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Anthropogenic and climatic influences on the eutrophication of large estuarine ecosystems

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Abstract

We examined the effects of anthropogenic and climatic perturbations on nutrient–phytoplankton interactions and eutrophication in the waters of the largest estuarine systems in the U.S.A., the Chesapeake Bay (CB), Maryland/Virginia, and the Neuse River Estuary/Pamlico Sound (NRE/PS) system, North Carolina. Both systems have experienced large post-World War II increases in nitrogen (N) and phosphorus (P) loading, and nutrient reductions have been initiated to alleviate symptoms of eutrophication. However, ecosystem-level effects of these nutrient reductions are strongly affected by hydrologic variability, including severe droughts and a recent increase in Atlantic hurricane activity. Phytoplankton community responses to these hydrologic perturbations, including storm surges and floods, were examined and when possible, compared for these systems. In both systems, the resulting variability in water residence time strongly influenced seasonal and longer-term patterns of phytoplankton biomass and community composition. Fast-growing diatoms were favored during years of high discharge and short residence time in CB, whereas this effect was not observed during high discharge conditions in the longer residence time NRE/PS. In the NRE/PS, all phytoplankton groups except summer cyanobacterial populations showed decreased abundance during elevated flow years when compared to low flow years. Although hurricanes affected the CB less frequently than the NRE/PS, they nonetheless influenced floral composition in both systems. Seasonally, hydrologic perturbations, including droughts, floods, and storm-related deep mixing events, overwhelmed nutrient controls on floral composition. This underscores the difficulty in predicting seasonal and longer-term phytoplankton production and compositional responses to nutrient input reductions aimed at controlling eutrophication of large estuarine ecosystems.

Nearly half the world's human population resides within 100 km of the coast, and this proportion is expected to continue to rise in the foreseeable future (Vitousek et al. 1997; National Research Council 2000). Large increases in pollutant discharge have accompanied the agricultural and urban development of coastal watersheds (Peierls et al. 1991; Hopkinson and Vallino 1995; Boesch et al. 2001). Deterioration of estuarine ecosystems that process this burgeoning nutrient load is accelerating, yet there is a paucity of information on how primary producer and higher-ranked consumer communities are being altered. Understanding how human-induced ecological change (e.g., declining biodiversity, water quality, and fisheries resources) interacts with and affects the structure and function of large estuarine ecosystems adjoining coastal waters is a major research challenge. The most pervasive and problematic anthropogenic influences on these waters include nutrient enrichment (Nixon 1995; Boesch et al. 2001) and decreases in grazer and higher-consumer populations (e.g., shellfish, finfish) (Jackson et al. 2001). Although there is considerable debate over the extent to which ''bottom-up'' (nutrient enrichment) and ''top-down'' (grazing) processes influence ecological change, their combined effects have, in many instances, dramatically increased estuarine and coastal primary production and phytoplankton biomass, promoting an excess accumulation of organic matter, or eutrophication (Nixon 1995). Increases in phytoplankton production affect nutrient (carbon, nitrogen, phosphorus, and silicon) cycling, water quality, and ecosystem health (Smetacek et. al 1991; Conley 1999). Increased nutrient loading to coastal waters has been the primary causative factor for increased algal blooms (Paerl 1988), decreases in water clarity (Cloern 2001), and expanded hypoxia (Rabalais et al. 1996).

Estuarine and coastal ecosystems are also influenced by seasonal and multi-annual hydrologic variability (e.g., droughts, wet periods, and El Niño vs. La Niña years) and shorter-term episodic perturbations such as floods, tropical

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storms, and hurricanes, the intensity and frequency of which appear to be increasing (Goldenberg et al. 2001). The combined effects of coastal population growth and a recent rise in Atlantic (and possibly Pacific) hurricane activity (Goldenberg et al. 2001) is a particularly troubling formula for the alteration of coastal watersheds and their receiving waters.

During 1972, Tropical Storm Agnes delivered record amounts of rainfall and caused catastrophic flooding in the Chesapeake Bay (CB) (Fig. 1). The ecological consequences of this event, including adverse effects on water quality, disruption of fisheries habitat, and depressed finfish and shellfish catches, persisted for a number of years (Ruzecki et al. 1976). More recently (fall 1999), Hurricanes Dennis, Floyd, and Irene inundated coastal North Carolina with up to 1 m of rainfall, causing a 100–500-yr flood (depending on location) in the watershed of Pamlico Sound (PS), the second largest estuary in the U.S.A. and a key nursery for the mid- and southeast Atlantic fisheries (Fig. 1). Sediment- and nutrient-laden floodwaters displaced over 80% of the Sound's volume, depressed salinity by more than 70%, and accounted for half the annual nitrogen (N) load to this N-sensitive system (Paerl et al. 2001; Peierls et al. 2003) (Fig. 2). The biogeochemical and ecological effects of this sequence of hurricanes included a threefold increase in algal biomass, hypoxic (<4 mg L^{-1} of O_2) bottom waters accompanied by changes in nutrient cycling, altered fish distributions, fish catches, and increased fish disease (Paerl et al. 2001, Tester et al. 2003; Adams et al. 2003). Almost exactly 4 yr later (September 2003), Hurricane Isabel made landfall in the same region (Fig. 1), crossed the PS as well as the Tidewater–CB region to the north, breached North Carolina's Outer Banks, and caused large-scale hydrologic (storm surges, flooding) and nutrient perturbations (enhanced runoff, washout of coastal developments, marinas, wetlands, and farmland) throughout the mid-Atlantic region.

Although large estuarine ecosystems exhibit a range of biogeochemical and trophic responses to short- and longer-term hydrologic changes, they are also affected by multiple stressors, including nutrients and other pollutants, changes in light regime (turbidity), temperature, mixing, and circulation, which are changing in time and space. Over time these stressors may alter the ecological characteristics of these large systems. For example, the delivery of anthropogenic nutrients and other pollutants to coastal waters is in a highly dynamic state, as development and accelerated loading and management loading reductions are occurring concurrently (Nixon 1995; Boesch et al. 2001; Elmgren and Larsson 2001). This may result in long-term changes in estuarine and coastal biogeochemical processes and trophic function. Integrating climatic and anthropogenic perturbations is difficult but essential to understand and manage these ecosystems.

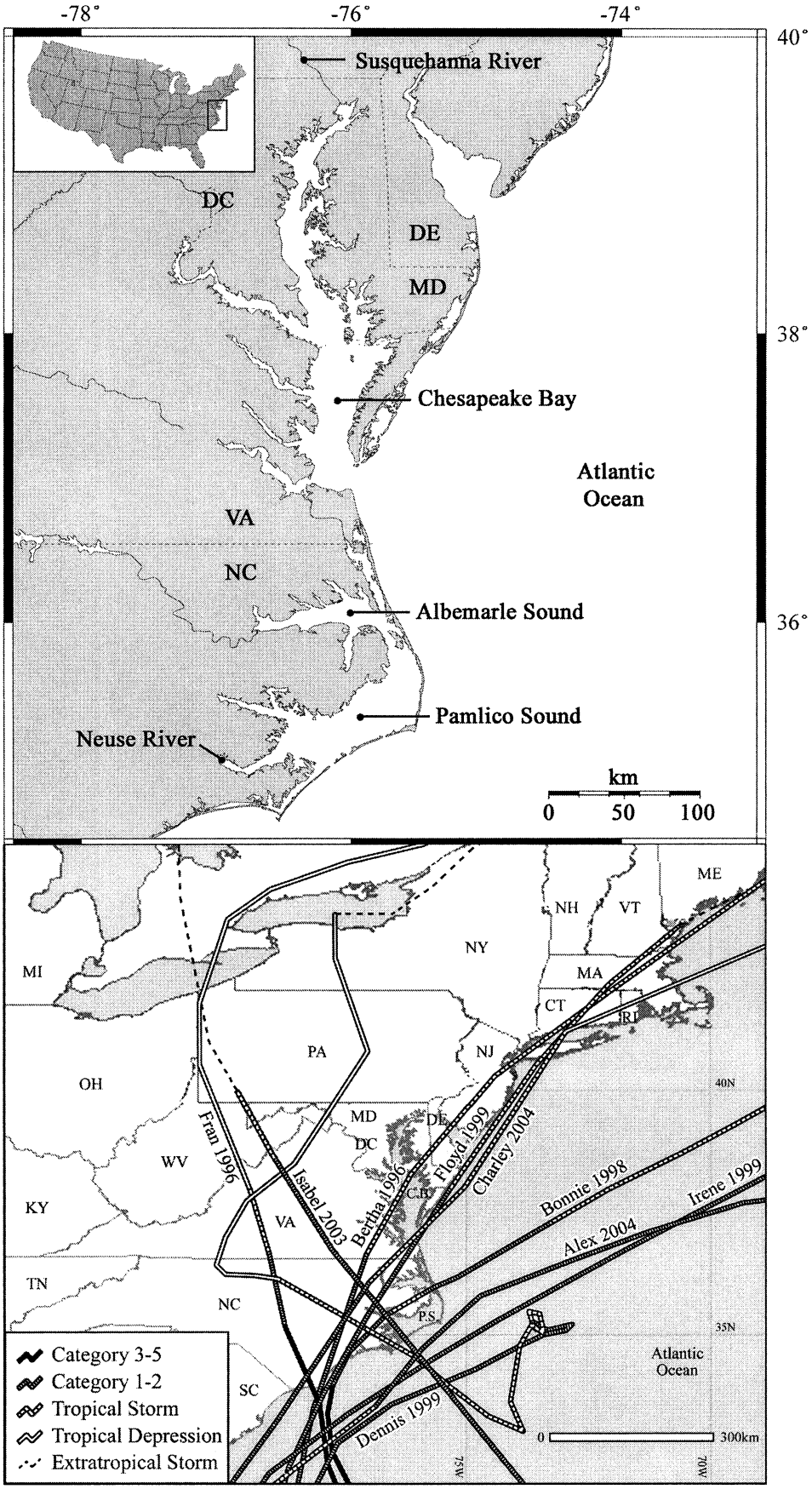
The effects of human and natural perturbations are readily detected at the microbial primary producer level, specifically phytoplankton, level where large amounts of ecosystem energy and nutrient flows are mediated. Phytoplankton generally have fast growth rates and exhibit a high degree of sensitivity, and in certain cases specificity, to an array of pollutants and environmental perturbations, making them useful indicators of ecological change.

