>4 mg $O_2 \cdot L^{-1}$) conditions, although higher-than-seasonally-normal freshwater discharge prevailed well into the spring months. This discharge most likely resulted from floodwaters still draining swamps and wetlands, as well as recharge from saturated groundwater sources [28, 29]. Significant residual discharge lasted at least 6 months after Fran. Increased estuarine nutrient loads also resulted. Dissolved inorganic nitrogen (DIN) loading to the Neuse River associated with Fran's floodwaters approximately doubled the annual nitrogen load to this estuary [13] (Figure 6). Fran's nutrient load occurred after the summer optimal phytoplankton production period [24]. Hence, much of this load was not use and flushed into the Pamlico Sound. Unfortunately, the sound was not routinely monitored for water quality until late 1999 (following hurricanes Dennis, Floyd, and Irene).

Hurricane Bonnie, which made landfall near Wilmington as a Category 3 hurricane, was another coastal storm. It rapidly moved up the North

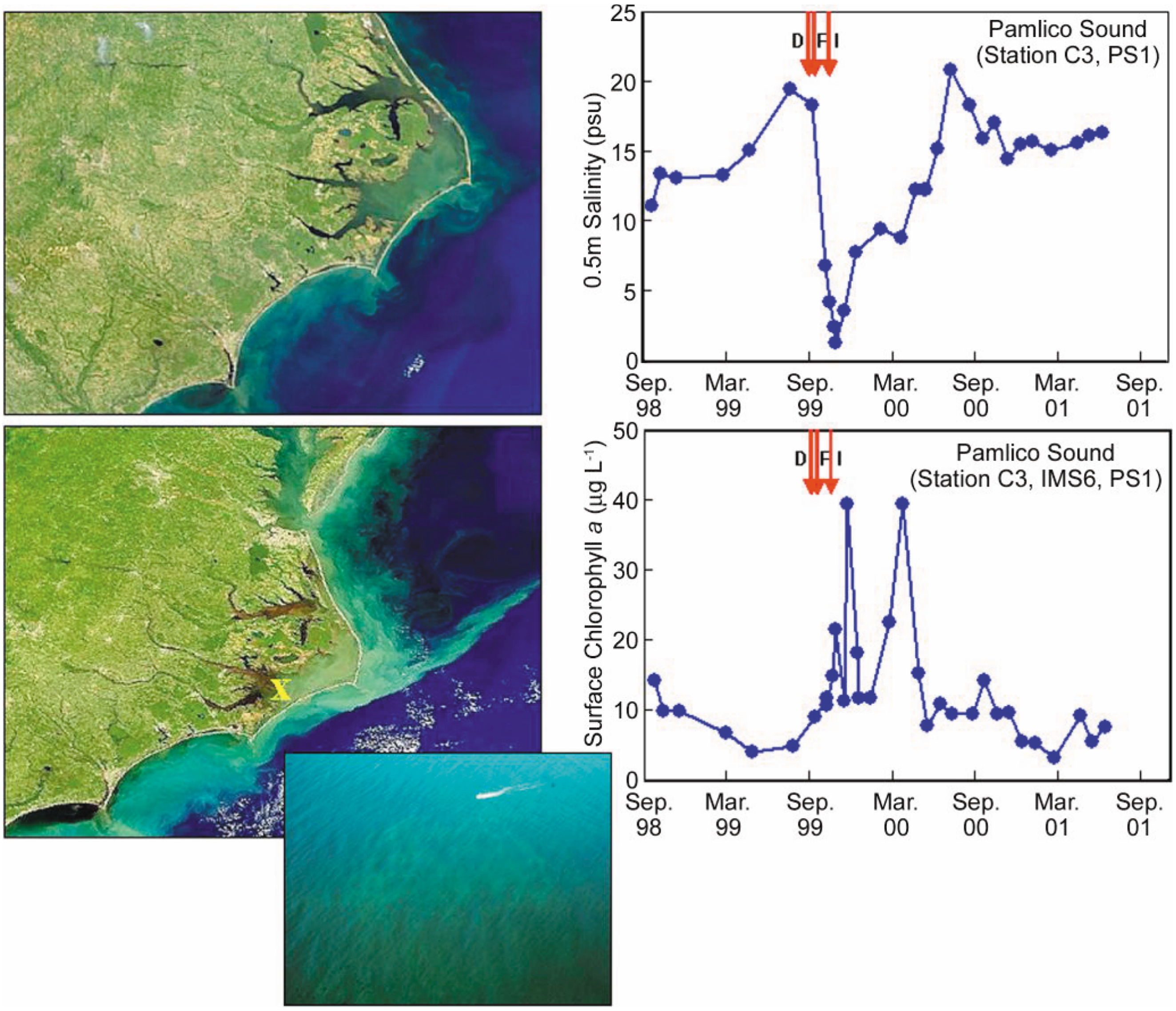

Figure 7. Effects of hurricanes Dennis (D), Floyd (F), and Irene (I) on salinity (psu) and phytoplankton production (chlorophyll *a* concentration) of Pamlico Sound. Upper left frame is a NASA SeaWiFS image of the sound on 16 September 1998, almost 1 year before the hurricanes. Middle left frame is the sound and adjacent coastal ocean on 23 September 1999, approximately 1 week after Floyd made landfall. Note the brown-stained freshwater runoff entering the sound as well as the sediment-laden water flowing from the sound into the ocean following post-Floyd flooding in the watershed. Salinity did not return to pre-hurricane levels at the sampling location (x) for approximately 9 months and elevated chlorophyll *a* concentrations occurred for at least 6 months after this event. Lower left frame shows one of several algal blooms occurring in response to Floyd's floodwaters in Pamlico Sound (note the fishing boat). Figure adapted from [3].

Carolina coast and crossed the western sound with over 45 $m \cdot s^{-1}$ winds, causing widespread structural damage, downed trees, and coastal erosion. Bonnie took a path similar to Hurricane Bertha and likewise proved to be a windy but relatively low rainfall storm. The hydrograph at Kinston showed relatively little freshwater discharge associated with Bonnie. As a result, this hurricane had no detectable impact on either seasonal or annual nitrogen loads to the Neuse River Estuary. While Bonnie completely mixed the waters of the estuary, no significant stimulation of primary production or phytoplankton biomass and no development of hypoxia or fish kills were evident after her passage.

