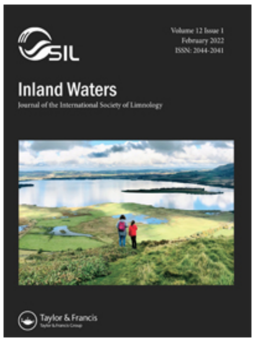

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Changes to water quality and sediment phosphorus forms in a shallow, eutrophic lake after removal of common carp (*Cyprinus carpio*)

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ABSTRACT

Pickerel Lake (Minnesota, USA) is a shallow, polymictic lake that has had eutrophication problems for decades. Although excess nutrient loading has been a problem in the past, the dominance of common carp (*Cyprinus carpio*) was considered to be a substantial factor driving and sustaining eutrophic conditions. To remove carp and restore the fish community, the lake was treated with rotenone in late 2009 and then restocked with native species. All water quality variables improved after carp removal, with mean values (May–Sep) for chlorophyll *a*, total phosphorus, and turbidity decreasing by 80% to 93% and Secchi disk transparency increasing nearly 600% when comparing means of pre- to post-treatment years. Macrophyte coverage also improved, from means of 4.6% before treatment to 90% after treatment, indicating a shift from an algal- to a macrophyte-dominated system. Sediment phosphorus (P) storage increased significantly after carp removal as well, with labile (releasable) forms of P increasing in the upper 10 cm of sediment in all cores ($n = 7$). The decrease in water column P equaled the increase in labile sediment P forms after treatment, indicating carp were a key driver of P transport from sediment to water. The results of this study indicate that an ecological (i.e., both abiotic and biotic) approach is needed when managing eutrophic lakes because management of nutrients alone will not likely be adequate to restore water quality in systems dominated by carp or other large benthic feeding fish.

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benthic fish; bioturbation; eutrophication; invasive species; restoration

Introduction

The common carp (*Cyprinus carpio*, or carp) is a large benthivorous fish native to Eastern Europe and Asia that has been widely introduced to other regions over the past century. It is considered one of the world's most invasive organisms (Kulhanek et al. 2011, Sorensen and Bajer 2011) and is often referred to as an ecosystem "engineer" because of its ability to transform its environment through direct and indirect influences on water transparency, sediments, nutrient cycling, plankton, and other aquatic biota (Cahn 1929, Northcote 1988, Parkos et al. 2003, Bajer et al. 2009, Weber and Brown 2009). Lakes with dense populations (typically >100–200 kg/ha) of carp are generally characterized by a lack of plants, low native diversity, and turbid, nutrient-rich water (Haas et al. 2007, Bajer et al. 2009, Kloskowski 2011b, Vilizzi et al. 2015). Carp dig in the bottom sediment while searching for food (Nikolsky 1963, Meijer et al. 1990b, Chumchal and Drenner 2004), uprooting aquatic plants, resuspending sediment, and increasing water turbidity (Crivelli 1983, Breukelaar et al. 1994, Lougheed et al. 1998, Zambrano et al. 2001, Bajer et al. 2009).

Carp may play an important role in nitrogen (N) and phosphorus (P) transport from sediment to the water column as a result of both physical sediment disturbance (i.e., bioturbation) and excretion (Lamarra 1975, Breukelaar et al. 1994, Cline et al. 1994, Moss et al. 2002, Chumchal et al. 2005, Driver et al. 2005, Vilizzi et al. 2015, Huser et al. 2016), but information on the relative importance of sediment P, and the forms that may be affected by foraging, have not been described. In addition, both direct and indirect processes can play a role in how carp affect nutrient cycling and water quality, such as nutrient release from suspended sediment (Sondergaard et al. 1992), light limitation,

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and other biological interactions that may exacerbate or limit effects of carp and resuspended sediment (Scheffer 1990), as well as a host of other factors (see review in Huser and Bartels 2015).

Although nutrient export from sediment to overlying waters has been suggested to be an important element of how carp alter ecosystems, this process has not been well documented. For example, debate exists about the magnitude of nutrient fluxes caused by carp foraging activity and whether these fluxes are primarily driven by excretion (Lamarra 1975, Morgan and Hicks 2013) and/or bioturbation (Driver et al. 2005). Although carp excretion rates have been estimated in experimental enclosures (Lamarra 1975, Morgan and Hicks 2013) and from bioenergetics models (Vanni et al. 2013), effects of bioturbation on sediment nutrient availability and release are poorly documented.

Nutrient release due to bioturbation is especially difficult to estimate because it is influenced by many factors, including sediment physical properties, chemical milieu (e.g., P-binding metals, pH, oxygen), availability of labile sediment P, water column mixing, and carp burrowing depth. A recent study showed that foraging activity of carp in a shallow, eutrophic lake in the United States increased the sediment mixing depth from 5 to 16 cm (Huser et al. 2016). The lake, however, was treated with aluminum to convert labile sediment P to aluminum-bound P and thereby reduce sediment P release. This action prevented studying changes to labile P forms in the sediment caused by carp.

Of the remaining studies available that investigate changes to sediment, one using aquaculture ponds with high-density sediment and low carp biomass suggested mixing depth might be as low as 3 cm (Ritvo et al. 2004). By contrast, a laboratory study suggested mixing depth could reach 15 cm in areas with soft sediments (Nikolsky 1963), similar to the findings by Huser et al. (2016). Regardless of the mechanism(s), the transfer of nutrients from sediment to water is a key aspect with respect to the effects carp and other benthivorous fish species have on water quality in lakes and other waterbodies. Because clear in situ information on carp sediment mixing is lacking, however, estimates of the effects of carp and other benthivorous fish on sediment P forms and availability are currently not available, which might hinder management of sediment and P in lakes with high biomass densities of benthic feeding fish.

This study determined the effect of common carp on sediment P forms and water quality in a shallow, hypereutrophic lake in Minnesota (USA), with the main hypothesis being that water column nutrients would decrease because of increased accumulation in the sediment via decreased flux from sediment to water. The lake was treated with rotenone in late 2009, and native fish species were stocked the following year in an attempt to restore the in-lake biological community and improve aquatic habitat. Water quality data covered years 2005–2016, and 7 sediment cores were collected from the same locations in 2009 (pre-treatment) and 2018 (post-treatment). Significant improvements in water quality-related variables and changes to sediment P forms were detected following treatment. Changes in sediment P stores could be directly related to improved water quality conditions in the lake.