The goal of this contribution was to examine and compare how nutrient enrichment and climatic perturbations interact to control phytoplankton composition, distribution, and activity in the two largest estuarine ecosystems in the U.S.A., the Chesapeake Bay system (CB), Maryland–Virginia and the Neuse River Estuary-Pamlico Sound system (NRE/PS), North Carolina (Fig. 1). Both systems have well-documented histories of such anthropogenic and natural perturbations.

Anthropogenic nutrient stressors: Their interactions with hydrology

Nitrogen (N) availability commonly controls phytoplankton and higher plant biomass and primary production in estuarine and coastal waters (Ryther and Dunstan 1971; Nixon 1992). Excessive N loading, much of it anthropogenic, is a chief causative agent of coastal eutrophication (Nixon 1995; Paerl 1997). Symptoms include phytoplankton blooms, which may accumulate as partially or ungrazed organic matter, providing the ''fuel'' for large-scale oxygen consumption and depletion in bottom waters and sediments. This cascading chain of events is particularly problematic in stratified bottom waters, where oxygen is not readily replenished from the atmosphere (Fig. 3). Under these conditions, persistent low oxygen or hypoxic conditions (<4 mg L^{-1} of O_2) can alter nutrient (N, P, and trace metals) cycling (Paerl et al. 1998; Conley 1999; Rabalais and Turner 2001) and promote fish disease and mortality (Diaz and Rosenberg 1995).

The composition, concentration, and delivery of nutrients depend on how the watershed has been modified by agricultural, urban, and industrial activities (Hopkinson and Vallino 1995; Paerl 1997). Futhermore, the timing, location, and intensity of storms and associated rainfall amounts also affect nutrient makeup and discharge to coastal waters (Paerl 1997). Freshwater discharge delivers nutrients to the coastal zone and determines the hydrologic properties of the water column, including vertical stratification, water residence time, salinity, turbidity, and clarity. All of these properties interact to mediate productivity, nutrient cycling, dissolved oxygen dynamics, and habitat condition (Figs. 3, 4). Residence time plays a critical role in determining the availability and utilization of nutrients by phytoplankton. As discharge also controls transport of phytoplankton through these systems, it interacts with nutrient supply to control growth, competition, and succession of the phytoplankton community. For example, high rates of freshwater discharge reduce both salinity and residence time. These conditions generally favor fast-growing phytoplankton such as chlorophytes (green algae) and various flagellates, members of which have been shown to demonstrate optimal growth under reduced salinity conditions (Pinckney et al. 1999). In contrast, low discharge promotes longer water residence times, favoring slower-growing taxa, including dinoflagellates and cyanobacteria. The influences of hydrologic forcing in relation to nutrient inputs, seasonality, and climatic variability were explored and compared for both of these large estuarine ecosystems.


-78°
-76°
-74°
40°
38°
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Susquehanna River
DC
DE
MD
Chesapeake Bay
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km
0 50 100
ME
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VT
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MD
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DC
WV
KY
VA
TN
NC
SC
C.B.
P.S.
Fran 1996
Isabel 2003
Bertha 1996
Floyd 1999
Charley 2004
Bonnie 1998
Irene 1999
Alex 2004
Dennis 1999
40N
35N
75W
70W
Atlantic Ocean
0 300km
Category 3-5
Category 1-2
Tropical Storm
Tropical Depression
Extratropical Storm

Hydrologic effects on estuarine phytoplankton composition

The different effects of nutrient and hydrologic changes on phytoplankton community composition were examined and compared in the CB and the NRE/PS estuarine complexes (Fig. 1). Diagnostic chlorophyll and carotenoid photopigments, measured by high-performance liquid chromatography coupled to a photodiode array spectrophotometer, were used as indicators of major phytoplankton taxonomic groups (PTGs), including diatoms, dinoflagellates, chlorophytes, cyanobacteria, and cryptomonads (Paerl et al. 2003). These photopigments were measured from water samples collected from the CB (1995–2000) and from the NRE/PS (NRE: 1994–present; PS: 1999–present) as part of ongoing monitoring studies. A statistical procedure, ChemTax (Mackey et al. 1996), was applied to these photopigment concentrations to partition total phytoplankton biomass, as chlorophyll *a* (Chl *a*), into the PTGs and quantify the relative and absolute contributions of each group. Diagnostic photopigment markers included Chl *b* and lutein (chlorophytes), zeaxanthin, myxoxanthophyll and echinenone (cyanobacteria), fucoxanthin (diatoms), peridinin (dinoflagellates), and alloxanthin (cryptomonads).

Seasonal or hurricane-induced (or both) variations in river discharge, and hence residence time, affect PTG dynamics in the CB and NRE/PS systems as a function of the interactions of freshwater discharge rates, volume and size of the receiving system (which affect water residence time), and resident phytoplankton community composition and growth characteristics. Multi-annual monthly means of streamflow rates for the largest tributaries of the CB (Susquehanna River) and PS (Neuse River) are shown in Figure 5. Although Susquehanna River flow is significantly greater in magnitude than Neuse River flow, overall, the discharge patterns of these two rivers were similar, reflecting regional seasonal wet and dry periods, including very wet spring years (e.g., 1994 and 1998) as well as severe summer droughts (e.g., 1997–1999, 2001–2002). However, large differences in discharge patterns were also apparent, depending on the occurrence of localized storm events. For example, during the early fall of 1999, hurricanes Dennis and Floyd severely affected the Neuse River watershed while the Susquehanna watershed was relatively unaffected (Fig. 5). The potential effects of high versus low flow seasons and years as well as individual events (e.g., the hurricanes of 1999) are reflected in these freshwater flows entering the respective receiving estuaries (Fig. 5).

The phytoplankton composition of the CB and the NRE/PS systems varied in response to nutrient enrichment, droughts (reduced flushing combined with minimal nutrient inputs), and elevated tropical storm and hurricane activity (high flushing accompanied by elevated nutrient inputs). For example, in the CB, diatom abundance was increased during high flow years, regardless of season, when compared to low flow years (Fig. 6). We hypothesize that this selective effect is due to the fast growth rates and enhanced nutrient uptake rates exhibited by this group under these conditions (Malone et al. 1988; Harding 1994; Pinckney et al. 1999). Contrary to the CB, diatoms in the NRE were reduced in abundance during high flow years, regardless of season, when compared to years characterized by reduced flow conditions. A possible explanation for this differential effect is that under high flow conditions, water residence time in various segments of the CB is substantially shorter (1–3 wk) than those in the NRE/PS (2 wk to 2 months). Under the relatively shorter residence time conditions typifying the CB, diatoms will most effectively compete, as they tend to have faster doubling times ($<$0.7 d) than other PTGs (generally 1–2 d). Furthermore, this effect may be due to differences in the native phytoplankton composition that characterize these two systems. Diatoms are generally predominant in the CB, whereas all five taxonomic groups are typically found in similar proportions in the NRE ($\sim$20%).

