Estuaries and Coasts
https://doi.org/10.1007/s12237-023-01258-y

Hurricane Effects on Benthic Nitrogen Cycling in an Emerging Coastal Deltaic Floodplain Within the Mississippi River Delta Plain

Song Li[1] · Robert R. Twilley[1] · Denise M. Poveda[1] · Robinson W. Fulweiler[2,3]

Received: 17 February 2023 / Revised: 7 July 2023 / Accepted: 5 August 2023

Abstract
Hurricanes are one of the most common natural events that disturb estuarine and coastal wetlands along the Gulf of Mexico. The episodic and energetic events of hurricanes modify wetland hydrodynamics, sedimentation, and vegetation structure, which can impact the connectivity of coastal deltaic floodplains in processing riverine nutrients. Hurricane effects on benthic nitrogen dynamics and their fluxes during ecosystem recovery following an event were investigated at three experimental sites with distinct sediment organic matter (SOM) concentrations (lower-, intermediate-, and higher-SOM) in Wax Lake Delta (WLD), Louisiana. Intact sediment cores were incubated with $^{15}NO_3^-$ enrichment prior to, 1 month, 2 years, and 3 years post Hurricane Barry. The disturbance of Hurricane Barry on benthic nitrogen dynamics was most significant at the higher-SOM site, where SOM concentrations significantly decreased together with a 50% reduction in rates of direct denitrification, coupled nitrification-denitrification, and dissimilatory nitrate reduction to ammonium (DNRA). Shifts in SOM and benthic nitrogen dynamics as result of hurricane sedimentation followed the linear function between increased denitrification (or NO_3^- fluxes) with greater SOM concentrations previously established by sampling along SOM gradients in WLD. The estimated NO_3^- removal capacity decreased by 8.5% (76 Mg N year^{-1}) compared to pre-hurricane conditions due to lower SOM concentrations associated with mineral sedimentation at the most disturbed site. The disturbed site had not recovered to pre-hurricane conditions in terms of SOM concentrations and benthic nitrogen dynamics three years after Hurricane Barry. NO_3^- removal capacity of an active delta such as WLD is a combination of SOM increase from ecological succession and SOM decrease associated with events that stimulate mineral deposition. Frequency of high energy events such as floods and storms along with wetland feedback in soil organic development and delta expansion will influence NO_3^- removal capacity.

Keywords Hurricane disturbance · Coastal deltaic floodplain · Denitrification · Sediment organic matter · Coupled nitrification-denitrification · Benthic biogeochemistry

Introduction

Anthropogenic fertilization dramatically increases bioreactive nitrogen loading to rivers and coastal oceans, which decreases coastal water quality, causes eutrophication, and generates harmful algal blooms (Canfield et al. 2010; Damashek and Francis 2018; Diaz 2009; Erisman et al. 2008; Paerl et al. 2002; Rabalais et al. 2002; Steffen et al. 2015). Coastal deltaic floodplains forming at the mouth of major river basins have potential capacity to remove excess riverine nitrate (NO_3^-) prior to export to coastal oceans (Henry and Twilley 2014; Li and Twilley 2021). Recent research reported that ~10 to 27% of riverine NO_3^- loading to a newly emergent coastal deltaic floodplain could be reduced through denitrification before export to the oceans (Li et al. 2020). Nitrogen removal rates increase with elevated sediment organic matter (SOM) concentrations as ecological succession of newly developed delta landscapes emerge from subtidal to supratidal hydrogeomorphic zones (Henry and Twilley 2014; Li et al. 2020). The increase in elevation as wetland soils age during delta formation causes a shift in wetland vegetation

Communicated by Lijun Hou

✉ Song Li
sli10@lsu.edu

1 Department of Oceanography and Coastal Sciences, College of the Coast and Environment, Louisiana State University, Baton Rouge, LA 70803, USA

2 Department of Earth and Environment, Boston University, Boston, MA 02215, USA

3 Department of Biology, Boston University, Boston, MA 02215, USA

Published online: 02 September 2023

that increases the SOM concentration, which further regulates rates of denitrification (Bevington and Twilley 2018; Li et al. 2020). There is evidence in other habitats of aquatic ecosystems that elevated SOM concentration enhances denitrification and N removal capacity (Arango et al. 2007; Cornwell et al. 1999; Eyre et al. 2013; Fulweiler et al. 2008, 2007; Hardison et al. 2015).

However, SOM concentrations in deltaic floodplains are not only a function of delta development and ecological succession, but also depend on natural disturbance events such as hurricanes, river floods, and coastal frontal passages (Bevington 2016; Bevington and Twilley 2018; Li et al. 2020; Turner et al. 2006a). Hurricanes are one of the most common natural events that create disturbance to estuarine and coastal environments along the Gulf of Mexico (Conner et al. 1989; Davis et al. 2004; Williams et al. 2008; Morton and Barras 2011; Liu et al. 2014; Carle and Sasser 2016). The episodic and energetic events of hurricanes alter wetland hydrodynamics, sedimentation rates, and vegetation structure, which may further impact the capacity of coastal wetlands to process riverine nutrients (Davis et al. 2004; Deng et al. 2010; Liu et al. 2014; Michener et al. 1997; Turner et al. 2006a; Wang et al. 2016). For example, hurricanes resuspend inorganic sediments from shallow bays and redeposit them into coastal wetlands (Liu et al. 2018), which decreases organic matter concentrations in the top layer of sediments (Bevington et al. 2017; Castañeda-Moya et al. 2010; Turner et al. 2006a; Walker 2001). The decreased SOM at the sediment-water interface may inhibit benthic denitrification and alter the relative importance of denitrification to other nitrogen processes like coupled nitrification-denitrification and dissimilatory nitrate reduction to ammonium (DNRA; Fulweiler et al. 2008, 2007; Li and Twilley 2021). Understanding how SOM variation associated with hurricane events may shift the relative significance of different nitrogen pathways is essential to understand the response of nitrogen removal capacity to hurricanes in different areas of an active coastal deltaic floodplain. Studies on wetland responses to hurricane events mainly focus on wetland landscape and plant and animal communities (Courtemanche et al. 1999; Guntenspergen et al. 1995; Reja et al. 2017), and the recovery rates vary among different wetland features (Morton and Barras 2011). Far less attention has been given to how hurricane disturbances alter nutrient biogeochemistry of coastal deltaic floodplains.

In addition to changes in SOM due to hurricane effects, saltwater intrusion and salt spray during a hurricane event also generate higher stress to vegetation and benthic microbes (Blood et al. 1991; Michener et al. 1997; Wang et al. 2016). An increase in salinity from 0.9 to 3.6 after a hurricane event is reported to generate substantial mortality of freshwater vegetation in the Mississippi River Delta (Chabreck and Palmisano 1973; Lacoul and Freedman 2006). Hurricanes could increase fluxes of labile organic carbon and nutrients leaching from dead vegetation and litter to overlying water column (Davis et al. 2004). Higher nutrient concentrations following hurricanes may increase chlorophyll *a* concentrations in coastal waters (Fogel et al. 1999; Huang et al. 2011). In summary, the impacts of a hurricane on coastal wetland ecosystems are diverse and complex, which are related to not only the track and magnitude of a hurricane event, but also the morphological and ecological characteristics of disturbed wetlands (Davis et al. 2004; Wang et al. 2016). More field research of how benthic sediment characteristics may change benthic fluxes in response to hurricane disturbances is necessary to better understand hurricane effects on nutrient biogeochemistry in coastal deltaic floodplains.

We tested how redistributed sediment during hurricane disturbance changes the nutrient biogeochemistry of coastal deltaic floodplains in Wax Lake Delta (WLD). At three experimental sites with distinct SOM concentrations intact sediment cores were incubated with $^{15}NO_3^-$ enrichment before Hurricane Barry and then again for comparison 1 month, 2 years, and 3 years following the hurricane (July 2019 and July 2021). We analyzed the changes of benthic biogeochemical characteristics (salinity, bulk density, chlorophyll *a*, SOM, and nutrients) and benthic nitrogen processes (direct denitrification, coupled nitrification-denitrification, and DNRA) prior to and following Hurricane Barry. The importance of coastal deltaic floodplains to benthic nitrogen cycling and coastal nitrogen removal may diminish in response to natural disturbance of hurricanes. As such, we hypothesized that mineral sedimentation associated with hurricane events decreases SOM concentrations leading to lower denitrification rates and changes in the relative importance of denitrification, coupled nitrification-denitrification, and DNRA on the fate of nitrogen in coastal deltaic floodplains.

Methods

Wax Lake Delta is a newly emergent (since 1973) coastal deltaic floodplain in the Atchafalaya Coastal basin within the Mississippi River Delta (Fig. 1b). WLD experienced more than 46 tropical storms and hurricanes passing within 400 km since 1973 (Carle and Sasser 2016). As a river-dominated delta with weak influences of tides and waves, WLD subaerial land grows at a rate of 2.62 km^2 $year^{-1}$ with minor anthropogenic manipulation from navigation (Edmonds et al. 2011; Paola et al. 2011; Shaw and Mohrig 2014; Twilley et al. 2019). The delta is primarily composed of mineral sediments with an increased gradient of SOM associated with morphological development along the chronosequence from younger to older deltaic area (Bevington and Twilley 2018;

