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RESEARCH ARTICLE

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Key Points:

- Downstream nitrate & ammonium concentrations were seasonally responsive to flow, while total phosphorus & orthophosphate were chemostatic
- Nutrient concentrations were strongly related to watershed inputs, and less consistently to regulatory releases
- Restoring downstream water quality will require reservoir and watershed management, and actions that go beyond modified release scheduling

Supporting Information:

Supporting Information may be found in the online version of this article.

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Downstream Nutrient Concentrations Depend on Watershed Inputs More Than Reservoir Releases in a Highly Engineered Watershed

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Abstract In this study, we characterized the impact of regulatory water releases relative to watershed inputs on the quality of receiving waters to identify if and how managed releases could be scheduled to mitigate nutrient export and downstream water quality impairment. We specifically investigated freshwater flow partitioning to the Caloosahatchee River and Estuary (CRE) from a large managed lake, Lake Okeechobee, and the CRE's upstream watershed, the C-43 basin, in southwest Florida (USA). A water balance was developed to identify dominant freshwater inflow sources (i.e., Lake Okeechobee vs. watershed inputs) over time. From the water balance, analyses of historical trends were performed to detect changes in freshwater inflow contributions to the CRE. Further, seasonal and annual concentration variations and long-term concentration-discharge (C-Q) relationships were analyzed to better understand biogeochemical and hydrological processes in the system in relation to freshwater source. Since 1966, we found the duration and magnitude of flows from the C-43 basin were higher than those from Lake Okeechobee releases. However, recent increases in the annual water volume and proportion of inflow coming from Lake Okeechobee to the CRE were observed. The C-Q analysis revealed that nitrate and ammonium concentrations in the CRE were responsive to changes in discharge, while total phosphorus and orthophosphate concentrations were chemostatic. While modifications to the Lake Okeechobee operation schedule could potentially mitigate downstream inorganic nitrogen loading, this potential is limited by complex, seasonal C-Q relationships and confounding effects from surrounding watersheds.

Plain Language Summary Water levels in large lakes at risk of flooding into surrounding areas are controlled using engineered structures like dams. To ensure water levels do not overtop a lake's banks, water is released from control structures and then flows into downstream waterways like rivers and estuaries. When a managed lake has water quality challenges, such as excess nutrient concentrations or harmful algal blooms, water releases may affect the quality of downstream waters, but determining the role of released waters on downstream water quality is challenging. In this study, we analyzed nitrogen and phosphorus concentrations in the Caloosahatchee River and Estuary (CRE), a waterway that receives released water from Lake Okeechobee, a large managed lake, to understand whether there were relationships between Lake Okeechobee water releases and nutrient concentrations in the CRE. We found that released water had an impact on downstream water quality, but that water runoff from the surrounding land area had a greater effect. Nitrogen concentrations varied based on the time of year and amount of flowing water, while phosphorus concentrations did not. Therefore, changes to the timing and volume of water releases may not affect downstream phosphorus concentrations, but could potentially improve downstream nitrogen concentrations.

1. Introduction

Human settlement has profoundly altered the natural landscape, increasing environmental pressures on watersheds across the globe. At the same time, demand for freshwater, energy and other resources has increased, driven by the growing needs of diverse sectors, including municipalities, agriculture, and industry (Dahm, 2010; Holland et al., 2015; Vörösmarty et al., 2010). To meet these needs, thousands of reservoirs have been constructed, often by damming and diking natural lakes and rivers (Chen et al., 2016; WCD, 2000).

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Today, there are more than 90,000 dams in the United States (USACE, 2022) and more than 500,000 large dams in the world (Downing et al., 2006).

Management of reservoirs and lakes has greatly modified the quality and quantity of freshwater inflow to downstream waterbodies (Benson, 1981; Cerco & Noel, 2016; Ling et al., 2017; Nilsson et al., 2005), which affect their structure and function (Grill et al., 2019; Lehner et al., 2011; Nilsson et al., 2005; Poff et al., 2007; Wu et al., 2019; Yi et al., 2010). Water quality degradation can be especially pronounced in downstream water bodies receiving large and frequent discharges containing high levels of nutrients and/or pollutants (Liu et al., 2009). Lakes and rivers located in human-dominated landscapes are particularly susceptible to loading from a wide range of nutrients and pollutants from agricultural, industrial, and urban land uses (Huang et al., 2013; Klatt et al., 2003; Motew et al., 2017; Rechcigl, 1997). Pollutant loads can accumulate in these systems, leading to discharges to downstream waters that result in significant water quality impacts, such as harmful algal blooms (Glibert et al., 2009; Paerl et al., 2008; Phlips et al., 2012, 2023). The challenge of managing water quality in water bodies subject to large discharges from developed watersheds is further complicated by the presence of dams, dikes and other water control structures, which alter hydrologic conditions. One of these challenges is the need to determine the extent to which downstream nutrient and pollutant loads are sourced directly from engineered water control structures versus more diffuse watershed inputs. Fortunately, multi-year time series of water quality and hydrology are now available for many aquatic systems across the US and can offer insights on how downstream water quality responds to different flow regimes and sources of water.

Long-term observations can be used to characterize concentration-discharge (C-Q) relationships, which describe a watershed's hydrological behavior and dominant biogeochemical processes (Godsey et al., 2009; Musolff et al., 2021). Depending on the slope of the C-Q relationship, three solute export patterns can be characterized: dilution, mobilization, and chemostasis (Godsey et al., 2009). Several studies have investigated C-Q relationships in forested and agricultural watersheds (Duncan et al., 2017; Godsey et al., 2009; Liu et al., 2022). However, research on C-Q relationships in highly engineered and managed watersheds has been comparatively limited, though relationships between nutrient loads and flows in some human-dominated basins have been investigated (e.g., Basu et al., 2010). Studying C-Q relationships in waters receiving regulatory releases from reservoirs or managed lakes could help to define the extent to which releases are responsible for worsening downstream water quality, as compared to the impacts of diffuse watershed inputs, and potentially inform operation schedules. In particular, the application of C-Q relationships to ecosystems with water control structures could be used to optimize operation schedules such that they improve downstream water quality (or degrade it less). For example, if time periods when nutrient mobilization is likely to occur through water releases were identified, operation schedules could be adjusted to avoid major discharges during these times, and instead prioritize releases when dilution is more likely to occur.

To determine the impact of regulatory water releases relative to watershed inputs on receiving waters and identify how releases could be scheduled to mitigate nutrient export and downstream water quality impairment, we analyzed trends in controlled releases from a large, managed, and eutrophic lake in Florida (Lake Okeechobee) and its downstream waterway (Caloosahatchee River and Estuary, CRE), located in southwest Florida. Our objectives were to: (a) Evaluate how operations schedules impacted downstream waters, (b) quantify the relative contribution of regulatory water releases on total flows in the downstream receiving waterbody, and (c) estimate how nutrient concentrations in receiving waters vary as a function of freshwater source (i.e., regulatory lake releases vs. diffuse watershed inputs to the CRE) across years and seasons. In addition to producing findings that can inform how Lake Okeechobee's operation schedule could be designed to mitigate downstream water quality impacts, the presented approach offers generalizable findings as to how analyses of observational data can provide practical insight for defining environmental flow criteria and lake-reservoir operational schedules.