Seasonality and interannual climatic differences (i.e., wet vs. dry years) strongly affect hydrologic conditions and PTG composition in these estuarine systems. Dinoflagellates showed greater competitive abilities in the nutrient-enriched spring months under moderate to high flow conditions in the CB. This effect is most noticeable in spring in the CB as opposed to summer and fall, when overall flows are lower and residence times appear to be long enough for other PTGs to increase in abundance. During summertime, flow has less of an effect in promoting dominance of either diatoms or dinoflagellates in each system, whereas during fall, high flow promotes diatom dominance in CB but not in the NRE/PS. In contrast, cyanobacteria tend to be most dominant in summertime in both systems, when low flow generally predominates and the distinction between low and high flow is minimized (Fig. 6). With the exception of summertime cyanobacteria populations, all PTGs in the NRE (and thus total Chl *a* concentrations) decreased during high flow years when compared to low flow years. On a seasonal basis, changes in flow regimes co-occur with changing irradiance and temperature patterns. In addition, zooplankton and benthic invertebrate (shellfish) and herbivorous fish (e.g., menhaden) grazing influence PTG abundance and dominance, thus creating a complex set of interactions with residence time that control PTG community structure.

Susquehanna River flow (SRF) is an important driver of seasonal to interannual hydrologic variability in the CB (Fig. 5) (Malone et al. 1988; Fisher et al. 1988; Boynton and Kemp 2000). Summer phytoplankton dynamics in CB, when SRF was low, were characterized by low biomass (compared

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Fig. 1. Upper panel: Map of the U.S. mid-Atlantic coast showing (from north to south) the Susquehanna River, the Chesapeake Bay, the Albemarle Sound, the Pamlico Sound, and the Neuse River. The abbreviations NJ, DC, DE, MD, VA, and NC refer to states or major cities bordering these systems. Lower panel: The tracks and intensities (Saffir–Simpson scale) of major hurricanes that have crossed this region since 1996. They include: Hurricanes Bertha and Fran (1996), Bonnie (1998), Dennis, Floyd, and Irene (1999), Isabel (2003), and Charley and Alex (2004).

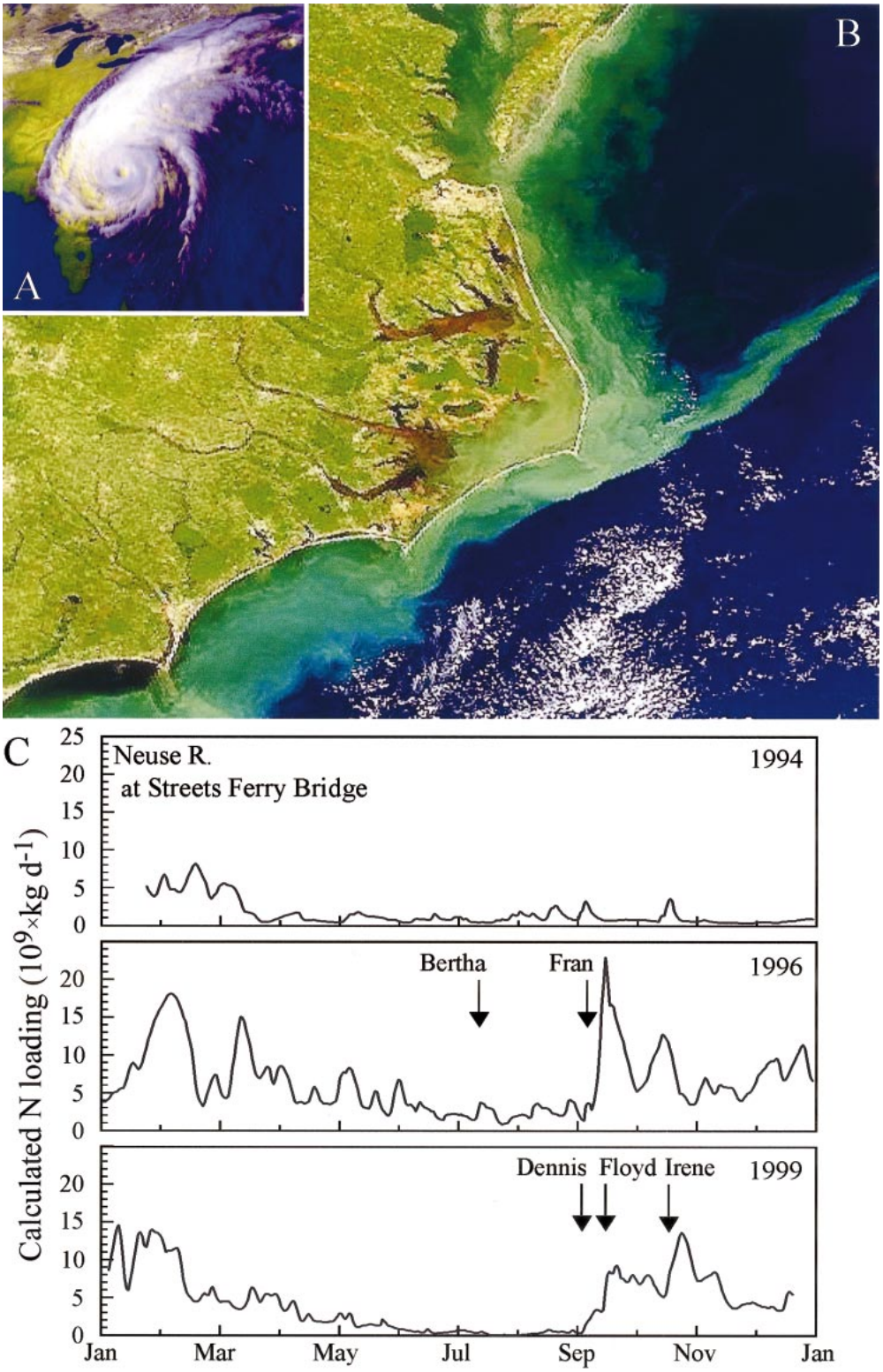

Fig. 2. (A–B) The Albemarle–Pamlico Sound Estuarine System and adjacent Atlantic Ocean coastal waters of eastern North Carolina, U.S.A., as observed by ocean color satellite remote sensing system SeaWiFS (photos courtesy of NASA). (A) Landfall of Hurricane Floyd along the North Carolina coast, 16–17 September 1999. (B) Approximately 1 wk after Floyd, 23 September 1999. Note the brown-stained floodwaters discharging into Pamlico Sound and overflowing into the coastal Atlantic Ocean. Some of the turbid, sediment-laden water is being carried out to sea by the Gulf Stream, which passes closely by the North Carolina coastline (from south to north). (C) Total nitrogen (dissolved and particulate inorganic and organic) loading calculated from discharge and concentration at the entrance to the Neuse River Estuary (Streets Ferry Bridge) during nonhurricane and hurricane (1996, 1999) years. Typically, a large percentage of annual N loading in nonhurricane (1984) years occurs during the rainy late-winter early-spring period from January through early-May. This is shown for a

to spring) and a phytoplankton assemblage dominated by small and flagellated forms (Marshall and Lacouture 1986). High SRF in the summer resulted in elevated total biomass and an increased contribution of diatoms, which contrasted with average low-flow summer conditions when diatoms were approximately equal in abundance with cyanobacteria, cryptophytes, and dinoflagellates (Fig. 6). In CB, as in the NRE/PS, seasonal and interannual variability in flow presents a dynamic backdrop against which indicators of anthropogenic influence must be evaluated.

Hydrologic variability interacts with nutrient-enriched conditions to control seasonal and interannual patterns and fates of phytoplankton communities. In the CB, strong seasonal signals in phytoplankton dynamics included accumulations of high biomass during the spring diatom bloom (Fig. 6), much of which sediments out of the photic zone during the spring–summer transition (Malone 1992; Malone et al. 1996; Harding et al. 2002). This flux of phytoplankton-based organic matter to the lower layer of the CB water column is retained by upper-Bay estuarine flow and is partially separated from the upper water column by strong salinity stratification (Kemp and Boynton 1984; Boicourt 1992). Microbial decomposition of this organic material supplies a significant fraction of nutrients that supports elevated summer productivity and contributes to bottom-water anoxia, a persistent feature during summer (Malone 1992).