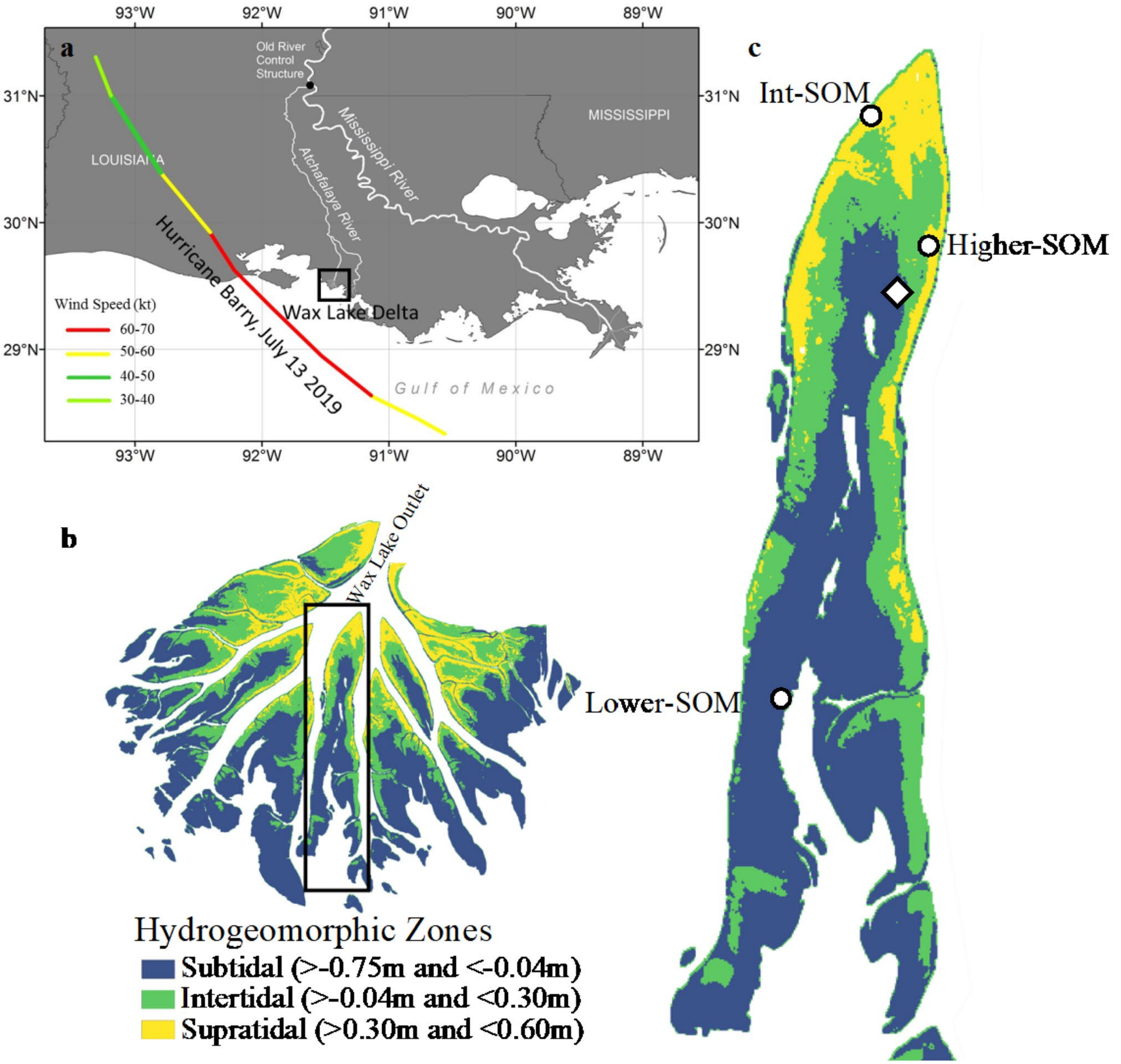


Fig. 1 **a** Hurricane Barry track with wind scales taken from anemometers above the standard 10 m observation height (data were from the NOAA Weather Prediction Center and national Hurricane Center), and **b** map of Wax Lake Delta (WLD), Louisiana, with **c** the location of study sites in Mike Island. Elevation records are from USGS Atchafalaya 2 project LiDAR Survey 2012 digital elevation model (4 m resolution). The diamond symbol indicates the location that we took pre- and post-hurricane photos shown in Fig. 2

Li et al. 2020). Sediment stoichiometry demonstrates that the productivity in WLD is primarily limited by nitrogen based on nitrogen:phosphorus molar ratios less than 16 (Henry and Twilley 2014; Aarons 2019; Li et al. 2020).

Hurricane Barry

Hurricane Barry made its landfall 70 km to the west of WLD at southern Louisiana on July 13, 2019 as a category 1 hurricane with peak wind speed of 120.3 km h^{-1} (65 kt; Fig. 1a). The Barry cyclone was asymmetric through landfall as most of its associated heavy rains occurred in the south and east part of the hurricane track. Hurricane Barry induced substantial mortality of semi-aquatic and aquatic macrophytes across the WLD (Fig. 2). Maximum wind speed at the Amerada Pass gauge (National Oceanic and Atmospheric Administration NOAA 8764227; https://tidesandcurrents.noaa.gov) was 48.6 km h^{-1} (Fig. 3a) together with a 2 m increase in water level (Fig. 3b). The storm surge elevated surface water salinity from 0.2 to 4.3 for 11 h during the hurricane. After

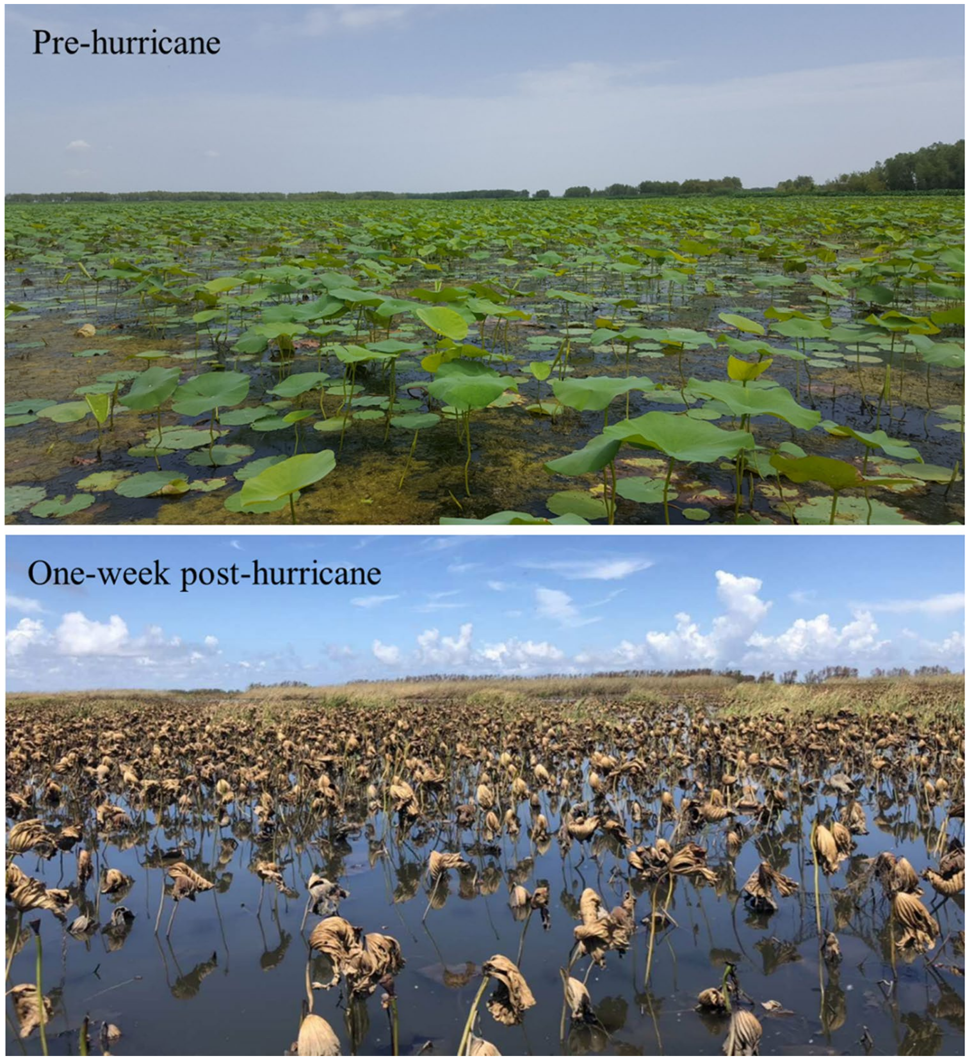


Fig. 2 Landscape change in Mike Island in WLD after Hurricane Barry. Post-hurricane photo was taken on July 20th, which is 7 days after Hurricane Barry. The location of this area is shown in Fig. 1 with a diamond symbol. The area is in intertidal zone dominated by freshwater macrophytes like *Nelumbo lutea* and *Colocasia esculenta*

Hurricane Barry, water level and salinity returned to pre-event conditions in several days (Coastal Resources Monitoring System (CRMS) 0464 station on the east side of WLD https://www.lacoast.gov/crms/Home.aspx).

Site Description and Lab Incubation

Field sampling and lab incubations were done at three experimental sites serving as lower (lower-SOM, 2.9% dry mass), intermediate (int-SOM, 6.5%), and higher (higher-SOM, 20.8%) sediment organic matter concentrations on Mike Island of WLD in August 2020 (1 month after Hurricane Barry) and July 2021 (2 years post Hurricane Barry, Fig. 1c). These experimental results were compared to the pre-hurricane results measured 1 month before Hurricane Barry in June 2019 in the int-SOM and higher-SOM sites (Li et al. 2021) and 1 year before Hurricane Barry in August 2018 in the lower-SOM site (Li and Twilley 2021). Another field sampling and lab incubation were added in Oct 2022 at the int-SOM and higher-SOM sites to track the recovery of benthic nitrogen dynamics at the disturbed site (higher-SOM) compared with the undisturbed site (int-SOM). In addition, we sampled the lower-SOM site 7 days post Hurricane Barry to measure the in situ water and sediment characteristics to support the hurricane effects. The lower-SOM site (29°28′48.4″N, 91°26′53.4″W) is located at the distal portion of the delta with lower elevation (−0.6 m NAVD 88), younger mineral sedimentation, and colonized by submersed aquatic vegetation (Bevington and Twilley 2018). The int-SOM site (29°30′47.9″N, 91°26′33.4″W) is on the west side levee of Mike Island along a primary channel (less than 5 m to channel edge) and colonized by trees (primarily *Salix nigra*) and *Colocasia esculenta*. The higher-SOM site (29°30′21.2″N, 91°26′18.5″) is located more interior of the island (37 m to channel edge) and colonized by *Colocasia esculenta* and *Nelumbo lutea* (Li and Twilley 2021). In situ surface water and porewater samples were sampled 4 cm within the air-water interface and sediment-water interface,

