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Ecological Response to Hurricane Events in the Pamlico Sound System, North Carolina, and Implications for Assessment and Management in a Regime of Increased Frequency

Hans W. Paerl[1,]*, Lexia M. Valdes[1], Alan R. Joyner[1], Benjamin L. Peierls[1], Michael F. Piehler[1], Stanley R. Riggs[2], Robert R. Christian[3], Lisa A. Eby[4], Larry B. Crowder[5], Joseph S. Ramus[5], Erika J. Clesceri[6], Christopher P. Buzzelli[7], and Richard A. Luettich Jr.[1]

[1] *Institute of Marine Sciences, University of North Carolina at Chapel Hill, Morehead City, North Carolina 28557*
[2] *Department of Geology, East Carolina University, Greenville, North Carolina 27858*
[3] *Department of Biology, East Carolina University, Greenville, North Carolina 27858*
[4] *Department of Ecosystem and Conservation Science, University of Montana, Missoula, Montana 59812*
[5] *Duke Center for Marine Conservation and Duke University Marine Laboratory, Beaufort, North Carolina 28516*
[6] *U.S. Agency for International Development, Washington, D.C. 20523*
[7] *National Oceanic Atmosphere and Administration, Hollings Marine Lab, Charleston, South Carolina 29412*

ABSTRACT: Since the mid 1990s, the Atlantic and Gulf Coast regions have experienced a dramatic increase in the number of hurricane landfalls. In eastern North Carolina alone, eight hurricanes have affected the coast in the past 9 years. These storms have exhibited individualistic hydrologic, nutrient, and sediment loading effects and represent a formidable challenge to nutrient management aimed at reducing eutrophication in the Pamlico Sound and its estuarine tributaries. Different rainfall amounts among hurricanes lead to variable freshwater and nutrient discharge and variable nutrient, organic matter, and sediment enrichment. These enrichments differentially affected physical and chemical properties (salinity, water residence time, transparency, stratification, dissolved oxygen), phytoplankton primary production, and phytoplankton community composition. Contrasting ecological responses were accompanied by changes in nutrient and oxygen cycling, habitat, and higher trophic levels, including different direct effects on fish populations. Floodwaters from the two largest hurricanes, Fran (1996) and Floyd (1999), exerted multi-month to multi-annual effects on hydrology, nutrient loads, productivity, and biotic composition. Relatively low rainfall coastal hurricanes like Isabel (2003) and Ophelia (2005) caused strong vertical mixing and storm surges, but relatively minor hydrologic and nutrient effects. Both hydrologic loading and wind forcing are important drivers and must be integrated with nutrient loading in assessing short-term and long-term ecological effects of these storms. These climatic forcings cannot be managed but should be considered in the development of water quality management strategies for these and other large estuarine ecosystems faced with increasing frequencies and intensities of hurricane activity.

Introduction

The Atlantic and Gulf of Mexico coasts of North America have entered a period of elevated tropical storm activity since the mid 1990s (Goldenberg et al. 2001; Emanuel 2005; Webster et al. 2005), with 2005 having been a record year in hurricane destructiveness (Emanuel 2005). North Carolina alone has experienced the effects of 8 hurricanes ranging up to category 3 ($\leq$ 209 km h^{-1}) between 1996 and 2005, including Hurricanes Bertha and Fran in 1996, Bonnie in 1998, four visits from three hurricanes (Dennis, Floyd, and Irene) in a 6-wk period during September–October 1999, and Hurricane Isabel in 2003 (Fig. 1). Most recently (September 2005), Hurricane Ophelia struck the region. Hurricanes Fran and Floyd lead to 100–500 yr flood events (Bales 2003), inundating coastal rivers and estuaries, and affecting Pamlico Sound (PS), North Carolina (Paerl et al. 2001; Peierls et al. 2003; Ramus et al. 2003; Burkholder et al. 2004).

Initial assessments of the water quality, habitat, and fisheries effects from these storms indicated that such effects vary substantially in magnitude and duration (Paerl et al. 2001; Adams et al. 2003; Peierls 2003; Tester et al. 2003), with large storm events leaving multi-annual effects (Peierls et al.

* Corresponding author; tele: 252/726-6841 ext. 133; fax: 252/726-2426; e-mail: hpaerl@email.unc.edu

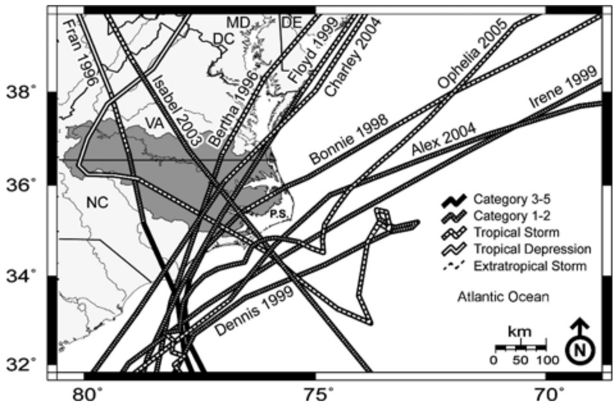

Fig. 1. Tracks and intensities of hurricanes that have made landfall in eastern North Carolina, 1996–2005. Shown are the Pamlico Sound and its watershed (gray shaded area).

2003; Burkholder et al. 2004; Paerl et al. 2006a). Climatologists have forecasted an increase in storm frequency and intensity of Atlantic hurricanes over the next 10–40 yr (Goldenberg et al. 2001; Webster et al. 2005). This poses a long-term threat to low-lying coastal regions. Fully evaluating the ecological effects of hurricanes and other intense storms affords a unique scientific opportunity to understand the linkages between coastal watershed geology, hydrology, biogeochemistry, water quality, fisheries production responses, and the resiliency of receiving waters.

The hurricanes of 1996, 1998, 1999, 2003, and 2005 provided such an opportunity. Fran, Dennis, and Floyd were large, high-rainfall systems that exerted extensive hydrologic (flooding) and biogeochemical (nutrient loading) effects on the PS watershed and its receiving waters (Paerl et al. 1998, 2001; Bales 2003). Watershed-altering hurricanes like Fran (1996) and Floyd (1999) can be compared to coastal hurricanes, such as Bertha (1996), Bonnie (1998), Irene (1999), Isabel (2003), and Ophelia (2005). The latter storms, while packing high winds and leading to considerable beach erosion and structural damage, did not deliver the excessive rainfall and external nutrient loads that the inland storms brought.

