Water-quality outcomes of wetland restoration depend on hydroperiod rather than restoration strategy

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Abstract: Land managers increasingly use wetland restoration to improve water quality, particularly in cultivated landscapes. In agricultural wetland restoration, managers regularly excavate accumulated sediments eroded from the surrounding landscape to increase water storage capacity, decrease invasive species cover, or improve water quality. However, it is unclear whether the effects of sediment excavation are influenced by wetland hydroperiod. Additionally, we lack data on how long excavation effects persist in restored wetlands. We examined dissolved nutrient concentrations (i.e., NH_4^+, NO_3^-, total dissolved N, soluble reactive P, total dissolved P, and dissolved organic C) as proxies for water quality in 54 restored agricultural wetlands ranging from 1 to 10 y post-restoration in the Prairie Pothole Region of west central Minnesota, USA. In 26 of these wetlands, restoration practitioners restored natural (i.e., either seasonal or semipermanent inundation) hydrological regimes by removing subsurface tile drainage and plugging surface drainage ditches (business-as-usual treatment). In 28 wetlands, practitioners removed accumulated sediment and redeposited it on the surrounding landscape (excavated treatment) prior to restoring hydrology. We found that wetlands in the excavated treatment group initially experienced reduced dissolved P concentrations, but over time P levels increased, particularly in wetlands with shorter hydroperiods. Excavated wetlands had lower NH_4^+ and dissolved organic C concentrations compared with business-as-usual wetlands, but the trend was driven by differences between restoration treatments in semipermanent wetlands. N and P dynamics were almost universally related to hydroperiod, both immediately following restoration and over the ensuing years. We postulate that the effects of hydroperiod are likely related to differences in redox conditions via direct mechanisms (water level fluctuations related to hydroperiod) and indirect mechanisms (development of dense emergent macrophyte communities in seasonal wetlands). In basins with seasonal hydroperiod, inorganic N concentrations decreased over time and inorganic P concentrations increased, suggesting net P mobilization concurrent with growing N limitation. Our results illustrate that hydroperiod regulates the expression of legacy P following wetland restoration, with little long-term effect of sediment removal on water quality outcomes.

Key words: depressional wetland, restoration, nitrogen, phosphorus, carbon, sediment, Prairie Pothole Region

Freshwater ecosystems continue to suffer from N and P nutrient enrichment through human activity, a process known as cultural eutrophication (Smith 2003). Eutrophication is the product of both chronic and episodic nutrient enrichment contributing to the degradation of aquatic ecosystem structure and function (Heisler et al. 2008). Eutrophication has far-reaching effects that have economic and cultural costs (Dodds et al. 2009, Scholte et al. 2016). For example, eutrophication can support the proliferation of harmful algal blooms (Heisler et al. 2008), create hypoxic conditions, and result in concomitant fish kills (Mallin et al. 2006). Eutrophication also affects aquatic food webs (Hall et al. 1999, Liston et al. 2008), alters plant assemblage composition (Woo and Zedler 2002), and increases the risk of harmful parasite loads in wildlife (Johnson and Chase 2004, Smith and Schindler 2009).

N and P enrichment is caused by a combination of increasing nutrient availability (e.g., fertilizers, human and animal wastewater effluent) and the systemic removal of water storage features across the landscape (e.g., wetland drainage, channelization; Mitsch and Day 2006, Harrison et al. 2009, Cheng and Basu 2017). Thus, landscape-level solutions to

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the eutrophication problem require a combination of decreasing nutrient amendments and restoring high-quality water storage features, including floodplains and wetlands.

The North American Prairie Pothole Region (PPR), which stretches from northwest Iowa in the United States to Manitoba and Alberta in Canada (Fig. 1), was characterized by an abundance of depressional wetlands prior to European settlement in the 19th century (Dahl 2014). Throughout the 19th and 20th centuries, 61% of PPR wetlands were drained for cultivation, both to increase the amount of arable land and to reduce the inconvenience of farming around wetlands (Gelso et al. 2008). Most drained PPR wetlands are relatively small (<0.5 ha; Dahl 2014), but large networks of small wetlands increase water residence time on the landscape (Mitsch et al. 2005, Cheng and Basu 2017), capture nutrients (Romero et al. 1999, Salk et al. 2018), and improve down-gradient water quality (Westbrook et al. 2011, Hansen et al. 2018). In the PPR, the presence of undrained depressional wetlands reduces spring discharge in nearby streams by 70% and nutrient export by 85 to 89% for N and P, respectively (Westbrook et al. 2011).

Restoration managers can improve a wetland's ability to capture and retain nutrients by removing accumulated agricultural sediments, a substantial source of internal nutrient loading in restored wetlands (Preston et al. 2013). Managers often use sediment dredging in eutrophic systems burdened by high rates of internal P loading from benthic sediments (Bormans et al. 2016). Core incubation studies have shown that removing nutrient-laden sediments should decrease the rates of internal P loading by as much as 95% in shallow eutrophic systems (Oldenborg and Steinman 2019). Removing accumulated sediment can diminish the pool of labile and mineralizable nutrients (Søndergaard et al. 2001, Gulati and van Donk 2002) and promote conditions favoring permanent N removal by extending the duration of soil saturation (Luo et al. 1997). However, in situ dredging experiments often fail to permanently reduce internal nutrient loading, likely because external nutrient loads remain elevated following manipulation (Liu et al. 2016, Li et al. 2020) and exposed soils may lack the appropriate chemical profile to adsorb dissolved P that is reintroduced from external sources (Liu et al. 2016, Oldenborg and Steinman 2019).

In agricultural wetland restorations, managers use sediment dredging to increase wetland depth and water storage capacity (Galatowitsch and van der Valk 1994). Removing accumulated eroded sediments can lengthen wetland hydroperiod, the number of consecutive days with standing water, by increasing maximum wetland volume (Luo et al. 1997, Tsai et al. 2007), with implications for nutrient cycling. Wetlands with seasonal hydroperiod retain standing water for most of the growing season but often dry out for at least a couple of weeks every year, whereas semipermanent wetlands retain standing water throughout the growing season in most years (Galatowitsch and van der Valk 1994). Prolonged water residence times promote nutrient assimilation and N removal via denitrification (Cheng and Basu 2017, Müller et al. 2021), whereas shorter hydroperiods can promote aerobic organic matter decomposition and nutrient

Figure 1. North American Prairie Pothole Region (shaded gray) within west central Minnesota, USA (inset). Each dot represents 1 or more wetlands.

mineralization (Richardson and Simpson 2011, Bünemann 2015). However, short periods of water drawdown that oxygenate soils can stimulate coupled nitrification–denitrification resulting in net N removal (Groffman et al. 2009). Competing pathways for N and P mineralization and removal make it difficult to predict how small changes in hydroperiod following sediment removal will affect dissolved nutrient availability.

Few published studies have considered the form and concentration of dissolved nutrients in restored prairie pothole wetlands (but see Detenbeck et al. 2002, Westbrook et al. 2011, Skopec and Evelsizer 2018) much less the effect of sediment removal as a restoration strategy. Studies conducted outside of the PPR suggest that improvements in water quality following sediment excavation may be short lived, particularly in the absence of substantial changes in nutrient application in the surrounding watershed (Liu et al. 2016).

In this study, we compared nutrient dynamics in agricultural wetlands located in the PPR that were restored by either re-establishing hydrology alone (business as usual [BAU]) or excavating accumulated eroded sediments (excavation [EXC]) prior to restoring hydrology (Fig. 2). Our objective was to determine whether restoration strategy (sediment removal) and wetland hydroperiod influenced water column dissolved nutrient dynamics over time (Fig. 2). We hypothesized that sediment removal would decrease dissolved N and P concentrations by removing nutrient enriched sediments. We also hypothesized that longer wetland hydroperiod would reduce dissolved N and P concentrations in the water column because longer water residence allows more time nutrient assimilation and deposition, and denitrification.

METHODS

Study design and site description

We used a series of experimentally restored wetlands to understand how alternative restoration strategies influence water quality outcomes over time. We observed spring dissolved nutrient concentrations over 4 consecutive y in 54 depressional prairie pothole wetlands with varying restoration strategy, hydroperiod, and time since restoration. We assessed the effects of restoration strategy, hydroperiod, time since restoration, and 2-way interactions between these variables using mixed effects models with site as a random intercept to account for repeated measures. Study wetlands were located in the PPR of west central Minnesota (Fig. 1). Wetlands were restored between 2009 and 2016 by the United States Fish and Wildlife Service in partnership with private landowners (see Appendix S1). Prior to restoration, wetlands and surrounding uplands were drained by subsurface tile or drainage ditches and were actively cultivated in row-crop agriculture. We noted additional land-use

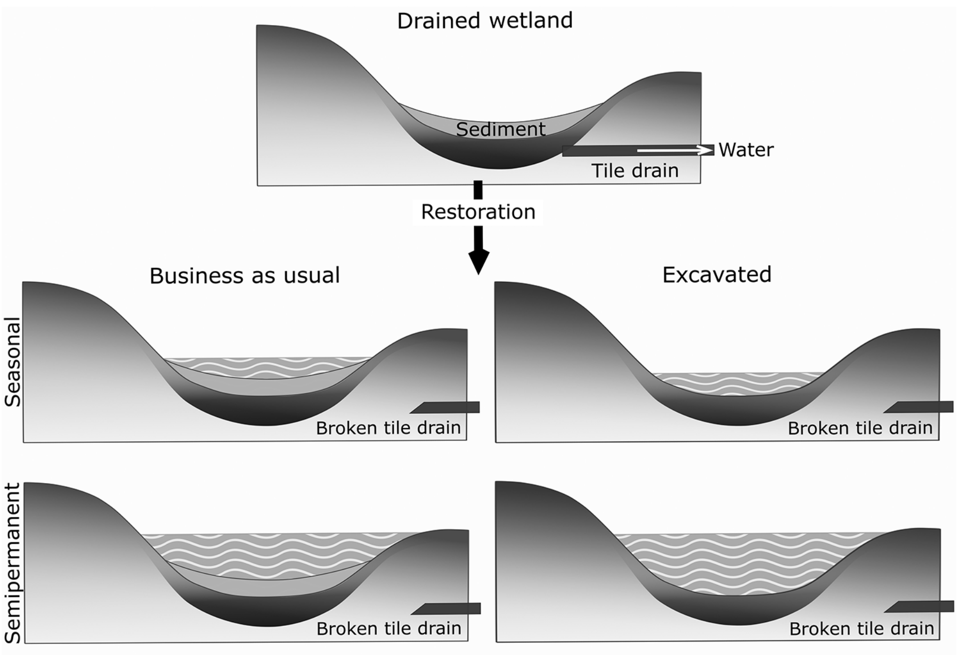

Figure 2. Study design conceptual diagram. Drained and cultivated wetlands accumulate eroded sediment from the surrounding landscape. Wetland restoration always included plugging surface drainage ditches and breaking subsurface tile drains to restore water to the wetland. In ½ of the restored wetlands, sediment was excavated and returned to the surrounding landscape (excavated), while in other wetlands sediment remained in the wetted portion of the basin (business as usual). Some wetlands had relatively permanent pools of standing water and submerged macrophytes (semipermanent hydroperiod), while others dried out for a few weeks annually (seasonal hydroperiod).

history information whenever it was made available by landowners (Table S1), including the presence of livestock. Property owners often elected to enroll the surrounding uplands into the Conservation Reserve Program at the same time as the restoration, but in some cases portions of the watershed continued to be actively cultivated throughout the study. The Conservation Reserve Program is a federally funded land-retirement program designed to improve soil and water health by restoring native vegetation on retired agricultural land. Landowners are financially compensated for enrolling land in the program for an extended period of time (10–15 y), with the potential for re-enrollment at the end of the contract (Stubbs 2014). Watersheds of ½ of the sites ($n = 23$) retained some contemporary agriculture; among those watersheds, cultivation was usually a minor component of overall land use (mean = 24 ± 20% SD). Three watersheds contained at least 50% cultivation, animal confinement, or impervious surface cover. Among the most heavily impacted watersheds, only 1 received runoff directly from row-crop agriculture via a drainage ditch. All other watersheds containing substantial contemporary agriculture maintained a minimum grassland buffer of no less than 24 m between cultivation and the wetland.