Methods

Study site

Pickerel Lake is a shallow, previously hypereutrophic lake (area 281 ha) with mean and maximum depths of 1.2 and 1.8 m, respectively. It is located adjacent to the city of Albert Lea (lake ID 24002500), Minnesota, in the Western Corn Belt Plains ecoregion (WCBP; Fig. 1). The watershed consists of mainly row crops, with smaller areas of wetlands, forest, and developed areas (Supplemental Table S1). Development (mainly conversion to agriculture) within the tributary watershed of the lake began in the mid-late 1800s, which likely resulted in excess external P inputs that might have contributed to high levels of internal P loading and the degraded ecological status of the lake (Shell Rock River Watershed District 2005, Barr Engineering 2009).

Reports of degraded water quality go back as early as 1948 (Shell Rock River Watershed District 2004) and include descriptions of poor water clarity (Secchi disk transparency of 0.08 m) along with heavy algal blooms. The lake was drawn down the following year to kill carp and black bullheads (*Ameiurus melas*) during winter. Although native to the region, black bullheads are often managed together with carp because they may also impact lake sediment and water quality via bioturbation (Hanson and Butler 1994), but their effects on lakes are hypothesized to be less severe than those of common carp (Braig and Johnson 2003, Fischer et al. 2013, Bajer et al. 2018). Secchi disk transparency increased to 0.5 m the year following drawdown, but conditions worsened again within a decade, likely due to an incomplete fish kill and/or a faulty carp barrier that was installed at the lake's outlet to prevent carp reinvading from downstream sources.

Manipulation of the fish population in Pickerel Lake has occurred regularly since the early 1900s, with both stocking and opportunistic and not well-documented commercial removal of carp occurring. Poor water quality conditions remained generally constant, however,

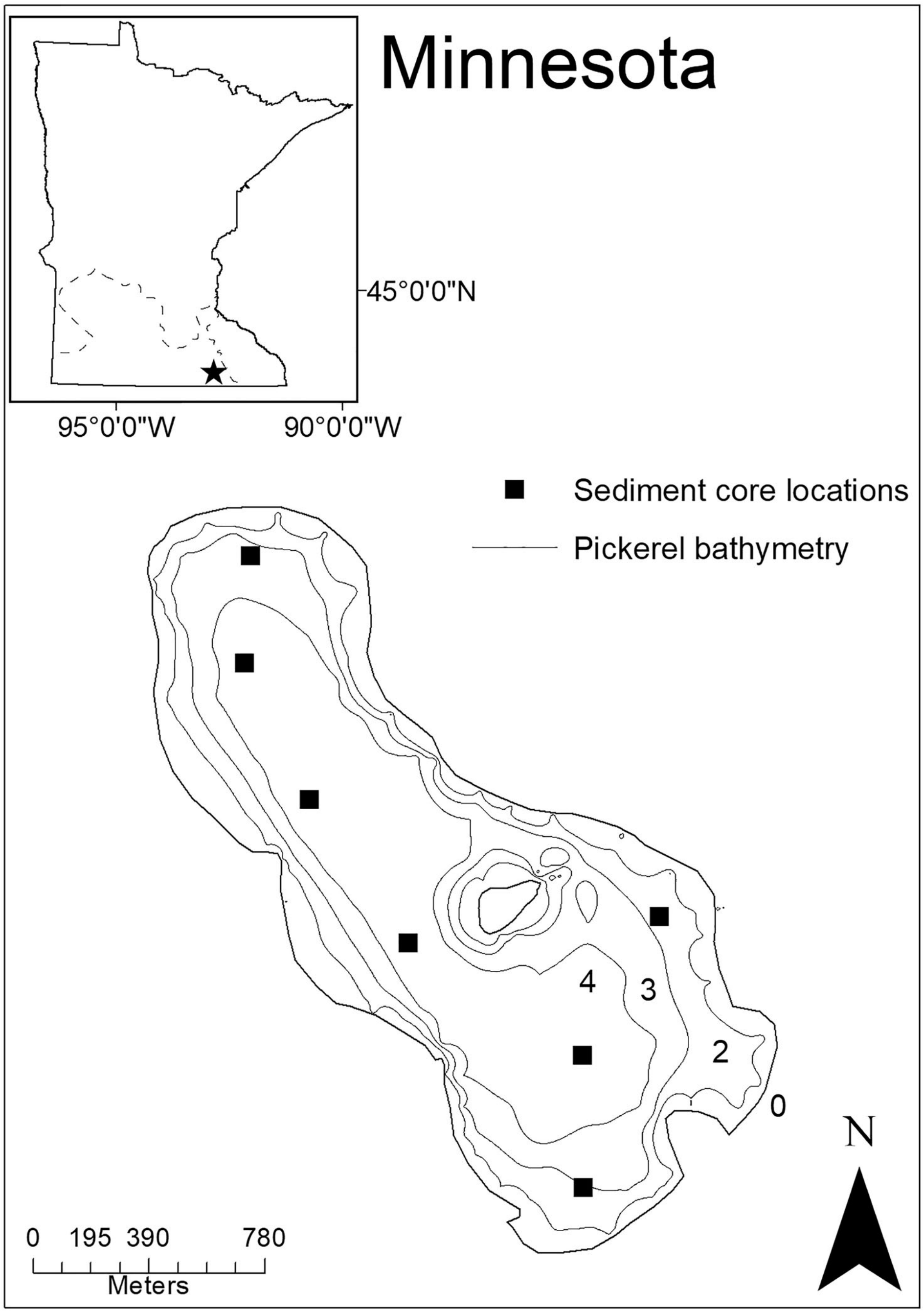

Figure 1. Pickerel Lake, located in southern Minnesota, with bathymetry (depth indicated in meters) and core locations (2008 and 2018). The dashed line in the upper figure box represents the boundary of the Western Corn Belt Plains ecoregion within the state of Minnesota.

until the year following the application of rotenone to eradicate the carp in late 2009. The lake was treated with rotenone (0.1 mg/L) during early October 2009 by a helicopter and drip stations placed at all inlets and ditches leading to the lake. The lake was then restocked with native fish species, including bluegill sunfish (*Lepomis macrochirus*), yellow perch (*Perca flavescens*), and northern pike (*Esox lucius*) in 2010 and 2014. Yellow perch and northern pike were again stocked in 2015 and 2016, respectively (Table 1). Fish stocking was conducted by the Minnesota Department of Natural Resources (MNDNR), primarily to support water quality objectives and secondarily to support sport fishing. Note that these species were also present prior to carp removal. An electric fish barrier was installed at the outlet of the system to prevent carp immigration into Lake Pickerel from downstream sources.