We will focus on the magnitude, duration, and qualitative nature of successive geomorphic, hydrologic, and nutrient perturbations resulting from these storms and the resultant phytoplankton and nekton community responses. In the PS and its tributaries, phytoplankton account for at least 80% of primary production sustaining the system's food webs (Paerl et al. 1998). The effects of these perturbations on the phytoplankton community are of considerable importance and relevance for evaluating ecosystem-level biogeochemical and trophic responses. We have tried to put these responses in perspective with regard to managing water quality and fisheries habitat during a protracted period of elevated hurricane activity that is affecting this and other large estuarine ecosystems along the U.S. East and Gulf Coasts.

Assessing hurricane-related perturbations is not straightforward and is a considerable challenge. These perturbations overlay seasonal and interannual variations in rainfall resulting from droughts, extra-tropical storms (local thunderstorms and nor'easters), large-scale multi-annual climatic oscillations, such as El Niño and the North Atlantic Oscillation (NAO), and anthropogenic watershed influences, such as stormwater runoff, wastewater, sediment, and agricultural discharges. The path and strength of storms relative to the estuarine watershed, the waters themselves, and in the case of PS, its barrier islands, play a critical role in the overall ecosystem response. Sampling and analysis of drivers and biotic responses are often not conducted equally intensively. Surveys prior to 1999 were confined to the Neuse River Estuary (NRE), the largest tributary of the PS system, and occurred semimonthly. Following the 1999 hurricanes, monthly sampling was extended into the PS, and the North Carolina Department of Transportation ferries have been monitoring water quality continuously since on three routes transecting the system (Buzzelli et al. 2003). With this information, we reconstructed ecosystem-level responses to these large, individualistic climatic perturbations.

The Pamlico Sound System and Its Watershed

Geologically, North Carolina's barrier islands and associated drowned-river estuaries are highly dynamic and have evolved for thousands of years. This history contains a record of changing climate, including periods of both minor and intense storm activity (Riggs 1999). Accretion and landward migration of barrier islands, and the dynamics and abundance of inlet systems through the barriers, are largely products of episodic, intense storm events. The recent breach of Hatteras Island by Hurricane Isabel (2003) serves as direct evidence for the latter (Paerl 2005). Coring, seismic, and sediment studies suggest that barrier islands and associated estuaries rapidly (weeks to months) respond to major patterns of fluctuating energy conditions (Fletcher et al. 2000; Anderson et al. 2001). The associated ecosystem that develops under such conditions must be resilient, characterized by sudden fluctuations followed by rapid (months to years) recovery. These estuaries and barrier islands represent a storm-dominated ecosystem, in which flood events periodically flush the system and reset the clock through the delivery of a major disturbance, comparable to a fire-dominated ecosystem on land (Riggs 2001). The problem is that the bulk of well-documented data on nearshore geologic processes from Atlantic and Gulf Coast systems comes from a period of relatively low Atlantic storm activity (early 1960s through mid 1990s). We have only a rudimentary understanding of system response and recovery.

Five major watersheds (Tar-Pamlico, Neuse, Roanoke, Chowan, and Pasquotank; see Fig. 1, and Bales 2003) with a total area of approximately 80,000 km^2 provide fresh water to the PS, which has a surface area of 4,350 km^2 and estimated volume of about 21 km^3 (Giese et al. 1985). An important geomorphologic feature of the PS is its lagoonal nature, created by the surrounding Outer Banks barrier island system. Water exchange with the coastal Atlantic Ocean and nearby Gulf Stream is mainly restricted to three narrow, shallow inlets, leaving PS with a relatively long residence time (c. 1 yr) during average years (Pietrafesa et al. 1996). This provides ample time for resident phytoplankton and vascular plants to assimilate nutrient inputs, and is a critical ingredient for PS's high productivity (per unit nutrient input) and fertility. Phytoplankton productivity and biomass accumulation are limited by nitrogen (N) supply (Paerl et al. 1995), and PS receives fewer riverine pulses of nutrients than the upstream NRE due to biological activity in the NRE (Piehler et al. 2004). The long residence time also makes PS sensitive to excessive nutrient loading and eutrophication (Paerl et al. 2001; Christian et al. 2004). The PS is an important fishing ground and provides critical nursery and foraging habitats for the surrounding mid Atlantic fishery (Copeland and Gray 1991).

Like other coastal regions of the mid Atlantic, conversion of watersheds to agriculture began after the Tuscaroran Indian War (1711–1715) when ditching and draining of the coastal plain wetlands began along with the severe deforestation of the Piedmont and Appalachian regions by the early 1900s. The recent shift (late 1950s to early 1960s) to large, fertilized corporate agriculture and silviculture operations, in combination with ongoing urbanization and industrialization, has greatly increased nutrient loading to the river estuaries of PS. This latter shift has resulted in at least a 50% increase in N and phosphorus loading since World War II (Stanley 1988; Dodd et al.1993; Stow et al. 2001), which has resulted in eutrophication in its estuarine tributaries (Copeland and Gray 1991; Cooper et al. 2004; Paerl et al. 2004).

The geomorphology and hydrology of PS's subestuaries (Chowan, Pamlico, and Neuse) predisposes them to accelerated eutrophication (Paerl et al. 1998, 2004); the consequences are well documented for the decades of the 1970s, 1980s, and 1990s (nuisance algal blooms, hypoxia, anoxia, toxicity, disease and mass mortalities of finfish and shellfish; Paerl et al. 2004), but the downstream consequences on the PS are not. Commercial fisheries landings for most species in the PS reached historic peaks in 1980 and have rapidly declined since (Copeland and Gray 1991). While overfishing and habitat destruction contribute to fisheries declines, the landings data signal major changes in the trophic dynamic structure of PS.

Effects of Hurricanes on Hydrological and Biogeochemical Conditions: 1996–2003

Prior to 1996, coastal North Carolina had not been seriously affected by a large hurricane since mid October 1954, when Hurricane Hazel struck. Hazel generated 200 km h^{-1} winds at landfall and stalled as it moved inland, delivering torrential rains to the Coastal Plain and Piedmont regions. From a meteorological and trajectory perspective, Hazel was similar to Fran (1996) and Floyd (1999), as it stalled after making landfall and then delivered a massive amount of rainfall to the coastal watersheds. No data exist on North Carolina estuarine water quality responses to Hazel, though fisheries landings were reduced for most of the major species for several years (NC DENR Division Marine Fisheries unpublished data).