During a six-week period from early September to mid-October 1999, hurricanes

Dennis, Floyd, and Irene inundated eastern North Carolina with up to 1 m of rainfall, exceeding the 30-year average rainfall value by more than 50 cm in some regions of the Pamlico Sound watershed [28] (Figure 7). This led to the "flood of the century" in the eastern part of the state [2]. The sediment- and nutrient-laden floodwaters turned the sub-estuaries of the sound fresh and were equivalent to more than 80% of the volume of the sound [2, 3] (Table 1). The floodwaters caused the sound's water residence time to drop from ~1 year to ~2 months, depressing salinity by 70%. The floodwater freshet entering the sound caused strong vertical salinity stratification, which "locked in" high salinity, nutrient-enriched bottom waters and triggered a very large hypoxia event. An estimated one third or more of the sound's bottom waters was hypoxic to anoxic during the 1- to 2-month period of stratification that followed the flooding [3]. This hypoxic condition would have probably lasted longer if it had not been for Hurricane Irene's winds completely mixing the sound's water column by mid-October. Stressful conditions on finfish and shellfish and an increase in fish disease were reported during the post-Floyd hypoxic period in the sound [3].

The nitrogen load associated with the floodwater was equivalent to at least the annual nitrogen load to this nitrogen-sensitive system [3]. In addition, the floodwaters were highly enriched with organic matter, quantified as dissolved and particulate organic carbon (DOC and POC). Floodwaters transiting the Neuse River Estuary contained up to three times higher DOC and POC concentrations than pre-floodwater discharge [3]. Between September and October 1999, roughly 2000 metric tons of particulate nitrogen (PN) or 60% of the annual freshwater external load entered the estuary [3, 4]. External loading of particulate N was likely an important contributor at the estuary head where productivity rates are typically the lowest [18]. Primary productivity and chlorophyll *a* (Chl *a*) concentration decreased during peak flow. Given the rapid flushing rates and dramatic decrease in residence time, much of this production was likely exported to the sound [4].