Table 1. Information on fish stocking conducted in Pickerel Lake since rotenone treatment in 2009.

Year	Species	Size	Number	Weight (pounds)
2016	Northern pike	fry	80 892	1.3
2015	Yellow perch	adults	392	14.0
2014	Bluegill sunfish	adults	480	100.0
	Northern pike	fry	149 814	2.9
	Yellow perch	adults	3198	310.0
2010	Bluegill sunfish	adults	76	19.0
	Northern pike	fry	126 581	2.0
	Yellow perch	adults	2656	320.0

Sediment

A Willner gravity sediment-coring device (Uppsala, Sweden) was used to collect all sediment cores (30 cm in length), which were sliced on-site (every 2 cm down to 10 cm and every 5 cm thereafter down to 30 cm), and stored at 4 °C in the dark until analysis within 1 week of collection. Sediment was collected on 15 May 2008 and 22 May 2019 from the same locations (water column depths from 0.9 to 1.7 m, mean 1.2 m; Fig. 1) during the different sampling periods. One extra sample was collected during the 2018 sampling (10–15 cm), and although it was excluded from calculations and testing because it was not collected during 2009 sampling, data are still presented. Meteorological conditions were similar during both sampling years, with wind averaging 2.7 and 1.8 m/s and temperature averaging 18.3 and 20 °C in 2009 and 2018, respectively.

Sediment P fractions were determined using the sequential P extraction technique for wet sediment by Psenner et al. (1988), modified by Hupfer et al. (1995). Soluble reactive P from sediment extracts was analyzed using the ammonium-molybdate blue method (Murphy and Riley 1962). All fractions were analyzed, but only mobile (pore water, loosely sorbed, and iron bound) P and organic P are presented. Background concentrations, used to estimate elevated amounts of mobile and organic P in surficial sediment, were estimated using the deepest sediment layers where generally recalcitrant fractions remain due to mineralization and diffusion processes. This approach is commonly used to determine the amount of labile P in sediment because the P in these fractions continuously moves toward the sediment surface over time (Reitzel et al. 2003, de Vicente et al. 2008, Schutz et al. 2017). Water content was determined by freeze-drying sediment after storage at −20 °C for ≥24 h, and sediment density was estimated after loss on ignition at 550 °C for 2 h (Håkanson and Jansson 1983). These data are not presented but were used for calculating concentration (dry weight) and mass of P forms in the sediment.

Water

Data used to determine mean surface water quality variables (2005–2016) were obtained from the Shell Rock River Watershed District in Albert Lea, Minnesota. Water chemical data have been collected consistently for total P (TP), soluble reactive P (SRP), chlorophyll *a* (Chl-*a*), turbidity, and Secchi disk transparency since 2005. Annual means were calculated from May to September, and measurements were generally conducted once per month. In cases where 2 or more values were available for a month, a monthly center analysis was conducted, and only the value closest to the center of the month was included in the analyses. Data were handled in this manner because using all data for months with multiple samples would lead to bias, and taking the mean of multiple sampling events during 1 month to standardize the data may influence variance (Helsel and Hirsch 2002).

Two years (2006 and 2008) were excluded from analysis because data for Chl-*a* and TP were limited. A limited number of profiles for dissolved oxygen (DO), pH, and water temperature (2006–2007) were downloaded from the Surface Water Environmental Data Access database (www.pca.state.mn.us/index.php/data). Some of these data had to be excluded because of ambiguous depth measurements (numbers seemed to be in feet but were listed as meters). P mass in the water column (as g/m^2) was calculated using annual mean P concentrations (pre- and post-treatment) and lake water volume.

Fisheries and macrophyte data

Fish populations were surveyed in 2008 and 2013 by the MNDNR using standard methods that included multi-panel gill nets, 250 feet long with five 50-foot panels with the following mesh (bar) sizes: 0.75, 1.0, 1.25, 1.5, and 2 inch. The surveys were conducted during summer for 24 h at the same location each year ($n = 2$). The nets were set overnight, and collected fish were identified to species, counted, and measured. Fish weight was estimated from length. Catch per unit effort (CPUE) was then calculated both in terms of the number per net and kilograms per net for each species. Thresholds for ecosystem damage (vegetation cover declines below 10%; Vilizzi et al. 2015, Bajer et al. 2016) and biomass density estimates for carp were calculated using the regression developed by Bajer et al. (2016). Both trap and gill net surveys were conducted, but only gill net survey results are presented because they can be used to estimate threshold for ecological impacts and biomass density, as noted earlier.

Macrophytes were sampled from sites placed at regular intervals in a point-intercept grid pattern across the entire lake (Madsen 1999) to determine species richness and coverage of aquatic plant species. Macrophyte coverage and richness was then estimated based on species found at each sampling point. Search area for each sampling point was ~1 m^2. A plant rake (~46 cm round grapple type) was randomly thrown at each grid survey point. Plants in the immediate area where the rake was thrown but not "collected" on the rake were counted as present (e.g., cattail, *Typha angustifolia* or *T.* × *glauca*).

Statistical analyses

Because variance between groups was not equal when comparing changes to sediment and water P, Mann-Whitney rank sum tests were used to test for significant differences between pre- and post-treatment. The Student's *t*-test was used to test for significant changes in sediment P fractions before and after treatment. Statistical testing was conducted with Sigmaplot 11.1.0.