We surveyed 26 BAU and 28 EXC wetlands ($n = 54$) between 2016 and 2019 (Fig. 2). Study wetlands were small, averaging 0.6 ha in area (range = 0.06–2.3) and were often in small watersheds averaging 11.4 ha (range = 0.3–91.9) with a mean watershed to wetland area ratio of 30.7 (median = 8.0). We characterized hydroperiod as seasonal ($n = 38$; 15 BAU, 23 EXC) or semipermanent ($n = 16$; 11 BAU, 5 EXC; Fig. 2) based on water retention throughout the growing season (Cowardin and Golet 1995) and the development and persistence of distinct vegetative communities (Stewart and Kantrud 1971). Before formally assigning a hydroperiod, we observed both variables during multiple visits over the course of the growing season during each year. Prior to data analysis, we examined differences in excavation depth between semipermanent wetlands (mean = 48.8 ± 25.1 cm SD) and seasonal wetlands (mean = 33.0 ± 26.9 cm SD) using analysis of variance (ANOVA, $p = 0.24$). Preliminary, descriptive statistics were performed using ANOVA in the statistical software R (version 4.0.5; R Project for Statistical Computing, Vienna, Austria). We defined wetland age following restoration as the difference between the sampling year and the restoration year.

In autumn of 2018 we identified 8 reference wetlands with no known history of drainage, though some wetlands had constructed spillways to minimize flooding beyond a specific elevation. We confirmed that wetlands had not been drained by inspecting digitally archived aerial imagery dating as far back as 1939 (University of Minnesota, Historical Aerial Photographs; https://apps.lib.umn.edu/mhapo/). Reference wetlands ranged in size from 0.4 to 5.1 ha (mean = 1.5 ± 1.5 SD) and were larger than restored wetlands (mean = 0.6 ± 0.4 ha SD). Watershed area was similar for reference wetlands (mean = 9.3 ± 7.3 ha SD) and restored wetlands (mean = 11.4 ± 21.5 ha SD) ($p = 0.78$). Cultivated land use in the watershed was higher in reference wetlands ($n = 6$, median = 68.5%, mean 47.9 ± 39.0% SD) than in the restored wetlands ($n = 23$, median = 0%, mean = 10.2 ± 17.6% SD; $p < 0.001$). We compared results from restored wetlands with results from reference wetlands as an indicator of deviation from the natural state. However, we recognize that many reference wetlands may have remained undrained over the last century because of attributes that made them distinct from wetlands that were drained, such as greater depth, persistent upwelling of groundwater, or inaccessibility.

Sample collection and chemical analysis

We processed 888 water samples collected between 2016 and 2019. In 2016, we collected surface water samples between June 29 and August 4. From 2017 to 2019, we collected annual surface water samples between May and July, sampling each site at least once/y, though some wetlands were opportunistically sampled more than once/y. We collected samples during daylight h between 07:00 and 19:00. On each sampling date, we collected samples from 3 points evenly spaced along a longitudinal transect that intercepted shallow and deep-water habitats within each wetland. We filtered water in the field with pre-ashed 25-mm glass fiber filters (0.7-μm pore size; Whatman, Maidstone, United Kingdom) and stored samples frozen in acid washed 60-mL high-density polyethylene bottles. We dried filters at 60°C for 48 h and stored them in individual containers until particulate N and P analysis.

We measured dissolved inorganic nutrients at the St Croix Watershed Research Station and Science Museum of Minnesota in St Croix, Minnesota, USA, on a SmartChem 170 discrete analyzer (AMS Alliance, Westborough, Massachusetts) with the following methods; NH_4-N (5 μg/L detection limit) by the phenol hypochlorite method (APHA 1998), NO_3-N (10 μg/L detection limit) by the cadmium reduction method (APHA 1992a), and soluble reactive P (SRP; 3 μg/L detection limit) by the ascorbic acid method (Murphy and Riley 1962). When sample concentrations fell below the method detection limit and >0 we assigned a concentration of ½ the method detection limit (Smith 1991). We measured total dissolved N (TDN) and dissolved organic C (DOC) using combustion-infrared and combustion-chemiluminescence methods on a Shimadzu TOC-L analyzer equipped with a chemiluminescence detector (TNM-L unit; Shimadzu, Kyoto, Japan) (APHA 2005, ASTM 2008). We measured total dissolved P (TDP) from water samples and particulate P from preserved water filters using persulfate digestion followed by the ascorbic acid method for colorimetric analysis (Murphy and Riley 1962, APHA 1992b). From 2017 to 2018, we measured particulate N from filters using a Costech ECS 4010 CHNSO Analyzer (Costech Analytical Technologies Inc, Valencia, California).

We calculated dissolved inorganic N (DIN) as the sum of NH_4-N and NO_3-N. We calculated dissolved organic N (DON) and dissolved organic P (DOP) as the difference between the total dissolved and the inorganic fractions. Total N and total P were calculated as the sum of the total dissolved and particulate nutrient pools. We also calculated the molar DOC:DON ratios and molar N:P ratios for the dissolved inorganic, dissolved organic, total dissolved, particulate, and total nutrient pools.

Assessing effects of restoration, hydroperiod, and time on N and P

We used linear mixed-effects models to assess if water column nutrient availability was associated with restoration treatment (BAU and EXC), hydroperiod (seasonal and semipermanent), and age since restoration (1–9 y). We also included fixed effects to account for the interactions between treatment and hydroperiod, treatment and wetland age, and hydroperiod and wetland age. To control for repeated measurements at each wetland and inherent interannual variability, our models included wetland-specific site identifiers and sampling year (e.g., 2016, 2017, 2018, 2019) as random effects.

Prior to analysis, we identified and truncated outliers to the 99th percentile, using the *OutlierDetection* package (version 0.15; Tiwari and Kashikar 2019) in R because it selects outliers based on consensus across multiple algorithms. We limited outlier detection to dissolved N species because of noise from transient N pulses following storm events, particularly at discrete inlets from agricultural drainage ditches. To assess the influence of elevated NO_3-N concentrations in a wetland receiving water from an agricultural drainage ditch (site FF.080; Table S1) on overall model results, we repeated DIN and NO_3-N analyses after removing samples taken near the wetland inlet, where NO_3-N was highest and reported these results. Whenever appropriate, we log transformed response variables to meet model assumptions of homogeneous residual error (Tables 1, 2). We included a quadratic term for wetland age when nonlinear relationships were visually apparent and improved model fit (ANOVA, critical P $\alpha = 0.05$). We performed all statistical analysis in R using the *lme4* (version 1.1-31; Bates et al. 2020) and *lmerTest* (version 3.1-3; Kuznetsova et al. 2020) packages with an α of 0.05. We evaluated interactions between fixed effects with Tukey's honestly significant difference post hoc test using the *emmeans* package (version 1.8.2; Lenth et al. 2020) in R.

RESULTS

Major nutrient pools

Dissolved nutrients dominated water column N and P pools, but the particulate nutrient fraction represented 22% of total N and 35% of total P in the water column. Particulate N and P concentrations did not vary substantially between wetlands with different restoration strategies or hydroperiods (Table 1, Figs S1A, B, 4A–D), though the relative contribution of the particulate fraction to total N and P did change substantially between treatments and hydroperiods. In EXC wetlands with semipermanent hydroperiod, particulate N contributed much less to total N (15%) compared with other EXC (23%) or BAU (22%) sites ($p = 0.001$; Tables 1, 3). Conversely, particulate P represented a larger proportion of total P in semipermanently flooded wetlands (43%; Figs S1A, B, 4A–D) than in seasonal wetlands (31%; $p = 0.026$; Tables 1, 3). Dissolved N and P contributed most to the nutrient fraction, so we focused on dissolved rather than particulate pools.

Dominant forms of dissolved N

TDN was primarily in the organic form, with 96.4% of TDN as DON (Figs 3A, B, 4A–D). The contribution of DON to TDN decreased over time in all semipermanently flooded wetlands ($p < 0.001$; Table 2), but organic N still represented >90% of the TDN pool (Fig. 4A–D). As wetlands aged, TDN and DON concentrations increased by an average 6.0 and 8.6 $\mu g\ L^{-1}\ y^{-1}$, respectively ($p = 0.034$ and 0.013, respectively; Tables 2, 4, Fig. 5A–F), but the rate of increase was lower in semipermanently flooded wetlands than in seasonal wetlands ($p = 0.022$ and < 0.001; slopes $= -0.018$ and -0.027 for TDN and DON, respectively). DOC concentrations followed similar patterns to DON (Tables 2, 4, Fig. S2).

DIN dynamics

Inorganic N, particularly NO_3-N, was scarce. We recorded only 6 samples with NO_3-N concentrations ≥ 200 µg/L and 62 samples with NH_4-N concentrations ≥ 100 µg/L ($n = 888$). Temporal trends in DIN concentration were difficult to interpret because the concentrations were so low, but we were able to detect a handful of patterns. DIN dynamics were largely driven by the interaction between hydroperiod and wetland age ($p < 0.001$; Table 2, Fig. 5A), with DIN concentrations decreasing as seasonally flooded wetlands aged and increasing in semipermanently flooded wetlands (Table 2, Fig. 5A). The relatively small DIN pool was primarily composed of NH_4-N, which made up >76% of DIN, while NO_3-N contributed <24% to DIN (Figs 3A, B, 4A–B).

NO_3-N concentrations were 23% higher in semipermanent sites compared with seasonal wetlands ($p = 0.039$; Tables 2, 4), but the trend was driven by BAU wetlands with semipermanent hydroperiod (Fig. 3A). One site (FF.080; Table S1) with particularly high NO_3-N concentrations drove elevated NO_3-N concentrations in semipermanent BAU wetlands. This site received water from a drainage ditch servicing an adjacent agricultural field. As one of the older wetlands included in the study, it also contributed to age-related increases in NO_3-N concentrations. Results of the

Table 1. Model coefficients indicating the effect of restoration treatment, hydroperiod, wetland age, and variable interactions on particulate and total nutrient concentrations and molar ratios. Treatment and hydroperiod model coefficients are shown as the deviation of excavated (EXC) wetlands from business as usual (BAU) and the deviation of semipermanent from seasonal wetlands, respectively. Wetland age refers to the effect of time since restoration. Goodness of model fit for fixed effects and for fixed and random effects (full model) are shown. Random effects included random intercepts for each wetland. *P*-values are indicated by superscripts following model coefficients. All responses were log transformed except particulate N:P.

