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RESEARCH ARTICLE

Quantifying effects of increased hydroperiod on wetland nutrient concentrations during early phases of freshwater restoration of the Florida Everglades

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Wetland restoration requires managing long-term changes in hydroperiod and ecosystem functions. We quantified relationships among spatiotemporal variability in wetland hydrology and total phosphorus (TP) and its stoichiometric relationships with total organic carbon (TOC:TP) and total carbon (TC:TP) and total nitrogen (TN:TP) in water, flocculent organic matter (floc), periphyton, sawgrass (*Cladium jamaicense*), and soil during early phases of freshwater wetland restoration—water year (WY) 2016 (1 May, 2015 to 30 April, 2016) to WY 2019—in Everglades National Park (ENP, Homestead, FL, U.S.A.). Wetland hydroperiod increased by 87 days, following restoration actions and rainfall events that increased median stage in the upstream source canal. Concentrations of TP were highest and most variable at sites closest (<1 km) to canal inputs and upstream wetland sources of legacy P. Surface water TOC:TP and TN:TP ratios were highest in wetlands >1 km downstream of the canal in wet season 2015 with spatial variability reflecting disturbances including droughts, fires, and freeze events. The TP concentrations of flocculent soil surface particles, periphyton, sawgrass, and consolidated soil declined, and TC:TP and TN:TP ratios increased (except soil) logarithmically with downstream distance from the canal. We measured abrupt increases in periphyton (wet season 2018) and sawgrass TP (wet season 2015 and 2018) at sites <1 km from the canal, likely reflecting legacy TP loading. Our results suggest restoration efforts that increase freshwater inflow and hydroperiod will likely change patterns of nutrient concentrations among water and organic matter compartments of wetlands as a function of nutrient legacies.

Key words: biogeochemistry, Everglades restoration, freshwater, hydroperiod, modified water deliveries, Northeast Shark River Slough

Implications for Practice

- Hydrologic restoration outcomes are a consequence of a combination of water management actions and climate variability, which influence hydroperiod, and nutrient uptake and allocation in managed aquatic ecosystems.
- Restoring wetland hydroperiod can change nutrient concentrations among ecosystem compartments, which likely varies based on legacies of nutrient loading.
- Long-term ecological research is essential to detect dynamic and emerging patterns of biogeochemical changes associated with restoration.

Introduction

Vast declines in wetlands worldwide have occurred due to human land use and climate changes, making wetland restoration a global imperative (Dahl & Stedman 2013; Gardner et al. 2015). Restoration in wetland ecosystems is a dynamic process that occurs over time, and spatiotemporal variability in ecological responses is largely based on relative changes in hydroperiod—that is, the number of days per year with water at or above a minimum depth threshold (Zedler 2000). The term ecological restoration often involves an attempt to return a system to near a former state, although the difficulty of achieving this aim is widely recognized (Palmer et al. 2016). Restoration requires adaptive efforts, because co-occurring disturbances (e.g. global climate change, human intervention, etc.) alter the capacity of ecosystems to return to a former state (Palmer et al. 2016). Usually in subtropical areas like Florida, significant challenges to restoring wetlands include disturbances associated with land-use change, extreme events (droughts, floods, hurricanes), and—for coastal wetlands—sea-level rise (National

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Research Council [NRC] 2018). These changes affect wetlands principally through altered hydrology, and there is an increasing need to understand how variability in hydroperiod interacts with the frequency, duration, and severity of these disturbances (Erwin 2009).

Assessment of hydrologic restoration effectiveness in wetland ecosystems requires comprehensive measurements of how changes in hydroperiod driven by management interact with other ongoing environmental changes (including disturbance) to impact ecological structure and functions. Restoring wetland ecosystems is often complex, as the physical factors that define a wetland environment at any specific time are often treated as independent variables compared to other ecosystem processes (Zedler & Kercher 2005). For instance, wetland hydrology affects soil, biogeochemistry, and biology of a wetland; however, the hydrology is in turn directly or indirectly affected by the soil, plants (i.e. sawgrass, *Cladium jamaicense*), benthic periphyton, and flocculent detrital organic matter (floc) underlying the wetland (Jackson et al. 2019). Wetland hydroperiods are important ecosystem control points (Bernhardt et al. 2017), because most aquatic organisms are associated with the water column and near-surface soil, and their life cycles are synchronized to the inundation periods of a wetland (Jackson et al. 2019). Therefore, wetland restoration (e.g. reestablishing hydroperiod, improving water management strategies, removing exotic species) is critical to maintain carbon and nutrient balance among the compartments of these globally threatened ecosystems (sensu Odum 1969; Kominoski et al. 2018). There is a need and opportunity to understand how changes in hydroperiod from restoration interact with biogeochemical changes to influence ecosystem properties.

The Florida Everglades is the largest freshwater peatland in the conterminous United States, and it is undergoing the largest and most expensive restoration effort in the world (NRC 2018). More than a century of draining and building of canals throughout the Florida Everglades has allowed for the expansion of urban and agricultural development, reducing the original size of the historic Everglades by half (Perry 2004; McVoy et al. 2011). These changes resulted in a cascade of environmental disruptions throughout the Everglades landscape (Davis et al. 1994). Landscape-scale hydrologic disturbances have reduced surface water flows and increased surface-groundwater interactions that likely interacted with historic elevated total phosphorus (TP) loading from intensive agriculture, leading to persistent ecosystem regime shifts (Gunderson 2001; Hagerthey et al. 2008; Newman et al. 2017). For example, elevated TP concentrations in inflowing water prior to the establishment of a protective criterion of 10 $\mu g\ L^{-1}$ in 2000 caused elevated soil TP concentrations (Osborne et al. 2014; Surratt & Aumen 2014), resulting in declines in native plant communities and shifts to dense monocultures of invasive *Typha* spp. near inflows (Doren et al. 1997; Childers et al. 2003). Collectively, wetland compartmentalization and TP loading resulted in the loss of historic Everglades ridge-and-slough landscape patterning in some parts of the Everglades (Larsen et al. 2007). Cascading effects of elevated TP loading are initiated by collapse of periphyton mats that are adapted to low nutrient availabilities (Gaiser et al. 2005), and the history of TP loading has culminated in a predictable distribution of communities downstream of canal inflow points (Gaiser et al. 2006). Phosphorus is first removed by microorganisms, and then cycles subsequently into plants, floc, and finally water (Noe et al. 2002). Long-term increases in wetland hydroperiod will likely influence P cycling and distribution among surface water, plants, and benthic organic matter in the Everglades (Noe et al. 2001; Hagerthey et al. 2008; Naja et al. 2017). In addition, changes in water flow through structures will influence downstream movement of P that has accumulated in upstream reaches as a result of a history of above-ambient TP loading to the system (legacy loading) (Childers et al. 2003; Bramburger et al. 2013; Gaiser et al. 2014).