Results

Water

Annual means were used to test for differences between pre- (2005, 2007, 2009) and post- (2010–2016) treatment water quality. All water quality variables improved significantly after rotenone treatment and restocking in 2009. TP and Chl-*a* decreased from 418 and 242 µg/L to 83.4 and 17.4 µg/L, respectively (Table 2, Fig. 2). Turbidity decreased as well (150–9.2 Formazin Nephelometric Units [FNU]), whereas Secchi disk transparency increased from 0.2 to 1.2 m. Note that Secchi disk transparency reached the bottom of the lake for 67% of the measurements after treatment (0% before), and thus the true increase in water clarity was likely underestimated. Improvements in water quality remained fairly constant after treatment (Fig. 3a–b). TP mass in the water column decreased from 0.49 to 0.10 g/m^2 following treatment, a difference of 0.39 g/m^2.

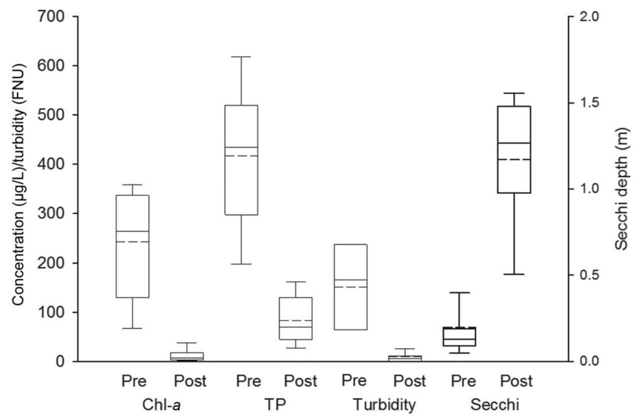

Figure 2. Box plot showing means for pre- and post-treatment Chl-*a*, TP, turbidity, and Secchi disk transparency. Dashed and solid horizontal lines represent the mean and median, respectively. 25th and 75th percentiles are the upper and lower bounds of each box, whereas the whiskers represent 5th and 95th percentiles.

Sediment

Mean concentrations ($n = 7$ cores) of mobile P increased significantly in the upper 10 cm of sediment from 2009 to 2018, between 45% and 127% depending on sediment depth, with the greatest changes occurring in the uppermost sediment layers (Table 3, Fig. 4a). Organic P was also significantly elevated after carp removal (38% increase) but only in the upper 0–2 cm of sediment

Table 2. Annual means (May–Sep) for water quality-related variables and macrophyte coverage, and May–Sept. mean for precipitation before and after treatment. Only the macrophyte survey in August 2010 was included because surveys earlier in the year (see Supplemental Material) were conducted while the lake was still recovering from treatment.

Period	Year	Chl-*a* (µg/L)	TP (µg/L)	SRP (µg/L)	Secchi (m)	Turbidity (FNU)	Macrophyte coverage (%)	Precip (cm)
Pre	2002						9.3	
Pre	2005	272	418	75.6	0.11			63.0
Pre	2007	314	453	86.6	0.08			72.4
Pre	2009	141	381	65	0.34	150	0	44.5
Post	2010	15	122	39.3	1.20	1.4	100	65.6
Post	2011	10	46	8.5	1.31	1.3	100	46.5
Post	2012	39	103	11.0	1.11	7.0	90.2	31.3
Post	2013	8	78	12.8	1.28		95.7	67.3
Post	2014	3	89	42.8	1.43	9.3		56.4
Post	2015	8	31	8.4	1.28	9.7	94.8	72.8
Post	2016	39	115	7.8	0.60	26.7	59.4	88.0
Mean Pre		242	417	76	0.18	150	5	60.0
Mean Post		17.4	83.4	18.7	1.2	9.2	90.0	61.1
Difference (%)		−93***	−80***	−75***	565**	−94**	1835***	2.0

$p \le 0.01$**, 0.001***.

