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Long-term temporal and spatial trends in phytoplankton biomass and class-level taxonomic composition in the hydrologically variable Neuse–Pamlico estuarine continuum, North Carolina, U.S.A.

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Abstract

Phytoplankton diagnostic photopigments in near-surface waters (≈0.5 m) were identified and quantified by high-performance liquid chromatography beginning in April 1994 in the Neuse River Estuary and in October 1999 in the Pamlico Sound, North Carolina. Photopigment concentrations were analyzed using ChemTax to determine the class-specific biomass of the dominant phytoplankton groups. Long-term annual and seasonal trends in phytoplankton biomass and composition were characterized along the river–estuarine continuum and compared to river flow rates, which were variable because of droughts, uncharacteristic seasonal rainfall patterns, and, since 1996, an increase in the frequency of tropical storms and hurricanes. We tested the hypothesis that temporal and spatial patterns of phytoplankton biomass and composition were largely controlled by changes in river flow rate through associated changes in salinity and residence time or through physical transport and advection of phytoplankton classes with river flow along the estuary. Significant interannual, seasonal, and spatial variability in phytoplankton biomass and composition was observed and coincided with variability in river flow rates. The five dominant phytoplankton classes (Chlorophyceae, Cryptophyceae, Cyanobacteria, Bacillariophyceae, and Dinophyceae) were physically displaced downstream during periods of elevated river flow. Dinoflagellates were reduced in abundance during high flow conditions, especially in the upper Neuse River Estuary. The abundance of cyanobacteria was also reduced throughout the system during elevated river flow conditions, although chlorophytes were more abundant. Changes in hydrology can be a useful indicator of seasonal phytoplankton distribution and higher level compositional changes along hydrologic gradients in these and similar systems.

Because of their small size, rapid nutrient uptake and growth rates, specific growth requirements, and susceptibility to grazing, phytoplankton are particularly responsive to variations in environmental condition (Reynolds 1984; Stolte et al. 1994). This sensitivity, combined with their ability to rapidly proliferate in waters affected by anthropogenic (agricultural, urban, and industrial watershed activities) and natural (droughts and elevated rainfall events) disturbances, implies that phytoplankton can be useful indicators of environmental change in freshwater, estuarine, and marine environments (Paerl 1988; Reynolds et al. 1993; Richardson 1997). Deviations from typical phytoplankton abundance and compositional patterns through time and space can thus be used to detect the occurrence of ecological change in estuaries (Malone et al. 1988; Harding 1994). In systems that have been eutrophic for many years and continue to be affected by anthropogenic and climatic perturbations, determining the normal cycles of phytoplankton abundance and composition from which to detect these deviations proves to be difficult. In addition, in many estuarine systems, few data exist on phytoplankton community structure prior to these impacts. In order to distinguish between typical and uncharacteristic temporal and spatial phytoplankton cycles and thus to be able to detect past, present, and future ecological change, long-term, continuous information on phytoplankton community structure is necessary to develop a site-specific reference or baseline condition of phytoplankton community dynamics (Harding and Perry 1997).

Previously, phytoplankton biomass and composition data were acquired by microscopic analysis of water samples. This technique proved to be time-consuming, analyst-specific, and prone to errors (Tester et al. 1995; Mackey et al. 1996). More recently, the use of high-performance liquid chromatography (HPLC) to identify and quantify concentrations of phytoplankton diagnostic photopigments (chlorophylls and carotenoids) and the subsequent analysis of these photopigment concentrations by mathematical computations (multiple linear regression or steepest-descent algorithm using ChemTax), has become

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a quicker and more cost-effective alternative for determining class-specific phytoplankton biomass (Mackey et al. 1996; Pinckney et al. 1997; Paerl et al. 2003). The HPLC–ChemTax approach relies on the specificity of photopigments to major phytoplankton classes. However, some photopigments are frequently present in more than one phytoplankton class, and variations in photopigment type and concentration may occur depending on the physiological state of the phytoplankton (light and nutrient conditions). To account for these discrepancies, this technique relies on the use of photopigment/chlorophyll *a* (Chl *a*) ratios that are specific to phytoplankton cells in the area of study, as well as on the routine verification of HPLC–ChemTax results with microscopy (Tester et al. 1995; Schluter et al. 2000; Lewitus et al. 2005). One disadvantage of the HPLC–ChemTax method is that it cannot determine species-specific biomass; only higher-level (division or class) information on phytoplankton composition can be derived. Previous studies have suggested that these higher levels of biological organization can sometimes prove to be better indicators of environmental condition and effects than species-specific data (Cottingham and Carpenter 1998; Pinckney et al. 2001). Furthermore, in estuarine systems, phytoplankton communities are frequently dominated by one or a few species during bloom events (Pinckney et al. 2001). The composition of these blooms would therefore be adequately classified by the HPLC–ChemTax approach.

The primary objective of this study was to illustrate the long-term temporal and spatial patterns of phytoplankton biomass and class-level composition in the Neuse River Estuary (NRE) and Pamlico Sound (PS). In particular, the study focused on the phytoplankton classes that dominate primary production in the NRE-PS; Chlorophyceae (chlorophytes), Cryptophyceae (cryptophytes), Cyanobacteria, Bacillariophyceae (diatoms), and Dinophyceae (dinoflagellates) (Mallin 1994; Tester et al. 1995). The availability of long-term data will allow us to estimate the patterns of phytoplankton communities in these dynamic systems and thus provide a means to potentially detect short and long-term estuarine ecological change in response to the combined stresses of anthropogenic nutrient enrichment, droughts, and increased tropical storm and hurricane frequency that have affected these systems. In addition, the continuous monitoring of phytoplankton can be used to evaluate the success of nutrient reduction efforts aimed at controlling unwanted symptoms of eutrophication (e.g., nuisance blooms).