	Main effects				Interaction terms				
Response variable	Treatment	Hydroperiod	Age	Age^2	Treatment × hydroperiod	Treatment × age	Hydroperiod × age	R^2 (fixed effects)	R^2 (full model)
Particulate C (mg/L)	0.020	0.031	0.009	–	−0.257[a]	−0.001	−0.008	0.06	0.12
Particulate N (μg/L)	0.187	0.334	0.049	–	−0.555[a]	−0.013	−0.040	0.09	0.21
Particulate P (μg/L)	0.084	0.164	0.033	–	−0.454[a]	0.005	−0.023	0.12	0.31
Total organic C (mg/L)	−0.252[a]	−0.101	−0.057[a]	0.004[a]	0.022	0.026	−0.027	0.35	0.78
Total N (μg/L)	−0.140	−0.121	−0.007	–	−0.117	0.017	−0.0006	0.16	0.53
Total P (μg/L)	−0.497	−0.310	−0.223[a]	0.026[a]	−0.151	0.072[a]	0.005	0.38	0.79
Particulate N:total N	0.025	0.034	0.003	–	−0.050[a]	−0.001	−0.003	0.06	0.18
Particulate P:total P	0.224	0.298	0.141[a]	−0.017[a]	−0.263	−0.004	0.0004	0.27	0.54
Particulate N:P	−2.596	−3.716	−0.419	–	−0.778	0.401	0.596	0.002	0.16

[a] $p \leq 0.05$.

DIN model did not change in response to removing elevated NO_3-N samples, but there was substantially less variation in means after removing samples taken near the wetland inlet at FF.080. Further investigation into NO_3-N dynamics across the longitudinal transect of this wetland showed patterns consistent with N removal and assimilation as water moved through a wetland (Fig. S3).

Dominant forms of dissolved P

In contrast to dissolved N, the dominant form of P varied between wetlands with seasonal and semipermanent hydroperiod. TDP was primarily comprised of the inorganic form in seasonal wetlands (52% SRP), while DOP was dominant in semipermanent wetlands (76% DOP; Figs 3C, 4A–D). In BAU wetlands, the contribution of SRP to TDP was initially high and subsequently decreased for the first 4 to 5 y following restoration before increasing between y 6 and 10 (Table 2, Fig. 4A–D), following the trends in overall SRP concentration over the same time frame (Fig. 5D). In EXC wetlands, the contribution of SRP to TDP was initially low (<50%) but increased over time to ~75% of TDP (Fig. 4D), following the pattern of SRP in the water column (Fig. 5D). After initially increasing, the contribution of DOP to the TDP pool decreased over time (Table 2, Fig. 4C). The contribution of SRP and DOP to the TDP pool was driven by temporal patterns in SRP availability ($p <$ 0.001; Fig. 5D) as DOP concentrations did not change over time ($p = 0.587$; Fig. 5E).

Dissolved P dynamics

Restoration treatment and hydroperiod were both reliable predictors of dissolved P availability (Table 2), but hydroperiod had a larger effect (Fig. 5D, F). Concentrations of TDP and SRP were 3.6 and 8× higher in seasonal than in semipermanent wetlands, respectively ($p = 0.001$; Tables 2, 4, Figs 3C, 4A–D). As predicted, sediment removal resulted in lower TDP and SRP concentrations (Table 4), particularly in EXC wetlands. Immediately following restoration, seasonally flooded wetlands had fairly high TDP (mean = 344 μg/L) and SRP (mean = 263 μg/L) concentrations, particularly in wetlands restored with the BAU strategy.

Temporal patterns in dissolved P availability were primarily driven by seasonally flooded wetlands (Fig. 5D, F), which had 3.5× more TDP than semipermanent wetlands ($p < 0.001$; Table 2). In general, TDP availability increased as wetlands aged ($p < 0.001$; Table 2), a trend that was driven by SRP dynamics ($p < 0.001$; Table 2, Fig. 5D−F). In BAU wetlands, TDP and SRP concentrations initially decreased and then rebounded to levels observed shortly after restoration (Fig. 5D, F). In EXC wetlands, TDP and SRP concentrations were initially low and remained low for 6 to 7 y before rapidly increasing, resulting in faster accumulation of

Table 2. Model coefficients indicating the effect of restoration treatment, hydroperiod, wetland age, and variable interactions on particulate and total nutrient concentrations and molar ratios. Treatment and hydroperiod model coefficients are shown as the deviation of excavated wetlands from business as usual (BAU) and the deviation of semipermanent from seasonal wetlands, respectively. Wetland age refers to the effect of time since restoration. DIN = dissolved inorganic N, DOC = dissolved organic C, DON = dissolved organic N, DOP = dissolved organic P, SRP = soluble reactive P, TDN = total dissolved N, TDP = total dissolved P. Goodness of model fit for fixed effects and for fixed and random effects (full model) are shown. Random effects included random intercepts for each wetland. Fixed effect p-values are indicated by superscripts following model coefficients. Response variables that were log-transformed to meet model assumptions are indicated with the superscript b.

	Main effects				Interaction terms				
Response variable	Treatment	Hydroperiod	Age	Age2	Treatment × hydroperiod	Treatment × age	Hydroperiod × age	R^2 (fixed effects)	R^2 (full model)
NO_3-N (μg/L)[b]	0.051	−0.234[a]	−0.017	–	−0.081	−0.009	0.045[a]	0.03	0.13
NH_4-N (μg/L)[b]	−0.489[a]	−0.886[a]	−0.079[a]	–	−0.086	0.069[a]	0.148[a]	0.08	0.39
DIN (μg/L)[b]	−0.375[a]	−0.801[a]	−0.067[a]	–	−0.102	0.053[a]	0.138[a]	0.09	0.39
DON (μg/L)[b]	−0.099	−0.031	−0.008	–	0.003	0.002	−0.027[a]	0.16	0.53
TDN (μg/L)[b]	−0.099	−0.070	−0.014[a]	–	−0.012	0.002	−0.018[a]	0.19	0.70
SRP (μg/L)[b]	−1.481[a]	−1.647[a]	−0.517[a]	0.035[a]	0.473	0.155[a]	0.083[a]	0.27	0.73
DOP (μg/L)[b]	0.031	−0.031	−0.037	–	−0.226	0.001	−0.001	0.03	0.24
TDP (μg/L)[b]	−0.783[a]	−0.943[a]	−0.321[a]	0.022[a]	0.200	0.073[a]	0.038	0.28	0.76
DOC (mg/L)[b]	−0.170[a]	−0.056	−0.030[a]	0.002[a]	0.069	0.005	−0.040[a]	0.35	0.85
DON : TDN	−0.001	0.041[a]	0.002	–	0.020	−0.0001	−0.010[a]	0.05	0.14
DIN : TDN	0.001	−0.041[a]	−0.002	–	−0.020	0.0001[a]	0.010[a]	0.05	0.14
DOP : TDP	0.423[a]	0.513[a]	0.173[a]	−0.014[a]	−0.171	−0.040[a]	−0.029	0.22	0.60
SRP : TDP	−0.423[a]	−0.513[a]	−0.173[a]	0.014[a]	0.171	0.040[a]	0.029	0.22	0.60
DOC : TDN	−2.456[a]	−0.432	0.346[a]	–	2.453	0.052	−0.621[a]	0.23	0.53
DOC : DON[b]	−0.078[a]	−0.029	0.005	–	0.057	0.005	−0.011[a]	0.22	0.50
DOC : DIN[b]	0.198	0.727[a]	0.067[a]	–	0.147	−0.046[a]	−0.170[a]	0.16	0.42
DOC : TDP	−71.110	−68.574	143.593	−13.544[a]	427.394	44.174	77.891	0.13	0.44
DOC : DOP[b]	0.133	0.312[a]	0.117[a]	−0.009[a]	0.105	−0.017	−0.046[a]	0.05	0.31
DOC : SRP[b]	1.243[a]	1.630[a]	0.551[a]	−0.038[a]	−0.392	−0.144[a]	−0.126[a]	0.22	0.68
TDN : TDP	−3.160	−11.366	5.174	−0.581	24.875	2.429	6.470[a]	0.15	0.40
DON : DOP[b]	0.203	0.325[a]	0.099[a]	−0.008[a]	0.061	−0.021	−0.035	0.07	0.29
DIN : SRP[b]	0.893[a]	0.646	0.489[a]	−0.041[a]	−0.578	−0.073[a]	0.090[a]	0.32	0.68

[a] $p \leq 0.05$.
[b] Log transformed.

dissolved P at EXC (slopes = 82.2 and 79.4 for TDP and SRP, respectively) than BAU wetlands (p = 0.002 and < 0.001; slopes = 37.8 and 31.9 for TDP and SRP, respectively; Table 2).

Molar ratios

Dissolved nutrient molar ratios changed dramatically over time, with the direction of change moderated by hydroperiod and sometimes by restoration treatment (Table 2, Fig. 6A–F). Dissolved C : N molar ratios were controlled by restoration treatment, hydroperiod, and time, whereas C : P ratios were primarily influenced by hydroperiod and time (Tables 2, 4). Molar DOC : DON ratios were lower in EXC sites (mean = 20.2 ± 3.4 SD) than BAU sites (mean = 19.4 ± 3.3 SD; p = 0.003; Tables 2, 4, Fig. 6A). Log-transformed DOC : DIN ratios increased over time in seasonal wetlands (slope = 0.044) and decreased over time in semipermanent wetlands (slope = −0.13; p < 0.001; Table 2, Fig. 6B), a pattern that was driven by DIN availability (Fig. 5A). Molar DOC : DOP ratios were lower and less variable at wetlands with seasonal (mean = 944.7 ± 1230.7 SD) than semipermanent hydroperiod (mean = 1233.6 ± 2123.9 SD; p = 0.042; Tables 2, 4, Fig. 6C). Initially following restoration, DOC : DOP ratios increased, but began to fall ~5 y after restoration. A similar pattern was observed for DOC : SRP molar ratios, where a sharp decline in DOC : SRP coincided with increasing SRP concentrations (Table 2, Figs 5D, 6D). Organic and inorganic N : P molar ratios also increased following restoration and then decreased around 5 y following restoration (Table 2, Fig. 6E, F). Inorganic N : P molar ratios were higher

Table 3. Mean particulate and total C, N, and P concentrations and molar ratios. Means with SD shown parenthetically are listed by restoration treatment (BAU = business as usual; EXC = excavated), wetland hydroperiod, and treatment × hydroperiod.

