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Invasion of common carp (*Cyprinus carpio*) reduces the quality of bottom sediments in shallow lakes

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HIGHLIGHTS

- Common carp significantly reduce phosphorus concentrations in the surficial sediment of shallow lakes
- Lakes with carp have higher sediment C/P ratios and decreased sediment organic matter quality
- Sediment phosphorus loss is largely retained in the water column, driving eutrophication in carp-infested lakes

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ABSTRACT

Species invasions are one of the main anthropogenic forces reshaping ecological structure and function in lakes during the 21st century. Common carp (*Cyprinus carpio*) are among the most globally widespread and damaging aquatic invasive species, with the capacity to significantly alter lake ecosystems. While it is well documented that carp feeding activity can disturb sediments, decrease water quality, and reduce macrophyte and fish diversity, less is known about how carp influence sediment chemistry and nutrient cycling. Here, we examined the effect of carp invasion on sediment phosphorus (P) dynamics and organic matter quality in shallow lakes. We compared P fractions in sediments of lakes with established carp populations and those from carp-free reference lakes. We found that lakes with carp had depleted surficial sediments, with significantly lower organic P (0.16 vs. 0.41 mg g^{-1}) and higher C/P ratios (972 vs. 639) than lakes without carp. Carp lakes had higher concentrations of water-column total P (370 vs. 160 μg L^{-1}), though a mass balance between sediment labile P and water-column P was similar for lakes with and without carp, indicating sediment P loss due to carp is largely kept in the water column. Sediments are a crucial component of lake ecosystems, and a reduction in sediment organic matter quality by invasive carp can alter food web dynamics and geochemical processes in invaded lakes.

1. Introduction

As human activity accelerates global connectivity, biological invasions are increasingly reshaping the structure and function of aquatic ecosystems (Gallardo et al., 2016; Havel et al., 2015). Invasive species not only affect native biodiversity, but can also transform entire ecosystems by altering food web dynamics, habitat structure, and biogeochemical processes. Freshwater ecosystems can be particularly susceptible to species invasions and ecosystem alterations, because they already face widespread degradation from urbanization and pollution (Vander Zanden et al., 2024), coupled with the ease of transporting and releasing aquatic species (Moorhouse & Macdonald, 2015).

Invasions in freshwaters may also pose severe consequences, given the numerous human services provided by freshwater ecosystems, and their importance as biodiversity hotspots and key terrestrial/aquatic interfaces (Havel et al., 2015; Moorhouse & Macdonald, 2015; Vander Zanden et al., 2024). Freshwater ecosystems have a high degree of endemism and greater biodiversity per surface area than both marine and terrestrial ecosystems (Dudgeon et al., 2006). Freshwaters also regulate the flow of water and materials across the landscape and are active sites of carbon and nutrient cycling, both at local and global scales (Battin et al., 2009; Wetzel, 2001). Invasive species have already deeply transformed freshwater ecosystems across many landscapes (Dudgeon et al., 2006; Gallardo et al., 2016), and it remains crucial to fully

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understand the impacts and subsequent consequences of freshwater invasive species.

One of the most widespread and damaging freshwater invasive species is the common carp (*Cyprinus carpio* or 'carp'; Sorensen & Bajer, 2011; Weber & Brown, 2009). Carp are originally native to eastern Europe and Asia, but have now been introduced to every continent except Antarctica. Carp were introduced to North America in the late 1800s, and in the past 100 years have established themselves in various ecosystem types throughout North America (Sorensen & Bajer, 2011). Carp are capable of dominating freshwater communities across entire regions (Bajer et al., 2016), and are pervasive across large areas of Australia, Africa, Mexico, North and South America, and Western Europe (Vilizzi, 2012; Weber & Brown, 2009).

Carp are large, benthivorous fish and are considered ecosystem engineers (Badiou et al., 2011; Matsuzaki et al., 2009). While searching for food in sediments, carp uproot aquatic plants and increase water turbidity. Sediment bioturbation from carp feeding activity has been well associated with a reduction or elimination of submerged plants (Bajer et al., 2016; Bajer & Sorensen, 2015), an increase of dissolved and suspended nutrients (Huser et al., 2016, 2022), and decrease of native fish, benthic invertebrate, and waterfowl diversity (Badiou et al., 2011; Bajer et al., 2009; Stewart & Downing, 2008). Despite numerous studies showing that carp reduce water quality and species diversity, however, their specific effects on sediment nutrients and organic matter remain unclear. Sediments are a crucial component of freshwater ecosystems as sites of intense microbial activity, nutrient cycling, and sequestration (Wetzel, 2001), and benthic resources can form the foundation of lake food webs (Schindler & Scheuerell, 2002). Bioturbation from carp feeding activity can potentially modify sediment processes, and while some studies have shown that carp bioturbation can alter nutrient cycling in single lakes (e.g. Huser et al., 2022), it is unknown how carp may change sediment dynamics at larger, regional scales.

In this study, we examined the influence of carp on the sedimentary environment of 17 shallow lakes in a region heavily impacted by carp invasion. We collected and analyzed sediment cores to compare phosphorus (P) dynamics, organic matter quality, and associated water quality parameters between lakes with and without established carp populations. We hypothesized that bioturbation by carp would reduce labile phosphorus and organic matter in the sediments of carp-invaded lakes, creating a low-quality sedimentary environment for benthic organisms.