In the sound, phytoplankton biomass (Chl *a*) showed a sudden and sustained increase above pre-hurricane levels. This increase was initially documented in monthly surveys using small boats in the western sound and then (starting in 2000) by ferry-based continuous water quality monitoring across the sound [30]. On average, Chl *a* concentrations increased approximately ten-fold, from pre-hurricane levels of 2–5 $\mu g \cdot L^{-1}$ to well over 25 $\mu g \cdot L^{-1}$ after the floodwaters fertilized the sound (Figure 7). Elevated Chl *a* concentrations were observed in the sound as well as the Neuse River Estuary until mid-2000, indicating at least a 6-month period of phytoplankton biomass enhancement. The stimulation of phytoplankton production was accompanied by changes in community composition [4, 27], discussed in the context of the 1996–2003 hurricanes.

These observations indicate that the nutrient load associated with Hurricane Dennis' and Floyd's floodwaters strongly affected primary production, nutrient cycling, and overall water quality of the sound. While hurricane-related floodwaters appeared to have a strong flushing effect on the estuarine tributaries of the sound [3, 4], the Pamlico Sound acted like a trap for the accompanying nutrient loads. These results indicate that hurricanes do not always or consistently have "cleansing" effects on estuarine ecosystems. Rather, they can become nutrient loading sinks or sources, depending on hydrologic, nutrient loading, and within-system cycling characteristics [3, 4].

Most recently, Hurricane Isabel made landfall as a Category 2 storm on 18 September 2003 between Cedar and Ocracoke islands on the Outer Banks. The storm crossed the Pamlico Sound on a northwesterly track, taking it through northeastern North Carolina and the Virginia Tidewater and Chesapeake Bay regions (Figure 4). Isabel's storm surges and high waves caused a breach in the Outer Banks, creating a new inlet near Hatteras Village (Figure 4). Her storm surges also caused extensive flooding and property damage throughout the Bay area. Despite the violent winds, rainfall amounts from Isabel were relatively small (less than 6 cm in coastal North Carolina) (NC Climatology Office,

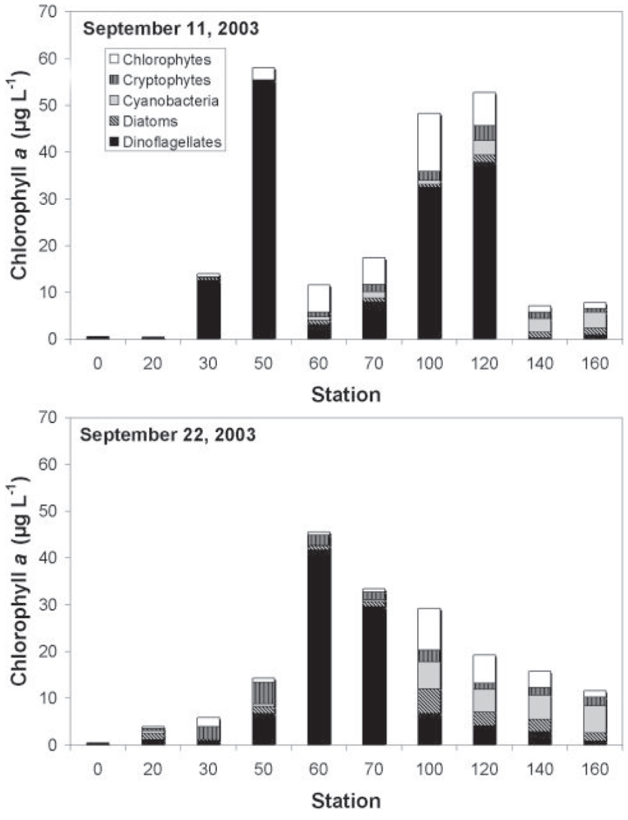

Figure 8. Effects of Hurricane Isabel on phytoplankton biomass (as total chlorophyll *a* concentration) and composition (as the absolute abundance of major taxonomic groups) in the Neuse River Estuary. Values were determined by HPLC-Chemtax analysis. Shown are data for ModMon station locations ranging from the freshwater head of the estuary (0) to the entrance to Pamlico Sound (160). Data are shown for the week prior to and 4 days following Isabel's passage.