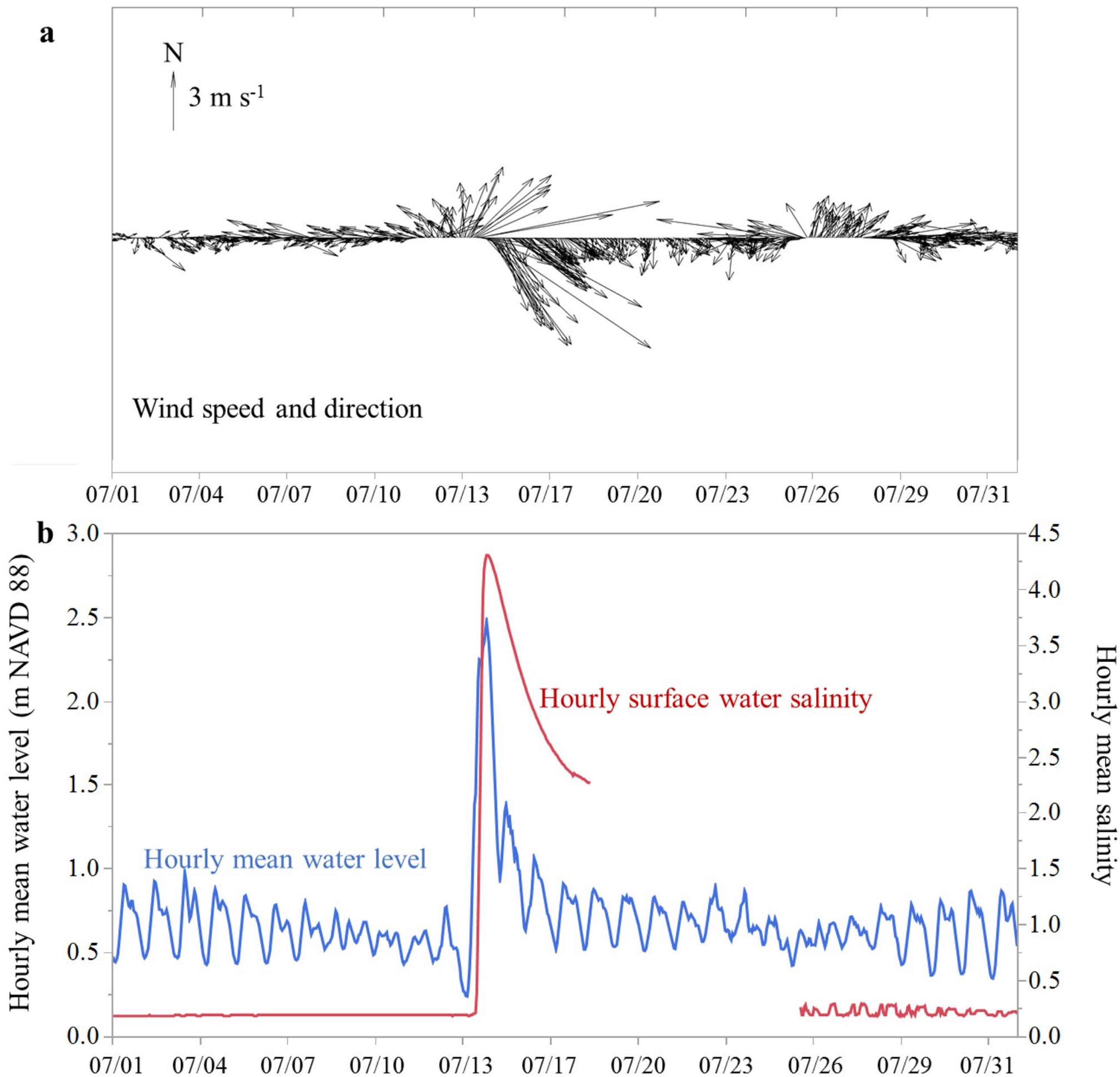


Fig. 3 **a** Time-series of wind speed and wind direction at Amerada Pass gauge 10 km southeast to the WLD (NOAA 8764227) in July 2019. **b** Corresponding water levels (m NAVD 88) at Amerada Pass gauge and surface water salinity at Coastal Resources Monitoring System (CRMS) 0464 station. Surface water salinity data had some missing values due to instrument failure

respectively, in each experimental site. Water samples were filtered through GF/F glass microfiber filters with 0.7 μm particle retention in lab and analyzed for NO_3^-, nitrite (NO_2^-), ammonium (NH_4^+), and phosphate (PO_4^{3-}) concentrations on a segmented flow solution IV autoanalyzer (OI analytical, College Station, TX). The in situ nutrient concentrations in surface water and porewater samples after Hurricane Barry were compared to the respective nutrient concentrations measured 1 month prior to Hurricane Barry (Li et al. 2021). However, the lower-SOM site had no recent pre-hurricane measurements of nutrient concentrations, so we used the observed results in summer 2018 at this site (Li and Twilley 2021) as the pre-hurricane records.

Triplicate sediment cores (10 cm internal diameter) were collected with 10 ± 1 cm depth of sediments and 10 ± 1 cm depth of ambient water from each of the three sites on each sampling date and moved to the lab within 4 h. Incubation water was collected from Wax Lake Outlet at the Calumet boat launch, LA and filtered through a five-stage filtration system (30, 20, 5, 1, and 0.2 μm) at lab to remove suspended particles and microbes in overlying water. The ambient NO_3^- of the incubation water was removed by flowing the water through a column of packed NO_3^--specific resin (NO_3^- removal efficiency ≥ 98%, ResinTech SIR-100-HP, West Berlin, NJ). About 100 μM of labelled $^{15}NO_3^-$ was then enriched to the incubation water before each incubation event ($K^{15}NO_3^-$, 99%, Cambridge stable isotope laboratories) to mimic real NO_3^- concentrations flowing from Atchafalaya River to WLD during the sampling season (58 to 110 μM, Li et al. 2020; Li and Twilley 2021).

Sediment cores from the experimental sites on each sampling date were incubated in a water chamber in dark at 19–21 °C with the treated incubation water flowing through the systems at a speed of about 4 mL min^{-1}. The overlying water residence time inside each core was controlled at 3 h and the incubation conditions are clearly described in Li and Twilley (2021). After 10 h of pre-incubation, influent and effluent water samples were collected and filtered for NO_3^-, NO_2^-, NH_4^+, and PO_4^{3-} analyses at every 3-h time interval for three times of sampling events. Duplicate influent and effluent samples were also collected into 12-mL gas-tight exetainers (Labco Limited, Lampeter, Wales, UK) with the injection of 200 μL $ZnCl_2$ solution (50% saturation concentration, Nielsen and Glud 1996) in each sampling event. Exetainers were then sealed and stored underwater at 4 °C for the analysis of dissolved $^{28}N_2$, $^{29}N_2$, and $^{30}N_2$ on a membrane inlet mass spectrometer (MIMS; Kana et al. 1994). Dissolved oxygen concentrations of influent and effluent waters were recorded with a Hach HQ30 dissolved oxygen probe at each sampling event. Benthic fluxes of nutrients and dissolved gases (N_2 and O_2) were calculated based on the equation:

$$\text{Flux} = \left[\left(C_e - C_i\right) \times \text{flow rate}\right] \div \text{Core surface area} \qquad (1)$$

where C_e and C_i refer to the effluent and influent concentrations of a certain compound in a sediment core as described in Li et al. (2020).

Denitrification includes direct denitrification that converts NO_3^- from overlying water columns to N_2 gas and coupled nitrification-denitrification that consumes NO_3^- oxidized from NH_4^+ through nitrification. Direct denitrification rates were calculated by summing the ^{15}N-N_2 released from the sediment-water interface and coupled nitrification-denitrification rates were calculated based on the equation outlined by Nielsen (1992) and Li and Twilley (2021). DNRA rates were determined by the production of $^{15}NH_4^+$ during the incubation using OX/MIMS method described in Yin et al. (2014). The DNRA rates using this method may be conservative as the occurrence of nitrification may release some unlabeled $^{14}NO_3^-$ that are used for DNRA, and denitrification may use some of the released $^{15}NH_4^+$ from DNRA (Gardner and McCarthy 2009; Yin et al. 2014). Pre-hurricane rates of direct denitrification, coupled nitrification-denitrification, and DNRA were measured in summer 2018 as initial nitrogen dynamics before the disturbance of Hurricane Barry (Li and Twilley 2021).

After three sampling events in each incubation, the top 2 cm layer of sediments was collected in each sediment core using a smaller piston core with 1.4 cm internal diameter. Samples were then stored frozen in dark for fluorometric determination of chlorophyll *a* following the method of Arar and Collins (1997). Briefly, chlorophyll *a* was extracted from wet sediment samples (3.1 mL) with 45 mL of 90% acetone and the sonicated for 30 s before 24 h storage at −20 °C in dark. Then, chlorophyll *a* concentrations were determined fluorometrically (Turner Designs TD-700) using the HCl acidification method (Arar and Collins 1997). In addition, we collected another set of top 4 cm sediment samples in each core and segmented at 2 cm depth intervals using a larger piston core (2.4 cm internal diameter) and oven dried these samples at 60 °C to a constant mass. Bulk density (g cm^{-3}) was then determined by dividing dry sediment mass by wet sediment volume. The dried sediment samples were ground to less than 250 μm and 1 ± 0.01 g subsamples were ignited at 550 °C for 2 h to measure SOM concentrations (% dry mass). Pre-hurricane bulk density and SOM concentration results at the intermediate- and higher-SOM sites were measured 1 month before Hurricane Barry (Li et al. 2021) while pre-hurricane results at the lower-SOM site were measured in summer 2018 (Li and Twilley 2021).

Data were tested for normality (Shapiro-Wilk) and transformed using log, square root, or Box-Cox transformations if $p < 0.05$ to achieve normality. One-way analysis of variance (ANOVA) with Welch's *F*-test was used to test significant variations ($p < 0.05$) of each parameter among the four sampling times (prior to, 1 month following, 2 years, and 3 years following Hurricane Barry) within each experimental site. Games-Howell post hoc tests ($p < 0.05$) were applied for pairwise comparisons as some response variables do not have equal variances through different sampling periods. Statistical analyses were done using JMP software and data were presented as means with error bars representing standard error (SE).

Results

Ambient surface water and porewater nutrients concentrations indicated no obvious trend except for sharp increase of porewater NH_4^+ concentrations after Hurricane Barry (Supplemental Table S-1). In brief, porewater NH_4^+ concentrations at the lower-SOM site increased from 91.7 to 182.6 μM 7 days following Hurricane Barry (Supplemental Table S-2) then dropped to 54.5 μM 1 month following Hurricane Barry and 29.2 μM 2 years following Hurricane Barry (Supplemental Table S-1). At the int-SOM site, porewater NH_4^+ concentrations increased from 41.3 to 142.1 μM 1 month after Hurricane Barry and to 535.3 μM 2 years following the hurricane, then decrease to 23.3 μM 3 years after the hurricane. The higher-SOM site demonstrated an increase of porewater NH_4^+ concentrations from 97.7 to 442.6 μM 1 month after Hurricane Barry, then decreased to 140.0 μM and 323.3 μM 2 years and 3 years following the hurricane, respectively.

The chlorophyll a concentrations of the top 2 cm sediments were 2.1 to 3.3 mg L^{-1} without significant site-to-site variation prior to Hurricane Barry (Fig. 4). One month following Hurricane Barry, the chlorophyll *a* concentrations significantly increased at the lower- and higher-SOM sites ($p = 0.0450$ and 0.0122, respectively, $n = 18$). Two years following Hurricane Barry, the chlorophyll *a* concentrations returned back to the pre-hurricane levels at the lower-SOM and higher-SOM sites.

Bulk density and SOM concentration results did not show obvious differences between 0 to 2 cm and 2 to 4 cm layers of sediments, so we averaged these two layers of results. The lower-SOM site had no significant variation of bulk density or SOM concentrations among sampling dates, indicating little impact of Hurricane Barry on sedimentation in this hydrogeomorphic zone (Fig. 5). The int-SOM site and higher-SOM site showed contrasting trends in both bulk density and SOM concentrations in response to hurricane disturbance. Bulk density at the int-SOM site decreased from 0.9 ± 0.05 to 0.7 ± 0.1 g cm^{-3} 1 month after Hurricane Barry. Two years after the hurricane, bulk density at the int-SOM site was even lower at 0.4 ± 0.03 g cm^{-3} but increased to 1.0 ± 0.05 g cm^{-3} 3 years following Hurricane Barry. In contrast, bulk density at the higher-SOM site increased from 0.2 ± 0.01 g cm^{-3} prior to the hurricane to 0.5 ± 0.1 g cm^{-3} 1 month after Hurricane Barry and stayed over 0.5 for the following 3 years. SOM concentrations at the int-SOM site were stable with a slight increase during the sampling period regardless of the impacts of Hurricane Barry (6.5–9.2%). In contrast, SOM concentrations at the higher-SOM site significantly decreased from 20.6 ± 0.6% in pre-hurricane conditions to 9.4 ± 1.4% 1 month following the hurricane ($p = 0.0006$, $n = 24$) and stayed around 7.8% in the following 3 years.

