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Author(s): Benjamin L. Peierls, Robert R. Christian and Hans W. Paerl
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Water Quality and Phytoplankton as Indicators of Hurricane Impacts on a Large Estuarine Ecosystem

BENJAMIN L. PEIERLS[1],*, ROBERT R. CHRISTIAN[2], and HANS W. PAERL[1]

[1] *University of North Carolina at Chapel Hill, Institute of Marine Sciences, 3431 Arendell Street, Morehead City, North Carolina 28557*

[2] *Department of Biology, East Carolina University, Greenville, North Carolina 27858*

ABSTRACT: Three sequential hurricanes in the fall of 1999 provided the impetus for assessing multi-annual effects on water quality and phytoplankton dynamics in southwestern Pamlico Sound, North Carolina. Two and a half years of post-hurricane data were examined for short- and long-term impacts from the storms and > 100 year flooding. Salinity decreased dramatically and did not recover until May 2000. Inorganic nitrogen and phosphorus concentrations were briefly elevated during the flooding, but later returned to background levels. Dissolved organic carbon concentrations declined through the whole study period, but did not appear to peak as was observed in the Neuse River estuary, a key tributary of the Sound. Light attenuation was highest in the fall to spring following the storms and was best correlated with chlorophyll *a* concentrations. Phytoplankton biomass (chl *a*) increased and remained elevated until late spring 2000 when concentrations returned to pre-storm levels and then cycled seasonally. Phytoplankton community composition varied throughout the study, reflecting the complex interaction between physiological optima and combinations of salinity, residence time, nutrient availability, and possibly grazing activity. Floodwater advection or dilution from upstream maxima may have controlled the spatial heterogeneity in total and group-specific biomass. The storms produced areas of short-term hypoxia, but hypoxic events continued during the following two summers, correlating strongly with water column stratification. Nitrogen loading to the southwestern sound was inferred from network analysis of previous nitrogen cycling studies in the Neuse River estuary. Based on these analyses, nutrient cycling and removal in the sub-estuaries would be decreased under high flow conditions, confirming observations from other estuaries. The inferred nitrogen load from the flood was 2–3 times the normal loading to the Sound; this estimate was supported by the substantial algal bloom. After 8-mos, the salinity and chl *a* data indicated the Sound had returned to pre-hurricane conditions, yet phytoplankton community compositional changes continued through the multi-year study period. This is an example of long-term aspects of estuarine recovery that should be considered in the context of a predicted 10–40 yr period of elevated tropical storm activity in the western Atlantic Basin.

Introduction

Tropical storms and hurricanes create large-scale, acute disturbances for coastal aquatic and terrestrial ecosystems (Valiela et al. 1998). In estuaries, extreme wind velocities, storm surges, and rainfall can cause intense mixing, alterations to circulation, and even changes to geomorphology (i.e., inlet formation or closure). An estuary is often classified by geomorphic type or water circulation patterns and both factors help control the ecological structure and function of these dynamic ecosystems (Day et al. 1989). When major storms make landfall on or near an estuary, their effects can be considerable, at least in the short term. Often, storms produce floodwaters that reduce salinity and increase organic matter and nutrients as happened in the Chesapeake Bay after Tropical Storm Agnes (Chesapeake Research Consortium 1976), in the Herbert River after Cyclone Sadie

(Mitchell et al. 1997), in Charleston Harbor after Hurricane Hugo (Van Dolah and Anderson 1991), and in the Cape Fear River after Hurricane Fran (Mallin et al. 1999). Similar impacts were observed in the Taiwan Strait after Typhoon Graff and Herb, although some of the nutrient increases were due to wind-driven upwelling (Shiah et al. 2000). Freshwater and nutrient loadings are not the only reported hurricane effects. Hurricane Donna had the opposite impact on Florida Bay when a massive storm surge temporarily increased salinity (Tabb and Jones 1962). Wind and storm surge from Hurricane Bob opened a new inlet into Waquoit Bay on Cape Cod (Valiela et al. 1998). Nor does every storm have the same effect on any one estuary; Mallin et al. (2002) documented variable responses by the Cape Fear River and its estuary to a series of hurricanes during latter half of the 1990s. Only a few studies have reported the longer-term impacts of major storms on estuaries.

In the fall of 1999, three sequential hurricanes passed through or near eastern North Carolina causing record flooding (Bales et al. 2000; Paerl et

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

al. 2001). Hurricane Dennis bypassed the coast, meandered offshore, and then made landfall as a tropical storm on September 4. Hurricane Floyd moved through the area as a category 2 hurricane September 15–16. Hurricane Irene never made landfall, but contributed additional rainfall and winds when it passed by North Carolina on October 17. Our Pamlico Sound research cruises began in early October in response to the storms and extended ongoing long-term monitoring and research on the Neuse River estuary, a sub-estuary of the Sound (Luettich et al. 2000). The goals for the Pamlico Sound study were to monitor multi-annual water quality and phytoplankton community responses to and recovery from the fall 1999 storms.

There are few reports on water quality in the Pamlico Sound, despite its critical role as a habitat resource for estuarine-dependent fisheries in the Mid-Atlantic region (Epperly and Ross 1986; Steel 1991). Previous research on Pamlico Sound focused mostly on hydrologic and hydrographic details (Williams et al. 1973; Giese et al. 1985; Pietrafesa et al. 1986). Woods (1967) briefly discussed nutrient concentrations and phytoplankton productivity in the sound. Aside from that report, most water quality research concentrated on the major sub-estuaries, the Neuse and Pamlico Rivers (Steel 1991; Luettich et al. 2000).

Previous and ongoing reports indicate that substantial quantities of dissolved nutrients entered the Neuse River and its estuary from the hurricane-induced flooding (Bales et al. 2000; Paerl et al. 2001). Under normal hydrologic regimes, the sub-estuaries of Pamlico Sound remove nutrients prior to their entry into the Sound (Christian et al. 1984, 1991; Rudek et al. 1991; Christian and Thomas 2000, 2003). This removal, or filtering capacity, results largely from sedimentation, burial, and denitrification. The ability of an estuary to cycle and remove nutrients is strongly influenced by its flushing or water residence time (Nixon et al. 1996; Eyre and Balls 1999; McKee et al. 2000). Nixon et al. (1996) found that for several North Atlantic estuaries, as residence time increased, the percent nitrogen (N) and phosphorus (P) exported decreased and the percent N denitrified increased. In a comparison of Scottish coastal rivers, Balls (1994) noted that greater flushing times caused nutrients to deviate from conservative mixing behavior, presumably due to increased exposure to biological activity. Similar observations were made in sub-tropical (Eyre and Twigg 1997) and tropical systems (Eyre and Balls 1999), except with greater variation of discharge and flushing times compared to temperate estuaries. Network analysis of N cycling for the Neuse River estuary (Christian and Thomas 2000, 2003) demonstrated that during periods of low discharge, low loading, and long residence time, biological processing removes considerable N before it can enter the sound. The opposite occurred when discharge and loading increased and residence time shortened. We hypothesize that, given the large nutrient inputs to and the short residence time in the sub-estuaries following the 1999 hurricanes, the nutrient loading to the sound was larger than usual and the response of the system was controlled in part by the excessive nutrient inputs.

The main objective of this paper is to describe the temporal and spatial patterns in the water quality and phytoplankton data since the hurricane disturbance. These patterns are used to quantify the time frame for recovery from the disturbance. We estimate the N loading to the sound from the hurricanes by extrapolating the network analysis results from earlier studies (Christian and Thomas 2000, 2003). We also examine the data for indications of long-term effects from the storms.

