Two decades of tropical cyclone impacts on North Carolina's estuarine carbon, nutrient and phytoplankton dynamics: implications for biogeochemical cycling and water quality in a stormier world

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Abstract Coastal North Carolina (USA) has experienced 35 tropical cyclones over the past 2 decades; the frequency of these events is expected to continue in the foreseeable future. Individual storms had unique and, at times, significant hydrologic, nutrient-, and carbon (C)-loading impacts on biogeochemical cycling and phytoplankton responses in a large estuarine complex, the Pamlico Sound (PS) and Neuse River Estuary (NRE). Major storms caused up to a doubling of annual nitrogen and tripling of phosphorus loading compared to non-storm years; magnitudes of loading depended on storm tracks, forward speed, and precipitation in NRE-PS watersheds. With regard to C cycling, NRE-PS was a sink for atmospheric CO_2 during dry, storm-free years and a significant source of CO_2 in years with at least one storm, although responses were storm-specific. Hurricane Irene (2011) mobilized large amounts of previously-accumulated terrigenous C in the watershed, mainly as dissolved organic carbon, and extreme winds rapidly released CO_2 to the atmosphere. Historic flooding after Hurricanes Joaquin (2015) and Matthew (2016) provided large inputs of C from the watershed, modifying the annual C balance of NRE-PS and leading to sustained CO_2 efflux for months. Storm type affected biogeochemical responses as C-enriched

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floodwaters enhanced air–water CO_2 exchange during 'wet' storms, while CO_2 fluxes during 'windy' storms were largely supported by previously-accumulated C. Nutrient loading and flushing jointly influenced spatio-temporal patterns of phytoplankton biomass and composition. These findings suggest the importance of incorporating freshwater discharge and C dynamics in nutrient management strategies for coastal ecosystems likely to experience a stormier future.

Keywords Tropical cyclones · Carbon/nutrient cycling · Estuarine · Coastal · Phytoplankton · North Carolina

Introduction

Since the mid-1990s, increased activity of tropical cyclones has been observed in both the Atlantic and Pacific Basins (Goldenberg et al. 2001; Emanuel 2005; Webster et al. 2005; Holland and Webster 2007; Bender et al. 2010; IPCC 2014; Kang and Elsner 2015); this active period has surpassed previous cycles in both frequency and intensity of cyclones (NOAA Hurricane Center; Bender et al. 2010; Seneviratne et al. 2012; IPCC 2014). Physical perturbations of estuarine and coastal ecosystems, such as erosion, sediment re-suspension, regional flooding, increased freshwater inputs, and over-wash of wetlands and marshes, are often accompanied by massive inputs of nutrients and organic matter from affected watersheds (Conner et al. 1989; Paerl et al. 2000, 2006a, b, 2010a, b; Christian et al. 2004; Roman et al. 2005; Crosswell et al. 2014). These inputs may stimulate primary production, promote harmful algal blooms, and culminate in bottom water hypoxia (Paerl et al. 2006a, b, c; Harding et al. 2016).

Negative consequences for higher trophic levels are commonly observed, including habitat degradation, increased disease and mortality of fish and shellfish, abrupt changes of salinity, dissolved oxygen, and pH, and inputs of contaminants from affected watersheds (Ruzecki et al. 1976; Conner et al. 1989; Eby and Crowder 2002; Adams et al. 2003; Roman et al. 2005; Miller et al. 2006; Paerl et al. 2006a, b, 2010a, b; Phlips et al. 2011; Hagy et al. 2004, 2006). Prior studies have documented the impact of tropical cyclones on major biogeochemical processes in estuarine and coastal systems, including air–water CO_2 exchange, nutrient loading and regeneration, and re-mineralization of soil organic carbon (C) (Bauer et al. 2013; Bianchi et al. 2013; Wetz and Yoskowitz 2013). However, most observational studies have focused on a single event or limited time period, which cannot be extrapolated to the broader impacts of changing storm activity. In order to quantify whether storms have a significant impact relative to baseline conditions requires long-term datasets that resolve a range of storms with diverse characteristics in a tractable study sytem.

Previous work documented profound impacts of tropical cyclones on lagoonal and semi-enclosed water bodies separated from oceans and seas by sandbars, barrier islands, and reefs because of restricted water exchange and relatively long water-residence times (Kennish and Paerl 2010; Paerl et al. 2010b; Laruelle et al. 2017). Lagoonal estuaries are low-energy ecosystems with small tidal amplitudes and low current velocities, promoting storage and recycling of materials (Kennish and Paerl 2010). These features prolong the recovery period following episodic perturbations, making them susceptible to cumulative impacts of closely spaced events (Paerl et al. 2006b). North Carolina's Pamlico Sound (PS) is the largest lagoonal ecosystem and second largest estuarine complex in North America. This ecosystem and its largest microtidal sub-estuary, the Neuse River Estuary (NRE) that feeds into PS, exemplify these conditions and represent the focus of this study.

The NRE-PS is an ecosystem subject to increasing human activity, resulting in nutrient enrichment, sedimentation, accumulation of pollutants, and habitat disturbances from rapidly expanding agriculture, industry, and urbanization in the airshed and watershed (Stanley 1988; Copeland and Gray 1991; Stow et al. 2001; Paerl et al. 2006a, 2007, Burkholder et al. 2006). The relatively long residence time of NRE-PS ($\sim$ 1 year), combined with efficient use of nutrients and organic matter, make this system highly susceptible to nutrient over-enrichment and eutrophication, resulting in nuisance algal blooms, hypoxia, anoxia, finfish and shellfish diseases, and mass mortalities (Copeland and Gray 1991; Christian et al. 1991; Paerl et al. 1995, 2006a, 2010a, 2014; Buzzelli et al. 2002; Eby 2001; Eby and Crowder 2002). This ecosystem is also strongly influenced by climatic perturbations, particularly the passages of tropical cyclones and "nor'easters", as it is located on the Atlantic "hurricane track" with a very active history of storm landfalls (NOAA Hurricane Center: http://www.nhc.noaa.gov). Climatologists have noted a "new climatic era" in the southeastern and mid-Atlantic coastal region of the United States, characterized by increased intensity and frequency of storms since the mid-1990s (Goldenberg et al. 2001; Webster et al. 2005; Holland and Webster 2007; Bender et al. 2010; Seneviratne et al. 2012; IPCC 2014; Wuebbles et al. 2014). The coastal region of North Carolina has experienced 35 tropical storm or hurricane-strength landfalls from 1996 through 2016, notably Hurricanes Bertha and Fran in 1996, Bonnie in 1998, three successive cyclones, Hurricanes Dennis, Floyd and Irene, in a 6-week period in September and October 1999, Isabel in 2003, Charlie and Alex in 2004, Ophelia in 2005, Tropical Storm Ernesto in 2006, Hurricanes Irene in 2011, Arthur in 2014, and most recently, Matthew in 2016 (Fig. 1). Three of these storms, Hurricanes Fran, Floyd and Matthew, caused "100–1000-year flood events" in the watershed of Bales (2003), Bales et al. (2000), https://www.colorlines.com/articles/noaa-declares-hurricane-matthew-1-1000-year-flood-event.

Effects of recent tropical cyclones on water quality, habitat, and fisheries in NRE-PS vary substantially in type, magnitude, and duration (Paerl et al. 2001a, b, 2006a, b; Peierls et al. 2003; Paerl and Peierls 2008; Adams et al. 2003; Tester et al. 2003), with large storm events exerting biogeochemical impacts lasting from several months into subsequent years (Peierls et al. 2003; Burkholder et al. 2004; Paerl et al. 2006a, b). As such, these storms pose a recurring threat to NRE-PS and other low-lying estuarine-coastal ecosystems along the US East Coast and Gulf of Mexico that have a number of large lagoonal or semi-lagoonal estuaries, bays, and sounds draining the

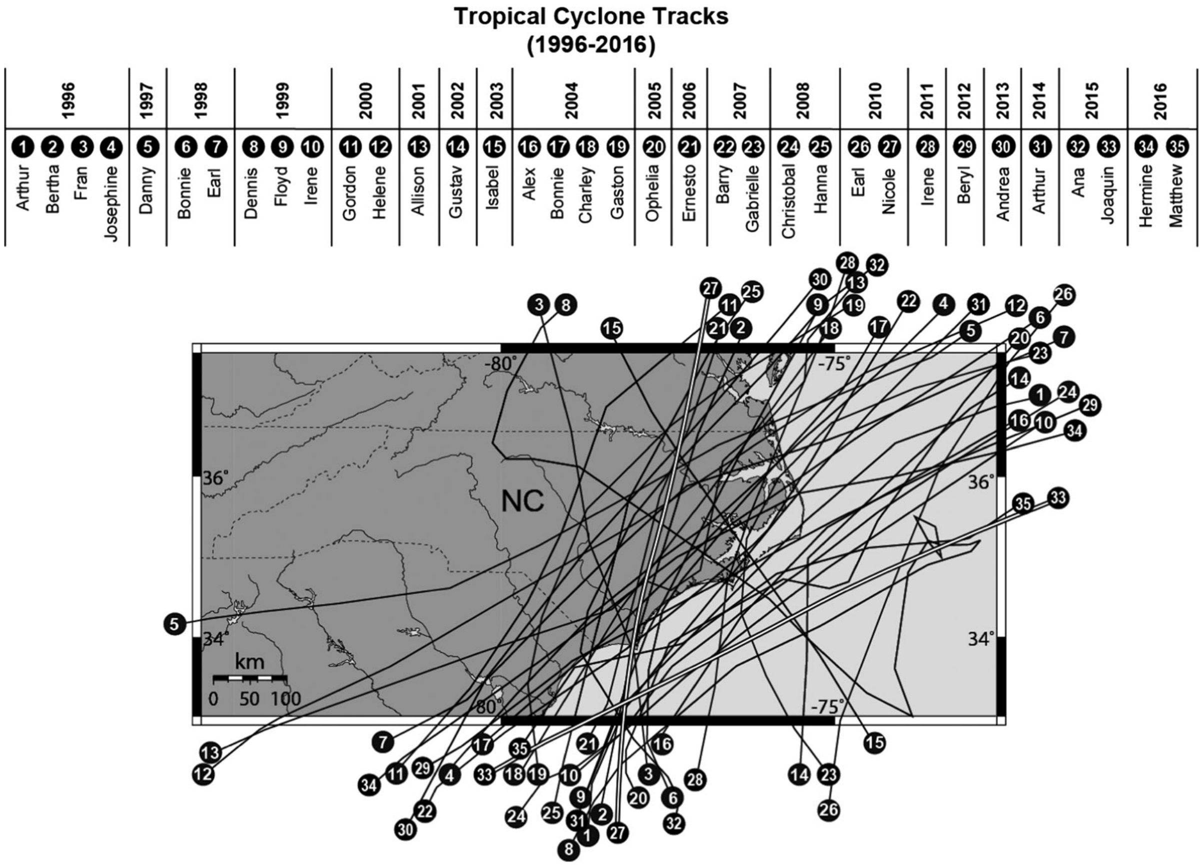

Fig. 1 Named storms that have impacted the North Carolina coastline since 1996. Storm track data are from the NOAA National Hurricane Center: Storm tracks with solid lines directly impacted the coastline, while tracks with open lines (e.g., Nicole, Joaquin) did not directly cross the study area, but impacted it with heavy rains and winds

coastal plains (i.e., Chesapeake Bay, Pamlico Sound, Florida Bay, Lake Ponchartrain, Texas lagoonal estuaries and bays). Fully evaluating the biogeochemical and ecological effects of hurricanes and other intense storms affords an opportunity to understand the linkages between coastal watershed geology, hydrology, biogeochemistry, water quality, and fisheries to resiliency of lagoonal ecosystems worldwide (e.g., S.E. Asia, Australia).