Hazel was followed by a 40-yr period of minor hurricane activity. Analyses of the weather records for the North Carolina coastline indicate that this region has experienced repeatable 10–40 yr periods of elevated Atlantic hurricane activity. The late 1880s to 1900 and mid 1930s to mid 1950s were particularly active periods interspersed with calm periods (Fig. 2). During the 1890s, there were several years (1893 and 1899) where multiple category 2 or higher hurricanes struck the North Carolina coastline. In 1893, there were 4 hurricanes in the Atlantic simultaneously, 3 of which eventually struck the North Carolina coast (September–October). The 1930s and 1940s were also very active years, with hurricane landfall frequencies matching those of the late 1890s and 1990s.

The most recent period of elevated hurricane landfalls started in 1996 with the arrival of Hurricanes Bertha and Fran. Bertha made landfall near Wilmington, North Carolina, on 12 July 1996, then rapidly moved north just inside of 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 (U.S. Geological Survey [USGS] Station No. 02089500), which is located approximately 25 km upstream from the entrance to the NRE, showed little effect on hydrologic loading to the estuary (Fig. 3).

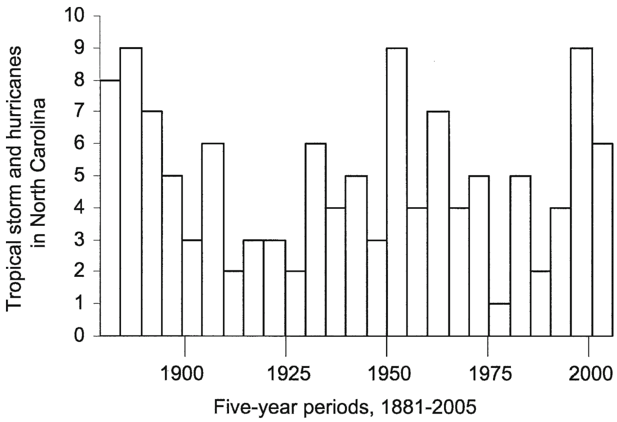

Fig. 2. Number of hurricanes and tropical storms in each five year period from 1881–2005 affecting Pamlico Sound, North Carolina.

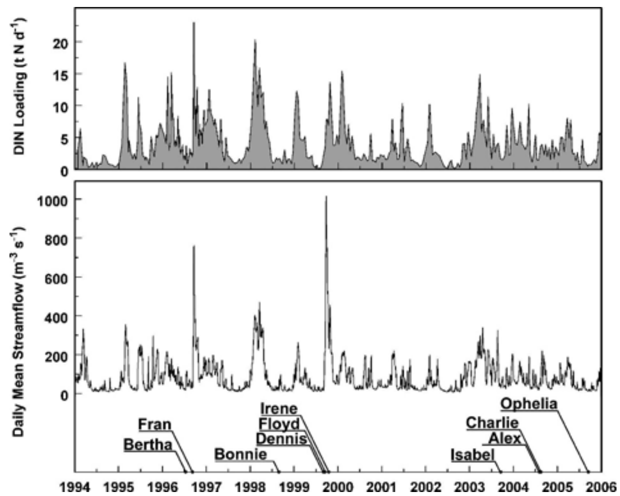

Fig. 3. Dissolved inorganic nitrogen (DIN) loading to the Neuse River estuary (NRE) calculated from concentrations measured near New Bern, NC and streamflow measured at Kinston, NC. Neuse River freshwater discharge patterns measured at the Kinston USGS gauging station (No. 02089500) between 1994–2005. The landfall dates and names for major storms striking the region are also indicated.

Hurricane Fran, which struck near Wilmington on 5 September 1996, moved inland and stalled over the Piedmont region. During its destructive course, which took it over the Raleigh-Durham area, this large hurricane delivered up to 50 cm of rainfall in the areas of the PS watershed, causing extensive, long-lasting (4 wk) flooding in the Neuse River and Pamlico River drainage basins. The Neuse River basin was particularly affected. Hydrographic data at the Kinston gauging station showed a massive amount of freshwater discharge to the NRE. This pulse of freshwater lead to very low dissolved oxygen concentrations (< 2 mg O_2 l^{-1}) throughout the NRE, which caused extensive finfish and shellfish kills that lasted several weeks (Paerl et al. 1998). Nearly 2 mo later, the NRE returned to pre-Fran oxic (> 4 mg O_2 l^{-1}) conditions, although higher than normal (seasonal) freshwater discharge conditions prevailed well into the following spring. This resulted from floodwaters continuing to drain from the land and recharge from saturated groundwater sources (Mew et al. 2002). Elevated discharge lasted at least 6 mo after Fran.

Increased estuarine nutrient loads also resulted from Fran. N loading to the NRE associated with Fran's floodwaters approximated the annual N load (Paerl et al. 2006a, Fig. 3). N loading due to Fran roughly doubled the annual N load to this estuary. Fran's nutrient load occurred after the summer optimal phytoplankton production period (Paerl et al. 1998), so a large proportion of this load was not used and flushed into the PS. PS was not routinely monitored for water quality until late 1999 (following hurricanes Dennis, Floyd, and Irene).

Hurricane Bonnie made landfall as a category 3 storm on August 26, 1998 near Wilmington. It rapidly moved up the North Carolina coast, and crossed the western PS with > 160 km h^{-1} winds, causing widespread structural damage, downed trees, and coastal erosion. Bonnie, like Bertha, was a windy but relative low rainfall storm, had no detectable effect on either seasonal or annual N loads to the NRE (Fig. 3), and no fish kills were reported following this storm.

Between early September and mid October 1999, Hurricanes Dennis, Floyd, and Irene inundated eastern North Carolina with up to 1 m of rainfall, exceeding the 30-yr average rainfall value by more than 50 to 100 cm in some regions of the PS watershed (Bales 2003), leading to historic flooding in eastern North Carolina. The volumes of sediment- and nutrient-laden floodwaters entering PS during September–October 1999 were approximately equivalent to 80% of the volume of PS (Bales 2003). As a result, the Sound's normal water residence time of 1 yr (Pietrafesa et al. 1996) was reduced to approximately 2 mo (Table 1), depressing salinity by 70%. The N load associated with the floodwater was equivalent to at least the annual N load to the NRE (Paerl et al. 2001) and 2–3 times the annual loading to PS from NRE (Peierls et al. 2003). The floodwaters also enriched the PS with large amounts of dissolved organic carbon (DOC) and less so particulate organic carbon (POC; Christian et al. 2004). Floodwaters entering via the NRE contained up to 3 times higher DOC concentrations than pre-floodwater discharge (Paerl et al. 2001, Fig. 4).