Materials and Methods

STUDY LOCATION

The Pamlico Sound is a part of the Albemarle-Pamlico Estuarine System (APES). This system is the second largest estuarine ecosystem of any type in the United States (Epperly and Ross 1986; Steel 1991). The APES drains an approximately 80,000 km² watershed that includes about one-third of North Carolina and parts of Virginia (Giese et al. 1985; Steel 1991). Pamlico Sound is the largest component of the APES with a surface area of 5,335 km² (Giese et al. 1985), also making it the largest lagoonal estuary in the U.S. (Pietrafesa et al. 1986). The major tributaries of Pamlico Sound are the Neuse River, Pamlico River, and Albemarle Sound (Giese et al. 1985). The average depth of Pamlico Sound is 4.9 m, but the bathymetry is distinguished by two major basins (maximum depth 7.3 m) separated by shoal regions (Giese et al. 1985). The circulation of the Sound is dominated by wind tides and river flow, except near the three major inlets from the Atlantic Ocean (Giese et al. 1985; Pietrafesa et al. 1986).

A series of 10 stations in southwestern Pamlico Sound (Fig. 1), covering the sub-basin extending from the Neuse River, were visited at least monthly immediately following the hurricanes from early October 1999 until February 2000. Starting in March 2000, the stations were relocated and reduced to nine (Fig. 1). The new locations were chosen to overlap with other research group stations and the track of the North Carolina Department of Transportation Cedar Island to Ocracoke ferry (Buzzelli et al. 2003). Trips continued at roughly monthly intervals through April 2002.
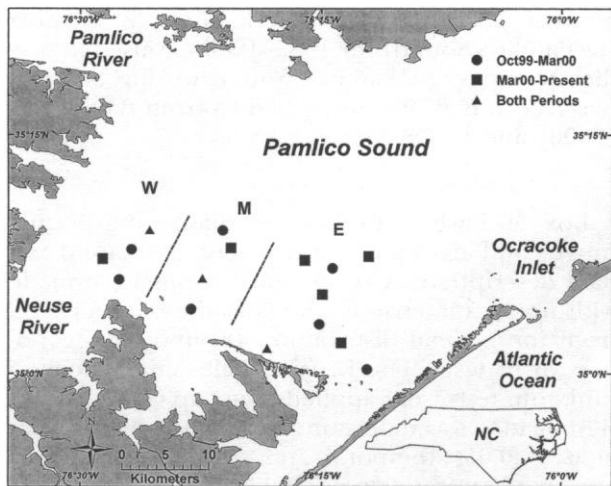
Fig. 1. Map of study area including sampling stations and coverage dates. Station groups, identified by West (W), Middle (M), and East (E), are used for spatial comparisons.

FIELD SAMPLING

Vertical profiles of hydrographic and light data were collected at each station. A YSI 6600 sonde coupled to a 610 or 650 logger was used to measure temperature, salinity, pH, and dissolved oxygen. Conductivity (salinity) and pH sensors were calibrated with commercial standards and the dissolved oxygen sensor was calibrated using water-saturated air. In November 1999, the YSI sonde did not record complete profiles, so bottom values for that date are from duplicate profiles measured with a Hydrolab H20 sonde. The diffuse light attenuation coefficient, K_d, was determined from profiles of photosynthetically active radiation (PAR) using a LI-COR LI-193SA spherical quantum sensor. The slope of the linear regression between natural log-transformed PAR data and depth was used as the diffuse attenuation coefficient (K_d).

Water samples were collected from the surface and near bottom layers and stored in acid-cleaned, high-density polyethylene (HDPE), 10 l containers. The bottom samples were collected near 0.5 m above the sediment with a horizontal plastic Van Dorn sampler, while the surface containers were either submerged just below the surface or filled from bucket casts. All containers were kept in dark coolers at ambient temperature until processed. All filtration was done within a few hours of collection and, when conditions permitted, on board the research vessel.

LABORATORY ANALYSES

Dissolved nutrients were measured after vacuum filtration (< 25 kPa) of the collected samples through pre-combusted (3–4 h at 450°C) Whatman GF/F glass fiber filters and frozen storage of the filtrate in acid-cleaned HDPE bottles. Nitrate plus nitrite, ammonium, and orthophosphate concentrations in μmol l^{-1} (μM) were determined using a Lachat QuikChem 8000 flow injection analyzer and standard colorimetric methods. The limits of detection were approximately 0.08 μM, 0.3 μM, and 0.01 μM for NO_3+NO_2, NH_4, and PO_4, respectively. Concentrations below these values were reported as one third of the method detection limits.

Additional aliquots of the GF/F filtrate were stored frozen in pre-combusted glass scintillation vials with Teflon-lined closures. These samples were used to measure dissolved organic carbon (DOC) concentrations using a Shimadzu TOC-5000A Analyzer. This instrument uses high temperature catalytic oxidation followed by non-dispersive infrared analysis of the CO_2 produced. Samples were acidified to pH < 2 and sparged with air before being analyzed for non-volatile organic carbon.

Particulate organic carbon (POC) and particulate nitrogen (PN) concentrations were determined by elemental analysis of material collected on pre-combusted GF/F filters. Carbonates were removed from the filters by vapor phase acidification (concentrated HCl). After drying at 60°C, the filters were rolled in tin disks and injected into a PE 2400 Series II CHNS/O Analyzer calibrated with acetanilide. POC and PN concentrations were converted to molar C to N ratios (C:N).

Phytoplankton chlorophyll a (chl a) concentrations were measured using the modified in vitro fluorescent technique in EPA Method 445.0 (Arar et al. 1997). Samples (50–75 ml) were collected on 25 mm GF/F filters (vacuum filtration, < 25 kPa), blotted dry, and frozen immediately. Chl a was extracted from the filter using a tissue grinder and 90% aqueous acetone. The samples remained in the acetone overnight at −20°C. The extracts were filter-clarified and analyzed on a TD700 fluorometer. The fluorometer was calibrated with chl a after determining the concentration using a Shimadzu UV160U Spectrophotometer and the extinction coefficients of Jeffrey and Humphrey (1975). The calibration was checked daily against a solid secondary standard (Turner Designs, proprietary formula).

Diagnostic phytoplankton photopigments were quantified using high-performance liquid chromatography (HPLC), coupled to photodiode array spectrophotometry (PDAS) separation and analysis (Jeffrey et al. 1997). Water samples (500–1,000 ml) were gently vacuum filtered (< 25 kPa) onto 47-mm GF/F filters, blotted dry, then immediately

frozen ($-20°C$). The filters were placed in 100% acetone, sonicated, and extracted at $-20°C$ for 12–24 h. The HPLC configuration and other details used in the current study are described in Pinckney et al. (1996). The matrix factorization program CHEMTAX (Mackey et al. 1996) was applied to chlorophyll and carotenoid (alloxanthin, antheraxanthin, chl *b*, total chl *a* [chl *a* + chlorophyllide *a*], fucoxanthin, lutein, peridinin, violaxanthin, and zeaxanthin) concentration data to determine the absolute contribution of five major phytoplankton divisions or classes (Cryptophyta, Cyanophyta, Bacillariophyta, Dinophyta, and Chlorophyceae) to total community biomass (Pinckney et al. 2001). The initial pigment matrix values came from Table 1 in Mackey et al. (1996) and the analyses were grouped by depth level and season.

We used photosynthetic rates to estimate phytoplankton N demand and compared that demand against N loading to the Sound (see below). The rates were measured using an adaptation of Steemann Nielsen's (1952) ^{14}C bicarbonate method (Paerl et al. 1998). Volumetric photosynthetic rates for each station and date were converted to areal carbon fixation by using a euphotic zone depth (1% of surface irradiance) calculated from K_d and assuming 8 h of daylight. N demand for September to December 1999 was calculated using trapezoidal integration and stoichiometric conversion to N (Redfield C:N = 6.6).