In this contribution, we focus on the magnitudes of nutrient, inorganic and organic C loading and cycling, and responses of phytoplankton production and composition to tropical storm events. Phytoplankton account for ~ 80% of "new" primary production to sustain planktonic and benthic food webs in NRE-PS (Paerl et al. 1998); thus quantifying phytoplankton responses is important to develop predictive capabilities for trophodynamic responses to tropical cyclones. Large-scale responses to tropical cyclones are superimposed on seasonal and inter-annual variability associated with human impacts and natural processes, requiring that we distinguish these effects to resolve impacts. To this end, we draw on extensive data from long-term monitoring programs to define relationships between nutrient and C inputs, impacts on water quality, habitat conditions, and biological responses from storm-related perturbations in comparison to more chronic, seasonal patterns. We classify three different types of storms based on rainfall and wind speed, and quantify estuarine responses to these different storm types relative to non-storm conditions.

Methods and materials

Neuse River Estuary-Pamlico Sound (NRE-PS) study site

NRE is the second largest tributary of PS in terms of freshwater discharge. Its watershed is comprised of managed forests and rapidly expanding agricultural (animal and row-crop operations), rural, urban (Raleigh-Durham-Research Triangle) and industrial land uses. Anthropogenic N and P loadings to NRE approximately doubled in the past four decades (Stow et al. 2001). Urban regions have sprawled in the upper NRE watershed, while industrial-scale animal (swine, poultry) farms in the coastal plain region proliferated, with an increase of swine from less than 1 million in 1989 to more than 12 million today. Excessive nutrient inputs dominated by non-point sources (80%) associated with these expanding human activities led to expressions of eutrophication, including nuisance algal blooms, hypoxia, and food web alterations (Copeland and Gray 1991; Rudek et al. 1991; Mallin et al. 1993; Paerl et al. 1995, 1998, 2006c; NC Dept of Environment and Natural Resources, Division of Water Qulaity 2001; Burkholder et al. 2006). Changes in the landscape fueling eutrophication are also reflected in organic matter loading to NRE (Osburn et al. 2016a).

PS has a surface area of 5335 km^2 and drains five major watersheds (Neuse, Tar-Pamlico, Roanoke, Chowan, and Pasquotank Rivers). These watersheds cover an area ~ 80,000 km^2, total freshwater discharge of ~21 km^3 y^{-1}, and drain about 40% of North Carolina's and 10% of Virginia's surface area (Table 1).

Tidal exchange with the coastal Atlantic Ocean and nearby Gulf Stream is restricted to three narrow inlets, resulting in a ~ 1 year residence time during average hydrologic years (Pietrafesa et al. 1996). The long residence time allows resident phytoplankton and vascular plants ample time to assimilate nutrients, resulting in high productivity per unit nutrient input. These characteristics are key to the PS serving as a highly productive nursery, supporting ~ 80% of US mid-Atlantic commercial and recreationally caught finfish and shellfish species (Copeland and Gray 1991; NC Dept. of Environmental Quality, http://portal.ncdenr.org/web/apnep/fastfacts).

Sampling sites and methodologies

Data analyzed here were obtained from two long-term monitoring programs in NRE, ModMon and FerryMon, designed to cover NRE and western PS (Fig. 2; Table 2). ModMon is a collaborative University—State of North Carolina (NC-Dept. of Environmental Quality-DEQ), and UNC-Chapel Hill Institute of Marine Sciences (IMS) program (www.unc.edu/ims/neuse/modmon/index.htm), that began in 1994. Sampling consisted of twice monthly visits to 11 mid-river stations along the estuarine portion of NRE (Fig. 2), including vertical profiles with collection of near-surface and near-bottom water for water quality (Paerl et al. 1995, 2006a, b). Monthly samples were also collected at nine stations in the western PS as part of the ModMon program starting in 2000 (Fig. 2).

Table 1 General characteristics of the Neuse River Estuary and Pamlico Sound, North Carolina

Characteristic	Neuse River Estuary	Pamlico Sound
Watershed size (km^2)	16,108	80,400
Surface area (km^2)	455	5335
Average depth (m)	2.7	5
Discharge (m^3 s^{-1})	50–1000	600–1500
Freshwater flushing time (d)	7–200	200– > 400
Hypoxic area (% of bottom)	20– > 70	Not known

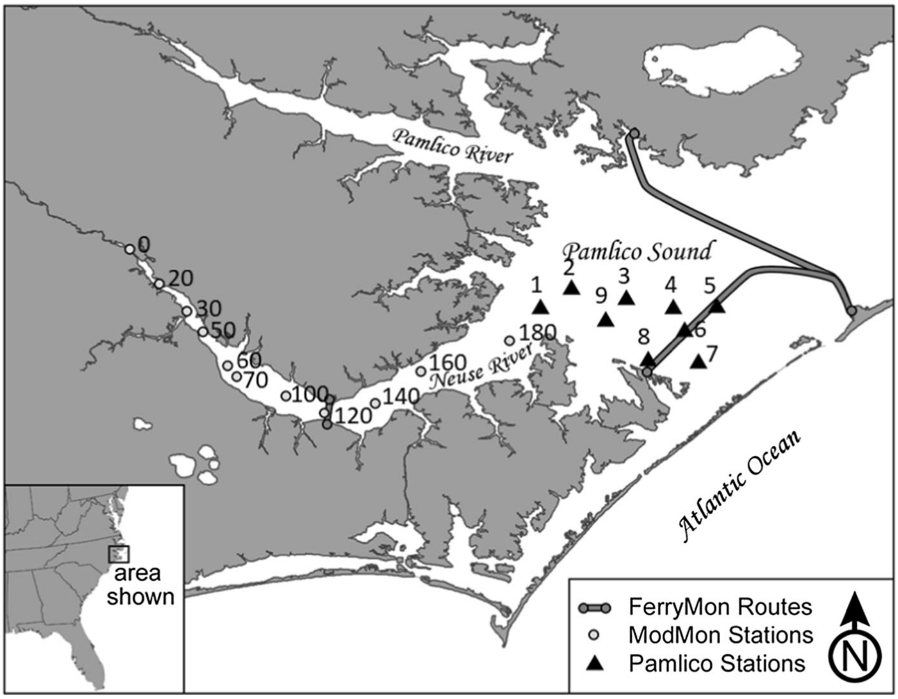

Fig. 2 Map of the Neuse River Estuary (NRE) and Pamlico Sound (PS) system, showing ModMon sampling stations (by numbers referred to in text) and the FerryMon crossings

Table 2 Comparison of sampling programs employed in this study

Program	Location	Resolution		Key measurements
		Spatial	Temporal	
ModMon	Along river axis	73 km coverage; 1–14 km (distance between sites)	Bi-weekly	YSI vertical sonde profiles (temperature, salinity, pH, O$_2$, chlorophyll *a*., turbidity); Discrete: DOM & POM, CDOM, inorganic nutrients, HPLC-pigments, preserved phytoplankton and microzooplankton, primary productivity
FerryMon	Across river channel and sound	~ 20 m horizontal (sampling resolution)	NRE = 34 crossings d^{-1} PS = 4 crossings d^{-1}	YSI sonde near surface (as above) Discrete: inorganic nutrients, DOM and POM, CHN, HPLC-pigments

Profiles of temperature, salinity, and dissolved oxygen were made at 0.5 m depth intervals using a YSI 6600 multi-parameter water quality sonde (Yellow Springs Inc., Yellow Springs, OH). Sondes were calibrated prior to each sampling trip according to the YSI User's Manual. Analytical uncertainties of all reported measurements are provided in Appendix I within the Supplementary Information.

Samples for nutrient concentrations, phytoplankton biomass, and community composition were collected along the ModMon transect in NRE from 1994 through 2016, and in the western PS from 2000 through 2016. Water samples were collected at the surface (0.2 m depth) and bottom (0.5 m above bottom) using a non-destructive diaphragm pump, dispensed into 4 L polyethylene bottles, and returned to the laboratory at the UNC-CH Institute of Marine Sciences, Morehead City (IMS) for processing within 4 h of collection.

FerryMon (www.ferrymon.org) consists of two N.C. Dept. of Transportation ferries equipped with automated, water-quality monitoring systems (Buzzelli et al. 2003; Ensign and Paerl 2006; Paerl et al. 2009). The NRE ferry makes 34 crossings per day between Cherry Point and Minnesott Beach, a mid-estuarine location in the mesohaline salinity zone of NRE characterized by high primary productivity and seasonal hypoxia (Fig. 2). Water is drawn from a through-hull intake located at ~ 1.5 m depth where it passes through a debubbler and a flow-through chamber that houses a YSI 6600 multi-parameter data sonde. Temperature, salinity, dissolved oxygen, turbidity, pH, and chlorophyll-a (Chl-*a*) via in vivo fluorescence are measured at a sampling rate of 0.25 Hz, and data are transmitted to a shore-based data server (IMS) via a cellular modem. Continuous data were augmented by discrete samples for nutrients and phytoplankton photopigments using automated ISCO samplers at programmed intervals. Physical–chemical parameters (Table 2) at NRE stations were also sampled monthly by NC-DEQ, and data were provided in a common database maintained by UNC-CH IMS and NC-DEQ.

Water Quality monitoring in NRE was expanded in 2009 to include high-resolution surveys of surface-water partial pressure of carbon dioxide (pCO_2) to estimate air–water fluxes (Crosswell et al. 2012). These spatial surveys of pCO_2 were coordinated with water-quality monitoring in PS, and the NRE ferry was fitted with an autonomous pCO_2 system in 2011 to study the impact of Hurricane Irene (Crosswell et al. 2014). For periods where direct pCO_2 measurements were unavailable (prior to 2009), pCO_2 was calculated from measured DIC and pH (NBS) via CO2Sys (Lewis et al. 1998), using the carbonic acid dissociation constants of Millero (2010). This approach may overestimate pCO_2 by upwards of 10% in organic rich, acidic water, due to the relatively large contribution of organic acids to total alkalinity (Abril et al. 2015). However, this error is reasonably small, relative to the large spatial and temporal variability of pCO_2 in these estuaries (Crosswell et al. 2012; Van Dam et al. 2018), particularly during storm events (Crosswell et al. 2014).

Wind, freshwater discharge, and material loading

Hourly average windspeed was gathered from the National Data Buoy Center station CLKN7 at Cape Lookout, NC. Daily average Neuse River discharge was measured by the United States Geological Survey (USGS) at Fort Barnwell (USGS 02,091,814), and divided by 0.69 to account for ungaged downstream inputs (Peierls et al. 2012). Daily Neuse River loads of carbon and nutrient forms were estimated using Weighted Regressions on Time Discharge and Season (WRTDS) (Hirsch and DeCicco 2014; Hirsch et al. 2010) based on daily average discharge and concentrations measured by ModMon (or NC DEQ for total N and total P) at the head of the estuary (Fig. 2). Half-window widths of the tricube weight function for seasonality, time, and discharge were set to default values of 6 months, 7 years, and 2 natural log units, respectively (Hirsch and DeCicco 2014).