Receding floodwaters had a dramatic effect on the flux of particulate organics in the NRE. Between

TABLE 1. Water residence time in days, calculated from monthly mean flow, for 2 key tributaries (Neuse and Pamlico River Estuaries) and the Pamlico Sound proper. Values are shown for September and October 1999 during the hurricane flood period. These were compared to normal conditions, based on mean flows over the previous 10 years.

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

September and October 1999 roughly 2000 metric tons of particulate nitrogen (PN) or 60% of the annual freshwater external load entered the estuary (Bales 2003). This externally supplied organic load also represents a large supply of reduced carbon (C) that upon aerobic degradation represents a large supply of oxygen demand in an estuary that already experiences large-scale bottom water anoxia (Paerl et al. 1998). For perspective, the external load represented up to 70% of the internally-supplied (by primary production) N load that accumulated during this period, based on productivity data integrated over the entire estuary from September to October (Paerl et al. 2001). Internal production of organic matter in the NRE also resulted from the large influx of nutrients associated with the floodwaters. Given the rapid flushing rates and dramatic decrease in residence time, much of this production was exported to the PS (Paerl et al. 2001; Christian et al. 2004). Both primary productivity and phytoplankton biomass showed extensive, long-lasting stimulation in PS, lasting into spring/summer of 2000 (Paerl et al. 2001; Peierls et al. 2003; Christian et al. 2004).

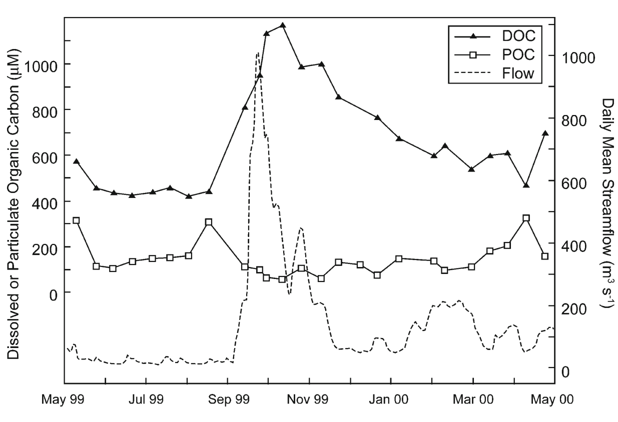

Fig. 4. Dissolved organic carbon (DOC) and particulate organic carbon (POC) concentrations at a Neuse River mid estuarine location along with streamflow at the Kinston USGS gauging station before, during, and after Hurricane Floyd struck eastern North Carolina. Floyd made landfall on September 16, 1999.

The floodwaters entering the NRE and PS altered both the quantity and quality of organics delivered. Stable isotope ratio (SIR) analysis of bulk organic matter is a nonspecific indicator of organic matter source and biogeochemical alteration that has been applied to ecosystem-scale studies (Peterson and Fry 1987). The SIRs of organic C and PN were measured in suspended particulate organic matter (SPOM) collected from surface and bottom waters along a longitudinal transect of the NRE before and after the 1999 hurricanes, as detailed by Clesceri (2003). Hurricane alterations to the SIRs of PN, in particular, were dramatic (Fig. 5). The low variability in SIR values across the 60-km transect suggested that the cause of isotopic alteration was related to changes in organic matter source, rather than isotopic fractionation or biological processing similar to the effect of winter conditions (i.e., high flow and low phytoplankton biomass) on SPOM source in other systems (Mariotti et al. 1984; Cifuentes et al. 1991; Kendall et al. 2001). Clesceri (2003) observed that the average δ^{15}N-PN value of SPOM in the NRE decreased (i.e., became depleted in ^{15}N) dramatically from 7.9 ± 0.25‰ (SE) before the hurricanes to 4.3 ± 0.17‰ during post-hurricane conditions. Such δ^{15}N-PN values that were uniformly depleted in ^{15}N were not otherwise observed in NRE SPOM during the study period or to our knowledge elsewhere (Matson and Brinson 1990).

Potential C and N sources in the watershed that may have been flushed into the estuary during the floodwater recession include topsoils, sewage, fertilizer, or animal waste lagoons and sprayfields. Swine livestock facilities have experienced a large increase in North Carolina in recent years (North Carolina Department of Agriculture 1997). In 1999 several animal operations flooded throughout eastern

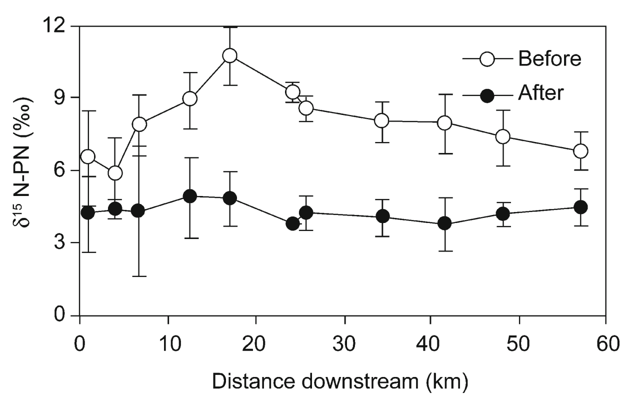

Fig. 5. Stable isotope ratio (δ^{15}N-PN [‰]) of particulate nitrogen from suspended particulate organic matter (SPOM) before (July 19 and August 2, 1999) and after (September 29 and October 25, 1999) the fall 1999 Hurricanes Dennis, Floyd, and Irene. Variability for surface and bottom water samples is shown as standard error, detailed in Clesceri (2003).

North Carolina (NC DENR Division Water Quality unpublished data). Effluent from sewage treatment plants in the Neuse watershed likely overflowed into receiving waters given extended power outages resulting from the hurricanes.

To differentiate among these complex particulate organic matter sources, the use of tracers having end members with extreme values can minimize uncertainties in a large ecosystem. Compared to synthetic fertilizers and soils that have characteristically low $\delta^{15}N$ values (0–2‰; Heaton 1986; Wada and Hattori 1991), swine wastes and human wastes have higher $\delta^{15}N$ values (swine manure 13.82 ± 7.03‰, swine slurry 29.68 ± 9.98‰, sewage treatment sludge 11.70 ± 7.21‰; Curt et al. 2004). Given the low average SIR value for SPOM (4.3 ± 0.17‰), the 1999 NRE floodwaters did not likely contain any significant content of swine or human waste particulates. Rather the estuarine SPOM pool was likely overwhelmed by topsoil and possibly fertilizer-related inputs, similar to the low N SIR values found in forested sites under nonstorm conditions in the headwaters of a neighboring North Carolina estuary (Ulseth and Hershey 2005). Although not measured in this study, it should be noted that animal waste and sewage effluent may have penetrated the dissolved N pool in the NRE. No isotopically heavy sources of dissolved N were biosynthesized into particulates, perhaps given the pre-dominance of physical mixing over biological processing in the aftermath of the 1999 hurricanes.