NETWORK ANALYSIS

The network analyses of Christian and Thomas (2000, 2003) were used to determine N loading to the sound. Their analyses were on 16 seasonal networks of N cycling (Spring 1985–Winter 1989) in the Neuse River estuary. The general network of the N cycle was divided into seven compartments (as mmol N m^{-2}) representing phytoplankton, aquatic heterotrophs, detritus, sediments and benthos, dissolved organic N (DON), nitrate plus nitrite, and ammonium. Fluxes (as mmol N m^{-2} season^{-1}) included import from loading, export into the Sound, denitrification, nitrogen fixation, and 27 internal flows among compartments. Networks were constructed largely on results from spring 1985–winter 1989 integrated over the entire estuary (Christian et al. 1991, 1992; Lackey 1992; Rizzo et al. 1992; Boyer et al. 1993, 1994; Rizzo and Christian 1996). NETWRK4 (Ulanowicz 1987) was used to interpret the nature of N cycling in the networks and by inference in the field. Full explanations of model construction and analysis can be found in Christian et al. (1992) and Christian and Thomas (2000, 2003). Mass balance of the networks provided seasonal total N (TN) export fluxes for each seasonal TN import flux. The relationship between TN import (riverine loading) and export (to Pamlico Sound) for 1985–1989 was used to predict N export to Pamlico Sound during September–December 1999 using N data from Bales et al. (2000) and USGS records of flow.

STATISTICS

Box and whisker plots (median, interquartile range, and extreme values) were used for basic data descriptions. Group comparisons were made with non-parametric methods as the data differed from the normal distribution (Kolmogorov goodness of fit test). The Kruskal-Wallis and Wilcoxon rank-sum tests were applied to group comparisons; significance was determined for these and all tests at $\alpha = 0.05$. Temporal and spatial comparisons were made using data pooled by flood period (October to March) or season (Fall = September, October, and November) and by station groups (Fig. 1), respectively. Surface and bottom values for DOC, C:N, dissolved nutrients, chl *a*, and algal group biomass were combined for the group comparisons. For correlations, the Spearman rank correlation procedure was used. The TN loading/export relationship was modeled with linear and polynomial least squares regression analysis. All statistical measures and tests were performed with S-Plus 6.0.

Results

TEMPORAL PATTERNS

The hurricanes of 1999 generated unprecedented rainfall in the watershed, record river flows, and record flooding (Fig. 2; Bales et al. 2000; Paerl et al. 2001; Bales 2003). Peak stream flow in the Neuse River at Kinston reached over 1,000 m^3 s^{-1} in late September and returned to more typical levels by November. Salinity in southwestern Pamlico Sound rapidly responded to the flooding from the tributaries, although the response was lagged due to travel time from the watershed. Median surface salinity was less than 10 psu in early October 1999 after Hurricane Floyd and continued to drop until the beginning of November (Fig. 2). Extreme low values of less than 2 psu were reported near the mouth of the Neuse River estuary (Paerl et al. 2001; Ramus et al. 2003). Salinity began to increase in the sound by the end of 1999. Summer 2000 brought a median surface salinity of about 22 psu, very close to the values for summer 1999 (Ramus et al. 2003) and 2001 (Fig. 2). The next period of low salinity was in November 2000–March 2001. This same early winter lag in salinity did not repeat in 2001, coincident with a very dry winter (Southeast Regional Climate Center, www.dnr.state.sc.us/climate/sercc/).

We defined a flood period (October 1999

through March 2000) based on the period when salinities never overlapped median values for any other time (Fig. 2). Comparing surface salinity from the flood period to the same months in the succeeding two years revealed significant differences between the years with a trend towards higher median salinity with time (Table 1). The same pattern appeared when the data were compared by the three fall seasons only (Table 1). Bottom salinities followed the same trends as the surface only with a greater range of values at each date (data not shown). Delta salinity (ΔS, bottom minus surface) was used as a measure of water column stratification. During most sampling trips, the sound exhibited varying degrees of stratification with ΔS at times exceeding 15 psu (Fig. 2). A notable exception was immediately following the passage of Hurricane Irene in late October 1999, when the entire southwestern basin appeared to be well mixed. ΔS did not differ significantly between the three years, except when comparing the fall seasons alone (Table 1). In that case, median ΔS was lowest in fall 1999.

All nutrient concentrations in Pamlico Sound were elevated at the beginning of the study, but decreased to background levels within a month of the last storm (Fig. 2). NO_3+NO_2 reached levels as high as 3 to 4 μM and then remained below detection limits except during October 2000–June 2001, when median concentrations hovered around 0.5 μM. NH_4 and PO_4 rose immediately after the storms (median values of about 5 and 0.5 μM, respectively) and were low or below detection shortly after. Elevated NH_4 and PO_4 conditions were observed in summer to fall periods. Nutrient concentrations pooled by flood period or season showed significant difference among all groupings, except for fall PO_4, which did not differ significantly between years (Table 1). Salinity was negatively correlated with NO_3+NO_2 and PO_4 for surface values during the two October 1999 cruises (N: r = -0.70, p = 0.0023; P: r = -0.52, p = 0.022; n = 20).

Water clarity was determined by measuring the diffuse light attenuation coefficient K_d. The temporal pattern for K_d is shown in Fig. 2. Large coefficients indicate that light is attenuated more rapidly with depth. Reduced light conditions characterized the flood period, as evidenced by median K_d values of about 2 m^{-1} or more. From May 2000 on, median K_d had decreased to about 1 m^{-1} or less; this corresponds to an approximate doubling of the euphotic zone depth. The K_d data grouped by flood period or fall season showed significant differences among years and lower median values in each succeeding year (Table 1).

The median dissolved organic carbon (DOC)

concentration over the entire collection period was 444 μM (n = 446) with extreme concentrations ranging from about 100 to almost 1,700 μM (Fig. 2). DOC concentrations appear to decline gradually over the study period. Group medians for flood period and fall season declined with year, and the groups all differed significantly (Table 1). About 26% of the variability in K_d is explained by DOC (r = 0.51, p < 0.0001, n = 270), but there was no significant correlation when using just the flood period data.

The pattern for particulate C and N resembles the chlorophyll a pattern (see below), and the box plots are not shown. Correlation coefficients for POC and PN versus chl a were 0.73 and 0.83, respectively (p < 0.0001, n = 552). The ratio of POC to PN (C:N) appears to follow a cyclical pattern with lower ratios in the summer and fall (Fig. 2). At several time points, median C:N values were at or near the Redfield ratio for phytoplankton (6.6), especially during the flood period. Group comparisons of the C:N data show significant differences among both sets of groupings; the lowest median was in the first flood period or fall.

Total phytoplankton community biomass was estimated using chl a concentrations (in vitro fluorescence technique). Chl a began the period relatively high, with median concentrations close to 18 μg l^{-1} and peak concentrations of 35 μg l^{-1} (Fig. 2). A small drop in chl a was followed closely by a bloom in February and March 2000, with values of similar magnitude as in October 1999 (Fig. 2). From then on, chl a decreased and median values stayed at 10 μg l^{-1} or less with small peaks in August–September of each of the following years. This concentration level corresponds to pre-hurricane values for the system (Paerl et al. 2001). The three years were significantly different from each other (p < 0.0001) when the chl a data was grouped by flood period or fall season and the group medians followed the observed decrease (Table 1). Over the whole study period, chl a and K_d were strongly correlated (r = 0.78, p < 0.0001, n = 270).