The secondary objective was to investigate whether these long-term temporal and spatial patterns in phytoplankton biomass and class-level composition were largely a result of changes in river flow rates that have influenced the NRE-PS continuum through time. Specifically, we used these objectives to test the hypotheses that (1) changes in river flow rates determined phytoplankton class composition as a result of changes in water residence time, salinity, and nutrient concentrations and (2) river flow physically transported or advected all phytoplankton classes along the estuary. The goal was to determine whether certain phytoplankton classes were more abundant during reduced river flow rates that occurred during drought conditions (long water residence time, increased salinity, and reduced nutrient concentrations) whereas other classes were possibly more abundant during periods of increased river flow associated with elevated rainfall events (reduced water residence times and salinity and increased nutrient concentrations). In the Chesapeake Bay, for example, increases in river flow rates have a strong influence on the abundance and distribution of diatoms (Paerl et al. 2006). Increases or decreases in river flow rates may be key determinants of the occurrence, location, magnitude and composition of phytoplankton blooms, because they are directly linked to water residence time, nutrient loading concentrations, and salinity variations, factors known to affect phytoplankton growth rates, distribution, and succession (Harding 1994; Pinckney et al. 1999; Paerl et al. 2006).

The NRE-PS system is an ideal location for investigating the effects of hydrologic variability on the abundance, composition, and spatial distribution of phytoplankton communities, because this microtidal lagoonal system has experienced large variations in freshwater inflow and water residence time caused by recurrent drought periods (1997, 2000–2002) and an increased frequency of tropical storms and hurricanes beginning in 1996. A total of seven hurricanes have impacted coastal North Carolina within the past 8 yr (Paerl et al. 2001, 2006; Peierls et al. 2003). These large-scale natural perturbations have caused large deviations in river flow, estuarine water residence time, salinity, and nutrient concentrations and loads, thereby altering the ecological condition of these systems, and potentially favoring opportunistic phytoplankton groups that exhibit optimal growth during these conditions (Paerl et al. 1995; Peierls et al. 2003; Christian et al. 2004).

Methods

Site characteristics—The NRE-PS continuum is located in coastal North Carolina and comprises the southernmost subestuary of the Albemarle-Pamlico Sound Estuarine System, the second largest estuarine system and largest lagoonal ecosystem in the U.S. (Fig. 1). The NRE-PS watershed has experienced rapid human population growth and development in the past several decades, including the highly urbanized triad of Raleigh, Durham, and Chapel Hill upstream and the intensive row crop agriculture, silviculture, and animal (e.g., hog) production towards the coast (Stow et al. 2001). As a result, the NRE-PS has exhibited the typical signs of eutrophication, including increases in phytoplankton biomass (Chl *a*) and phytoplankton blooms, frequent hypoxic and anoxic conditions, fish kills, and habitat decline (Luettich et al. 2000; Paerl et al. 2004). The NRE is a river-dominated, oligohaline to mesohaline estuarine system with an average depth of 2.2 m. Salinity in the NRE is primarily a function of precipitation, river flow, and wind-driven mixing events. Tidal influence plays only a minimal role in regulating salinity (Luettich et al. 2000). Nitrogen limitation in the NRE increases downstream (Paerl et al. 2004; Piehler et al. 2004) and residence time generally varies from 2 weeks to 3 months during extended periods of drought. Chl *a* concentrations in the NRE are variable and range from less

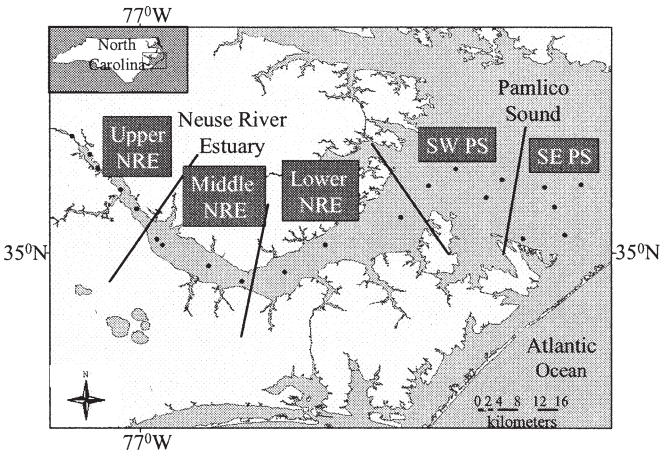

Fig. 1. Map of the Neuse River Estuary–Pamlico Sound system delineating the five geographical regions; Upper NRE (Upper Neuse River Estuary), Middle NRE (Middle Neuse River Estuary), Lower NRE (Lower Neuse River Estuary), SW PS (Southwest Pamlico Sound), and SE PS (Southeast Pamlico Sound). Black dots represent the fixed long-term monitoring stations.

than 1 μg L^{-1} to greater than 100 μg L^{-1}, with an average Chl *a* concentration of approximately 14 μg L^{-1} (Luettich et al. 2000; Paerl et al. 2004). The NRE flows into PS, a large (129 km long and up to 48 km wide) relatively shallow (mean depth $\approx$ 5 m) lagoon separated from the Atlantic Ocean by the Outer Banks barrier island system. Tidal mixing of PS with the Atlantic Ocean occurs through four small inlets (Pietrafesa et al. 1996). The salinity of PS typically ranges from 15 to near 30 (Paerl et al. 2001; Peierls et al. 2003). Because of the disparity between its large size and its limited access to the open ocean, residence times in this system are long, averaging 11 months (Pietrafesa et al. 1996). Its three major riverine tributaries (Neuse, Tar–Pamlico, and Chowan–Roanoke) serve as effective traps for dissolved and particulate nutrients and organic matter (Matson et al. 1983; Luettich et al. 2000; Clesceri 2003), rendering the open Sound a nutrient-deplete, oligotrophic to mesotrophic system, with a mean Chl *a* concentration of approximately 9 μg L^{-1} (Paerl et al. 2001; Peierls et al. 2003). Nitrogen limitation is generally more pronounced and chronic in the PS than in the NRE. Deviations from these conditions have occurred during extended periods of drought and, since the mid-1990s, during flooding events associated with an upsurge in the occurrence of Atlantic tropical storms and hurricanes (Goldenberg et al. 2001) that have impacted the watersheds of the NRE-PS (Paerl et al 2001; Bales 2003; Peierls et al. 2003). In particular, a large pulse of nutrient-laden discharge resulted from the category 2 or greater hurricanes, Dennis, Floyd, and Irene, that affected the area during a 6-week period in fall 1999. This pulse led to a protracted period (at least 9 months) of elevated primary production, with Chl *a* levels exceeding 30 μg L^{-1} in PS (Paerl et al. 2001; Peierls et al. 2003; Tester et al. 2003).