We lack a comprehensive understanding about how changes in freshwater hydroperiod, associated with restoration, interact with extreme events and legacy nutrients, mostly P historically loaded into the system, to affect wetland biogeochemistry. Although it is understood that increasing wetland hydrology influences nutrient cycling and concentrations in the Everglades (Noe & Childers 2007; Gottlieb et al. 2015; Sola et al. 2018), it is uncertain how spatiotemporal variability in hydroperiod—driven by both water management and the interaction with climate-driven disturbances—mobilizes legacy nutrients and subsequently affects nutrient concentrations and ratios of surface water and other ecosystem compartments (i.e. floc, periphyton, sawgrass, soil). Shortened hydroperiods have led to changes in the distribution and dynamics of marsh plant communities and associated periphyton assemblages (Gottlieb et al. 2005; Saunders et al. 2006; Lee et al. 2013). Both spatial and temporal variabilities in hydroperiod increase periphyton mat TP concentrations, as drying and rewetting is associated with enhanced nutrient concentrations (Sola et al. 2018). In addition, legacy P inputs from canal point sources (i.e. culverts) have impacted algal and plant communities (Gaiser et al. 2014; Sah et al. 2014; Sullivan et al. 2014). The Everglades is a model ecosystem to assess how early phases of freshwater restoration drive changes in hydroperiod and ecological responses due to the implementation of the modified water deliveries (MWD) to ENP Project, an initial foundation project of the Comprehensive Everglades Restoration Plan (NRC 2018). The MWD project allows incremental increases of water flow into Northeast Shark River Slough (NESRS), ENP (McLean 2015). After long delays in planning and construction, the first incremental test of this multiyear project was started in October 2015 (McLean 2015). The goal of the MWD project is to increase water flows that are expected to change species composition and relative abundance of different species by increasing the length of the hydroperiod and improving seasonal timing and distribution of water deliveries (McLean 2015).

Here, our objective was to quantify how changes in freshwater delivery into a previously reduced hydroperiod wetland via MWD interacts with multiple climate-driven extreme events (e.g. droughts, floods, hurricanes) to affect biogeochemistry across ecosystem compartments in NESRS, ENP. We quantified how increases in hydroperiod and distance from an upstream canal (source of restorative fresh water) interact with natural disturbances to drive changes in nutrient concentrations, especially of the limiting nutrient phosphorus (as TP), and its stoichiometric relationships with total organic carbon (TOC:TP), total carbon (TC:TP), and total nitrogen (TN:TP) in surface water, floc, periphyton, sawgrass (*Cladium jamaicense*), and soil in NESRS, ENP. We tested the following questions: (1) What is the spatiotemporal variability in freshwater hydroperiod during the early phases of restoration? (2) How does variability in hydroperiod differentially affect nutrient concentrations and ratios in surface water, floc, periphyton, sawgrass, and soil? and (3) How does distance from an upstream source of restorative fresh water and legacy P differentially affect nutrient concentrations and ratios in surface water, floc, periphyton, sawgrass, and soil? We hypothesized that increases in hydroperiod would be variable spatially and temporally with increases in the stage of the upstream canal (L-29) associated with restoration, water management, and climate-driven extreme events (floods, droughts, and hurricanes). Increases in hydroperiod were expected to increase downstream transport of legacy P (Bramburger et al. 2013) and decrease TOC:TP, TC:TP, and TN: TP in surface water, floc, periphyton, sawgrass, and soil to a greater extent in wetlands closest to the upstream L-29 Canal and culvert-associated vegetation halos compared to wetlands further downstream.

Methods

Site Description

The historic Everglades was previously a continuous marsh network extending from north of Lake Okeechobee southward to Florida Bay. The water flowed mostly as sheet flow during the wet season (May–November) when the region receives 70% of its rainfall (Sandoval et al. 2016; NRC 2018). However, hydrologic modification has altered water flow by subdividing the region into several basins via drainage canals (e.g. water conservation areas; WCAs and ENP). The creation of WCAs (1960) resulted in hydrologic impoundments, droughts, and loss of ecological connectivity between the central and southern Everglades, greatly reducing seepage and flow.

NESRS is an approximately 50,000 ha watershed contained entirely within the Everglades and extends from the eastern boundary of ENP westward to the L-67 Canal Extension (25°18′45″N, 80°41′15″W) (Fig. 1). The L-29 Canal (also called the Tamiami Canal) with a WCA levee on its northern bank and Tamiami Trail roadway on its southern bank eliminated the connectivity with and natural sheet flow from the central Everglades into Shark River Slough (SRS) (Fig. 1). The NESRS largely receives water from upstream via L-29 water control structure S-333 (Fig. 1), culverts beneath the Tamiami Trail, and since 2012, overland flow from the L-29 Canal when water stage is higher than 2.3 m (National Geodetic Vertical Datum 1929 [NGVD29]) (McLean 2015). This overland flow has been enabled by the MWD project, with construction of a 1.6-km bridge in 2012 to increase the connectivity between central and southern Everglades. Two additional bridges (totaling 4.2 km) to the west of the 1.6-km bridge were constructed in 2018 to further increase water deliveries southward from the L-29 Canal into NESRS. The MWD began operations on 15 October, 2015 with testing phases (MWD incremental tests) that increased the maximum stage in the L-29 Canal from 2.2 to 2.6 m NGVD29. This study focuses on the ecological effects in surface water, floc, periphyton, sawgrass, and soil in NESRS of ENP due to increasing hydroperiod and distance from the upstream canal water source, associated with these initial operations during the MWD incremental tests.

This study project was originally established in 2006 to document the patterns and abundance of key ecological indicators (e.g. surface water, floc, periphyton, sawgrass, and soil) across the NESRS landscape (Gaiser 2009). Sites were selected to cover the broader NESRS landscape as well as capture ecological changes with downstream increases in hydroperiod associated with freshwater restoration (Fig. 1). Sites located closest and perpendicular to the L-29 Canal distributed along eight 3-km transects (T1-T8) were selected to be approximately parallel to expected flow vectors from the canal (Fig. 1). The first transect (T1) location was considered as a reference as it was selected east of the 1.6-km bridge, while the others transects (T2-T8) were selected to be downstream of the bridges (Fig. 1).

Sample Collection

Surface water and particulate organic matter samples were collected from the wet season of 2015 and 2018 to coincide with multiple climate-driven disturbances (droughts, floods, hurricanes) and the onset of enhanced freshwater management (MWD incremental tests).

Surface water samples ($n = 1$ replicate per site) were collected at each site when water was present (at a minimum water depth of 10 cm). Both filtered and unfiltered surface water grab samples were collected into plastic bottles from mid-depth of the water column (lower boundary floc/water interface, upper boundary water/air interface) at each location. Approximately 500 mL unfiltered and 250 mL filtered surface water were collected. Filtered sample were collected by syringe with 0.4-μm filter cap. After collecting, samples were acidified and kept on ice until returning to the lab.

Soil and the overlying floc were sampled by intact coring. The flocculent detrital organic matter—floc—was defined as the "unconsolidated" layer lacking the coherence of soil that "flows" off the soil when extruded from a core. Three replicate samples (triplicate) of soil and floc (if present) were collected from each location. Cores were collected by inserting a 5-cm-diameter polycarbonate tube through the floc and into the soil. By using a thin-walled (2 mm) polycarbonate corer, soil was collected to reduce compaction as much as possible. Once collected, the cores were separated into the floc (unconsolidated layer on top of the soil) and the 0–2- and 2–10-cm soil depth increments. We analyzed 0–2 and 2–10 cm separately and include data from both increments in soil analyses.