2. Materials and Methods

2.1. Study Area

Lake Okeechobee is a large (1,890 km^2), shallow (mean depth 2.7 m) lake in South Florida. It is a highly eutrophic lake with substantial internal nutrient loads and recurring intense harmful algal blooms, including of the cyanobacteria *Microcystis aeruginosa*, *Dolichospermum* spp. (formerly *Anabaena*), *Raphidiopsis raciborskii* (formerly *Cylindrospermopsis raciborskii*) (Kramer et al., 2018; Phlips et al., 2020). Although of natural origin, the lake is surrounded by a human-made dike and operated as a reservoir, making it central to the hydrology and

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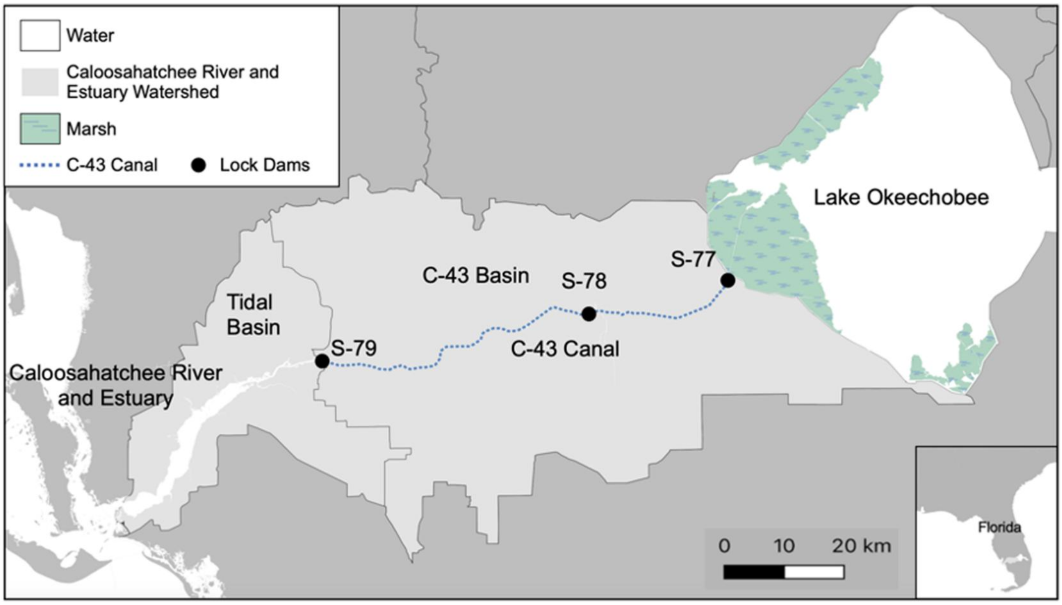

Figure 1. Study area illustrating the Caloosahatchee River and Estuary (CRE) and the S-77, S-78, and S-79 lock and dams. The CRE watershed is composed of the C-43 basin (upstream of S-79) and the tidal basin (downstream of S-79).

water management of the region (SFWMD, 2009). Historically, Lake Okeechobee was the primary source of freshwater to the Everglades, an extensive sawgrass marsh complex that stretched across most of the southern peninsula of Florida. To prevent deadly flooding, as well as facilitate navigation and agriculture, the U.S. Army Corps of Engineers (USACE) constructed over 30 water control structures since the 1930s to manage Lake Okeechobee water levels and a canal system to divert Lake Okeechobee discharges to the east and west coasts of Florida. Over the past 30 years, an average of 38% (±13% SD; range: 11%–59%) of total Lake Okeechobee annual outflows have been artificially discharged to the Caloosahatchee River Estuary (CRE) on Florida's southwest coast (Figure 1); average flows to the St. Lucie and south to the Everglades account for 17% and 45% of Lake Okeechobee discharges, respectively (Zacharias & Kaplan, 2023). While successful in preventing catastrophic floods, controlled water releases from Lake Okeechobee fundamentally transformed the hydrology and ecology of South Florida. Today's Everglades span only 50% of the original area (Sklar et al., 2005), resulting in the loss of significant amounts of water storage on the southern Florida peninsula.

Several Lake Okeechobee operation schedules have been implemented over the past few decades, with the schedules dictating when and how much water is discharged to the CRE and other downstream ecosystems. Since 1978, five operation schedules have been authorized to control floods and meet other demands, with each successive plan increasing in complexity in response to growing concerns over an expanding human population and declining ecosystem health (Table 1) (Julian & Reidenbach, 2023; Tarabih & Arias, 2021). Currently, under the Lake Okeechobee Regulation Schedule (LORS), Lake Okeechobee releases are "pulsed" to the CRE in the dry season on a regular basis. This approach was adopted to mitigate the occurrence of hypersaline conditions in the CRE (Tarabih & Arias, 2021), but it may have the unintended consequence of providing persistent nutrient loads to the estuary.

Three lock and dam structures, referred to as the S-77, S-78, and S-79 structures, are used to release water from Lake Okeechobee to the CRE and maintain water levels in the C-43 canal (Figure 1). Lock S-77 serves as an outlet from Lake Okeechobee, and S-79 is 68 km downstream of S-77 and serves as a salinity and tide barrier at the upstream boundary of the CRE (SFWMD, 2009). The C-43 canal connects S-77–S-79, and receives watershed inputs from the surrounding basin. The S-78 structure was constructed for navigation, irrigation, flood, drought, and regulatory control, and is located between S-77 and S-79 on the C-43 canal. In addition to direct inputs from Lake Okeechobee, the CRE receives surface runoff from a 4,370 km^2 watershed (SFWMD, 2009) that includes the C-43 basin (70% of watershed land area) and the "tidal" basin (30% of watershed land area) (Julian & Osborne, 2018). Lake Okeechobee releases and C-43 watershed inputs both arrive to the CRE via the S-79

Table 1
Authorized Operations Schedules of Lake Okeechobee Since 1978 (Cadavid et al., 2012; Tarabih & Arias, 2021)

Lake Okeechobee operation schedule	Date of implementation	Objectives
1978 Rules	1978	• Maintain water levels between 4.72 and 5.64 m
Run 25	1991	• Maintain water levels between 4.77 and 5.11 m
Water Supply and Environment (WSE)	2000	• Maintain water levels from 4.1 to 5.6 m • Decrease water discharges into the estuaries • Decrease the frequency of littoral zone flooding • Meet water user's demands, while allowing water levels to drop lower than antecedent schedule
Lake Okeechobee Regulation Schedule (LORS) 2008	2008	• Prevent lake level exceedance above 4.88 m • Identify seasonal high-water levels for which water is discharged to prevent saltwater intrusion during the dry season
System Operating Manual (LOSOM)	Plan under final stages of review	• Incorporate flexibility in water management to better balance different needs (e.g., navigational, flood control, preservation of fish and wildlife)

structure, and the tidal basin drains to the CRE downstream of S-79 through a number of small creeks (Figure 1). The primary land use in the C-43 watershed is irrigated agriculture, accounting for 27% of the area, followed by pasture and hay at 23%, and urban land use at 6%, according to the 2019 National Land Cover Database (NLCD) (Dewitz, 2021). In contrast, residential and commercial developments are the predominant land uses in the tidal basin (SFWMD, 2009). Analyses carried out by the South Florida Water Management District (SFWMD) revealed that nutrient loads from the C-43 basin were much higher than those coming from the tidal basin (SFWMD, 2009). However, additional research is needed to separate the effects of C-43 watershed inputs and Lake Okeechobee releases on water quality in the region to better understand the impact of regulatory water releases relative to watershed inputs.

2.2. Flow and Water Chemistry Data

Average daily discharge from the S-77 and S-79 structures were obtained from DBHYDRO, a database maintained by the SFWMD (accessed at: https://my.sfwmd.gov/dbhydroplsql/show_dbkey_info.main_menu). The data set includes daily mean flow observations dating back to 1966, and the period of record analyzed here spanned from January 1966 to August 2022. Daily rainfall observed at S-79 was also retrieved from DBHYDRO from 1965 to 2022. The S-78 data record was not considered in the analysis due to limited records compared to S-79.