Water quality assessments—Because of the sensitivity of the NRE-PS to the combined effects of anthropogenic and natural disturbances, several continuous water quality monitoring programs were initiated to detect estuarine ecological change in response to these perturbations. Continuous long-term monitoring since 1994 has generated a comprehensive dataset for the NRE-PS that has been used to establish baseline and change information for this study. The Neuse River Bloom Project (Pinckney et al. 1999), the Neuse River Modeling and Monitoring Project (ModMon) (Luettich et al. 2000; Paerl et al. 2004) and the Atlantic Coast Environmental Indicators Consortium Project-ACE-INC (www.aceinc.org) (Paerl et al. 2006) were used as data sources.

Water samples were collected at a depth of approximately 0.5 m from fixed stations located within the NRE-PS and analyzed for primary productivity and nutrient, Chl *a*, and diagnostic photopigment concentrations. Ambient physical and chemical conditions (salinity, temperature, conductivity, dissolved oxygen concentrations, pH, and photosynthetically active radiation levels) were also assessed at each sampling site. To assess the long-term temporal and spatial patterns of phytoplankton community structure, only data pertaining to phytoplankton photopigments were analyzed in this study.

To determine the spatial distribution of the phytoplankton classes along the NRE-PS river–estuarine continuum, the study area was divided into five geographical regions: upper, middle, and lower NRE (Upper NRE, Middle NRE, and Lower NRE, respectively) and southwest and southeast PS (SW PS and SE PS, respectively) (Fig. 1). These spatial delineations also reflect changes in the temporal sampling of this system, as the sampling of each region began at different times. The Upper NRE and Middle NRE regions of the NRE have been continuously monitored for water quality parameters on a biweekly basis since 1994. The Upper NRE encompasses the narrow upper portion of the estuary and represents the area where the majority of nutrients are delivered to the estuary with river flow. The Middle NRE region was characterized as the area where the estuary begins to broaden until just upstream of where the river bends in a northeast direction. This region tends to accumulate the highest concentrations of Chl *a* because of the widening and increased residence time that occurs at this location (Luettich et al. 2000; Buzzelli et al. 2002). Sampling was later spatially extended downstream in 1997 by incorporating the lower portion of the NRE (Lower NRE) in the routine monitoring. The Lower NRE region includes the section of the river downstream of the bend and continuing to the mouth of the river before it drains into PS. In October 1999, immediately following the three sequential hurricanes, water quality monitoring was extended into the southern portion of PS. Initially, 10 stations were sampled monthly in PS. The number of PS stations was reduced to nine in March 2000. This southern portion of PS that is adjacent to the mouth of the NRE was divided into two regions: SW PS and SE PS. The data presented in this study include data from all five regions through December 2003.

Concentrations of diagnostic phytoplankton photopigments—Phytoplankton photopigments (chlorophylls and carote-

noids) generally representative of specific phytoplankton taxa were separated and quantified using high-performance liquid chromatography (HPLC, Spectra-Physics SP8800) coupled to an inline photodiode array spectrophotometer (Shimadzu SPD M10av) (Tester et al. 1995; Jeffrey et al. 1997). Up to a liter of water sample was vacuum-filtered using 47-mm glass fiber filters (Whatman GF/F) to generate sufficient pigment concentrations for detection and analysis. Filters were subsequently frozen and stored at −80°C prior to analysis. Photopigments were later extracted from the frozen filters by placing them in 100% acetone, followed by sonication and storage at 20°C for 12–24 h. Extracts (200 μL) were injected into the HPLC for analysis. The HPLC column configurations and pigment separation procedures are described in Pinckney et al. (1996, 1998, 2001). Photopigments were identified according to their characteristic absorption spectra as determined from pure crystalline pigment standards (Sigma Chemical Company and Hoffman-LaRoche and Company) or from pigments extracted from phytoplankton cultures (Wright et al. 1991).

ChemTax analysis—Photopigment concentrations were subsequently analyzed using ChemTax, a matrix factorization program that determines the absolute and relative contribution of specific phytoplankton taxonomic groups to the total Chl *a* pool based on an initial pigment ratio matrix specific to the study area (Mackey et al. 1996, 1997). The initial pigment ratio matrix used in this study was obtained from a matrix characteristic of coastal phytoplankton groups (Mackey et al. 1996) and consisted of nine photopigments (alloxanthin, antheraxanthin, chlorophyll b, total Chl *a* [Chl *a* + chlorophyllide a], fucoxanthin, lutein, peridinin, violaxanthin, and zeaxanthin) indicative of five algal groups: chlorophytes, cryptophytes, cyanobacteria, diatoms, and dinoflagellates. To minimize the variation in pigment ratios that accompany changes in phytoplankton species composition with season and salinity regime, homogenous data groupings of the HPLC-derived photopigment concentrations were delineated prior to running on ChemTax. Pigment concentrations were grouped by season (winter, spring, summer, and fall) and then by salinity regime (oligohaline [<5.0], mesohaline [5.01–18.0], and polyhaline [>18.01]).

Although species composition as determined from microscopy would have generated more in-depth information on changes in phytoplankton composition through time, class-specific phytoplankton abundance as determined by the HPLC–ChemTax procedure was used in order to be able to most effectively analyze and interpret the large amount of long-term photopigment data that was collected.

River flow rates—Daily means of Neuse River flow rates were obtained from a long-term (1930–present) United States Geological Survey streamflow gauging station located approximately 20 km upstream of the Neuse River Estuary, near Kinston, North Carolina (Station 02089500). Because of the long-term data available from this station, and its proximity to the Neuse River Estuary, this station has been routinely used for estimating river flow and nutrient loading into the Neuse River Estuary (Bales 2003; Peierls et al. 2003).

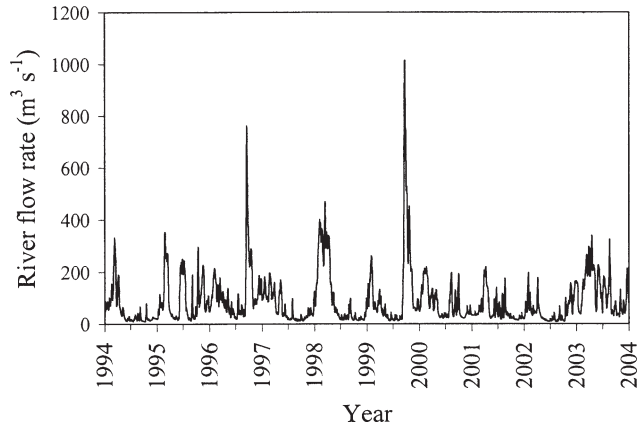

Fig. 2. Daily means of Neuse River flow rates measured by the United States Geological Survey at Kinston, North Carolina (USGS Station No. 02089500).