Sediment cores were incubated under similar physical and chemical conditions prior to and following Hurricane Barry in our experiments (Supplemental Table S-3). Negative values of dissolved O_2 fluxes indicate net benthic O_2 consumptions in all experimental sites during all sampling periods (Fig. 6a). Benthic fluxes of dissolved O_2 at the lower-SOM site were similar prior to and 1 month following the hurricane (2.2 ± 0.1, 2.3 ± 0.2 mmol m^{-2} h^{-1}), then increased to 3.6 ± 0.7 mmol m^{-2} h^{-1} 2 years after Hurricane Barry. Dissolved O_2 fluxes at the int-SOM site had no significant variation with time associated with Hurricane Barry. Benthic O_2 consumptions at the

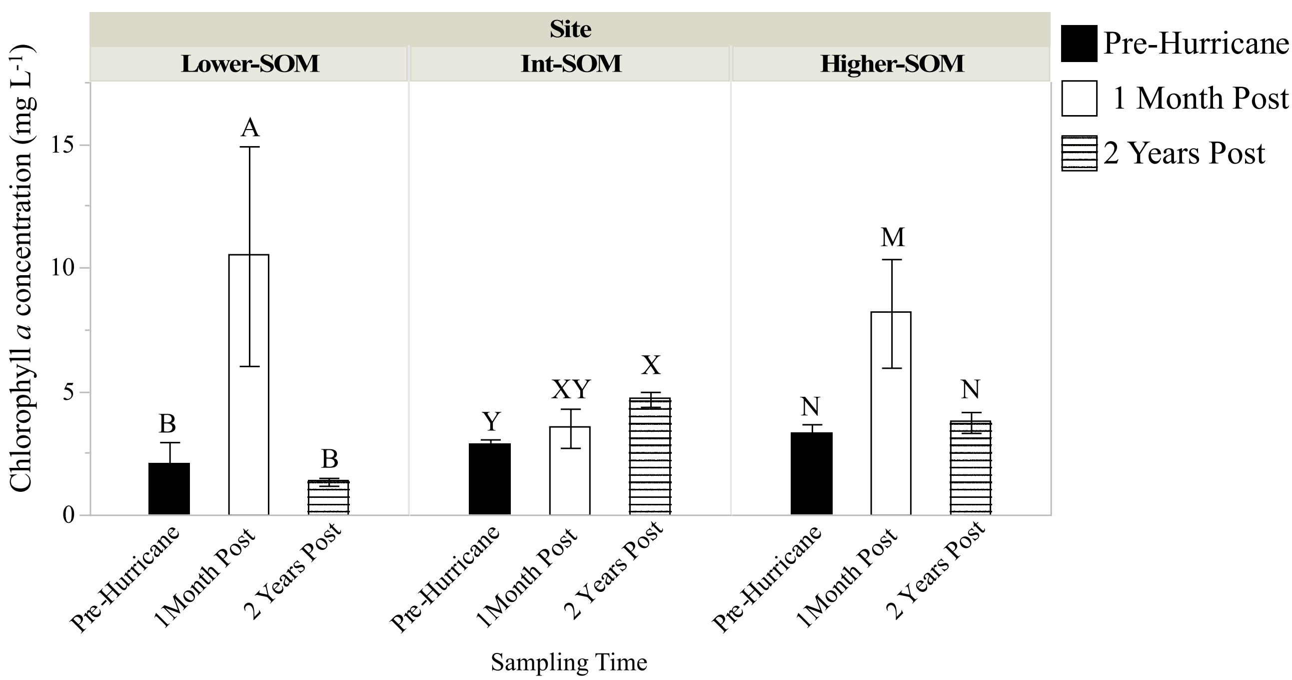


Fig. 4 Chlorophyll *a* concentrations in the 0 to 2 cm layer of sediments prior to, 1 month following, and 2 years following Hurricane Barry among the experimental sites (mean ± standard error, there is no chlorophyll result three years post Hurricane Barry due to technic issue). The pre-hurricane results in the int- and higher-SOM sites were measured 1 month before Hurricane Barry in 2019 while the pre-hurricane results in the lower-SOM site were from summer 2018 (Li and Twilley 2021). Letters designate significant differences among sampling dates (prior to, 1 month, 2 years following Hurricane Barry) within each experimental site using Games-Howell post hoc tests ($p < 0.05$)

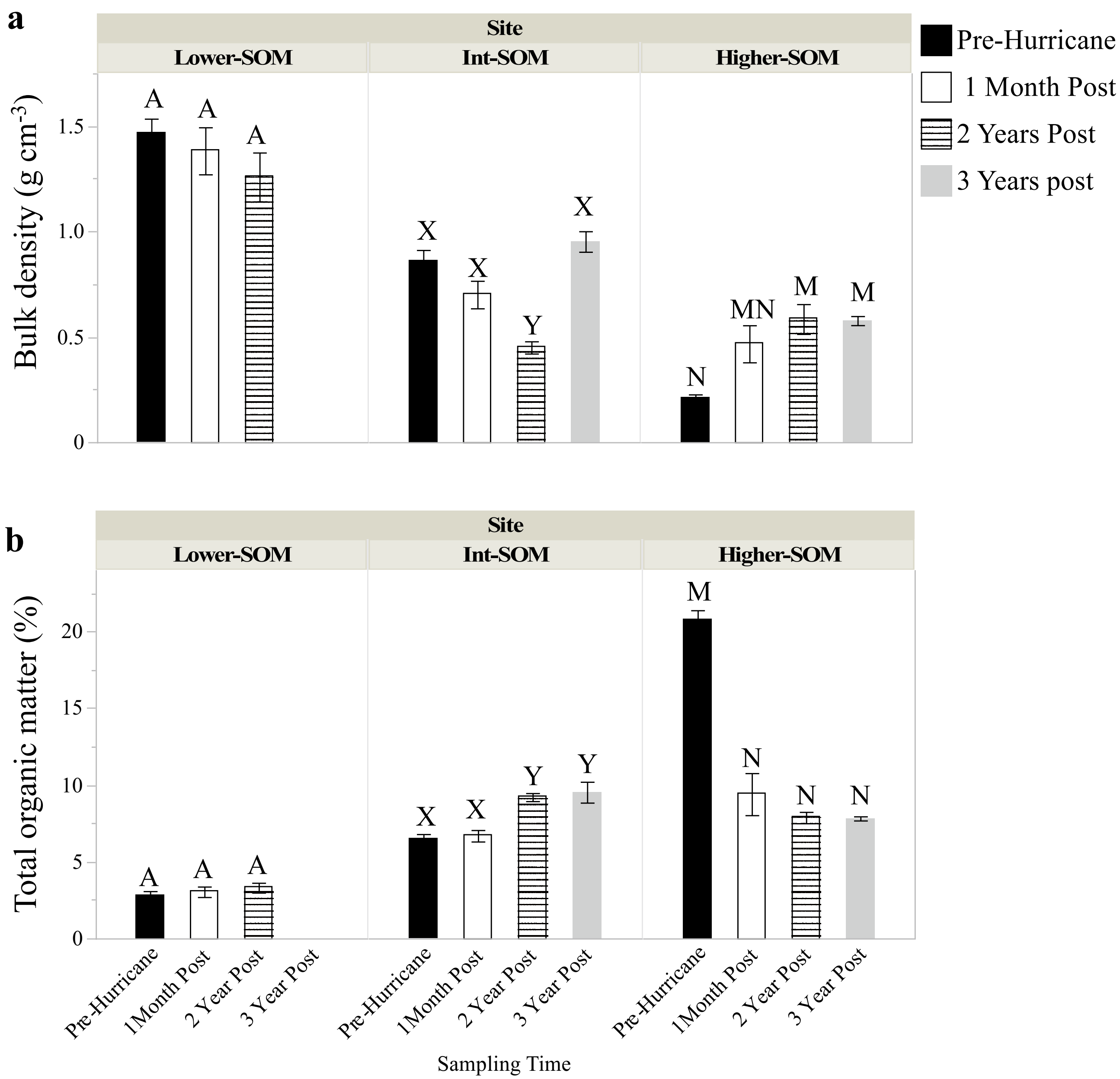


Fig. 5 Averaged **a** bulk density and **b** sediment organic matter (SOM) concentrations from 0 to 4 cm layer of sediments prior to, 1 month following, 2 years following, and 3 years following Hurricane Barry among three experimental sites in WLD (mean ± standard error). The pre-hurricane results in the intermediate- and higher-SOM sites were measured 1 month prior to Hurricane Barry in 2019 while the pre-hurricane results in the lower-SOM site were from summer 2018 (Li and Twilley 2021). The lower-SOM site has no data 3 years post Hurricane Barry for technic reason. Letters designate significant differences among four sampling dates (prior to, 1 month, 2 years, and 3 years following Hurricane Barry) within each experimental site using Games-Howell post hoc tests ($p < 0.05$)

higher-SOM site significantly decreased from 7.3 ± 0.7 prior to the hurricane to 4.8 ± 0.2 1 month following ($p = 0.0004$, $n = 36$) and then to 2.0 ± 0.1 mmol m^{-2} h^{-1} 2 years following the hurricane event ($p < 0.0001$, $n = 36$). Three years after Hurricane Barry, the dissolved O_2 fluxes at the higher site increased to 4.3 ± 0.2 mmol m^{-2} h^{-1} but were still significantly lower than the pre-hurricane O_2 fluxes ($p < 0.0001$, $n = 36$).

Benthic NO_3^- fluxes were negative, indicating net benthic NO_3^- uptake in the study area during all sampling periods. Benthic NO_3^- uptake at the lower-SOM site significantly increased from 4.3 ± 21.5 to 134.2 ± 24.7 then to 227.9 ± 12.8 μmol m^{-2} h^{-1} prior to compared to 1 month and 2 years following hurricane conditions ($p = 0.0448$ and 0.0047, respectively, $n = 27$, Fig. 6b). NO_3^- uptake at the higher-SOM site significantly decreased from 731.0 ± 82.1