Nutrient and carbon analyses

Nutrients measured at ModMon stations included: total dissolved nitrogen (TDN), nitrate plus nitrite ($NO_3^- + NO_2^-$), ammonium (NH_4^+), soluble reactive phosphate (SRP), dissolved organic carbon (DOC), dissolved inorganic carbon (DIC), particulate organic carbon (POC), and particulate nitrogen (PN). Dissolved inorganic nitrogen (DIN) was $NO_3^- + NO_2^- + NH_4^+$. Dissolved organic nitrogen (DON) was computed by difference as TDN–DIN. Nutrient analyses used 100 mL aliquots filtered through pre-combusted (4 h at 525 °C) 25 mm diameter Whatman

GF/F filters into acid-washed and sample-rinsed 150 mL polyethylene bottles that were subsequently frozen at − 20 °C. Filtrates were analyzed for dissolved N forms and SRP with a Lachat/Zellweger Analytics QuickChem 8000 flow injection autoanalyzer using standard protocols (Lachat method numbers 31-107-04-1-C, 31-107-06-1-B, and 31-115-01-3-C, respectively) (Peierls et al. 2012). Particulate organic carbon (POC) and nitrogen (PON) were measured on seston collected on pre-combusted GF/F filters, analyzed by high-temperature combustion using a Costech ECS 4010 analyzer (Peierls and Paerl 2011). DIC and DOC were measured on a Shimadzu Total Organic Carbon Analyzer (TOC-5000A) (Crosswell et al. 2012).

Phytoplankton biomass and community composition

Chlorophyll *a* (Chl-*a*) was measured for near-surface and near-bottom samples by filtering 50 mL of NRE water onto GF/F filters. Filters were frozen at −20 °C and subsequently extracted using a tissue grinder in 90% acetone (EPA method 445.0, Arar et al. 1997). Chl-*a* of extracts was measured using the non-acidification method of Welschmeyer (1994) on a Turner Designs Trilogy fluorometer calibrated with pure Chl-*a* standards (Turner Designs, Sunnyvale, CA). Taxonomic-group diagnostic photopigments were used to estimate spatio-temporal changes in abundance of algal taxonomic groups. Samples were analyzed by high performance liquid chromatography (HPLC) using a Shimadzu model LC-20AB HPLC equipped with a SIL-20AC autoinjector and a Shimadzu SPD-M20AC photodiode array spectrophotometric detector. Pigment extraction and processing techniques were described by Pinckney et al. (1998, 1999, 2001) and Van Heukelem et al. (1994). Absorption spectra were used to identify photopigments using commercial standards (DHI, Denmark). Major phytoplankton taxa and diagnostic pigments included; chlorophytes or green algae (chlorophyll *b*, lutein, violaxanthin), cyanobacteria (zeaxanthin, myxoxanthophyll, echinenone, canthaxanthin), diatoms, raphidophytes (fucoxanthin, chlorophyll c, diadinoxanthin, diatoxanthin), dinoflagellates (peridinin), and cryptophytes (alloxanthin) (Jeffrey et al. 1999).

Data analysis

Thirty-five named storms that affected the North Carolina coast from 1996 through 2016 (Fig. 1) were designated as wet or dry and windy or calm, based on recorded wind speeds near the NRE-PS and the impact of their precipitation on freshwater delivery to the NRE (Table 3). Wet storms produced a 7 day mean Neuse River flow, (Fort Barnwell, NC) that was greater than 191 $m^3\ s^{-1}$, the 90th percentile of weekly average flows for the storm season (May–October). Windy storms were defined as having a 36 h (12 h before landfall and 24 h after landfall) maximum hourly average wind speed that was greater than 14.1 $m\ s^{-1}$, the 90th percentile of 36 h maximum hourly average wind speeds during the storm season. Named storms that were not categorized as wet or windy (8 storms) were considered as part of the baseline conditions upon which to compare storm impacts. Using these criteria, storms were assigned to three groupings: windy but not wet = dry and windy (16 storms), wet but not windy = wet and calm (3 storms), and wet and windy (8 storms) (Table 3). Storm flow periods were defined for each “wet” storm as the time period that encompassed the rise in river flow associated with the storm through the falling limb of the hydrograph, and ended at the first increase in flow once baseflow conditions occurred (see Fig. 3). Storm loads were calculated by summing daily loads over each storm period. To determine the relative importance of storm loads on annual and long-term loading to the NRE, the sum of storm loads was compared directly against total loads on an annual basis and for the long-term (21 years) record. The proportion of storm to total loads, however, minimizes the importance of storm loading to some degree because storm loads also increase the total load. To determine the increase in annual loads directly attributable to storms, the total storm load was divided by a theoretical total load where the storm period loadings were substituted with average non-storm period loading values from the months of May through October.

Impacts of tropical cyclones on estuarine carbon, nutrient and algal biomass related parameters were determined for each storm type for the NRE and southern PS. For each parameter and for both the NRE and PS, volume weighted averages were calculated to provide a single metric for examining the response of

Table 3 Named storms affecting North Carolina from 1996 through 2016, with storm designation and dates

Storm	Date	Classification	Storm	Date	Classification
Arthur	20 Jun 1996	Dry and windy	Gaston	30 Aug 2004	–
Bertha	12 Jul 1996	Dry and windy	Ophelia	14 Sep 2005	Dry and windy
Fran	6 Sep 1996	Wet and windy	Ernesto	1 Sep 2006	Wet and windy
Josephine	8 Oct 1996	Wet and windy	Barry	3 Jun 2007	Dry and windy
Danny	24 Jul 1997	–	Gabrielle	9 Sep 2007	–
Bonnie	27 Aug 1998	Dry and windy	Christobol	20 Jul 2008	–
Earl	4 Sep 1998	Dry and windy	Hanna	5 Sep 2008	–
Dennis	4 Sep 1999	Wet and windy	Earl	3 Sep 2010	Dry and windy
Floyd	16 Sep 1999	Wet and windy	Nicole	29 Sep 2010	Wet and calm
Irene	18 Oct 1999	Wet and windy	Irene	27 Aug 2011	Wet and windy
Gordon	19 Sep 2000	Wet and windy	Beryl	30 May 2012	Dry and windy
Helene	23 Sep 2000	Dry and windy	Andrea	7 Jun 2013	Dry and windy
Allison	13 June 2001	–	Arthur	4 Jul 2014	Dry and windy
Gustav	10 Sep 2002	Dry and windy	Ana	7 May 2015	Wet and calm
Isabel	18 Sep 2003	Dry and windy	Joaquin	3 Oct 2015	Wet and windy
Alex	3 Aug 2004	–	Hermine	2 Sep 2016	Dry and windy
Bonnie	13 Aug 2004	–	Matthew	8 Oct 2016	Wet and windy
Charley	14 Aug 2004	Wet and calm			

"–" The storms were not classified as wet or windy

each water body. For the NRE, volume weighted concentrations were calculated according to Peierls et al. (2012) based on segment volumes assigned to each NRE station. Due to the even spatial distribution and weaker spatial gradients in PS, the volume weighted average was assumed equal to the arithmetic mean of observations from the nine PS sampling stations (Fig. 2). Pigment data were log transformed prior to all analyses. Volume weighted average parameter values from sampling cruises within two weeks following a storm were averaged and the resulting averages were aggregated by storm type. Kruskal–Wallis tests were used to determine significance of differences in each parameter between four storm types: (1) baseline, non-event, (2) dry and windy, (3) wet and calm, and (4) wet and windy storms. Tukey–Kramer post hoc tests on ranks within each storm type grouping were used to determine which groups were different when Kruskall Wallis tests indicated significant differences of medians between groups ($\alpha = 0.05$). To evaluate the evolution of storm impacts over time, this process was repeated for samples collected 3–4 weeks after the storms (Table 4).

Following these estuary-wide analyses, phytoplankton biomass as Chl-*a* was examined with a greater degree of spatial resolution in the NRE, where averaging across the estuary may obscure significant differences in downstream Chl-*a* spatial gradients due to storm impacts. Volume weighted Chl-*a* concentrations were calculated for upper (stations 0–30), middle (stations 50–120) and lower estuary (stations 140–180) segments, and Chl-*a* responses to the different storm types were determined as for the whole estuary.

Results and discussion

Freshwater discharge

Major storms, including Hurricanes Floyd in September 1999 and Matthew in October 2016, resulted in peak daily average discharges more than ten and twenty times higher than the long-term mean ($\sim$ 110 m^3 s^{-1}) and median ($\sim$ 70 m^3 s^{-1}), respectively (Fig. 3). These significant storm pulse events are superimposed on a highly dynamic flow regime regulated by seasonal cycles of evapotranspiration, years of very high non-tropical storm related precipitation (e.g. 1998 and 2003), and multi-year droughts (e.g. 2007–2012). Consequently, storm impacts on annual discharge depend on the intensity of storm discharge, relative to background annual flow. For

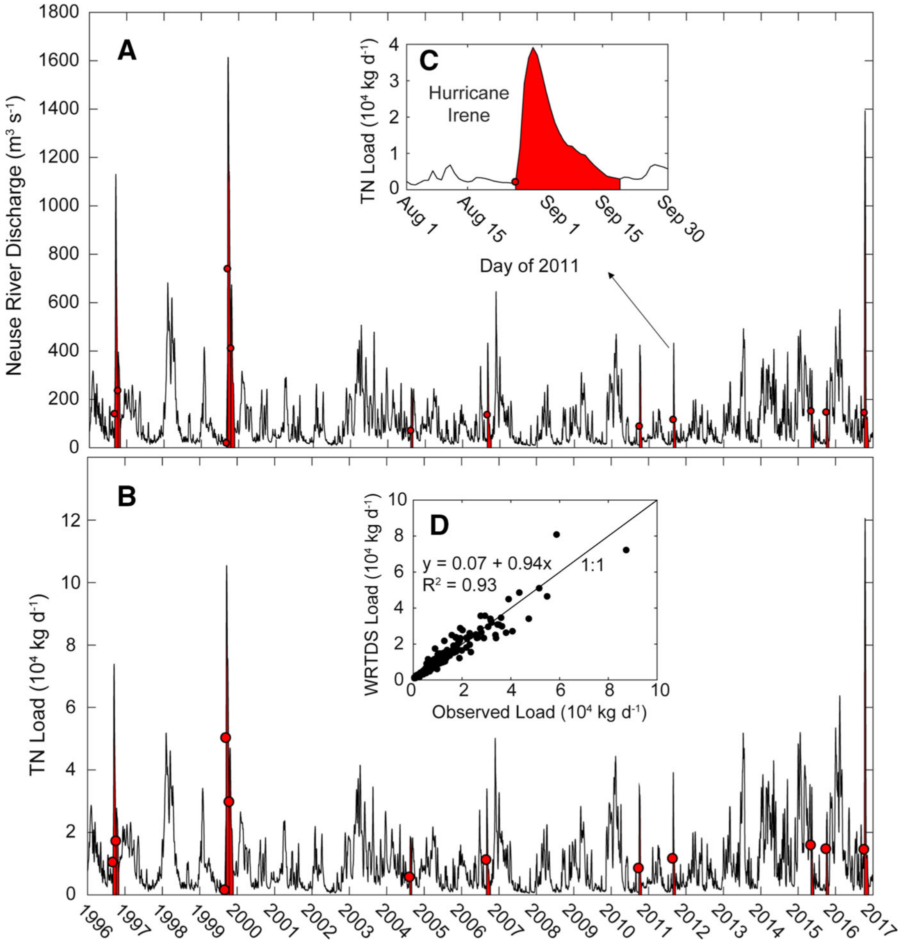

Fig. 3 Impacts of "wet storms" on river flow and total N (TN) loading to the Neuse River Estuary. **a** Daily Neuse River discharge. **b** Daily TN load estimated by Weighted Regressions on Time Discharge and Season. Filled red circles indicate the landfall dates of "wet storms". Time periods defined as storm flows are shaded red. **c** Expanded view of TN load resulting from Hurricane Irene. **d** Relationship between observed TN load based on monthly TN measurements and WRTDS estimates of load for the same set of dates. (Color figure online)

Table 4 Influence of "wet" storms on long-term (1996–2016) material loads to the Neuse River Estuary

Parameter	Percent of long term load during storm flows	Percent increase over baseline due to storms
Water	13.9	15.5
TN	11.6	12.6
DIN	7.2	7.5
DON	16.0	18.3
PN	16.0	18.2
TP	21.5	25.7
SRP	26.0	32.8
DOC	21.2	25.6
POC	17.0	19.6
DIC	14.1	15.7

example, 1999 was an otherwise dry year but the cumulative sequential impacts of Hurricanes Dennis, Floyd, and Irene more than doubled the annual discharge, making annual flows in 1999 the highest during the 21 year period of study (Fig. 4A). Although the storm pulse from Hurricane Matthew was a significant event, 2016 was a year marked by high rainfall to the watershed, and Matthew only constituted about 10% of the annual total flow. Hurricane Irene (2011) produced about half the discharge of Matthew but occurred during the prolonged drought when annual flows were the lowest during the 21 year study period. As a result, discharge following Irene was twice the fraction of the annual total compared to Matthew.