2. Materials and Methods

2.1. Study area and Carp abundance

The 17 shallow lakes in this study were located in southern Minnesota, USA (Fig. S1; Rabaey et al., 2025), a region where over 70% of lakes harbor abundant carp populations (biomass >200 kg ha^{-1}; Bajer et al., 2016). We chose shallow lakes as they are productive systems (Rabaey et al., 2024), where carp thrive across much of the Great Plains ecoregion of North America (Egertson & Downing, 2004). Carp are considered a destructive invasive species in this region, but spread to lakes via natural waterways or accidental introduction. The 17 study lakes were chosen to have similar characteristics outside of the carp infestation, and all were natural, lentic systems, though most had natural inflow and outflow streams. All lakes were polymictic, in agricultural watersheds, and followed the definition of shallow lakes (approximately 5m or less in maximum depth with less than 30% of surface area covered by emergent vegetation; Richardson et al., 2022). Lake surface area ranged from 0.563 to 10.8 km^2, and maximum depth ranged from 1.1 to 5.49 m.

To assess carp presence and abundance, we conducted electrofishing transect surveys (Bajer & Sorensen, 2012). Each lake was surveyed in the summer of 2023 between June and July, and surveys consisted of three 20-minute electrofishing transects. Each transect was conducted in a different area of the lake and confined to areas less than 1.5 m in depth. We used a flat-bottom aluminum boat that generated a pulsed DC electric field (5–12 A, 80–150 V, 20% duty cycle, 120-pulse frequency). The boat was equipped with two anodes located approximately 3 m in front of the boat, while the boat hull functioned at the cathode. The boat was maneuvered at a slow speed (~0.5 to 1 m s^{-1}) in a zigzagging fashion along the shore while stunned carp were collected and placed in a live well. The length of captured carp was measured and the total catch per unit effort from surveys was used to estimate carp density based on a regression analysis from eight Minnesota lakes (R^2 = 0.83; Bajer & Sorenson, 2012): Carp density (carp ha^{-1}) = 4.71*Electrofishing CPUE + 3.04. The average carp length was then used to estimate total lake carp biomass (kg ha^{-1}). The presence of other non-carp fish species was obtained from the most recent Minnesota Department of Natural Resources lake surveys, or from onsite observations during electrofishing surveys. Ten of the 17 study lakes had detectable carp populations at the time of this study according to electrofishing surveys, while the other seven had no carp detected. These two lake categories are referred to here as "carp" and "carp-free" lakes.

2.2. Water quality and macrophyte abundance

Each study lake was sampled twice in the summer of 2023 (June - August) for water quality and water chemical variables. At each sampling event, profiles were taken at the deepest point of the lake to measure water temperature, dissolved oxygen concentration, pH, and chlorophyll *a* concentration at 1 s intervals using an EXO2 Sonde (YSI, Yellow Springs Ohio, United States). At the same location, a depth-integrated water sample was collected using a 3 m PVC tube to measure total phosphorus (TP) concentration using the molybdenum blue reaction (Murphy & Riley, 1962).

Submerged macrophyte surveys were conducted in each lake once during the second sampling event. Macrophytes were sampled at 10 randomly selected points in each lake, with all points selected to be within 0.5-2.5 m deep. Macrophyte samples were collected using a 0.33-m wide, 14-tine, single-headed rake attached to a 3-m long pole. The rake was lowered to the sediment surface and slowly turned in 3 rotations before slowly lifting the rake straight up while continuing to rotate. Each sample collected macrophytes from approximately 0.09 m^2 of sediment (Johnson & Newman, 2011). The samples were identified to the genus or species level, drained of excess water and dried in a salad spinner for 1 minute, then weighed to estimate wet biomass.

2.3. Sediment analysis

To determine P forms and concentrations in the sediment, we collected sediment cores from each study lake in November 2023. We collected sediment cores after the fall mixing period to maximize the amount of P in the sediment and equalize any effect of internal loading during summer periods of elevated organic matter mineralization or anoxia. A rod-deployed piston corer was used to collect all sediment cores, which were sliced on-site (every 2 cm), and stored at 4°C in the dark until analysis. Sediment P fractions were determined for the top 40 cm of each core using a sequential phosphorus extraction technique for wet sediment (Hupfer et al., 1995, 2009; Psenner et al., 1988), adapted to the following steps: extraction with ultrapure H_2O for 2 h, extraction with 0.11 M BD bicarbonate/dithionite for 2 h, extraction with 0.1 M NaOH for 16 h, and extraction with 0.5 M HCl for 16 h. Soluble reactive P from all sediment extracts, as well as digested extracts from the NaOH step, was analyzed using the molybdenum blue method (Murphy & Riley, 1962). We define the fractions based on the expected P species from each extraction step (Hupfer et al., 2009), which includes mobile P (pore water, loosely sorbed, and redox-sensitive P; extracted as H_2O-P and BD-P), aluminum-bound P (ligand exchangeable P, extracted as NaOH-P), organic P (extracted as autoclave digested NaOH-P), calcium-bound P (extracted as HCl-P), and total P as the sum of these fractions. We define the mobile and organic P fractions together as labile P (i.e., potentially releasable P).

To estimate elevated amounts of P in surficial sediment and compare across lakes in different watersheds, we estimated background concentrations of sediment P for each fraction in each lake. To determine the sediment depth at which P concentrations stabilized, we calculated running slopes of P vs. sediment depth for each fraction, using a sliding window of 8 cm. Across all lakes and all P fractions, the slope of P concentrations were much more stable below 20 cm compared to above 20 cm, and mean slopes below 20 cm were all within one standard deviation of the slope at the deepest depth (Fig. S2). As a result, we considered P concentrations from 20-40 cm as background concentrations, and scaled all P fractions in each lake by subtracting the mean concentrations from this layer. This is supported by previous work showing carp can mix sediments down to 20 cm in some cases (Huser et al. 2016). Deeper sediment layers often have more stable P concentrations and contain more recalcitrant fractions due to mineralization and diffusion processes. Because labile P continuously moves toward the sediment surface over time, this approach is commonly used to compare patterns of labile P in sediment (Huser et al., 2022; Schütz et al., 2017).

