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Phytoplankton and nutrient dynamics in a tidally dominated eutrophic estuary: daily variability and controls on bloom formation

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ABSTRACT: To better understand nutrient dynamics and factors that promote the initiation of algal blooms, the Lafayette River, a tidal subestuary of Chesapeake Bay that experiences seasonal algal blooms, was sampled daily for a period of 54 d in the fall of 2005. Three phytoplankton blooms (chl a concentrations exceeding twice the average of monthly measurements from 2000 to 2009) occurred during this period: a mixed bloom of *Akashiwo sanguinea* and *Gymnodinium* sp., a monospecific *Skeletonema costatum* bloom, and a monospecific *Gymnodinium* sp. bloom. Over the sampling period, nutrient concentrations increased following precipitation events and were elevated between bloom periods but low during blooms. All measured forms of nitrogen (N) were positively correlated with dinoflagellate abundance with a lag time of 3 to 5 d, suggesting a possible triggering effect, although not by any single form of N. Concentrations of NO_2^- reached 10 µM between September and October, indicative of incomplete nitrification. Over a 24 h period, nutrient concentrations and chl a biomass varied by an order of magnitude (0.1 to 1 µM N and 4.5 to 45 µg chl a l^{-1}, respectively) and were strongly linked to the tidal phase. In the highly eutrophic Lafayette River, when nutrient concentrations are high, phytoplankton blooms appear to be controlled by spring-neap tidal modulation and wind-driven mixing; however, picoplankton abundance does not appear to be linked to the spring-neap tidal cycle.

KEY WORDS: Nutrient dynamics · Bloom formation · Dinoflagellates · Estuarine variability · Nitrite · Nitrification · Nitrogen

INTRODUCTION

Since the early 1800s, Chesapeake Bay and its tributaries have experienced a decrease in water quality characterized by decreased overall diversity of diatom species, increased occurrences of anoxic events, increased rates of sedimentation (Cooper & Brush 1991, 1993, Kemp et al. 2005), and a shift from benthic to pelagic production. The latter has been associated with an increase in the ratio of centric to pennate diatoms and a decrease in water clarity (Cooper & Brush 1993). Over the last 20 yr, sections of the lower Chesapeake Bay and its tributaries have experienced a decrease in phytoplankton diversity and an increase in the abundance of potentially harmful algal taxa (Dauer et al. 2005, Marshall et al. 2005). Algal blooms occur seasonally in Chesapeake Bay and its tributaries, and many of the bloom-forming taxa are potentially harmful or toxin-producing species (Marshall et al. 2005, 2009). Since 2007, major blooms of the harmful dinoflagellate *Cochlodinium polykrikoides* have occurred annually during summer in the lower Chesapeake Bay and its tributaries (Mulholland et al. 2009, Morse et al. 2011, 2013).

Worldwide, algal blooms appear to be increasing in frequency because of cultural eutrophication (Paerl 1988, Smayda 1990, Pinckney et al. 2001). Eutrophication from nutrient over-enrichment, usually attrib-

uted to nitrogen (N) and/or phosphorus (P), is often implicated as a causative factor in the formation of both harmful and ecosystem-disrupting algal blooms (EDABs) (Anderson et al. 2002, 2008, Sunda et al. 2006, Heisler et al. 2008). Blooms have also been linked to perturbations in the ratios at which inorganic nutrients are input relative to the Redfield ratio (N:P of 16:1) (Hodgkiss & Ho 1997). Elevated ratios of dissolved organic carbon (DOC) to dissolved organic nitrogen (DON) (DOC:DON) (Heil et al. 2001, Lomas et al. 2001, Anderson et al. 2002) have also been implicated in bloom formation, while elevated N:silica (Si) or P:Si ratios are thought to select for dinoflagellates over diatoms (Smayda 1990, 1997). In contrast, the development of many EDABs has also been linked to prolonged periods of lower than normal nutrient concentrations (Gobler et al. 2005, Sunda et al. 2006). This may be because of a positive feedback scenario, where a noxious or otherwise unpalatable EDAB species experiences decreased grazing pressure, and thus nutrient recycling and availability are reduced to competing taxa, thereby prolonging bloom duration (Sunda et al. 2006). While it is certain that nutrients play a major role in the formation of algal blooms, no single nutrient or combination of nutrients has emerged as a causative factor for the formation of blooms, and the environmental conditions promoting bloom development are still poorly understood (Anderson et al. 2002).

Because algal blooms are seldom visible until cell numbers exceed 10^6 cells l^{-1}, blooms in the natural environment are usually sampled only after the bloom is already well established, nutrients have been drawn down by the bloom organism, and competing taxa are absent. Rarely are the conditions leading up to or promoting bloom formation captured in sampling programs because the temporal resolution of sampling is insufficient. Consequently, most reports characterize fully mature or even senescent blooms; thus, factors promoting blooms remain largely unknown.

In coastal and estuarine environments, physical forcing from tides and estuarine circulation play a major role in the distribution and patchiness of phytoplankton populations (Cloern et al. 1985, 1989). Tidal forcing, estuarine circulation, and the behavior of many bloom-forming organisms (e.g. vertical migration) all contribute to temporal and spatial patchiness of blooms. Tidal transport and advection tend to 'smear' phytoplankton patches horizontally along estuarine gradients (Lucas et al. 1999). Further, physical boundaries within an estuary can interrupt and deflect density and wind-driven flows, often result-

ing in the formation of complex eddy circulation (Geyer & Signell 1992, Shen et al. 1999). The importance of tidal transport processes on estuarine phytoplankton populations is highlighted in continuous chl a monitoring programs and timeseries records, where chl a concentrations vary in conjunction with the tidal stage, and the chl a maximum often occurs at a particular stage of the tidal cycle (Mallin et al. 1999, Li & Smayda 2001). The transient and ephemeral nature of these processes, which occur on tidal and subtidal timescales, are rarely captured in fixed-station monitoring programs in which samples are collected weekly to monthly (Dustan & Pinckney 1989, Trigueros & Orive 2000). Consequently, most monitoring programs are temporally and spatially insufficient to capture blooms and their progression from initiation to senescence, and small-scale, high-frequency targeted studies on bloom initiation are required to gain a better understanding of the processes involved in the formation of algal blooms.

To better understand the timescales of variability in phytoplankton populations and conditions promoting algal blooms, we sampled the Lafayette River, a shallow, eutrophic subtributary of the lower Chesapeake Bay where algal blooms regularly occur, at a fixed station on a daily basis at the same phase of the tidal cycle for a period of 54 d in fall of 2005, a period when blooms routinely occur (Fig. 1). Ambient dissolved inorganic nitrogen (DIN) concentrations in the Lafayette River are often >10 µM, and the concentration of dissolved inorganic phosphorus (DIP) is typically above 1 µM. Between 2000 and 2009, the Chesapeake Bay monitoring program station LFB01 in the Lafayette River had an average DIN concentration of 5.8 µM (SD = 8.8 µM), and the average DIP concentration at this station was 0.74 µM (SD = 0.84 µM) (Chesapeake Bay Program 2009, www.chesapeakebay.net/data_waterquality.aspx). The Lafayette River has a water residence time of 1 to 4 mo, depending on the amount of rain in a given year (White 1972) or event-scale processes such as nor'easters and tropical storms, which may modulate the residence time (Paerl et al. 2006). The combination of a long residence time and high nutrient loads favors the growth of dinoflagellates (Margalef 1978, Sellner et al. 2001), making this an ideal location to observe algal bloom dynamics.

The goal of this study was to identify factors promoting the initiation of algal blooms and to relate changes in phytoplankton community structure with nutrient concentrations on short timescales characteristic of developing blooms. Sampling on a daily basis allowed for higher temporal resolution of

phytoplankton populations, nutrient dynamics, and physical forcing than most monitoring programs afford.