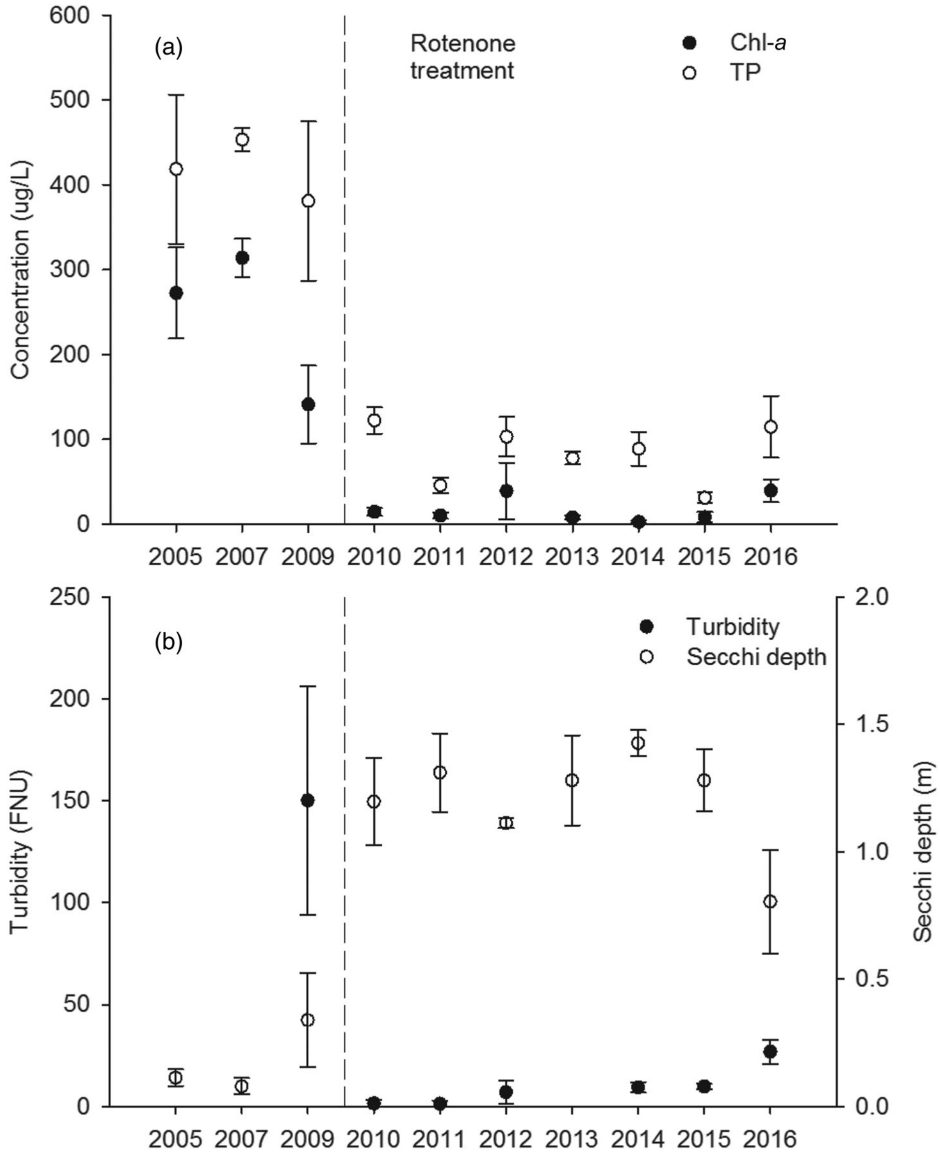

Figure 3. Annual means (May–Sep) for (a) Chl-*a* and TP and (b) Secchi disk transparency and turbidity. Timing of the rotenone treatment is indicated by the dashed line, and whiskers represent standard error.

(Table 3, Fig. 4b). The mean mass of labile (mobile + organic) P in all cores increased by 0.40 g/m^2 in the upper 10 cm of sediment when comparing sediment collected before (2009) and after (2018) carp removal (Fig. 5).

Mobile P concentrations also increased significantly at all individual sampling stations (mean of upper 10 cm) after carp removal (Table 4, Supplemental Fig. S1). Mean mobile P concentrations ranged from 0.041 to 0.060 mg/g before treatment and from 0.066 to 0.12 mg/g after treatment. Organic P concentration increased in all cores (0–2 cm) except one after treatment (P4), ranging from 0.19 to 0.37 mg/g before treatment to 0.31–0.54 mg/g after treatment (Table 4, Supplemental Fig. S2).

Fish community

Pre-treatment data (2008) showed extremely high numbers and mass of carp in Pickerel Lake. CPUE for carp in 2008 was 36.4 kg/net in Pickerel Lake, 26 times greater than the threshold for causing ecological damage (Table 5). Mean weight of carp captured in gill nets in 2008 was 1 kg and average length was 44 cm. No carp were found in fish surveys in 2013. Following treatment, northern pike, yellow perch, and black bullhead were the most abundant species, both in number caught and weight per net (Table 5). The black bullhead population in 2013 seemed to be dominated by relatively small (likely juvenile) individuals (mean weight 0.03 kg; Table 5). Total number of black bullheads caught in 2013

Table 3. Lake-wide means (standard error) for mobile and organic sediment P pre- and post treatment. Note: no sample collected at 12.5 cm in 2009.

P form	Depth	Pre	Post	Difference
Mobile	(cm)	(mg/g DW)		%
	1	0.059 (0.004)	0.135 (0.015)	127***
	3	0.055 (0.004)	0.093 (0.005)	70***
	5	0.057 (0.004)	0.089 (0.009)	57**
	7	0.057 (0.005)	0.086 (0.008)	51*
	9	0.062 (0.006)	0.09 (0.011)	45*
	12.5		0.084 (0.006)	
	17.5	0.074 (0.008)	0.078 (0.007)	5
	27.5	0.074 (0.008)	0.077 (0.007)	4
Organic	1	0.289 (0.019)	0.399 (0.028)	38*
	3	0.259 (0.023)	0.286 (0.029)	10
	5	0.241 (0.012)	0.244 (0.024)	1
	7	0.222 (0.01)	0.22 (0.021)	−1
	9	0.191 (0.01)	0.191 (0.022)	0
	12.5		0.173 (0.019)	
	17.5	0.138 (0.005)	0.144 (0.016)	5
	27.5	0.09 (0.007)	0.103 (0.012)	15

$p \leq 0.05$*; 0.01**; 0.001***.

was nearly 5 times greater than the next most abundant species (yellow perch), yet black bullhead was not stocked after the rotenone treatment. Possibly enough bullheads survived the rotenone treatment to repopulate the lake.

Macrophytes

During the 2 point-intercept macrophyte surveys conducted pre-treatment, macrophyte coverage was between 0% (2009) and 9% (2002) across the lake (Supplemental Table S2). Species abundance was also low, with only 2 species detected in 2002 and 0 in 2009, ~2 months before treatment. Macrophyte coverage increased substantially following treatment, covering 32.4% of sampled plots in June 2010 during the transition period just 8 months after treatment. Coverage reached 100% in August 2010, 10 months after treatment. Number of species detected also increased to 6 during the August 2010 survey. During the following years, coverage ranged from 90.2% to 100% and species richness ranged from 6 to 10. The exception to this was the 2016 survey, in which plant coverage decreased to 59.4% but number of species detected remained relatively high ($n = 7$).

Discussion

Pickerel Lake was treated with rotenone in late 2009 primarily to remove the invasive common carp and thereby restore the in-lake biological community and improve water quality and aquatic habitat. The lake was restocked with native fish species (black bullheads recovered without stocking), and carp were not detected in the lake after treatment using either trap or gill nets (Table 5). All measured water quality-related variables indicated substantially improved water quality after treatment. Post-treatment means (2010–2016) for TP, Chl-*a*, and Secchi disk transparency met Minnesota water quality standards of ≤90 µg/L, ≤30 µg/L, and ≥0.7 m, respectively, for the WCBP ecoregion (Table 2). The removal of carp led to a switch from a turbid, algal-dominated state, to a lake dominated by macrophytes. The decline in water column TP was nearly equivalent to the increase in labile sediment P (0.39 vs. 0.40 g/m^2, respectively), indicating that the removal of carp increased sediment retention of P, thereby improving water quality in the lake.