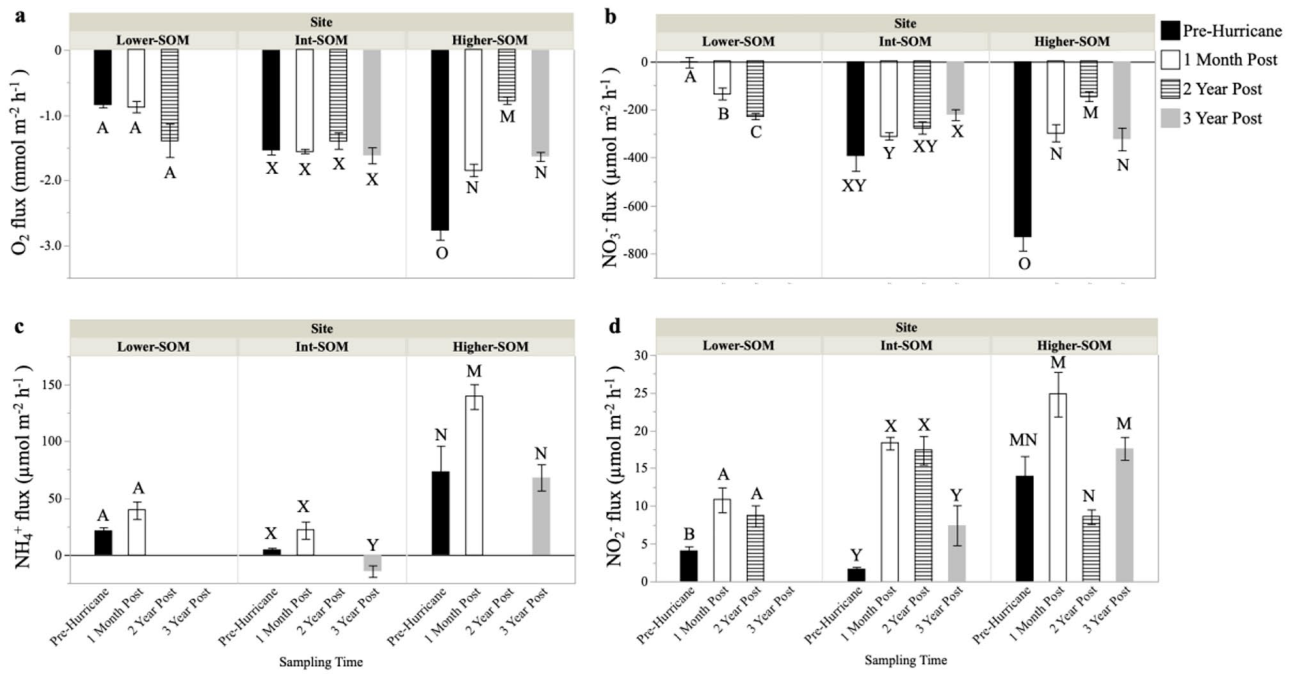
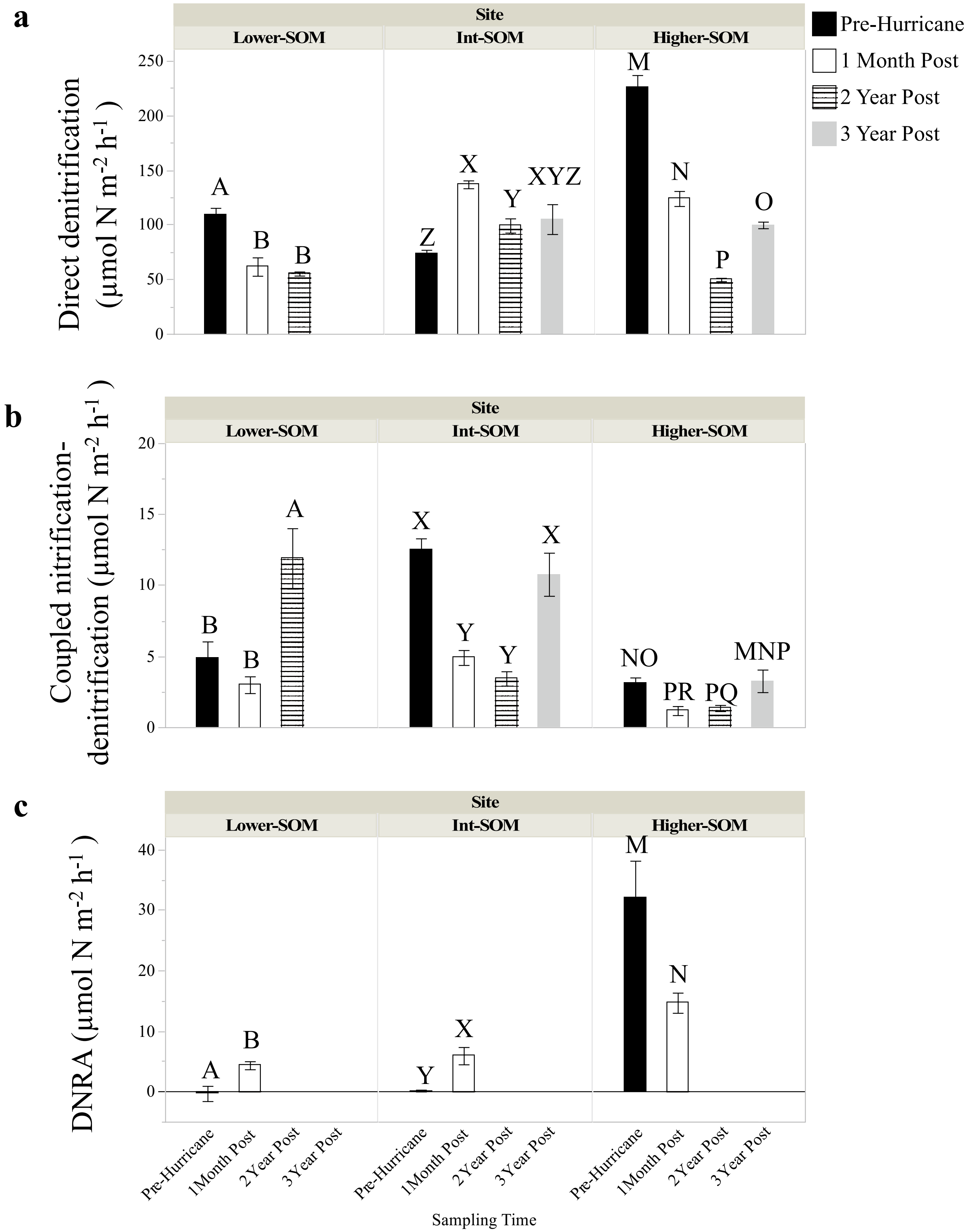


Fig. 6 Benthic fluxes of **a** dissolved O_2, **b** NO_3^-, **c** NH_4^+, and **d** NO_2^- prior to, 1 month following, 2 years, and 3 years following Hurricane Barry at three experimental sites in WLD (mean ± standard error). The lower-SOM site has no data three years post Hurricane Barry for technic reason. The pre-hurricane NH_4^+ flux at the higher-SOM site was from summer 2017 (Li et al. 2020) as there was no available NH_4^+ flux in summer 2018. All other pre-hurricane results were from summer 2018 (Li and Twilley 2021). Letters designate significant differences among four sampling dates within each experimental site using Games-Howell post hoc tests ($p<0.05$). Results of NH_4^+ fluxes prior to Hurricane Barry at the higher-SOM site and 2 years following Hurricane Barry at all three sites were missing due to analytical errors

prior to the hurricane to 297.2 ± 35.6 1 month post the hurricane ($p<0.0001$, $n=36$) and to 145.2 ± 20.6 µmol m^{-2} h^{-1} 2 years after Hurricane Barry ($p<0.0001$, $n=36$). Three years after Hurricane Barry, the NO_3^- uptake increased back to 323.4 ± 47.2 µmol m^{-2} h^{-1} but was still significantly lower than the pre-hurricane NO_3^- uptake ($p=0.0001$, $n=36$). The variation of benthic NO_3^- fluxes at the int-SOM site was not significant to sampling times relative to Hurricane Barry. NH_4^+ fluxes significantly increased from 64.7 ± 21.7 to 139.4 ± 10.9 µmol m^{-2} h^{-1} at the higher-SOM site 1 month after Hurricane Barry compared to the pre-hurricane results ($p=0.0250$, $n=27$, Fig. 6c). NH_4^+ fluxes at the lower-SOM and int-SOM sites also increased 1 month after Hurricane Barry (from 21.5 ± 7.6 to 39.2 ± 7.7 µmol m^{-2} h^{-1} and 4.7 ± 1.4 to 21.7 ± 2.7 µmol m^{-2} h^{-1}, respectively), but the increase was not significant. NO_2^- fluxes in each of the three experimental sites increased 1 month following Hurricane Barry compared to pre-hurricane results ($p=0.0084$, $n=27$ at lower-SOM site; $p<0.0001$, $n=36$ at int-SOM site; $p=0.0750$, $n=36$ at higher-SOM site) then decreased to about pre-disturbance levels 2 years following Hurricane Barry and later (Fig. 6d). Benthic PO_4^{3-} fluxes at the experimental sites had no clear pattern with time associated with disturbance from Hurricane Barry (Supplemental Fig. S-1).

Direct denitrification rates significantly decreased from 109.9 ± 5.4 to 61.5 ± 8.4 then to 55.1 ± 1.9 µmol N m^{-2} h^{-1} at the lower-SOM site prior to compared to 1 month and 2 years following the hurricane event ($p=0.0008$ and <0.0001, respectively, $n=27$, Fig. 7a). Similarly, direct denitrification at the higher-SOM site significantly decreased from 226.3 ± 10.7 prior to the hurricane to 123.9 ± 6.9 1 month after Hurricane Barry then to 49.7 ± 1.5 µmol N m^{-2} h^{-1} 2 years after the hurricane (both $p<0.0001$, $n=36$). Three years after Hurricane Barry, the direct denitrification rates at the higher-SOM site raised to 99.6 ± 3.0 µmol N m^{-2} h^{-1}, which accounts for 45% of pre-hurricane denitrification rates. Direct denitrification rates at the int-SOM site ranged from 74.1 ± 2.8 to 136.8 ± 3.6 µmol N m^{-2} h^{-1} with the highest rates occurred 1 month post the hurricane and lowest rates occurred before the hurricane. Coupled nitrification–denitrification rates varied from 1.2 ± 0.32 to 12.5 ± 0.75 µmol N m^{-2} h^{-1}, which were around 10 times lower than direct denitrification rates in the study area. Coupled nitrification–denitrification rates at the int-SOM and higher-SOM sites decreased significantly 1 month following Hurricane Barry compared to pre-hurricane conditions ($p<0.0001$ and $p=0.0032$, $n=36$, respectively), remained low 2 years after the hurricane, and then raised to


a
Site
Lower-SOM
Int-SOM
Higher-SOM
Pre-Hurricane
1 Month Post
2 Year Post
3 Year Post
Direct denitrification (μmol N m-2 h-1)
250
200
150
100
50
0
A
B
B
Z
X
Y
XYZ
M
N
P
O
b
Coupled nitrification-denitrification (μmol N m-2 h-1)
20
15
10
5
0
B
B
A
X
Y
Y
X
NO
PR
PQ
MNP
c
DNRA (μmol N m-2 h-1)
40
30
20
10
0
A
B
Y
X
M
N
Pre-Hurricane
1Month Post
2Year Post
3Year Post
Sampling Time

◂**Fig. 7** **a** Direct denitrification, **b** coupled nitrification–denitrification, and **c** dissimilatory nitrate reduction to ammonium (DNRA) rates among the experimental sites prior to, 1 month following, 2 years, and 3 years following Hurricane Barry (mean ± standard error). The lower-SOM site has no data 3 years post Hurricane Barry for technic reason. The pre-hurricane results were from summer 2018 (Li and Twilley 2021). Letters designate significant differences among four sampling dates (prior to, 1 month, 2 years, and 3 years following Hurricane Barry) within each experimental site using Games-Howell post hoc tests ($p < 0.05$). DNRA rates were not measured 2 years and 3 years following Hurricane Barry due to analytical issue

pre-hurricane conditions 3 years after the hurricane. DNRA rates at the higher-SOM site significantly decreased from 32.3 ± 5.9 to 14.7 ± 1.7 μmol N m^{-2} h^{-1} 1 month after Hurricane Barry ($p = 0.0213$, $n = 18$), but the higher-SOM site remained with greater DNRA rates prior to and following Hurricane Barry compared to the other experimental sites.