Diagnostic photopigments add to the phytoplankton community analysis by providing estimates of group-specific biomass. The CHEMTAX program converted pigment concentrations into cryptomonad (Cryptophyta), cyanobacteria (Cyanophyta), diatom (Bacillariophyta), dinoflagellate (Dinophyta), and green algae (Chlorophyceae) biomass, reported as chl a. It was evident that there were different temporal patterns in the group-specific biomass record (Fig. 2). At the beginning of the study, the community was an approximately equal mixture of cryptomonads, cyanobacteria, diatoms, and green algae. Cryptomonads showed a
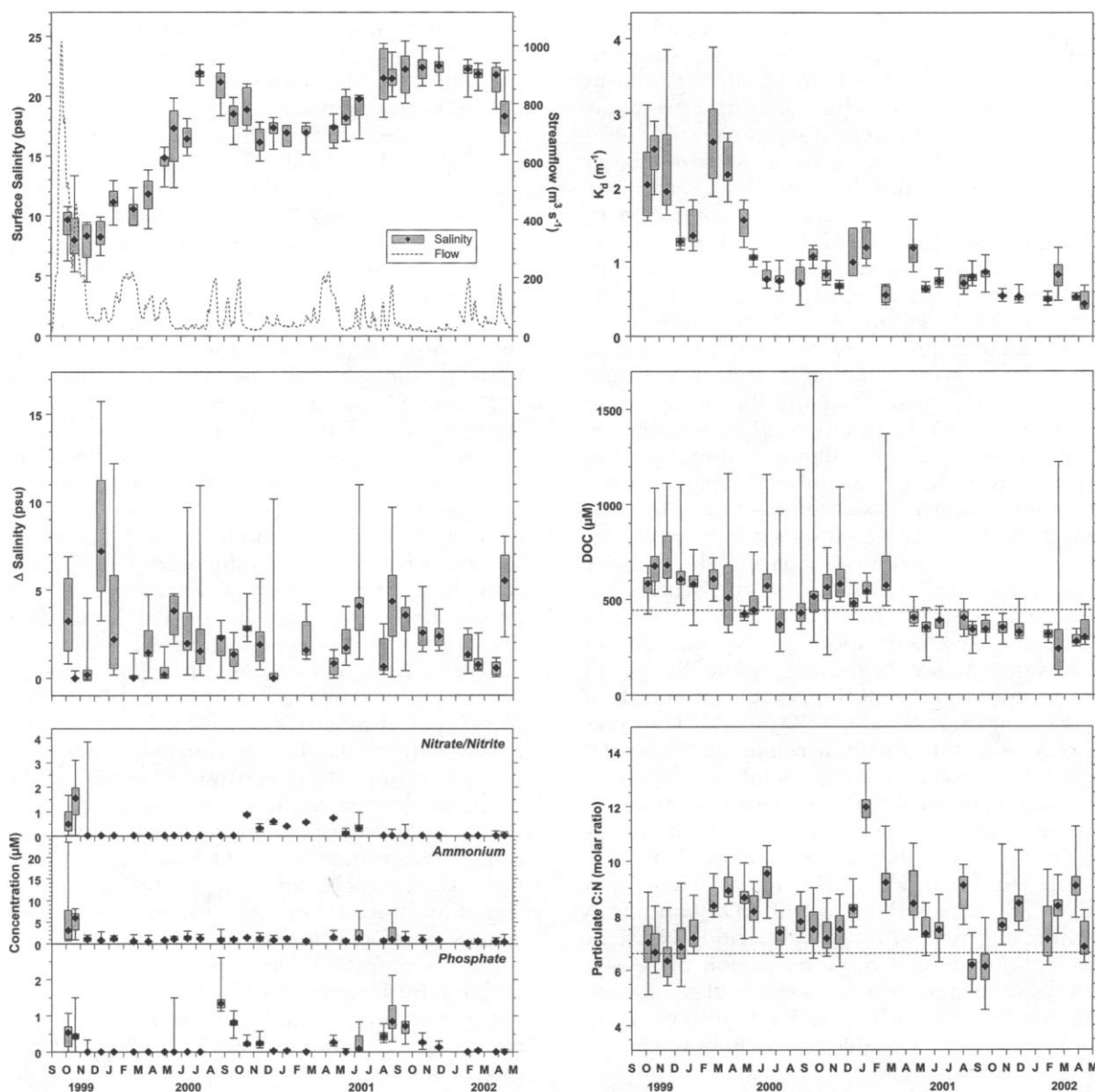
Fig. 2.   Box and whisker plots of surface salinity; ΔS (difference between bottom and surface salinity); surface and bottom water nitrate plus nitrite (top), ammonium (middle), and orthophosphate (bottom); diffuse light attenuation coefficient, K_d (m^{-1}); surface and bottom dissolved organic carbon (DOC) (dotted line represents the long-term median concentration for October 1999–April 2002); the molar ratio of POC to PN in surface and bottom water samples (the dotted line is the Redfield C:N ratio); surface and bottom chl a; group-specific algal biomass; and bottom water DO in mg l^{-1} (upper dashed line is EPA criterion continuous concentration [4.8 mg l^{-1}] and the lower dotted line is the criterion minimum concentration [2.3 mg l^{-1}; USEPA 2000]. These limits signify critical hypoxic conditions) in Pamlico Sound over time. The diamond symbol is the median value, shaded boxes indicate interquartile range (25th to 75th percentile), and the whiskers are the minimum and maximum values (n = 9–10 or 18–20). The flow data comes from the USGS gauging station at Kinston, North Carolina (station no. 02089500, N35°15′29″, W77°35′09″), and is daily mean stream flow in m^3 s^{-1}.

gradual decrease from the beginning of the record except for a peak in November 2000. Diatoms and green algae became most dominant during the first winter and spring; dinoflagellates also reached maximum biomass during this period. Cyanobacteria declined to minimal levels after the storms,

but maintained median biomass values of from 2–3 µg l^{-1} during the warm months. Diatom biomass peaked again in fall 2000 and spring 2001, but had only a small peak in fall 2001. After the flood period, dinoflagellates rarely contributed much to the total community biomass. Green algal biomass
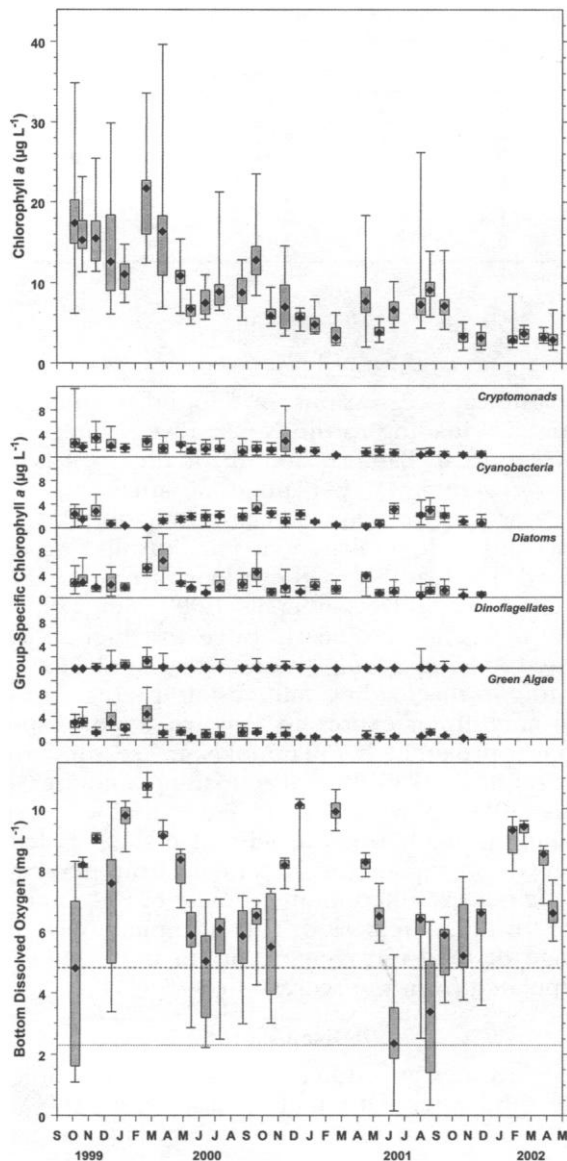
Fig. 2. Continued.

dropped off in April 2000, and median values rarely exceeded 1.5 $\mu g\ l^{-1}$ for the rest of the study. All the phytoplankton groups had significant differences across the three years when pooled by time period (Table 2). Except for cyanobacteria, the median values declined from highest values in the first year. Cyanobacteria appeared to remain constant or increase; summer 2001 median biomass was higher than summer 2000 (data not shown) and the two seasonal groups were different at $p < 0.0001$.