METHODS

24 h tidal phase sampling

To understand how algal abundance and nutrient dynamics are controlled by tidal forcing, we sampled a tidal subestuary of the lower Chesapeake Bay, the Lafayette River (Fig. 1; Center for Coastal Physical
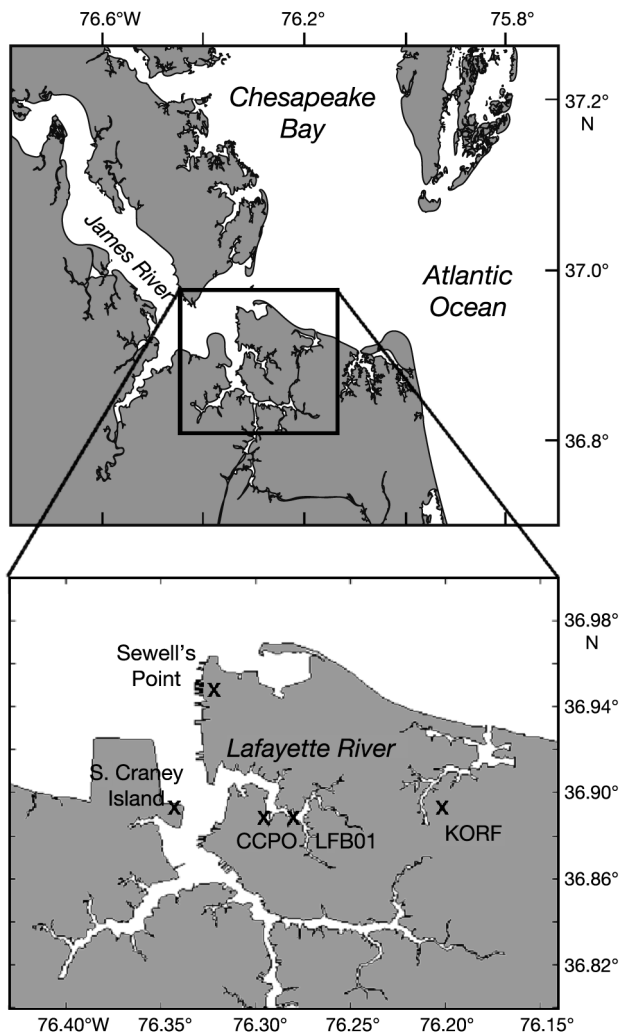

Fig. 1. Study area, showing sampling sites on the Lafayette River at the Center for Coastal Physical Oceanography (CCPO), Norfolk International Airport (KORF), NOAA Physical Oceanography Real-Time System (PORTS) station at Sewell's Point, NOAA PORTS station at S. Craney Island, and Virginia Department of Environmental Quality water quality station LFB01

Oceanography, CCPO), on an hourly basis for a period of 24 h. A Hydrolab DataSonde 4*a* water quality multiprobe was used to measure conductivity and water temperature at each sampling time. Water was collected, beginning on July 18, 2005, at 06:00 h local time, in an acid-cleaned carboy. In the lab, water was withdrawn and filtered onto Whatman GF/F glass fiber filters for chl *a* analysis. Nutrient samples were collected after filtration through 0.2 μm Supor filters. Nutrient and chl *a* samples were immediately frozen and stored in a freezer until analysis. Tidal height data were obtained from the NOAA Physical Oceanography Real-Time System (PORTS) station at Sewell's Point in the Elizabeth River (Fig. 1). The distance between the sampling site in the Lafayette River and the NOAA Sewell's Point tide gauge is <12 km, and on average, tidal height predictions for the Lafayette River lag those for Sewell's Point by approximately 20 min. Since data were collected on an hourly basis, the time of measured low water at Sewell's Point and low salinity in the Lafayette River are offset by approximately 1 h.

Daily tidal phase sampling

Based on the results from the hourly sampling, daily sampling of surface water from the Lafayette River was timed to coincide with the highest observed algal biomass, which was at the incoming tide approximately 2 h after the low tide in the Lafayette River. Samples were only collected during daylight hours. When the flood tide occurred at night, the sampling interval was extended approximately 12 h to coincide with the subsequent flood tide during daylight; this happened on August 22 and September 2 and 7. Prior to water sampling, dissolved oxygen, salinity, and water temperature were measured *in situ* using a Hydrolab DataSonde 4*a* water quality multiprobe. Because of the arrangement of the sensors on the sonde, all parameters were measured at the bottom of the water column. The average depth of the water during the sampling period was 1 m. Water samples were collected from the surface using an acid-cleaned bucket, placed into a 20 l acid-cleaned polycarbonate carboy, and transported to the laboratory <3 km away.

Sample handling and analyses

Once at the laboratory, water samples were kept well mixed by adding a magnetic stir bar to the car-

boys and gently stirring their contents. Samples for nutrient analyses were immediately filtered through a 0.2 μm Pall sterile microculture capsule using a peristaltic pump. The filtrate was placed into acid-cleaned bottles and stored frozen until analysis. NO_3^- + NO_2^-, NO_2^-, urea, PO_4^{-3}, and silicate (SiO_4^{4-}) were measured using an Astoria Pacific nutrient autoanalyzer according to manufacturer specifications and consistent with the colorimetric techniques outlined by Parsons et al. (1984). Ammonium (NH_4^+) concentrations were measured by the phenolhypochlorite method of Solorzano (1969). Total dissolved nitrogen (TDN) and total dissolved phosphorus (TDP) were analyzed at Old Dominion University's Water Quality Laboratory, following the standard procedures and protocol outlined for the Chesapeake Bay water quality monitoring program (http://archive.chesapeakebay.net/pubs/quality_assurance/doc-EPA903-R-96-006.pdf). DON was calculated as the difference between TDN and DIN. Dissolved organic phosphorus (DOP) was calculated as the difference between TDP and DIP. Nutrient concentrations that were below the detection limit were assigned values of the detection limit for statistical purposes.

Whole water samples (500 ml) were preserved with Utermohl's modified Lugol's solution for enumeration of microplankton and nanoplankton and with 1% glutaraldehyde (final concentration) for enumeration of picoplankton. Phytoplankton were quantified microscopically as described by Marshall & Nesius (1996), and autotrophic picoplankton (0.2 to 2 μM) were enumerated via epifluorescent microscopy following filtration onto polycarbonate Nuclepore filters with a pore size of 0.2 μm (Affronti & Marshall 1994, Marshall & Nesius 1996). Chl *a* samples were collected onto glass fiber filters (Whatman GF/F) and stored frozen until analysis using the non-acidification fluorometric technique of Welschmeyer (1994) within 3 wk of collection. Phytoplankton blooms are hereafter defined as when the cell abundance of a single taxon exceeded 0.5×10^6 cells l^{-1} for a period of 3 d or longer and/or daily chl *a* concentrations exceeded 44 μg l^{-1}, twice the average chl *a* concentration for the nearby Chesapeake Bay monitoring program station LFB01 (Fig. 1) from 2000 to 2009 (Morse et al. 2011).

Correlation and statistical analyses

Phytoplankton taxonomic abundance (as phyla) was compared to nutrient concentrations by calculating the cross-correlation function using The Math-Works MATLAB software, which follows the cross-correlation function equation given by Box et al. (2008). Because phytoplankton growth rates are on the order of days, a time lag in the response of phytoplankton abundance to nutrient loading events was expected. Therefore, we compared nutrient concentrations with phytoplankton abundance at 1 d intervals ranging from 7 d previous through 7 d forward in time. Additionally, to explore the effect of autocorrelation among nutrients, the autocorrelation function of each nutrient compound was plotted for a 7 d period. The 95% CI was calculated by the program using 2 SDs of either the cross-correlation function or the autocorrelation function.

Meteorological and supplementary data

Atmospheric pressure and tidal height data were obtained from the NOAA PORTS station at Sewell's Point (Fig. 1, Sewell's Point), and wind speed data were obtained from the NOAA PORTS Craney Island station near the mouth of the Lafayette River (Fig. 1, S. Craney Island). Precipitation data were obtained from Norfolk International Airport (Fig. 1, KORF). Surface nutrient and chl *a* data for the Virginia Department of Environmental Quality (VADEQ) Lafayette River station LFB01 (approximately 1 km upriver from the CCPO sampling site) from 2000 to 2009 were obtained from the Chesapeake Bay Program's data hub (http://chesapeakebay.net/data/downloads/cbp_water_quality_database_1984_present).

RESULTS

Hourly nutrient and chl *a* variability

Nutrient and chl *a* concentrations were measured hourly over a 24 h period from July 18 to 19, 2005, in the Lafayette River to determine the effect of tides on these water quality parameters. There was no precipitation during the sampling period, and the Lafayette River has no freshwater tributaries or inputs other than runoff from precipitation. The Lafayette River experiences semidiurnal tides, and the concentrations of both chl *a* and nutrients appear to have semidiurnal maxima and minima linked to the tidal phase (Fig. 2).