Discussion

Hurricane Disturbance Differs Across Hydrogeomorphic Zones

Prior to hurricane disturbance by Barry, trends of benthic nitrogen dynamics with SOM concentrations along hydrogeomorphic and chronologic zones represented 7 years of undisturbed delta successional development (Supplemental Fig. S-2; Li et al. 2020). Organic matter concentrations increased from younger to older deltaic sediments from subtidal to supratidal hydrogeomorphic zones, which were coupled with increasing benthic nitrogen fluxes (Li et al. 2020). Undisturbed sites in WLD had patterns of SOM concentrations and benthic nitrogen fluxes during our study that may be expected with delta development (Mermillod-Blondin et al. 2003; Michaud et al. 2003; Stockdale et al. 2009; Wenzhöfer and Glud 2004). The lower-SOM site showed similar SOM concentrations over the three sampling periods within 2 years, demonstrated some variations of dissolved O_2 consumptions and benthic nitrogen fluxes, which may be related to spatial and temporal heterogeneity of deltaic sediments. Since SOM concentration is already low in this hydrogeomorphic zone, there is little change in benthic nitrogen dynamics given the strong influence of SOM on benthic fluxes in coastal deltaic floodplains. For the int-SOM site, SOM concentrations 2 years and 3 years after Hurricane Barry were significantly higher than SOM concentrations pre Hurricane Barry ($p < 0.0001$ and $p = 0.0200$, respectively, $n = 36$), indicating organic matter accumulation associated with ecological succession (Bevington and Twilley 2018). Annually different benthic nitrogen fluxes at the int-SOM site illustrated ecological succession in wetlands that changes benthic communities and biogeochemical dynamics (Michaud et al. 2003).

The site-to-site variation of hurricane effects across hydrogeomorphic zones of the coastal deltaic floodplain demonstrate how multiple factors resulting from vegetation mortality and mineral sedimentation control soil characteristics and benthic nitrogen cycling (Morton and Barras 2011). Short-term hurricane effects include substantial mortality of *Nelumbo lutea*, *Colocasia esculenta*, and other plants 1 week after Hurricane Barry. Associated with a decrease density at the sites vegetated with emergent macrophytes was a significant increase of chlorophyll *a* concentrations at the lower-SOM and higher-SOM sites in the top layer of sediments 1 month after Hurricane Barry. The post-hurricane blooms may be related to increased availability of inorganic nutrients released from dead vegetation and litter after Hurricane Barry (Fogel et al. 1999; Huang et al. 2011). Substantial mortality of macrophytes across the delta during Hurricane Barry allowed greater light penetration to the benthic zone that along with higher porewater nutrients such as NH_4^+ could have stimulated the growth of benthic algae (Pennock 1985).

The higher-SOM site located along the interdistributary bay with a dominance of *Colocasia esculenta* and *Nelumbo lutea* showed the most significant disturbance in sediment characteristics after Hurricane Barry. Previous research demonstrates that hurricane deposition of mineral sediment differed with distance from channel edge (Supplemental Fig. S-3; Bevington et al. 2017). Sites with higher-SOM located around 37 m to the primary channel edge had more hurricane sediment deposition based on responses of elevation gain to hurricanes Gustav and Ike (Bevington et al. 2017). The significant increase of bulk density and decrease of SOM concentrations at the higher-SOM site were related to redeposit of resuspended mineral sedimentation attributed to Hurricane Barry (Liu et al. 2018). Storm surge, wind, waves, and currents associated with hurricanes resuspend significant amounts of mineral sediments from shallow inshore zones and redeposit them onto wetland platforms during storm surge inundation (Bevington et al. 2017; Walker 2001). Hurricane-related mineral deposition at the higher-SOM site was at least 4 cm in depth. The ≥ 4 cm sediment deposition at the higher-SOM site resulting from Hurricane Barry was more than three times greater than the long-term annual accretion rate of 1.1 cm $year^{-1}$ in WLD from 2010 to 2019 (based on Coastwide Reference Monitoring System site at 29°31′36.7″N, 91°26′52.9″W). The hurricane deposition at the higher-SOM site was also comparable to recent measurements of annual accretion rate in Louisiana coastal marshes varying from 1.6 to 5.9 cm $year^{-1}$ (Cahoon et al. 2011). Increased mineral sedimentation significantly reduced SOM concentrations at the higher-SOM site, leading to 50% reduction in direct denitrification, coupled nitrification-denitrification, and DNRA rates at this site 1 month following Hurricane Barry.

In between the sampling period from 2019 to 2022, tropical storm Olga (Oct, 2019) and hurricane Zeta (Oct, 2020) also occurred within 100 km distance to WLD, which may disturb the study area. However, unlike hurricane Barry landing on the left side of the wetland, tropical storm Olga and hurricane Zeta landed on the right side of the wetland (Fig. S-2). Hurricanes are counterclockwise cyclones in the North, which cause serious storm surge on their right rather than on their left (Fritz et al. 2007; Sebastian et al. 2014). Also, water levels and surface water salinities during the periods of tropical storm Olga and hurricane Zeta did not show significant variation to these two events (Supplemental Fig. S-4). As such, we speculate that the effects of tropical storm Olga and hurricane Zeta to the study area are minimal. Our study indicates that the disturbed area (higher-SOM site) did not recover to pre-hurricane condition 3 years post the hurricane Barry. Three years tracking period may not be enough to indicate wetland resilience as SOM concentrations together with benthic nitrogen dynamics need longer time than that to recovered to pre-hurricane condition as a result of ecological succession (Mitsch et al. 2005). For example, previous research reported that SOM concentrations in created wetlands increased by about 1% every 3-year period (Mitsch et al. 2005). Hurricane Barry induced about 11% decrease of SOM concentrations at the higher-SOM site, which may need more than 30 years to recover to pre-hurricane condition. However, our study does indicate a short-term restoration trajectory of wetland benthic biogeochemistry after hurricane events. Long-term monitoring of benthic nitrogen dynamics was necessary to understand the resilience and recovery of coastal deltaic floodplain to natural disturbances like hurricanes.

N Dynamics Controlled by SOM

Recent studies at the same experimental sites prior to Hurricane Barry showed that denitrification, as the dominant N pathway in WLD, is positively correlated with SOM concentrations at high overlying NO_3^- concentrations (around 100 μM, Li et al. 2020). As discussed above, mineral sedimentation with hurricane disturbance decreased SOM concentrations and denitrification rates at the higher-SOM site by 50% of the pre-hurricane values. The decrease in SOM concentrations following Hurricane Barry decreased denitrification rates without significantly changing the linear correlation between these two parameters discovered prior to the hurricane (Fig. 8a, $p=0.80$, see supplemental materials for statistic test). Benthic NO_3^- fluxes had a similar response with SOM concentrations based on linear correlation between these two parameters established prior to the hurricane (Fig. 8b; from Li et al. 2020). Benthic NO_3^- fluxes into sediments and denitrification rates are positively correlated with SOM concentrations based on SOM concentrations manipulated by hurricane sediment deposition, strengthening the cause and effect relationship of SOM control of these processes in coastal deltaic floodplains. Changes in SOM concentration with mineral sedimentation following hurricane disturbance reduced benthic NO_3^- fluxes into sediment at the higher-SOM site without impacting the linear correlation between SOM concentrations and NO_3^- fluxes. In summary, the changes of denitrification and benthic NO_3^- fluxes following Hurricane Barry were mainly due to the changes in SOM concentrations associated with hurricane-induced mineral sedimentation in our study area. Hurricane Barry reset the deltaic successional changes in sediment development at the higher-SOM site by decreasing SOM concentrations causing shifts in how benthic nitrogen dynamics process NO_3^-.

Sediment organic matter is an important factor controlling benthic nitrogen dynamics in coastal deltaic floodplains (Henry and Twilley 2014; Li et al. 2020). Previous research demonstrated that hurricanes (e.g., Katrina, Gustav, and Ike) create a net elevation gain due to allochthonous mineral sedimentation in coastal deltaic floodplains like WLD (Bevington et al. 2017; Turner et al. 2006b; Tweel and Turner 2012; Williams and Flanagan 2009). Significant mineral sediment deposits on coastal wetlands decrease SOM concentrations at the sediment-water interface which in turn alters benthic nitrogen dynamics. Wetland soils with significant decrease of SOM after a hurricane event will have decreased denitrification and coupled nitrification-denitrification and DNRA rates and experience a reduction of NO_3^- removal capacity. Previous research showed that sediment surface elevation along seven transects across WLD had 53 of 85 sites increase due to hurricane-induced mineral deposition from Hurricanes Gustav and Ike (Bevington et al. 2017). Using assumptions that the decrease in SOM and NO_3^- removal capacity in the higher-SOM site after Hurricane Barry can be applied to 53/85% of the supratidal zone in WLD (9.8% of the delta area), and the disturbed area has not recovered in 3 years since Hurricane Barry, the NO_3^- removal capacity of WLD has been reduced by 76 Mg N $year^{-1}$. This reduction accounts for 8.5% of total NO_3^- removal capacity of 896 Mg N $year^{-1}$ estimated before the hurricane (Li et al. 2020). Increased mineral deposition has benefits to sediment surface elevation of wetlands but decreases the immediate NO_3^- removal capacity of the coastal deltaic floodplain.

The manipulation of mineral sedimentation on decreasing SOM has other implications to nutrient dynamics in coastal deltaic floodplains. Major river floods deposit significant mineral sediments that may also change SOM concentrations and cause similar changes in denitrification and NO_3^- processes at the sediment-water interface. Based on the manipulations of SOM caused by hurricane deposition,

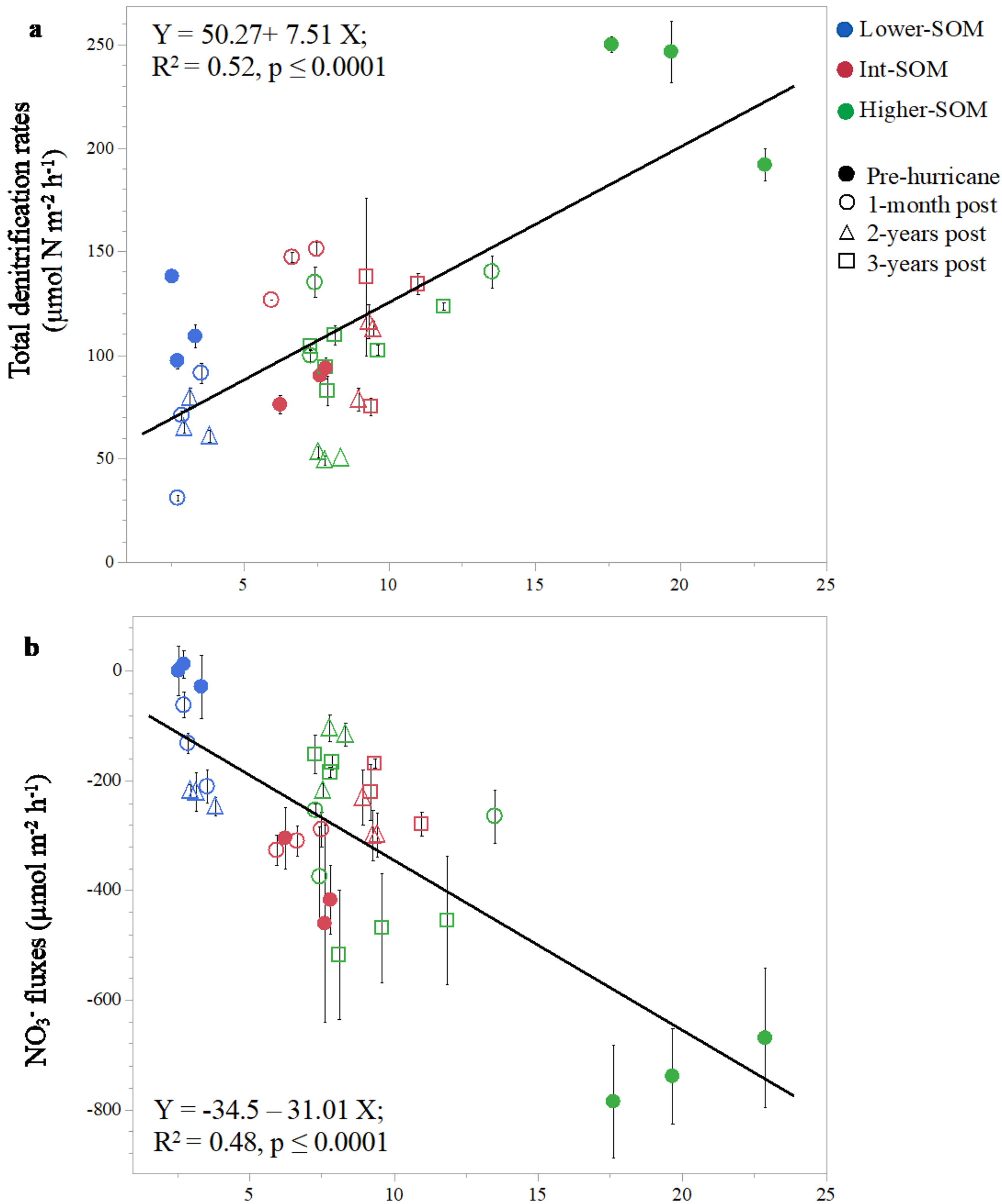


Fig. 8 **a** Total denitrification rates and **b** NO_3^- fluxes as functions of sediment organic matter concentrations prior to and following Hurricane Barry. Solid circles represent pre-hurricane results, while open circles, triangles, and squares indicate 1 month, 2 years, and 3 years following hurricane results, respectively