	Restoration treatment		Hydroperiod		Treatment × hydroperiod			
Response variable	BAU	EXC	Seasonal	Semipermanent	BAU × seasonal	BAU × semipermanent	EXC × seasonal	EXC × semipermanent
Particulate C (mg/L)	2.95 (3.13)	2.92 (4.42)	3.28 (4.52)	2.27 (1.80)	3.24 (3.93)	2.66 (1.99)	3.30 (4.84)	1.35 (0.57)
Particulate N (μg/L)	362 (419.7)	325.9 (381.3)	380.5 (453)	271 (255.5)	391.7 (521.2)	331.7 (279)	373.9 (408.8)	126.2 (76.6)
Particulate P (μg/L)	69.6 (70.6)	75.7 (112.2)	82.9 (108)	53 (54.3)	74.7 (80.1)	64.5 (59.2)	87.7 (121.4)	25.6 (23.4)
Total organic C (mg/L)	21.77 (8.33)	19.21 (9.56)	23.10 (9.58)	15.28 (4.85)	26.83 (7.91)	16.59 (4.84)	20.90 (9.80)	12.16 (3.18)
Total N (μg/L)	1572.9 (1519.2)	1353.2 (758.5)	1549.3 (776.1)	1284 (1728.3)	1684.8 (731.9)	1458.5 (2028.3)	1469.8 (791.7)	867.3 (265.6)
Total P (μg/L)	320.6 (343.2)	286.6 (355.4)	388.9 (397.4)	135.5 (101.6)	479.4 (414.1)	158 (105)	335.7 (378.3)	81.8 (68.3)
Particulate N : total N	0.22 (0.13)	0.22 (0.13)	0.23 (0.13)	0.21 (0.12)	0.20 (0.13)	0.24 (0.12)	0.23 (0.13)	0.15 (0.07)
Particulate P : total P	0.32 (0.22)	0.37 (0.21)	0.31 (0.21)	0.43 (0.21)	0.22 (0.17)	0.43 (0.21)	0.36 (0.21)	0.42 (0.2)
Particulate N : P	14.5 (10.9)	14.2 (12.2)	14.4 (12.9)	14.2 (8.6)	14.4 (12.6)	14.5 (8.9)	14.4 (13.1)	13.5 (7.9)

Table 4. Mean dissolved nutrient concentrations and molar ratios with SD shown parenthetically. Values are listed by wetland restoration treatment (BAU = business as usual; EXC = excavated), wetland hydroperiod, and treatment × hydroperiod. DIN = dissolved inorganic N, DOC = dissolved organic C, DON = dissolved organic N, DOP = dissolved organic P, SRP = soluble reactive P, TDN = total dissolved N, TDP = total dissolved P.

Response variable	Restoration treatment		Hydroperiod		Strategy × hydroperiod			
	BAU	EXC	Seasonal	Semipermanent	BAU × seasonal	BAU × semipermanent	EXC × seasonal	EXC × semipermanent
NO_3-N (μg/L)	20 (146.3)	7.2 (17.1)	6.9 (14.9)	28 (183)	5.7 (4.5)	37.4 (216.5)	7.7 (18.7)	4.7 (1.5)
NH_4-N (μg/L)	38.8 (57.1)	30.4 (50.9)	35.8 (58.8)	31.5 (41.6)	40.4 (64)	36.9 (47.6)	33 (55.4)	18.2 (13.4)
DIN (μg/L)	58.9 (171.2)	37.6 (57.6)	42.7 (63.9)	59.4 (206.5)	46.1 (66.1)	74.4 (243.5)	40.6 (62.6)	22.8 (13.6)
DON (μg/L)	1132.1 (407)	995.9 (455)	1138.5 (442.6)	889.3 (372.9)	1271.6 (357.1)	963.1 (400.4)	1055.9 (469.9)	708.2 (203.7)
TDN (μg/L)	1191 (505.1)	1033.4 (491.9)	1181.2 (481.7)	948.7 (517.4)	1317.7 (396.7)	1037.4 (576.1)	1096.5 (510)	731 (211.9)
SRP (μg/L)	193.3 (280.3)	135.8 (240.4)	224.1 (293.2)	27.8 (54)	324.1 (320.2)	34.9 (62.1)	162 (256.6)	10.5 (13.2)
DOP (μg/L)	84.4 (94)	79 (101.1)	93.4 (111.5)	55.1 (45.6)	104.2 (116.5)	60.5 (45.6)	86.7 (107.8)	41.8 (43)
TDP (μg/L)	277.8 (312.5)	214.8 (283.7)	317.5 (331.3)	82.9 (80.5)	428.4 (349.5)	95.3 (86)	248.7 (300)	52.3 (54.2)
DOC (mg/L)	19.39 (6.88)	16.30 (6.88)	19.82 (7.17)	13.24 (4.00)	23.63 (5.82)	14.26 (3.96)	17.46 (6.91)	10.75 (2.85)
DON:TDN	0.96 (0.06)	0.97 (0.03)	0.97 (0.03)	0.96 (0.07)	0.97 (0.03)	0.95 (0.09)	0.97 (0.03)	0.97 (0.01)
DIN:TDN	0.04 (0.06)	0.03 (0.03)	0.03 (0.03)	0.04 (0.08)	0.03 (0.03)	0.05 (0.09)	0.03 (0.03)	0.03 (0.01)
DOP:TDP	0.56 (0.33)	0.65 (0.3)	0.53 (0.33)	0.76 (0.22)	0.42 (0.32)	0.73 (0.24)	0.61 (0.31)	0.83 (0.14)
SRP:TDP	0.44 (0.33)	0.35 (0.3)	0.47 (0.33)	0.24 (0.22)	0.58 (0.32)	0.27 (0.24)	0.39 (0.31)	0.17 (0.14)
DOC:TDN	19.5 (3.6)	18.8 (3.3)	20 (3.3)	17.3 (3.2)	21.3 (2.6)	17.2 (3.4)	19.1 (3.4)	17.5 (2.7)
DOC:DON	20.2 (3.4)	19.4 (3.3)	20.6 (3.2)	18 (3)	22 (2.4)	18 (3.1)	19.7 (3.3)	18 (2.8)
DOC:DIN	973.7 (687.4)	943.3 (828)	1063.7 (845.8)	720.5 (449.8)	1171.4 (767.8)	734.1 (477.2)	996.8 (885.2)	687.1 (374.8)
DOC:TDP	497.5 (481.3)	727.5 (1008.4)	503.6 (598)	869.4 (1102.9)	366.5 (412)	656.1 (511.6)	588.6 (675.4)	1392.8 (1789.7)
DOC:DOP	945.6 (1517.1)	1122 (1637.3)	944.7 (1230.7)	1233.6 (2123.9)	869.7 (733.7)	1024.7 (2035.4)	986.3 (1433)	1730.2 (2257.5)
DOC:SRP	3998.3 (7236.5)	4736.7 (7896.3)	3622.1 (7528.4)	6169.3 (7411.8)	2693.1 (6737.6)	5701 (7525)	4238.7 (7960.1)	7483.7 (6975.6)
TDN:TDP	26.8 (27.5)	39.1 (57.6)	25.3 (28.9)	50.7 (67.5)	17 (18.6)	38.6 (31.6)	30.5 (32.7)	80.5 (110.3)
DON:DOP	48.3 (83.2)	59 (85.9)	46.4 (59.6)	69.5 (119.8)	39.2 (33.8)	57.9 (113.1)	50.5 (69.6)	97.1 (131)
DIN:SRP	6.9 (17.2)	5.9 (9.2)	3.9 (7.7)	12.5 (21.3)	2.3 (5.5)	12.9 (24.1)	5 (8.7)	11.2 (10.2)

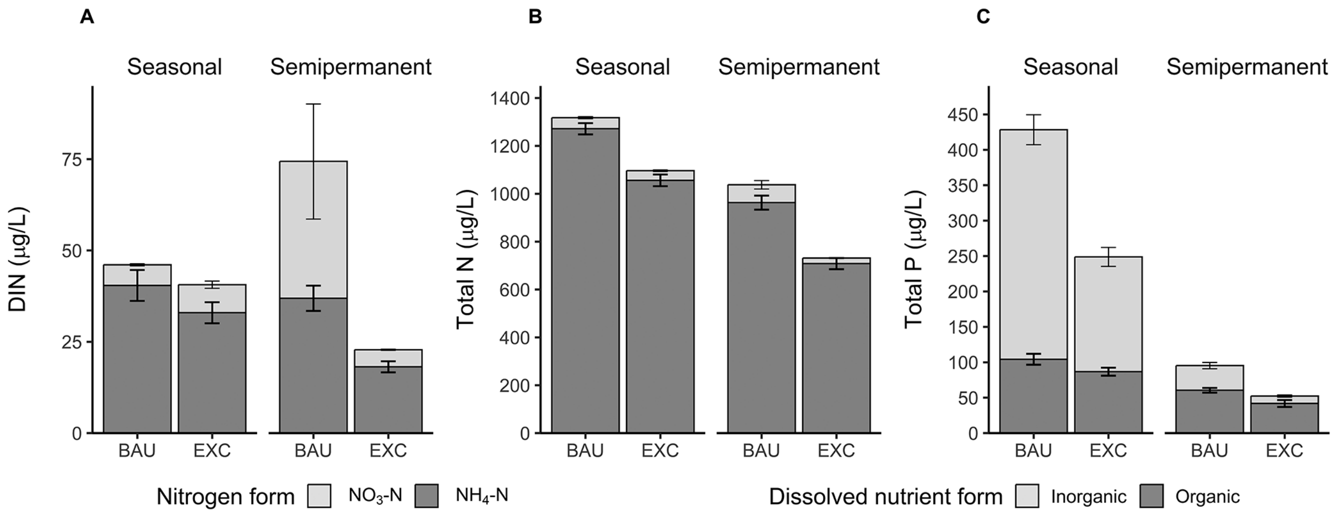

Figure 3. Dissolved inorganic N (DIN; A) as the sum of NH_4-N (bottom) and NO_3-N (top), and the contribution of dissolved organic (bottom, dark gray) and dissolved inorganic (top, light gray) nutrient fractions to total dissolved N (TDN; B) and total dissolved P (TDP; C). Nutrient fractions are shown stacked atop each other. Error bars represent the SE about the mean.