Location is also an important determinant of PTG composition in these systems; however, it appears to interact less with flow and discharge than seasonality. For example, in CB diatoms are dominant in high-flow years regardless of location, whereas dinoflagellates increase in dominance at both upper and mid, but not lower, estuarine locations (Malone et al. 1988; Malone 1992). The lack of uniformity of dinoflagellate dominance along the entire estuary during low-flow years may be due to the increasing influence of salinity under low-flow conditions (Malone et al. 1988). Downstream locations typically exhibit high salinity during low-flow years, conditions that are unfavorable for common bloom-forming estuarine dinoflagellate species. This effect is less dampened in the NRE, which maintains lower salinity (<20) than CB even at its lower estuarine location, because of the buffering effects of the downstream PS, which acts as a large lagoonal, mesohaline reservoir. For the same reasons, the lower NRE location is well-suited for supporting periodic dinoflagellate blooms when flow is enhanced (e.g., late-winter *Heterocapsa triquetra* blooms) (Fig. 7) (Paerl et al. 1995), as the system typically maintains its lagoonal, nontidal nature, ensuring favorable (to dinoflagellates) oligo- to mesohaline conditions downstream.

Nutrient-enriched conditions interact with both hydrologic discharge and seasonality to determine PTG composition in these systems. In CB, studies have emphasized that the Bay, as we know it today, is in a more eutrophic state than it was only 50–100 years ago (c.f., Boesch et al. 2001). Eutrophication of CB, as well as the NRE/PS, is strongly expressed in several aspects of phytoplankton dynamics. Declining diatom diversity and a shift toward dominance by pelagic diatoms preserved in CB sediment cores indicate accelerating eutrophication since the time of European settlement (Cooper and Brush 1991). Within the last 50 yr, an increasing trend in CB Chl *a* concentrations was detected that paralleled increased N loading that occurred over the same time period (Harding 1994; Harding and Perry 1997). These studies demonstrated that the effects of anthropogenic activities in the CB watershed have affected the ecosystem in ways that are observable over long time scales (tens to hundreds of years). They also emphasized the potential for natural variability to cause similar changes to the phytoplankton as might be anticipated as a result of anthropogenic activities.

When large storms and hurricanes affect both the CB and the NRE/PS, PTG responses to these sudden and large hydrologic perturbations can be large and distinct from the longer-term seasonal shifts in flow and residence time. The individual and cumulative effects of these episodic events can be seen in both CB and the NRE/PS (Figs. 6 and 7). Decreases in the occurrence of winter–spring dinoflagellate blooms and increases in the abundance of chlorophytes coincided with an increased frequency and magnitude of tropical storms and hurricanes since 1996 in the NRE/PS (Fig. 7). Interestingly, this effect was not evident in CB, which was not nearly as severely affected by hurricanes in 1996 (Fran) or 1999 (Dennis and Floyd) (data not shown). The relatively slow growth rates of dinoflagellates may have led to their reduced abundance during the extremely high river discharge events that accompanied landfall of Fran and subsequent hurricanes in the NRE/PS watershed. In addition, changes in residence time may influence the composition and interactions of PTGs and their grazers, including micro- and macrozooplankton, and larval and juvenile fish. Such shifts will affect trophic transfer pathways and efficiencies, with ramifications for food web structure, function, and carbon and nutrient (N, P, Si, minor nutrients) cycling (Kleppel and Burkart 1995; Turner et al. 1998, Conley 1999). Phytoplankton composition in the NRE/PS estuarine system has changed since 1995, largely in response to persistent periods of flooding and elevated freshwater discharge resulting from the 1996 and 1999 hurricanes. Such changes are not nearly as evident in CB.

Although these results indicate that physical–chemical forcing features strongly influence estuarine phytoplankton dynamics mediating eutrophication, can we manipulate these features to control this process in these large ecosystems? The answers to this question depend on the scale of the system and the availability of freshwater. Aside from aqua-

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relatively dry year (1994), as well as for more ''normal'' years (1996 and 1999). During drought conditions (early summer of 1999), very little N loading takes place. Also shown are N inputs due to hurricanes that affected the Neuse River Estuary watershed with heavy rainfall. During 1996, Hurricanes Bertha (category 2) and Fran (strong category 3) affected the watershed, whereas in the summer–fall of 1999, Dennis (category 2), Floyd (strong category 3), and Irene (category 2) sequentially affected the watershed within a 6-wk period. Note that the amounts of N loading due to large hurricanes (Fran and Floyd) accounted for large percentages of annual N loading to this estuary.

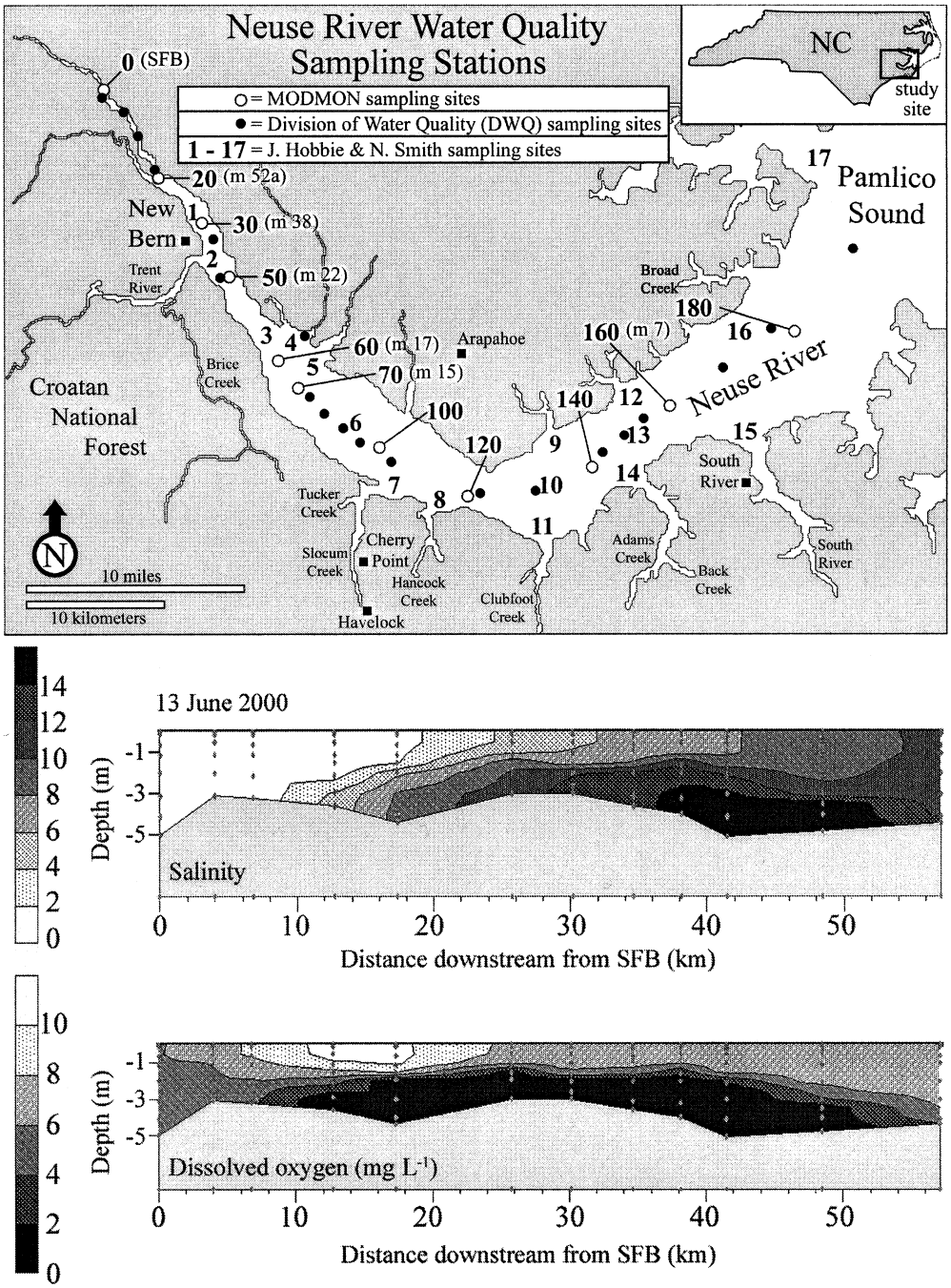

Fig. 3. Upper panel: Map of the Neuse River Estuary showing the historic and currently monitored water quality stations. Lower panel: Contour plots of water column salinity and dissolved oxygen along a vertical axial transect of the eutrophic Neuse River Estuary, North Carolina, ranging from the freshwater head of the estuary (left hand side) to the mesohaline entrance into Pamlico Sound. The contours were generated from profiles collected on 13 June 2000 as part of the Neuse River Estuary Modeling and Monitoring Program, ModMon; the profile data points are indicated by dots on plot.