we suggest that denitrification rates per area may follow a function of SOM using the model $Y = 50.2 + 7.5X$ (X is SOM concentrations in % dry mass). Another mineral deposition event in coastal Louisiana may occur in response to operations of sediment river diversions. Diversion operations that enhance the frequency of wetland inundation have been shown to increase the capacity of flooded intertidal sediments to remove river NO_3^- (Twilley et al. 2021). However, anticipated mineral sedimentation in outfall areas in wetland areas with higher SOM concentrations (above 20%) during diversion operations may see reductions in NO_3^- removal capacity.

To our knowledge, this research is the first assessment on benthic nitrogen dynamics in response to hurricanes disturbance using intact core incubations. Hurricane Barry resets the successional stage of coastal deltaic floodplains by reducing SOM concentrations within the hurricane track resulting in reduced NO_3^- removal capacity by 8.5% compared to pre-hurricane levels (896 Mg N year^{-1}) in the delta. The reduced NO_3^- removal capacity had not recovered to pre-hurricane conditions 3 years following the hurricane. However, mineral sedimentation from river floods and hurricanes can expand wetland areas in coastal deltaic floodplains, leading to coastal nitrogen removal with long-term delta development. For example, some hurricanes' deposition creates a net gain of soil elevation which transform subaqueous delta to emergent ecosystems with an expansion of wetland areas (Bevington et al. 2017; Bevington and Twilley 2018; Ma et al. 2018). Though the newly emergent area has reduced benthic nitrogen dynamics at first due to lower SOM concentrations, the area will be colonized by vegetation during growing season to stimulate SOM accumulation as well as nitrogen removal capacity with long-term ecological succession (Ma et al. 2018; Twilley et al. 2019). As such, more research regarding long-term hurricane effects on benthic nutrient dynamics and soil and hydrogeomorphic characteristics are necessary to clarify the response and recovery ability of coastal deltaic floodplains to natural hurricane disturbances.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s12237-023-01258-y.

Acknowledgements We would like to thank Alexandra Christensen, Andre Rovai, and Andy Cassaway for assistance in field. We thank Sophia Lingo as an undergraduate student assisting with experiments. We also want to thank Thomas Blanchard and Sara Gay for assistance on sample processing and Amanda Vieillard for help with the membrane inlet mass spectrometry measurements. We would like to thank Andre Rovai for constructive suggestions in writing the "Discussion."

Funding This study was supported by the National Science Foundation via the Coastal SEES program at LSU [EAR-1427389]. This manuscript was prepared under award R/MMR-33 to Louisiana Sea Grant College Program by NOAA's Office of Ocean and Atmospheric Research, U.S. Department of Commerce.

Data Availability The data that support the findings of this study are available from the corresponding author upon reasonable request.

References

Aarons, A.A. 2019. Spatial and temporal patterns of ecological succession and land development along a coastal deltaic floodplain chronosequence. PhD Diss.

Arango, C.P., J.L. Tank, J.L. Schaller, T.V. Royer, M.J. Bernot, and M.B. David. 2007. Benthic organic carbon influences denitrification in streams with high nitrate concentration. *Freshwater Biology*. https://doi.org/10.1111/j.1365-2427.2007.01758.x.

Arar, E.J., and G.B. Collins. 1997. In vitro determination of chlorophyll a and pheophytin a in marine and freshwater algae by fluorescence.

Bevington, A. 2016. Dynamics of land building and ecological succession in a prograding deltaic floodplain, Wax Lake delta, LA, USA.

Bevington, A.E., and R.R. Twilley. 2018. Island edge morphodynamics along a chronosequence in a prograding deltaic floodplain wetland. *Journal of Coastal Research* 344: 806–817. https://doi.org/10.2112/jcoastres-d-17-00074.1.

Bevington, A.E., R.R. Twilley, C.E. Sasser, and G.O. Holm. 2017. Contribution of river floods, hurricanes, and cold fronts to elevation change in a deltaic floodplain, northern Gulf of Mexico, USA. *Estuarine, Coastal and Shelf Science* 191: 188–200. https://doi.org/10.1016/j.ecss.2017.04.010.

Blood, E.R., P. Anderson, P.A. Smith, C. Nybro, and K.A. Ginsberg. 1991. Effects of Hurricane Hugo on coastal soil solution chemistry in South Carolina. *Biotropica*. https://doi.org/10.2307/2388251.

Cahoon, D.R., D.A. White, and J.C. Lynch. 2011. Sediment infilling and wetland formation dynamics in an active crevasse splay of the Mississippi River delta. *Geomorphology* 131: 57–68. https://doi.org/10.1016/j.geomorph.2010.12.002.

Canfield, D.E., A.N. Glazer, and P.G. Falkowski. 2010. The evolution and future of earth's nitrogen cycle. *Science* (80-). https://doi.org/10.1126/science.1186120.

Carle, M.V., and C.E. Sasser. 2016. Productivity and resilience: Long-term trends and storm-driven fluctuations in the plant community of the accreting Wax Lake Delta. *Estuaries and Coasts* 39: 406–422. https://doi.org/10.1007/s12237-015-0005-9.

Castañeda-Moya, E., R.R. Twilley, V.H. Rivera-Monroy, K. Zhang, S.E. Davis, and M. Ross. 2010. Sediment and nutrient deposition associated with hurricane wilma in mangroves of the Florida coastal everglades. *Estuaries and Coasts* 33: 45–58. https://doi.org/10.1007/s12237-009-9242-0.

Chabreck, R.H., and A.W. Palmisano. 1973. The effects of Hurricane Camille on the marshes of the Mississippi River delta. *Ecology*. https://doi.org/10.2307/1935578.

Conner, W.H., J.W. Day, R.H. Baumann, and J.M. Randall. 1989. Influence of hurricanes on coastal ecosystems along the northern Gulf of Mexico. *Wetlands Ecology and Management* 1: 45–56. https://doi.org/10.1007/BF00177889.

Cornwell, J.C., W.M. Kemp, and T.M. Kana. 1999. Denitrification in coastal ecosystems: methods, environmental controls, and ecosystem level controls, a review. *Aquatic Ecology*. https://doi.org/10.1157/13077763.

Courtemanche, R.P., M.W. Hester, and I.A. Mendelssohn. 1999. Recovery of a Louisiana barrier island marsh plant community following extensive hurricane-induced overwash. *Journal of Coastal Research*.

Damashek, J., and C.A. Francis. 2018. Microbial nitrogen cycling in estuaries: From genes to ecosystem processes. *Estuaries and Coasts* 41: 626–660. https://doi.org/10.1007/s12237-017-0306-2.

Davis, S.E., J.E. Cable, D.L. Childers, C. Coronado-Molina, J.W. Day, C.D. Hittle, C.J. Madden, E. Reyes, D. Rudnick, and F.

Sklar. 2004. Importance of storm events in controlling ecosystem structure and function in a Florida gulf coast estuary. *Journal of Coastal Research* 204: 1198–1208. https://doi.org/10.2112/03-0072r.1.

Deng, Yang, Helena M. Solo-Gabriele, Michael Laas, Lynn Leonard, Daniel L. Childers, Guoqing He, and Victor Engel. 2010. Impacts of hurricanes on surface water flow within a wetland. *Journal of Hydrology* 392: 164–173. https://doi.org/10.1016/j.jhydrol.2010.08.004.

Diaz, R.J. 2009. Spreading dead zones and consequences for marine ecosystems. *Science* 80: 926–930. https://doi.org/10.1126/science.1156401.

Edmonds, D.A., C. Paola, D.C.J.D. Hoyal, and B.A. Sheets. 2011. Quantitative metrics that describe river deltas and their channel networks. *Journal of Geophysical Research Earth Surface* 116: 1–15. https://doi.org/10.1029/2010JF001955.

Erisman, J.W., M.A. Sutton, J. Galloway, Z. Klimont, and W. Winiwarter. 2008. How a century of ammonia synthesis changed the world. *Nature Geoscience* 1: 636.

Eyre, B.D., D.T. Maher, and P. Squire. 2013. Quantity and quality of organic matter (detritus) drives N2 effluxes (net denitrification) across seasons, benthic habitats, and estuaries. *Global Biogeochemical Cycles*. https://doi.org/10.1002/2013GB004631.

Fogel, M.L., C. Aguilar, R. Cuhel, D.J. Hollander, J.D. Willey, and H.W. Paerl. 1999. Biological and isotopic changes in coastal waters induced by Hurricane Gordon. *Limnology and Oceanography*. https://doi.org/10.4319/lo.1999.44.6.1359.

Fritz, H.M., C. Blount, R. Sokoloski, J. Singleton, A. Fuggle, B.G. McAdoo, A. Moore, C. Grass, and B. Tate. 2007. Hurricane Katrina storm surge distribution and field observations on the Mississippi Barrier Islands. *Estuarine, Coastal and Shelf Science*. https://doi.org/10.1016/j.ecss.2007.03.015.

Fulweiler, R.W., S.W. Nixon, B.A. Buckley, and S.L. Granger. 2007. Reversal of the net dinitrogen gas flux in coastal marine sediments. *Nature*. https://doi.org/10.1038/nature05963.

Fulweiler, R.W., S.W. Nixon, B.A. Buckley, and S.L. Granger. 2008. Net sediment N2 fluxes in a coastal marine system-experimental manipulations and a conceptual model. *Ecosystems* 11: 1168–1180. https://doi.org/10.1007/s10021-008-9187-3.

Gardner, W.S., and M.J. McCarthy. 2009. Nitrogen dynamics at the sediment-water interface in shallow, sub-tropical Florida Bay: Why denitrification efficiency may decrease with increased eutrophication. *Biogeochemistry* 95: 185–198. https://doi.org/10.1007/s10533-009-9329-5.