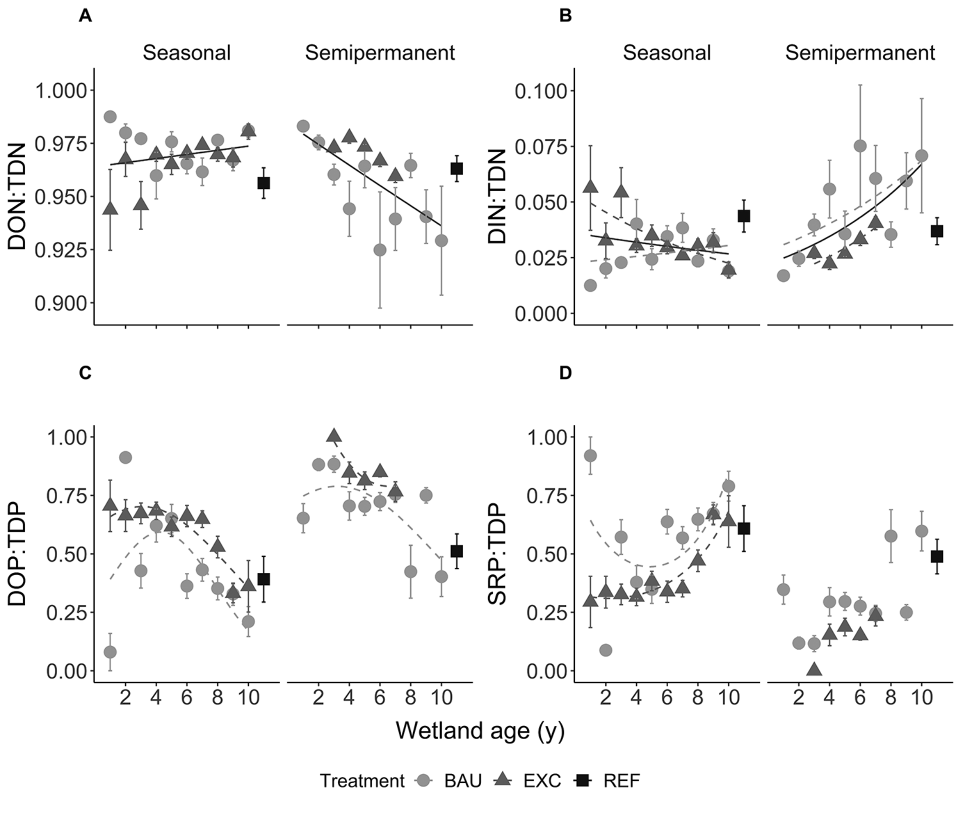

Figure 4. Contribution of dissolved inorganic and organic nutrient fractions to the total dissolved nutrient pool over time in restored (BAU = business as usual, circles; EXC = excavated, triangles) and reference (REF = squares) basins. Total dissolved N (TDN) species shown for dissolved organic N (DON; A) and dissolved inorganic N (DIN; B), and total dissolved P (TDP) species shown for dissolved organic P (DOP; C) and soluble reactive P (SRP; D). Seasonally inundated basins shown in the left panel and semipermanent basins in the right panel. Trend lines are shown for temporal relationships with $p \leq 0.05$. Solid lines represent wetland age interaction with hydroperiod. Broken lines represent wetland age interaction with restoration treatment. Each point represents a mean across multiple sites with SE. Note difference in *y*-axis scale among panels.

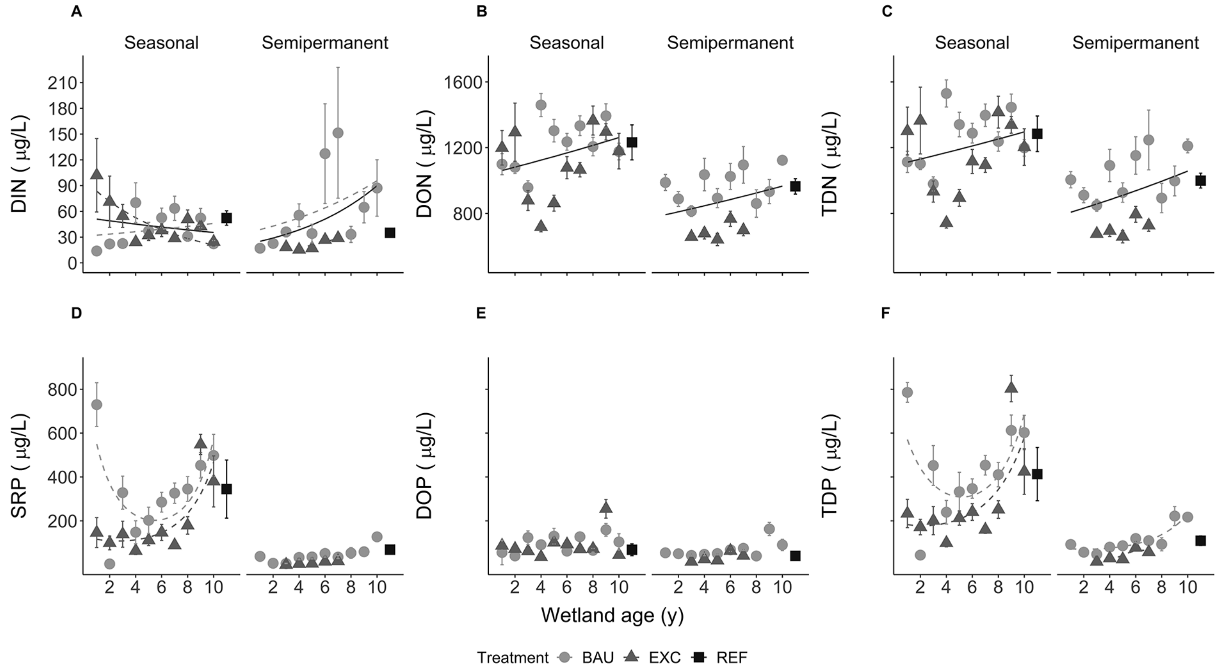

Figure 5. Dissolved nutrient concentrations over time in restored (BAU = business as usual, circles; EXC = excavated, triangles) and reference (REF = squares) basins. Seasonally inundated basins shown on the left side of each panel and semipermanent basins on the right side. Dissolved inorganic N (DIN; A), dissolved organic N (DON; B), and total dissolved N (TDN; C), soluble reactive P (SRP; D), dissolved organic P (DOP; E), and total dissolved P (TDP; F). Seasonally inundated basins shown in the left panel and semipermanent basins in the right panel. Trend lines are shown for temporal relationships with $p \leq 0.05$. Solid lines represent temporal interaction with hydroperiod. Broken lines represent temporal interaction with restoration treatment. Each point represents a mean across multiple sites with SE. Note difference in *y*-axis scale among panels.

in EXC wetlands, where sediment was removed (mean = 6.9 ± 17.2 SD), than in BAU restorations (mean = 5.9 ± 9.2 SD; $p = 0.015$; Table 2), but this trend was driven by differences in wetlands with seasonal hydroperiod rather than semipermanent wetlands (Table 4). Organic N : P ratios were ~50% higher in semipermanently flooded wetlands than seasonal wetlands, regardless of restoration strategy ($p = 0.016$; Tables 2, 4).

Particulate N : P molar ratios were smaller (~14.3 ± 11.6 SD; Table 3) in contrast to the molar ratios of DOC : TDN (mean = 19.1 ± 3.5 SD; $p < 0.01$, repeated measures ANOVA) and TDN : TDP (mean = 33.1 ± 46.0 SD; $p < 0.01$, repeated measures ANOVA). The relative availability of more bioavailable DIN : SRP averaged 6.4 (13.8 SD), suggesting lower relative availability of inorganic N to P compared to organic N and P. In general, total N : P ratios were enriched in P (mean = 23.1 ± 19.0 SD), slowly increasing until 5 y following restoration ($p = 0.01$), at which point values decreased ($p < 0.001$), regardless of restoration strategy or hydroperiod.

DISCUSSION

We studied 54 restored wetlands over a 4-y period to identify how water quality responds to sediment removal and hydroperiod over time (Fig. 2). Water quality was primarily influenced by hydroperiod. Accumulated sediment excavation decreased dissolved inorganic P concentrations immediately following restoration, but the effect lasted only 6 y, and increases in P were primarily driven by dynamics in seasonal wetlands. As wetlands aged, dissolved nutrient concentrations increased, primarily from rising inorganic P and organic N, with relatively larger increases in P compared to N. Rising DOC : DON and falling DIN : SRP suggest that both seasonal and semipermanent wetlands grew increasingly N limited over time. Differences in N and P cycling appear to have driven stronger N-limited conditions in seasonal compared with semipermanent wetlands. Below, we explore possible mechanisms underlying these patterns and their implications for wetland management.

Dissolved P dynamics in seasonal and semipermanent wetlands

Hydroperiod emerged as the most important characteristic controlling available P as wetlands aged, though excavation removed substantial amounts of P-enriched sediment and initially reduced dissolved P concentrations. SRP concentrations were higher and more dynamic in seasonal wetlands, suggesting that hydroperiod shapes the environmental conditions involved in P cycling within wetlands. In contrast, DOP and particulate P concentrations were similar

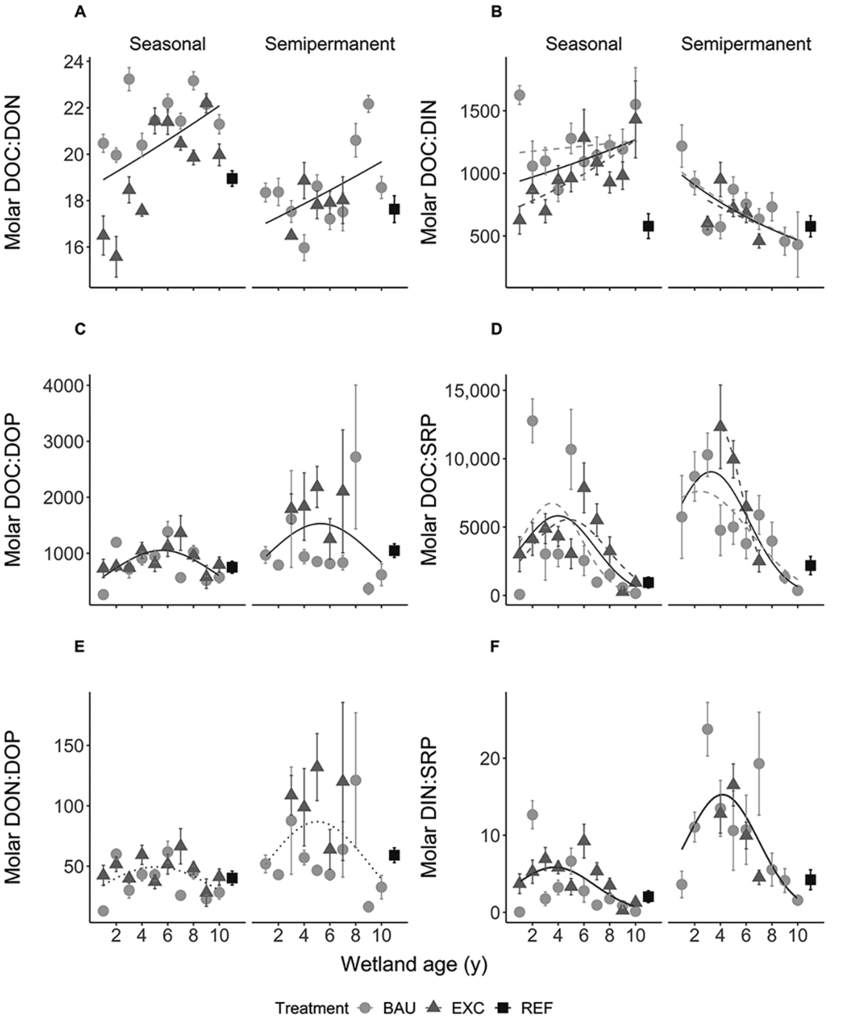

Figure 6. Dissolved nutrient molar ratios across time in restored (BAU = business as usual, circles; EXC = excavated, triangles) and reference (REF, squares) wetlands. Seasonal wetlands shown on the left side of each panel and semipermanent basins on the right side. Dissolved organic C (DOC) to dissolved organic N (DON) ratios (A), DON to dissolved inorganic N (DIN) ratios (B), DOC to dissolved organic P (DOP) ratios (C), DOC to soluble reactive P (SRP) ratios (D), DON to DOP ratios (E), and DIN to SRP ratios (F). Seasonally inundated basins shown in the left panel and semipermanent basins in the right panel. Trend lines are shown for temporal relationships with $p \leq 0.05$. Solid lines represent temporal interaction with hydroperiod. Broken lines represent temporal interaction with restoration treatment. Dotted lines represent overall temporal trend without associated variable interactions.

in both seasonal and semipermanent wetlands. Higher dissolved P mobilization in seasonal wetlands could arise from multiple mechanisms. First, regular periods of water drawdown in seasonal wetlands can promote decomposition of detritus and subsequent nutrient mineralization (Olila et al. 1997, Freeman et al. 2004). Second, continuous dense stands of emergent macrophytes throughout restored seasonal wetlands may limit gas exchange across the air–water interface, resulting in hypoxic conditions that promote internal loading of P in the presence of standing water (Rose and Crumpton 1996).