NC State University, Raleigh), largely because it was a fast-moving storm. As a result, freshwater discharge associated with Isabel was quite low—comparable with more localized summer-fall thunderstorm activity.

Phytoplankton productivity and biomass responses to Isabel were measurable but small, because little freshwater discharge and nutrient enrichment resulted from this storm. No significant increases in Chl *a* were observed in the Neuse River Estuary following Isabel (Figure 8). Most likely, the lack of phytoplankton growth response to the storm was attributable to the lack of external nutrient loading due to low runoff and the fact that the water columns of these systems were already vertically well-mixed prior to Isabel's arrival. As a result, little, if any, nutrient enrichment of the euphotic, upper water column took place [13].

A different scenario occurred in response to Isabel's passage in the Chesapeake Bay. Aircraft remote sensing and two baywide cruises after this hurricane showed a significant phytoplankton bloom in the mainstem Bay between the York and Patuxent rivers (L. Harding and J. Adolf, personal communication). This bloom appears to have resulted from water column mixing and reintroduction of nutrients to the surface layer. Approximately 7 weeks after Isabel, a large dinoflagellate bloom was observed in the mainstem Bay between the Patuxent and Choptank rivers. This bloom, which lasted for several weeks, proved unusual when compared to historic analyses of the same region during this period (L. Harding and J. Adolf, personal communication) [13]. Mixed-layer depths increased after Isabel, substantially exceeding the mixed-layer depths in a long-term average dataset for some regions of the Bay (W. Boicourt, personal communication). This increase suggests that significant water column mixing occurred, leading to the introduction of subpycnocline nutrients, which helped trigger and sustain this bloom. Although it remains unclear why dinoflagellates specifically took advantage of these conditions, it is evident that long-term averages for the rich and well-documented Chesapeake Bay hydrologic and phytoplankton data can be overwhelmed by episodic events such as hurricanes [13, Roman et al. submitted]. The overall effects of Isabel on phytoplankton dynamics in the Neuse River Estuary/Pamlico Sound and Chesapeake Bay were short-lived, a striking contrast to >6-month stimulation of primary production and phytoplankton biomass in response to nutrient enrichment from Floyd's floodwaters during 1999 to 2000 in both the estuary and the sound.

Impacts of Hurricanes on Phytoplankton, Trophic State, and Habitat Conditions

Data from 1994 to the present show that North Carolina's estuarine systems have experienced the combined stresses of anthropogenic nutrient enrichment, droughts (reduced flushing combined with minimal nutrient inputs), and elevated hurricane activity (high flushing accompanied by elevated nutrient inputs) since 1996. These distinct perturbations have allowed us to examine impacts of anthropogenic and natural stressors on phytoplankton community structure. Seasonal and/or hurricane-induced variations in river discharge with resulting changes in flushing rates (and hence, estuarine residence times) have differentially affected phytoplankton taxonomic groups as a function of their contrasting growth characteristics. For example, the relative contribution of chlorophytes, cryptophytes, and diatoms to the total Chl *a* pool appeared to be strongly controlled by periods of elevated river flow in the Neuse River Estuary (Figure 9). These effects are most likely due to the rapid growth rates and enhanced nutrient uptake rates of these groups [31]. Cyanobacteria, which generally have slower growth rates, were more abundant when flushing was minimal (i.e., longer residence times) during summer (Figure 9).