Water content was determined by freeze-drying frozen sediment (stored at −18°C until completely frozen). Sequential loss on ignition was performed on all core samples, first for 2 h at 550°C to determine organic matter content, and second for 2 h at 1050°C to determine inorganic C ($CaCO_3$) content. Organic matter (%) and water content were used to estimate sediment density (Håkanson & Jansson, 1983), which was used to calculate the concentration (dry weight) and mass of P forms in the sediment. Organic carbon (C) content was calculated using the equation: organic C (%) = organic matter (%) x 0.4 (Hobbs et al., 2013; Rosén et al., 2010). C/P ratios were calculated for the organic sediment fraction using organic C and organic P molar concentrations.

2.4. Phosphorus mass balance

To compare different pools of P between carp lakes and carp-free lakes, we performed a mass balance of P by calculating areal concentrations (g m^{-2}) of labile P in the sediment, water-column P, and P in carp biomass for each lake. Labile sediment P included the total mass of organic and mobile P in the top 15 cm, which is the deepest sediment depth where significant differences were seen between carp-free and carp lakes. Areal concentrations of water-column P were determined by multiplying volumetric concentrations by lake mean depth. To determine the concentration of P within carp biomass, we multiplied the density of carp by 0.0074, which is the estimated fraction of P in common carp tissue (Nwanna et al., 2010).

2.5. Data analysis

All data analyses were performed using R statistical software (R Core Team, 2022). Because of small sample sizes, Wicoxon rank sum tests were used for all comparisons between carp and carp-free lakes. Simple linear regressions were used to assess relationships between variables, and all analyses used a significance level (α) of 0.05.

3. Results

3.1. Carp regimes and water quality

The 10 carp lakes had estimated carp densities ranging from 5.3 to 30.7 individuals ha^{-1}, and biomass ranging from 39.9 to 283.3 kg ha^{-1} (Table S1). Carp dominated the fish populations in most of the carp lakes, and all but three carp lakes had densities of over 100 kg ha^{-1}, a biomass threshold that has been shown to lead to dramatic declines in aquatic vegetation and species diversity (Table S1; Bajer et al., 2009). The seven carp-free lakes had no detectable carp populations during this study; however, several had documented carp populations within the previous 5 years, with complete removal occurring from winter deoxygenation or management activities (i.e. water level drawdown or rotenone treatment; Table S1). All lakes had populations of bullhead (*Ameiurus sp.*), a native benthic fish species, and most had piscivorous predator species present (Table S1).

All lakes were eutrophic to hypereutrophic, with mean water-column TP concentrations ranging from 53.6 to 807.9 μg l^{-1} (Table S2). Carp lakes had more than twice the mean TP concentrations of carp-free lakes (163 vs. 373 μg L^{-1}, $P = 0.088$), along with significantly higher chlorophyll *a* (Chl *a*, $P = 0.022$), turbidity ($P = 0.043$), and significantly lower submerged macrophyte abundance ($P = 0.028$; Table 1). Three of the lakes with carp had no detectable submerged macrophytes (Table S3), and all carp lakes were highly turbid.

3.2. Sediment characteristics

Across all study lakes, sediment organic C concentrations ranged from 5.2 to 17% dry weight, and inorganic C concentrations ranged from 5 to 53% (Table S4). Inorganic C concentrations were significantly correlated to the log of the drainage ratio (watershed area/lake surface area; $R^2 = 0.45$, $P = 0.0023$), with lakes with larger drainage ratios having higher concentrations of inorganic C.

Patterns of P fractions in the sediment varied between lakes (Fig. 1). Organic P decreased with increasing sediment depth in all cores and tended to be the dominant fraction in surficial sediments, with surface concentrations ranging from 0.16 to 0.67 mg g^{-1}. Calcium-bound P remained stable throughout the cores in most lakes with mean concentrations ranging from 0.11 to 0.45 mg g^{-1}. Patterns of mobile P varied widely between lakes, increasing in the surface layers of some cores, while decreasing in others (Fig. 1). Surface concentrations of mobile P were low but varied by an order of magnitude, ranging from 0.013 to 0.31 mg g^{-1} (Table S4). Concentrations of aluminum-bound P were also low (mean concentrations ranging from 0.021 to 0.095 mg g^{-1}), and increased in the surface layers or remained stable in all lakes (Fig. 1).

3.3. Phosphorus fractions in carp and carp-free lakes

Patterns of sediment organic P, aluminum-bound P, and total P differed significantly between carp lakes and carp-free lakes. Organic P

Table 1
Lake and water quality characteristics in lakes with and without carp. Row crop agriculture represents the percentage of watershed area occupied by row crops. DO represents dissolved oxygen; surface DO was defined as the mean DO concentration in the top 0.5 m of the water column, while bottom DO was defined as the mean DO concentration in the bottom 0.5 m. Macrophyte biomass represents submerged, rooted aquatic vegetation. TP represents total phosphorus concentration.

Variable	All Lakes[1] N = 17	Carp-free Lakes[1] N = 7	Carp Lakes[1] N = 10	**p value**[2]
Carp biomass (kg ha^{-1})	-	0 ± 0	160 ± 82	<0.001*
Maximum depth (m)	2.9 ± 1.2	3.0 ± 1.7	2.9 ± 0.86	0.9
Surface area (km^2)	2.9 ± 3.0	2.2 ± 2.7	3.3 ± 3.3	0.2
Watershed area (km^2)	6.8 ± 13	2.0 ± 2.0	10 ± 17	0.019*
Row crop agriculture (%)	51 ± 15	47 ± 11	54 ± 18	0.4
Surface DO (mg L^{-1})	10 ± 3.2	9.6 ± 3.5	11 ± 3.1	0.9
Bottom DO (mg L^{-1})	6.3 ± 3.0	5.7 ± 3.9	6.8 ± 2.2	0.5
Macrophyte biomass (kg m^{-2})	9.2 ± 13	17 ± 17	4.0 ± 6.0	0.028*
Turbidity (FNU)	26 ± 35	13 ± 9.0	34 ± 43	0.043*
Chl *a* (μg L^{-1})	23 ± 10	17 ± 11	26 ± 9.0	0.022*
TP (μg L^{-1})	290 ± 250	160 ± 130	370 ± 280	0.088