Data analysis—Phytoplankton community structure data were averaged by year, season, and the previously mentioned five regions of the NRE-PS. These means were compared to mean annual river flow rates. The seasonal classifications used were: winter (December through February), spring (March through May), summer (June through August), and fall (September through November). Class-specific phytoplankton abundance was also correlated to the average daily river flow rate on the day of sampling (T0). In addition, to account for the time lags of river flow effects downstream, phytoplankton abundance was also directly related to average daily river flow rates 1 (T1), 2 (T2), 3 (T3), and 4 (T4) wk prior to the sampling date. This helped determine the approximate length of time that each phytoplankton class responded to changes in river flow rate in each region of the NRE-PS.

All statistical tests were performed using the statistical package SPSS for Windows, version 11.5 (SPSS Inc.). Because of the violations of the assumptions for parametric statistical testing, nonparametric statistical analyses were performed for all parameters to account for the lack of parameter normality, unequal group variances, and unequal sample number between groups. For each parameter, Kruskal–Wallis or Mann–Whitney nonparametric tests were performed to test for significant differences in phytoplankton community structure between years, seasons, and regions of the NRE-PS. Nonparametric Spearman correlations were also performed to relate the abundance of the five phytoplankton classes to river flow. An alpha level of 0.05 was used for all hypotheses testing except where noted.

Results

Neuse River flow rates—Mean daily river flow rates (m^3 s^{-1}) were highly variable during the 1994–2003 study period (Fig. 2). In particular, three large peaks in river flow rates were prominent. These peaks resulted from elevated

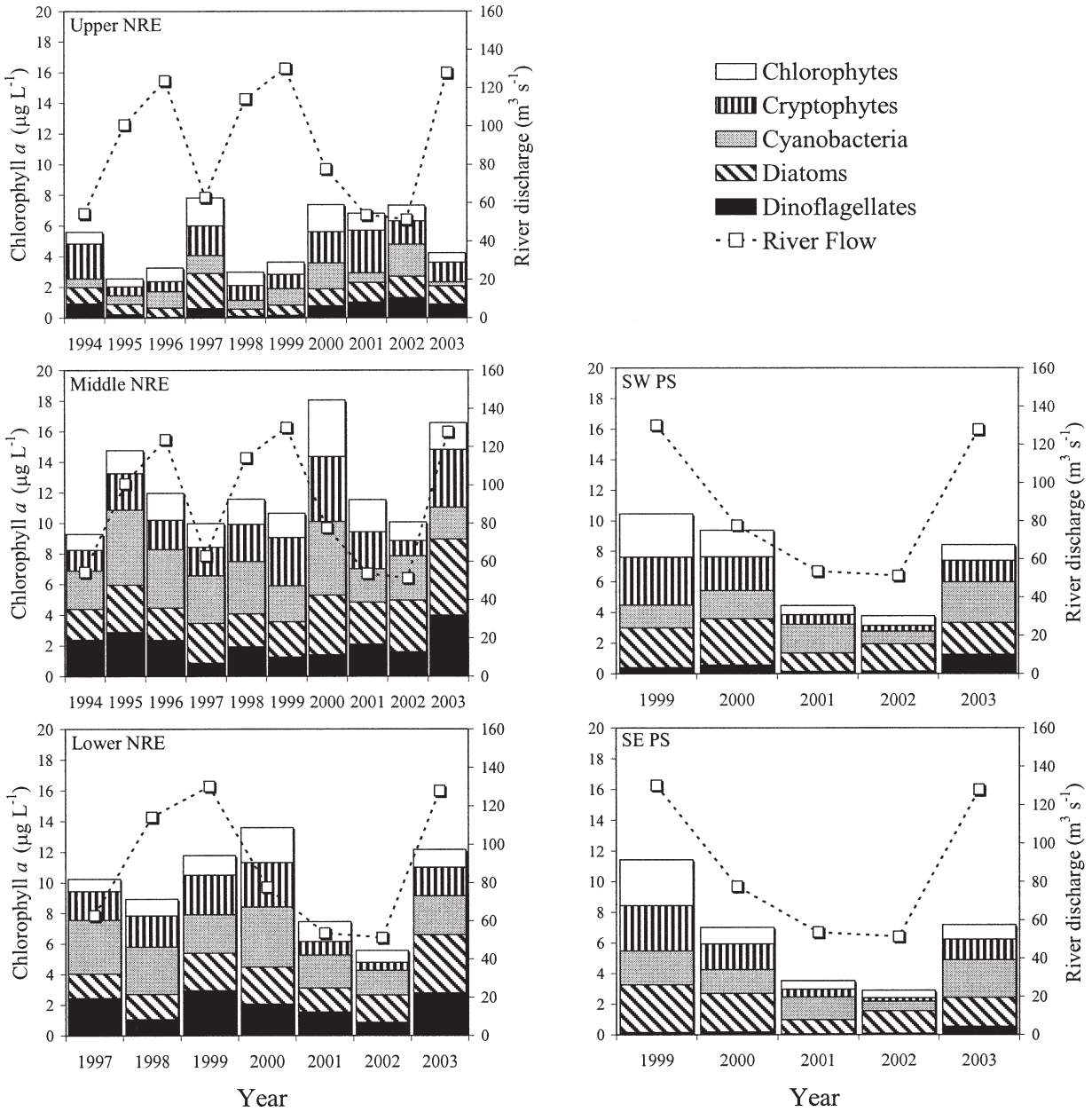

Fig. 3. Mean annual abundance of chlorophytes, cryptophytes, cyanobacteria, diatoms, and dinoflagellates as determined from ChemTax analysis of HPLC-derived diagnostic photopigment concentrations for all five regions of the NRE-PS river–estuarine continuum. Mean annual total Chl *a* concentrations are represented by the total length of each bar. The dashed line refers to mean annual river flow rate (see Fig. 2).