culture and retention ponds, small lagoons, and reservoirs, or a few large river systems where sufficient water is available for hydrologic manipulations such as flushing of nutrient-enriched impoundments, reservoirs, estuaries, coastal lagoons, and embayments (e.g., Mississippi River Delta), it is generally difficult to control water quality and eutrophication solely by controlling freshwater discharge. In most coastal watersheds, flow controls are not likely to be technically or economically feasible and realistic because large-scale, unpredictable weather events such as hurricanes and droughts

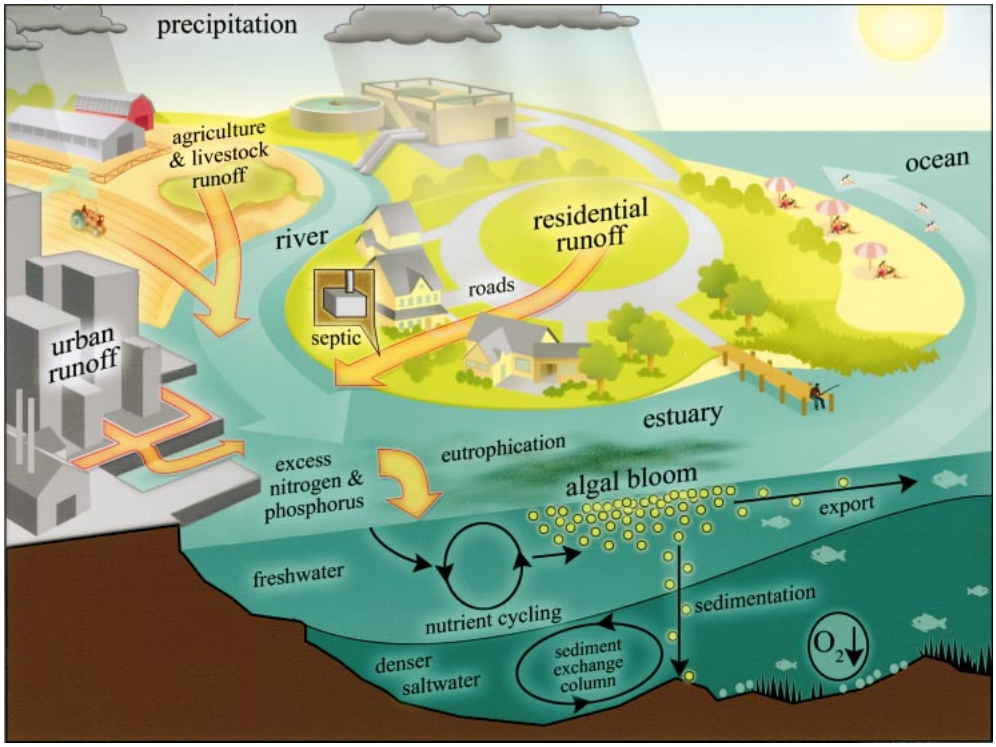

Fig. 4. Conceptual diagram showing the various watershed and airshed anthropogenic nutrient sources, their input to estuarine and coastal waters via freshwater discharge, the establishment of hypoxia due to freshwater overlaying denser saltwater, and the stimulation of primary production (eutrophication) and algal booms due to coastal nutrient enrichment. Note the linkage between nutrient-enriched primary production and hypoxia as phytoplankton sink into stratified bottom water. Also, note the potential negative effects of hypoxia on bottom-dwelling finfish and shellfish and submersed aquatic vegetation communities.

tend to dominate the hydrologic characteristics of these systems. This leaves nutrient and sediment inputs as the chief controllable variables.

Biology and scaling: Their roles in estuarine and coastal eutrophication

Primary productivity and growth responses to nutrient inputs and hydrologic modifications can be nonlinear, may involve long lag periods, and may be insensitive to short-term (days–weeks) nutrient reductions. In part, this is because primary producer communities are comprised of metabolically coupled assemblages of microorganisms and higher-ranked flora and fauna, whose interactions promote effective utilization, retention, and recycling of nutrients and energy. More often than not, phytoplankton and benthic microalgal species exhibit maximum growth rates in the presence of bacterial, protozoan, and other microbial consorts (Paerl and Pinckney 1996). These mutually-beneficial, or consortial, associations appear to be the rule rather than the exception in nature (Paerl and Pinckney 1996). Furthermore, they play vital roles in the development, maintenance, and proliferation of planktonic algal blooms and benthic microbial ''fouling'' communities, common manifestations of coastal eutrophication (Paerl 1988; La Pointe 1997; Paerl and Kuparinen 2002). Once established, consortia retain and recycle nutrients among their constituent microbial members, thereby keeping nutrients from being ''lost'' by physical processes such as diffusion, advection, sedimentation, or by biogeochemical transformations like denitrification. We suggest that consortial conservation of nutrients has evolved in response to the pulsed, episodic manner by which nutrients are often delivered to estuarine and coastal water bodies after storms and anthropogenic nutrient discharges. By using effective uptake, retention (e.g., intracellular storage capabilities), and consortial exchange and recycling mechanisms, bloom species can thrive and persist on pulsed sources of nutrients that may have entered the system weeks or months before bloom conditions prevailed. Conversely, reductions of nutrient inputs during optimal growth and bloom periods may not have the immediate desired effects, namely rapid reduction or control of blooms and epiphytic microalgal growth. Over longer time scales (i.e., months, seasons, and years), persistent nutrient reductions are likely to have beneficial effects. Therefore, the ''payoff'' from nutrient reductions may not be realized until subsequent years or even decades.

The homeostatic modulating roles that consortia play in productivity and growth responses to variable nutrient enrichment must be examined and evaluated in the context of interacting bottom-up physical–chemical drivers such as hydrologic, nutrient, light, temperature regimes, and top-down controls exerted by grazing and predation. These interactions

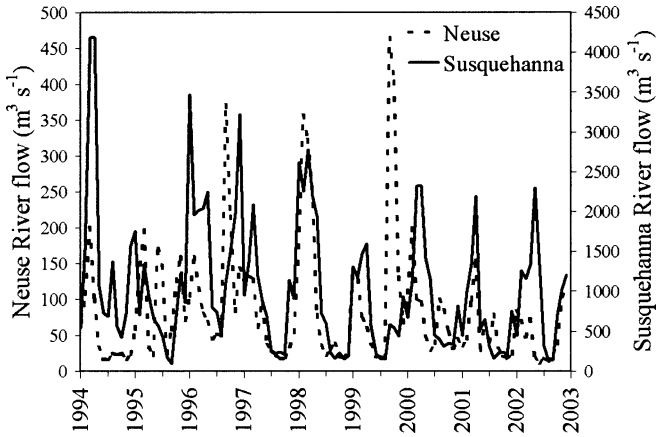

Fig. 5. Monthly mean river flow rates of the major tributaries of the Chesapeake Bay (Susquehanna River) and the Pamlico Sound (Neuse River) during the 1994–2003 period. Values were obtained from gauging stations monitored by United States Geological Survey in the Susquehanna River at Conowingo, Maryland (USGS Station No. 1578310) and in the Neuse River at Kinston, North Carolina (USGS Station No. 2089500).