[1] Mean ± SD
[2] Wilcoxon rank sum test
* Indicates statistical significance ($P < 0.05$)

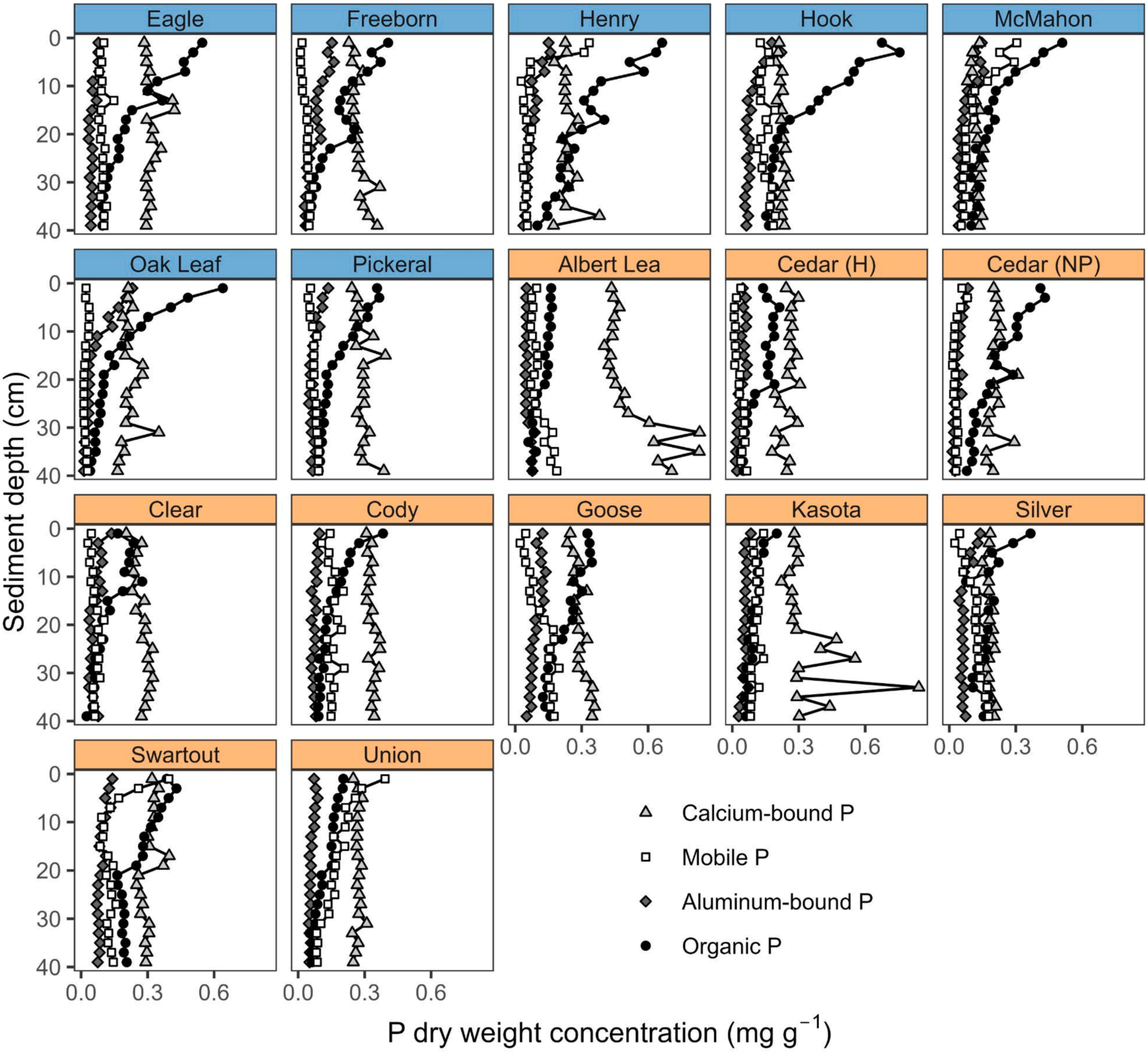

Fig. 1. Phosphorus (P) fractions in the top 40 cm of the 17 study lakes. Mobile P represents pore water, loosely sorbed, and redox-sensitive P. Carp-free lakes are highlighted in blue; carp lakes are highlighted in orange. Since two lakes were named Cedar, the nearest town abbreviation was added in parentheses to distinguish between lakes.

concentrations, relative to background concentrations, were significantly higher in the upper 10 cm of sediment of carp-free lakes, and surficial sediment concentrations were over 250% higher compared to carp lakes (0.41 vs. 0.16 mg g^{-1}; Fig. 2a). Organic P also increased more rapidly towards the sediment surface in carp-free lakes, with a significantly steeper slope in the top 20 cm ($P < 0.001$; Fig. 2b). Aluminum-bound P concentrations followed similar trends, and were significantly higher in the upper 8 cm of carp-free lakes, though the magnitude of difference was smaller compared to organic P (Fig. 2b). Several carp-free lakes had an increase of aluminum-bound P in the surficial sediment layers, while all carp lakes had stable concentrations through depth (Fig. 1). Total P concentrations were significantly higher concentrations in the top 15 cm of carp-free lakes, which also had a steeper slope of increase in surficial sediments compared to carp lakes (Fig. 2a, b). There were no significant differences in mobile P (Fig. 2a) or calcium-bound P (Fig. S1) concentrations between carp and carp-free lakes.