rainfall associated with Hurricane Fran in September 1996 (762 $m^3 s^{-1}$), an abnormally wet winter-spring in 1998 (470 $m^3 s^{-1}$), and the three consecutive hurricanes in fall 1999 (1,014 $m^3 s^{-1}$). Interspersed between these peaks in river flow were periods of extended drought, specifically during the summer and fall months of 1994 and 1997 (also an El Niño year), during fall 1998, during summer 1999, and during 2000–2002, when river flow rates were comparatively reduced, especially during the summer months. These hydrologic events caused significant interannual ($p < 0.001$) and seasonal ($p < 0.001$) variability in river flow rates. Overall, elevated mean annual river flow rates were observed for 1995 (101 $m^3 s^{-1}$), 1996 (124 $m^3 s^{-1}$), 1998 (114 $m^3 s^{-1}$), 1999 (130 $m^3 s^{-1}$), and 2003 (128 $m^3 s^{-1}$), whereas reduced river flow was observed for 1994 (54 $m^3 s^{-1}$), 1997 (63 $m^3 s^{-1}$), and 2000–2002 (78 $m^3 s^{-1}$, 54 $m^3 s^{-1}$, and 51 $m^3 s^{-1}$, respectively) (Fig. 3). During the 10-yr study, river flow rates were not significantly different between winter and spring months ($p = 0.504$) and were significantly greater during the winter ($p < 0.001$) and spring ($p < 0.001$) than during the fall (data not shown). Summer river flow rates were significantly reduced when compared to the other seasons ($p < 0.001$).

Annual trends—During 1994–2003, significant interannual variability in total Chl *a* concentrations, an indicator of total phytoplankton biomass, and in the mean abundance of chlorophytes, cryptophytes, cyanobacteria, diatoms, and dinoflagellates was observed within each of the five regions of the NRE-PS ($p < 0.001$) (Fig. 3). Annual total and class-specific Chl *a* trends also differed between the five regions. In the Upper NRE, mean annual total Chl *a* concentrations and class-specific algal abundances (except cyanobacteria) were higher during years characterized by reduced mean annual river flow rates than during elevated river flow years. This inverse relationship between mean annual total Chl *a* concentrations and mean annual river flow rates was not observed in the other four regions of the NRE-PS. In fact, the opposite effect was observed at the other extreme of the system in the SW PS and SE PS regions, where annual trends in total Chl *a* concentrations closely paralleled changes in mean annual river flow rates. In the Upper NRE, the mean annual abundance of dinoflagellates was, in particular, reduced during the elevated river flow rate years of 1995 (0.21 μg L^{-1}), 1996 (0.05 μg L^{-1}), 1998 (0.09 μg L^{-1}), and 1999 (0.16 μg L^{-1}). In this region, chlorophytes demonstrated greater mean annual abundances during dry years that immediately followed hurricane years, specifically in 1997 (1.82 μg L^{-1}) and 2000 (1.77 μg L^{-1}). Diatoms also showed a large peak in mean annual abundance during the reduced river flow year of 1997 (2.28 μg L^{-1}). Contrary to these groups, cyanobacteria in the Upper NRE region did not demonstrate a clear relationship between abundance and mean annual river flow rates.

The Middle and Lower NRE regions demonstrated very similar interannual patterns in total Chl *a* concentrations during the extended drought period that occurred from 2000 through 2002 and during the high flow year of 2003 (Fig. 3). Only during these years (2000–2003) were mean annual total Chl *a* concentrations in these two regions positively related to mean annual river flow rates. In 2000, the year following the passage of the three sequential hurricanes in fall 1999, mean annual total Chl *a* concentrations and the abundance of chlorophytes, cryptophytes, and cyanobacteria in the Middle NRE and Lower NRE were considerably higher when compared to the other years studied. After 2000 and coinciding with a decrease in mean annual river flow rate, annual total Chl *a* concentrations incrementally decreased with each successive year through 2002 in these regions. In 2003, when river flow rates were once again elevated, total Chl *a* concentrations in both regions once again increased. Contrary to these patterns, the Upper NRE demonstrated consistently elevated mean annual total Chl *a* concentrations throughout 2000–2002 (>6.8 μg L^{-1}) and a reduced mean annual Chl *a* concentration in 2003 (4.2 μg L^{-1}).

The two PS regions, SW PS and SE PS, demonstrated very similar interannual trends in mean annual total Chl *a* concentrations and class-specific algal abundance (Fig. 3). Mean annual total Chl *a* concentrations and the abundance of all phytoplankton classes studied were greater immediately following the three sequential hurricanes in fall 1999 than during the reduced flow rate period (2000–2002). After fall 1999 and similar to what was observed in the Middle NRE and Lower NRE regions, mean annual total Chl *a* concentrations and the mean annual abundance of all phytoplankton classes in these two regions decreased with each successive year through 2002 . Then, coinciding with the increase in mean annual river flow rate in 2003, mean annual total Chl *a* concentrations and the abundance of all phytoplankton classes, especially cyanobacteria and dinoflagellates, considerably increased. Overall, mean annual phytoplankton community structure in the two regions of PS changed from a community dominated by chlorophytes, cryptophytes, and diatoms in fall 1999 and 2000 to one primarily dominated by cyanobacteria and diatoms during 2001–2003. The community structure observed in these latter years may be more reflective of the typical community composition of PS.

Seasonal trends—With the exception of the Lower NRE region, significant seasonal variability in mean total Chl *a* concentrations was observed in each region of the NRE-PS ($p < 0.032$) (Fig. 4). Overall, in the Upper NRE and Middle NRE regions, mean total Chl *a* concentrations were significantly greater in the summer than during the other seasons ($p < 0.001$), whereas average total Chl *a* concentrations in the two PS regions were greatest during the fall.

Diatoms were the dominant phytoplankton class during the winter and spring months throughout all regions of the NRE-PS except the Upper NRE, which showed dominance by chlorophytes in the spring (Fig. 4). Cyanobacteria were the most abundant phytoplankton group during the summer in all five regions, when river flow rates were reduced, water temperatures were warmer, and water residence times were longer (Fig. 4). During the fall, the phytoplankton community structure throughout the NRE-PS was comprised primarily of cryptophytes in the Upper NRE, whereas in the Middle NRE and Lower NRE regions all phytoplankton groups contributed nearly equal percentages to total Chl *a* concentrations (Fig. 4). The two PS regions also demonstrated equal proportions of all phytoplankton classes during the fall, with the exception of dinoflagellates, which showed reduced mean abundance.