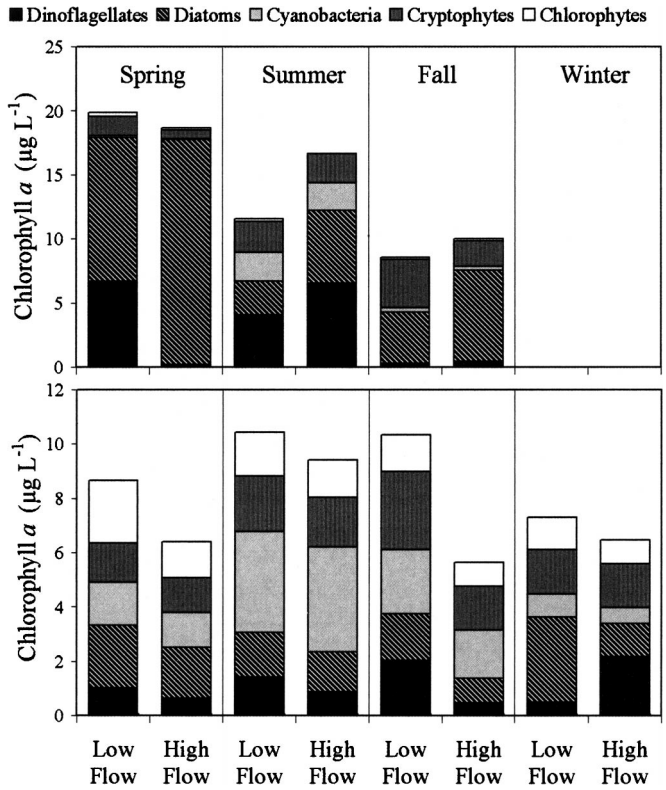

Fig. 6. Seasonal means of phytoplankton community structure and biomass in the Chesapeake Bay (upper panel) and in the Neuse River (lower panel) during low and high flow years. Seasons are defined by month (spring = March through May, summer = June through August, fall = September through November, and winter = December through February). Low-flow years represent years with mean river flow rates below the long-term mean, whereas high-flow years represent years with mean river flow rates above the long-term mean (1968–2000 for the Susquehanna River and 1931–2002 for the Neuse River). Years defined as low-flow years in the Chesapeake Bay were 1995, 1997, 1999, and 2000, whereas 1996 and 1998 were designated as high-flow years. In the Neuse River, low-flow years included 1994, 1997, 2000, 2001, and 2002, whereas high-flow years were defined as 1995, 1996, 1998, and 1999. Biomass (Chl *a*) is represented by the total length of each bar. Bar portions represent the fraction of Chl *a* attributable to different taxonomic groups as determined from photopigment and ChemTax analyses. Chesapeake Bay was not sampled during winter months.

influence nutrient availability, recycling, and stoichiometric controls on production, biomass, species composition, and resultant eutrophication dynamics on the larger ecosystem scale.

P versus N controls of eutrophication in the estuarine–coastal continuum

Because estuarine and coastal ecosystems are hydrologic and biogeochemical continua of freshwater and marine environments, they represent a unique and formidable challenge to formulating nutrient reductions aimed at controlling eutrophication. At upstream freshwater locations, P is often the growth-limiting macronutrient (Boynton et al. 1982; Larsson et al. 1985). At the freshwater–saltwater transition zone, P and N may both be colimiting, while the downstream mesohaline, polyhaline zones are usually N limited (Fisher et al. 1988; Rudek et al. 1991; Elmgren and Larsson 2001). The spatial and temporal overlaps of N and P limitation vary widely, and are closely controlled by hydrology, morphometry, geography, and climate.

Numerous studies have examined nutrient limitation along the freshwater–marine continuum (c.f., Ryther and Dunstan 1971; Pennock et al. 1994; D'Elia et al. 1986). These studies have provided the impetus and quantitative basis for nutrient input reduction strategies. There are numerous freshwater "success stories" in which appropriate input reductions have helped to alleviate the most visible and problematic symptoms of eutrophication, including phytoplankton blooms, hypoxia, and losses of fisheries and recreational habitat (Edmondson 1970; Schindler 1978; Paerl 1988). However, the estuarine–coastal continuum encompasses a broad range of varying hydrology, salinity, and nutrients, such that reduction of one nutrient may not necessarily lessen eutrophication along the entire length of an estuary.

One example is the effect of P control in estuaries where nutrient limitation shifts from P in the freshwater to N in the more saline downstream waters. Starting in the 1960s and continuing throughout the 1980s, the identification of P as the limiting nutrient in freshwater ushered in a period of aggressive P reductions in the watersheds of lakes and rivers draining into estuaries (Likens 1972, Schindler 1978; Vollenweider 1982). This trend was highlighted by a P-detergent ban and advances in wastewater P treatment in the 1970s–1990s in North America, Europe, and parts of Asia, the combined effect of which was marked reductions of P loading in the headwaters of many estuaries. Parallel N reductions were generally not undertaken at that time, largely because eutrophication problems in downstream N-limited waters were either not recognized, detected, or ignored, i.e., the solution to pollution was dilution. Not until the mid-1980s

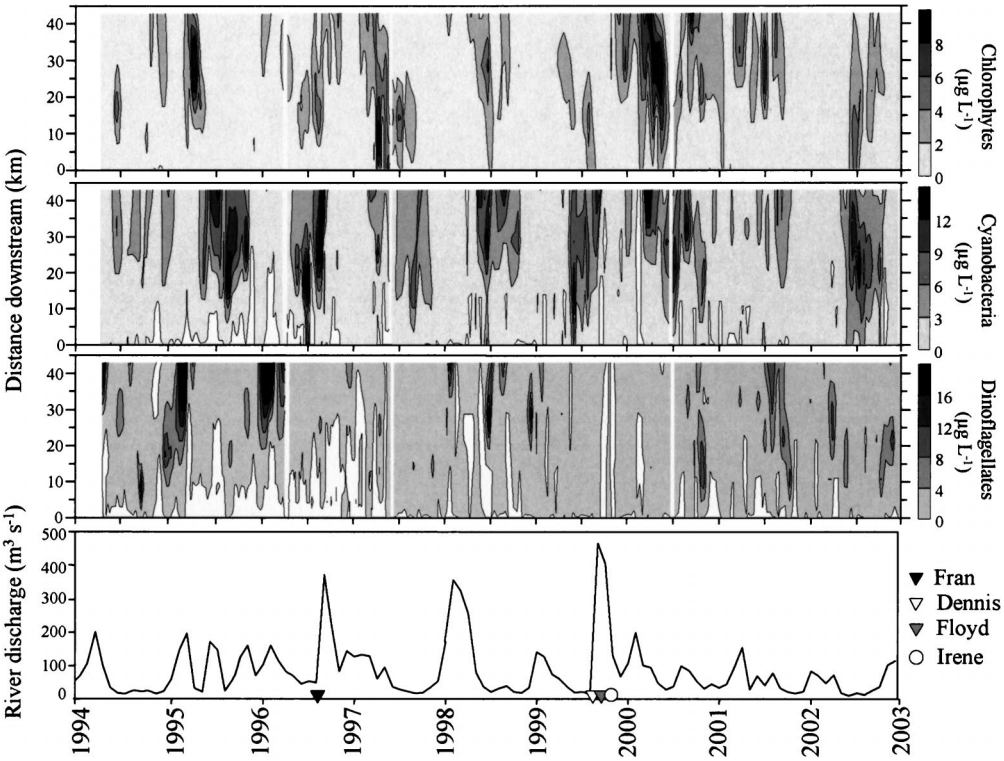

Fig. 7. Surface concentrations of chlorophyll *a* (μg L^{-1}) contributed by chlorophytes, cyanobacteria, and dinoflagellates along the upper and middle regions of the Neuse River Estuary (1994–2002). Values were determined from ChemTax analyses of high-performance liquid chromatography-derived diagnostic photopigment concentrations. Data were collected biweekly and were temporally and spatially extrapolated. White areas indicate instances when data were not collected. ChemTax data were plotted along with freshwater discharge at the head of the estuary. The dates of landfall of the four major hurricanes that have significantly affected flow since mid-1996 are shown.

were the broader ramifications of N-driven eutrophication and benefits of N reductions widely realized (cf. Boynton et al. 1982; Fisher et al. 1988). Even then, there was considerable reluctance to tackle the ''nitrogen problem'' as aggressively as that of P overenrichment in upstream freshwater segments. This was because, unlike P inputs, which are often dominated by point sources, N inputs are dominated by diffuse nonpoint sources that include agricultural runoff, groundwater, and atmospheric deposition (Paerl 1997) that are difficult to identify, generally regional in scale, and challenging to reduce.

Although P reductions have reduced eutrophication of freshwater parts of estuaries, they have had no such effect downstream. To the contrary, P reductions may have actually exacerbated eutrophication in more seaward regions of estuaries (cf. Elmgren and Larsson 2001). This is because reductions in upstream eutrophication potentials will also lower the amount of biomass that assimilates, retains, and in effect ''filters'' nutrients other than P (e.g., N, Fe, Si) that may limit downstream productivity.