Water quality parameters were also accessed via DBHYDRO, specifically for orthophosphate (Ortho-P), total phosphorus (TP), total nitrogen (TN), dissolved phosphorus (DP), nitrate and nitrite (NO_x), and ammonium (NH_4^+) concentrations. Flagged observations that did not meet quality control checks were excluded. For consistency, only surface samples (depth ≤0.5 ft) were considered. Nutrient concentrations were compared against reported Minimum Detection Limits (MDL); when an observation was less than its MDL, the value was replaced with the MDL concentration, and an observation was excluded if no MDL was reported. 2% of NH_4^+ ($n = 13$), 15% of NO_x ($n = 92$), 1% of Ortho-P ($n = 6$), and 1% of TP ($n = 6$) samples were below the MDL. If multiple sample values were reported for the same analyte on the same day, these values were averaged. After screening and cleaning, water quality data were available from 803 sampling events at the S-79 structure. Prior to May 2010, most samples were collected monthly. However, starting in May 2010, most samples were collected approximately weekly, and in 2016, the sampling frequency changed to approximately biweekly. Accordingly, nutrient concentrations prior to May 2010 were excluded from subsequent analysis as data were too scarce. Of the available sampling dates from May 2010 to August 2022 ($n = 605$), NH_4^+, NO_x, Ortho-P, and TP had few missing observations ($n = 20$, 14, 3, and 1, respectively), whereas TN and DP had many more missing values ($n = 215$ and 437, respectively) and were thus excluded from analysis. The final data set included 585 observations of NH_4^+, 591 of NO_x, 602 of Ortho-P, and 604 of TP.

2.3. Water Balance

A daily water balance was developed to identify the dominant source of freshwater inflow to the CRE (i.e., C-43 basin runoff vs. Lake Okeechobee releases). Flow from the C-43 basin was assumed to come via the C-43 canal and was calculated as the difference between S-79 and S-77 discharge ($Q_{C\text{-}43} = Q_{S\text{-}79} - Q_{S\text{-}77}$) for periods when the following criteria were met: (a) Flow at S-77 was positive (i.e., no backflow into the lake); and (b) the difference between S-79 and S-77 flows was positive (i.e., flow was greater at S-79 than S-77). Backflow from S-77 into Lake Okeechobee only occurred for 3% of the period of record. As a simple metric of flow dominance, we calculated the flow ratio between C-43 inputs and total flow at S-79. When this value was greater than or equal to 0.5, the dominant source of flow was from the C-43 watershed; when this ratio was less than 0.5, the dominant flow source to the estuary was from Lake Okeechobee releases. Discharge dominance was analyzed over the overlapping period of record for the S-77 and S-79 stream gauges stations and broken out over three hydro-climatological seasons defined by Julian and Osborne (2018): Dry = November through May; Early Wet = May through July; and Wet = August through October.

2.4. Trend and Concentration-Discharge (C-Q) Analyses

To investigate the hydrological and biogeochemical characteristics of the watersheds, we performed trend and C-Q analyses. To gain a comprehensive understanding of the role of freshwater source on nutrient concentrations in the CRE, seasonal variation within and across years needed to be considered to account for intra- and inter-annual hydrologic dynamics. Therefore, we assessed nutrient concentrations in relation to freshwater source within seasons and years.

The trend analysis was conducted using the rank-based, non-parametric Mann-Kendall test (MK) (Kendall, 1948; Mann, 1945) using the statistical software R (R Core Team, 2020) to test for temporal trends in annual average daily discharge proportion and the annual average daily volume attributed to Lake Okeechobee at the S-79 stream gauge between 1966 and 2022. The non-parametric MK method is less sensitive to outliers than parametric tests and does not require specification as to whether the trend is linear or nonlinear. The Kendall Tau statistic, which varies from −1 to 1, measures the monotonicity of the slope, with +1 being a consistently increasing trend, and −1 being a consistently decreasing trend.

Additionally, we conducted a C-Q analysis to assess the relationship between the concentrations of TP, Ortho-P, NH_4^+, and NO_x and the discharge rate at S-79 throughout the entire study period, as well as on a monthly basis. All C and Q data were log-transformed, and the linear regression slope of the log-log relationship was computed. The slope (β) of the log(C)-log(Q) regression was considered significantly different from zero at $\alpha = 0.05$. A slope ranging from −0.1 to 0.1 is generally considered to correspond to chemostatic export behavior, while slopes >0.1 correspond to mobilization and those <−0.1 correspond to dilution (Godsey et al., 2009; Herndon et al., 2015).

3. Results

3.1. Partitioning Flows to the Caloosahatchee River Estuary

Daily discharge into the CRE at the S-79 structure was highly variable over the 57-year period, with large spikes in discharge corresponding to wet years and hurricanes (e.g., Hurricane Irma in 2017) and several drought years characterized by extremely low flows (less than 0.30 m^3/s). The daily discharge median was 25.4 m^3/s (10th percentile = 0.28, 90th percentile = 161 m^3/s).

Water releases from Lake Okeechobee were the dominant surface water source to the CRE for 49% of days in the period of record. Freshwater inputs from the lake were generally dominant from October through May, while runoff from the C-43 basin was usually dominant from June through September (Figure 2). However, these seasonal observations were not consistent throughout the period of record. Monthly (Figure 2b) and seasonal (Figure 2c) long-term flow observations revealed that, from the 1970s until the 2000s, annual discharge to the CRE came mainly from the C-43 basin; prior to 2003, Lake Okeechobee was the dominant source of flow to S-79 for a median of 3 months per year, increasing to 7 months per year from 2003 onwards (Figure 3a).

We found a significant increasing trend in the proportion of annual average daily discharge to the CRE coming from Lake Okeechobee (tau = 0.233, $p = 0.01$) as well as in the annual volume attributable to Lake Okeechobee at the S-79 station (tau = 0.206, $p = 0.02$) (Figures 3b and 3c). The changes in source partitioning appeared to