Across all lakes, calcium-bound P concentrations were significantly correlated with watershed size, with lakes in larger watersheds having higher concentrations of calcium-bound P throughout the sediment. Aluminum-bound P, Mobile P, and organic P were not correlated with watershed size (Fig. 3). While lake surface area and depth were similar between carp and carp-free lakes, watershed size was larger among carp lakes (mean 10.7 vs. 70.2 km^2, $P = 0.13$; Table 1), and larger watersheds have been shown to be more susceptible to carp invasion in this region (Herwig et al., 2026). Inorganic C ($CaCO_3$) was also positively correlated with watershed size ($P = 0.0022$, $R^2 = 0.45$), and highly correlated with calcium-bound P ($P < 0.001$, $R^2 = 0.52$).

3.4. Sediment organic matter quality

$(C/P)_{organic}$ ratios increased with increasing depth for all lakes, and were all well above the Redfield Ratio (417-1550 in top 2 cm of sediment). Carp lakes had significantly higher $(C/P)_{organic}$ ratios in the top 4 cm, with surface sediment ratios over 150% higher than carp-free lakes

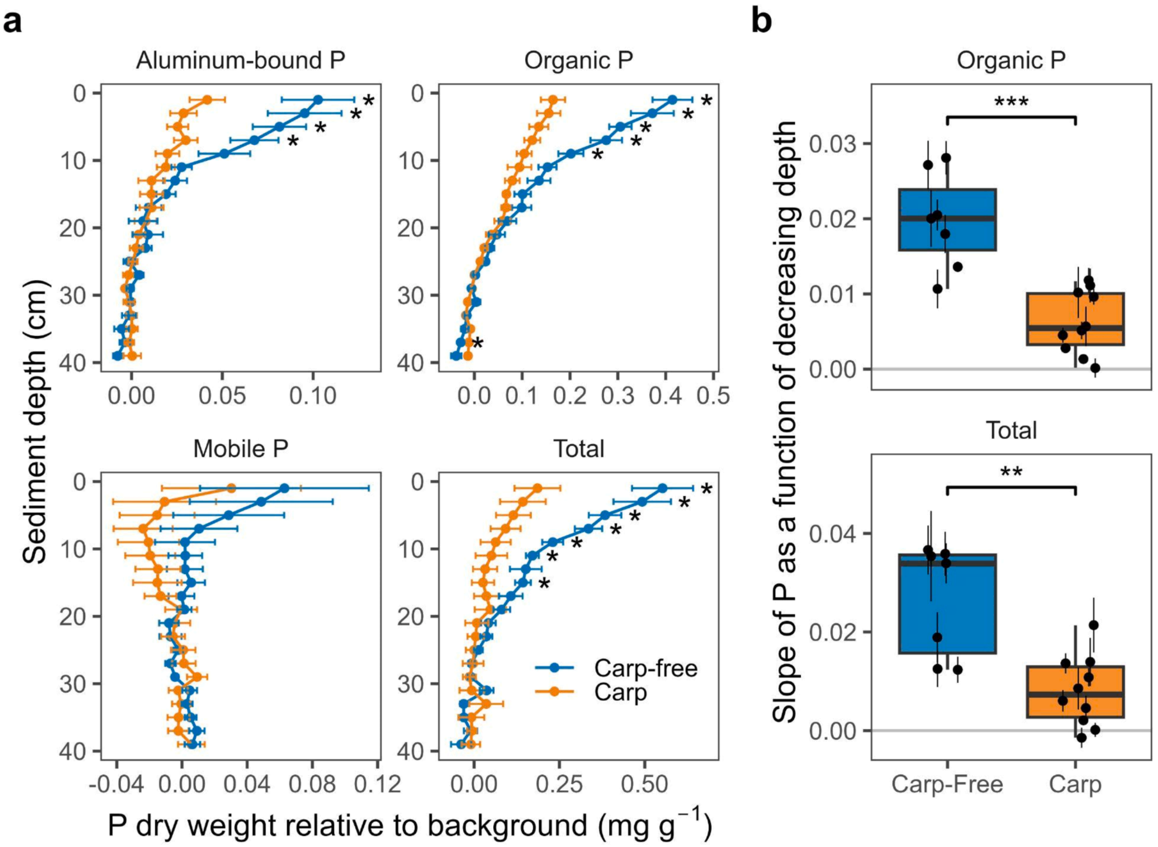

Fig. 2. Comparisons of phosphorus (P) fractions between carp (orange) and carp-free (blue) lakes. **a**, P dry weight concentrations relative to background (mean concentration 20-40 cm) for each fraction. Total represents the sum of all fractions. Asterisks (*) indicate a significant difference between carp and carp-free lakes ($P < 0.05$). Error bars represent ± SE. Calcium-bound P was relatively stable through depth in all lakes, and is shown in Fig. S1. **b**, The slope of P as a function of decreasing sediment depth in the top 20 cm between carp-free and carp lakes for organic P ($P = 0.0004$), and total P ($P = 0.0046$). Points represent the slope for each lake, and error bars represent ± SE.

(972 vs. 639, $P = 0.0038$; Fig. 4). Across all lakes, mean $(C/P)_{organic}$ ratios were not correlated with mean sediment organic C concentrations ($R^2 = 0.01$, $P = 0.69$), but were inversely correlated with mean organic P concentrations ($R^2 = 0.38$, $P = 0.0068$), indicating that the decrease in organic phosphorus is the main reason for the increase in C/P ratio.