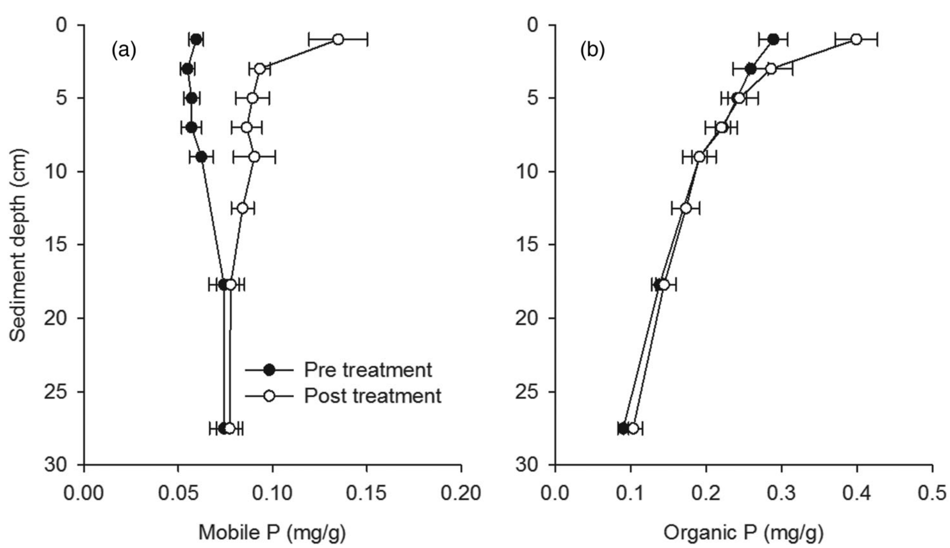

Figure 4. Mean concentrations (dry weight) of (a) mobile and (b) organic P for the 7 cores collected from Pickerel Lake.

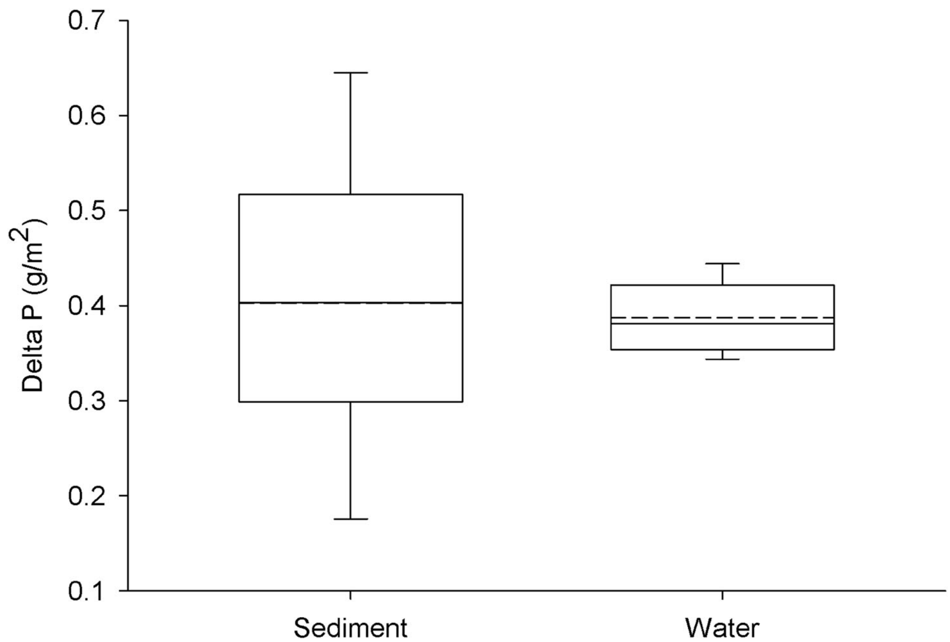

Figure 5. Differences (Delta P) in labile (mobile + organic) sediment P in each core (Sediment; 2009 vs. 2018) and between pre-treatment (mean of 2005, 2007, 2009) and post-treatment (2010–2016) annual means for water column TP mass (Water). Dashed and solid horizontal lines represent the mean and median, respectively. 25th and 75th percentiles are the upper and lower bounds of each box, whereas the whiskers represent 5th and 95th percentiles.

Table 4. Sediment concentrations of organic and mobile P (mean of 0–10 cm) pre- and post-treatment.

	GIS coordinates (m)		Depth	Mean organic P (mg/g)		Mean mobile P (mg/g)	
Core	X	Y	(m)	Pre	Post	Pre	Post
1	467577	4829861	0.95	0.23	0.38	0.041	0.085*
2	467572	4830305	1.34	0.32	0.36	0.069	0.120*
3	466986	4830683	1.37	0.29	0.39	0.059	0.117**
4	466654	4831167	1.37	0.35	0.31	0.063	0.099**
5	466436	4831627	1.22	0.37	0.36	0.067	0.116***
6	466456	4831986	1.16	0.27	0.54	0.061	0.089**
7	467831	4830774	1.01	0.19	0.44	0.046	0.066**

P-value ≤ 0.05*, 0.01**, 0.001***

Table 5. Catch per unit effort (CPUE, gill net) and other information on fish community structure before (2008) and after (2013) the rotenone treatment. According to Minnesota Department of Natural Resources, normal range (95% of values) for common carp gill net CPUE is 0.8–3.7 carp/net in lakes of similar type (shallow, productive prairie lakes).

Year	Species	CPUE (N/net)	Mean weight (kg)	Total caught (N)	CPUE (kg/net)
2008	Common carp	37	0.98	74	36.4
	Black bullhead	52.5	0.13	105	6.7
	Black crappie	6.5	0.18	13	1.1
	Yellow perch	89	0.03	178	2.4
2013	Black bullhead	281.5	0.03	563	8.9
	Black crappie	1	0.35	2	0.4
	Bluegill	5.5	0.18	11	1.0
	Hybrid sunfish	1	0.19	2	0.2
	Northern pike	14.5	1.68	29	24.3
	Yellow perch	63	0.16	126	10.0

Changes in fish community composition

Carp density and biomass were extremely high before the treatment. CPUE for carp (kg/net) was 26 times greater in Pickerel Lake than the threshold for severe ecosystem disruption of 1.4 kg/gill net (equivalent to ~190 kg/ha) determined for other lakes in the region (Bajer et al. 2016) and globally (Vilizzi et al. 2015). The estimated biomass of carp in Pickerel Lake before treatment was 3100 kg/ha according to the equation developed by Bajer et al. (2016) and a CPUE of 36 kg/net. This value is almost certainly an overestimate, however, because mark–recapture studies show that carp biomass typically does not exceed 1200 kg/ha and usually remains below 500 kg/ha in lakes of the region (Bajer et al. 2009, Vilizzi et al. 2015, Weber et al. 2016). Trap net surveys (1984, 1993, 2008) also had high carp catch rates ranging from

34 to 88.5 carp/net (MNDNR). According to the MNDNR, the normal range (95% of observed values) for common carp trap net CPUE is 0.8–3.7 carp/net in lakes of similar type (shallow, productive prairie lakes). Even though the exact carp biomass (i.e., biomass in kg/ha) before treatment was not quantified, the CPUE values from standard fish surveys and macrophyte data suggest it was high and likely exceeded the threshold for ecosystem disruption.