Over the 24 h sampling period, NO_3^- + NO_2^- concentrations in the Lafayette River varied by an order of magnitude, chl *a* varied by a factor of 8, and this variability appeared to be tidally controlled
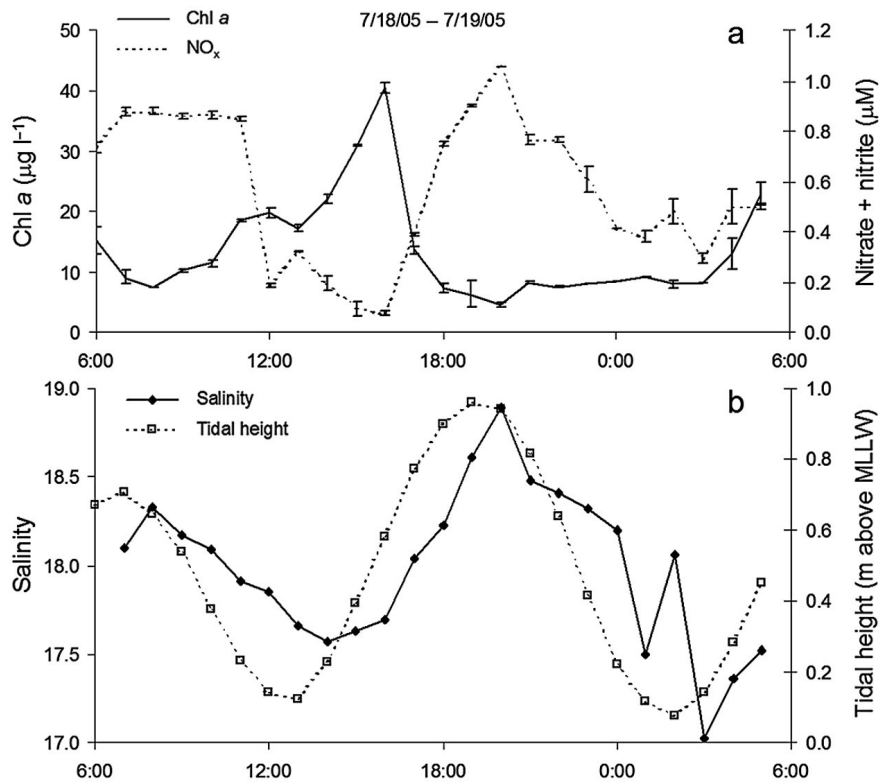
Fig. 2. (a) Hourly chl *a* (µg l^{-1}) and NO$_3^-$ + NO$_2^-$ (NO$_x$, µM) measured in the Lafayette River at the Center for Coastal Physical Oceanography (CCPO); NO$_3^-$ and NO$_2^-$ displayed similar concentrations and trends between time points and, thus, are reported as NO$_x$ for clarity. (b) Hourly tidal height (m above mean lower low water, MLLW) measured at Sewell's Point in the Elizabeth River and salinity measured in the Lafayette River at CCPO. All measurements made on July 18 to 19, 2005

(Fig. 2a,b). Chl *a* concentrations were highest approximately 2 to 3 h after low tide (Fig. 2a,b). Nutrient concentrations were highest at maximum flood tide, when chl *a* concentrations were low. The salinity measured in the Lafayette River lagged behind tidal height observations for Sewell's Point by approximately 1 h (Fig. 2b). Based on the chl *a* variability observed over the tidal cycle, we elected to collect samples for our 54 d daily study (August 15 to October 8, 2005) approximately 2 h after the predicted low tide in the Lafayette River, when chl *a*, and thus phytoplankton biomass, was highest.

Phytoplankton abundance

Between August 15 and October 8, 2005, 3 major blooms occurred in the Lafayette River (Fig. 3a). The first bloom, a mixed-species dinoflagellate bloom dominated by *Akashiwo sanguinea* (3.2 × 10^6 cells l^{-1}, >88.4% total abundance), was already in progress at the start of the daily sampling period on August 15, 2005. However, on August 16, an unidentified *Gymnodinium* sp. was the dominant species (0.5 × 10^6 cells l^{-1}), comprising 48 and 42% of the total phytoplankton abundance on August 16 and 17, respectively (Fig. 3a). At this time, concentrations of dissolved urea, NH$_4^+$, NO$_3^-$, and NO$_2^-$ were at or near

their limits of analytical detection (Fig. 3b). Subsequently, dinoflagellate abundance decreased until populations were <14 000 cells l^{-1} by August 18, 2005. At this time, dissolved N concentrations increased, and NO$_2^-$ and NH$_4^+$ concentrations reached 7.2 and 10.4 µM, respectively, by August 24 (Fig. 3a,b). Diatoms and cryptophytes comprised 86% of the phytoplankton at this time, but total phytoplankton abundance was still <1.0 × 10^6 cells l^{-1}.

The second bloom occurred between August 28 and September 3, 2005. Beginning about August 25 and between August 27 and September 3, the relative abundance of diatoms and cryptophytes increased, and the greatest total phytoplankton abundance observed during the study period occurred on September 1, at 1.2 × 10^7 cells l^{-1} (Fig. 3a). Diatoms were the dominant taxa on August 28 and 31 and September 1, while cryptophytes were dominant on August 29 to 30 (Fig. 3c). Between August 31 and September 3, *Skeletonema costatum* was the dominant phytoplankter enumerated in our samples (Fig. 3a,c). Diatoms comprised 96.9% of the total phytoplankton abundance on August 31, with 9.2 × 10^6 diatom cells l^{-1}, and increased to 10.7 × 10^6 diatom cells l^{-1} on September 1, when they comprised 89.7% of the phytoplankton population (Fig. 3a,c). Diatoms remained abundant through September 5. As diatoms and cryptophytes increased in abun-
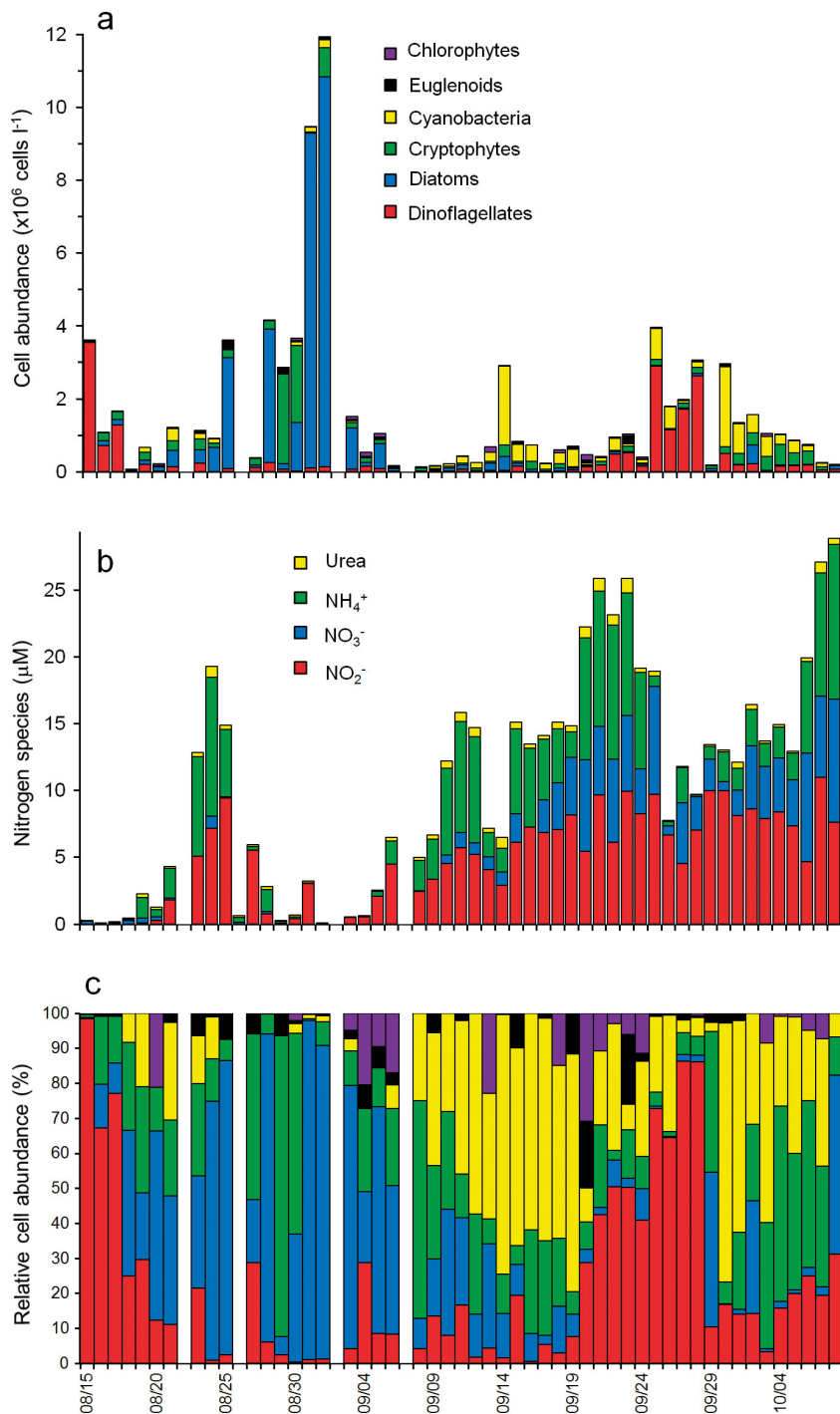
Fig. 3. (a) Stacked daily abundance of cyanobacteria and phytoplankton taxa ($\times\ 10^6$ cells l^{-1}) measured in the Lafayette River at the Center for Coastal Physical Oceanography (CCPO). (b) Stacked concentrations of dissolved inorganic nitrogen species (NO_3^-, NO_2^-, ammonium [NH_4^+]) and urea (µM measured at CCPO). (c) Relative taxonomic abundance of plankton expressed as a daily percent of the total cell count (legend is the same as in [a]). Dates given as mm/dd in 2005