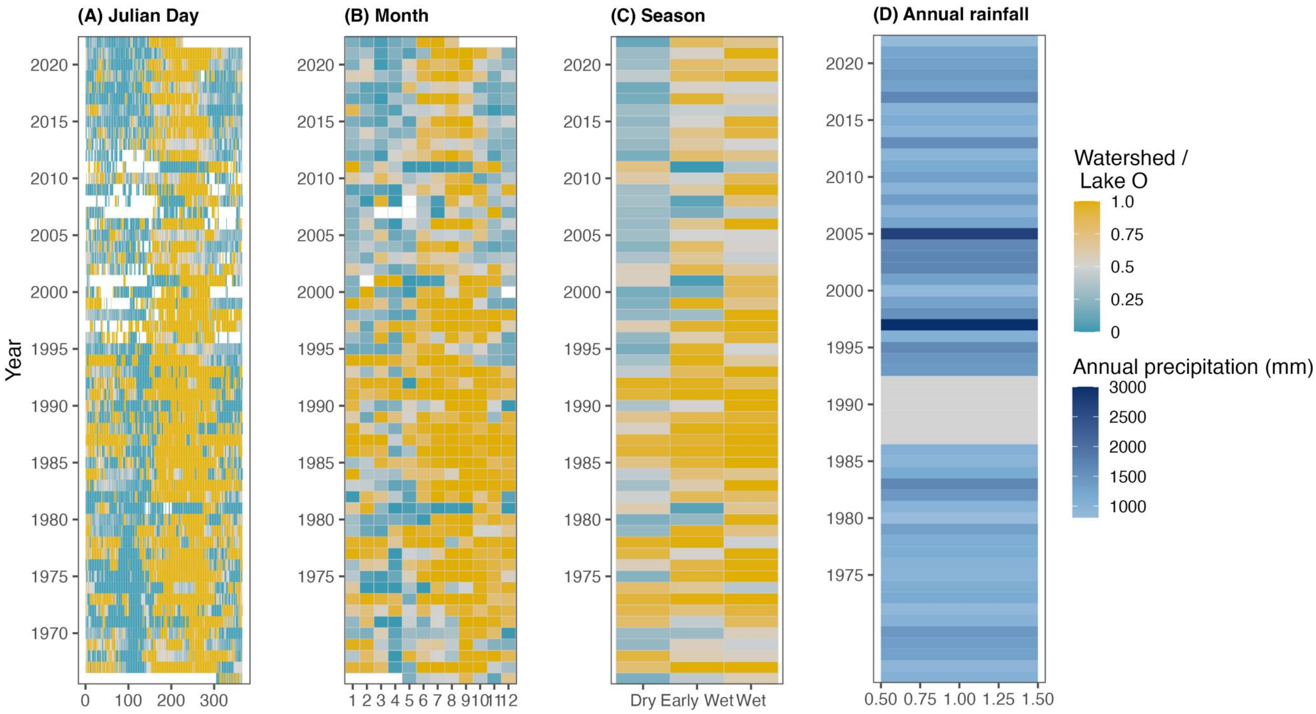

Figure 2. S-79 freshwater discharge heatmap for the Julian day (a), month (b), and season (c), and annual precipitation at S-79 (d). The color ramp in panels (a)–(c) corresponds to the proportion of S-79 discharge attributed to watershed inputs relative to Lake Okeechobee (Lake O) water releases. For values greater than 0.5 (i.e., more yellow), the dominant source of flow comes from the watershed (C-43 basin) and for values less than 0.5 (i.e., more blue), the dominant source of flow comes from Lake Okeechobee. From 1987 to 1992, over 30% of the daily precipitation data were missing, therefore, annual rainfall was reported as NA for these years (d).

coincide with the Lake Okeechobee regulatory management change from Run25 to WSE (Table 1), the adoption of which resulted in regulatory releases occurring more frequently (Figure 2). However, S-79 hydrographs from individual years (Figure 4) show that the duration and magnitude of flows from the C-43 basin were generally higher than those from Lake Okeechobee releases. While Lake Okeechobee was more frequently the dominant flow source on a daily basis (i.e., Lake Okeechobee was the dominant freshwater source to the CRE on most days in the period of record), the C-43 basin was the primary source of freshwater inflow to the CRE *by volume* for 41 of 57 years in the period of record (Figure 3c). Of note, although C-43 watershed inputs dominated the total freshwater flow volumes to the CRE, most freshwater flow from C-43 occurred during the wet season (Figure 2c).

3.2. Nutrient Responses in Relation to Dominant Water Source

For TP and Ortho-P, similar monthly patterns were observed, with the lowest concentrations observed from November to May (dry season), which corresponded to periods when Lake Okeechobee was the dominant source of inflow. Higher concentrations were observed for the rest of the year (Figure 5), when the C-43 basin was the primary source of freshwater inflow. For NO_x, higher concentrations were observed in November (median of 0.32 mg/L) and the lowest concentrations were observed in May (median of 0.018 mg/L). For NH_4^+, the concentration was consistent over the year (Figure 5).

When considering all data, statistically significant patterns of mobilization were observed for all water quality parameters, except TP, for which chemostasis was observed ($\beta_{TP} = 0.09$). The strongest effects were observed for NH_4^+ ($\beta_{NH_4^+} = 0.37$) and NO_x ($\beta_{NO_x} = 0.25$), while the effects were relatively weak for Ortho-P ($\beta_{Ortho\text{-}P} = 0.11$, i.e., just above the threshold for chemostasis) (Figure 6). These results indicate there was little influence of discharge on variation in TP and Ortho-P concentrations but a stronger influence on NH_4^+ and NO_x concentrations. In particular, NH_4^+ exhibited mobilization behavior for all the months of the year except from March to May, for which insignificant relationships were found (Figure 7). The dominant source of inflow does not seem to affect the mobilization pattern of NH_4^+ (Figure 6). Contrary to NH_4^+, NO_x showed both mobilization and dilution behaviors; significant mobilization patterns were observed in February and April to

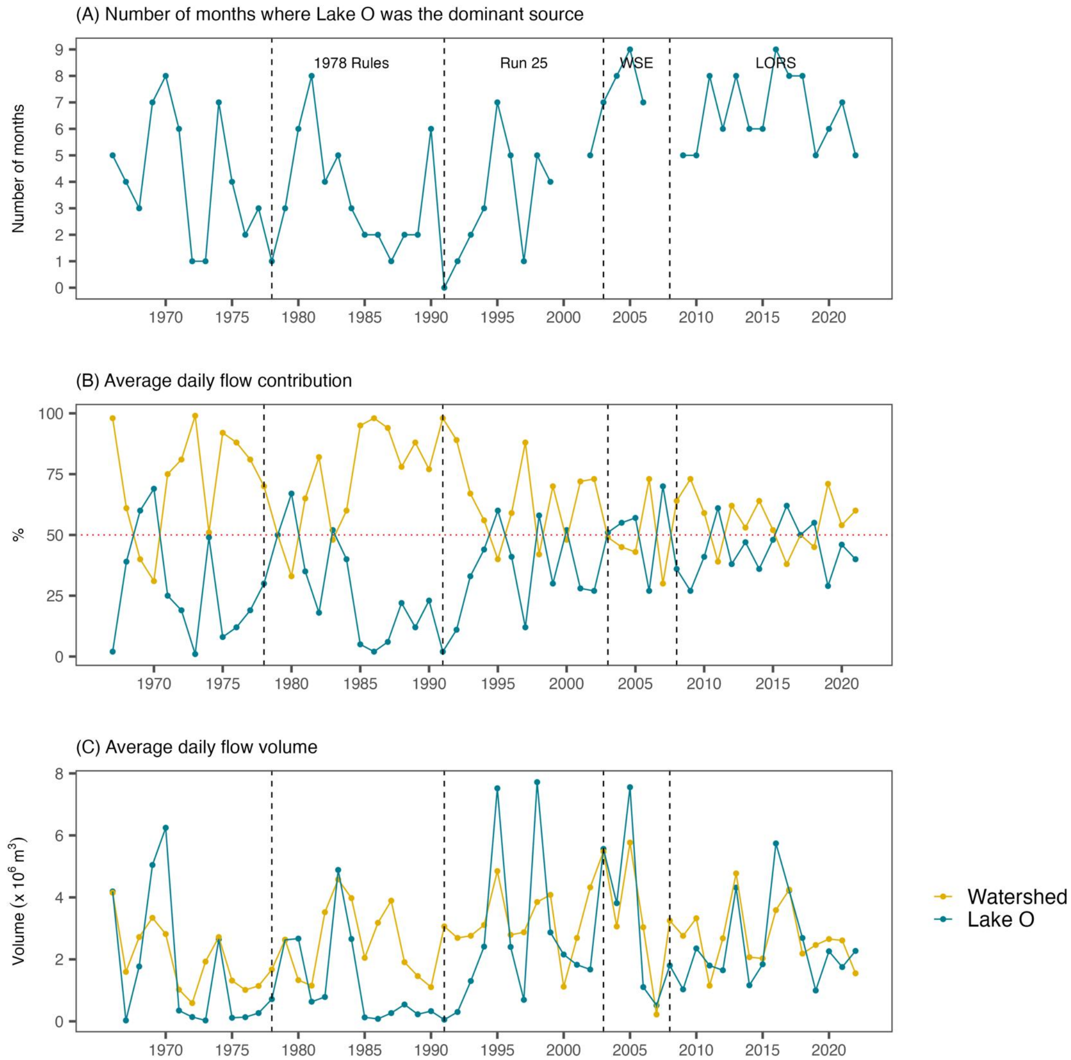

Figure 3. Number of months where Lake Okeechobee (Lake O) was the dominant source at S-79 (a), average daily discharge proportion (%) attributable to Lake Okeechobee (MK test: tau = 0.233, p-value = 0.01) and C-43 watershed at S-79 (b), and average daily volume attributable to Lake Okeechobee (MK test: tau = 0.206, p-value = 0.02) and C-43 watershed at S-79 (c). All values shown on an annual basis. The vertical dashed lines correspond to different Lake Okeechobee operation schedules (Table 1). The horizontal red dotted line at 50% (panel b) is used to differentiate dominant flow source.