Carp can increase turbidity even at low abundance levels (Richardson et al. 1990, Drenner et al. 1998, Zambrano et al. 1998), but a switch from clear water to a turbid ecosystem is more likely to occur once biomass surpasses a critical threshold. This switch seems likely for Pickerel Lake, which had elevated turbidity and a nondetectable aquatic plant community before carp removal in October 2009. Reported thresholds vary for such ecosystem disruption, but several papers suggest that the impacts become noticeable at 100 kg/ha (Bajer et al. 2009) and severe above 190 kg/ha (Vilizzi et al. 2015, Bajer et al. 2016). Also possible is that smaller population densities could cause a shift in state over longer periods (Zambrano and Hinojosa 1999) as well, especially as benthic invertebrate populations decline and carp increase foraging time, resulting in increased sediment disturbance and resuspension (Werner and Anholt 1993). Given the pre-treatment fish survey results, degraded water quality and ecological status were likely due to a combination of high biomass density and increased foraging time due to the extremely high number and biomass density of carp in the lake.

Changes in water quality

TP decreased significantly from 417 to 83.4 µg/L following carp removal (80% decline; Table 2). The decline in P availability also likely drove declines in algal productivity, with Chl-*a* means decreasing by 94% (from 242 to 17.4 µg/L). Turbidity decreased by 94% (from 150 to 9.2 FNU) because of declines in algal productivity and sediment resuspension by carp, leading to an increase in water clarity (0.18–1.2 m). These types of changes have been detected in numerous studies where carp or other benthic feeding fish populations have been reduced (see review in Huser and Bartels 2015).

Bottom-feeding fish are considered to be important regulators (or engineers) of aquatic community structure through their direct and indirect influence on water transparency, nutrient cycling, plankton, macrophytes, and benthic macroinvertebrates (Northcote 1988, Parkos et al. 2003, Bajer et al. 2009, Weber and Brown 2009). Similar to conditions in Pickerel Lake before carp removal, increases in sediment resuspension, nutrient concentrations, and algal biomass were commonly associated with increased biomass density of benthivorous fish species in other studies (Meijer et al. 1990a, Richardson et al. 1990, Breukelaar et al. 1994, Roberts et al. 1995, Lougheed et al. 1998, Driver et al. 2005, Weber and Brown 2011, Akhurst et al. 2012).

A host of indirect effects resulting from carp foraging can also lead to increased nutrients in aquatic systems. Increased internal nutrient loading has been linked to loss of macrophytes and sediment bed stability (Moss et al. 2002, Parkos et al. 2003, Schrage and Downing 2004, Bajer et al. 2009), potentially leading to increased wind-driven mixing of sediment due to increased water velocity at the sediment surface (Håkanson and Jansson 1983). Before carp removal in Pickerel Lake, internal loading of P was estimated at 50–75% of the total P load (Shell Rock River Watershed District 2005), whereas after removal it was estimated to be ∼15% based on mobile sediment P mass and the empirical relationship developed by Pilgrim et al. (2007) relating mobile P to sediment P release. Indications that legacy sediment P contributes to excess internal P loading (increases in water column TP during later summer months) persist, but the lake generally met water quality goals during the post-treatment study period.

Increases in water column nutrients associated with common carp can lead to increased phytoplankton production (Andersson et al. 1988, Qin and Threlkeld 1990, Breukelaar et al. 1994, Vanni 2002, Chumchal and Drenner 2004, Matsuzaki et al. 2007, Akhurst et al. 2012, Fischer et al. 2013). At least 50% of P excreted by carp is easily available for uptake and production by phytoplankton (Lamarra 1975) but varies based on carp size, diet, and habitat variability. In a review of studies available in the literature, 81% showed a positive relationship between carp and phytoplankton biomass, whereas only 4% showed a decline, and 15% showed no trend either way (Huser and Bartels 2015). Physical mixing of sediment can also lead to increased recruitment of planktonic species resting on the sediment surface (e.g., Brunberg and Blomqvist 2003, Roozen et al. 2007, Vilizzi et al. 2015).

Carp effects on sediment

Some differences in opinion remain on whether excretion (Lamarra 1975), sediment disturbance (Driver et al. 2005), or both are the major drivers of increased nutrients in the water column when carp invade aquatic systems. Unfortunately, comparisons of many early studies on carp size and water quality are difficult because of variability in carp size within a study and inconsistent reporting of actual carp sizes (Driver 2002). A number of researchers (Driver et al. 2005, Weber and Brown 2009, Kloskowski 2011a) suggest a continuum of P mobilization from excretion to sediment disturbance as carp size increases. Driver et al. (2005) showed that larger carp mobilized more P per unit weight than smaller carp, even though larger fish retain more P, have lower mass specific ingestion rates, and excrete less P per unit size. The additional P mobilized was attributed to direct input from the sediment. Unfortunately, excretion rates were not studied in Pickerel Lake before treatment occurred, so it is difficult to estimate the relative importance of excretion versus sediment disturbance. However, elevated water column TP due to carp activity in the sediment should generally return to the sediment after removal, regardless whether it was released via excretion or due to sediment disturbance.