Periphyton is a common feature of Everglades freshwater wetlands and is comprised of algae, detrital material, and associated living organisms in floating or epiphytic mats. Periphyton

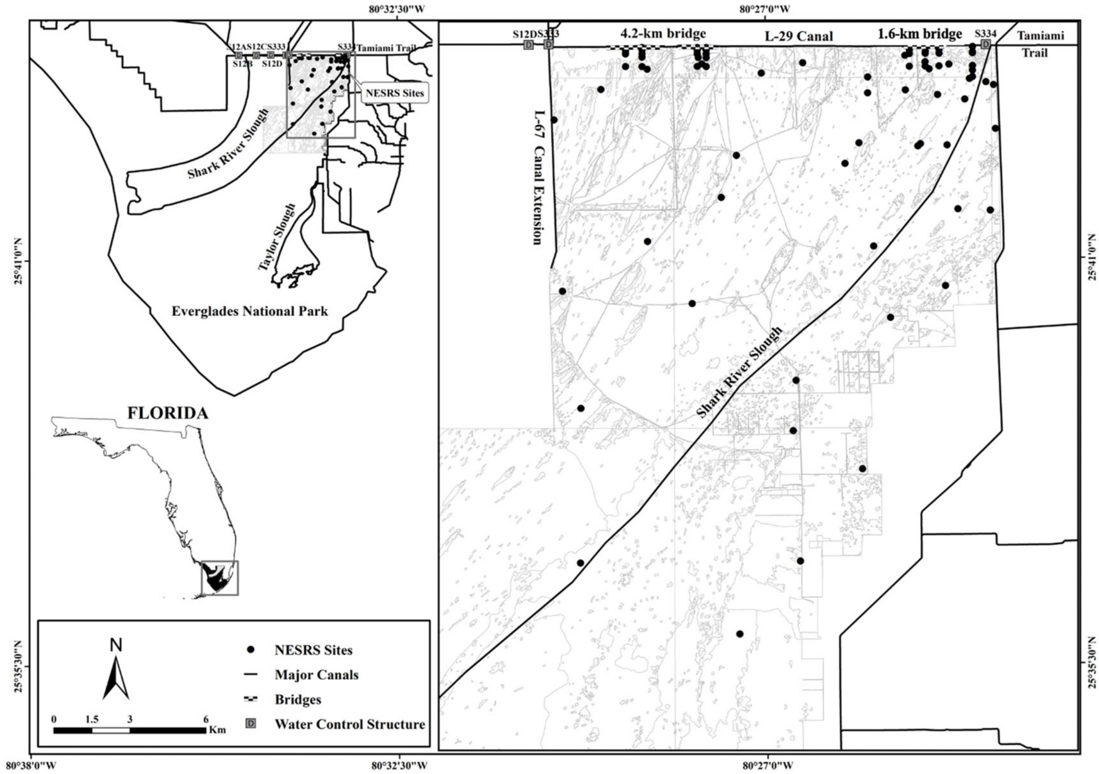

Figure 1. Map locating the geographical settings and sampling sites along the Northeast Shark River Slough, Everglades National Park (Homestead, FL, U.S.A.). Map was produced in ArcGIS 10.7.

serves as an excellent early responder to environmental changes and can be used as an indicator of impending change (Gaiser 2009). We estimated the biovolume of calcareous floating and epiphytic periphyton (data not shown), as well as the percent cover of benthic calcareous periphyton at all sites, where present. We collected 120 mL grab samples (n = 3 replicates per site) of benthic periphyton from each site, where present. Periphyton was mostly absent during the dry season and at sites closest to the L-29 Canal. Periphyton samples were stored in labeled, sealed bags (Whirl-Pak or equivalent) and immediately placed on ice until returned to the lab.

Sawgrass (*Cladium jamaicense*) is a dominant native macrophyte of Caribbean karstic freshwater wetlands like the Florida Everglades (Ross et al. 2003). Fifteen-centimeter sections from the middle of three leaves of sawgrass were collected from each site (n = 3 replicates per site), where present.

All collected surface water, floc, periphyton, sawgrass, and soil samples were stored on ice until returned to the lab. After returning, all samples were packed in pre-labeled plastic bottles or tubes and delivered to the analytical lab on ice on the same day of sample collection for analyses. Detailed procedures and methods for sample nutrient analyses can be found in Sarker et al. (2019).

Canal Stage and Wetland Hydroperiod

Stage data for L-29 Canal from 2006 to 2018 were obtained from the DBHYDRO database (www.sfwmd.gov/science-data/dbhydro). To improve data accuracy, stage data measured before 2010 based on NGVD29 were upgraded to North American Vertical Datum 1988 (NAVD88) standard (www.sfwmd.gov/science-data/dbhydro). To maintain data coherency, all stage data from 1 January, 2006 to 31 December, 2018 were analyzed based on the NAVD88 standard.

Surface water-depth data for downstream wetlands were obtained from the Everglades Depth Estimation Network (EDEN) database. Daily water-depth maps from EDEN are computed by subtracting the ground elevation from the daily water level for each grid cell (400 m × 400 m). The water-depth data for NESRS sites were extracted from the EDEN water-depth maps using a script in R. Water depths <5 cm were considered dry and water depths >5 cm were considered wet to account for known error associated with EDEN depth estimates. Total wet and dry days for each site were summed for a particular year at each site to calculate hydroperiod (i.e. numbers of days per year with water depth >5 cm). We calculated hydroperiod from 1 May, 2015 through 30 April, 2019 based on daily water depth at each site for each water year (WY). Hydroperiod was calculated for a full WY starting from May to April of the following year, that is, hydroperiod for WY2016 was calculated from 1 May, 2015 to 30 April, 2016. Hydroperiod for WY2019 was calculated from 1 May, 2018 to 30 April, 2019.

Nutrient Concentrations and Molar Ratios

Samples of surface water, floc, periphyton, sawgrass, and soil were collected from all sites, where present, in wet season

2015 and 2018 and analyzed for TP, TN, TOC (surface water samples), and TC (Table 1). Samples from half of sites were processed by FIU's Center for Aquatic Chemistry and Environment Nutrient Core Facility, and duplicate samples from 10% of those sites (for QA/QC [quality assurance/quality control]) were collected and processed by the South Florida Water Management District (SFWMD). Samples from the other half of sites were processed by the SFWMD, duplicate samples from 10% of those sites were processed by FIU. Both FIU and SFWMD analytical labs follow strict internal and external QA/QC practices and have National Environmental Laboratory Accreditation Conference certification for nonpotable water-General Chemistry under State Lab ID E76930 (FIU) and E46077 (SFWMD).

For water samples, TP was analyzed following Solórzano and Sharp (1980), TN was measured with an Antek TN analyzer (Antek Instruments, Houston, TX, U.S.A.), and TC and TOC were analyzed by using a Shimadzu TOC Analyzer (Shimadzu Corporation, Columbia, MD, U.S.A.).

TC and TN of oven-dried floc, periphyton, sawgrass, and soil samples were analyzed by the high-temperature dry combustion method using a Carlo-Erba NA-1500 CNS Analyzer (Nelson & Sommers 1996). Determination of TP was done by oxidation

Table 1 Summary of elemental concentrations (total organic carbon, TOC; total carbon, TC; total nitrogen, TN; total phosphorus, TP) and molar ratios (TOC:TP or TC:TP, TOC:TN or TC:TN, TN:TP) of surface water (μg L^{-1} TP, mg L^{-1} TOC and TN), floc, periphyton, sawgrass and soil (μg g^{-1}) from wet seasons in 2015 and 2018 (during initial phases of modified water deliveries [MWD] incremental tests) from sites along the northeast Shark River Slough, Everglades National Park (Homestead, FL, U.S.A.).