Hurricane Isabel made landfall as a category 2 storm on 18 September 2003 on the Outer Banks. The storm crossed the PS on a northwesterly track, taking it through northeastern North Carolina, the Virginia Tidewater, and Chesapeake Bay regions (Fig. 1). The storm surges and high waves associated with Isabel created a new inlet near Hatteras Village on the Outer Banks (Paerl 2005). Despite the violent winds, rainfall amounts from Isabel were relatively small (< 6 cm in coastal North Carolina; North Carolina Climatology Office, North Carolina State University, Raleigh, North Carolina), in part because it was a fast moving storm. Freshwater discharge associated with Isabel was quite low compared to the 1999 hurricanes and comparable to more localized thunderstorms. Moderate storm surges within the PS locally caused severe shoreline erosion with significant sediment loads and resulting fish kills (Riggs and Ames 2003).

We note that, in addition to being affected by hurricanes, North Carolina's coastal region is also strongly affected by large scale climatic oscillations, including El Niño years (e.g., winter of 1998), shifts in the NAO, which strongly affect freshwater and nutrient discharge. Examples can be seen in the freshwater discharge record for the NRE (Fig. 3). These events can alter nutrient loads, productivity, phytoplankton community composition, and higher trophic levels and were factored in to overall ecosystem responses for NRE and PS. Following the El Niño in 1998, significant changes in the biogeochemistry of the NRE were documented, most notably the presence of active N_2 fixing cyanobacteria (Piehler et al. 2002a,b).

Effects on Phytoplankton Community Composition

Data from 1994 to present show that these estuarine systems have experienced the multiple stresses of anthropogenic nutrient enrichment, and since 1996, elevated hurricane activity. Following the 1999 hurricanes, chlorophyll *a* (chl *a*) concentrations, which reflected total phytoplankton biomass, showed a sudden and sustained increase above pre-hurricane levels throughout the lower NRE and PS. On average, chl *a* concentrations increased at least 5 fold, from pre-hurricane (mid 1999) levels of 2–10 $\mu g\ l^{-1}$ to well over 25 $\mu g\ l^{-1}$ after the floodwaters fertilized the lower NRE and PS (after fall 1999; Ramus et al. 2003; see Fig. 9 in Paerl et al. 2006a). Elevated chl *a* concentrations (> 10 $\mu g\ l^{-1}$) were observed in PS as well as the NRE until mid 2000.

Phytoplankton community responses to hurricanes, storms (floods), and droughts were examined using diagnostic photopigments as indicators of the major phytoplankton taxonomic groups. High performance liquid chromatography (HPLC), coupled to photodiode array spectrophotometry (PDAS) was used to determine phytoplankton group composition based on the diagnostic photopigments (Millie et al. 1993). Pigments include specific chlorophylls (*a, b, c*) and carotenoids. A statistical procedure, ChemTax (Mackey et al. 1996) partitions chl *a* (i.e., total microalgal biomass) into the major algal groups, to determine the relative and absolute contributions of each group (Paerl et al. 2003). HPLC pigment analyses were adapted to routine monitoring programs, including the NRE modeling and monitoring program (ModMon, www.marine.unc.edu/neuse/modmon), and the ferry-based water quality monitoring program, FerryMon (www.ferrymon.org).

Seasonal and hurricane induced variations in river discharge, flushing rates, and as a result, estuarine residence times affected phytoplankton taxonomic group composition as a function of their contrasting growth characteristics. The relative contribution of chlorophytes to the total chl *a* pool appeared strongly controlled by periods of elevated river flow in the NRE (see Fig. 7 in Paerl et al. 2006a). These effects were most likely due to the efficient nutrient uptake and fast growth rates under relatively fresh conditions by members of this group (Pinckney et al. 1998). Cyanobacteria and dinoflagellates, which generally have slower growth rates and can thrive under mesohaline conditions, were more abundant when flushing was minimal (i.e., longer residence times) during summer.

Historic trends in dinoflagellate and chlorophyte abundance provide additional evidence that storm-related hydrologic changes have altered phytoplankton community structure in the NRE. Both decreases in the occurrence of winter-spring dinoflagellate blooms and increases in the abundance of chlorophytes coincided with the increased frequency and magnitude of hurricanes since 1996 (see Fig. 7 in Paerl et al. 2006a; Valdes et al. 2006). The relatively slow growth rates of dinoflagellates appear responsible for their reduced abundance during the ensuing high river discharge events. Phytoplankton composition has been altered since 1994 in response to large hydrologic changes, such as the floods following Hurricanes Fran and Floyd.

Phytoplankton productivity and biomass responses to Isabel were measurable but small, in large part because of the low freshwater discharge and nutrient inputs from this storm. Slight increases in chl *a* were observed in NRE immediately after the storm's passage (see Figs. 7 and 9 in Paerl et al. 2006a), but these lasted only a week or so. These increases were likely due to complete vertical mixing of PS, introducing sediment-related nutrients into the upper water column (Paerl et al. 2006a). A similar scenario was observed in response to Isabel's passage in the Chesapeake Bay, where deep mixing caused hypolimnetic nutrients to be injected into the surface waters, spawning post-hurricane blooms (Roman et al. 2005). These effects were short lived, in contrast to $>$ 6 mo stimulation of phytoplankton biomass in response to Floyd's floodwaters in 1999–2000.

Fish Health and Population Effects

Like the other estuarine characteristics, there were differences in the response of the finfish and shellfish to the various hurricanes that occurred in this system. Finfish and shellfish were sampled in the upper NRE from 1997 to 2001 and lower NRE from 1998 to 2000 by randomly selecting approximately 30 stations from an estuary-wide fixed grid. Fourteen stations in PS were sampled monthly by mongoose trawls from 1999 to 2001. Individuals were identified, enumerated, and measured for length in the trawl catches (Paerl et al. 2001; Eby and Crowder 2002).

Observed differences in nekton responses to the hurricanes were associated with differences in the freshwater discharge and subsequent changes to estuarine salinity and dissolved oxygen. Hurricane Bonnie (1998) produced little rain, minor changes in estuarine salinity, and few direct effects on the NRE fish community. Hypoxia ($<$ 4.0 mg O_2 l^{-1}) was present after this hurricane, and fish avoided hypoxic patches (Eby and Crowder 2002). A fish kill was reported after the hurricane (www.esb.enr.state.nc.us/Fishkill/fishkillmain.htm), but our trawl catches were similar to or higher than before the hurricane, implying that this kill was not large in relation to the total population.