3.5. *Phosphorus mass balance in carp and carp-free lakes*

On an areal basis (g m^{-2}), carp lakes had roughly half of the labile P in the top 15cm of the sediment compared to carp-free lakes, while carp lakes had more than twice the amount of P in the water column (Fig. 5). The amount of P in carp biomass was not negligible, and was on the same order of magnitude as water-column P. However, the higher water-column P and carp biomass P in carp lakes only accounted for one third of the gap in labile sediment P, and carp-free lakes had higher P concentrations when adding up the three P pools (Fig. 5).

4. Discussion

Among the shallow lakes in this study, invasive carp had a profound impact on sediment P dynamics and organic matter quality. Carp lakes had significantly lower concentrations of sediment P, and C/P ratios of sediment organic matter were significantly higher. The reduced retention of sediment P in carp lakes corresponded with reduced water quality, including higher Chl *a* concentrations, TP, and turbidity. These results clearly show that invasive carp alter the sedimentary environment of shallow lakes, and are capable of shifting biogeochemical cycles at both ecosystem and regional scales.

4.1. *Carp effects on sediment*

Carp had a distinct effect on the quantity and pattern of total P (total of all measured fractions) concentrations in the sediment. Sediment P profiles generally display distinct patterns within different trophic states, due to limited ability of eutrophic lakes to effectively bury P as P loads increase (Carey & Rydin, 2011). In eutrophic lakes, total P generally increases towards the sediment surface, with the slope of P increase (P as a function of decreasing sediment depth) being greater in more eutrophic systems. In these eutrophic-hypereutrophic study lakes, carp lakes had significantly lower total P concentrations in the top 15 cm of sediment, as well as a significantly lower slope of total P increase, despite higher water-column TP concentrations (Fig. 2b, Table 1). Several carp lakes had slopes near zero, and one carp lake had a negative slope for total P (Goose Lake, mean water-column TP of 100 μg L^{-1}), a phenomenon not seen in any eutrophic lakes in a previous study of sediment phosphorus patterns in 94 lakes (Carey & Rydin, 2011).

The majority of the difference in total sediment P between carp and carp free lakes was due to labile P (organic and mobile P) concentrations. Eutrophic lake sediments typically have higher concentrations of labile P in surface sediments, followed by a decrease until a stabilization depth in the burial zone (Boström & Pettersson, 1982). This labile P pool in surficial sediment can potentially be released back to the water column under certain conditions, as sediment in eutrophic lakes typically has a poor ability to permanently bind and bury P (Boström & Pettersson, 1982; Rydin, 2000). Carp lakes in this study, however, had little to no increase in organic P in the surficial sediment layers (Figs. 1, 2), similar to results seen in a single-lake carp removal study (Huser et al., 2022). While differences in mobile P were not significantly different

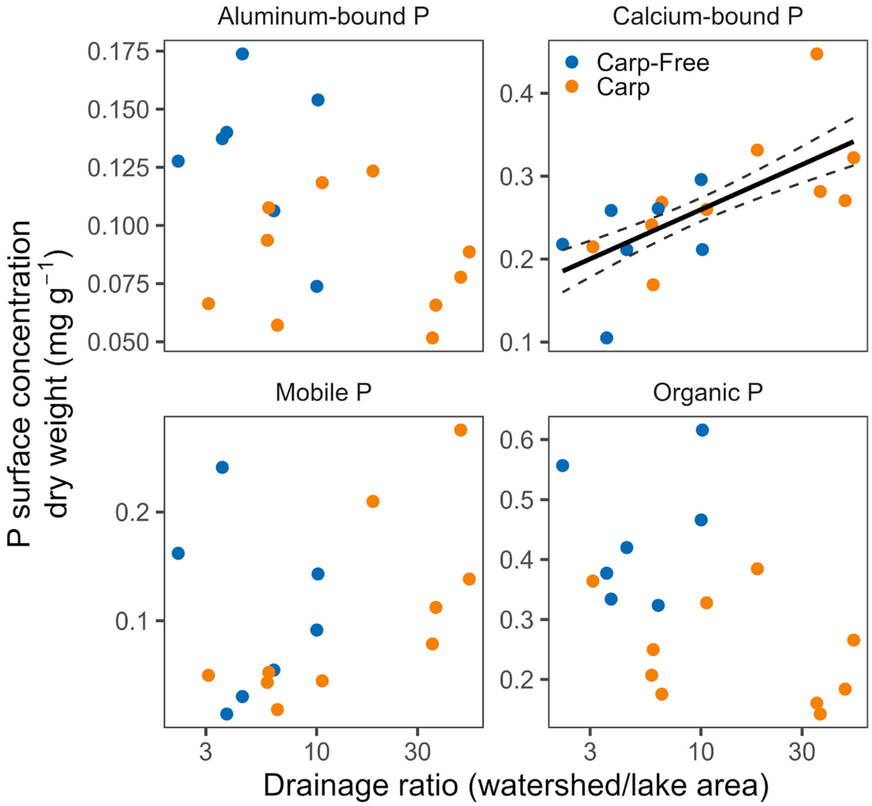

Fig. 3. The relationship between surface P concentrations and the drainage ratio for each lake among different P fractions. Calcium-bound P was significantly correlated with lake drainage ratio ($P = 0.0032$, $R^2 = 0.45$), while aluminum-bound P, mobile P, and Organic P were not. All surface P concentrations are means of the top 10 cm of sediment. Dashed lines represent ± 1 standard error.