	Wet Season 2015					*Wet Season 2018*			
	Median	*Min*	*Max*	n		*Median*	*Min*	*Max*	n
Surface water									
TP	5	2	50	77	TP	20	4	72	78
TN	1.28	0.62	3	77	TN	1.10	0.27	2	78
TOC	15	11	23	77	TOC	16	6	25	78
TOC:TP	7,750	1,011	16,017	77	TOC:TP	2,357	467	12,271	78
TOC:TN	13	7	30	77	TOC:TN	18	10	51	78
TN:TP	660	52	1770	77	TN:TP	151	29	620	78
Floc									
TP	976	270	1,695	39	TP	296	40	1,277	123
TN	30	11	38	39	TN	21	3	40	123
TC	373	203	442	39	TC	305	171	476	123
TC:TP	903	601	3,725	39	TC:TP	2,683	626	16,009	123
TC:TN	14	12	22	39	TC:TN	18	9	77	123
TN:TP	62	31	291	39	TN:TP	152	37	674	123
Periphyton									
TP	67	21	1,379	148	TP	74	5	400	167
TN	10	3	37	148	TN	10	5	23	167
TC	245	190	467	148	TC	240	187	353	167
TC:TP	9,089	562	27,683	148	TC:TP	7,923	2070	99,098	167
TC:TN	29	12	66	148	TC:TN	28	16	43	167
TN:TP	287	47	1,007	148	TN:TP	278	105	3,124	167
Sawgrass									
TP	284	74	1937	110	TP	247	121	1,055	145
TN	11	3	36	110	TN	8	5	29	145
TC	452	274	504	110	TC	465	311	504	145
TC:TP	4,092	555	15,387	110	TC:TP	4,883	1,109	9,727	145
TC:TN	49	13	171	110	TC:TN	68	13	113	145
TN:TP	80	36	191	110	TN:TP	74	18	176	145
Soil (0–2 cm)									
TP	432	68	1,459	216	TP	391	43	1,351	210
TN	6	1	37	216	TN	22	3	44	210
TC	156	18	450	216	TC	325	129	513	210
TC:TP	933	77	7,180	216	TC:TP	2,232	588	12,917	210
TC:TN	17	13	47	216	TC:TN	19	12	61	210
TN:TP	51	3	265	216	TN:TP	119	32	911	210
Soil (2–10 cm)									
TP	413	91	1,503	211	TP	292	43	952	209
TN	4	1	36	211	TN	24	1	39	209
TC	120	17	529	211	TC	356	68	504	209
TC:TP	964	38	6,199	211	TC:TP	2,685	736	17,879	209
TC:TN	18	13	73	211	TC:TN	18	12	188	209
TN:TP	36	2	352	211	TN:TP	128	26	1,117	209

(dry combustion) and hydrolysis of the P-containing compounds in the sample to soluble forms (soluble reactive, ortho-P [SRP]) using $MgSO_4/H_2SO_4$ and HCl (Solórzano & Sharp 1980), and then followed by standard colorimetric analysis of the resultant SRP (United States Environmental Protection Agency [USEPA] 1996, method 365.1). Elemental ratios (TC:TP, TN:TP) were calculated as molar.

Data Analyses

We compiled all data collected from 2006 to 2018 for surface water, floc, periphyton, sawgrass, and soil in a publicly accessible database (Sarker et al. 2019). Data from surface water, floc, periphyton, sawgrass, and soil were not consistently available for each season in each location. To develop a general summary of all parameters, we here compared the data from wet season 2015 and 2018 from all sites along the NESRS (Fig. 1) and calculated minimum, median, and maximum values for each compartment (Table 1). We chose median as the central tendency of these skewed (non-normal) data.

Time series of water stage in the L-29 from 1 January, 2006 to 31 December, 2018 was used to illustrate climate-driven extreme events and water management impacts on downstream water availability. By using Geographic Information System (GIS) proximity analysis (e.g. near tool), we measured the distance of all NESRS sites from the upstream L-29 Canal. Hydroperiod calculated for WY2016 were compared to WY2019 to determine the spatial and temporal changes of hydroperiod across the NESRS. A non-parametric Mann–Whitney test was conducted to determine the statistical significance of hydroperiod between 2 years. A GIS interpolation technique inverse-weighted analysis was applied to visualize the comparison of hydroperiod between WY2016 to WY2019. We tested changes in hydroperiod with downstream distance from the L-29 Canal using linear regression and compared slopes of regressions for WY2016 and WY2019 with analysis of covariance (ANCOVA).

A subset database for median TP, TC:TP, and TN:TP was created for each matrix type (e.g. surface water, floc, periphyton, sawgrass, and soil) including hydroperiod, and distance from the L-29 Canal. Relationships between hydroperiod and downstream distance from the L-29 Canal were tested with simple linear regressions. Nutrient concentrations and molar ratios were compared with downstream distance from the L-29 Canal for wet season 2015 and 2018, respectively, using simple linear regressions. We tested how increases in hydroperiod affected downstream transport of legacy P by comparing slopes of regressions with ANCOVA. All statistical analyses were performed in R version 3.6 and RStudio version 0.97.124 (R Core Team 2019).

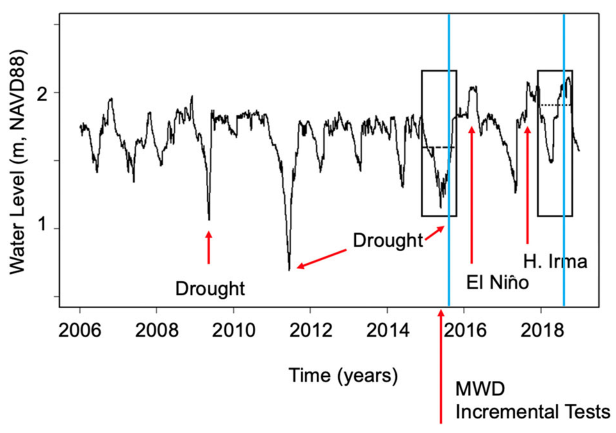

Figure 2. Temporal variation of daily stage (m, NAVD 88) of L-29 Canal from calendar years 2006–2018 (x-axis tick marks indicate 1 January in a given year). Dashed lines indicate median water level the in L-29 Canal in calendar years 2015 and 2018. Blue vertical lines denote sampling events. Red arrows indicate climate-driven extreme events and a freshwater management operational change (initiation of modified water deliveries [MWD] incremental tests).

Results

Canal Stage, Wetland Depth, and Hydroperiod

The stage of L-29 Canal increased and decreased with climate-driven extreme events (droughts, El Niño, and Hurricane Irma) as well as during the MWD incremental tests (Fig. 2). Water depth at all sites (data not shown) increased in accordance with increases in the stage of the L-29 Canal. Wetland hydroperiod was highly variable over space and time and increased from WY2016 to WY2019 throughout the NESRS sites (Figs. 3 and 4). Median hydroperiod increased by 107 days in wetlands following climate-driven flooding events in WY2016 that coincided with initiation of MWD incremental tests (NRC 2018), collectively increasing median canal stage from 1.55 to 1.81 m (Fig. 2). In some sites, hydroperiod was increased from 15 to 89 days comparing WY2016 to WY2019 (Fig. 3). Non-parametric Mann–Whitney U test showed that there was a difference between 2016 and 2019 hydroperiod across the NESRS ($w = 805$, $p < 0.001$). Hydroperiod was generally negatively correlated with downstream distance from the L-29 Canal, and the slope of this relationship decreased from WY2016 to WY2019 (ANCOVA, $F_{1,173} = 194.5$, $p < 0.001$), following increases in water stage in the L-29 Canal and freshwater flows into downstream wetlands (Fig. 4).