July, while significant dilution patterns were observed from September to November (Figure 7). The dominant source of freshwater inflow to the CRE was C-43 basin runoff from June to October and Lake Okeechobee for the rest of the year (Figure 2b). Thus, temporal patterns observed in NO_x mobilization and dilution do not perfectly align with periods of either dominant C-43 basin runoff or Lake Okeechobee releases.

4. Discussion

Designing optimal operating strategies for reservoirs and managed lakes to meet water supply demand and flood prevention needs without impacting downstream water quality is challenging. This study aimed to better understand the impacts of regulatory water releases of a managed lake (Lake Okeechobee) on a downstream estuarine system (the Caloosahatchee River and Estuary; CRE) to identify if releases could be scheduled to mitigate nutrient export and downstream water quality impairment. We quantified the relative contribution of the different freshwater inflow sources (i.e., regulatory water release from the lake vs. surface runoff from the surrounding watershed), and evaluated how nutrient concentrations varied as a function of freshwater source.

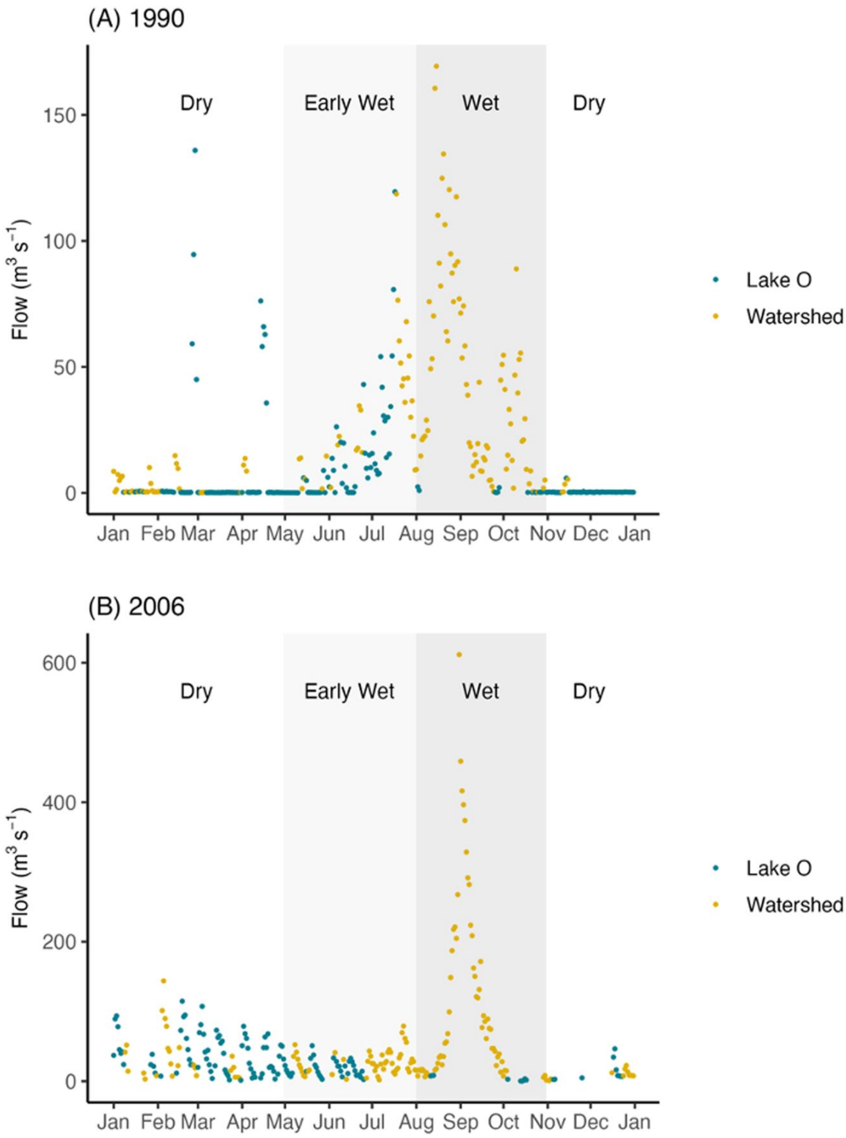

Figure 4. S-79 freshwater discharge for the years 1990 (a) and 2006 (b). Points are colored by the dominant source of freshwater inflow, with yellow corresponding to C-43 basin inputs and blue to Lake Okeechobee (Lake O) water releases. Relatively rainfall-driven discharge patterns were observed for some years (e.g., 1990 corresponding to the 1978 Rules operation schedule) while others had pulsed released flows (e.g., in the dry and early wet seasons of 2006, which corresponded to the WRE operation schedule). The years 1990 and 2006 were selected as illustrative examples of system hydrology across different operation schedules.

While loads are also important to consider, we focused on concentrations given their importance for explaining biological processes such as algal growth (NRC, 2000).

Our study found that C-43 inputs are more strongly related to water quality and quantity in the CRE, particularly in the wet season, than Lake Okeechobee water releases. Prior studies arrived at the same conclusion (Caloosahatchee Estuary Basin Technical Stakeholders, 2012; Julian & Osborne, 2018). Notably, Rumbold and Doering (2020) observed that the majority of the water quality parameters (e.g., NO_x, TP, Secchi disk depth) they studied along the CRE increased significantly in one or more regions of the estuary when the C-43 basin was the dominant source of freshwater. Our results build on the work of others by quantifying how the C-43 basin impacts water quality and quantity in the CRE relative to Lake Okeechobee using C-Q relationships, and providing more specificity on biogeochemical behaviors by characterizing intra-annual variation in mobilization, dilution, and chemostatic behaviors.