Bottom water dissolved oxygen (DO) followed a seasonal pattern with highest values during the coldest periods (Fig. 2). The first occurrence of hypoxia was after the first two storms in early October 1999, but the bottom layer was rapidly re-saturated after the mixing effect of Hurricane Irene (Fig. 2). During the warmer periods, DO concentrations ranged from supersaturated to values that were at or below the criteria set by EPA for hypoxia (i.e., 2.3–4.8 mg l^{-1}; U.S. Environmental Protection Agency 2000). The periods of lowest DO coincided with periods of significant salinity stratification (Fig. 2); summertime bottom DO and ΔS were significantly correlated ($r = -0.68$, $p < 0.0001$). Hypoxia was evident in the 2000 summer and fall season, but median DO concentrations were above the upper hypoxia limit. In the summer of 2001, however, extreme hypoxia and even anoxia prevailed on two sampling dates. While there were differences between years, the most significant difference was when comparing fall periods (Table 1). Median DO concentrations decreased with each succeeding fall season.

SPATIAL PATTERNS

The sampling stations covered an approximately 450 km² portion of the southwest basin of Pamlico Sound. Some of the variables showed large variation over this spatial scale during the flood period. We evaluated spatial differences in stratification, hypoxia and phytoplankton by comparing three

TABLE 1. Group comparisons for Pamlico Sound data pooled by time period. Flood period is October 1999–March 2000 compared against the same months in the succeeding two years. Fall is September, October, and November. Numbers are median values for each group. Significant difference between groups as determined by the Kruskal-Wallis rank-sum test is indicated by italics (p < 0.05), italics + bold (p < 0.01), and bold (p < 0.0001). Salinity = surface salinity; ΔS = bottom salinity-surface salinity; DOC = dissolved organic carbon; C:N = molar carbon to nitrogen ratio; NO_3 = nitrate+nitrite; NH_4 = ammonium; PO_4 = orthophosphate; DO = bottom dissolved oxygen; Chl a = fluorometrically determined chl a.

Period or Season	Salinity (psu)	ΔS (psu)	NO_3 (μM)	NH_4 (μM)	PO_4 (μM)	K_d (m^{-1})	DOC (μM)	C:N	Chl a ($\mu g\ l^{-1}$)	DO (mg l^{-1})
Flood	**9.6**	1.3	**0.03**	0.9	*0.004*	2.0	606.7	7.3	15.3	*9.0*
Flood + 1 y	**17.3**	1.9	**0.6**	1.1	*0.05*	0.8	547.0	8.3	5.5	*8.4*
Flood + 2 y	**22.1**	1.5	**0.03**	0.7	*0.04*	0.5	316.9	8.1	3.2	*8.3*
Fall 1999	**8.7**	*0.4*	**0.5**	**2.4**	0.3	2.2	631.9	6.6	15.9	8.2
Fall 2000	**17.6**	*2.0*	**0.3**	**1.2**	0.3	0.8	537.8	7.4	8.6	6.9
Fall 2001	**22.4**	*2.6*	**0.03**	**1.0**	0.3	0.6	344.6	7.6	3.8	5.9

TABLE 2. As in Table 1, but for algal taxonomic groups determined from diagnostic photopigments. All units are μg chl a l^{-1}.

Period or Season	Cryptomonads	Cyanobacteria	Diatoms	Dinoflagellates	Green Algae
Flood	1.9	*1.1*	2.6	*0.2*	2.5
Flood + 1 y	1.0	*1.2*	1.4	*0.05*	0.5
Flood + 2 y	0.3	*0.9*	0.4	*0.03*	0.3
Fall 1999	2.3	2.2	2.5	BD	2.4
Fall 2000	1.3	2.4	1.8	0.1	0.9
Fall 2001	0.3	1.1	0.5	0.03	0.4

sampling areas (west, middle, and east; Fig. 1), pooling results from stations within each. In early October 1999, the greatest stratification (measured as ΔS) was evident in the western and northern portions of the sampling area (Fig. 3). The most stratified area moved to the eastern stations during December and January 2000. The winter season was the only season of the three that the station groups exhibited significant differences in ΔS (Table 3). When considering all of the data, stratification was different among the station groups with eastern stations having a higher median. Hypoxia varied over space as well. On October 6, low bottom DO water concentrations were found in the western and northern stations, parallel to the maximum stratification pattern (Fig. 3). Low DO appeared in December 15 at a few stations, but overall, there were no significant differences among station groups in any of the seasons or when considering all of the data (Table 3).

Chl a, however, did display significant variation in space for the fall and spring period (Table 3). Wintertime station groups were only just outside of the significance level (p = 0.056). The highest median chl a was in the east group in fall 1999, shifting to the west group by spring; Fig. 3 illustrates some of this heterogeneity. The pattern of higher biomass in the west was still detectable when considering all of the data (Table 3). Given that the lowest salinity levels tended to be near the river mouth, the spatial trend was also evident in the negative correlation between surface chl a and salinity (r = −0.69, p < 0.0001, n = 270). When the phytoplankton groups were analyzed separately, not all the groups showed spatial differences. Diatoms and cyanobacteria had significant spatial differences (higher medians in the east stations) in fall 1999, while only dinoflagellates had wintertime differences (Table 3). By spring, cryptomonads, cyanobacteria, dinoflagellates, and green algae differed among station groups (higher medians in the west). Over the entire study, cryptomonads, dinoflagellates, and green algae showed a significant spatial difference.

N Loading

Significant regressions were found between seasonal TN loading to the Neuse River estuary and TN export to Pamlico Sound for the 16 seasonal networks (Fig. 4). Explained variance in export (r^2) was 0.94 for a linear relationship and 0.98 for a second order polynomial relationship. We estimated TN loading to the estuary from mid-September to mid-December as 1,000 mmol N m^{-2} season^{-1}. This was nearly twice the highest estimated loading during the four-year study. Extrapolating to this loading value using the regressions, the amount of export to Pamlico Sound ranges from approximately 750 mmol N m^{-2} season^{-1} (linear regression) to the entire loading amount (second order polynomial regression). This corresponds to a filtering capacity of 0–25%. Calculations of phytoplankton N demand from photosynthetic rates resulted in an estimate of 874 mmol N m^{-2} for the same period. This is comparable to the range of total nitrogen export to the Sound extrapolated from the regressions.