Spatial trends—Regardless of season, the highest average total Chl *a* concentrations in the NRE-PS occurred in the Middle NRE region (>11.4 μg L^{-1}; Fig. 4). Specifically, mean total Chl *a* concentrations were significantly greater in the Middle NRE region than in the other regions during the spring ($p < 0.004$) and summer ($p < 0.001$) months. Downstream of the Middle NRE, mean total Chl *a* concentrations decreased with each successive region. Mean total Chl *a* concentrations were significantly lowest in the Upper NRE ($p < 0.030$) during all seasons except summer, when mean total Chl *a* concentrations in the Upper NRE were comparable to mean total Chl *a* concentrations in the SE PS region ($p = 0.261$).

Spatial differences in phytoplankton community structure were attributed primarily to changes in dinoflagellate abundance throughout the NRE-PS (Fig. 4). Regardless of season, average dinoflagellate abundance was greatest in the Middle NRE and Lower NRE regions when compared

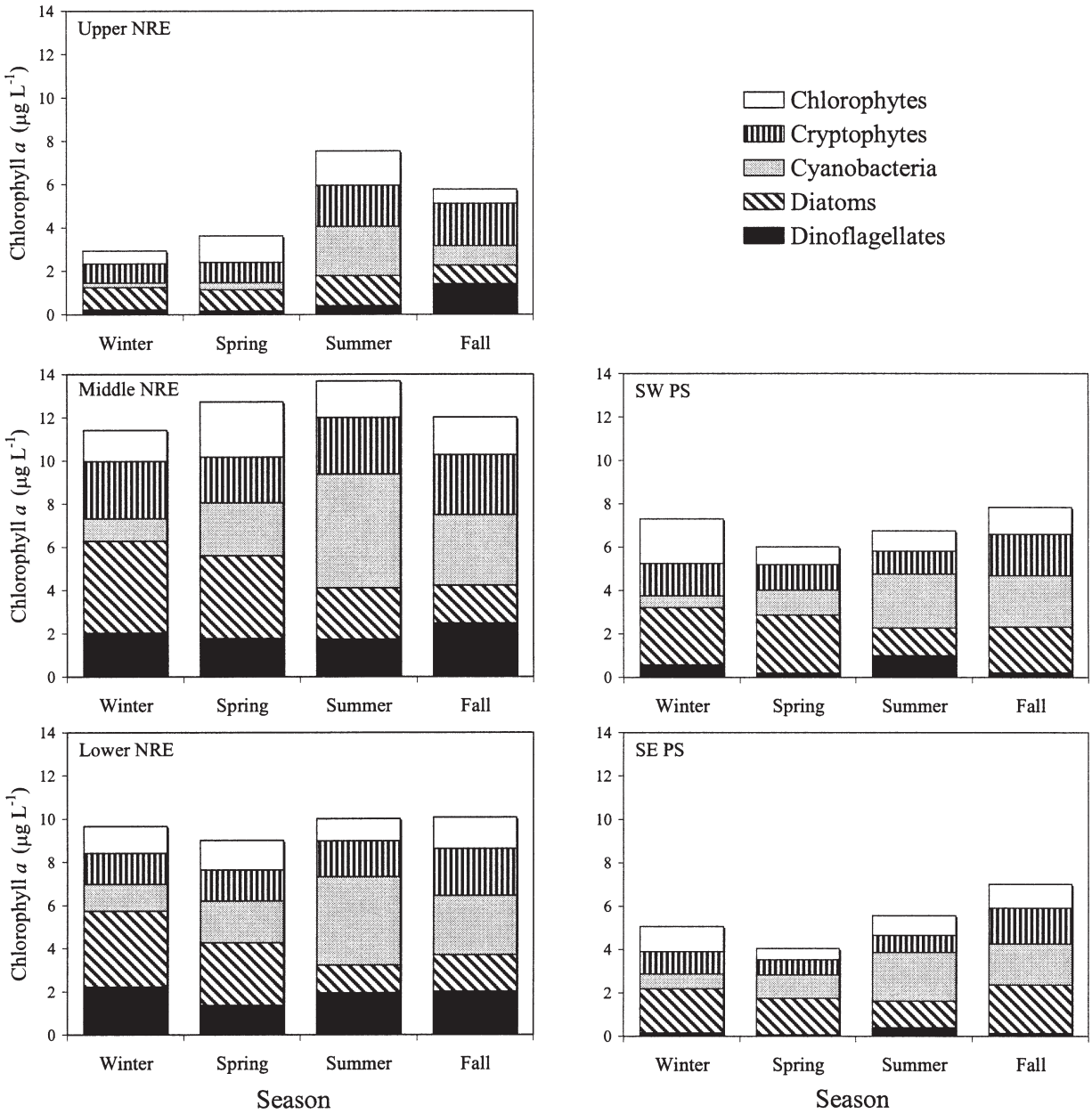

Fig. 4. Seasonal mean abundance of each phytoplankton class and of total Chl *a* concentrations in the five regions of the NRE-PS.

to the other regions. Moreover, the average abundance of dinoflagellates was not significantly different between these two regions ($p > 0.233$). The only exception to this pattern occurred during the winter months, when mean dinoflagellate abundance in the SW PS region was not significantly different from that observed in the Middle NRE ($p = 0.354$) and Lower NRE ($p = 0.141$) regions.

Table 1 illustrates the average percent contribution of chlorophytes, cryptophytes, cyanobacteria, diatoms, and dinoflagellates to total Chl *a* concentrations in each of the five regions of the NRE-PS for all years combined. Overall, dinoflagellates comprise a greater proportion of the phytoplankton community in the NRE regions than in the PS regions, whereas diatoms contribute more to total Chl *a* concentrations in the PS regions than in the NRE regions. Diatoms were also the dominant phytoplankton group in the PS regions. In the Upper NRE, cryptophytes were the most dominant phytoplankton group, whereas cyanobacteria and diatoms were the most dominant groups in the Middle NRE and Lower NRE regions.