While it is clear that tropical cyclones can contribute significant pulses of freshwater to the NRE-PS system, no significant effects of storms on volume weighted average salinities were determined for either the NRE or PS (Fig. 5A, F). Although the median salinities did decrease for wet and calm and wet and windy storms in both first 2 weeks and following weeks three and four after the storm (Fig. 5A, F), the high degree of variability resulted in these difference being statistically insignificant. River flow exerts a strong influence on the salinity of the NRE-PS. However, the salinity budget of the system is also strongly impacted by changes in exchange with shelf waters driven by differences in water level between PS and nearby Raleigh Bay (Jia and Li 2012), the occasional formation of new inlets (Paerl et al.

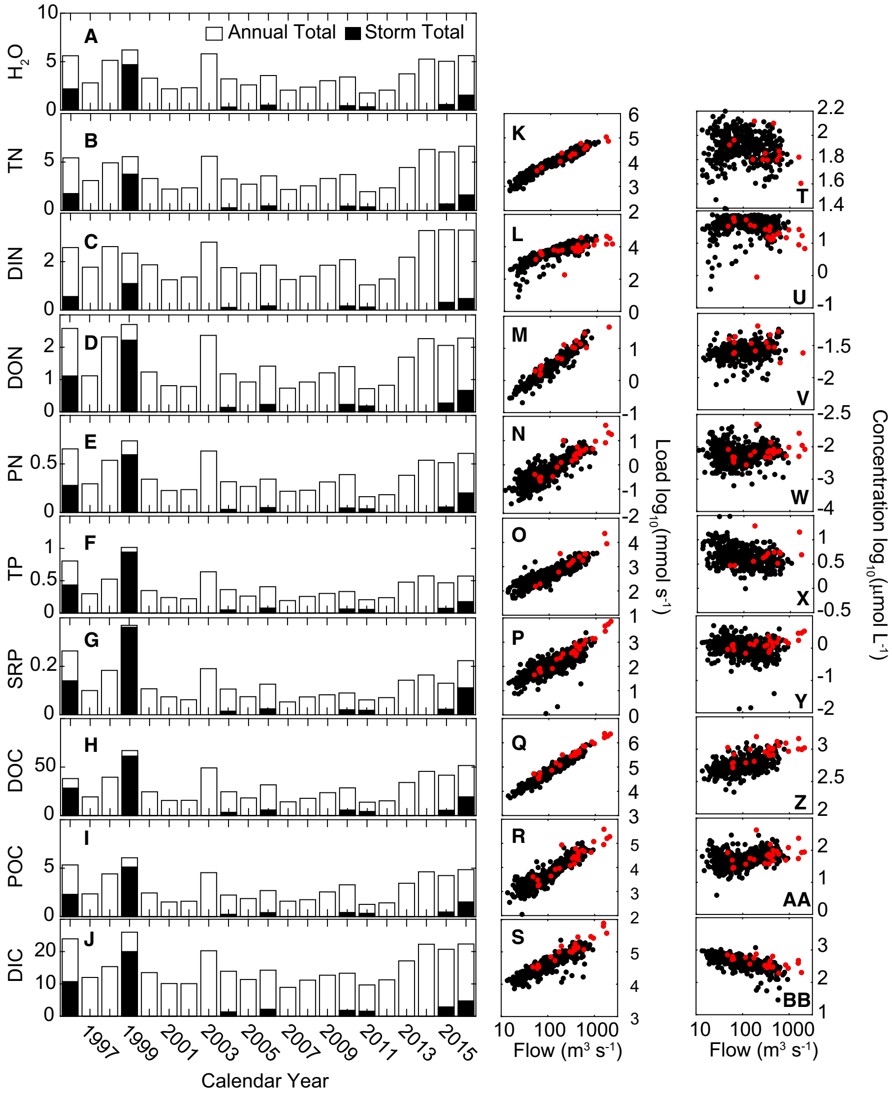

Fig. 4 Total annual and storm flow loading of nutrients and carbon forms (left panels). Flow versus concentration relationships during non-storm in black symbols and storm flows in red symbols (left panels). Annual water loads are in units km^{-3} per year. N, P, and C loads are in units 10^6 kg of N, C, or P per year. Concentrations at Streets Ferry Bridge are in units log10 (μmol L^{-1}). (Color figure online)

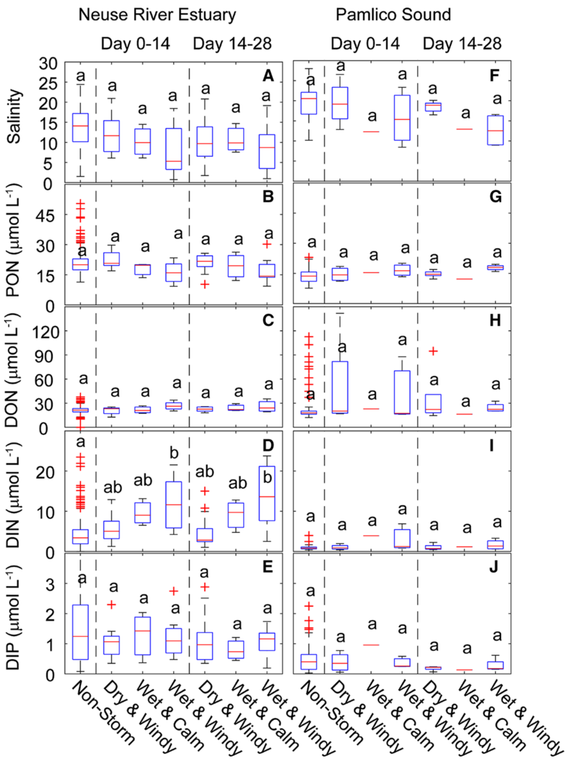

Fig. 5 Box plots of volume weighted nutrient-related parameters within the NRE & PS. during non-storm conditions and two time spans following the passage of dry and windy, wet and calm, and wet and windy tropical cyclones. Boxes represent the interquartile range. Whiskers represent 1.5 times the interquartile range, and red, plus symbols represent outliers. Different letters above boxes identify statistically distinguishable rank values between groups. (Color figure online)

2009), and wind-forced salinity intrusion (Jia and Li 2012).

Continuous monitoring of salinity in PS by FerryMon provided an excellent example of how creation of a new inlet can affect exchange and salinity regimes within PS. Prior to Hurricane Isabel in September 2003, the eastern side of PS was growing increasingly fresh compared to the western basin due to higher than usual riverine discharge to the Roanoke and Chowan rivers that eventually drain into eastern PS (Paerl et al. 2009). The inlet created by Hurricane Isabel enhanced exchange of the eastern basin with Atlantic shelf waters causing a relative increase in salinity in the eastern basin compared to the western basin of PS. This trend of increasing relative salinity in the eastern basin continued until later in the fall of 2003 when the new inlet was filled by the N.C. Dept. of Transportation and the east–west gradient in salinity began to once again decrease (Fig. 6).

Nutrient (N and P) and carbon loadings

Variability in river flow spanned nearly three orders of magnitude while concentrations of nutrient and C forms generally varied only by 1–1.5 orders of magnitude (Fig. 4, K-BB). Consequently, flow rather than concentration was the strongest driver of loading of nutrients and C forms to the estuary. High river flows following “wet” storms consistently led to periods of intense C and nutrient loading to the estuary, and often contributed significantly to annual total loading. For example, in 1999 loading of TP and SRP during the back to back storm flow periods following Dennis, Floyd, and Irene constituted greater than 90% of the annual load (Fig. 4F, G). These same storm flows, however, only constituted about 50% of the annual DIN loading (Fig. 4C). Similarly, SRP loading during Hurricane Matthew constituted about half of the annual load while DIN loading was less than 20%.

These differences in the relative importance of storm loadings to the annual total can be explained by examining the relationship between flow and concentrations of each parameter during storm and non-storm flows. Under non-storm flow condtions, both TP and SRP exhibit weak negative relationships with increasing flow (Fig. 4X, Y), which is indicative of a dominant contribution by point sources in the watershed. In contrast, under storm flows, concentrations of

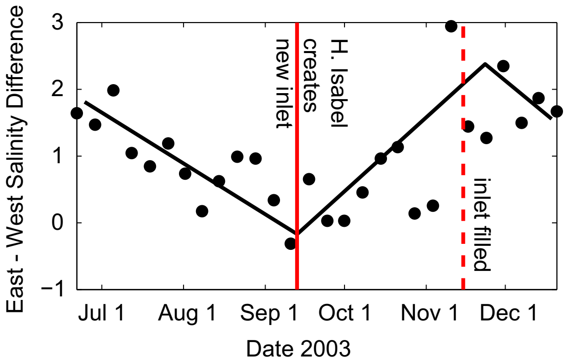

Fig. 6 Difference in weekly average FerryMon salinity measurements between the east and west basins of Pamlico Sound during the period prior to the creation of a new inlet by Hurricane Isabel through its eventual closure in late fall 2003. Figure reproduced with permission from Paerl et al. (2009)

P forms increase as flow increases, which magnifies the impact of elevated water loading to the estuary on P delivery. The mechanism behind the enhancement of P concentration under storm flow conditions may involve sediment P release from inundated wetlands and agricultural fields under the hypoxic river water conditions that often occur following the passage of tropical cyclones. DOC concentrations exhibited a similar positive slope with flow under both storm and non-storm flow conditions (Fig. 4Z). However, under storm flows, DOC concentrations are higher than non-storm flows (Fig. 4Z), with a similar effect of magnifying the relative importance of storm flow loading of terrigenous DOC to the estuary. It seems very likely that high P and DOC loadings following storms are linked. Tropical cyclones occur during summer and fall when waters are still warm and favorable for bacterial growth (Peierls et al. 2012). High loading of labile terrigenous DOC during storm flows likely fuels water column oxygen consumption, creating hypoxic conditions that promotes redox sensitive P release from surficial sediments (Paerl et al. 1998).

Both TN and DIN exhibited a non-monotonic relationship with flow with concentrations increasing from the lowest flows up to about 30 $m^3 s^{-1}$ and then subsequently declining weakly with increasing flows (Fig. 4T, U). This pattern has been previously recognized and ascribed to the initial importance of overland, non-point source delivery of N as flows begin to increase followed by a dilution effect of increasing flows (Alemeddine et al. 2011). Within the range of storm-flows, the relationship between flow and concentrations of TN and DIN is negative (Fig. 4T, U), and therefore mutes the impact of storm flows on loading relative to P forms and DOC. DON and PON showed no clear relation with flow (Fig. 4V, W), and therefore the fraction of storm loading to total loading for these N forms closely mirrored the fraction storm water loading to total water loading.