Hurricane Floyd's floodwaters substantially altered salinity and dissolved oxygen concentrations. One week after Hurricane Floyd, the upper NRE was completely fresh from surface to bottom. Further downstream, the surface waters remained fresh, but saline bottom waters produced a strong pycnocline (a 15 psu difference; Paerl et al. 2001). The strong stratification resulted in bottom water hypoxia in the lower NRE and reduced dissolved oxygen concentrations in western PS ($<$ 4.0 mg O_2 l^{-1}). Strong stratification continued until mid October, when Hurricane Irene fully mixed the system (Paerl et al. 2001). Prior to Irene, benthic fishes were forced to choose between hypoxic and extremely low salinity waters. More fish were captured in the hypoxic waters than usual, indicating that the low salinity was perhaps more physiologically challenging for fish than low oxygen conditions. Since fish did not move out of hypoxic zones, both catch per unit effort (CPUE) and species richness were similar inside and outside of the low oxygen patches (Eby 2001).

After Floyd, fish disease increased both external lesions and evidence of a systematic bacterial infection. Like other studies (Noga 1987; Levine et al. 1990a,b) prior to the hurricane (from 1997), we seldom observed similar evidence of disease in species other than Atlantic menhaden, with whom ulcerative mycosis lesions are typical. Over 95% of Atlantic menhaden *Brevoortia tyrannus* had external lesions after Floyd, but prior to the storm, we found about 80% of menhaden captured had lesions. What was atypical was the occurrence of disease in demersal fishes, specifically Atlantic croaker *Micropogonias undulatus* and spot *Leiostomus xanthurus*. Typical incidences of disease during 1997 and 1998 in the NRE spot and Atlantic croaker population were less than 0.2%. External lesions and signs of bacterial disease were first observed in October 1999, with an incidence of 1–2% for external lesions and 10–40% for systematic bacterial infections. The progression front of diseased fish was tracked from the Neuse and Pamlico Rivers into the PS in the weeks following the hurricanes with only low occurrences of disease in fishes in the furthest PS stations by mid December (Fig. 6). Although we do not know the cause of this high occurrence of

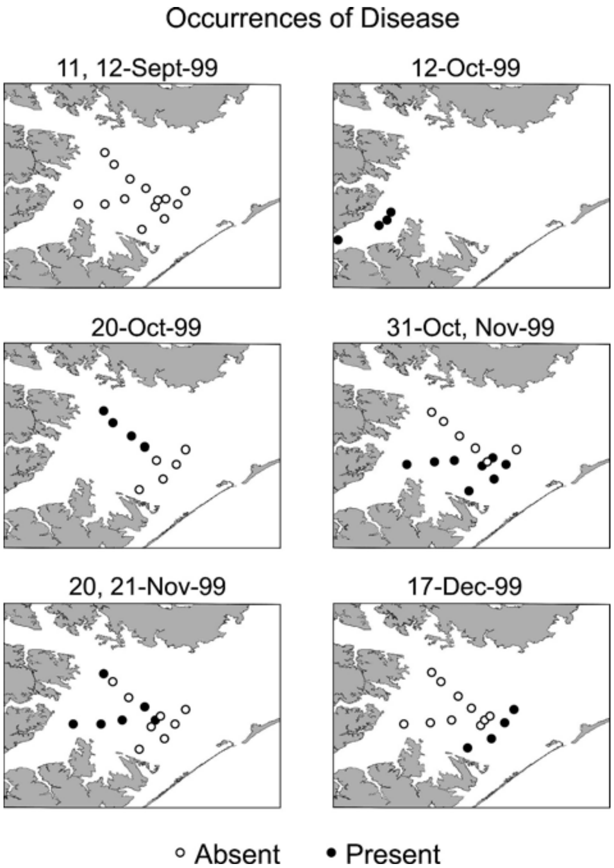

Fig. 6. Spatial occurrence of disease (detection or nondetection from visual surveys) in the fish collections before and after the arrival of Hurricane Floyd (landfall September 16, 1999).

disease after the hurricanes, environmental stresses that affect physiological condition can pre-dispose fish to additional stressors (e.g., Peterson and Black 1988), potentially explaining the increase in disease after Hurricane Floyd. Several physiological, reproductive, immunological, and histopathological indices demonstrated that southern flounder *Paralichthys lethostigma* and spot in the PS after the hurricane were sublethally stressed and in poorer condition than fish sampled from the relatively unaffected Core Sound, North Carolina (Adams et al. 2003).

Upper NRE trawl surveys conducted in the fall of 1999 revealed large declines in CPUE after Hurricane Floyd. This decrease in catches in the fresh upper river coincided with higher catches downstream (Table 2). Fish were likely moving out of the upper estuary site because of the rapid change in salinity and subsequent formation of low oxygen zones. The largest declines occurred in bay anchovies *Anchoa mitchilli* and shrimp *Penaeus* spp., but a reduction in catch of croaker, menhaden, and blue crabs *Callinectes sapidus* was also apparent. We captured an atypical pulse of shrimp in the PS, indicating their movement into PS with the low salinity front out of the estuary (Eby and Crowder 2002, Table 2). Another indicator of movement of the shrimp out of the NRE was the increased commercial catch in PS after the storm (Burkholder et al. 2004). Responses of fish moving out of the estuary, not avoiding hypoxic zones, and demonstrating a higher prevalence of disease associated with high fall freshwater discharge associated with Hurricane Floyd in the NRE were not seen during the high spring discharge in 1998 that resulted in similar salinity values in the upper site (Eby 2001). We attributed differences in fish responses to rapid salinity changes following hurricanes, causing sudden, radical increases in freshwater exposure during late fall as the fish are physiologically preparing to migrate out of estuaries to the marine, high salinity environment (Eby 2001).