Discussion

Hurricanes and other large storms can directly affect the water column of estuaries in several ways. Substantial rainfall reduces local salinity, increases stratification, and washes in dissolved and particulate material from connected watersheds (Chesapeake Research Consortium 1976; Van Dolah and Anderson 1991; Mallin et al. 1999). Increased freshwater input also reduces estuarine water residence time as seen in the seasonal patterns of temperate (Balls 1994), subtropical (Eyre and Twigg 1997), and tropical (Eyre and Balls 1999) estuaries. In the case of the 1999 hurricanes, the sound's residence time decreased from approximately 1 yr to less than 2 mos (Paerl et al. 2001). High wind velocity disrupts water column stratification and mixes bottom sediments into the water column (Tabb and Jones 1962; Valiela et al. 1998). Storm surges can increase salinity and change circulation patterns by modifying geomorphology (e.g., opening a new inlet) (Tabb and Jones 1962; Valiela et al. 1998). Not all of these storm effects occurred
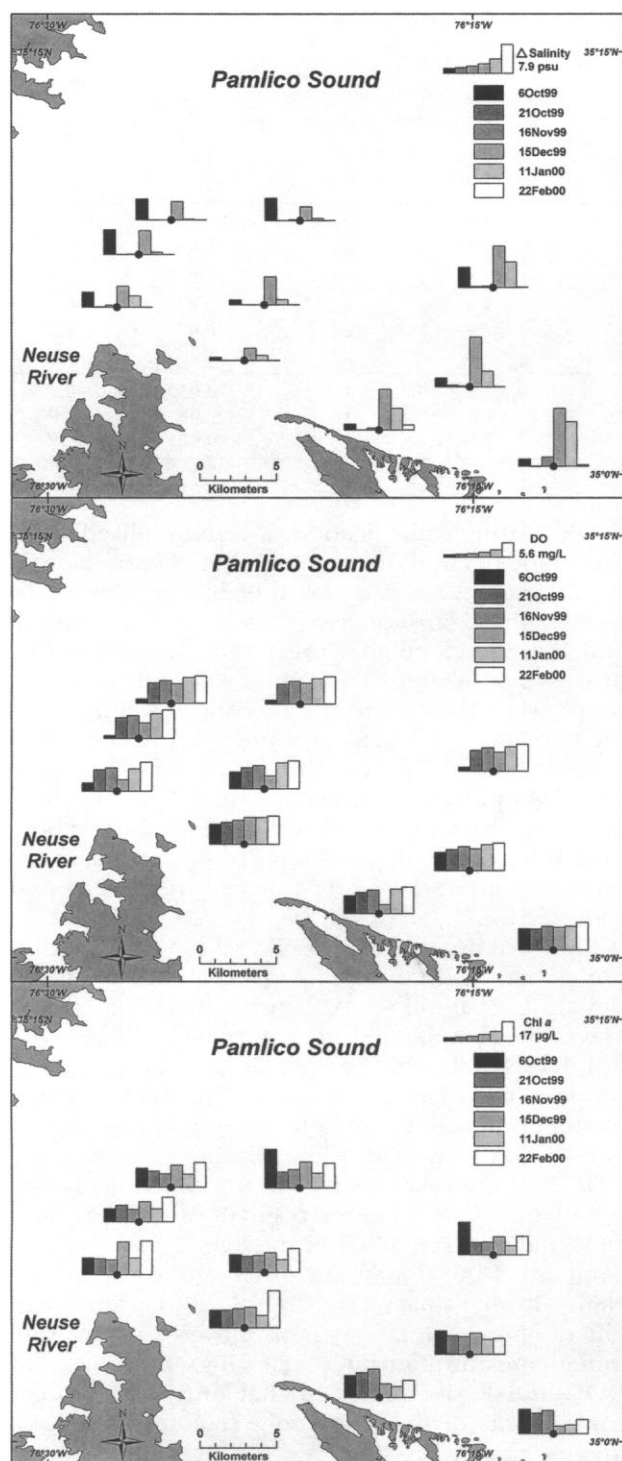
Fig. 3.   Spatial distribution of ΔS (psu), bottom DO (mg l^{-1}), and surface chl a (μg l^{-1}) from October 6, 1999–February 22, 2000. Closed circles indicate actual station locations and each bar indicates the value for a specific date at that station. A scale bar is in the upper right corner.

for Pamlico Sound in 1999. Since the sound is isolated from the Atlantic Ocean by barrier islands, direct storm surge effects on the sound water column were minimal. The basic morphology of the sound stayed intact despite severe erosion and overwash on the barrier islands. Heavy rainfall and powerful winds did have impacts on the entire APES. The combined rains from Hurricane/Tropical Storm Dennis and Hurricane Floyd brought significant freshwater, particulate and dissolved organic matter, and nutrients into the Neuse and Pamlico Rivers (Bales et al. 2000; Paerl et al. 2001), while the winds from Hurricane Irene mixed the entire water column and resuspended sediments.

The impact of the freshwater flood was obvious in the surface salinity time course for Pamlico Sound (Fig. 2 and Table 1). Beyond May 2000, the salinity returned to pre-hurricane conditions (Paerl et al. 2001; Ramus et al. 2003) and the record shows seasonal variability, probably related to local climate. Except for the extreme flood from the storms, the salinity record in the southern portion of the sound did not show significant response to the river discharge peaks at Kinston, over 120 km upstream. This suggests that other factors such as direct rainfall, evaporation, and seawater intrusion play a role in controlling the sound's salinity. Furthermore, modulation of freshwater pulses occurs in the Neuse River, as the water may take weeks to months to pass through the sub-estuary under average flow rates (Christian et al. 1991). The flux of freshwater from the storms decreased water residence time in the sub-estuary and promoted intervals of density stratification in the sound. In December 1999, the combination of low salinity river water and seawater from the ocean inlets produced salinity differences much greater than typically reported (1 to 6 psu; Pietrafesa et al. 1986). Aside from that extreme, stratification during the flooding was either lower or not different than in later years (Table 1), although the ΔS record could be biased due to the tendency to sample on relatively calm days. Spatial differences in salinity and stratification were expected based on previous hydrologic research (Giese et al. 1985; Pietrafesa et al. 1986). During the flood period, highest ΔS shifted east from near the Neuse River estuary mouth to near the ocean inlet, as seawater returned underneath the fresher storm water (Fig. 3) .

Inorganic nutrients showed a clear short-term increase from the flood (Fig. 2 and Table 1). NO_3+NO_2 was transported with the freshwater as demonstrated by the negative correlation with salinity. The lack of correlation between salinity and NH_4 was evidence that the NH_4 came from remineralized particulate and dissolved organic matter

TABLE 3. As in Table 1 and 2, but for data pooled by station groups. Spatial comparisons were conducted for three different seasons during 1999 and 2000 and for all available data.

Season/Year	Station Group	ΔS (psu)	DO (mg l^{-1})	Chl a (µg l^{-1})	Cryptomonads	Cyanobacteria	Diatoms	Dinoflagellates	Green Algae
Fall 1999	East	0.4	8.2	*19.7*	2.2	*3.1*	**3.6**	BD	2.8
	Middle	0.0	8.2	*16.2*	2.4	*2.1*	**2.4**	BD	2.5
	West	0.03	8.1	*14.0*	1.9	*1.7*	**2.0**	BD	2.1
Winter 1999	East	*6.4*	9.5	12.5	1.7	0.3	2.5	*0.2*	2.7
	Middle	*1.3*	10.2	15.4	1.6	0.4	2.3	*0.8*	2.8
	West	*0.6*	9.6	17.6	2.3	0.4	3.0	*1.0*	3.9
Spring 2000	East	1.9	8.3	*9.0*	*1.2*	1.4	2.5	*0.05*	*0.8*
	Middle	0.4	8.5	*11.0*	*2.0*	1.4	2.9	*0.07*	*1.2*
	West	1.4	8.1	*13.4*	*2.2*	1.8	2.6	*0.1*	*1.6*
All data	East	*2.1*	7.1	*6.4*	*0.9*	1.5	1.7	*0.05*	*0.7*
	Middle	*1.0*	7.7	*7.8*	*1.4*	1.5	1.9	*0.08*	*1.0*
	West	*1.6*	7.0	*8.3*	*1.4*	1.5	1.7	*0.09*	*0.9*

flushed to the sound. PO_4 correlated with salinity, also suggesting dilution of a riverine source, although elevated PO_4 may have come from internal sources given the similar peaks during the next two summer/fall seasons. All nutrients rapidly decreased after reaching the sound in fall 1999, presumably to support the growing algal community. Under non-storm conditions, the nutrient patterns, particularly of NH_4 and PO_4, were likely dominated by sediment remineralization and planktonic uptake rather than loading from the sub-estuary (Day et al. 1989). From October 2000 to June 2001, $NO_3 + NO_2$ unexpectedly remained above detection, ranging from about 0.5 to 1 µM (Fig. 2). This $NO_3 + NO_2$ could have been pro-