The strong correlation of N loadings with freshwater discharge (Fig. 4K–N) confirmed the importance of non-point sources, including agricultural and urban storm-water runoff, as major sources of N in the NRE-PS basin. These results were consistent with earlier estimates of annual point vs. non-point sources of N in the NRE-PS basin that showed ∼ 80% of total N loading is of non-point origin, much of it organic N (NC DENR 2001; Lebo et al. 2012; Osburn et al. 2016a). Moreover, results presented here illustrate the importance of event-scale loadings, with “wet” storms contributing significant fractions of annual totals for N loading to the NRE and PS. Years with large wet storm events corresponded to increased annual loadings compared to years with no events or that experienced “dry” storms. Fall 1999 (Floyd and Dennis), fall 2006 (Ernesto) and fall 2016 (Matthew) are examples of years whose N loadings were dominated by storm events (Fig. 4B). Several other years had rainy seasons in an absence of major storms, exemplified by summer 2003. In contrast, seasons and years that featured dry and windy storms and droughts showed lowest seasonal and annual N loadings to the NRE and PS. These data documented that the frequency and magnitude of “wet” events strongly affected N loadings to the NRE-PS.

Although storms do increase N loading to the NRE-PS, of the forms of N investigated (PON, DON, and DIN), only DIN showed significantly elevated concentrations compared to the baseline conditions, and only in the NRE during the first 2 weeks following wet and windy storms (Fig. 5B–D).

While phytoplankton in the NRE-PS were N-limited from spring to fall, P was a “co-limiting” factor occasionally (Rudek et al. 1991; Paerl et al. 1995, 2014). Co-limitation by N and P was observed during periods of high freshwater discharge accompanied by exceptionally high N loadings. Compared to baseline, non-storm conditions, volume weighted phosphate concentrations were not significantly different in either the NRE or PS following any storm type (Fig. 5E, J).

Organic matter (OM)

Storms appear to affect pools of DOC and POC differently in NRE-PS. Pulses of terrigenous DOC occurred throughout NRE-PS following wet and calm and wet and windy events, and the spatial extent of these DOC pulses often reached the mid-estuary, depending on the magnitude of freshwater discharge (Figs. 7, 8). Exceptional DOC pulses affected PS, particularly following large, wet tropical storm events in 2006 and 2016 (Figs. 7, 8). This result was consistent among wet and windy storms and resulted in median volume-weighted DOC values that were significantly higher than non-storm conditions in NRE (Fig. 7). DOC concentrations in NRE were

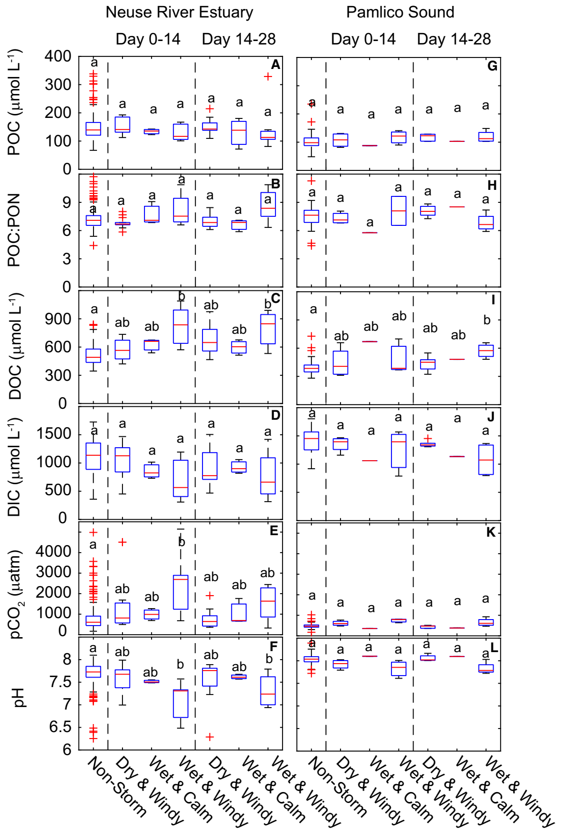

Fig. 7 Box plots of volume weighted carbon-related parameters within the NRE & PS. Figure configuration follows Fig. 5

approximately 200 and 300 μmol L^{-1} higher during the first three to 4 weeks following wet and windy storms (Fig. 7). In PS, the same trend was observed but DOC concentrations were only significantly higher than baseline conditions ($\sim$ 100 μmol L^{-1} higher) during the three to 4 week period following wet and windy storms (Fig. 7). Median values of volume-weighted POC concentrations in NRE and PS were remarkably consistent at $\sim$ 150 and 120 μmol L^{-1}, respectively.

While DOC concentrations are often used to track the influence of terrigenous OM in estuarine systems, C:N serves as an indicator of the origin and quality of DOM and POM, with lower C:N (4–10) attributed to phytoplankton biomass and the higher C:N (> 20) characteristic of terrigenous material (Bianchi and Bauer 2011). In NRE, DOM is largely terrigenous with some modulation of its quality by planktonic processes during low discharge (Osburn et al. 2012; Dixon et al. 2014). For example, just prior to Hurricane Irene, NRE experienced low-flow conditions and DOM quality reflected high Chl-*a* (Osburn et al. 2012). After passage of that storm, both DOM and POM pools reflected terrigenous sources, including increases in terrigenous DON. Another major source of autochthonous DOM originated in sediments, as evidenced by changes of DOM quality under moderate discharge and wind-driven mixing (Dixon et al. 2014). C:N ratios in DOM for NRE ranged from 12 to 30, indicating the predominantly terrigenous influence.

In NRE, increases of particulate C:N ($p = 0.09$) were observed during wet and windy storms four weeks following Hurricane Irene (Fig. 7B), suggesting that storms with high freshwater delivery increased the ratios of terrigenous to phytoplankton-derived organic matter. Particulate C:N ratios in PS primarily reflected phytoplankton OM (C:N < 10) as the influence of terrigenous OM was negligible. Tropical cyclones and precipitation extremes are known to produce significant changes in terrigenous OM loading to NRE and PS (Brown et al. 2014; Osburn et al. 2012; Paerl et al. 1998, 2001a). The significant increase of DOC for wet and windy storms (Fig. 7C, I) was consistent with an impact of these storms on DOC loading (Fig. 4H, Q). Large pulses of terrigenous OM into NRE were observed for days to months following storm passages. DOC pulses following high freshwater discharge affected microbial production and respiration, exacerbating eutrophication and habitat degradation, i.e., hypoxic/anoxic zones; fish kills; decreased water clarity and quality (Brown et al. 2014; Paerl et al. 1998; Peierls and Paerl 2010, 2011).

Understanding how the impact of these DOC pulses on the eutrophic NRE-PS is important in the context of their roles in accelerating eutrophication, given a predicted increase of major tropical cyclones (Category 3 or higher) in the western Atlantic in future climate scenarios (Bender et al. 2010). Our findings suggest that storm-driven flushing of terrigenous OM to NRE-PS, confirmed by DOC and particulate C:N signals (Fig. 7), results in a shift to terrigenous-dominated OM from phytoplankton-dominated OM, stretching from riverine sources to the marine end-member (Dixon et al. 2014; Osburn et al. 2016b). Extreme events, particularly events that resulted in historic floods (i.e., Hurricanes Floyd, Matthew) resulted in extreme pulses of terrigenous DOC that

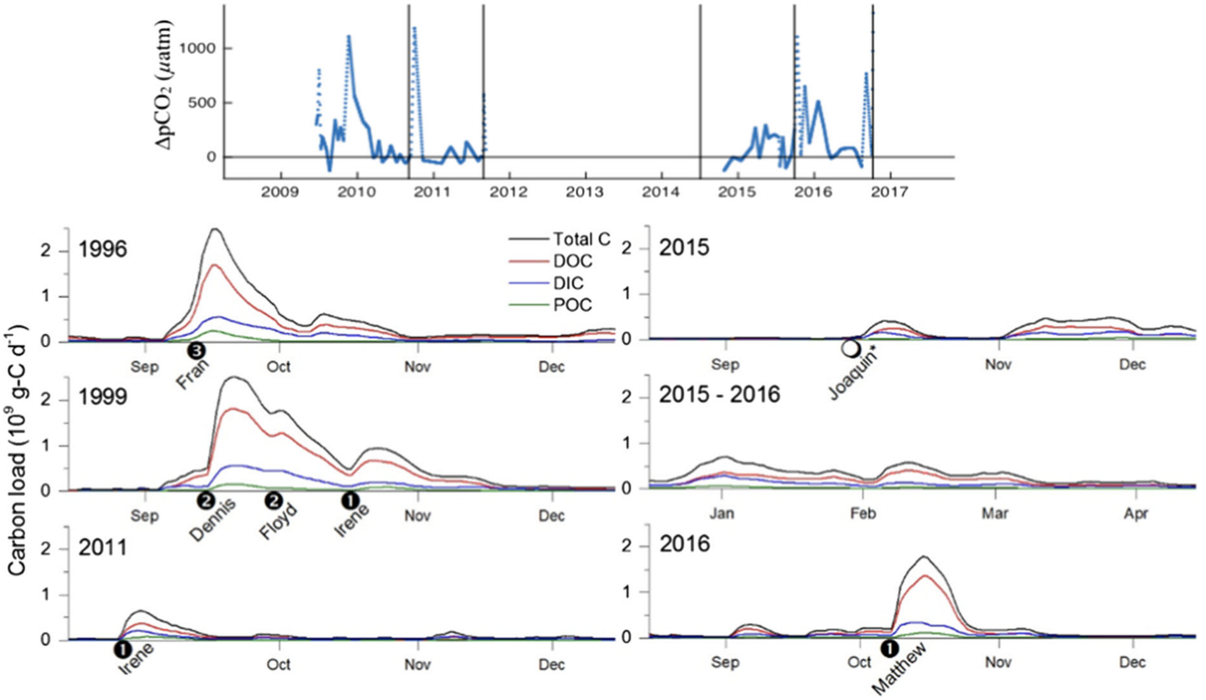

Fig. 8 Carbon loading and air–water CO_2 gradients (ΔpCO_2) in the NRE, where positive ΔpCO_2 indicates CO_2 exchange from the water to the atmosphere. Hurricane Joaquin (2015) did not make landfall (also shown in Fig. 1), but indirectly impacted NC as part of a large 'multiple-low' storm complex

extended through NRE and into PS, indicating these extreme discharge events follow the pulse-shunt concept whereby NRE acts as a pipeline for terrigenous DOC that is exported to PS largely unaltered (Osburn et al. 2012; Paerl et al. 2001a, b, 2006a, b, c; Osburn et al. 2016b; Raymond et al. 2016).

CO_2 fluxes

Average estuarine pCO_2 in NRE was significantly elevated above baseline conditions during the two week period following wet and windy storms (Fig. 7E). This increase in pCO_2 was also reflected in significant decreases in pH (Fig. 7F). Although individual storms did produce elevated pCO_2 in PS (e.g. Hurricane Irene: Crosswell et al. 2014), there were no consistent, statistically significant differences in PS pCO_2 or pH following any storm type compared to non-storm conditions (Fig. 7K, L). Due to the high bicarbonate concentration of seawater and its dominance of the DIC pool at estuarine pH, changes of DIC by storm type resembled those for salinity (compare Figs. 5A, F and 7D, J) and no significant changes from baseline, non-storm conditions were observed.

Extreme winds dramatically increase gas exchange via increased turbulence and physical processes associated with wave breaking. Crosswell et al. (2014) reported increases of pCO_2 and piston velocity following Hurricane Irene led to air–water CO_2 efflux from NRE and PS of 57–170 and 5–16 mmol C m^{-2} h^{-1}, respectively, for the 42-h period when NRE-PS experienced hurricane-force winds. By contrast, air–water CO_2 efflux over the 17 days following Irene were only 4.2–6.0 and 0.2–0.3 mmol C m^{-2} h^{-1} in NRE and PS, respectively. A significant increase in calculated pCO_2 after wet and windy storms (Fig. 7E) was consistent with pCO_2 directly measured during the case study of Hurricane Irene. Median calculated pCO_2 following wet and windy storms was at least three times higher than wet and calm storms, dry and windy storms, or non-storm conditions.