Even though immediate effects of the storm were substantial and negative, many aspects of the finfish and shellfish community have returned to normal 6 yr after Floyd. Although Hurricane Floyd had strong, short-term, system-wide effects on the fish community, the large dispersal capability of estuarine fishes allow them to move out of stressful and potentially hostile habitat conditions. Adult life stages of many of these species are offshore and buffered from many of the estuarine hurricane effects. By 2000, catches of most finfish in the NRE had rebounded to within or above their previous values, demonstrated by both trawl catches and commercial landings within or above their previous range, but blue crabs had yet to recover in 2001 (Table 2; Burkholder et al. 2004). In the PS, finfish and blue crabs in the commercial landings remained low through 2001, nearly 2 yr after the storms (Burkholder et al. 2004). If we compare landings of blue crabs (North Carolina's most valuable fishery) for the 5 yr prior to Hurricane Floyd (1995–1999) with the 5 yr after (2000–2004), landings were reduced by nearly one third (32.2%, North Carolina Division of Marine Fisheries; www.ncfisheries.net). Although chronic stressors, such as fishing or decreased habitat quality that affect demographic rates may impede the ability of the community to recover, as observed in coral reef assemblages (Hughes and Connell 1999), we do not know what factors (habitat quality, recruitment, fishing, offshore environmental changes) delayed the recovery of blue crabs. The North Carolina blue crab fishery was experiencing record landings in the late 1990s before the hurricane, but population analyses indicated the lack of sustainability of this exploitation rate (Eggleston 1998; Eggleston et al. 2004). Blue crab landings increased slightly in 2002 and 2003, but it fell in 2004 to the second lowest

TABLE 2. Catch per unit effort (number per 100 m trawled) for selected species in the study sites. nd is no data for that time. Bold indicates the month that Hurricanes Dennis and Floyd arrived.

	1998			1999			2000			2001		
	August	September	October	August	September	October	August	September	October	August	September	October
Blue crab												
NRE up	2.2	3.5	5.1	8.6	**6.0**	2.7	1.0	0.5	0.0	0.3	0.1	0.2
NRE down	0.4	0.8	2.6	0.3	**4.0**	3.4	0.0	0.1	0	nd	nd	nd
PS	nd	1.7	1.1	nd	**0.2**	0.7	1.3	0.1	0.1	0.1	0.1	0.0
Shrimp												
NRE up	0.1	2.5	0.5	1.9	**0.1**	0	0.0	1.0	0	0.0	0.2	0.2
NRE down	1.0	2.8	2.4	0.8	**6.7**	1.1	0.3	1.2	0.9	nd	nd	nd
PS	nd	1.6	1.8	nd	**1.7**	4.9	1.6	2.1	1.2	0.6	0.2	0.4
Flatfish												
NRE up	0.1	0.3	0.3	1.0	**5.9**	4.4	0.0	0.4	0.0	0.1	0.1	0.2
NRE down	0.5	1.5	1.1	0.9	**1.4**	2.4	0.3	0.2	0.1	nd	nd	nd
PS	nd	1.1	0.6	nd	**0.1**	0.5	0.3	0.8	0.1	0.2	0.1	0.2
Spot												
NRE up	8.2	16.8	7.2	63.8	**34.0**	39.4	23.0	12.9	4.6	0.7	1.0	6.7
NRE down	16.3	13.4	16.7	22	**68.4**	99.5	7	3.6	1.1	nd	nd	nd
PS	nd	4.2	3.1	nd	**6.4**	17.6	1.2	2.4	0.3	1.3	0.4	0.2
Croaker												
NRE up	8.8	19.8	31.8	10.1	**6.8**	2.4	9.2	8.5	1.5	0.6	0.5	3.0
NRE down	22.7	13.7	35.7	7.7	**15.0**	24.8	2.1	1.5	0.7	nd	nd	nd
PS	ND	6.3	7.0	ND	**4.7**	10.4	0.9	10.3	1.3	0.7	0.2	0.8
Bay anchovy												
NRE up	19.9	32.5	27.0	1.9	**0.0**	0.2	36.5	33.1	0.6	4.8	3.3	0.9
NRE down	8.5	51.4	18.9	0.4	**0.3**	0.1	6.2	2.0	0.7	nd	nd	nd
PS	nd	36.3	22.3	nd	**0.7**	0.1	18.8	31.2	9.4	1.5	1.2	1.3
Menhaden												
NRE up	20.4	16.3	12.7	1.5	**2.1**	0.1	0.1	8.1	9.3	0.1	0.0	0.3
NRE down	0.8	1.3	1.9	0	**6.7**	14.1	0	0.3	1.4	nd	nd	nd
PS	nd	0.0	0.1	nd	**0.1**	3.4	0.1	0	0	0	0	0.1

level in the past 15 yr (only 2001 was lower; www.ncfisheries.net).

Implications for Assessment and Management

Based on the findings from PS, and previous studies of hurricane effects in other large estuarine systems (e.g., Hurricane Agnes on the Chesapeake Bay in 1972; Ruzecki et al. 1976), we conclude that an increase in high rainfall, flood-producing hurricanes will lead to increased nutrient loading, higher frequencies, intensities, and spatial coverage of phytoplankton blooms, as well as expansion of low oxygen conditions. Low rainfall hurricanes will yield far lower nutrient inputs accompanied by low to moderate stimulation of primary production and phytoplankton biomass. While it can be argued that primary production and standing stocks of phytoplankton will sporadically increase as a result of the large nutrient loads accompanying hurricane floodwaters, there was little short-term evidence that the enhanced primary production of PS was translated into increased production at higher trophic levels. If anything, the increased production of phytoplankton organic matter appeared to support expanded hypoxia and anoxia in the NRE and PS bottom waters and sediments (Paerl et al. 1998, 2001). While large river discharge can enhance shelf fisheries or anadromous fishes in oligotrophic estuaries, high discharges are more likely to have a negative effect in lagoonal estuaries such as the PS. Flooding not only adds nutrients, organic materials, sediments, and toxic chemicals to the estuary, it can also enhance vertical stratification of the water column, a pre-requisite to low oxygen concentrations in the bottom water (Buzzelli et al. 2002).

Although hypoxia reduces habitat quality and can be physiologically challenging or even lethal, oxygenated refuges often exist in the surface or nearshore waters and mobile organisms evade areas of low habitat quality. In the wake of Fran and Floyd, refuge areas in the NRE were eliminated by the rapid and dramatic change in salinity. The combined effects of low dissolved oxygen and low salinity as environmental stressors were probably greater than either would present alone. Fin and mobile shellfish responded with changes in abundance, composition, and distribution that were largely species specific, but most populations were resilient to this disturbance.

Pulsed ecosystem perturbations such as hurricanes result in a spectrum of responses (Odum et al. 1995). No discernible change may occur, change may be transient, or it may be permanent. The response depends upon the turnover time of a chemical constituent, which in turn depends on the rates of transfers (e.g., physical exchange) and transformations (e.g., biogeochemical cycling) relative to its standing stock. The rapidly cycled nutrients demonstrated quick return to their nominal state, whereas recovery of the conservative property of salinity took months. The transfer rates of organisms depend on their mode of mobility. Plankton move with the flow of water and are under similar controls as chemical constituents. Nekton can either lengthen or shorten recovery times, depending on response to habitat conditions. The generation times of the affected organisms also helps determine their turnover time and recovery rate. These generation times can be hours to days for phytoplankton, months to years for benthos, and years to decades for fishes and large nekton. The net result of all of these features is a changing state of the ecosystem, with a return to some nominal state occurring incrementally, if at all. Successive pulses may cause recognizable changes in the ecosystem as the proportions of the various components are altered.