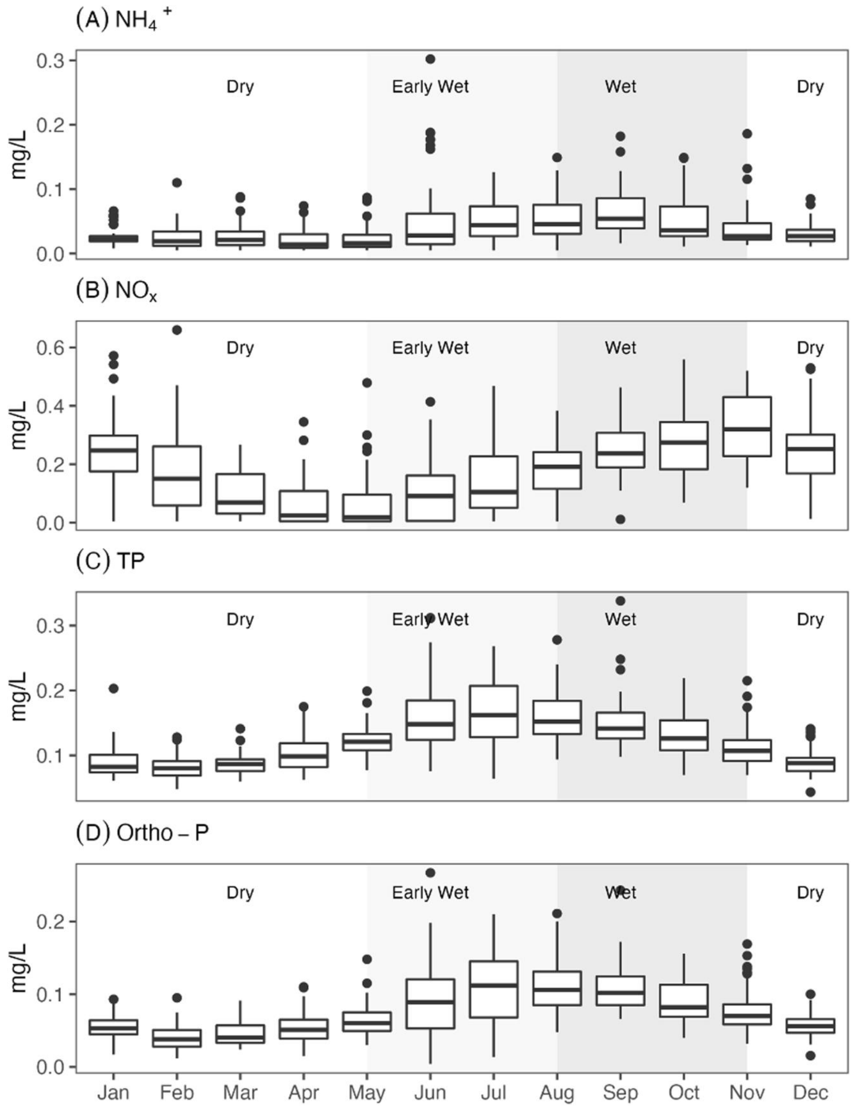

Figure 5. Monthly boxplots of NH_4^+, NO_x, orthophosphate (Ortho-P), and total phosphorus (TP) concentrations at S-79.

The C-43 basin has undergone several modifications over time to facilitate drainage and irrigation in the surrounding agriculturally dominant landscape. Rainfall-driven watershed runoff is a significant contributor to freshwater inflow in the estuary (Julian & Osborne, 2018), notably during the wet season (Figure 2). The combination of artificial drainage and intensive agricultural land use likely explains why C-43 watershed inputs are more strongly related to elevated nutrient concentrations in the CRE. As far as the lesser importance of Lake Okeechobee releases on CRE nutrient concentrations, previous research proposed two potential explanations: (a) nutrients are taken up by plants in extensive marshes located between S-77 and Lake Okeechobee and (b) water residence times are long in Lake Okeechobee, which would allow biological and chemico-physical processes to remove nutrients from the water prior to being discharged to the CRE. Although these mechanisms may help to explain why Lake Okeechobee releases are less consequential in driving elevated nutrient concentrations in the CRE, managed releases still play a major role, and Lake Okeechobee remains a considerable source of nutrients that must be considered in management actions.

Although the C-43 basin was the major contributor of freshwater volume to the CRE over the period of record, Lake Okeechobee releases are highly consequential as a driver of CRE hydrology (Figure 2). Lake Okeechobee operation schedules have evolved over the last decades to improve downstream conditions, prevent flooding, and increase the water supply. These operational changes (Table 1) were associated with an increasing trend in Lake

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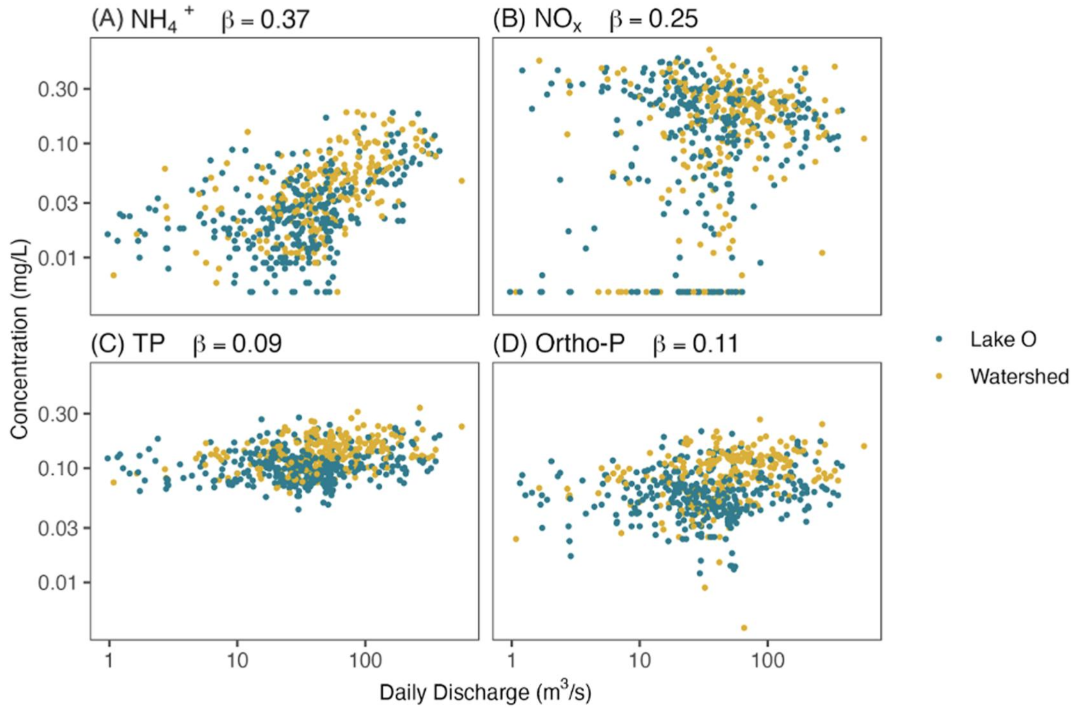

Figure 6. Nutrient concentrations (*y*-axis) and daily discharge at S-79 (*x*-axis) plots using the log-scale. The dominant source of flow (blue for Lake Okeechobee (Lake O, yellow for watershed) was determined through the water balance. Significant mobilization patterns were observed for NH_4^+ and NO_x and chemostatic behaviors were observed for orthophosphate (Ortho-P) and total phosphorus (TP). The slopes (β) of the log(C)–log(Q) regressions were all significant (p-value < 0.05).

Okeechobee water releases discharged to CRE, specifically starting in the late 1990s and early 2000s (Table 1, Figure 2). This increase aligns with prior studies demonstrating how the LORS2008 schedule was responsible for most of the increasing trends in water flows to the CRE (Tarabih & Arias, 2021). Prior to the implementation of LORS2008, flow releases from Lake Okeechobee were more variable, after which they became more frequent and regularly pulsed (e.g., Figure 4). LORS2008 was adopted to mitigate impacts to the downstream estuary by decreasing the maximum lake stage and releasing smaller volumes of water more frequently, as opposed to large volumes of water all at once. These smaller water releases aimed to create a salinity gradient in the estuary that would support sea grasses and oyster reefs, which are particularly vulnerable to periods of prolonged elevated salinity (Doering et al., 2002; Douglass et al., 2020; Volety et al., 2009). Thus, the approach of releasing relatively small volumes of water can provide water quality benefits by mitigating deleterious increases in salinity. However, the LORS2008 modification resulted in greater total water volumes of Lake Okeechobee water being delivered to the CRE.

The recent increasing influence of Lake Okeechobee water releases through more frequent pulse releases during the dry season was also shown to correspond to changes in downstream nutrient responses, but not consistently. Our results revealed that the relationship between nutrient concentrations and discharge in the study area was complex and varied by nutrient type and season. While concentrations of Ortho-P and TP were invariant to discharge, NH_4^+ showed a strong, significant, and positive response to increasing discharge in January, February, and July through November (Figure 7). In contrast, NO_x exhibited both dilution and mobilization behaviors in response to discharge depending on the season. Specifically, during the wet season (September–November), when flows were generally highest and primarily sourced from the C-43 watershed, NO_x showed dilution behavior. On the other hand, during the late dry season (April) and the transition from the early wet to wet season (July and August), when flows were lower and primarily sourced from Lake Okeechobee water releases, NO_x showed mobilization behavior (Figure 7). Observing both dilution and mobilization patterns of NO_x in the same system is in line with findings from prior research, which have reported the coexistence of these patterns in various watershed settings (Knapp et al., 2020; Moatar et al., 2017). For example, Knapp et al. (2020) observed dilution behavior during wetter conditions and mobilization behavior during drier conditions.