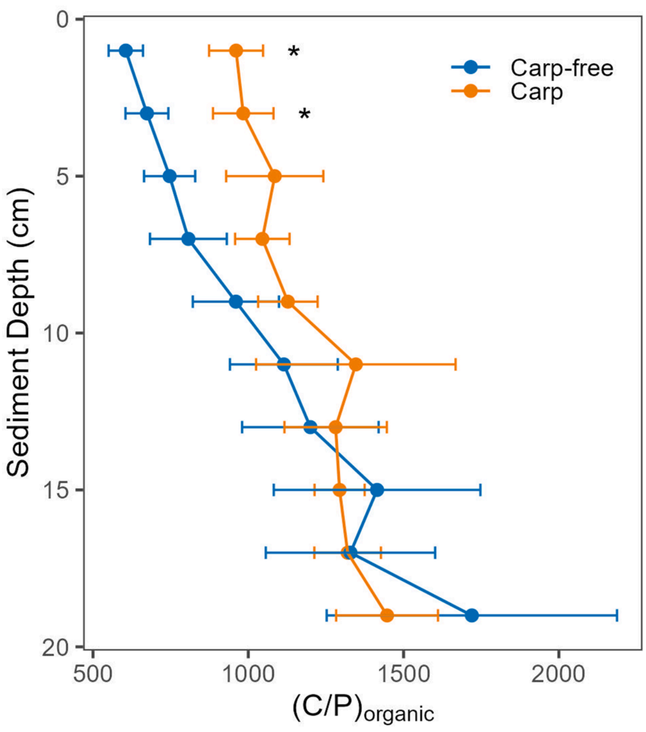

Fig. 4. $(C/P)_{organic}$ ratios in the top 20 cm of carp and carp-free lakes. Asterisks (*) indicate a significant difference between carp and carp-free lakes ($P < 0.05$). Error bars represent ± SE.

between carp and carp-free lakes, carp lakes also had lower mean surface concentrations, with mobile P even decreasing towards the surface in some carp lakes (Figs. 1, 2a). Mobile P concentrations were the most variable among lakes (Fig. 2a), and this variability may have made it difficult to see differences between carp and carp-free lakes.

Aluminum-bound P concentrations were also significantly higher in carp-free lakes, which can be a consequence of more organic matter availability and increased retention (Huser & Pilgrim, 2014), and aluminum-bound P was highly correlated to organic P ($R^2 = 0.62$, $P < 0.001$) in the upper 5 cm of sediment. Aluminum-bound P was also weakly correlated to water pH above the sediment ($R^2 = 0.18$, $P = 0.078$; Fig. S2), with concentrations decreasing at higher pH levels corresponding with the solubility of aluminum (Stumm & Morgan, 1996). There were no significant differences in calcium-bound P concentrations between carp and carp free lakes (Fig. S3), as concentrations were likely mediated by hydrogeological conditions and were positively correlated with $CaCO_3$ and watershed size. Calcium-P compounds are considered a stable form of P and create long-term burial of P (Anderson et al., 2001; Von Gunten et al., 2023), and are likely not heavily influenced by carp bioturbation.

Carp bioturbation can influence the depletion of sediment labile P in multiple ways. Physical disturbance of sediment can increase the sediment mixing depth and the flux of loosely bound and porewater P to the water column (Huser et al., 2016). In addition, sediment mixing from carp can expose deeper sediments to oxygen (Phan-Van et al., 2008), which can increase aerobic mineralization of organic matter that is usually limited to the top few millimeters of sediment (Håkanson & Jansson, 1983). The lakes in this study often had fully oxic water columns (72% of all sampling events; Table 1, S2), allowing for oxic bottom waters to mix with sediments. Enhanced aerobic conditions lead to the rapid degradation of P-rich organic material (Bastviken et al., 2004; Kristensen et al., 1995), and likely explains the significantly higher