Annual fluctuations between wet and dry conditions throughout the growing season are a defining feature of PPR seasonal wetlands and may have meaningful impacts on dissolved nutrient availability when standing water is present. Semipermanent wetlands rarely experience complete water loss that exposes sediment to air, whereas seasonal wetlands are smaller and water levels are more vulnerable to annual variability in precipitation (Wetzel 1990, Downing et al. 2006, van der Kamp and Hayashi 2009). In seasonal wetlands, periods of drawdown stimulate aerobic decomposition and nutrient mineralization from decomposing plant litter (LaBaugh et al. 1987, Reddy et al. 1999). Mineralized nutrients can move into the water column upon rewetting, resulting in higher dissolved nutrient content in seasonal wetlands compared with their semipermanent counterparts. In a post hoc analysis, we found a modest negative relationship between water-column depth at the point of collection and dissolved P concentration (Table S2, Fig. 7A–D, Appendix S1). However, water-column depth only explained 1% of variation in this simple model while site identity, included as a random effect to account for repeated measurements over multiple dates, accounted for 68% of variability in TDP concentrations (Table S2). This suggests that while wet–dry cycling contributes somewhat to mobilization of dissolved P, it is unlikely the most important control.

The restored seasonal wetlands in our study were usually colonized by dense stands of emergent macrophytes throughout the entire wetted area, whereas semipermanent wetlands had an open pool colonized by floating and submerged vegetation surrounded by an emergent macrophyte ring (Winikoff et al. 2020). Seasonal wetlands were often quickly colonized by *Typha* × *glauca* (hybrid cattail) and *Phragmites australis* ssp *australis* (common reed) (Winikoff et al. 2020), with substantial stands of *Phalaris arundinacea* (reed canary grass) that often expanded well into the emergent macrophyte zone immediately following restoration and retreated over time (personal observation). Previous studies in prairie pothole wetlands have shown that within emergent macrophyte zones, the water column exists in a nearly permanent state of hypoxia (≤3 mg oxygen/L; Rose and Crumpton 1996). Emergent macrophyte stems and stalks can limit water-column dissolved oxygen by intercepting incident photosynthetically active radiation and decreasing in situ oxygen production (Morris and Barker 1977, Larkin et al. 2012) and decreasing wind velocity and shear forces that promote gas exchange across the air–water interface (Liss and Slater 1974). The combination of shading and sheltering within the emergent macrophyte zone can result in persistent hypoxia throughout the growing season (Rose and Crumpton 1996) leading to mobilization of sedimentary P (Patrick and Khalid 1974, Carlton and Wetzel 1987). In contrast, submerged aquatic vegetation in semipermanent wetlands can stabilize sediment P by delivering oxygen to the benthos and by physically protecting sediments from resuspension by wind and wave action, while allowing for air–water gas exchange (Søndergaard et al. 1992, Jeppesen et al. 1997).

To test whether differences in dissolved P concentration may be moderated by the physical and chemical effects of the emergent macrophyte community, we performed a post hoc analysis of emergent macrophyte cover and dissolved P concentration (Appendix S1). We found a positive relationship between both SRP and TDP concentrations and cumulative % cover of 3 aggressive invasive species common to the region: hybrid cattail, common reed, and reed canary grass (Table S2, Fig. 7B, D). Invasive emergent macrophyte cover and the interaction between cover and hydroperiod explained 55 and 48% of variability in SRP and TDP concentrations, respectively (Table S2). When considered alone, emergent macrophyte cover explained 21 and 20%

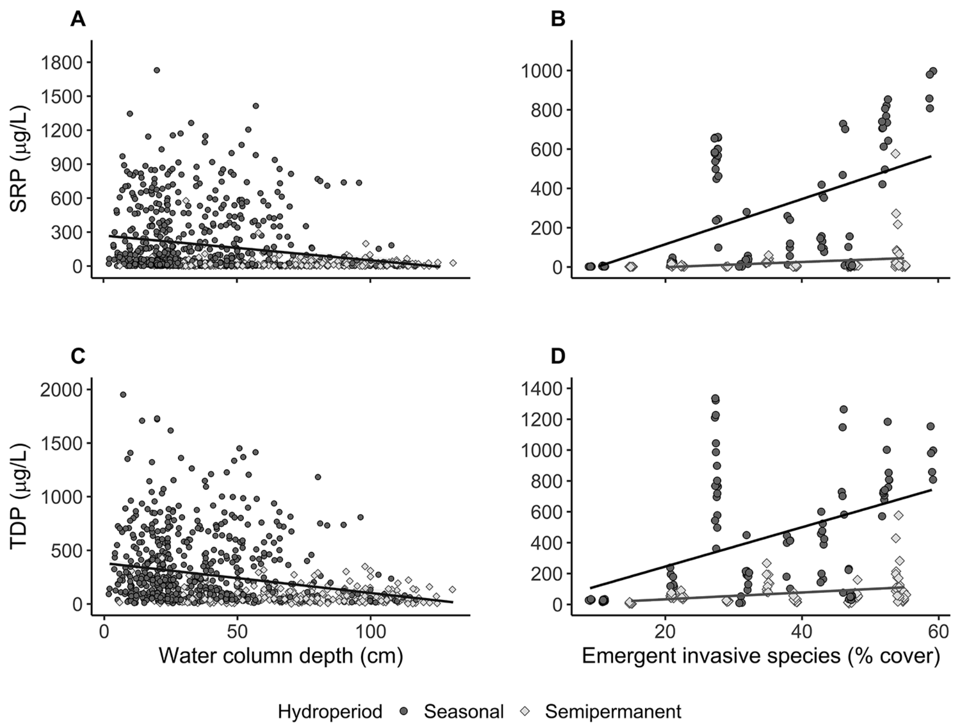

Figure 7. Soluble reactive P (SRP; A, B) and total dissolved P (TDP; C, D) concentrations across water column depth (A, C) and invasive emergent macrophyte cover (B, D) in wetlands with seasonal and semipermanent hydroperiod. Note difference in *y*-axis scale among panels.

of variability in SRP and TDP, respectively, suggesting that emergent macrophytes may alter the physical and chemical conditions that lead to P mobilization. Taken together, our post hoc analyses provide some evidence that the effect of hydroperiod on dissolved P is mediated through wet–dry cycling that promotes mineralization of organic sediment P and the physical effects of the emergent macrophyte community that promote P mobilization. Future research should evaluate differences in sediment P mobility by performing fractionation studies in restored seasonal and semipermanent wetlands with varying densities of emergent macrophytes.

Hydroperiod influences the expression of legacy P

The presence of high levels of dissolved P may be indicative of legacy P accumulated from past agricultural activities, although we only observed these legacy effects in environmental settings that promoted P mobilization, regardless of sediment excavation. Semipermanent wetlands, which tended to be slightly deeper and maintained more open water area over the study period, had low SRP and total P even several years after restoration, irrespective of restoration method. In contrast, shallower wetlands with seasonal hydroperiod had extremely high concentrations of SRP even when P-rich agricultural sediment had been excavated. For example, we found 16 seasonal wetlands with SRP concentrations >278 μg/L, which was in excess of total P concentrations found in 75% of shallow Danish lakes of similar size (Søndergaard et al. 2005). The legacy of past disturbance and fertilization can augment P runoff for decades or even centuries (e.g., Jeppesen et al. 2005, McCrackin et al. 2018). Recent evidence suggests that legacy P may also contaminate groundwater supplies (Domagalski and Johnson 2011), which complicates our understanding of effective mitigation efforts by slowly increasing surface water P far away from the point of disturbance. These spatial and temporal asynchronies make it difficult to identify how legacy P remediation efforts influence contemporary water quality at the landscape scale.

N dynamics in restored wetlands

Despite low DIN concentrations, DON was fairly high for shallow lentic systems with small surface areas (Detenbeck et al. 2002, Jeppesen et al. 2005). Limited availability of DIN with concomitant increases in DON are indicative of N removal and recycling (Mitsch et al. 2005, Vymazal and Březinová 2018). Small lentic systems are particularly effective N sinks (Müller et al. 2021), permanently removing up to 100% of N inflow (Harrison et al. 2009). Wetlands and shallow lakes are also efficient N traps, removing inorganic N from the water column via assimilation and recycling (Wetzel 1990). In flow-through wetlands, macrophytes and associated epiphytes can be responsible for capturing up to 100% of inorganic N flowing into a wetland and may hold up to 86% of all N within the wetland (van Donk et al. 1993, Romero et al. 1999). Since assimilated N often re-enters the dissolved nutrient pool as DON following plant senescence or decomposition (Wetzel 1990), watersheds with abundant wetland cover tend to export a larger proportion of TDN as DON (Pellerin et al. 2004, Fasching et al. 2019). Evidence suggests that labile forms of organic N, such as amino acids and proteins, are biologically available to microbes and primary producers (Johnson and Tank 2009, Mackay et al. 2020). In primarily closed systems with very little surficial connectivity between wetlands, it is reasonable to expect DON concentrations to increase over time as more bioavailable forms of organic N are mineralized and reassimilated while less bioavailable forms grow more concentrated.

Biogeochemical drivers of shifting nutrient stoichiometry

We found evidence that all wetland types experienced increasing N limitation over time. Long-term patterns of decreasing DIN with concurrent increases in DON and SRP, combined with steadily decreasing inorganic N : P molar ratios, are consistent with inorganic N limitation. Furthermore, using the framework proposed by Stutter et al. (2018) wherein dissolved C : N ratios between 11 and 100 indicate net N sequestration by aquatic microbial communities (i.e., limitation), DOC : DON molar ratios in this study were consistently suggestive of N limitation (Table 4). As wetlands aged, DOC : DON ratios increased, a pattern that is consistent with either the utilization of DON at a faster rate than DOC or the favorable production of DOC over DON in systems that regularly cycle through wet and dry periods, a pattern known as the Birch effect (Birch 1964, Steinman et al. 2012). In our study, both DOC and DON concentrations increased over time (Figs 5B, S2), but the rate of DOC increase was lower at semipermanent wetlands compared with seasonal sites (Fig. S2). Meanwhile, DOC : DON ratios increased at a similar pace in both seasonal and semipermanent wetlands (Fig. 6A–F). Taken together, these data suggest that DON may have been utilized at a faster rate than DOC, at least in semipermanent basins, indicating some degree of N limitation. Since DON is often considered less labile than DIN, steadily increasing DOC : DON molar ratios also suggest high inorganic N demand, which could reflect either N assimilation or removal. Taken together, our data suggest that restored agricultural wetlands may be more limited by N availability than by C or P, and this limitation likely increases over time.