dance, dissolved N concentrations became depleted, and NO_2^- or NH_4^+ were the dominant forms of dissolved N in the system (Fig. 3b).

After September 5, the relative abundance of filamentous cyanobacteria increased (Fig. 3c), although the total cell number was much lower than that observed during the diatom bloom (Fig. 3a). At the same time, on September 6, dissolved N concentrations increased and remained >5.0 µmol l^{-1} for the duration of the study (Fig. 3b).

The third bloom occurred between September 25 and 28, 2005. Beginning September 20, dinoflagellate relative abundance increased, and dinoflagellates comprised 72.9% of the phytoplankton community by September 25, with an unidentified *Gymnodinium* sp. reaching an abundance of 1.4×10^6 cells l^{-1} and dominating the assemblage (Fig. 3a,c). On September 28, the abundance of *Gymnodinium* sp. reached 2.0×10^6 cells l^{-1}, while cryptophyte abundance was at or near its lowest level during the 54 d study.

Picoplankton abundance was greatest in late August, with a maximum abundance of 2.8×10^9 cells l^{-1} on August 21 (Fig. 4a). Picoplankton abundance generally declined throughout the study period, with the minimum abundance occurring on October 6, at 8.0×10^8 cells l^{-1} (Fig. 4a); however, brief fluctuations in picoplankton abundance (lasting 2 to 4 d) occurred at approximately weekly timescales throughout the study period (Fig. 4a).

Nutrient concentrations

DIN (NO_2^-, NO_3^-, and NH_4^+) and urea concentrations were at or near the limits of detection at the start of the study, between August 15 and 18 (Fig. 3b), when dinoflagellate abundance was high (Fig. 3a). NO_2^- concentrations increased after August 20, reaching nearly 7 µmol l^{-1} on August 25. NH_4^+ concentrations also increased,

Fig. 4. (a) Picoplankton abundance ($\times 10^9$ cells l^{-1}; left *y*-axis) and total microplankton and nanoplankton abundance ($\times 10^6$ cells l^{-1}; right *y*-axis). (b) Dissolved organic nitrogen (DON, µM N; left *y*-axis) and dissolved inorganic phosphorus (DIP, µM P) and dissolved organic phosphorus (DOP, µM P); right *y*-axis. DOP concentrations below detection limit (0.027 µM) were assigned values of the detection limit for statistical purposes. Dates given as mm/dd in 2005
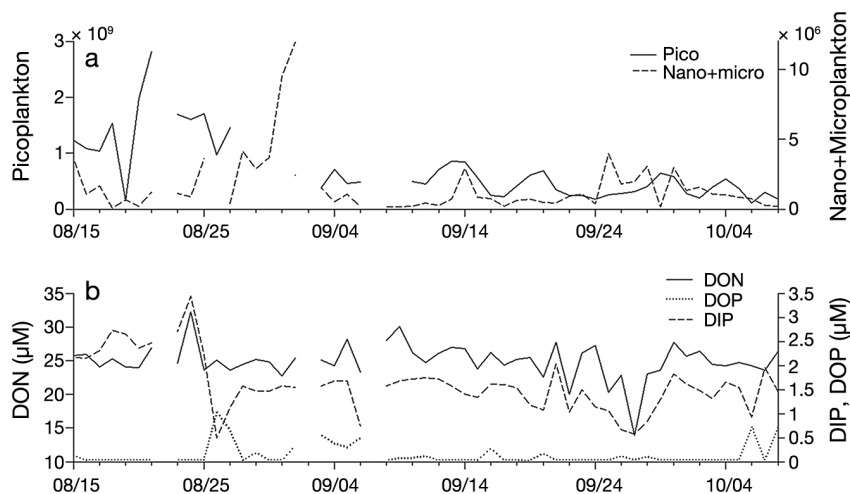
but then both NO_2^- and NH_4^+ were drawn down as phytoplankton biomass increased between August 24 and September 3 (Fig. 3a,b). Beginning September 5, NO_2^- concentrations increased from near the detection limit (0.02 µmol l^{-1}) to 10 µmol l^{-1} by the end of the study period (Fig. 3b).

NO_3^- concentrations were generally low relative to other forms of N, typically <2 µmol l^{-1} and <2% of TDN until September 14 (Figs. 3b & 4b). In mid-September, NO_3^- concentrations increased, reaching a maximum of 9 µmol l^{-1} by October 8, and NO_3^- represented a substantial fraction of the DIN pool (up to 30%) during the latter third of the study period (Fig. 3b). NO_3^- concentrations were lower during the September dinoflagellate bloom, when cyanobacterial abundance was also high (Fig. 3a,c).

Concentrations of NH_4^+ ranged from below the detection limit (<0.02 µmol l^{-1}) to >10 µmol l^{-1} and were highly variable over the course of the 54 d study. The highest NH_4^+ concentrations were observed between bloom periods, while large decreases in NH_4^+ concentrations occurred during periods when phytoplankton cell abundance increased (Fig. 3a,b). NH_4^+ concentrations were highest prior to the diatom bloom at the end of August (10.4 µmol l^{-1} on August 24) and prior to and after the September dinoflagellate bloom (10.1 µmol l^{-1} on September 21 to 22 and 11.6 µmol l^{-1} on October 8). NH_4^+ concentrations were near or below the detection limit on August 31 during the diatom bloom and during the dinoflagellate blooms on August 15 to 16 and September 28.

Urea concentrations were low throughout the sampling period, with a maximum concentration of 1 µmol l^{-1} on September 23 (Fig. 3b). Urea concentrations comprised only a small portion of the TDN pool at any given time (generally <1% of TDN, but always

<2.5% of TDN). SiO_4^{4-} concentrations were high, ranging from 30 to 70 µmol l^{-1} throughout the study period (data not shown), and the ratio of dissolved SiO_4^{4-} to DIN was always >1. SiO_4^{4-} concentrations decreased from 80 µmol l^{-1} to 60 µmol l^{-1} as a diatom bloom formed in late August but were never depleted (data not shown).

DIP concentrations were also relatively high throughout the study period, ranging from 0.5 to 3.5 µmol l^{-1}, well above the limit of analytical detection (Fig. 4b). At the onset of the study in mid-August, DIP concentrations were higher (maximum of 3.4 µmol l^{-1}) but decreased by nearly a factor of 2 following the diatom bloom in late August and remained lower for the remainder of the study period (average 1.6 ± 0.6 µmol l^{-1}) (Figs. 3a & 4b).

DON concentrations did not change much over the 54 d study period (average 24.9 ± 2.6 µmol l^{-1}), with one exception; DON concentrations were lower during the dinoflagellate bloom from September 25 to 28, and the lowest concentration was observed on September 27 (13.9 µmol l^{-1}) (Figs. 3a & 4b). DOP concentrations were lower (maximum of 1.0 µmol l^{-1}) than DIP concentrations and were often below the limit of analytical detection (Fig. 4b). Because the DOP concentrations were so low and the variance was so great, patterns in DOP concentrations relative to phytoplankton abundance could not be elucidated.