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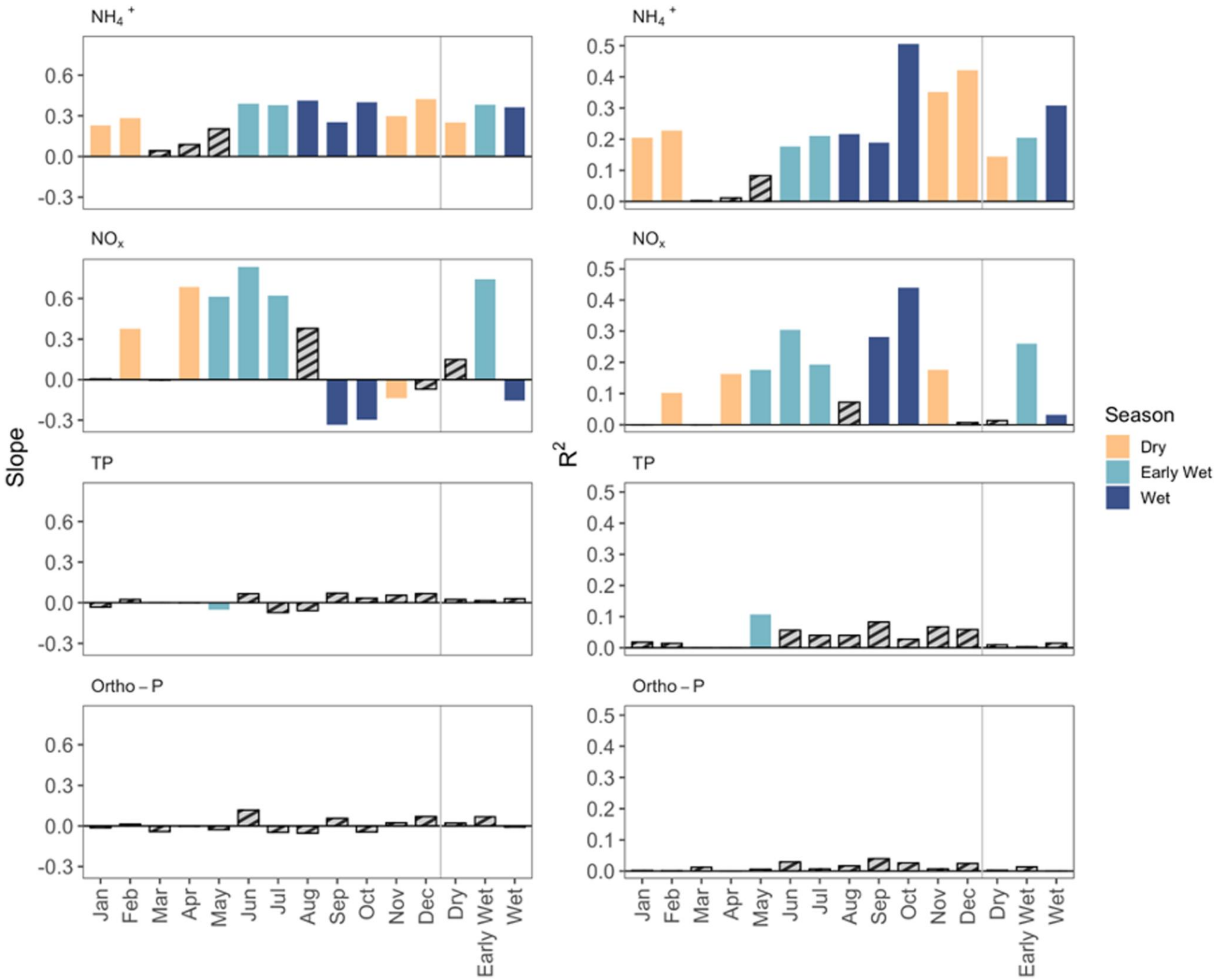

Figure 7. Slope (left column) and coefficient of determination (R^2; right column) from the log(C)–log(Q) regression models for each nutrient species across months and seasons. Bars are filled by the season they correspond to; bars shown in gray with hatch marks were not significantly different from zero.

The complex and dynamic relationships observed in NO_x transport and delivery can be attributed to various driving factors, including land-use type (e.g., agriculture, urban) (Fazekas et al., 2020), hydrological characteristics (e.g., water flows, rainfall) (Anderson et al., 1997; Jones et al., 2018), and biological processes (e.g., nutrient removal or transformation by aquatic organisms) (Birgand et al., 2007). In the CRE, the observed NO_x mobilization pattern may be largely attributable to agricultural operations. C-43 watershed inputs are largely sourced from agricultural lands (SFWMD, 2009), and could be delivering nutrients generated through fertilizer or manure application, explaining why high NO_x concentrations were observed during the months dominated by C-43 inputs. Several studies have found positive relationships between NO_3^- and the proportion of arable lands in a watershed (Minaudo et al., 2019; Moatar et al., 2017). Due to the lack of publicly available data on nutrient application, agricultural practices were not directly studied here, but greater understanding of the timing and type of nutrient application in the C-43 basin would facilitate the development of specific and targeted strategies for mitigating nutrient export to the downstream estuary. Furthermore, water residence time can also partially explain the observed mobilization pattern of NO_x. Lower flows can result in longer water residence time and increased contact time with the streambed surface, favoring NO_3^- uptake by denitrifying microorganisms (Birgand et al., 2007; Peterson et al., 2001), which could result in lower concentrations during low flow conditions. In contrast, when flow increases, especially from the C-43 basin, residence time and the potential for denitrification decrease, likely resulting in higher concentrations.

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On the other hand, groundwater input may also partially explain the NO_x dilution patterns observed in the CRE in September through November. The hydraulic conductivity of the unconfined aquifer in Lee County, where the CRE is located, is high (Scott & Missimer, 2001), and submarine groundwater inputs to the CRE are substantial (Charette et al., 2013). Hence, groundwater might account for the observed dilution pattern by contributing water with lower nitrate concentrations than surface water during baseflow conditions (Rose et al., 2018). Further, riparian and biogeochemical processes occurring along the western edge of Lake Okeechobee, which is composed of a large wetland marsh area (Figure 1), can filter water before it leaves the lake and therefore might result in lower NO_x concentrations in Lake Okeechobee releases (Doering & Chamberlain, 1999). Previous research has posited that biogeochemical processes, including nitrate uptake and denitrification within streams or riparian zones, exert a more substantial relative impact on nitrate export during low-magnitude events (Moatar et al., 2017).

Overall, our results indicate that water releases from Lake Okeechobee could be scheduled to potentially mitigate downstream nitrogen loading, but that modified scheduling may have little impact on downstream phosphorus concentrations. In particular, releases could be scheduled when dilution of NO_x, rather than mobilization, is more likely to happen (i.e., September–November), or when the response of NH_4^+ is likely to be invariant as opposed to strongly positive (i.e., January, February, May through December). Unfortunately, these time periods do not overlap, demonstrating the complexity of establishing a schedule that mitigates all forms of downstream nutrient loading. The largely chemostatic behavior of TP and Ortho-P relative to discharge indicates that the Lake Okeechobee operation schedule may not be capable of being revised to appreciably impact downstream phosphorus concentrations in the CRE. This is in part related to the large legacy load of phosphorus in the lake (Reddy et al., 2011), which is reflected in the results of nutrient bioassay experiments, which show that nitrogen is the most commonly limiting nutrient for phytoplankton growth rates in the lake (Aldridge et al., 1995).