Variation in storm intensity and frequency

Over the past two decades, the largest effects on riverine C-loadings (DIC, DOC, and POC) followed intense (1996, 2016) and back-to-back (1999) hurricanes (Fig. 8). Riverine C-loading following these types of storms was 10× greater than occurred immediately after Hurricane Irene (2011) or Hurricane Joaquin (2015) (Fig. 8). Storm intensity is typically characterized by the Saffir-Simpson scale that is based on wind speed. However, other metrics of storm intensity, such as rainfall, location, and duration may better capture the extent to which C is mobilized from the watershed and transported through rivers to estuaries (Fig. 8). The largest riverine C-loadings were in response to Hurricane Dennis (1999), the longest-duration storm to impact the state of North Carolina during the study period. Hurricane Fran (1996) was a more intense storm in terms of rainfall and wind speed, but Fran was a relatively fast-moving system that followed a northern track, and riverine C-loading was slightly less than after Dennis. A similar trend was observed among the less intense storms. The northern track of Hurricanes Dennis (1999) and Irene (2011) across the NC coastline led to relatively low riverine C loading. By contrast, the curved track of Hurricane Matthew along the South Atlantic Bight extended the time of impact on Piedmont watersheds and produced extreme flooding and C-loadings from rivers to coastal waters (Fig. 8).

Fate of terrigenous C in NRE-PS

The role of rivers as passive conduits or 'pipelines' that deliver terrigenous DOC and POC to estuaries and coastal waters has long been recognized as a major component of global biogeochemical cycles (Schlesinger and Melack 1981; Bianchi 2007; Bianchi and Bauer 2011; Bauer et al. 2013). However, the concept of streams and rivers as active, rather than passive "pipelines" for OC (Cole et al. 2007) has received support in the past few decades (Battin et al. 2009; Tranvik et al. 2009). This has led to a recognition of inland waters as globally significant sources of CO_2 (Butman and Raymond 2011; Raymond et al. 2013) and CH_4 (Cole et al. 2007, Bastviken et al. 2011) to the atmosphere, driven by the re-mineralization of terrigenous OC (Cole and Caraco 2001; Regnier et al. 2013). Hydrologic events significantly alter both the timing and quality of OC flux from streams to receiving bodies such as estuaries (Hilton et al. 2008; Osburn et al. 2012; Bauer et al. 2013; Bianchi et al. 2013; Osburn et al. 2016b; Almeida et al. 2017). DOC and POC concentrations generally increase with freshwater discharge as a larger fraction of runoff occurs in overland flow rather than infiltration and percolation through soils (Schlesinger 2005). Hence, freshwater discharge affects the quality and quantity of terrigenous OC delivered by rivers, and the residence time of this material within receiving waters. The recently described 'pulse-shunt' concept (Raymond et al. 2016) is an extension of earlier frameworks describing OC dynamics in drainage networks, including 'active pipe' (Cole et al. 2007) and nutrient spiraling (Ensign and Doyle 2006; Hall et al. 2013). This concept argues that hydrologic events alter the delivery of terrigenous OC through drainage networks by mobilizing a 'pulse' of labile material, which is rapidly 'shunted' downstream.

The fate of this labile OC depends on the capacity of estuarine waters to buffer changes in pCO_2 generated during the respiration and photochemical oxidation of organic matter. If waters are poorly buffered, more of the remineralized OC will be lost to the atmosphere as CO_2, but if the buffering capacity is high, a greater fraction may be exported to the coastal ocean as HCO_3^- and CO_3^{2-}. Because this buffering capacity varies with DIC and alkalinity (Egleston et al. 2010; Hu and Cai 2013), delivery of these materials to the estuary will shape the response of the estuary to OC loading.

The data presented here for NRE-PS support the pulse-shunt concept and extend its applicability to estuarine systems. Storms mobilize large pulses of terrigenous OC and deliver this C to the estuary (Osburn et al. 2012). The eventual fate of this terrigenous OC is determined by the relative importance of three processes: burial, flushing to the coastal ocean, and degradation to CO_2, resulting in exchange with the atmosphere. We were able to constrain one of these loss terms, air–water CO_2 exchange in this study. 'Dry' events, such as Hurricane Irene (2011), were associated with enhanced physical mixing that increased CO_2 loss to the atmosphere relative to terrigenous OC flux and storage in PS (Crosswell et al. 2014). 'Wet' storms, exemplified by Joaquin and Matthew, were associated with relatively low CO_2 fluxes during storm passage. Instead, the main impact of wet storms on CO_2 fluxes occurred after the storm due to enhanced net heterotrophy, and possibly photochemical oxidation, in response to large terrigenous DOC loadings generated by extreme rainfall. Figure 9 illustrates this effect as increased DOC loadings associated with the large freshwater pulse from Hurricane Matthew, concurrent flushing of phytoplankton biomass from NRE, and dilution of POC associated with phytoplankton biomass in NRE-PS that saturated these ecosystems with terrigenous DOC. Within 1–2 months, freshwater discharge decreased, allowing phytoplankton-driven production of POC to increase in importance as the large terrigenous DOC in freshwater discharge subsides (Figs. 8, 9).

Responses of phytoplankton biomass (Chl-a) to storm events

Within NRE and PS, volume-weighted phytoplankton pigment concentrations following the different storm types showed no consistent, statistically significant differences from non-storm conditions (Fig. 10). However, this finding did not indicate a lack of response by the phytoplankton community to storm events, rather it suggested there was not a predictable estuary-wide response. At finer degrees of spatial and temporal aggregation, significant changes in Chl-*a* due to storm type were observed in NRE. In the upper and mid-estuary, wet and windy storms led to decreased Chl-*a*, with impacts persisting up to four weeks following storm passage (Fig. 11A, B). In the

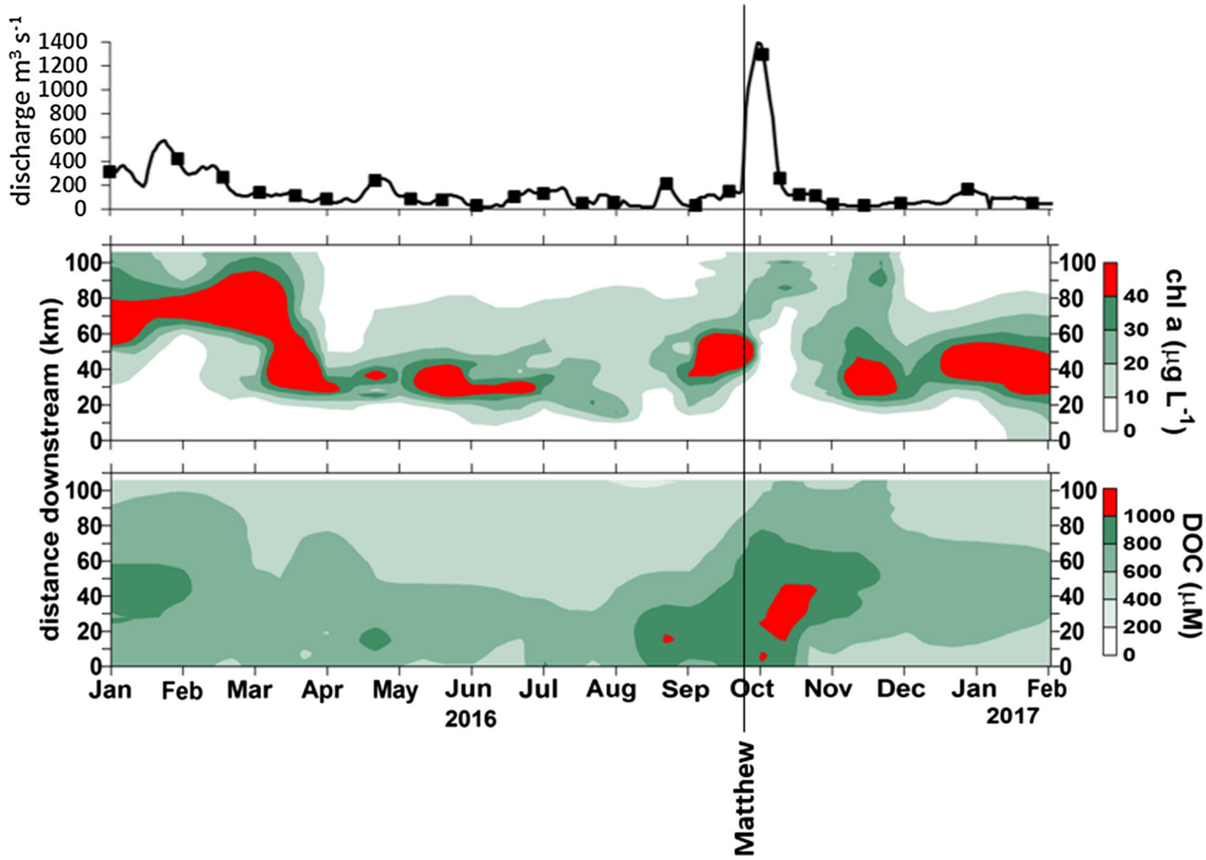

Fig. 9 An example of the pulse-shunt concept as shown by the organic matter-enriched freshwater pulse that discharged to the NRE-PS after very wet Hurricane Matthew struck coastal North Carolina in the fall of 2016. Note the rapid enrichment of DOC associated with the pulse. This caused a rapid shift from an authochthonous-driven system, as shown by phytoplankton-based Chl-*a*, to a allochthonous-dominated condition in response to Matthew's floodwaters, which flushed much of the phytoplankton biomass out of the estuary. Two months after this event, the system returned to authochthonous-dominated conditions, mediated by nutrient-driven phytoplankton production and reduced flushing rates

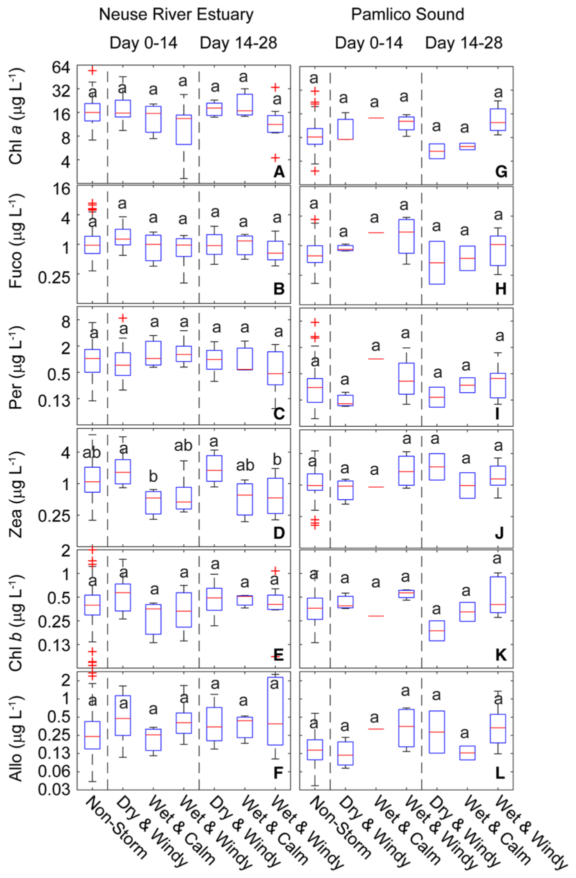

Fig. 10 Box plots of volume weighted log2 tranformed phytoplankton pigment concentrations within the NRE & PS. Figure configuration follows Fig. 6

upper estuary, even small increases of freshwater discharge promoted rapid flushing and prevented an accumulation of phytoplankton biomass (Peierls et al. 2012; Paerl et al. 2014). Though less sensitive to flushing than the upper estuary, the middle NRE was susceptible to rapid flushing by major wet and windy storms. Examples included Hurricanes Bertha and Fran in 1996 and Hurricane Floyd in 1999 (Paerl et al. 2001a, b, 2006a, b) that caused the middle NRE to become a freshwater, highly turbid, lotic system. The lack of a significant flushing effect from wet and calm storms is likely due to sample size as only three storms were designated as wet and calm. Although not statistically significant, the lower NRE responded to wet and wet and windy storms with increased phytoplankton biomass for up to 4 weeks following the storms (Fig. 11C). Under baseline conditions, riverine nutrients are assimilated by phytoplankton far upstream, within the upper and middle regions of NRE, leading to chronic nutrient-limitation in the lower NRE-PS (Pinckney et al. 1998; Piehler et al. 2004; Peierls et al. 2012; Paerl et al. 2014). Increased phytoplankton biomass in the lower NRE following wet and wet and windy storms was consistent with an alleviation of chronic nutrient-limitation by pulsed nutrient loadings to NRE-PS and sufficient residence time to allow significant biomass accumulation.