Nutrient Concentrations and Molar Ratios

Surface Water. Median (from across all sites) surface water nutrient concentrations were similar in wet season 2015 and 2018 for TOC (15 and 16 mg L^{-1}) and TN (1 mg L^{-1}), except for TP concentrations that increased 4× in wet season 2018 (20 μg L^{-1}) compared to wet season 2015 (5 μg L^{-1}; Table 1). Exceedance of the TP criterion of 10 μg L^{-1} was detected in 17.5% of discrete surface water samples collected in wet season 2015 and 70% of samples collected in wet season 2018. However, median TP in the L-29 Canal was similar in 2015 (6 μg L^{-1}) and 2018 (7 μg L^{-1}) and below the nutrient criterion level. Median TOC:TP ratios in surface water declined by −3.3× from wet season 2015 to wet season 2018 (Table 1).

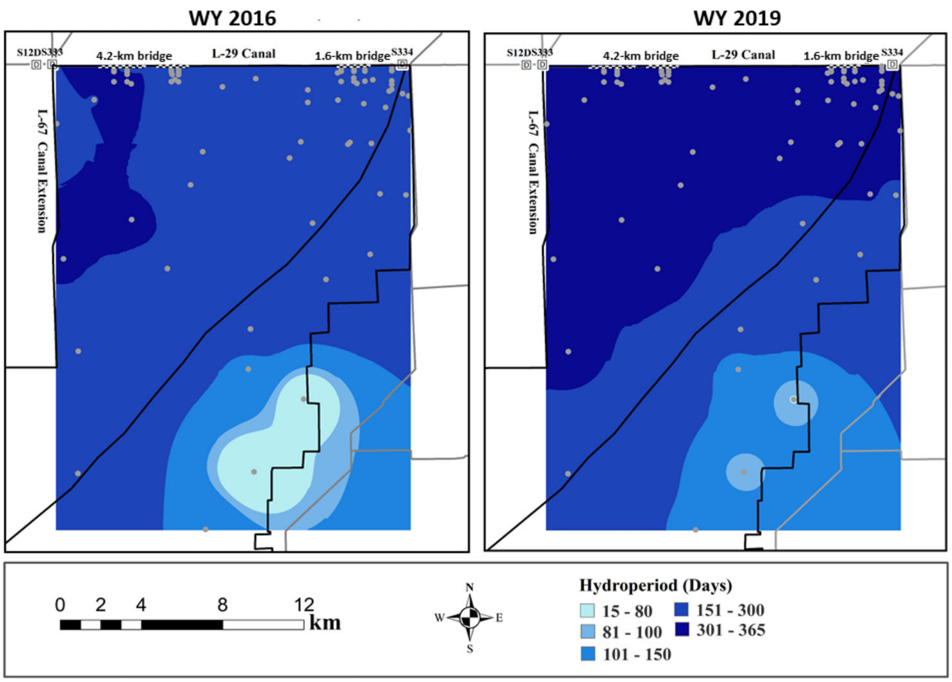

Figure 3. Spatial and temporal changes in hydroperiod in water year (WY) 2016 and 2019 along the Northeast Shark River Slough, Everglades National Park (Homestead, FL, U.S.A.). Dark color indicates higher hydroperiod where light color indicates lower hydroperiod. Map was produced in ArcGIS 10.7.

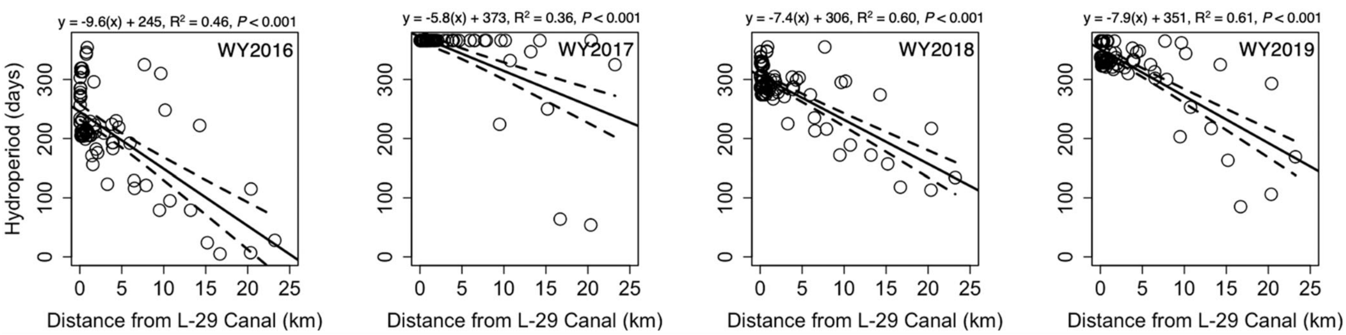

Figure 4. Relationship between hydroperiod with distance from the upstream L-29 canal during water years (WY) 2016–2019 along Northeast Shark River Slough, Everglades National Park (Homestead, FL, U.S.A.). Water year was 1 May –30 April in each year. Onset of modified water deliveries incremental tests began in WY2016. Fitted lines are linear regressions and 95% confidence intervals.

The highest TP concentrations were observed closest to the L-29 Canal in wet season 2015 and 2018, and downstream decreases in TP concentrations were observed with increasing distance from the L-29 Canal in wet season 2015 but not 2018 (Fig. 5A). Surface water TOC:TP and TN:TP ratios increased with distance downstream of L-29 Canal in wet season 2015, but TOC:TP and TN:TP ratios decreased with distance downstream in wet season 2018 (ANCOVA, $F_{1,165} = 82.4$, $p < 0.001$; Fig. 5F & 5K).

Floc, Periphyton, Sawgrass, and Soil. Median TP concentrations were highest for floc and soil in wet season 2015 and 2018 compared to all other water and particulate samples (Table 1). From wet season 2015 to 2018, median TP concentrations declined for floc (−3.3×) and soil (−1.2×), increased for periphyton (+1.1×), and declined for sawgrass (−1.1×). From wet season 2015 to 2018, median TC:TP and TN:TP ratios increased for floc (+3×, +2.5×) and soil (+1.4×, 1.4×), and were similar for periphyton. From wet season 2015 to wet season 2018, sawgrass median TC:TP ratios increased by +1.2× and TN:TP ratios slightly decreased by −1.1×. Median concentrations of TN were also highest in floc and soil in both wet season 2015 and 2018, and TN remained largely unchanged for all compartments when comparing wet season 2015 to 2018 (Table 1). Median TC concentrations were highest in sawgrass and remained largely unchanged for sawgrass and periphyton when comparing wet season 2015 to 2018 (Table 1). Periphyton had the highest