Meteorological and physical controls on estuarine variability

Between August 6 and 12, prior to the start of the daily sampling, 11.5 cm of precipitation was measured at KORF (data not shown). Precipitation oc-
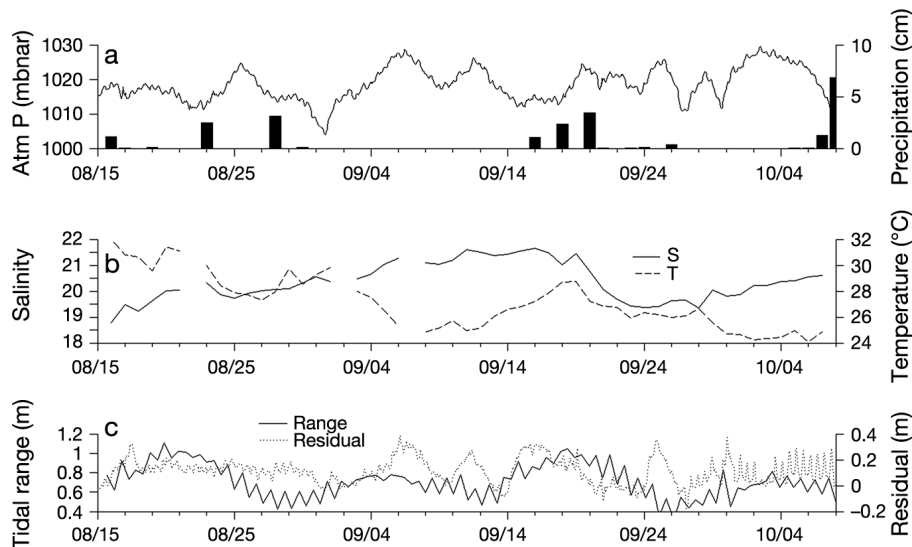
Fig. 5. (a) Atmospheric pressure (Atm P, mbar) recorded at Sewell's Point and daily precipitation (cm) measured at Norfolk International Airport. (b) Salinity and temperature (°C) measured at the Center for Coastal Physical Oceanography. (c) Tidal range (m) and tidal residual (measured; predicted height, m) recorded at Sewell's Point. Dates given as mm/dd in 2005. Breaks in the data of (b) are due to the unavailabillity of the sonde on these days

curred on August 15 and 16 (1.1 cm) after a dinoflagellate bloom had formed in the Lafayette River (Figs. 3a & 5a), on August 23 (2.5 cm) and 28 (3.1 cm), between September 16 and 20 (6.8 cm), and between October 6 and 8 (8.0 cm) (Fig. 5a). Nutrient concentrations increased following rainfall events, except on August 15 (Figs. 3b & 5a).

The wind was predominantly from the northeast during 4 periods: August 24 to 25, September 5 to 16, September 24, and September 29 (Fig. 6a), during which times the chl *a* concentration generally decreased (Fig. 6b), often resulting in the end of a bloom. As the remnants of Hurricane Katrina (downgraded to a tropical storm) passed to the west of the region beginning August 30, the wind speed increased and the direction shifted from the south to the southwest as the atmospheric pressure decreased to <1005 mbar on August 31 (Figs. 5a & 6a). This period of high wind coincided with a decrease in the

abundance of cryptophytes and an increase the abundance of diatoms; a bloom of *Skeletonema costatum* followed the August 30 to 31 wind event (Figs. 3a,c & 6a). There was a prolonged period of high winds beginning September 3 as a high-pressure system moved through the region following the remnants of Hurricane Katrina (Figs. 5a & 6a), and this corresponded to the demise of the diatom bloom (Fig. 6b). The high winds blew predominantly from the northeast during this period (Fig. 6a) and resulted in a positive tidal residual at Sewell's Point in the Elizabeth River (Fig. 5c). This positive tidal residual also coincided with an increase in salinity in the Lafayette River after September 5 (Fig. 5b). In addition, the water temperature in the Lafayette River cooled by 4°C during this event (Fig. 5b).

The winds increased again from September 10 to 12 as another high-pressure system passed through the region, and the winds were again predominantly
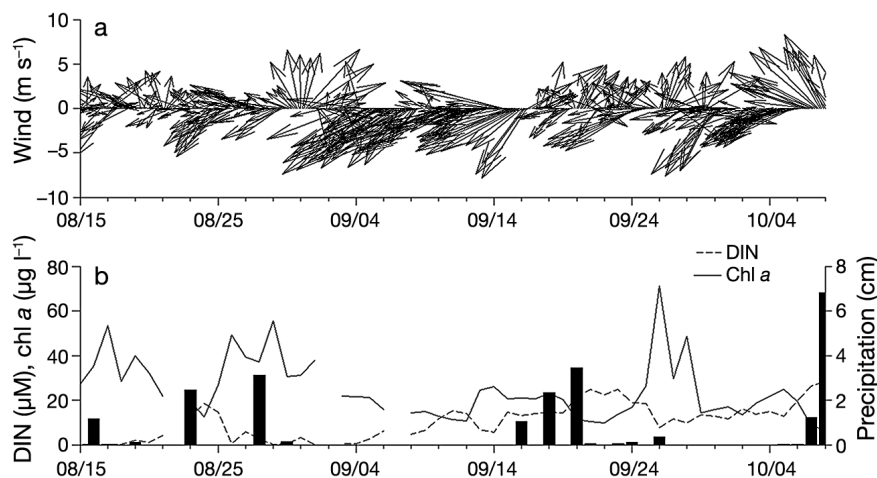

Fig. 6. (a) 3 h mean wind vector velocity (m s^{-1}) measured at Craney Island. (b) Chl *a* (µg l^{-1}) and dissolved inorganic nitrogen concentration (DIN, µM N; left *y*-axis) measured at the Center for Coastal Physical Oceanography and daily precipitation (cm; right *y*-axis) measured at Norfolk International Airport. Dates given as mm/dd in 2005

from the northeast (Figs. 5a & 6a). A third high-wind event occurred as the effects from Hurricane Ophelia passed over the Outer Banks of North Carolina and moved off the coast of Virginia from September 14 to 16 (Figs. 5a & 6a). Although below hurricane strength, this storm system was associated with substantial precipitation between September 16 and 20 (Fig. 5a). The predominantly northeasterly winds associated with this system again resulted in a positive tidal residual in the Elizabeth River at Sewell's Point (Figs. 5c & 6a) as well as increased salinity and water temperature in the Lafayette River (Fig. 5b). Water temperature and salinity in the Lafayette River decreased abruptly on September 20 (Fig. 5b) as the remnants of Hurricane Ophelia passed by the region, resulting in >3 cm of precipitation (Fig. 5a). Two more high-wind events occurred in late September and one occurred in October, but the duration of the high winds was short and the direction from which they came was not constant for >24 h (Fig. 6a); however, the dinoflagellate bloom in September ended as the winds increased in intensity from the northeast on September 29.

Spring-neap tidal modulation appeared to affect nanoplankton and microplankton abundance more than picoplankton abundance (Figs. 4a & 5c). Total phytoplankton (nanoplankton plus microplankton) abundance was higher during neap tides and lowest during spring tides. The dinoflagellate blooms in August and September, the diatom bloom in August, and the high cyanobacterial abundance in September all occurred during neap tides (Figs. 3a & 5c). Both the maximum and minimum picoplankton abundances occurred during spring tides. Picoplankton abundance was not as strongly controlled by the tidal cycle, and their abundance appeared to cycle on a 7 to 9 d basis regardless of the tidal phase (Figs. 4a & 5c).

DISCUSSION

Near-monospecific algal blooms are now common occurrences in Chesapeake Bay and its tidal tributaries, as well as other highly eutrophic estuarine systems worldwide. However, despite decades of research, our understanding of the controls on bloom formation are poorly understood because the conditions antecedent to bloom formation are seldom characterized with the necessary temporal resolution; most nutrient monitoring programs sample too infrequently (weekly to monthly), and ad hoc bloom sampling is largely focused on blooms only after they

have formed. In addition, chl a and nutrient concentrations can vary by an order of magnitude over diurnal time scales, and phytoplankton abundance is often strongly linked to the tidal phase (Fig. 2). To capture changing environmental conditions as blooms initiate, develop, and dissipate, we sampled the Lafayette River on a daily basis during late summer, when blooms are common, at the same portion of the tidal cycle for a period of 54 d in 2005. During this time, there were 2 dinoflagellate blooms and 1 diatom bloom. Sampling on a daily basis allowed for detailed observations regarding the sequence of events leading up to blooms as well as comparisons of phytoplankton abundance, ambient nutrient concentrations, and physical forcing (wind, precipitation, and spring-neap modulation of the tidal cycle) on timescales relevant to phytoplankton growth and bloom formation.