Guntenspergen, G.R., D.R. Cahoon, and J. Grace. 1995. Disturbance and recovery of the Louisiana coastal marsh landscape from the impacts of Hurricane Andrew. *Journal of Coastal Research*.

Hardison, A.K., C.K. Algar, A.E. Giblin, and J.J. Rich. 2015. Influence of organic carbon and nitrate loading on partitioning between dissimilatory nitrate reduction to ammonium (DNRA) and N<inf>2</inf> production. *Geochimica Et Cosmochimica Acta* 164: 146–160. https://doi.org/10.1016/j.gca.2015.04.049.

Henry, K.M., and R.R. Twilley. 2014. Nutrient biogeochemistry during the early stages of delta development in the Mississippi River deltaic plain. *Ecosystems* 17: 327–343. https://doi.org/10.1007/s10021-013-9727-3.

Huang, W., D. Mukherjee, and S. Chen. 2011. Assessment of Hurricane Ivan impact on chlorophyll-a in Pensacola Bay by MODIS 250m remote sensing. *Marine Pollution Bulletin*. https://doi.org/10.1016/j.marpolbul.2010.12.010.

Kana, T.M., C. Darkangelo, M.D. Hunt, J.B. Oldham, G.E. Bennett, and J.C. Cornwell. 1994. Membrane inlet mass spectrometer for rapid environmental water samples. *Analytical Chemistry* 66: 4166–4170.

Lacoul, P., and B. Freedman. 2006. Environmental influences on aquatic plants in freshwater ecosystems. *Environmental Reviews* 14: 89–136. https://doi.org/10.1139/A06-001.

Li, S., and R.R. Twilley. 2021. Benthic nitrogen dynamics in an emerging coastal deltaic floodplain in Mississippi River Delta using isotope pairing technique to test response to nitrate loading and sediment organic matter. *Estuaries and Coasts* 44:1899-1915. https://doi.org/10.1007/s12237-021-00913-6.

Li, S., A. Christensen, and R.R. Twilley. 2020. Benthic fluxes of dissolved oxygen and nutrients across hydrogeomorphic zones in a coastal deltaic floodplain within the Mississippi River delta plain. *Biogeochemistry*. https://doi.org/10.1007/s10533-020-00665-8.

Li, S., R.R. Twilley, and A. Hou. 2021. Heterotrophic nitrogen fixation in response to nitrate loading and sediment organic matter in an emerging coastal deltaic floodplain within the Mississippi River Delta plain. *Limnology and Oceanography* 66: 1961–1978. https://doi.org/10.1002/lno.11737.

Liu, K., Q. Chen, K. Hu, K. Xu, and R.R. Twilley. 2018. Modeling hurricane-induced wetland-bay and bay-shelf sediment fluxes. *Coastal Engineering*. https://doi.org/10.1016/j.coastaleng.2017.12.014.

Liu, K., T.A. McCloskey, T.A. Bianchette, G. Keller, N.S.N. Lam, J.E. Cable, and J. Arriola. 2014. Hurricane Isaac storm surge deposition in a coastal wetland along Lake Pontchartrain, southern Louisiana. *Journal of Coastal Research* 70: 266–271. https://doi.org/10.2112/si70-045.1.

Ma, H., L.G. Larsen, and R.W. Wagner. 2018. Ecogeomorphic feedbacks that grow deltas. *Journal of Geophysical Research. Earth Surface* 123: 3228–3250. https://doi.org/10.1029/2018JF004706.

Mermillod-Blondin, F., S. Marie, G. Desrosiers, B. Long, L. De Montety, E. Michaud, and G. Stora. 2003. Assessment of the spatial variability of intertidal benthic communities by axial tomodensitometry: Importance of fine-scale heterogeneity. *Journal of Experimental Marine Biology and Ecology*. https://doi.org/10.1016/S0022-0981(02)00548-8.

Michaud, E., G. Desrosiers, B. Long, L. De Montety, J.F. Crémer, E. Pelletier, J. Locat, F. Gilbert, and G. Stora. 2003. Use of axial tomography to follow temporal changes of benthic communities in an unstable sedimentary environment (Baie Des Ha! Ha!, Saguenay Fjord). *Journal of Experimental Marine Biology and Ecology*. https://doi.org/10.1016/S0022-0981(02)00532-4.

Michener, W.K., E.R. Blood, K.L. Bildstein, M.M. Brinson, and L.R. Gardner. 1997. Climate change, hurricanes and tropical storms, and rising sea level in coastal wetlands. *Ecological Applications* 7: 770–801. https://doi.org/10.1016/s1240-1307(97)87735-7.

Mitsch, W.J., L. Zhang, C.J. Anderson, A.E. Altor, and M.E. Hernández. 2005. Creating riverine wetlands: ecological succession, nutrient retention, and pulsing effects. *Ecological Engineering*. https://doi.org/10.1016/j.ecoleng.2005.04.014.

Morton, R.A., and J.A. Barras. 2011. Hurricane impacts on coastal wetlands: A half-century record of storm-generated features from Southern Louisiana. *Journal of Coastal Research* 275: 27–43. https://doi.org/10.2112/jcoastres-d-10-00185.1.

Nielsen, L.P. 1992. Denitrification in sediment determined from nitrogen isotope pairing. *FEMS Microbiology Ecology* 86: 357–362.

Nielsen, L.P., and R.N. Glud. 1996. Denitrification in a coastal sediment measured in situ by the nitrogen isotope pairing technique applied to a benthic flux chamber. *Marine Ecology Progress Series* 137: 181–186. https://doi.org/10.3354/meps137181.

Paerl, H.W., R.L. Dennis, and D.R. Whitall. 2002. Atmospheric deposition of nitrogen: Implications for nutrient over-enrichment of coastal waters. *Estuaries* 25: 677–693. https://doi.org/10.1007/BF02804899.

Paola, C., R.R. Twilley, D.A. Edmonds, W. Kim, D. Mohrig, G. Parker, E. Viparelli, and V.R. Voller. 2011. Natural processes in delta restoration: Application to the Mississippi Delta. *Annual Review of Marine Science* 3: 67–91. https://doi.org/10.1146/annurev-marine-120709-142856.

Pennock, J.R. 1985. Chlorophyll distributions in the Delaware estuary: Regulation by light-limitation. *Estuarine, Coastal and Shelf Science*. https://doi.org/10.1016/0272-7714(85)90068-X.

Rabalais, N.N., R.E. Turner, Q. Dortch, D. Justic, V.J. Bierman, and W.J. Wiseman. 2002. Nutrient-enhanced productivity in the northern Gulf of Mexico: Past, present and future. *Hydrobiologia* 475–476: 39–63. https://doi.org/10.1023/A:1020388503274.

Reja, M.Y., S.D. Brody, W.E. Highfield, and G.D. Newman. 2017. Hurricane recovery and ecological resilience: Measuring the impacts of wetland alteration post Hurricane Ike on the upper TX coast. *Environmental Management*. https://doi.org/10.1007/s00267-017-0943-z.

Sebastian, A., J. Proft, J.C. Dietrich, W. Du, P.B. Bedient, and C.N. Dawson. 2014. Characterizing hurricane storm surge behavior in Galveston Bay using the SWAN+ADCIRC model. *Coastal Engineering*. https://doi.org/10.1016/j.coastaleng.2014.03.002.

Shaw, J.B., and D. Mohrig. 2014. The importance of erosion in distributary channel network growth, Wax Lake Delta, Louisiana, USA. *Geology* 42: 31–34. https://doi.org/10.1130/G34751.1.

Steffen, W., K. Richardson, J. Rockström, S.E. Cornell, I. Fetzer, E.M. Bennett, R. Biggs, S.R. Carpenter, W. de Vries, C.A. de Wit, C. Folke, D. Gerten, J. Heinke, G.M. Mace, L.M. Persson, V. Ramanathan, B. Reyers, and S. Sörlin. 2015. Planetary boundaries: guiding human development on a changing planet. *Science* 80 (347): 1259855. https://doi.org/10.1126/science.1259855.

Stockdale, A., W. Davison, and H. Zhang. 2009. Micro-scale biogeochemical heterogeneity in sediments: A review of available technology and observed evidence. *Earth-Science Reviews*. https://doi.org/10.1016/j.earscirev.2008.11.003.

Turner, R.E., J.J. Baustian, E.M. Swenson, and J.S. Spicer. 2006a. Wetland sedimentation from hurricanes Katrina and Rita. *Science* 314 (80): 449–452. https://doi.org/10.1126/science.1129116.

Turner, R.E., J.J. Baustian, E.M. Swenson, J.S. Spicer, R. Eugene, J.B. Joseph, M.S. Erick, and S.S. Jennifer. 2006b. Wetland sedimentation from hurricanes Katrina and Rita. *Science* 314 (80): 449–452. https://doi.org/10.1126/science.1129116.

Tweel, A.W., and R.E. Turner. 2012. Landscape-scale analysis of wetland sediment deposition from four tropical cyclone events. *PLoS ONE*. https://doi.org/10.1371/journal.pone.0050528.

Twilley, R., J.W. Day, A.E. Bevington, E. Castañeda-Moya, A. Christensen, G. Holm, L.R. Heffner, R. Lane, A. McCall, A. Aarons, S. Li, A. Freeman, and A.S. Rovai. 2019. Ecogeomorphology of coastal deltaic floodplains and estuaries in an active delta: insights from the Atchafalaya Coastal Basin. *Estuarine, Coastal and Shelf Science* 106341. https://doi.org/10.1016/j.ecss.2019.106341.

Twilley, R.R., S. Rick, D.C. Bond, and J. Baker. 2021. Benthic nutrient fluxes across subtidal and intertidal habitats in breton sound in response to river-pulses of a diversion in mississippi river delta. *Water (Switzerland)* 13. https://doi.org/10.3390/w13172323.

Walker, N.D. 2001. Tropical Storm and Hurricane wind effects on water level, salinity, and sediment transport in the river-influenced Atchafalaya-Vermilion Bay system, Louisiana, USA. *Estuaries*. https://doi.org/10.2307/1353252.

Wang, X., W. Wang, and C. Tong. 2016. A review on impact of typhoons and hurricanes on coastal wetland ecosystems. *Acta Ecologica Sinica* 36: 23–29. https://doi.org/10.1016/j.chnaes.2015.12.006.

Wenzhöfer, F., and R.N. Glud. 2004. Small-scale spatial and temporal variability in coastal benthic O2dynamics: Effects of fauna activity. *Limnology and Oceanography*. https://doi.org/10.4319/lo.2004.49.5.1471.

Williams, C.J., J.N. Boyer, and F.J. Jochem. 2008. Indirect hurricane effects on resource availability and microbial communities in a subtropical wetland-estuary transition zone. *Estuaries and Coasts* 31: 204–214. https://doi.org/10.1007/s12237-007-9007-6.

Williams, H.F.L., and W.M. Flanagan. 2009. Contribution of hurricane rita storm surge deposition to long-term sedimentation in Louisiana coastal woodlands and marshes. *Journal of Coastal Research*.

Yin, G., L. Hou, M. Liu, Z. Liu, and W.S. Gardner. 2014. A novel membrane inlet mass spectrometer method to measure 15NH4+ for isotope-enrichment experiments in aquatic ecosystems. *Environmental Science and Technology* 48: 9555–9562. https://doi.org/10.1021/es501261s.