This shift appears to have taken place in the NRE, where severe eutrophication problems dating back to the 1970s and 1980s, including freshwater cyanobacterial blooms, hypoxia, and fish kills (Paerl 1983; Christian et al. 1986), were addressed through P reductions in the form of a P-detergent ban (early 1988) and improved P removal by wastewater treatment plants (mid to late 1980s). No parallel N reductions were pursued, even though early studies showed N to be colimiting upstream and exclusively limiting downstream of these algal blooms (Hobbie and Smith 1975; Paerl 1983). The success of P reductions is illustrated in Fig. 8, which shows significant decreases of mean annual dissolved inorganic and total P concentrations during the mid- to late 1980s in both upstream and downstream portions of the NRE. Effects of this selective nutrient reduction on nutrient stoichiometry and phytoplankton production included a sudden increase in molar N : P ratios for total (T) and dissolved inorganic (DI) forms (from approximately 12 DIN : DIP in 1986 to >60 DIN : DIP by 1992 and from 15 TN : TP to 25 TN : TP during the same time frame), and a protracted decrease in mean annual phytoplankton biomass (as Chl *a*) in the upstream freshwater section (Fig. 8). Further downstream in the NRE, an increase in mean annual total and dissolved inorganic N : P was also observed, although not as large as in the upstream region (Fig. 8).

During the decade following the large decrease of P loading (late 1980s through late 1990s), Chl *a* reached high concentrations in more downstream areas of the estuary (Fig. 8). It appears that the Chl *a* maxima migrated from the P-

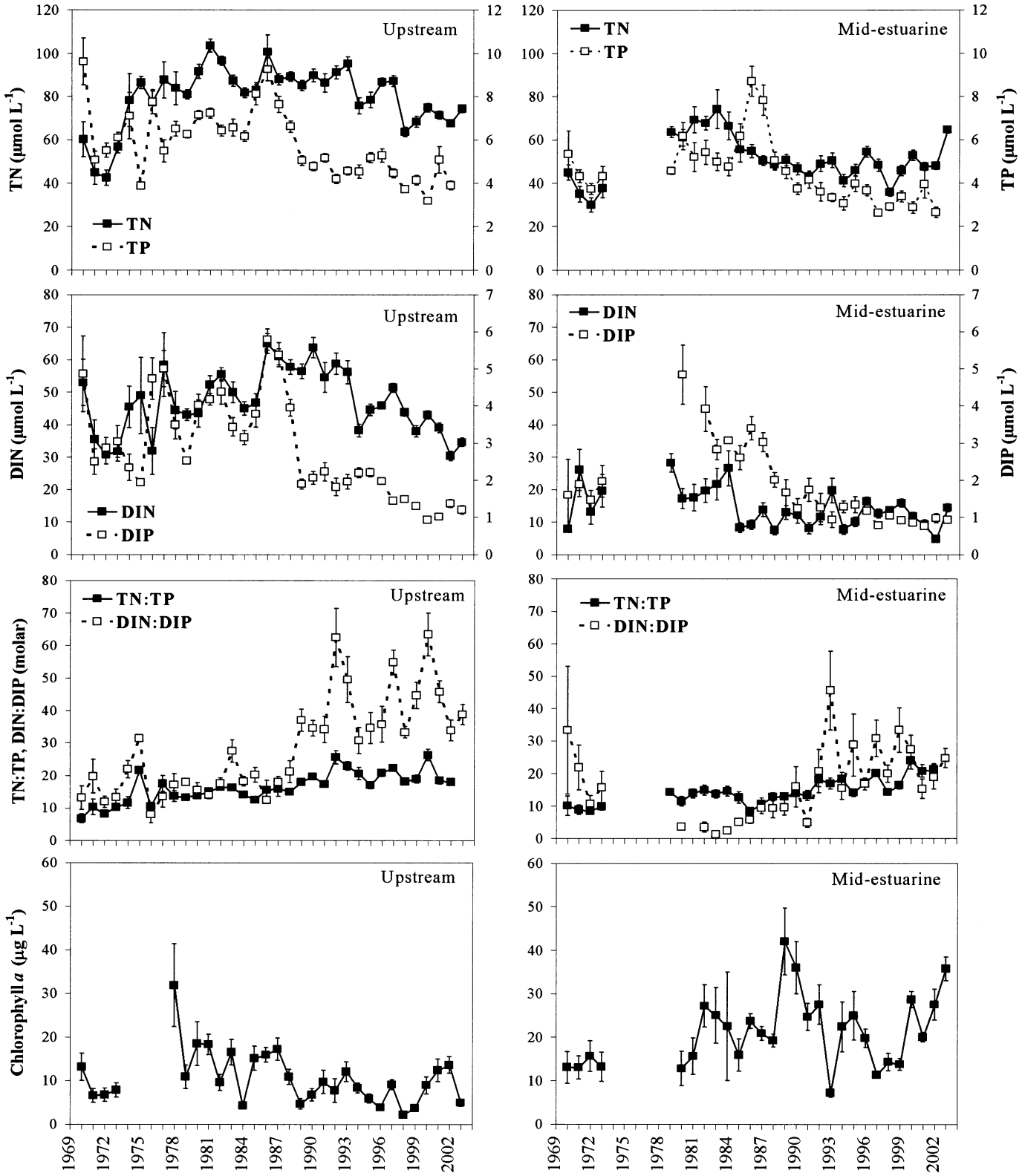

Fig. 8. Mean annual total and dissolved inorganic concentrations and ratios of N and P, and chlorophyll *a* concentrations at the upstream and mid-estuarine segments of the Neuse River Estuary. The upstream region includes water quality data collected from stations located between 0 and 30, whereas the mid-estuarine region includes data collected from stations located between 60 and 120 as shown in Fig. 3. Years for which data are not reported were not sampled at these locations. Error bars represent standard error of the mean.

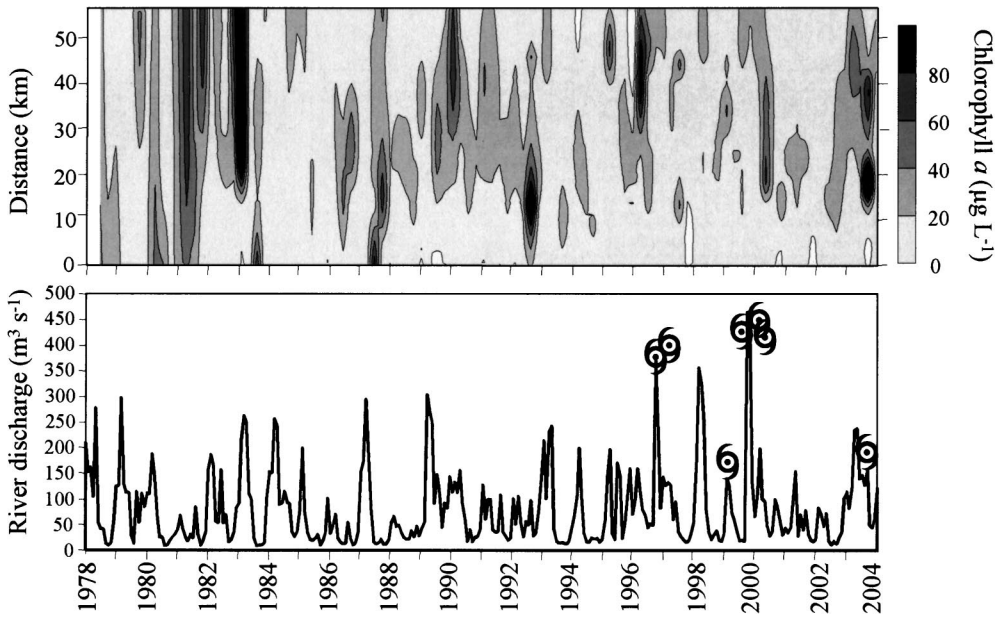

Fig. 9. Upper frame: Spatiotemporal plot of chlorophyll *a* distribution in the Neuse River Estuary 1978–2003. Data are plotted as distance downstream from the uppermost Neuse River Estuary station, Streets Ferry Bridge (SFB), shown in Fig. 3. Lower frame: Mean annual freshwater discharge to the Neuse River Estuary measured at the U.S. Geological Survey gauging station (No. 02089500) located at Kinston, North Carolina, approximately 20 km upstream from SFB. The seven hurricanes that have affected the watershed from 1996–2002; Bertha and Fran (1996), Bonnie (1998), Dennis, Floyd, and Irene (1999), and Isabel (2003), are indicated by symbols.

limited freshwater to the N-limited mesohaline region in response to selective nutrient reduction (Figs. 8, 9).