Nutrient dynamics and climatological controls on the formation of blooms

Nutrient loading because of precipitation and associated runoff and subsequent water column stratification play a key role in stimulating the formation of *Cochlodinium polykrikoides* blooms in the Lafayette River (Morse et al. 2011). Similarly, during the present study, precipitation and associated increases in ambient nutrient concentrations preceded the diatom and dinoflagellate blooms in late August and September, respectively (Figs. 3a,b & 5a). Despite periods of intense rainfall prior to the start of this study, ambient nutrient concentrations were depleted at the start of this study, likely because the nutrient demand of a mixed bloom of *Akashiwo sanguinea* and *Gymnodinium* sp. already in progress was removing nutrients as quickly as they were supplied. *A. sanguinea* and *Gymnodinium* sp. are bloomforming dinoflagellates typical during the summer months in Chesapeake Bay and its tributaries (Marshall 1995, Marshall et al. 2005). Subsequent to this bloom, large increases in DIN concentrations were observed after rainfall events, and increases in phytoplankton biomass were generally associated with decreases in DIN. Following precipitation on August 22 to 23, nutrient concentrations increased by a factor of 5, and a diatom bloom dominated by *Skeletonema costatum* formed during a neap tide period (Figs. 3a & 5a), rapidly drawing down dissolved N concentrations to the limit of detection (Fig. 3b). The relatively high wind speed at this time (Fig. 6a) may have contributed to the formation of a diatom rather

than a dinoflagellate bloom since dinoflagellates typically thrive when wind-driven mixing and turbulence are low (Margalef 1978, Sellner et al. 2001, Smayda & Reynolds 2001). Rain events associated with high nutrient inputs accompanied a frontal system associated with Hurricane Ophelia in mid-September. After this system passed, nutrient concentrations were high, the wind velocity decreased, and a dinoflagellate bloom ensued, likely because of high nutrient concentrations and decreased turbulence (Margalef 1978, Sellner et al. 2001, Cloern & Dufford 2005). While nutrients were not depleted during this dinoflagellate bloom, the concentrations of both DIN and DON were reduced during the bloom, consistent with previous observations that many dinoflagellates are able to use organic nutrients (Graneli et al. 1999, Burkholder et al. 2008) to supplement their nutrition.

Subsequent to the diatom bloom at the end of August and the dinoflagellate bloom in September, there were numerous high-wind (but low-precipitation) events, and this resulted in low phytoplankton abundance, higher cyanobacterial abundance (Figs. 3a & 5a), and the accumulation of NH_4^+ and NO_2^- (Fig. 3b), likely because of N regeneration as bloom organisms settled and decayed, as well as incomplete nitrification, a process common during this time of the year (McCarthy et al. 1977, 1984, Horrigan et al. 1990). It is likely that regenerated nutrients were also contributed from benthic fluxes as high winds allow mixing of surface and bottom water and sediment resuspension in these shallow-water systems (Horrigan et al. 1990, Rizzo 1990). In September and early October, prior to and following the September dinoflagellate bloom, NO_3^- also accumulated in the water column, likely because of nitrification. At these times, cyanobacterial abundances were high relative to other phytoplankton taxa and picoplankton abundance was also higher at these times (Figs. 4a & 5a). Cyanobacteria are important components of most phytoplankton communities and thrive under stratified conditions common in the summer, where they can take advantage of regenerated nutrient compounds (Paerl et al. 2006). Regenerated N is thought to fuel the bulk of primary production during summer months when new inputs of N are limited to stochastic events. Many dinoflagellate mixotrophs can also graze on picocyanobacteria including *Synechococcus* (Jeong et al. 2005, Burkholder et al. 2008), a common component of the cyanobacterial community in Chesapeake Bay (Marshall & Nesius 1996, Chen et al. 2006), and picoplankton abundance was lowest during the September dinoflagellate bloom.

The Redfield ratio of carbon, N, and P nutrient elements in the environment has long been used to infer which nutrient is in shortest supply. Selection for or against diatoms has been associated with the supply of SiO_4^{4-} relative to other nutrient elements (e.g. Si:N and/or Si:P ratios) (Conley & Malone 1992, Smayda 1997). Justic et al. (1995) combined stoichiometric and absolute concentration criteria to assess the potential nutritional limitation of phytoplankton and defined N limitation as DIN:P <10, Si:DIN >1, and total DIN <1 µM. Similarly, P limitation was defined as DIN:P >22, Si:P >22, and P <0.1 µM (Justic et al. 1995). During the present study period, the DIN:DIP ratio was <10 prior to September 15, indicative of potential N limitation, but DIN concentrations were only depleted (<1 µM) during the first 2 blooms in August. After August 31, neither DIN nor DIP was depleted, and therefore it is unlikely that phytoplankton were limited by N or P during the remainder of the study (Justic et al. 1995). Similarly, throughout the duration of the study, the Si:DIN ratio was always >1, the Si:DIP ratio was always >16, and the minimum concentration of Si was 28.4 µM, suggesting that SiO_4^{4-} concentrations were never limiting to diatom growth (Conley & Malone 1992, Justic et al. 1995).

Estuarine environments are often N-limited systems (Howarth 2008); however, in contrast to our observations that Si and P were unlikely to limit productivity during our sampling period, monthly data from VADEQ's monitoring station in the Lafayette River (LFB01) (Fig. 1) suggest that P might regulate productivity, at least seasonally. Between the years 2000 and 2009, chl *a* and DIN concentrations at LFB01 showed some seasonality, with higher concentrations during spring and fall (Fig. 7a,c). In contrast, PO_4^{3-} concentrations were highest between August and October in all years (Fig. 7b). While DIN and DIP concentrations were positively correlated (Pearson moment correlation, *t*-test, p < 0.05) at this station, chl *a* concentrations were positively correlated only with DIP (Pearson moment correlation, *t*-test, p < 0.001) and not DIN concentrations. It is important to remember that the VADEQ data are collected at a monthly interval and bi-weekly during the summer months; thus, the time interval is not particularly relevant to the life cycle of bloom organisms.

To explore these relationships further using data collected at a relevant timescale to bloom formation and because phytoplankton growth and bloom formation often lag nutrient inputs by several days, we calculated the time-lagged correlations between nutrient species and algal abundance from our data
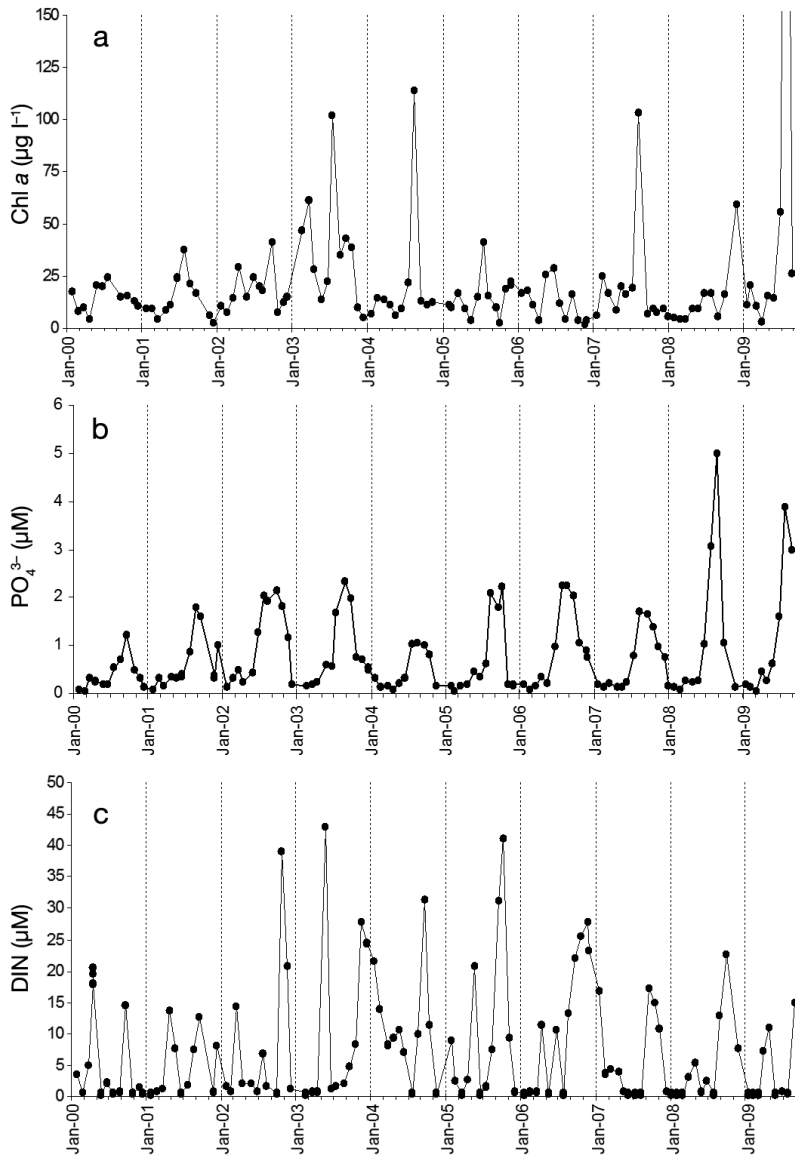
Fig. 7. Virginia Department of Environmental Quality water quality data showing (a) chl *a* (µg l^{-1}), (b) PO$_4^{3-}$ (µM P), and (c) dissolved inorganic nitrogen (DIN, µM N), measured at station LFB01 between January 2000 and December 2009. Dates given as mo-yr. In (a), the value of the peak in August 2009 was >300 µg l^{-1} and was caused by a *Cochlodinium polykrikoides* bloom (see Morse et al. 2013)