The relatively greater ability to influence nitrogen, as opposed to phosphorus, concentrations as a function of Lake Okeechobee operation scheduling could have nuanced repercussions for mitigating downstream water quality impacts, particularly harmful algal blooms (HABs). Previous studies report that the CRE can transition between nitrogen and phosphorus limitation in the freshwater portion of the system, while nitrogen limitation predominates in the saline regions of the CRE and nearshore Gulf of Mexico (Doering et al., 2006; Phlips et al., 2023). More specifically, nutrient loading to the CRE can affect HABs by: (a) driving the formation of autochthonous blooms within the estuary, and (b) enhancing nearshore red tides of toxic dinoflagellates, specifically through nitrogen loading (Medina et al., 2020, 2022; Phlips et al., 2023). In the latter scenario, the dominant red tide species along the southwest FL coast is the toxic dinoflagellate *Karenia brevis* (Heil et al., 2014a; Steidinger, 2009; Vargo, 2009). *K. brevis* is mixotrophic, and can take advantage of a wide range of nitrogen sources, including soluble inorganic and organic forms of nitrogen (Heil et al., 2014b), as well as particulate organic nitrogen through the direct phagotrophic consumption of pico/nanoplankton (Glibert et al., 2009). Several studies have observed the positive effect between nitrogen-levels in the CRE and the intensity of red tides (Medina et al., 2020, 2022; Phlips et al., 2023). Therefore, our findings indicate that there is some promise to adjust the Lake Okeechobee operation schedule to mitigate *K. brevis* blooms given the relationship between *K. brevis* concentrations in offshore waters and N concentrations from the CRE. However, autochthonous blooms occurring within the CRE, as opposed to in the nearshore environment, may require management of both N and P, depending on specific loading scenarios. The potential for algal blooms in the CRE can also be influenced by water residence time. During periods of sustained high discharge rates into the CRE, water residence times can be too short to support the accumulation of high biomass (Phlips et al., 2023). Therefore, the potential for autochthonous blooms in the CRE can be highest during low to moderate discharge rates.

When considering management actions that go beyond modifying operation schedule, our study's findings highlight how management efforts pursued in the surrounding C-43 basin could have great impact in terms of improving the quality of estuarine receiving waters. Large efforts are currently being undertaken to reduce nutrient loads from the C-43 basin to the CRE. Notably, several Basin Management Action Plans have been developed to implement Total Maximum Daily Loads (TMDLs), and the construction of the C-43 reservoir is currently underway (Caloosahatchee Estuary Basin Technical Stakeholders, 2012; Florida Department of Environmental Protection, 2020, 2022; Taylor et al., 2023). The C-43 reservoir aims to store excess water from the wet season when the CRE has too much freshwater and augment flow during the dry season. Previous C-43 reservoir modeling efforts have demonstrated that high flow releases could be reduced by 80% and nutrient loads by 30% (NRC, 2010). With the new construction of the C-43 reservoir, particular attention should be given to the coordination of the C-43 reservoir and Lake Okeechobee operation schedules so as to not compromise water quality conditions of the downstream estuary. Additionally, future changes to the Lake Okeechobee operation schedule (i.e., LOSOM; Table 1) will allow for further exploration as to how modified release scheduling affects downstream nutrient concentrations, and the upcoming adoption of LOSOM also creates opportunities to coordinate its schedule with that of the C-43 reservoir.

Lastly, though we have focused on the role of C-43 watershed runoff and Lake Okeechobee releases on nutrient concentrations in the CRE, it is important to acknowledge that nutrient availability in the CRE is also influenced by inputs from the watershed directly adjacent to the estuary, also referred to as the "tidal basin" (Brewton et al., 2022; Rumbold & Doering, 2020). The relative balance of inputs from the tidal basin, upstream watershed, and Lake Okeechobee defines the nutrient signature of the CRE. In order to mitigate the effects of nutrient loading in the estuary, it is critical to understand all nutrient sources and their role in driving HABs and other water quality hazards. Furthermore, since the CRE is subject to both tidal mixing and strong river influences, the potential for autochthonous algal blooms is not only related to nutrient availability, but also to hydrologic conditions, such a water residence time (Mathews et al., 2015; Phlips et al., 2023; Sun et al., 2022; Wan et al., 2013). Thus, an understanding of the ways in which Lake Okeechobee water releases affect CRE residence time could also be useful for informing operation scheduling improvements to mitigate downstream water quality impacts. Finally, blooms in the CRE could also be directly introduced through Lake Okeechobee releases instead of growing locally within the CRE (i.e., allochthonous vs. autochthonous) (Reynolds et al., 2023), and understanding the risk of bloom export from Lake Okeechobee will require additional assessment of spatial and temporal dynamics of blooms within the lake itself (Tarabih et al., 2023).

5. Conclusions

To implement lake and reservoir management strategies that preserve downstream ecosystems, managers need to take into account the many nutrient sources to a downstream waterway, while also considering that nutrient contributions from different sources are affected by hydrologic conditions. This study investigated freshwater flow partitioning to the Caloosahatchee River and Estuary from a large managed lake, Lake Okeechobee, and the watershed associated with the river and estuary (i.e., the C-43 basin). The results demonstrate that Lake Okeechobee plays a significant role in defining nutrient concentrations in the CRE, but inputs from the C-43 basin watershed have relatively greater impacts on total water volume and nutrient concentrations. These findings highlight the importance of considering both lake and watershed management in efforts to improve water quality and reduce harmful algal blooms in downstream waters.

Our C-Q analyses revealed that NO_x and NH_4^+ concentrations in the CRE were responsive to changes in discharge from Lake Okeechobee, while TP and Ortho-P concentrations were invariant to changes in discharge. Thus, modifications to the Lake Okeechobee operation schedule would predominantly affect downstream inorganic nitrogen concentrations in the CRE. Our study does not address whether reductions in nitrogen associated with modified discharge scheduling would significantly improve ecological conditions in the estuary, such as less intensive cyanobacteria and *K. brevis* blooms. Additionally, only concentrations, and not loads, were considered in this analysis, therefore some of the conclusions presented here may differ when analyzing loads. Moreover, we only considered nutrient concentrations measured from surface samples (depth $\leq$0.5 ft), and additional insights could be gained by analyzing measurements from samples collected at a range of depths to explore how nutrient concentrations relate to stratification, algal growth, dissolved oxygen concentrations, and the presence of submerged aquatic vegetation.

Overall, we conclude that modified lake release schedules have the potential to affect downstream nutrient concentrations, but the potential is limited by complex C-Q relationships and confounding effects from surrounding watersheds. The approaches and methods used in our study, such as C-Q analysis and the assessment of lake and watershed nutrient sources, could be applied to other freshwater systems confronting similar challenges with nutrient inputs from multiple sources, provided that sufficient data are available. Expanding this research to multiple sites could offer valuable insights into the variability of findings related to engineered water releases, phosphorus and nitrogen levels, and their impact on downstream waters. This broader investigation has the potential to enhance the generalizability of the study's findings across various environmental contexts, thereby contributing to the development of informed management strategies for the preservation of downstream ecosystems.

Conflict of Interest

The authors declare no conflicts of interest relevant to this study.

Data Availability Statement

All data were accessed from DBHYDRO, a publicly available database maintained by the South Florida Water Management District (https://my.sfwmd.gov/dbhydroplsql/). Daily average discharge data were accessed for the S-77 and S-79 structures. Water quality parameters and daily total rainfall were also downloaded at the S-79 site. Analyzed data and a R script including analysis code are included in supplementary material.

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