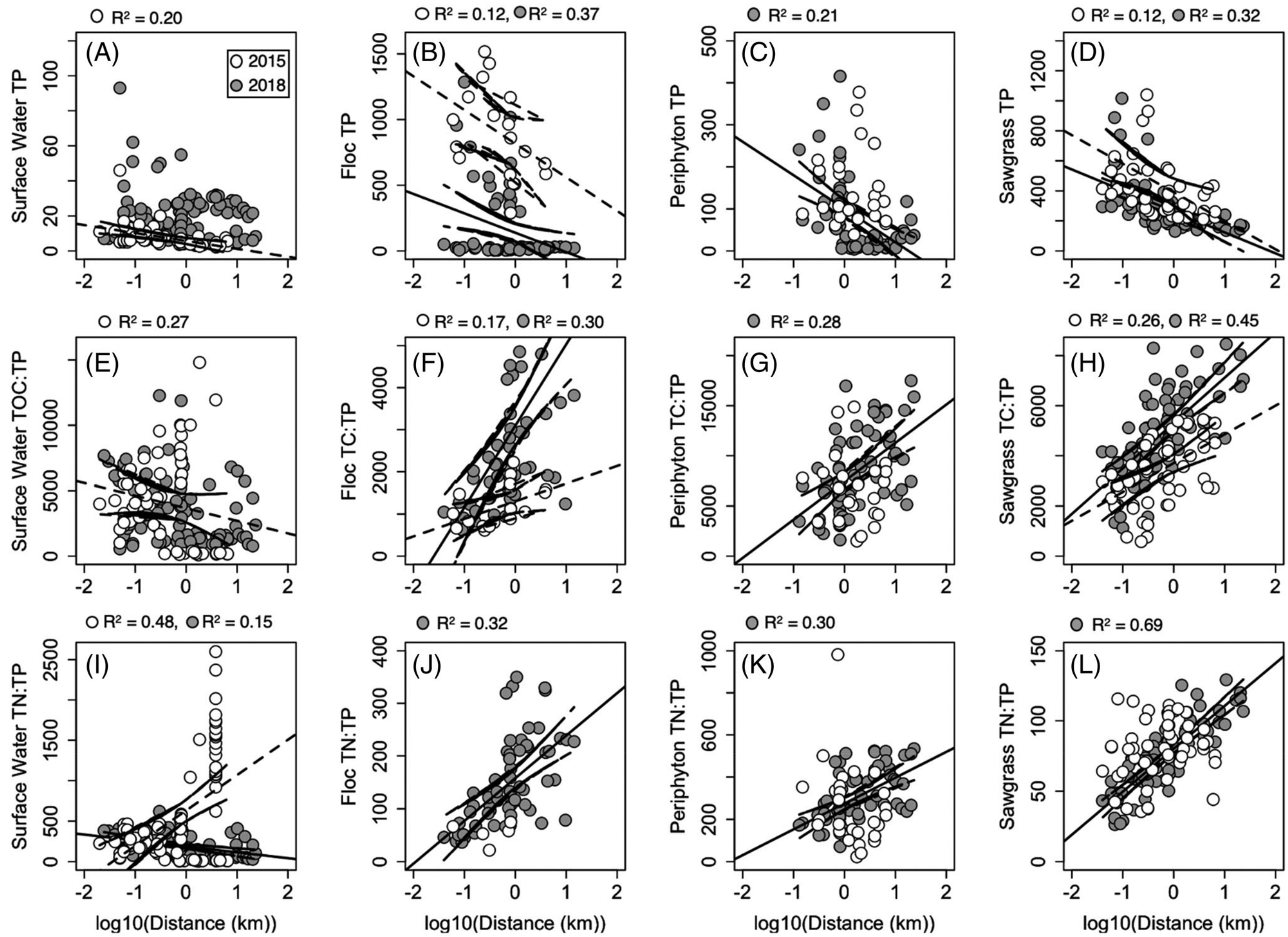

Figure 5. Changes in water and particulate nutrient concentrations and ratios with distance from the upstream L-29 canal in wet season 2015 (open symbols) and wet season 2018 (filled symbols) from all sites along Northeast Shark River Slough, Everglades National Park, (Homestead, FL, U.S.A). Values are individual water samples and median of replicates ($n = 3$) for floc, periphyton, and sawgrass. Total phosphorus (TP) concentrations ($\mu g\ L^{-1}$, $\mu g\ g^{-1}$) (A–D), and total organic carbon to TP (TOC:TP) for surface water, total carbon to TP (TC:TP) (E–H) and total nitrogen to TP (TN:TP) molar ratios (I–L) in surface water, floc, periphyton, and sawgrass. Onset of modified water deliveries incremental tests occurred from October 2015. Fitted lines are linear regressions ($p \le 0.05$), dashed representing 2015, solid representing 2018. When downstream trends occurred in both 2015 and 2018, slopes of regressions were compared using analysis of covariance (ANCOVA).

median TC:TP, sawgrass the highest TC:TN, and surface water the highest TN:TP (Table 1). From wet season 2015 to wet season 2018, median TC concentrations increased by +2.1× for 0–2 cm and + 3.0× for 2–10 cm soil, and decreased slightly by −1.2× for floc (Table 1). Median soil TN increased from wet season 2015 to wet season 2018 (+3.7× for 0–2 cm and + 6.0× for 2–10 cm), whereas median soil TP concentrations slightly decreased (−1.1× for 0–2 cm and −1.4× for 2–10 cm). We measured increases in median soil TC:TP ratios (+2.4× for 0–2 cm and + 2.8× for 2–10 cm) and TN:TP ratios (+2.3× for 0–2 cm and + 3.6× for 2–10 cm), whereas median soil TC:TN ratios were similar between 2015 and 2018 for both soil depths (Table 1).

Floc. Floc was present only at long hydroperiod sites. Concentrations of floc TP declined steadily with distance from the L-29 Canal in wet season 2018 but not in wet season 2015 (ANCOVA, $F_{1,83} = 19.6$, $p < 0.001$; Fig. 5B). Floc TC:TP and TN:TP ratios steeply increased with distance from the L-29 Canal in wet season 2018 compared to wet season 2015 (ANCOVA, $F_{1,75} = 9.5$, $p < 0.01$; Fig. 5G & 5L).

Periphyton. Periphyton TP concentrations and TC:TP and TN:TP ratios were influenced by hydroperiod and distance from the L-29 Canal. TP concentrations declined and TC:TP and TN:TP ratios increased with distance from the L-29 Canal in wet season 2018 but not in wet season 2015 (Fig. 5C, 5H, & 5M).

Sawgrass. Variation in sawgrass TP concentrations was explained by hydroperiod and distance from the L-29 Canal. Higher concentrations of sawgrass TP were measured at distances less than 1 km from the upstream L-29 Canal, and sawgrass TP steadily declined with downstream distance in wet season 2015 and 2018 (ANCOVA, $F_{1,129} = 11.5$, $p < 0.001$; Fig. 5D). Sawgrass TC:TP increased with downstream distance from the L-29 Canal in both wet season 2015 and 2018 (ANCOVA, $F_{1,129} = 27.6$, $p < 0.001$; Fig. 5I), and TN:TP increased with downstream distance in 2018 (Fig. 5N). Sawgrass was absent from sites that had hydroperiod less 100 days throughout the study period across the NESRS landscape.