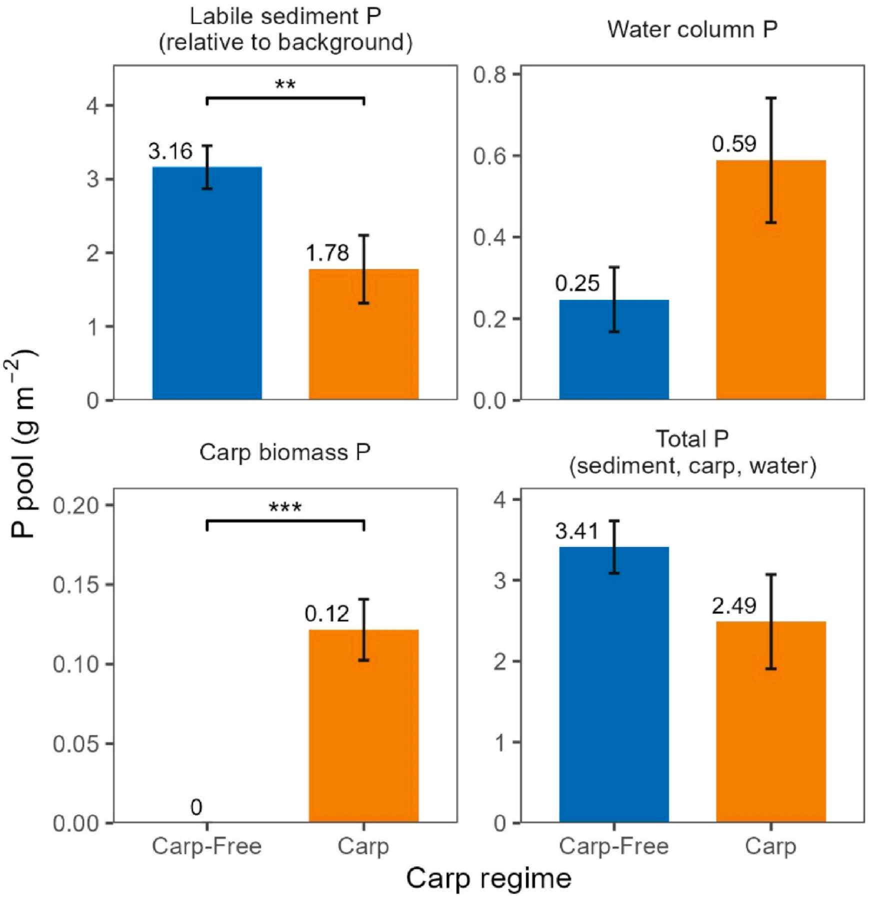

Fig. 5. A comparison of phosphorus (P) pools between carp-free (blue) and carp (orange) lakes. Labile sediment P includes pore water, loosely sorbed, redox-sensitive, and organic P. There were significant differences between carp-free and carp lakes in labile sediment P ($P = 0.0097$) and carp biomass P ($P < 0.001$), but not in water-column P ($P = 0.088$) or the total P among the pools ($P = 0.23$). Sediment labile P is the total concentration in the top 15 cm, which is the deepest sediment depth where significant differences were seen between carp-free and carp lakes. All P concentrations are expressed in g m^{-2}. Error bars represent ± SE.

$(C/P)_{organic}$ ratios in the surficial sediments of carp lakes if only more refractory organic material remains (Fig. 4). Differences in aquatic macrophytes may have also influenced sediment organic P, as macrophytes can mobilize sediment P as well as contribute P from decaying biomass (Barko & Smart, 1980). While submerged macrophyte density did not directly correlate with sediment organic P concentrations ($R^2 = 0.11$, $P = 0.17$), carp lakes had significantly lower abundance or even the absence of submerged macrophytes (Table 1). Macrophyte-derived organic matter degrades more slowly compared to phytoplankton-derived matter (Qu et al., 2013), which may degrade directly in the water column and be recycled before reaching the sediment (Meyers & Eadie, 1993). Rooted macrophytes also stabilize the sediment, while reducing sediment resuspension and increasing particle settling rates (Scheffer, 1990).

4.2. *Ecological effects of carp bioturbation*

The particularly large effect of carp on P cycling in shallow lakes has been widely observed (Jackson et al., 2010; Schrage & Downing, 2004; Zhang et al., 2016), and this study provides mechanisms by which carp elevate water-column P. Carp largely eliminated the retention of labile P in the surface sediment, which was coupled with a reduction in water quality similar to results described in previous research (Bajer & Sorensen, 2015; Schrage & Downing, 2004). Sediment disturbance from carp acts as a P pump from the sediment to the water (Huser et al., 2022), depleting the sedimentary environment while simultaneously maintaining eutrophic-hypereutrophic conditions in the water column. Sediments from carp lakes in this study had significantly lower labile P concentrations, while the total of sediment labile P, water-column P, and carp biomass P (in g m^{-2}) was not significantly different between carp and carp-free lakes (Fig. 5), indicating the majority of mobilized sediment P remains in the water column. However, the total P present in these pools (sediment, water, carp biomass) in carp lakes was only ~70% of the total P found in the same pools in carp-free lakes (Fig. 5), suggesting that some P may be lost over time and exported via lake outlets (Barton et al., 2000). Over long enough time scales, this may lead to the phenomenon that carp slowly drain internal stores of P from the sediment, exacerbating eutrophication both within the lake and in connected downstream systems.

While invasive carp are widely associated with eutrophication, a lesser-known impact may be the long-term depletion of the sedimentary environment. Carp feed on a variety of aquatic invertebrates (Huser & Bartels, 2015) and have been documented to reduce benthic invertebrate abundance and diversity (Badiou et al., 2011; Huser & Bartels, 2015; Schrage & Downing, 2004). In addition to direct impacts from predation, however, the impact of carp on benthic organisms may also be due to a reduction of sediment organic matter quality. Organic matter is a key driver of invertebrate abundance (Stewart & Downing, 2008), and provides both food and physical habitat. Carp lakes in this study had significantly higher $(C/P)_{organic}$ ratios in surficial sediments, a nutrient imbalance that can constrain growth and reproduction of benthic organisms (Elser et al., 2000; Frost et al., 2005). Given the importance of the benthic environment to lake food webs (Schindler & Scheuerell, 2002; Vander Zanden & Vadeboncoeur, 2002), a depletion of sediment quality could also contribute to decreases in other fish species found in carp-infested lakes (Egertson & Downing, 2004).

4.3. Implications of widespread carp invasion

Shallow lakes are biogeochemical hotspots and sites of intense productivity, nutrient processing, and carbon sequestration (Cheng & Basu, 2017; Downing et al., 2008; Rabaey et al., 2024). Although this study is restricted to Minnesota (USA), the lakes included are representative of shallow lakes throughout the Great Plains region, one of the largest ecoregions of North America extending from Canada to the Gulf of Mexico. Carp have been reported to be abundant throughout this entire region (Kulhanek et al., 2011; Weber & Brown, 2009; Zambrano et al., 2006), and have the potential to alter the important ecological role of shallow lakes across this expansive landscape, as shown in this study. Widespread carp invasion could change the balance between nutrient retention and export for entire watersheds (e.g. Barton et al., 2000).

Human activities have only increased species invasions over time, and freshwater ecosystems continue to be reshaped by invasive species. Although ecosystems are diverse and respond to invasion in varied and context-dependent ways, this study demonstrates that some invasive species can have consistent and significant impacts at regional scales. Expanding ecosystem-specific research to broader spatial contexts remains an essential goal for fully understanding the impacts of invasive species.

CRediT authorship contribution statement

Joseph S. Rabaey: Writing – review & editing, Writing – original draft, Visualization, Investigation, Formal analysis, Data curation. **Brian J. Huser:** Writing – review & editing, Supervision, Investigation, Conceptualization. **John A. Downing:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.watres.2025.125316.

Data availability

The data used in this study are available at the Environmental Data Initiative (EDI) Repository (https://doi.org/10.6073/pasta/943ba921ab0aebd63403134e242e7a4a; Rabaey et al., 2025).

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