Historic trends in dinoflagellate and chlorophyte abundance provide additional evidence that hydrologic changes have altered phytoplankton community structure, at least on a seasonal scale, in the Neuse River Estuary. Both decreases in the occurrence of winter-spring dinoflagellate blooms and increases in the abundance of chlorophytes coincided with the increased frequency and

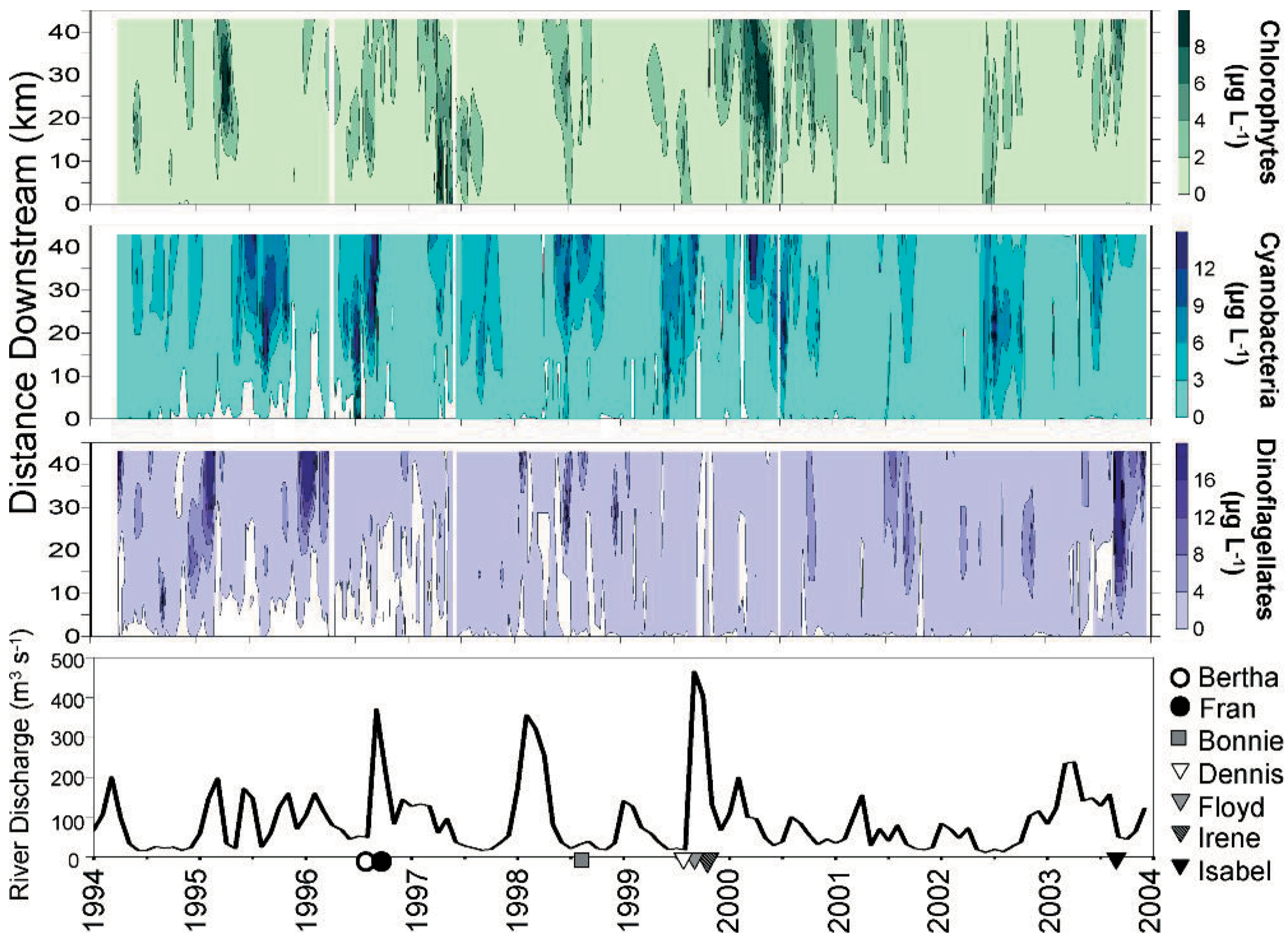

Figure 9. Phytoplankton taxonomic group biomass distributions, based on diagnostic photopigments, from 1994 to 2003 in the Neuse River estuary. Shown are changes in biomass of chlorophytes, cyanobacteria, and dinoflagellates along a segment of the estuary stretching from the most upstream, freshwater location (0 km) to a downstream, mesohaline location (40 km). Also shown is freshwater discharge from the Kinston, NC gauging station and the times of hurricane landfalls. Figure adapted from [13].