Broader implications

Healthy wetlands provide essential ecosystem services and are remarkably robust to physical and chemical disturbance, but decades of wetland consolidation (McCauley et al. 2015, Van Meter and Basu 2015), cultivation, and nutrient enrichment (Van Meter et al. 2016, McCrackin et al. 2018) have left the remaining wetlands under considerable strain to maintain historical ecosystem services. Our study shows that by restoring conditions conducive to microbially mediated N removal and deposition, wetlands can recover from a history of N amendments. Unfortunately, wetland recovery from long-term P enrichment remains a significant challenge. Restoration practitioners may need to consider either an active management approach or novel restoration strategies to restore high-quality seasonal wetland habitat. Active management practices designed to remove or control the remineralization of P warrant investigation with respect to their efficacy, impacts on plant and animal communities, and the cost of widespread implementation. A handful of ideas that continue to resurface include chemically capping sediments using alum treatments and Phoslock (Steinman et al. 2004, Copetti et al. 2016) and physically removing P by harvesting invasive species biomass (Lishawa et al. 2015) or maintaining grazing livestock in restored wetlands (Biró et al. 2019, 2020). Numerous studies have shown that sediment dredging can be an effective P management tool when there are sufficient time and funds to perform preliminary adsorption studies that can inform project design (Oldenborg and Steinman 2019) or when used in combination with chemical treatment (Lürling and Faassen 2012). In our study, land managers involved in the restoration had neither the time nor resources to perform detailed preliminary studies and post hoc chemical treatments. Wetlands have somewhat predictable patterns of nutrient availability in the years following restoration and the effects of sediment excavation on water quality are more pronounced in shallow wetlands that experience periodic drawdown than in wetlands with fairly stable hydrology.

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Author contributions: SGW conceived, designed, and implemented the study; analyzed and interpreted the data; and wrote the manuscript. JCF contributed to data interpretation and analysis and contributed to writing the manuscript.

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LITERATURE CITED

APHA (American Public Health Association). 1992a. 4500-NO_3^- nitrogen (nitrate). Pages 87–94 *in* A. E. Greensberg, L. S. Clesceri, A. D. Eaton, and M. A. H. Franson (editors). Standard methods for examination of water and wastewater. 18th edition. American Public Health Association, Washington, DC.

APHA (American Public Health Association). 1992b. 4500-P phosphorus. Pages 108–117 *in* A. E. Greensberg, L. S. Clesceri, A. D. Eaton, and M. A. H. Franson (editors). Standard methods for examination of water and wastewater. 18th edition. American Public Health Association, Washington, DC.

APHA (American Public Health Association). 1998. 4500-NH_3 nitrogen (ammonia). Pages 108–117 *in* S. Stieg, B. R. Fisher, O. B. Mathre, and T. M. Wright (editors). Standard methods for examination of water and wastewater. 20th edition. American Public Health Association, Washington, DC.

APHA (American Public Health Association). 2005. 5310 total organic carbon (TOC). Pages 19–26 *in* E. W. D. Huffman, K. O. Brinkmann, R. C. Dage, P. S. Fair, L. A. Kaplan, P. L. Meschi, J. W. O'Dell, and M. Plam (editors). Standard methods for the examination of water and wastewater. 21st edition. American Public Health Association, Washington, DC.

ASTM (American Society for Testing and Materials). 2008. Standard test method for total chemically bound nitrogen in water by pyrolysis and chemiluminescence detection. American Society for Testing and Materials International, West Conshohocken, Pennsylvania.

Bates, D., M. Maechler, B. Bolker, S. Walker, R. H. B. Christensen, H. Singmann, B. Dai, F. Scheipl, G. Grothendieck, P. Green, and J. Fox. 2020. *lme4*: Linear mixed-effects models using "Eigen" and S4. (Available from: https://cran.r-project.org/web/packages/lme4/index.html)

Birch, H. F. 1964. Mineralisation of plant nitrogen following alternate wet and dry conditions. Plant and Soil 20:43–49.

Biró, M., Z. Molnár, D. Babai, A. Dénes, A. Fehér, S. Barta, L. Sáfián, K. Szabados, A. Kiš, L. Demeter, and K. Öllerer. 2019. Reviewing historical traditional knowledge for innovative conservation management: A re-evaluation of wetland grazing. Science of the Total Environment 666:1114–1125.

Biró, M., Z. Molnár, K. Öllerer, A. Lengyel, V. Ulicsni, K. Szabados, A. Kiš, R. Perić, L. Demeter, and D. Babai. 2020. Conservation and herding co-benefit from traditional extensive wetland grazing. Agriculture, Ecosystems & Environment 300:106983.

Bormans, M., B. Maršálek, and D. Jančula. 2016. Controlling internal phosphorus loading in lakes by physical methods to reduce cyanobacterial blooms: A review. Aquatic Ecology 50:407–422.

Bünemann, E. K. 2015. Assessment of gross and net mineralization rates of soil organic phosphorus—A review. Soil Biology and Biochemistry 89:82–98.

Carlton, R. G., and R. G. Wetzel. 1987. Distributions and fates of oxygen in periphyton communities. Canadian Journal of Botany 65:1031–1037.

Cheng, F., and N. B. Basu. 2017. Biogeochemical hotspots: Role of small water bodies in landscape nutrient processing. Water Resources Research 53:5036–5056.

Copetti, D., K. Finsterle, L. Marziali, F. Stefani, G. Tartari, G. Douglas, K. Reitzel, B. M. Spears, I. J. Winfield, G. Crosa, P. D'Haese, S. Yasseri, and M. Lürling. 2016. Eutrophication management in surface waters using lanthanum modified bentonite: A review. Water Research 97:162–174.

Cowardin, L. M., and F. C. Golet. 1995. US Fish and Wildlife Sevice 1979 wetland classification: A review. Vegetatio 118:139–152.

Dahl, T. E. 2014. Status and trends of prairie wetlands in the United States 1994 to 2009. United States Department of the Interior, Fish and Wildlife Service, Ecological Services, Washington DC.

Detenbeck, N. E., C. M. Elonen, D. L. Taylor, A. M. Cotter, F. A. Puglisi, and W. D. Sanville. 2002. Effects of agricultural activities and best management practices on water quality of seasonal prairie pothole wetlands. Wetlands Ecology and Management 10:335–354.

Dodds, W. K., W. W. Bouska, J. L. Eitzmann, T. J. Pilger, K. L. Pitts, A. J. Riley, J. T. Schloesser, and D. J. Thornbrugh. 2009. Eutrophication of U.S. freshwaters: Analysis of potential economic damages. Environmental Science & Technology 43:12–19.

Domagalski, J. L., and H. M. Johnson. 2011. Subsurface transport of orthophosphate in five agricultural watersheds, USA. Journal of Hydrology 409:157–171.

Downing, J. A., Y. T. Prairie, J. J. Cole, C. M. Duarte, L. J. Tranvik, R. G. Striegl, W. H. McDowell, P. Kortelainen, N. F. Caraco, J. M. Melack, and J. J. Middelburg. 2006. The global abundance and size distribution of lakes, ponds, and impoundments. Limnology and Oceanography 51:2388–2397.

Fasching, C., H. F. Wilson, S. C. D'Amario, and M. A. Xenopoulos. 2019. Natural land cover in agricultural catchments alters flood effects on DOM composition and decreases nutrient levels in streams. Ecosystems 22:1530–1545.

Freeman, C., N. J. Ostle, N. Fenner, and H. Kang. 2004. A regulatory role for phenol oxidase during decomposition in peatlands. Soil Biology and Biochemistry 36:1663–1667.

Galatowitsch, S. M., and A. G. van der Valk. 1994. Restoring prairie wetlands: An ecological approach. Iowa State University Press, Ames, Iowa.

Gelso, B. R., J. A. Fox, and J. M. Peterson. 2008. Farmers' perceived costs of wetlands: Effects of wetland size, hydration, and dispersion. American Journal of Agricultural Economics 90:172–185.

Groffman, P. M., K. Butterbach-Bahl, R. W. Fulweiler, A. J. Gold, J. L. Morse, E. K. Stander, C. Tague, C. Tonitto, and P. Vidon. 2009. Challenges to incorporating spatially and temporally explicit phenomena (hotspots and hot moments) in denitrification models. Biogeochemistry 93:49–77.

Gulati, R. D., and E. van Donk. 2002. Lakes in the Netherlands, their origin, eutrophication and restoration: State-of-the-art review. Hydrobiologia 478:73–106.

Hall, R. I., P. R. Leavitt, R. Quinlan, A. S. Dixit, and J. P. Smol. 1999. Effects of agriculture, urbanization, and climate on water quality in the northern Great Plains. Limnology and Oceanography 44:739–756.

Hansen, A. T., C. L. Dolph, E. Foufoula-Georgiou, and J. C. Finlay. 2018. Contribution of wetlands to nitrate removal at the watershed scale. Nature Geoscience 11:127–132.

Harrison, J. A., R. J. Maranger, R. B. Alexander, A. E. Giblin, P. A. Jacinthe, E. Mayorga, S. P. Seitzinger, D. J. Sobota, and W. M. Wollheim. 2009. The regional and global significance of nitrogen removal in lakes and reservoirs. Biogeochemistry 93:143–157.

Heisler, J., P. M. Glibert, J. M. Burkholder, D. M. Anderson, W. Cochlan, W. C. Dennison, Q. Dortch, C. J. Gobler, C. A. Heil, E. Humphries, A. Lewitus, R. Magnien, H. G. Marshall, K. Sellner, D. A. Stockwell, D. K. Stoecker, and M. Suddleson. 2008. Eutrophication and harmful algal blooms: A scientific consensus. Harmful Algae 8:3–13.

Jeppesen, E., J. P. Jensen, M. Søndergaard, T. Lauridsen, L. J. Pedersen, and L. Jensen. 1997. Top-down control in freshwater lakes: The role of nutrient state, submerged macrophytes and water depth. Hydrobiologia 342–343:151–164.

Jeppesen, E., M. Søndergaard, J. P. Jensen, K. E. Havens, O. Anneville, L. Carvalho, M. F. Coveney, R. Deneke, M. T. Dokulil, B. Foy, D. Gerdeaux, S. E. Hampton, S. Hilt, K. Kangur, J. Köhler, E. H. H. R. Lammens, T. L. Lauridsen, M. Manca, M. R. Miracle, B. Moss, P. Nõges, G. Persson, G. Phillips, R. Portielje, S. Romo, C. L. Schelske, D. Straile, I. Tatrai, E. Willén, and M. Winder. 2005. Lake responses to reduced nutrient loading—An analysis of contemporary long-term data from 35 case studies. Freshwater Biology 50:1747–1771.

Johnson, L. T., and J. L. Tank. 2009. Diurnal variations in dissolved organic matter and ammonium uptake in six open-canopy streams. Journal of the North American Benthological Society 28:694–708.

Johnson, P. T. J., and J. M. Chase. 2004. Parasites in the food web: Linking amphibian malformations and aquatic eutrophication. Ecology Letters 7:521–526.