system or a lower removal rate compared to other nutrient compounds (e.g. lower uptake rates). NH$_4^+$ concentrations showed the least amount of autocorrelation among measured nutrient compounds (Fig. 8a), with correlations exceeding the CI for 1 d forward in time only, suggesting variable concentrations of NH$_4^+$ over time and enhanced removal rates compared to other nutrients, particularly given the high concentrations of NH$_4^+$ observed in mid- to late September.

To observe the effect of DIN concentrations on the abundance of different algal taxa, the cross-correlation function was calculated for DIN versus phytoplankton and cyanobacteria for 7 d in both forward and reverse time (Fig. 8b). DIN concentrations were strongly positively correlated with cumulative precipitation from 4 d in reverse time through 7 d in forward time, suggesting that DIN concentrations are tightly coupled to precipitation totals (Fig. 8b). DIN was negatively correlated with chl *a* concentrations at zero time lag and 1 to 2 d in reverse time and was positively correlated with dinoflagellate abundance from 3 to 7 d in forward time (Fig. 8b). To explore this relationship further, the cross-correlation function of dinoflagellate abundance versus nutrient compounds was plotted. There was a strong positive correlation (correlations exceeding the 95% CI) between dinoflagellate abundance and all N compounds from 2 to 7 d in reverse time (Fig. 8c). This suggests that when N concentrations increase, dinoflagellate abundance increased 2 to 7 d later, and likewise when N concentrations decrease, dinoflagellate abundance decreased accordingly. It is important to point out that correlation does not imply cause; however, because phytoplankton growth is dependent on nutrients and an increase in biomass requires N inputs, the increase in nutrient concentration likely caused the increase in dinoflagellate abundance.

The positive correlations between dinoflagellate abundance and all forms of measured N suggest that no particular nutrient species was required for bloom
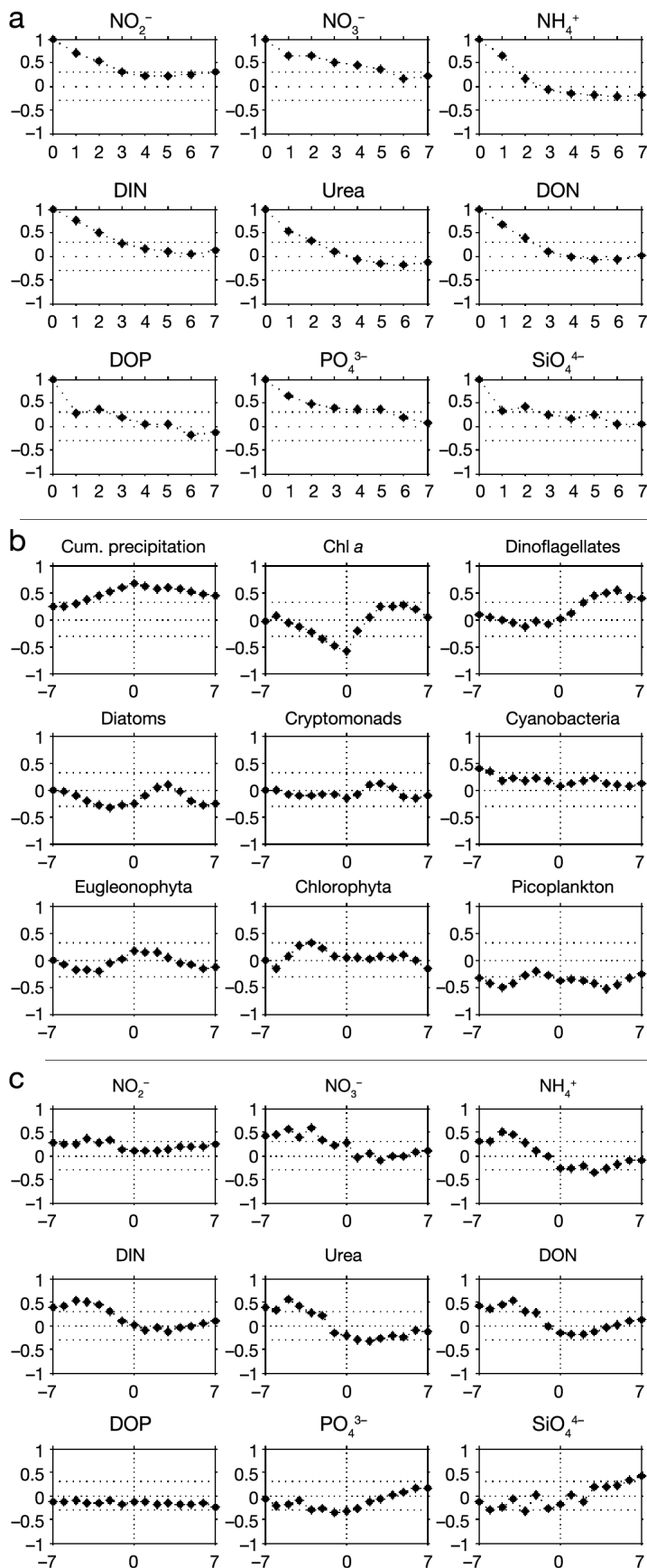
in the Lafayette River. To explore the effect of autocorrelation on nutrient concentrations (i.e. the serial correlation of a variable over time), the autocorrelation function of each nutrient compound was calculated for a 7 d period (Fig. 8a). All nutrient compounds showed some degree of autocorrelation, but NO$_3^-$ and PO$_4^-$ had the greatest amount, with positive autocorrelations exceeding the 95% CI from 1 to 5 d forward in time (Fig. 8a), suggesting either a relatively steady source of these nutrients within the

development but rather that the N concentration in general (NO_3^-, NO_2^-, NH_4^+, urea, and DON), regardless of N species, was important. Dinoflagellates have been shown to be nutritionally flexible (Anderson et al. 2002, Burkholder et al. 2008), and they appear to thrive in eutrophic estuarine systems where there is variability in the form of N supplied.

While the positive-lagged correlation between N concentrations and dinoflagellate abundance may be indicative of growth stimulation by N, the negative correlation between PO_4^{3-} and dinoflagellate abundance with little to no lag may suggest that P is drawn down during blooms to support cellular P demand and growth but is not growth limiting. Consistent with this observation, as dinoflagellate abundance increased during the September *Gymnodinium* sp. bloom, PO_4^+ concentrations decreased by the largest amount observed during the study period, but PO_4^+ was never depleted (Figs. 3a & 4).

There was a strong positive correlation between diatom abundance and PO_4^+ concentrations from 3 to 5 d in reverse time and a strong positive correlation with SiO_4^{4-} concentrations from 2 to 3 d in reverse time (data not shown). Additionally, there was a strong negative correlation between diatom abundance and NO_2^- and DIN concentrations 2 d in forward time (data not shown). This suggests that diatom abundance increased in response to increases in PO_4^+ and SiO_4^{4-} concentrations, but when diatom abundance decreased, the concentrations of DIN and NO_2^- increased 2 d later, perhaps because of nutrient recycling following the collapse of the diatom bloom in early September.