The influence of large-scale, episodic hydrologic pertubations: A recent rise in hurricane frequency

The nutrient–production relationships and estuarine eutrophication responses discussed above were significantly affected by a sudden increase in the frequency of hurricanes affecting the NRE watershed since 1996 (Figs. 1, 9). The extreme runoff and flooding events associated with these storms flushed nutrients and Chl *a* from the NRE into PS, changing what had been a consistent shift in phytoplankton production from the upper to the lower estuary before this disruptive sequence of storms. Such responses followed each large storm event, including Hurricanes Fran in 1996, and Dennis and Floyd in 1999. After these storms, a period of elevated discharge persisted for several months to a year (in the case of Floyd), after which freshwater flow decreased and Chl *a* peaks reestablished themselves within the estuary. Overall, the period of elevated hurricane activity has disturbed, but not eliminated, what appears to have been a shift in phytoplankton biomass (Chl *a*) in the NRE (Fig. 9).

In contrast to the 1996 and 1999 hurricanes, Hurricane Isabel, which affected CB and NRE/PS on 18 September 2003, was an intense but relatively low-rainfall storm. Its effects on hydrology and phytoplankton community dynamics proved quite different from the prior, wetter storms (Fig. 10). This storm provided an opportunity to compare the differential effects of a category 2 hurricane on these geomorphologically and hydrologically different, yet regionally close, systems (Fig. 1). In CB strong winds and a nearly 2-m storm surge caused damage and temporary (1–2 d) coastal flooding in low-lying areas throughout the Bay. The effects of Isabel contrast with the effects of hurricane Agnes (June 1972), which delivered extremely high rainfall amounts to CB, resulting in flooding and persistent shifts in baywide

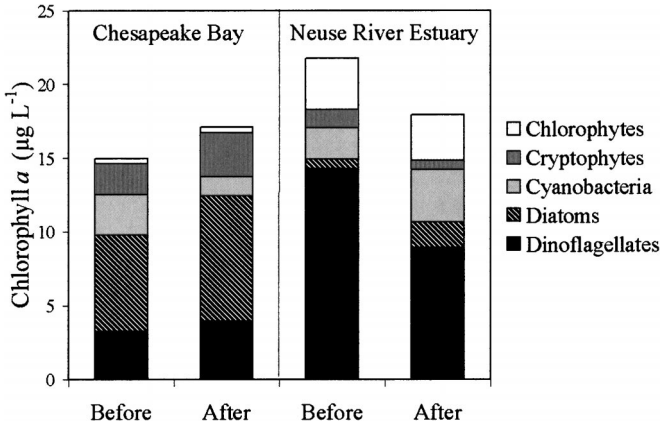

Fig. 10. Phytoplankton community structure and biomass in the Chesapeake Bay and in the Neuse River Estuary before and after Hurricane Isabel (18 September 2003). For the Neuse River, ''Before'' values represent data collected 1 wk before the hurricane, whereas ''After'' values were collected 4 d after the hurricane. For the Chesapeake Bay, phytoplankton community structure data were collected in August, one month prior to the hurricane Isabel (Before), and one month after the hurricane, i. e. in November (After).

salinity distributions due to freshwater input from the Susquehanna River and other tributaries (Schubel et al. 1977).

Aircraft remote sensing and two CB-wide cruises conducted after Hurricane Isabel were used to examine distributions of phytoplankton biomass and composition. We detected deviations from long-term averages for fall that had been established in past studies (Harding 1994; Harding et al. 2002). One week after the storm (24 September 2003), an increase in Chl *a* and a significant phytoplankton bloom in the main-stem Bay were detected by aircraft and field sampling between the York and Patuxent Rivers (not shown). This increase was ephemeral, resulting from water column mixing and reintroduction of nutrients to the surface mixed layer, as it was not observed in subsequent overflights. Shipboard sampling conducted 2 wk after Isabel showed a typical fall pattern (Figs. 6, 10), consisting mainly of diatoms and cryptophytes. Seven weeks after Isabel, both dinoflagellates and diatoms were responsible for sustained stimulation of phytoplankton biomass throughout much of the Bay (Fig. 10). It was particularly surprising that dinoflagellate blooms persisted well into the fall, since long-term average data show relatively small contributions of dinoflagellates to Chl *a*, typical of fall conditions (average = 3% of total Chl *a*, max. = 9% of total Chl *a*). Mixed-layer depths (Z_m) increased after Isabel, exceeding long-term averages and suggesting that significant water column mixing had occurred. The dinoflagellate blooms we sampled after Isabel occurred in regions of the Bay that returned to more typical Z_m values 2–7 wk after storm passage. Although it is difficult to say why dinoflagellates took advantage of these conditions, or whether selective grazing had an effect, it is clear that robust long-term averages can be disrupted by episodic events such as hurricanes in this system.

In contrast, Chl *a* concentrations failed to increase and actually showed a slight decrease after the passage of Isabel over the NRE/PS system (Fig. 10). In part, the lack of a positive response in Chl *a* in the NRE/PS can be attributed to geomorphological differences between CB and the NRE/PS. While the deeper CB exhibits partial vertical stratification in fall that was disrupted by Isabel, the shallower NRE/PS shows intermittent stratification during summer and fall (Peierls et al. 2003). Because the NRE/PS system was destratified before the arrival of Hurricane Isabel, wind mixing induced by this storm had far less of an effect on vertical structure and phytoplankton distributions than observed for CB. Also, Isabel delivered little rain to the watershed of the NRE/PS. Hence, there was minimal nutrient enhancement (due to runoff) on phytoplankton communities, in stark contrast to the effects of Hurricane Floyd (Fig. 2). Lastly, the violent wind mixing and high turbidity associated with Isabel negatively affected the NRE/PS phytoplankton communities by reducing clarity and creating suboptimal photosynthetic conditions.

Our observations of effects of anthropogenic nutrient enrichment in large estuarine systems affected by climatic perturbations yield the following conclusions and recommendations: (1) Reductions of nutrients aimed at controlling ecosystem-scale eutrophication need to consider the *entire* freshwater–marine continuum, spanning both P- and N-limited waters. From a nutrient management perspective, this means that *both* N and P reductions must be considered. In retrospect, it would have been timely and prudent if dual nutrient reductions had been initiated in the 1970s and 1980s when estuarine eutrophication was first identified. (2) Climatic changes, including an increase in the frequency of large storm events, floods, droughts, and other hydrologic perturbations, can cause short-term (months) to longer-term (several years) deviations in nutrient loading and productivity in estuaries, especially ecosystems that undergo significant changes in residence time in response to variable freshwater discharge.

Whereas these ecosystems may be expected to biologically and chemically ''rebound'' and re-establish prestorm nutrient and productivity gradients within a matter of months to a few years, longer periods (i.e., decades) of elevated storm activity, such as those we are experiencing along the U.S. Atlantic and Gulf of Mexico Coasts (Goldenberg et al. 2001), may lead to more severe and longer-lasting alterations of productivity, biotic community composition, biogeochemical cycling, and trophodynamics (Paerl et al. 2001; Adams et al. 2003; Peierls et al. 2003). In addition, a more protracted period of ''recovery'' from the effects of elevated storm activity may be expected if parallel increases in top-down pressure from expanding and diversifying fisheries (Jackson et al. 2001) accompany physical–chemical stresses from these events. These pressures, combined with continued increases in nutrient loading from agricultural, industrial, and urban development in coastal watersheds (Vitousek et al. 1997; National Research Council 2000, Boesch et al. 2001), represent an unprecedented combination of anthropogenic and climatic stresses on large estuaries and coastal waters, previously not considered to be prone to rapid and prolonged ecological change.

Acute and chronic responses to climatic and anthropogenic perturbations in estuarine and coastal ecosystems underscore the need for long-term, spatially and temporally intensive monitoring, modeling, and assessment of water quality and habitat condition in support of adaptive management aimed at reducing the unwanted symptoms of eutrophication. Monitoring and assessment should include detection of (1) trends, (2) changes in state, and (3) biogeochemical and trophic consequences of infrequent, but large-scale, events, using continuous and integrative approaches. In large estuarine ecosystems these requirements may at least partially be met by satellite- and aircraft-remote sensing, large-scale long-term, real-time monitoring using existing infrastructure such as bridges, platforms, ''ships of opportunity'' including ferries (Buzzelli et al. 2003), as well as unattended moorings and buoys using meaningful, sensitive, and easily deployed indicators of environmental stress and biotic responses to stressors. Although we have focused on diagnostic photopigments as indicators of phytoplankton community response, a wide array of deployable molecular, bio-optical, microchemical, and physical sensing technologies are now available to meet specific research and management requirements for these large ecosystems.

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