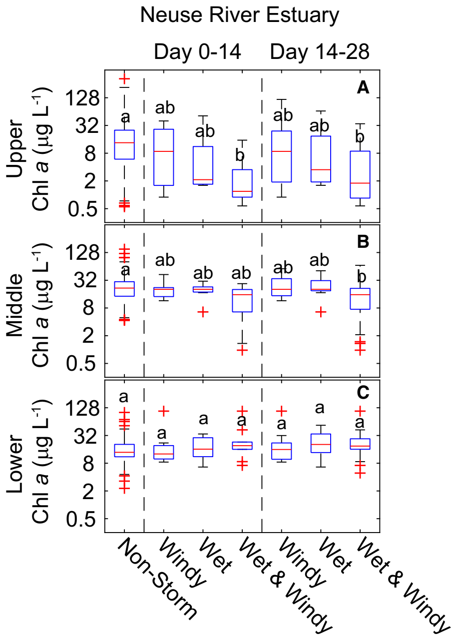

Fig. 11 Box plots of volume weighted log2 tranformed chlorophyll a concentrations within the upper, middle, and lower reaches of the NRE. Figure configuration follows Fig. 6

Previous studies suggested dry storms stimulate phytoplankton biomass, presumably by promoting sediment re-suspension and release of pore-water nutrients to the water column (Wetz and Paerl 2008). However, results presented here showed that windy storms with little precipitation had no detectable impact on phytoplankton biomass in nutrient-limited regions of NRE-PS. Freshwater discharge associated with tropical cyclones was the strongest modulator of phytoplankton biomass along NRE-PS, with impacts explained by dual influences of enhanced nutrient loading and enhanced flushing. Previous studies showed low to moderate rainfall and freshwater discharge stimulated phytoplankton biomass in the upper to middle regions of NRE where high Chl-*a* was observed, while high rainfall and freshwater discharge either stimulated biomass in downstream locations, or prevented biomass from accumulating in NRE due to excessive flushing (Peierls et al. 2012). In the latter case, such as we observed following the very wet Hurricane Floyd, significant increases of biomass occurred in the long-residence time PS (Paerl et al. 2001a, b, 2006b). Moderately wet storms, such as Ernesto (2006), led to significant biomass peaks at mid-NRE locations, including blooms of a toxic dinoflagellate (*Karlodinium venificum*) that were responsible for several fish kills (Hall et al. 2008).

Two recent examples of variable Chl-*a* responses to interactive effects of residence time and nutrient loadings occurred following Hurricane Joaquin (September 23, 2015) and Hurricane Matthew (October 18, 2016) (Fig. 12). Effects on freshwater discharge were both chronic (i.e., sustained, above-normal precipitation leading to a prolonged, weeks-to-months increase of discharge) and acute (i.e., precipitation not sustained, resulting in a brief, days, increase of discharge) following these storms. Chronic discharge followed multiple precipitation events that occurred concurrently within a time period leading to saturated soil conditions, resulting in increased overland flow, a higher water table, and stream base flow conditions. High chronic discharges occurred following Hurricane Joaquin from October 2015 through early March 2016, with a peak of 566.4 $m^3\ s^{-1}$ on February 2, 2016. Increased Chl-*a* developed in surface and bottom waters of PS following Joaquin and persisted until April 2016, returning to low baseline conditions in summer 2016, until Hurricane Matthew made landfall on October 8, 2016 (Fig. 12). Such high acute discharges also occurred immediately following Matthew from October 8, 2016 to October 26, 2016, with a peak discharge of 1393.2 $m^3\ s^{-1}$ on October 15, 2016.

A pair of surface Chl-*a* maxima occurred in PS before and after Hurricane Matthew. The first maximum closely followed increased rainfall from several tropical storms prior to Matthew, and the second maximum occurred following increased freshwater discharge from Matthew (Fig. 9). There was a slight increase of surface Chl-*a* for stations closest to the mouth of NRE, but no blooms affected Chl-*a* in bottom samples following Matthew. Most likely, this was due to salinity stratification that isolated surface from bottom waters as the freshet from Matthew moved downstream over denser, saltier bottom water in the lower NRE. This effect was distinct from the increase of Chl-*a* throughout the water column that we observed in PS as a response to chronic high discharges following Hurricane Joaquin. Persistent high freshwater discharge in the 2–3 week aftermath of high rainfall and flooding from Hurricane Joaquin led to complete flushing and vertical mixing of NRE, triggering high Chl-*a* throughout the well-mixed PS. In contrast, acute and extreme freshwater discharge associated with Hurricane Matthew in October 2016 produced a sharp increase of N- and P-loadings, followed by an abrupt return to low levels as the storm subsided. Thus, the distinct hydrologic impacts of these large storms included significantly different responses of phytoplankton biomass (Figs. 9, 10, 11, 12).

Flushing rates and nutrient loadings interacted to determine responses of phytoplankton biomass, production, and composition to storm events in NRE. Extreme freshwater discharge led to high nutrient loadings, but concurrently led to rapid flushing that exceeded phytoplankton growth rates (Peierls et al. 2012; Paerl et al. 2014) (Figs. 9, 11, 12). We suggest there is a tradeoff between nutrient loadings and flushing rates wherein moderately wet storms stimulate higher biomass in NRE than extremely wet storms. Two of the "wettest" storms on record confirmed this suggestion. Hurricanes Floyd and Matthew had extremely high nutrient loadings but did not stimulate blooms as rapid flushing precluded biomass accumulation in NRE. Distinct from storm effects on NRE, phytoplankton biomass was stimulated in PS where the residence time is much longer.

Storm effects on phytoplankton composition

Extensive data on HPLC diagnostic photopigments showed that nutrient loading and flushing interacted to influence phytoplankton community composition. During high discharge (e.g. post Ernesto in 2006, post Joaquin in 2015), phytoplankton were flushed down the estuary; how far depended upon the magnitude and duration of the event (Figs. 11, 12). Blooms often followed farther downstream. During low discharge periods (e.g. summers of 2002, 2007), higher pigment concentrations could be found farther upstream and even near SFB (0 km) with occasional blooms (Fig. 12).

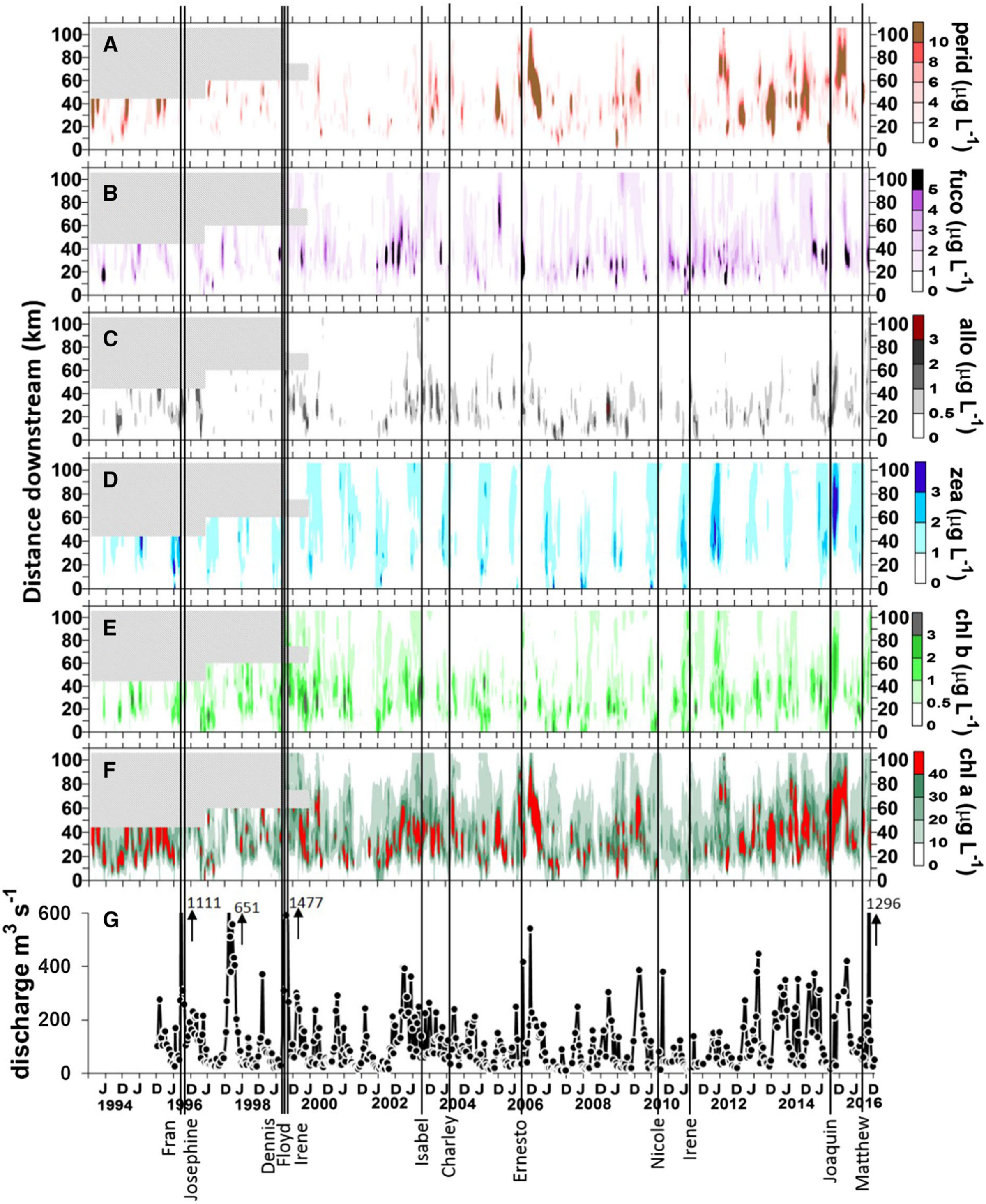

Fig. 12 Chlorophyll *a* and high performance liquid chromatography determinations of Chlorophyll *a* and diagnostic pigments for the dominant phytoplankton groups plotted for the NRE-PS as well as mean freshwater discharge and major storm events from 1994 to 2016. Blooms over 40 µg L^{-1} are seen in red; *J* June, *D* December, *Perid* peridinin, *fuco* fucoxanthin, *allo* alloxanthin, *zea* zeaxanthin, *chl b* chlorophyll b, and chl a = chlorophyll a

At baseline conditions, total pigment concentrations were often highest ∼ 20–50 km downstream in NRE where the river widens and residence time increases (Fig. 12a–c, e–f; Paerl et al. 2014). However, there were exceptions, as discussed below for individual taxonomic groups. Alloxanthin (cryptophytes) and Chl-*b* (chlorophytes) were responsive to storm events, displaying significant spatial heterogeneity and temporal lags (Fig. 12c, e, respectively). These pigment markers for cryptophytes and chlorophytes responded rapidly to storm events as inherent growth rates of these taxa are higher than other groups (Paerl et al. 2013, 2014), and both are favored by relatively low salinity and high nutrient conditions associated with storm passage.