magnitude of hurricanes since 1996 (Figure 9). The relatively slow growth rates of dinoflagellates appear responsible for their reduced abundance during the ensuing high-river discharge events. Overall, phytoplankton composition has been altered since 1994 in conjunction with major hydrologic changes, specifically floods following major hurricanes such as Fran and Floyd [13]. These phytoplankton community changes signal potential trophic shifts and biogeochemical alterations.

CONCLUSIONS

Phytoplankton communities are sensitive, relevant indicators of hydrologic and nutrient changes accompanying a recent upward shift in the frequency of Atlantic hurricanes making landfall along the U.S. East and Gulf coasts. A large proportion, from 50% to well over 80%, of primary production sustaining estuarine food webs in these regions is attributable to phytoplankton. Because they dominate within-system production of organic matter, phytoplankton communities supply the "fuel" for respiration and decomposition, the oxygen-consuming processes underlying hypoxia and anoxia in estuarine and coastal waters. Phytoplankton communities also strongly influence the *qualitative* aspects of production and fertility of these waters since not all phytoplankton taxa are alike in how they are consumed and used by consumers, starting with the zooplankton and benthic invertebrate grazers and terminating with finfish and shellfish. In addition, some species of dinoflagellates and cyanobacteria may be toxic, posing additional water quality and habitat problems.

On the whole, hurricanes and other large climatic perturbations—including frontal passages and intense winter-spring lows such as such nor'easters—can have profound effects on altering phytoplankton primary production, composition, and biogeochemical cycling. Some events have more profound and long-lasting effects. These events and critical "drivers" from the ecosystem-response perspective are the duration and amounts of rainfall associated with these events. Storm intensity is another important factor. Clearly, Category 2 or higher storms that move slowly once they make landfall are the most catastrophic from both human infrastructure and ecological perspectives. Overall, results from this synthesis indicate that hydrological and wind forcing assume relatively high levels of importance and must be integrated with nutrient-loading effects in assessing the ecological effects of hurricanes on large estuarine ecosystems.

Because ecosystem response and recovery can take months, if not years, following large storms, careful attention should be paid to the potential long-term, ecosystem-altering effects of the protracted period of elevated hurricane frequency that seems to be taking place [1]. Thus, while estuarine ecosystems are still recovering from one storm, they may be impacted by a new one, leading to long-term biogeochemical and trophic instability. Such instability may mandate close attention from fisheries and habitat managers; unstable conditions may require greater protection of fisheries stocks and resources until a more stable period of fewer and reduced frequency of climatic perturbations is entered.

Based on the findings from Pamlico Sound and prior studies of hurricane impacts in other large estuaries (e.g., Hurricane Agnes on the Chesapeake Bay in 1972 [32]), an increase in major storm activity can cause increased nutrient loading (both external and internal), enhanced algal bloom activity, expansion of low-oxygen conditions, and potential impacts on fisheries. While primary production and standing stocks of phytoplankton may sporadically increase in response to the large nutrient loads accompanying hurricane flood-waters, little short-term evidence suggests that the observed, enhanced primary production of Pamlico Sound translated into increased production at higher trophic levels [3, 17]. If anything, the increased production of phytoplanktonic organic matter adds more "fuel" to support hypoxia and anoxia in the sound's bottom waters and sediments [3]. While increased river discharge can enhance shelf fisheries or anadromous fishes in oligotrophic estuaries, high-discharge events are more likely to have a negative effect in lagoonal estuaries. Flooding not only adds nutrients, organic materials, sediments, and toxic chemicals to estuaries, it also leads to strong stratification of the water column—a prerequisite to low-oxygen concentrations in the bottom water [22], which has proven true for both the Pamlico Sound system and the Chesapeake Bay.

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