Correlations between class-specific phytoplankton abundance and river flow rate—In the Upper NRE, the abundance of all phytoplankton classes was significantly ($p < 0.05$) and negatively correlated with river flow rates at all time points (T0, T1, T2, T3, and T4; Table 2). Furthermore, the strength of the correlations decreased with increases in time lags of river flow rate; correlations were stronger at instantaneous river flow rates (T0) than at

Table 1. Percent contribution of each phytoplankton class to total Chl *a* concentrations in each region of the NRE-PS. Results are for all data combined.

Region	Chlorophytes	Cryptophytes	Cyanobacteria	Diatoms	Dinoflagellates
Upper NRE	21	28	19	21	11
Middle NRE	15	20	25	24	16
Lower NRE	13	17	27	23	20
SW PS	18	21	24	30	7
SE PS	17	20	27	33	3

river flow rates 1–4 wk prior to the sampling date (T1–T4). These relationships were not as evident in the four other regions of the NRE, because significant correlations became less apparent downstream, with very few significant correlations in the two PS regions. In the three NRE regions, the abundance of cyanobacteria was significantly ($p < 0.05$) and inversely related to both instantaneous and lagged river flow rates. With the exception of the Upper NRE region, chlorophytes, cryptophytes, and diatoms were positively correlated with river flow rate in all regions of the NRE-PS.

Discussion

The degree to which the interactions of flow and nutrient supply mediate estuarine phytoplankton abundance and compositional responses to environmental perturbations varies. In river-dominated estuaries like the NRE, distinguishing the effects of flow and nutrients on phytoplankton community structure is highly problematic because of their frequent linkage and the role that flow plays in controlling other variables such as salinity and turbidity (Borsuk et al. 2004). When high flow reduces residence time below phytoplankton growth rates, loss through physical advection can control the accumulation of phytoplankton biomass (Cloern et al. 1985). Advective loss of phytoplankton from the upper reaches of temperate estuaries is commonly observed during high flow periods (Fisher et al. 1988; Gallegos et al. 1992). Other physical conditions associated with pulses of storm discharge to estuaries have negative effects on phytoplankton, including turbidity increasing light attenuation (Cloern 1987; Ritzrau and Graf 1992) and increased mixing depths decreasing the time phytoplankton spend in euphotic conditions.

Table 2. Spearman correlation coefficients for relationships between the abundance of each phytoplankton class and river flow rates on the day of sampling (T0) and 1 (T1), 2 (T2), 3 (T3) and 4 (T4) wk prior to the day of sampling.

Region		T0	T1	T2	T3	T4
Upper NRE	Chlorophytes	−0.434**	−0.330**	−0.224**	−0.165**	−0.160*
	Cryptophytes	−0.540**	−0.445**	−0.400**	−0.354**	−0.343**
	Cyanobacteria	−0.631**	−0.604**	−0.503**	−0.472**	−0.455**
	Diatoms	−0.482**	−0.399**	−0.281**	−0.269**	−0.262**
	Dinoflagellates	−0.598**	−0.556**	−0.464**	−0.442**	−0.418**
Middle NRE	Chlorophytes	0.066	0.136*	0.177**	0.169**	0.188**
	Cryptophytes	0.207**	0.226**	0.183**	0.119	0.096
	Cyanobacteria	−0.449**	−0.432**	−0.412**	−0.389**	−0.360**
	Diatoms	0.120	0.133*	0.102	0.092	0.092
	Dinoflagellates	−0.138*	−0.167**	−0.177**	−0.140*	−0.123
Lower NRE	Chlorophytes	0.281**	0.288**	0.292**	0.290**	0.304**
	Cryptophytes	0.172*	0.207**	0.228**	0.237**	0.212**
	Cyanobacteria	−0.303**	−0.347**	−0.293**	−0.314**	−0.257**
	Diatoms	0.380**	0.445**	0.425**	0.384**	0.366**
	Dinoflagellates	0.144	0.162*	0.137	0.179*	0.144
SW PS	Chlorophytes	0.263	0.384*	0.321*	0.354*	0.362*
	Cryptophytes	0.042	0.283	0.313*	0.327*	0.400**
	Cyanobacteria	−0.241	−0.064	−0.138	−0.018	−0.031
	Diatoms	0.290	0.277	0.358*	0.251	0.362*
	Dinoflagellates	−0.007	−0.051	0.036	−0.066	0.036
SE PS	Chlorophytes	0.259	0.389**	0.341*	0.409**	0.403**
	Cryptophytes	0.097	0.318*	0.377*	0.292	0.421**
	Cyanobacteria	−0.132	0.064	−0.069	0.032	0.032
	Diatoms	0.295	0.326*	0.388*	0.270	0.345*
	Dinoflagellates	−0.043	−0.067	0.027	−0.099	0.022

* $p<0.05$; ** $p<0.01$.

The data presented here indicate that phytoplankton community structure in the NRE-PS was profoundly affected by changes in hydrology that resulted from droughts and/or large pulses in river flow associated with seasonal increases in rainfall or with tropical storms and hurricanes. This was especially evident at the two endpoints of our study area, in the Upper NRE, SW PS, and SE PS regions. Overall, elevated river flow rates were associated with reduced phytoplankton biomass and class-specific algal biomass in the Upper NRE region. Downstream of the Upper NRE, the reverse effect was observed; total phytoplankton biomass and the biomass of chlorophytes, cryptophytes, cyanobacteria, diatoms, and dinoflagellates were increased during conditions of elevated river flow rates. Conversely, during reduced river flow conditions, phytoplankton biomass was increased at upstream locations, where nutrient limitation is minimized. These trends suggest that phytoplankton were physically transported downstream during conditions of elevated river flow, an observation similar to those made by Malone et al. (1988) and Harding (1994) for the Chesapeake Bay and by Borsuk et al. (2004) for the NRE. With recent predictions of increased tropical storm and hurricane activity (Goldenberg et al. 2001), the elevated rainfall and river flow rates associated with these disturbances may increase phytoplankton biomass in the currently oligotrophic to mesotrophic regions of the estuarine continuum, especially in the PS. Increases in river flow rates can be used as an indicator of reduced biomass of all dominant phytoplankton classes in the Upper NRE and increased biomass of all groups downstream of this region. The reverse applies to reduced river flow rates.