Peridinin (dinoflagellates) increased during typical winter/spring blooms in NRE since 2011 and long-term data showed high concentrations persisted for weeks to months throughout the estuary (Fig. 12a). Growth rates of dinoflagellates are typically low, limiting responses to hydrologic perturbations and making members of this taxonomic group susceptible to flushing. Nonetheless, we observed storm effects on dinoflagellate biomass including a mixed bloom of perdinin- and fucoxanthin-containing dinoflagellates in 2006 following TS Ernesto (Fig. 12; Hall et al. 2008). Moderately wet storms supported increased peridinin as nutrient loadings and freshwater discharge provided suitable conditions for biomass accumulation with minimal flushing. These storm events also enhanced vertical stratification in NRE, favoring motile taxonomic groups such as dinoflagellates that use vertical migration to access light and nutrient resources (Hall and Paerl 2011).

Of the diagnostic pigments used to identify major taxa, zeaxanthin (cyanobacteria) was the only indicator of significant differences between storm types. Compared to wet and calm storms, cyanobacteria biomass was significantly higher following dry and windy storms in NRE. This stemmed from a slight, though statistically insignificant, increase above baseline conditions following dry and windy storms, and a stronger decrease following wet and calm storms (Fig. 10). Low growth rates characteristic of this taxonomic group and their susceptibility to flushing may explain this observation. Additionally, reduced N forms (e.g. ammonium and DON) that would be prevalent during resuspension events (Giffin and Corbett 2003) favor the growth of picoplanktonic cyanobacteria (Glibert et al. 2004) that are predominant members of the cyanobacteria assemblage in NRE (Gaulke et al. 2010).

Seasonal patterns of cyanobacteria growth and biomass were related to the annual temperature cycle, with biomass maxima typically occurring during warm summer and fall periods (Pinckney et al. 1998, 1999; Gaulke et al. 2010; Paerl et al. 2013, Fig. 12d). Over multiple years, cyanobacteria abundance tracked surface water temperatures, consistent with observations that cyanobacteria "like it hot" (Paerl and Huisman 2008). Furthermore, fucoxanthin (diatom) abundance was relatively unaffected by storm events, although a slight time lag was observed at some locations (Fig. 12b). Growth rates of diatoms are relatively high, but this taxonomic group generally comprised less than 20% of phytoplankton biomass in NRE-PS (Pinckney et al. 1998, 1999). This may explain the "insensitivity" of diatom abundance to storm events.

Major storm events strongly affected biogeochemical cycling and phytoplankton production, with storms exhibiting interactive effects of nutrient loadings and flushing. Some phytoplankton taxa, notably cyanobacteria, are highly seasonal with spatial–temporal distributions primarily associated with the annual temperature cycle and secondarily by flushing. From a predictive perspective, a period of elevated storm activity favors fast-growing chlorophytes and cryptophytes, especially if the ecosystem "freshens up" following high freshwater discharge from storm events. Dinoflagellates, such as *Karlodinium veneficum*, are also susceptible to removal by flushing, but intermediate conditions with modest flushing accompanied by vertical density stratification, permit this taxonomic group to form blooms by virtue of motility that confers an advantage in responding to nutrient pulses (Hall et al. 2008).

Conclusions

Estuarine and coastal systems such as NRE-PS are highly susceptible to hydrologic perturbations from storm events that deliver pulsed inputs of nutrients and OM. In this overview, we report the scales, magnitudes, and extent of biogeochemical and biotic responses for a variety of storm types spanning 2–3 decades. A conceptual diagram (Fig. 13) depicts

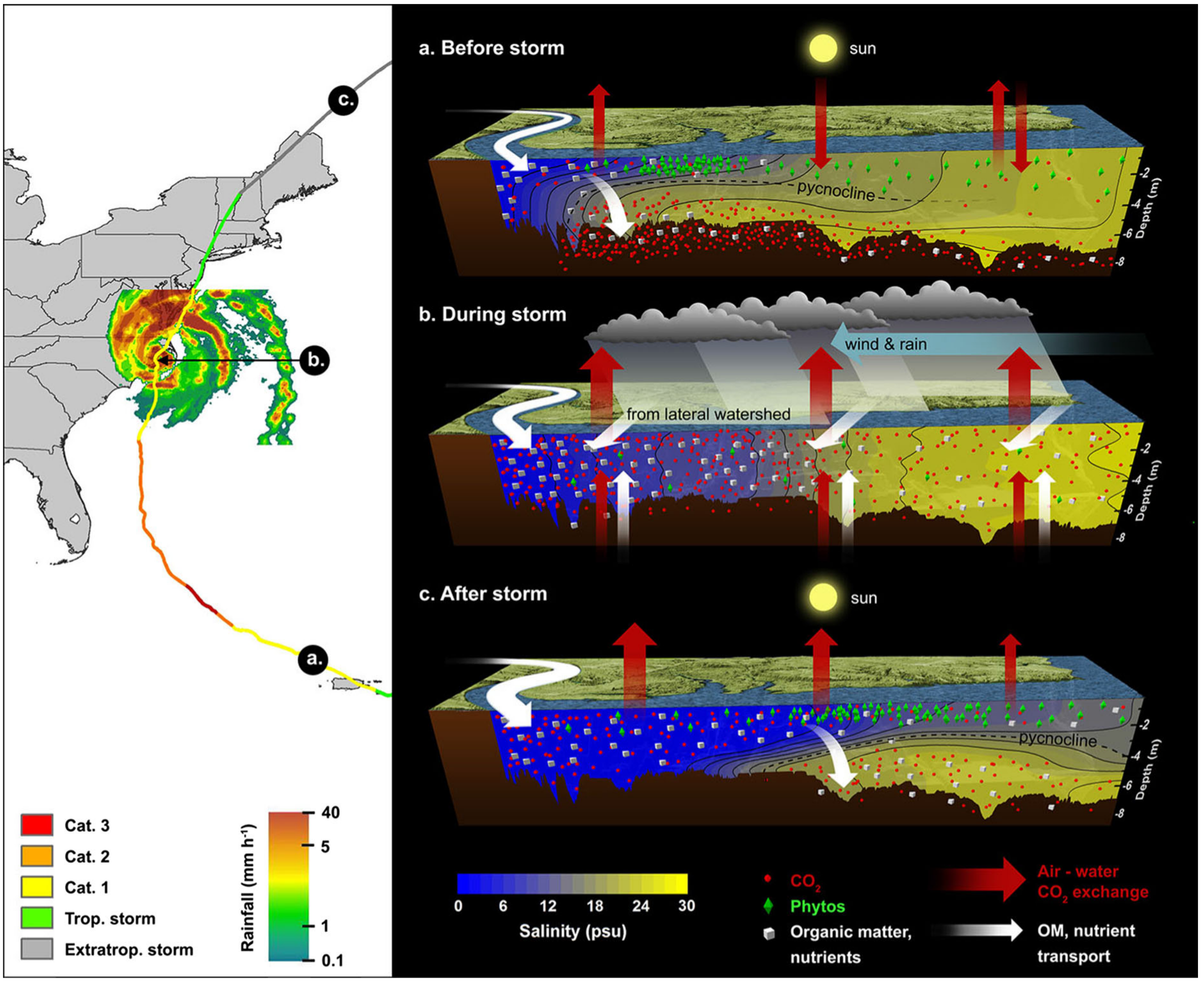

Fig. 13 Conceptual diagram, adapted from Crosswell (2013), showing the idealized response of the NRE to Hurricane Irene, a model 'windy' storm (right)*. The track and intensity of Hurricane Irene as it impacted the study area is also shown (left). *Salinity profiles were constructed from direct measurements before and after the storm. Data shown are 15 Aug. 2011 (a), hypothetical salinity values under well-mixed conditions (b), and 30 Aug. 2011 (c)

important ramifications of storm impacts, focusing on time-scales and magnitudes. Storms with high rainfall mobilized terrestrial material from inland watersheds and river channels, whereas storms with extreme winds mobilized previously stored terrigenous nutrients and OM. Perturbations of NRE-PS by storm winds or high freshwater flow were expressed at time scales from hours to weeks. Enhanced DOC, POC, and nutrient fluxes following storms exceeded annual fluxes observed in baseline years lacking major storms. Sequences of intense, frequent storms, exemplified by years with multiple tropical cyclones in a single season, exerted the largest impact on C and nutrient cycling. Each storm showed a unique signature based on physical attributes, such as duration, wind speed, precipitation, and geographic track. Widely used indices of storm intensity, however, such as the Saffir-Simpson Hurricane Wind Scale (SSHWS), were insufficient to predict storm effects on C and nutrient fluxes.

The upper region of NRE-PS was dominated by terrigenous DOC loading following storm events that delivered high rainfall to the watersheds (Fig. 13). Steep increases of DOC were recorded following storm events of all types. These responses were not limited to tropical cyclones, but occurred following major precipitation events that were sufficient to flush terrigenous material with high DOC from the watersheds (e.g., Dixon et al. 2014). The mid- and lower regions of NRE-PS also showed effects of increased terrigenous DOC, but effects were dampened compared to the upper region. PS experienced a lagged increase of DOC reflecting movement of the freshwater pulse down NRE to lower regions and PS. This lag suggests NRE acts as a "pipeline" during extreme storm events of sufficient strength to flush terrigenous material through NRE and into PS. Residence times are longer in PS, allowing water rich in nutrients and OM to fuel primary productivity. This finding is reflected in Chl-*a* data that reveal phytoplankton blooms following storm events. While the upper estuary was dominated by terrestrial flushing following storm events, the lower estuary and PS were dominated by in situ processes fueled by deliveries of nutrients and OM (Fig. 13).

Storm events can influence phytoplankton community composition through the interaction of nutrient loading and flushing rates. While very high freshwater discharge is responsible for maximum nutrient loads, they are also responsible for maximum flushing rates that can exceed phytoplankton growth rates. Some taxa (cyanobacteria) are most sensitive to seasonal temperature changes and their spatial–temporal biomass largely reflect the annual temperature cycle, with a secondary influence of flushing. From a predictive perspective, a period of elevated storm activity favors fast-growing chlorophytes and cryptophytes, especially if the system "freshens up" following major discharge events. Dinoflagellates are strongly affected by flushing, but under moderate and intermediate flushing conditions wherein nutrient enrichment from runoff and vertical stratification coincide, they can take advantage of advantageous conditions and form harmful blooms (Valdes-Weaver et al. 2006; Paerl et al. 2013).

The fate and impacts of terrigenous OM on estuarine and coastal ecosystems such as NRE-PS following storm events remains an open question. Bacterial production is responsive to loads of "fresh" terrigenous OM stored in watersheds and exported to coastal waters where increased residence time facilitates degradation of OC to CO_2 (Peierls and Paerl 2010). Photochemical oxidation of DOC is also an important process in long residence times. Nutrients that transit the "estuarine filter" of NRE should fuel secondary production in PS, but insufficient observations are available to confirm this conclusion. We suggest that storm events can "prime" coastal waters for intense biogeochemical cycling as a result of nutrient and OM pulses to receiving waters such as PS.

Lastly, we report storm effects on freshwater discharge, nutrient loadings, and C dynamics with commensurate influences on spatial–temporal distributions of phytoplankton biomass and composition in NRE-PS, responses that should be considered in management strategies for coastal ecosystems as we encounter stormier, increasingly extreme climate conditions.

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