Fig. 4. Relationship of total N (TN, in mmol m^{-2} season^{-1}) exported to Pamlico Sound as a function of TN loaded to the Neuse River estuary as determined by network analysis. Each point represents one season from the 16 consecutive seasonal networks for 1985–1989. The most extreme import and export values occurred as a result of major storms in winter 1987. Lines are least squares linear and non-linear (2nd order polynomial) regression. Dotted sections of lines indicate extrapolation beyond the data.

duced through nitrification of remineralized N in the flood-derived organic matter. There is not strong evidence to support this, but oxygen levels were high, algal biomass (N demand) was lower, and NH_4 increased after this period suggesting the process had abated. We cannot rule out external supply (i.e., from runoff; see reduced salinity during same period, Fig. 2) or some other process that might account for the $NO_3 + NO_2$ temporal pattern. Except for the immediate spatial pattern driven by floodwater dilution and some occasional bottom water hotspots, the sound remained relatively homogenous and oligotrophic with respect to nutrients.

Light attenuation increased in direct response to the storms and continued to be elevated during the algal bloom in winter/spring 2000 (Fig. 2). By May 2000, K_d appeared to be at stable, perhaps typical, levels, although we have no pre-storm data to support this. Dissolved and particulate organic matter control much of light attenuation variability in estuaries (Day et al. 1989). K_d did correlate with DOC, but the relationship was not as strong as the correlation with chl a (see results). Also, the Sound DOC data never exhibited the large pulse that accompanied the floodwater discharge in the upper Neuse River estuary (Paerl et al. 2001), although our sampling effort may have missed some of the initial concentration increase. This comparison of DOC and K_d is limited in that only the colored components of the DOC pool (colored dissolved organic matter or CDOM) affect light attenuation (Tester et al. 2003). The other major control of light attenuation is particulate matter, usually a mixture of allochthonous material, resuspended sediments, and planktonic organisms. We did not attempt to separate these particulate sources, but the C:N during the flood period (Fig. 2, near Redfield ratio) suggests a seston dominated by phyto-
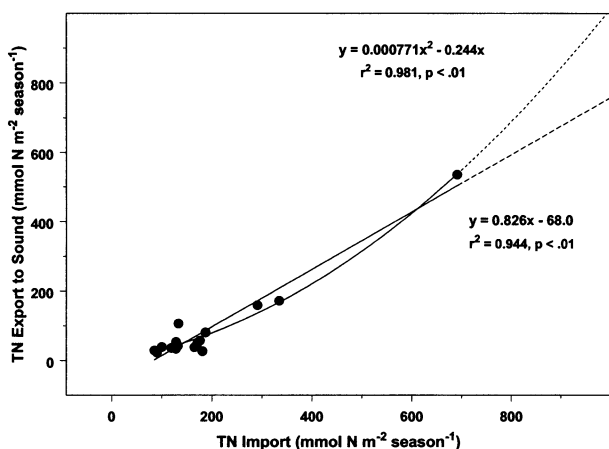
plankton. Chl *a* and K_d were significantly correlated over the whole study period, suggesting that overall, even during the flood, phytoplankton were the main particulate component of light attenuation. While sediment can change light penetration through wind-driven resuspension, we have observed this turbidity to decrease rapidly with reduced wind stress.

Phytoplankton community biomass was enhanced during the flood period (Fig. 2), beginning with a rapid increase from pre-storm chl *a* levels of 5 to 10 μg l^{-1} (Paerl et al. 2001; Ramus et al. 2003). While many variables regulate estuarine phytoplankton (Day et al. 1989), N inputs were the most probable controlling factor for the biomass increase (Paerl 1988; Nixon 1995; Pinckney et al. 1998). Light may have limited production early in the study (euphotic zone ranged from 1 to 2.8 m deep), but after May 2000, light was sufficient throughout the water column. Another river discharge peak in January and February probably supplied enough N to maintain high biomass levels in the winter/spring period, although N concentrations remained low, perhaps because uptake was rapid. After spring 2000, chl *a* decreased and then cycled seasonally. Nutrient limitation could explain the drop in algal biomass, but it is also possible that the grazer community re-established itself and began to strongly influence chl *a* levels. This is supported by observations of large populations of gelatinous and crustacean zooplankton that appeared in net hauls from spring 2000 onward (Kleppel personal communication). The initial phytoplankton bloom was unevenly distributed across the Sound. Peak chl *a* concentrations were found at northern and eastern stations, away from the river mouth, perhaps a result of advection in the flood waters (Tester et al. 2003). As discharge decreased, the phytoplankton biomass maximum shifted towards the western stations and the river mouth. After the flood period, the sound became more homogeneous with respect to chl *a*, but a trend towards higher biomass near the Neuse remained. This pattern may be related to higher nutrient supply or biomass dilution from upstream maxima; the negative correlation between chl *a* and salinity supports the latter possibility.

While chl *a* (total phytoplankton biomass) re-established itself to pre-hurricane levels within about 8 mo (Paerl et al. 2001; Ramus et al. 2003), the phytoplankton community composition proved far more dynamic and changed both spatially and temporally over the study period (Fig. 2). Phytoplankton community composition is controlled by a complex interaction of environmental factors, physiological preferences, competition, and herbivory (Day et al. 1989; Cloern 1996; Pinckney et

al. 1998). The mechanisms driving the observed pattern of community structure are difficult to distinguish, but it is clear that the N loading and lowering of salinity by the floodwaters had a profound effect on the phytoplankton community. The initial post-hurricane community was a mixture of all the taxonomic groups except dinoflagellates. Previous bioassay work using Neuse River phytoplankton assemblages revealed a similar community composition under N enriched conditions (Pinckney et al. 2001). In the sound, green algae and diatoms responded to the floodwaters with dramatic biomass increases, although green algae became a minor component of the community after February 2000. This loss of green algae may have resulted from increased salinity, decreased nutrients, or increased selective grazing. Diatoms maintained biomass dominance throughout the following year. Peak diatom biomass coincided with river discharge peaks, pointing to rapid utilization of external N (Collos 1986; Pinckney et al. 1999). Dinoflagellates, which are a seasonally-dominant component of local estuarine communities (Pinckney et al. 1998; Litaker et al. 2002), had only a modest bloom in the first winter/spring period and were otherwise rare. Either this group could not meet its resource requirements after the flood, or an efficient grazer community kept dinoflagellate biomass low. As a group, cyanobacteria have relatively slow growth rates (i.e., long doubling times) and show a strong preference for relatively warm conditions (> 15°C; Paerl 1999). This is reflected in both their lack of immediate response to the floodwaters and relatively large growth responses throughout the sound during the following two summers (2000 and 2001). It is unclear why cryptomonads maintained a significant presence in the first year, yet were much lower in 2001. Not all the taxonomic groups showed spatial differentiation at all times (Table 3), but for those that did, the pattern found for the whole community applied.