Hurricanes also complicate estuarine water quality management over longer time scales. The N load to the estuary appeared to begin to decrease in the mid 1990s, at a time when both the Neuse nutrient management strategy was enacted and the intensity of hurricane activity in the region increased (Paerl et al. 2006b). Discerning the effects of nutrient management from the flushing effects of tropical storms is a significant management challenge.

In considering potential management actions that can be taken to minimize deleterious nutrient, sediment, and other adverse effects of large hydrologic perturbations, the following options and recommendations emerge. Restore floodplain function on the landscape; restoring vulnerable floodplains will help capture and retain at least a portion of the pulse of nutrients before it reaches sensitive estuarine waters. Total (allowable) maximum daily loads (TMDL) of nutrients, sediments, and other pollutants may need to be modified to accommodate episodic hydrologic perturbations accompanying large storms, especially if their frequency is increasing. Instead of an empirically derived, static TMDL, a probability-based model with the ability to model these infrequent events may be more appropriate. Such models will help formulate the most realistic and achievable nutrient loading goals that reflect the frequencies, magnitudes, and effects of these events. With regard to fisheries management, decreases in habitat quality resulting from storm activity can decrease potential population growth rates of estuarine-dependent species. Attempts should be made to identify sensitive species (e.g., blue crabs) and adjust management (allowable harvest) to account for reduced growth potential or recovery.

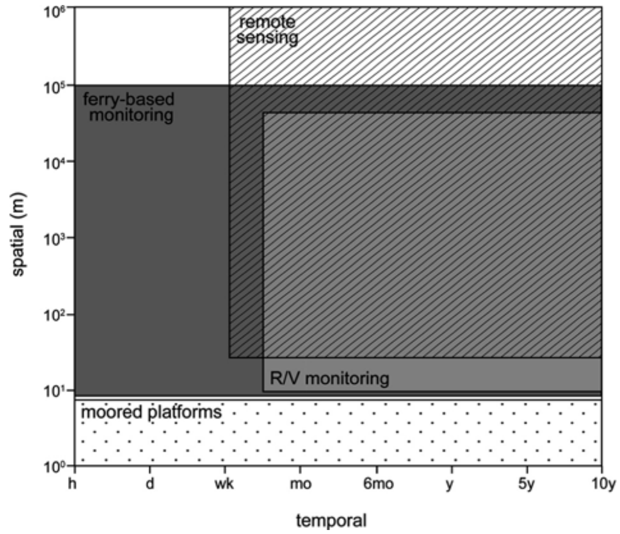

Fig. 7. Spatio-temporal coverage capabilities of monitoring and assessment tools and programs used to examine environmental responses to and effects of large hurricanes (e.g., Floyd) in a large estuary like Pamlico Sound. R/V indicates research vessels.

It has become obvious through recent events that integrated observation, research, and assessment programs for large East Coast and Gulf of Mexico estuarine systems must account for effects by large storms that result in hydrologic, nutrient, and trophodynamic alterations. First and foremost, long-term water quality and habitat monitoring programs should be in place prior to and following macroscale events. These programs should cover appropriate spatial and temporal scales, including relevant indicators and response variables capable of capturing the effects of human (i.e., nutrient, sediment) and climatic stresses and perturbations (Fig. 7). These programs must link human activities and land use with aquatic resources. Useful features of these programs should include:

- Detection and quantification of trends, changes in state equivalent to step functions, and consequences of infrequent, but large-scale events.
- Planning for event response well in advance of the approach of a storm. This is a challenge, given the uncertainties and changes in condition of both the natural ecosystems and human infrastructure associated with major storms.
- Optimizing existing infrastructure (bridges, platforms, commercial ships, ferries, and other ships of opportunity) and continuous and time-integrative sampling devices to assess water quality,

productivity, and turbidity, making use of remote sensing when possible and appropriate (Fig. 7; Harding et al. 1994; Woodruff et al. 1999).

- Assessing sediment dynamics. The sediments that have filled estuarine basins contain a wealth of paleoclimate and paleosea level information for the past 10,000 yr of coastal history (Riggs 1999; Fletcher et al. 2000; Anderson et al. 2001).
- Integrating and aggregating meteorological data on storm paths, winds, rainfall, and flooding to provide a quantitative context for large storms. In the case of PS, this analysis must consider the fact that until recently, the most active period of hurricanes in North Carolina (1930–1950s) occurred when the State's human population was much lower and the amount of landscape modification was significantly less.
- Identifying and using specific indicator communities (e.g., phytoplankton, submerged aquatic vegetation, benthic invertebrates, fish) affected by anthropogenic and climatic change.
- Linking human activities and land use within watersheds with aquatic resources. This recognizes the extensive feedbacks between humans and their ecosystems. Storm disruption of these feedbacks results in natural systems being affected in ways different from a nonhuman influenced state, and humans having important goods and services altered.

Appropriate modeling of watershed, water quality, habitat, and fisheries effects of intense storms should also be a key component of an integrated assessment program and is an important tool for synthesizing information and providing options for environmental management. For the PS basin, there are models for land use effects on nutrients (Stanley 1988; Stow et al. 2001), transfer of materials through soils (Chescheir et al. 1996), hydrodynamics (Luettich et al. 2002), water quality (Reckhow 1999; Bowen and Hieronymus 2000; Borsuk et al. 2003a,b), and fisheries (NC DENR, Division Marine Fisheries). These models could be used to address different aspects of storm effects, but most if not all have major limitations. The recent spate of hurricanes produced conditions beyond those for which most models have been constructed or validated. Extension of model predictions to cover a wide range of infrequent and extreme conditions and validation of those predictions are both challenges to, and requirements of, an effective assessment program.

A critically important component of an effective and broadly used integrated assessment program is cooperation and coordination among state, federal, and private research and monitoring entities. The North Carolina experience since 1999 proved that a strong working relationship among these entities was essential for sharing resources and expertise and using research aimed at understanding and managing a large system affected by interacting human and climatic forcing features. Cross-cutting multidisciplinary, multiagency approaches and analyses provide the necessary broad perspective needed to assess ecological change in a system that simultaneously affects and is affected by human economics and cultural activities and values.

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