The inherent characteristics of the Upper NRE region provide an explanation as to why phytoplankton abundance was reduced in this area of the estuary only when river flow rates were elevated. The Upper NRE region is closer in proximity to the station where instantaneous river flow rates are measured. As a result, time lags between when river flow rates are changed upstream and when this effect is observed in the estuary are shorter in the Upper NRE region compared to the other regions. It takes a greater amount of time for increases in river flow rates to be observed in the more downstream regions of the estuary; thus, phytoplankton community responses will typically lag in these regions in comparison to the Upper NRE. The Upper NRE region is also narrower than the other regions. As a result, flushing rates in this region are faster than those observed in the other four regions of the estuary. Because of these features, the relationship between phytoplankton abundance and river flow rates is more rapid and stronger in the Upper NRE region than in the other NRE-PS regions.

Dinoflagellates were especially reduced in abundance during periods of elevated river flow and reduced water residence time in the Upper NRE. Dinoflagellates appear to be both sensitive and ecologically relevant indicators of changes in hydrology in the Upper NRE, because they are consistently more abundant during periods of long residence time, when flushing rates are minimal. Unlike dinoflagellates, cyanobacteria in the Upper NRE region did not demonstrate a clear relationship between abundance and mean annual river flow rates. The reason for this is that cyanobacteria dominate phytoplankton composition during the summer months, when river flow rates are greatly reduced. By focusing on annual means, this pattern was concealed. However, when the abundance of cyanobacteria was compared to instantaneous and lagged river flow rates, their abundance was always reduced with increases in river flow rates. These results imply that class-specific phytoplankton abundance is strongly regulated by river flow rates.

In the SW PS and SE PS regions, river flow rates increased phytoplankton abundance, especially following the occurrence of large climatic events such as the fall 1999 hurricanes. The observed trends in phytoplankton community structure have demonstrated how phytoplankton classes are sensitive to these shorter-term climatic perturbations. For example, after the occurrence of these storms, mean annual total Chl *a* concentrations in both PS regions declined with each successive year through 2002, indicating that this system may have still been recovering from the effects of these hurricanes up to 3 yr later. This supports the suggestion of Peierls et al. (2003) that floodwaters associated with large hurricane events are followed by multiannual periods of phytoplankton community recovery, gauged as a return to prehurricane biomass data. In the SW PS and SE PS regions, greater mean annual total Chl *a* concentrations were observed in years characterized by elevated river flow rates, whereas decreased Chl *a* concentrations were observed during low flow years. During elevated river flow rates generated from large rainfall pulses (i.e., hurricanes), the phytoplankton abundance of all groups is increased in PS. In addition, recovery from these pulses in river flow may still be occurring 3 yr following the event. These results demonstrate the short- and long-term impacts that these storms can have on phytoplankton biomass and composition in these systems.

In the NRE, phytoplankton community structure was also strongly impacted by these hurricane events. Large peaks in phytoplankton biomass were observed in 2000, the year immediately following the hurricanes in the Middle NRE and Lower NRE regions. Conditions following the hurricanes were particularly favorable for the growth of chlorophytes. In the Upper NRE, chlorophytes demonstrated greater mean annual abundances during the winter–spring months that immediately followed hurricane years, specifically in 1997 and 2000. Nutrients that were delivered from the effects of these fall storms may have remained in the system until the following spring.

The results from this study suggest that the abundance and distribution of chlorophytes, cryptophytes, cyanobacteria, diatoms, and dinoflagellates are regulated to a large extent by the physical effects of changes in river flow (hydrology and flushing). All phytoplankton groups were advected downstream with increases in river flow. This was also observed by Borsuk et al. (2004) in the NRE. Contrary to those results, however, both chemical (nutrient loading) and physical factors (residence time) were found to regulate phytoplankton in the Suwannee River Estuary, Florida (Bledsoe et al. 2004). Spatially, the highest mean annual

total Chl *a* concentrations in the NRE-PS occurred in the Middle NRE region. Phytoplankton biomass had previously been shown to accumulate in this region because of its physical features and the frequent stratification that occurs in this region (Paerl et al. 1995; Luettich et al. 2000).

Trends in phytoplankton community structure were previously documented during 1994–1996 by Pinckney et al. (1998) for the Upper NRE and Middle NRE regions. Over those 3 yr, phytoplankton composition in these regions was found to be divided fairly evenly among chlorophytes, cryptophytes, cyanobacteria, diatoms, and dinoflagellates (e.g., 17%, 23%, 18%, 20%, and 22%, respectively). Analogous to those findings, dominance by one or a few phytoplankton taxonomic groups was not observed in any region of the NRE-PS system during this 10-yr study. However, there were slight differences in the contributions of cyanobacteria, diatoms, and dinoflagellates to total Chl *a* concentrations between the 1994–1996 study and this 1994–2003 study for the combined Upper NRE and Middle NRE regions; the percentage contribution of cyanobacteria and diatoms increased slightly from 18% to 24% and from 20% to 24% for these groups respectively. The contribution of dinoflagellates, however, decreased from 22% during 1994–1996 to 14% during 1994–2003. Because dinoflagellates' abundance is generally reduced during periods of high river flow and reduced water residence times, the increase in the frequency of tropical storms and hurricanes in the more recent years may be reducing the abundance of dinoflagellates in the two uppermost regions of the system. This shift is likely to have food web ramifications, because crustacean zooplankton grazers in the NRE are known to prefer dinoflagellate genera (*Heterocapsa*, *Gymnodinium*, and *Scrippsiella*) that dominate this phytoplankton group (Mallin and Paerl 1994). In addition, such hydrologically-forced shifts in phytoplankton community structure are likely to have biogeochemical effects, including changes in sediment carbon flux and hypoxia dynamics (Paerl et al. 1998).

These results have strengthened our understanding of phytoplankton community responses to hydrologic forcing and stress the importance of incorporating variability in river flow as a major factor in management strategies. Long-term analyses like the one presented here serve as a baseline from which to compare future ecological condition and assess change. Long-term monitoring of phytoplankton photopigments is a broadly applicable tool for examining and separating the impacts of these physical–chemical forcings. The methods for determining the abundance of each phytoplankton group are cost-effective and can be incorporated into already existing water quality monitoring programs. Discharge may be an indicator of phytoplankton biomass and community structure in estuarine systems worldwide that are affected discretely or simultaneously by natural (hydrologic) and anthropogenic factors.

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