Fig. 8. (a) Autocorrelation function of nutrient compounds measured at the Center for Coastal Physical Oceanography (CCPO), (b) Cross-correlation function of dissolved inorganic nitrogen (DIN) versus environmental variables and phytoplankton taxa at CCPO, (c) Cross-correlation function of dinoflagellate abundance versus nutrient compounds at CCPO. A 7 d forward time lag is shown along the *x*-axis in (a), with Day 0 being the present (i.e. no time lag), and a 7 d forward and reverse time lag is shown along the *x*-axis in (b) and (c). In all plots, the correlation coefficient at each time lag is shown along the *y*-axis, with the 95% CI for correlations shown as dashed lines. DON: dissolved organic nitrogen; DOP: dissolved organic phosphorus, NH_4^+: ammonium; SiO_4^{-4}: silicate

The high concentrations of NO_2^- observed during the present study and the importance of NO_2^- to bloom formation suggest that NO_2^- may play a larger role in estuarine environments than previously believed. The uptake of NO_2^- is well documented in oceanic environments, where it can be an important source of N (Collos 1998, Lomas & Lipschultz 2006). While McCarthy et al. (1977, 1984) reported high NO_2^- concentrations (up to 10 µM) in Chesapeake Bay and speculated that NO_2^- was derived from incomplete nitrification associated with destratification and mixing of surface and bottom waters, the abundance and utilization of this N source has not been widely examined in most estuarine systems. Concentrations of NO_2^- were observed that were consistent with those reported for Chesapeake Bay (McCarthy et al. 1977) and in the York River (L. Killberg & D. Bronk unpubl. data). NO_2^- can be formed during incomplete nitrification and be released by phytoplankton during NO_3^- uptake and less commonly during incomplete denitrification (Zehr & Ward 2002, Lomas & Lipschultz 2006). Because the process of nitrification is carried out by 2 separate groups of organisms, ammonium-oxidizing bacteria (AOB) and/or ammonium-oxidizing archaea (AOA) and nitrite-oxidizing bacteria (NOB) (Zehr and Ward 2002, Ward et al. 2007), the process of nitrification can become uncoupled, and NO_2^- may accumulate in the water column (McCarthy et al. 1984). AOB are abundant throughout Chesapeake Bay, with the highest diversity in the oligohaline upper bay region (Ward et al. 2007). In the polyhaline portion of the bay, AOA may be the dominant nitrifiers (Wuchter et al. 2006, Ward et al. 2007). Based on the tight coupling of NO_2^- and NH_4^+ concentrations, the low NO_3^- concentrations prior to mid-September (Fig. 3b), and the presence of sufficient oxygen in the water column (data not shown), the accumulation of high NO_2^- concentrations in the present study was likely a result of incomplete nitrification. This may occur when populations of AOB and NOB become de-coupled over space and time.

Physical controls on phytoplankton community dynamics

Wind-driven mixing in shallow estuaries can both inject nutrients from the benthos (Rizzo 1990) and result in the demise (Morse et al. 2011) or dissipation of algal biomass (Figs. 3a,b & 6a). Although the Lafayette River is generally sheltered from the wind, wind speed and direction may be important factors controlling taxonomic dominance and bloom development. For example, during a period of low and variable winds (August 28 to 30), phytoplankton biomass was high, and cryptophytes and diatoms were both abundant (Figs. 3a,c & 6a). However, following a period of high winds from the southwest (Fig. 6a), diatom abundance increased while cryptophyte abundance decreased drastically (Fig. 3a,c). The increase in wind velocity likely mixed the entire water column in the shallow Lafayette River, causing particle resuspension including diatoms, sediments, and other passive particles and creating unfavorable conditions for flagellates.

Following Hurricane Katrina, a high-pressure system in the region resulted in an extended period of high winds (> 7 m s^{-1}) from the northeast. This type of atmospheric system forces oceanic water landward, resulting in decreased riverine flushing, accumulation of oceanic water in Chesapeake Bay, positive tidal residuals at Sewell's Point, and saltwater intrusion into the Lafayette River. Chesapeake Bay and its tributaries are more vulnerable to northeasterly winds because of the fetch over which they develop and the north-south orientation of the bay mouth. The combined wind-driven and tidal mixing caused by this high-pressure system likely contributed to the decreased algal biomass observed during this period (Figs. 3a & 6a).

In contrast, winds from the southwest typically result in enhanced riverine flushing and offshore transport of water through the bay mouth. The Lafayette River is sheltered from the southwesterly winds by the landmass; thus, the effects of high wind from this direction are reduced. Therefore, although the winds were strong between August 30 and September 2, the winds were from the southwest and so did not result in the same degree of mixing and turbulence in the system, while allowing nutrient inputs from mixing to stimulate diatom growth. Diatoms characteristically thrive better in higher energy environments than dinoflagellates (Margalef 1978, Smayda & Reynolds 2001, Huisman et al. 2004). In contrast, the high-pressure system that dominated from September 4 through 9 resulted in northeasterly winds that resulted in a large oceanic influence on the lower Chesapeake Bay and its subtributaries, including the Lafayette River. Salinity in the Lafayette increased, there was a high positive tidal residual during this period, phytoplankton abundance decreased, and DIP concentrations decreased despite the lower algal biomass, suggesting increased turbidity and particle-associated nutrient removal (Froelich 1988).

Timescales of variability important to phytoplankton

One of the problems associated with sampling blooms is coping with estuarine variability on time-scales ranging from minutes to months and biological variability associated with the lifecycles and behavior of phytoplankton cells and populations (Hubertz & Cahoon 1999, Lucas et al. 2006, Glibert et al. 2008). Within a 24 h period of fixed-station sampling, nutrient concentrations and phytoplankton abundance varied by an order of magnitude, and nutrient and chl *a* concentrations were strongly linked to the tidal cycle (Fig. 2), as had been observed in this system previously (M. R. Mulholland et al. unpubl.). Shallow estuaries and coastal systems are highly dynamic areas where a multitude of physical, chemical, and biological factors concomitantly influence the distribution, growth, and transport of the phytoplankton community, which in turn modify the nutrient regimes of the surrounding waters. This variability makes it difficult to understand controls on blooms using data collected during most long-term monitoring programs that may sample systems only at weekly to monthly intervals, a frequency insufficient to capture ephemeral blooms. The tidal control of biomass and nutrient concentrations in estuarine environments has direct implications for interpreting monitoring data that are not tidally resolved (Cloern 1991, Lucas et al. 1999). In addition, it is now known that stochastic events are important for controlling nutrient inputs during large parts of the year, and these affect nutrient loading from the water- and air-sheds as well as nutrient inputs from the benthos (Paerl 1997).

When daily measurements of chl *a* concentrations from the present study are compared to chl *a* concentrations measured monthly at LFB01 (Fig. 1), it is apparent that short-term variability is missed in the monthly sampling record. In addition, when chl *a* concentrations are compared at the 2 sites (<1 km apart) on the same date in August, a factor of 2 difference is observed between the sites, highlighting the often patchy spatial distribution of chl *a* in these tidally dominated systems. While the VADEQ chl *a* monitoring record between 1999 and 2009 includes periods of high chl *a* concentrations in the Lafayette River, the magnitude of these peaks is far less than those measured during targeted studies of blooms (Mulholland et al. 2009, Morse et al. 2011). It is important to remember that the Chesapeake Bay monitoring program and associated sampling by VADEQ was not and is not designed to capture the

dynamics of ephemeral blooms but rather was designed as a statewide effort to understand long-term changes in Chesapeake Bay phytoplankton communities. A wide suite of methods, including *in situ* monitoring devices, remote sensing, and targeted sampling at a high temporal frequency, can be used to supplement long-term monitoring systems, such as those in place in Chesapeake Bay, to fully capture the dynamics associated with algal populations in stochastic estuarine ecosystems. To this end, continuous monitoring of nutrients and chl *a* provides a much more exhaustive and complete view of estuarine dynamics, but these data sets are still limited (Glibert et al. 2008). In addition, most long-term monitoring programs do not collect tidally resolved data. Timing sampling to a specific portion of the tidal cycle may help to resolve processes occurring at least at tidal time scales. With the advent of technologies such as *in situ* monitoring devices (e.g. Lucas et al. 2006) and *in situ* nutrient analyzers (e.g. Glibert et al. 2008), targeted sampling aimed at understanding conditions promoting the initiation of blooms will become easier. However, integrating the complex coupled climatological, physical, and biological forcings associated with blooms is likely to remain a challenge into the future.

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