Soil. Median TP concentrations in soil was higher at sites located closer to the L-29 Canal, and steeply declined downstream in both wet season 2015 and 2018 (0–2 cm: ANCOVA, $F_{1,120} = 24.9$, $p < 0.001$, 2–10 cm: ANCOVA, $F_{1,120} = 43.3$, $p < 0.001$; Fig. 6A & 6B). Median TP concentrations in subsurface soils were lower in wet season 2018 than wet season 2015 (2–10 cm: ANCOVA, $F_{1,120} = 11.4$, $p < 0.001$; Fig. 6B). Soil TC:TP (0–2 cm: ANCOVA, $F_{1,120} = 38.3$, $p < 0.001$, 2–10 cm: ANCOVA, $F_{1,120} = 29.2$, $p < 0.001$; Fig. 6C & 6D) and TN:TP ratios in wet season 2015 and 2018 increased with downstream distance from the L-29 Canal (0–2 cm: ANCOVA, $F_{1,120} = 22.1$, $p < 0.001$, 2–10 cm: ANCOVA, $F_{1,120} = 10.5$, $p < 0.01$; Fig. 6E & 6F). Median soil TC:TP (0–2 cm: ANCOVA, $F_{1,120} = 15.0$, $p < 0.01$, 2–10 cm: ANCOVA, $F_{1,120} = 53.5$, $p < 0.001$; Fig. 6C & 6D) and TN:TP ratios were higher in wet season 2018 than wet season 2015 (0–2 cm: ANCOVA, $F_{1,120} = 26.4$, $p < 0.001$, 2–10 cm: ANCOVA, $F_{1,120} = 68.7$, $p < 0.001$; Fig. 6E & 6F).

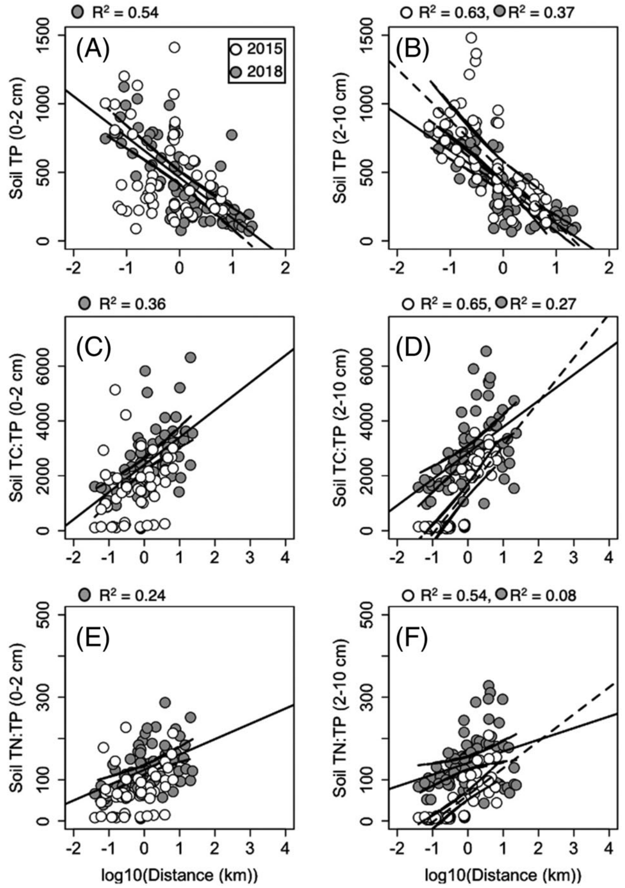

Figure 6. Changes in surface (0–2 cm) and subsurface soil (2–10 cm) nutrient concentrations and ratios with distance from the upstream L-29 canal in wet season 2015 (open symbols) and wet season 2018 (filled symbols) from all sites along Northeast Shark River Slough, Everglades National Park (Homestead, FL, U.S.A.). Values are median of replicates ($n = 3$) for both soil depths. Total phosphorus (TP) concentrations (μg L^{-1}, μg g^{-1}) (A, B), and total organic carbon to TP (TOC:TP) for surface water, total carbon to TP (TC:TP) (C, D), and total nitrogen to TP (TN:TP) molar ratios (E, F) in soil. Onset of modified water deliveries incremental tests occurred from October 2015. Fitted lines are linear regressions ($p \leq 0.05$), dashed representing 2015, solid representing 2018. When downstream trends occurred in both 2015 and 2018, slopes of regressions were compared using analysis of covariance (ANCOVA).

Discussion

From WY2016 to WY2019, hydroperiod increased with increases in stage of the L-29 Canal associated with MWD incremental tests and climate-driven hydrologic events (high rainfall events including hurricanes). The increased hydroperiod extended into wetlands up to 20 km downstream of the L-29 Canal. We predicted that increases in hydroperiod would increase TP concentrations and decrease TOC:TP, TC:TP, and TN:TP ratios in surface water, floc, periphyton, sawgrass, and soil due to potential mobilization of legacy P. Median TP in the L-29 Canal was similar in 2015 (6 μg L^{-1}) and 2018 (7 μg L^{-1}) and below the nutrient criterion level (10 μg L^{-1}). In general, we found higher TP concentrations in water and particulate matter during both wet season 2015 and 2018 at sites closest to the L-29 Canal. This suggests that legacy nutrient loading (prior to the TP criterion, 2000), and not increases in nutrients associated with increased water inflows from the L-29 Canal per se, could explain elevated surface water nutrient concentrations (Doren et al. 1997, 2009;Childers et al. 2003; Gaiser et al. 2014). For example, legacy TP can be released from soil and organic matter via oxidative decomposition during extended dry periods resulting in particulate matter that can be resuspended in the water column and transported downstream during storms (Davis et al. 2018). We detected high variability in surface water TP concentrations nearest to the L-29 Canal, and median surface water TP concentrations increased above the nutrient criterion level (10 μg L^{-1}) during MWD incremental tests in wet season 2018 compared to wet season 2015 (from 17.5 to 70% of samples). Uniformly low surface water TP concentrations are expected in an oligotrophic ecosystem like the P-limited Florida Everglades. If ecosystem state changes are to be avoided, restoration efforts must continue to avoid P-enrichment as well as identify how hydrologic restoration may interact with sources of legacy P. Surface water TOC:TP and TN:TP molar ratios were more variable >1 km downstream of the L-29 in wet season 2015, likely due to landscape-scale disturbances (e.g. droughts, fires, freeze events) that increased downstream export of TOC and TN (Davis et al. 2018). Soil and floc TP concentrations declined with increased distance during the study period and were lower in wet season 2018, suggesting that enhanced freshwater hydroperiod reduced soil and floc TP that can increase with drought (Davis et al. 2018). However, abrupt increases in periphyton and sawgrass TP during early restoration at sites <1 km downstream of the L-29 Canal and likely associated with sources of legacy P suggest that these wetland compartments may be responding to both current and legacy TP loading (Childers et al. 2003; Gaiser et al. 2014).