Kuznetsova, A., P. B. Brockhoff, R. H. B. Christensen, and S. P. Jensen. 2020. *lmerTest*: Tests in linear mixed effects models. (Available from: https://cran.r-project.org/web/packages/lmerTest/index.html)

LaBaugh, J. W., T. C. Winter, V. A. Adomaitis, and G. A. Swanson. 1987. Hydrology and chemistry of selected prairie wetlands in the Cottonwood Lake area, Stutsman County, North Dakota, 1979–82. Professional Paper 1431. United States Geological Survey, Reston, Virginia.

Larkin, D. J., M. J. Freyman, S. C. Lishawa, P. Geddes, and N. C. Tuchman. 2012. Mechanisms of dominance by the invasive hybrid cattail *Typha* × *glauca*. Biological Invasions 14:65–77.

Lenth, R., H. Singmann, J. Love, P. Buerkner, and M. Herve. 2020. *emmeans*: Estimated marginal means, aka least-squares means. (Available from: https://cran.r-project.org/web/packages/emmeans/emmeans.pdf)

Li, Y., L. Wang, Z. Yan, C. Chao, H. Yu, D. Yu, and C. Liu. 2020. Effectiveness of dredging on internal phosphorus loading in a typical aquacultural lake. Science of the Total Environment 744:140883.

Lishawa, S. C., B. A. Lawrence, D. A. Albert, and N. C. Tuchman. 2015. Biomass harvest of invasive *Typha* promotes plant diversity in a Great Lakes coastal wetland. Restoration Ecology 23: 228–237.

Liss, P. S., and P. G. Slater. 1974. Flux of gases across the air–sea interface. Nature 247:181–184.

Liston, S. E., S. Newman, and J. C. Trexler. 2008. Macroinvertebrate community response to eutrophication in an oligotrophic wetland: An in situ mesocosm experiment. Wetlands 28:686–694.

Liu, C., J. Zhong, J. Wang, L. Zhang, and C. Fan. 2016. Fifteen-year study of environmental dredging effect on variation of nitrogen and phosphorus exchange across the sediment-water interface of an urban lake. Environmental Pollution 219:639–648.

Luo, H.-R., L. M. Smith, B. L. Allen, and D. A. Haukos. 1997. Effects of sedimentation on playa wetland volume. Ecological Applications 7:247–252.

Lürling, M., and E. J. Faassen. 2012. Controlling toxic cyanobacteria: Effects of dredging and phosphorus-binding clay on cyanobacteria and microcystins. Water Research 46:1447–1459.

Mackay, E. B., H. Feuchtmayr, M. M. De Ville, S. J. Thackeray, N. Callaghan, M. Marshall, G. Rhodes, C. A. Yates, P. J. Johnes, and S. C. Maberly. 2020. Dissolved organic nutrient uptake by riverine phytoplankton varies along a gradient of nutrient enrichment. Science of the Total Environment 722:137837.

Mallin, M. A., V. L. Johnson, S. H. Ensign, and T. A. MacPherson. 2006. Factors contributing to hypoxia in rivers, lakes, and streams. Limnology and Oceanography 51:690–701.

McCauley, L. A., M. J. Anteau, M. P. van der Burg, and M. T. Wiltermuth. 2015. Land use and wetland drainage affect water levels and dynamics of remaining wetlands. Ecosphere 6:1–22.

McCrackin, M. L., B. Muller-Karulis, B. G. Gustafsson, R. W. Howarth, C. Humborg, A. Svanbäck, and D. P. Swaney. 2018. A century of legacy phosphorus dynamics in a large drainage basin. Global Biogeochemical Cycles 32:1107–1122.

Mitsch, W. J., and J. W. Day. 2006. Restoration of wetlands in the Mississippi-Ohio-Missouri (MOM) River Basin: Experience and needed research. Ecological Engineering 26:55–69.

Mitsch, W. J., J. W. Day, L. Zhang, and R. R. Lane. 2005. Nitrate-nitrogen retention in wetlands in the Mississippi River Basin. Ecological Engineering 24:267–278.

Morris, P. F., and W. G. Barker. 1977. Oxygen transport rates through mats of *Lemna minor* and *Wolffia* sp. and oxygen tension within and below the mat. Canadian Journal of Botany 55:1926–1932.

Müller, B., R. Thoma, K. B. L. Baumann, C. M. Callbeck, and C. J. Schubert. 2021. Nitrogen removal processes in lakes of different trophic states from on-site measurements and historic data. Aquatic Sciences 83:37.

Murphy, J., and J. P. Riley. 1962. A modified single solution method for the determination of phosphate in natural waters. Analytica Chimica Acta 27:31–36.

Oldenborg, K. A., and A. D. Steinman. 2019. Impact of sediment dredging on sediment phosphorus flux in a restored riparian wetland. Science of the Total Environment 650:1969–1979.

Olila, O. G., K. R. Reddy, and D. L. Stites. 1997. Influence of draining on soil phosphorus forms and distribution in a constructed wetland. Ecological Engineering 9:157–169.

Patrick, W. H., and R. A. Khalid. 1974. Phosphate release and sorption by soils and sediments: Effect of aerobic and anaerobic conditions. Science 186:53–55.

Pellerin, B. A., W. M. Wollheim, C. S. Hopkinson, W. H. McDowell, M. R. Williams, C. J. Vörösmarty, and M. L. Daley. 2004. Role of wetlands and developed land use on dissolved organic nitrogen concentrations and DON/TDN in northeastern U.S. rivers and streams. Limnology and Oceanography 49:910–918.

Preston, T. M., R. S. Sojda, and R. A. Gleason. 2013. Sediment accretion rates and sediment composition in prairie pothole wetlands under varying land use practices, Montana, United States. Journal of Soil and Water Conservation 68:199–211.

Reddy, K. R., R. H. Kadlec, E. Flaig, and P. M. Gale. 1999. Phosphorus retention in streams and wetlands: A review. Critical Reviews in Environmental Science and Technology 29:83–146.

Richardson, A. E., and R. J. Simpson. 2011. Soil microorganisms mediating phosphorus availability. Plant Physiology 156:989–996.

Romero, J. A., F. A. Comín, and C. García. 1999. Restored wetlands as filters to remove nitrogen. Chemosphere 39:323–332.

Rose, C., and W. G. Crumpton. 1996. Effects of emergent macrophytes on dissolved oxygen dynamics in a prairie pothole wetland. Wetlands 16:495–502.

Salk, K. R., A. D. Steinman, and N. E. Ostrom. 2018. Wetland restoration and hydrologic reconnection result in enhanced watershed nitrogen retention and removal. Wetlands 38:349–359.

Scholte, S. S. K., M. Todorova, A. J. A. van Teeffelen, and P. H. Verburg. 2016. Public support for wetland restoration: What is the link with ecosystem service values? Wetlands 36:467–481.

Skopec, M., and V. Evelsizer. 2018. Spring nutrient levels in drained wetlands of Iowa's Prairie Pothole Region. Wetlands 38:261–273.

Smith, R. L. 1991. Chemical concentration data near the detection limit. EPA/903/8-91/001. Region III technical guidance manual. Office of Superfund, Hazardous Waste Management, Philadelphia, Pennsylvania.

Smith, V. H. 2003. Eutrophication of freshwater and coastal marine ecosystems: A global problem. Environmental Science and Pollution Research 10:126–139.

Smith, V. H., and D. W. Schindler. 2009. Eutrophication science: Where do we go from here? Trends in Ecology and Evolution 24:201–207.

Søndergaard, M., P. J. Jensen, and E. Jeppesen. 2001. Retention and internal loading of phosphorus in shallow, eutrophic lakes. The Scientific World Journal 1:427–442.

Søndergaard, M., E. Jeppesen, and J. P. Jensen. 2005. Pond or lake: Does it make any difference? Archiv fur Hydrobiologie 162:143–165.

Søndergaard, M., P. Kristensen, and E. Jeppesen. 1992. Phosphorus release from resuspended sediment in the shallow and wind-exposed Lake Arresø, Denmark. Hydrobiologia 228:91–99.

Steinman, A., R. Rediske, and K. R. Reddy. 2004. The reduction of internal phosphorus loading using alum in Spring Lake, Michigan. Journal of Environmental Quality 33:2040–2048.

Steinman, A. D., M. E. Ogdahl, M. Weinert, K. Thompson, M. J. Cooper, and D. G. Uzarski. 2012. Water level fluctuation and sediment-water nutrient exchange in Great Lakes coastal wetlands. Journal of Great Lakes Research 38:766–775.

Stewart, R. E., and H. A. Kantrud. 1971. Classification of natural ponds and lakes in the glaciated Prairie Region. United States Department of the Interior, Fish and Wildlife Service, Bureau of Sport Fisheries and Wildlife, Washington, DC.

Stubbs, M. 2014. Conservation Reserve Program (CRP): Status and issues. Report No. R42783. Congressional Research Service, Washington, DC. (Available from: https://crsreports.congress.gov/product/pdf/R/R42783)

Stutter, M. I., D. Graeber, C. D. Evans, A. J. Wade, and P. J. A. Withers. 2018. Balancing macronutrient stoichiometry to alleviate eutrophication. Science of the Total Environment 634:439–447.

Tiwari, V., and A. Kashikar. 2019. *OutlierDetection*: Outlier detection. (Available from: https://cran.r-project.org/src/contrib/Archive/OutlierDetection/)

Tsai, J.-S., L. S. Venne, S. T. McMurry, and L. M. Smith. 2007. Influences of land use and wetland characteristics on water loss rates and hydroperiods of playas in the Southern High Plains, USA. Wetlands 27:683–692.

van der Kamp, G., and M. Hayashi. 2009. Groundwater–wetland ecosystem interaction in the semiarid glaciated plains of North America. Hydrogeology Journal 17:203–214.

van Donk, E., R. D. Gulati, A. Iedema, and J. T. Meulemans. 1993. Macrophyte-related shifts in the nitrogen and phosphorus contents of the different trophic levels in a biomanipulated shallow lake. Hydrobiologia 251:19–26.

Van Meter, K. J., and N. B. Basu. 2015. Signatures of human impact: Size distributions and spatial organization of wetlands in the Prairie Pothole landscape. Ecological Applications 25: 451–465.

Van Meter, K. J., N. B. Basu, J. J. Veenstra, and C. L. Burras. 2016. The nitrogen legacy: Emerging evidence of nitrogen accumulation in anthropogenic landscapes. Environmental Research Letters 11:35014.

Vymazal, J., and T. D. Březinová. 2018. Removal of nutrients, organics and suspended solids in vegetated agricultural drainage ditch. Ecological Engineering 118:97–103.

Westbrook, C. J., N. Brunet, I. Phillips, and J.-M. Davies. 2011. Wetland drainage effects on prairie water quality: Final report. University of Saskatchewan, Saskatoon, Saskatchewan, Canada.

Wetzel, R. G. 1990. Land-water interfaces: Metabolic and limnological regulators. Internationale Vereinigung für Theoretische und Angewandte Limnologie: Verhandlungen 24:6–24.

Winikoff, S. G., D. J. Larkin, S. L. Meier, and J. C. Finlay. 2020. Vegetation trajectories of restored agricultural wetlands following sediment removal. Restoration Ecology 28:612–622.

Woo, I., and J. B. Zedler. 2002. Can nutrients alone shift a sedge meadow towards dominance by the invasive *Typha* × *glauca*? Wetlands 22:509–521.