Evaluating the phytoplankton group-specific responses with the concurrent hydrologic and water quality data indicates that physical-chemical drivers are largely responsible for community composition shifts following large climatic perturbations. The combination of salinity, water residence time (flushing), and nutrient availability appears to exert a strong control on the spatial-temporal response of each taxonomic group. Other researchers have also suggested this mechanism to explain phytoplankton community changes in, for example, a Norwegian fjord after an extreme flooding event (Kristiansen 1998) and a seasonal Australian estuary (Chan and Hamilton 2001). When considered in the context of a predicted 10–40 yr in-

crease in Atlantic tropical storm and hurricane activity (Goldenberg et al. 2001), our observations indicate that the higher and more long-lasting incidences of freshening associated with such a scenario may have profound short- and long-term effects on the phytoplankton community supporting the base of these estuarine food webs. Changes in primary producers could produce changes in grazer communities and higher trophic levels (finfish and shellfish), critical elements of Pamlico Sound's ecology and economy. Both finfish and shellfish catches in the sound were depressed in the 2 yr following the storms (Crowder personal communication). Whether the observed changes at the phytoplankton group level have precipitated these changes (via differences in phytoplankton palatability or toxicity) remains to be investigated. If the sound continues to be affected by more frequent and elevated floodwater discharge due to increased storm frequency, this system may further experience phytoplankton community shifts while it is still recovering from previous freshening events. Such climatically driven ecological instability should be investigated with long-term monitoring, food web and fisheries management-oriented research.

The hypoxia created by the floodwaters caused concern for its potential impact on fisheries (Paerl et al. 2001). After a short period of patchy, low DO, the system seemed to return to a seasonal pattern controlled by temperature and water stability (Buzzelli et al. 2002), apparently unrelated to the storms (Fig. 2). Hypoxic events still occurred in the following two summers and some of the lowest DO readings occurred in June and August 2001. These events correlated with high stratification and may have been enhanced by the residual sediment organic matter deposited during and after the storms. Low DO concentrations appeared where stratification was pronounced (e.g., west/north in October and middle/south in December 1999; Fig. 3), but the lowest DO concentration did not always coincide with the highest salinity difference, especially at the east stations where sediments were sandy and organic-poor (Giese et al. 1985). Given that sediment organic matter content varies across the sound (Giese et al. 1985) and there are frequent wind mixing events, hypoxia in Pamlico Sound is probably local and ephemeral as was observed by Woods (1967) in the mid-1960s. The main effect of the storms on DO was to add organic matter to the sediment pool and increase biological oxygen demand.

The nutrient filtering capacity of the Neuse River estuary was significantly reduced during the hurricane period. We estimate that 75–100% of TN loaded from the Neuse River passed through into the Sound during September–December 1999 (Fig. 4). This would be equivalent to 2–3 yr of normal loading as calculated for the 4 yr of study used for the network analysis. In contrast, for the same 4-mo period, the Neuse River estuary received less than 1.5 yr of TN loading based on the years 1985–1989. Paerl et al. (2001) estimated that dissolved inorganic N loading to the Neuse River estuary from September to October 1999 was 71% of annual loading, based on the years 1994–1997. The N loading to the sound is potentially much greater than what would be predicted from calculations of loading to the sub-estuaries and assumptions that the sub-estuaries were functioning as nutrient filters.

The mechanism for reduced filtering capacity appears to be the balance between the time scales of physical transport and biological processing (Christian et al. 1991; Balls 1994; McKee et al. 2000). Nixon et al. (1996) found that among several estuaries, those with longer residence times have higher fractions of N denitrified and lower fractions of N exported. Other studies have documented similar control of N export within individual estuaries, especially tropical and sub-tropical systems dominated by episodic flooding (Eyre and Balls 1999; Eyre 2000). At the extremes of low discharge, low loading, and high residence time during the 1985–1989 study, less than 25% of TN entering the Neuse River estuary was estimated to export into the sound (Christian and Thomas 2000, 2003). Recycling, as indexed through network analysis, was extensive during these times; the average N atom entering the sub-estuary as nitrate was estimated to cycle through phytoplankton over 20 times within the sub-estuary (Christian and Thomas 2000, 2003). When discharge and loading increase and residence time decreases because of major storms, less cycling and removal occurs. If the storm is strong enough, potentially all N entering the sub-estuary can pass through. This prediction is based on extrapolation from network analysis of a data set that did not include such high flow conditions and from a power curve relationship (Fig. 4). We used both a power curve and linear relationship of TN import and export to bracket possible results in the extrapolation. Both curves gave r^2 values greater than 0.9. The results should be considered indicative of what occurred, but within the limitations of extrapolation and curve fitting.

Once past the sub-estuaries, the exported N could have been assimilated and cycled within the Sound or transported, unprocessed out of the system to coastal waters. The freshwater replacement time for the Sound (normally about 11 mo) dropped to less than 2 mo during the storm period

(Bales et al. 2000), but this still would have provid-
ed plenty of time for the alternate possibility of
biochemical filtration (Sharp et al. 1984). We test-
ed this idea by calculating phytoplankton N de-
mand, and found a value very similar to the ex-
trapolated estimates of N exported to the Sound,
suggesting that the biochemical filter could have
converted most of the loaded N to particulate mat-
ter. Assuming the N was immediately transformed
to particulate matter, the fate of that N could be
transfer to higher trophic levels, remineralization
and recycling, storage in sediments, denitrification,
export to the coastal ocean, or some combination
thereof (Day et al. 1989). We hope that continued
work in this system will provide more insight into
these processes.

In comparison to other estuarine flooding
events, the hurricane flooding in Pamlico Sound
produced similar responses. The increase in algal
biomass due to N loading is a typical flood re-
sponse seen in a range of systems (Kristiansen
1998; Eyre 2000; Chan and Hamilton 2001). The
highly episodic nature of the flood resembled the
hydrology of tropical estuaries (Eyre and Balls
1999), although the Sound was never completely
freshened. The Sound has limited connection with
coastal shelf waters, so most of the nutrient and
organic matter processing proceeds within the ba-
sin. In this way, the mass of floodwater in the
Sound resembles shelf waters that receive plumes
from well-flushed estuaries (Balls 1994; Eyre and
Balls 1999). The Sound is much more shallow and
enclosed than shelf waters and is probably more
sensitive to excess nutrient and organic inputs. The
future frequency of this type of extreme event may
control the Sound's resilience to potential eutro-
phication.

This study has provided critical baseline infor-
mation on the Pamlico Sound ecosystem and ex-
tends our understanding of the Sound's sub-estu-
aries (Rudek et al. 1991; Christian et al. 1991; Boy-
er et al. 1993; Paerl et al. 1998; Luettich et al.
2000). The water quality data collected for over 2
yr after the hurricanes revealed a range in recovery
times to more normal conditions from 1 to 2 mo
for dissolved nutrients to about an 8-mo recovery
for particulate matter and salinity. We acknowledge
that normal is difficult to define, particularly since
we have limited pre- and post-hurricane data and
cannot fully evaluate interannual variability. Most
of the other reports on estuaries impacted by hur-
ricanes also indicated rapid recovery, but this usu-
ally meant 3 mo or less (Chesapeake Research
Consortium 1976; Van Dolah and Anderson 1991;
Valiela et al. 1998). While total phytoplankton bio-
mass (chl *a*) returned to pre-hurricane levels with-
in a year, the community composition appeared to

be still changing more than two years later. Costan-
za et al. (1993) suggest that the lack of structure
and prevalence of highly mobile and generalist
species in estuaries creates resilience to distur-
bance. The Pamlico Sound water quality record af-
ter the hurricanes supports this notion of resil-
ience in estuaries. The observed phytoplankton
community structure, however, was less resilient
and took longer to recover, if at all. The commu-
nity shifts may be further affected by a predicted
increase in tropical storm frequency. The biogeo-
chemical and trophic implications of these climatic
and ecological changes may be significant, and still
need to be evaluated, especially at higher trophic
levels (i.e., fish). Continued long-term monitoring
will certainly add to an understanding of this sys-
tem as it responds to additional storm events and
more chronic, anthropogenic disturbances.

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KLEPPEL, G. Personal Communication. Department of Biological Sciences, State University of New York at Albany, 1400 Washington Avenue, Albany, New York 12222.