Sources and Spatiotemporal Patterns of Nutrient Compartmentalization

Nutrient concentrations in Everglades wetlands have been shown to follow an exponential decay with distance from water and nutrient sources (Childers et al. 2003), but concentrations in biota and ecosystem P budgets vary temporally with exposure to P loads (Gaiser et al. 2005; Noe & Childers 2007). Periphyton, floc, sawgrass, and soil respond to changing P load at different time scales (periphyton and floc faster, sawgrass and soil slower) (Noe et al. 2003; Gaiser et al. 2005; Noe & Childers 2007). Declines in water and soil TP concentrations with distance from canals are often observed over longer distances (>10 km) than we measured in our current study (<10 km) (Doren et al. 1997; Childers et al. 2003; Sarker 2018). Exponential declines in periphyton TP have been measured within <1 km of canals in Taylor Slough, which is dominated by marl prairie marshes (Gaiser et al. 2014). Although we detected declines in periphyton TP with downstream distance from the L-29 Canal, periphyton TP concentrations above the 150 $\mu g\ g^{-1}$ criterion that indicate excess P enrichment (Gaiser et al. 2006) occurred at sites nearest (<1 km) the L-29 Canal in wet season 2018 compared to sites furthest (>1 km) from the L-29 Canal in 2015. Higher sawgrass TP concentrations were observed nearest (<1 km) the L-29 Canal in both wet season 2015 and wet season 2018. Collectively, this indicates that periphyton and sawgrass—some of the fastest P-acquiring compartments of Everglades marshes—are critical to retaining both current and legacy P loads during periods of increased water flows (Surratt & Aumen 2014).

Despite known decreases in periphyton and floc TP with distance from canals (Gaiser et al. 2006), the presence of floc and periphyton is also driven by water depth, hydroperiod, and light availability, leading to the formation of marl soil in shorter- and floc in longer-hydroperiod wetlands (Childers et al. 2003; Gaiser et al. 2014). However, our ability to explain how changes in hydroperiod affect patterns in floc nutrient concentrations and ratios is limited by lower sample size (floc is not present at many sites) compared to other parameters. Similar to our findings from this study, Childers et al. (2003) found the highest soil TP concentrations within 1 km of an inflow canal. In addition to canal sources of TP to adjacent wetlands, upstream wetlands of the central Everglades remain a major potential source of TP for downstream wetlands in ENP, including the NESRS (Zapata-Rios et al. 2012; Surratt & Aumen 2014).

Although surface water TP concentrations from central to southern Everglades have generally decreased since the 1980s and are lowest when upstream wetland water depths (e.g. WCA-3A) were deepest (Noe et al. 2001), detection of TP concentrations exceedances in surface water and periphyton signals some concerns that enrichment may be occurring. Hydrologic variability upstream impacts nutrient concentrations downstream in Everglades wetlands. For example, water depths in WCA-3A declined from 2000 to 2012, and surface water TP concentrations subsequently increased in downstream freshwater inflows (Surratt & Aumen 2014). Water depth, nutrient loads, and nutrient cycling and allocation are a delicate balance that must be better understood and integrated into effective wetland restoration.

Everglades Restoration Is Increasing Water Levels and Depth

Restoration of the Florida Everglades is beginning to indicate ecological responses to restored hydrologic regimes (Sullivan et al. 2014). Hydrologic restoration in Everglades wetlands is increasing hydrologic connectivity between areas by redistributing water sources, removing levees, and plugging or filling canals (United Stated Army Corp of Engineers [USACE] 2005). A new large-scale restoration project directly upstream of the sites in this study, the Central Everglades Planning Project, is likely to increase hydrologic connectivity between the downstream wetlands in ENP and upstream freshwater sources in WCA-3A. Our comprehensive, long-term assessment of nutrient concentrations among ecosystem compartments in freshwater marshes found enhanced hydroperiod and nutrient removal in downstream wetlands. In addition, multiple hydrologic (i.e. droughts, floods, hurricanes) and non-hydrologic extreme events (e.g. fires, freezes) in the past decade have caused episodic increases in surface water nutrient concentrations throughout the landscape (Davis et al. 2018). South Florida experienced a massive drought in wet season 2015 followed by a strong El Niño period that caused extensive flooding and discharge of upstream flow into downstream wetlands. Then in September 2017, Hurricane Irma further increased water flows from upstream wetlands into downstream wetlands, resulting in increases in hydroperiod. Enhanced freshwater restoration is increasing water levels throughout the Everglades (Dessu et al. 2018), and our results suggest that continued increases in water depth and hydroperiod and in freshwater marshes downstream of the L-29 Canal will likely cause detectable changes in plant and benthic organic matter composition and biogeochemistry into the future.

Restoration of Water Depth and Hydroperiod as Ecosystem Control Points

Effective wetland restoration must balance the hydroperiod and water depth as well as the timing of both for meeting the ecological needs of dominant native plant species (Zedler 2000). Prolonged inundation and drought caused by climate change (both observed in NESRS in 2015) and freshwater management (e.g. onset of MWD incremental tests) can alter the carbon balance of freshwater marshes by transforming them from sinks of atmospheric carbon to terrestrial sources of carbon (Malone et al. 2013; Wilson et al. 2018; Zhao et al. 2019). Although wetlands can adapt to water management and climate changes, changes in freshwater flows that affect the seasonality and duration of hydroperiod as well as water depth can lead to changes in plant biomass. For example, sawgrass aboveground biomass and productivity have declined in freshwater marshes of Taylor Slough in ENP where increased water depths and hydroperiods have yielded a transition from sawgrass to spikerush (*Eleocharis cellulosa*) (Troxler et al. 2014). Shifts in wetland foundation species can occur when long-term changes in water depth and hydroperiod can cause soil and vegetation state changes that are stabilizing (Larsen et al. 2007; Zweig & Kitchens 2009; Newman et al. 2017; Marazzi et al. 2019).

Wetland ecosystems contain unique species adapted to flooding, drought, erosion, and deposition, and hydroperiod is a principle control point of wetland biogeochemical cycling and organic matter processing (Malone et al. 2013; Bernhardt et al. 2017; Zhao et al. 2019). Whether or not or how restoration of hydroperiod interacts to increase or decrease nutrient storage and organic matter accrual is critical to the long-term trajectory of wetland ecosystems (Odum 1969; Kominoski et al. 2018). As many ecosystems are increasingly exposed to multiple stressors, how restored ecosystems respond to climate-driven extreme events, disturbance legacies, and other drivers of environmental change should inform effective management of organic matter and nutrients in rapidly changing ecosystems worldwide. Wetland restoration that increases freshwater hydroperiod can alter nutrient cycling from local to landscape scales, likely influenced by legacies of nutrient loading. Therefore, restoration of wetlands must balance water depth and hydroperiod in upstream wetlands with mitigation of excess nutrient loading from legacy and modern sources. It is evident that episodic hydrologic disturbances (e.g. floods, droughts, etc.) and the MWD incremental tests have increased upstream canal stage that increased hydroperiod in the NESRS landscape. Continued long-term research during restoration is critical to quantifying integrated ecosystem responses to changing environmental conditions as well as differential constraints of restoration among ecosystem components due to disturbance legacies.

Wetlands are recognized as highly productive and vulnerable ecosystems worldwide (Keddy et al. 2009). Due to their high productivity, fertile soil, and importance for provision of water, many wetlands have been extensively used by humans, resulting in worldwide degradation, loss, and modification of wetlands (Reis et al. 2017). The vast decline in wetlands due to human uses and climate change has led to global efforts for wetland restoration (Gardner et al. 2015). Effective and proven restoration strategies and efforts are needed to rehabilitate degraded ecosystems and their functions, given rapid global changes that are transforming ecosystem services that support life on the planet.

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