Physical disturbance of sediment by adult carp can have a number of effects on chemistry and P forms in sediment. First, flux rate increases due to the physical movement of sediment bound and pore water constituents caused by carp; and second, aerobic decomposition increases as greater amounts of sediment are exposed to oxygen (Graneli 1979, Kadir et al. 2006, Phan-Van et al. 2008). Increased flux rate was likely one of the causes of reduced mobile sediment P before treatment (Table 3). Mobile P concentration in sediment profiles in eutrophic–hypereutrophic lakes are generally greatest in the uppermost layers and then decline to a stable background at a depth determined by both chemical and physical constraints (Carey and Rydin 2011). Instead, mobile P was actually lower in surficial sediment in all cores collected from Pickerel Lake before carp removal, both as an average (Fig. 4a) and at each of the 7 sampling stations across the lake (Supplemental Fig. S1), likely because the physical disturbance of carp acted as a P pump from sediment to water.

Aerobic mineralization generally occurs in the uppermost few millimeters of sediment (Håkanson and Jansson 1983) and in the cavities created by animal burrowing/foraging (Kristensen and Blackburn 1987), with mixing of sediment by carp potentially increasing the rate of mineralization of organic matter. Increases in oxygen availability, however, should lead to a decrease in P release from redox-sensitive metals like iron (Fe). Increased turbidity and organic matter mineralization caused by carp foraging may be the drivers behind most studies in the literature (88%) showing decreased DO concentration in lakes with moderate to high biomass densities of carp (Huser and Bartels 2015). Oxygen was not measured frequently in Pickerel Lake during regular sampling, but a limited number of profile data were available from 2006 to 2007, before carp removal (Supplemental Table S3); 38.4% of the bottom water measurements (1.2–1.5 m) had DO concentration <2 mg/L. Thus, the low levels of mobile (loosely bound, pore water, and Fe-bound) P before removal were likely due to a combination of degraded oxygen conditions and bioturbation of sediment. Unfortunately, data for DO were not available for post-treatment years.

Carp foraging in the sediment also results in a direct conversion of sediment organic matter to available nutrients in the water column via excretion. Excretion rates for some benthic species have been shown to exceed the sum of external loading sources for both N and P (Gido 2002). In addition, Brabrand et al. (1990) concluded that P loading from benthic feeding fish could be nearly twice that coming from external sources. The increase in organic P detected in Pickerel Lake sediment following carp removal was likely due to reduced uptake of plant matter and benthic invertebrates by foraging carp and potentially lower rates of organic matter degradation (i.e., macrophytes instead of phytoplankton). The significant increase was only detected in the 0–2 cm layer, which is not surprising given the likely sedimentation rate after restoration. Assuming the uppermost 2 cm layer with elevated organic matter was newly deposited would result in an average sedimentation rate of 0.22 cm/yr. This rate is on the low end compared to other shallow lakes with degraded water quality (e.g., Xu et al. 2017) and similar to rates detected in other macrophyte-dominated systems (e.g., Gąsiorowski 2008).

Increased sediment retention after carp removal

The decline in water column TP of 0.39 g/m^2 was not significantly different ($p = 0.9$) from the increase in sediment P of 0.40 g/m^2 after carp removal. As noted earlier, increased sediment retention of P was likely caused by a number of factors. Decreased physical disturbance increased the retention of the most labile forms of sediment TP, such as pore water and loosely sorbed P. Improved oxygen conditions due to a reduction in production and mineralization of easily degradable forms of organic matter (i.e., phytoplankton) likely improved retention of P bound to reductant soluble metals like Fe.

The conversion from an algal- to a macrophyte-dominated system likely contributed to increased sediment P retention in other ways as well. Macrophytes stabilize sediment, leading to less resuspension (Scheffer 1990). They can also supply oxygen to sediment via the root system, minimizing or preventing the release of reductant soluble P (Horppila and Nurminen 2005). Some macrophytes sequester P from the water column via direct uptake (Burkholder and Wetzel 1990, van Donk et al. 1993), which is then incorporated as organic matter in the sediment after dieback. Macrophytes also provide refuge for zooplankton (Jeppesen et al. 1997) and increase particle settling rates (Kufel and Kufel 2002), increasing the transfer of P from the water column to sediment. These processes should lead to an increase in sediment P retention, especially mobile and organic P, which was the case for Pickerel Lake.

Other factors potentially affecting water quality

External loading

One of the main factors that could affect in-lake nutrient concentrations and water quality, but was not studied due to lack of data, was the effect of external loading during the study period. Mean precipitation (May–Sep) pre- and post-treatment was similar but with some interannual variability, especially during 2011–2012 with lower than average precipitation for both the study months (May–Sep; Table 2) and for annual totals. Water quality in 2012 was second worst for the post-treatment period (excluding turbidity, which was low), but the averages for 2011–2012 were similar to the entire post-treatment average for all water quality-related variables except for turbidity (again lower).

Macrophyte and fisheries management

Curly-leaf pondweed (*Potemogeton crispus*) is an invasive macrophyte in the United States that can grow under the ice during winter with senescence occurring during late June and early July. Curly-leaf pondweed was detected in 2010 (15% coverage) and peaked during 2011 (27.1%). Herbicide treatment to control curly-leaf pondweed was conducted in 2011 and 2012, and although curly-leaf was still elevated during 2013, it declined to 1% in 2015 and was not detected during the 2016 survey.

According to observations by the Shell Rock River Watershed District, a partial fish kill occurred during summer 2013 and a winter fish kill during 2014/2015. Bluegill, yellow perch, and northern pike were stocked in 2010 after treatment and again in 2014. Stocking of yellow perch and northern pike occurred during 2015 and 2016, respectively. None of the above management actions seem to have significantly altered water quality in the lake, although they may have helped maintain the improved conditions. Species richness, excluding carp, increased from 3 to 6 when comparing pre- and post-treatment data (Table 5). In addition, 2 species not found before treatment in 2008 were detected after treatment: bluegill sunfish and black crappie (*Pomoxis nigromaculatus*).

P availability in suspended sediment

The argument that resuspension of sediment may have led to the elevated levels of TP and turbidity, but that increases in bioavailable P were minimal before carp removal, is not supported by the data, with both Chl-*a* and SRP concentrations declining substantially after carp removal. Large net transport of SRP into the water column during resuspension events has been documented (20–30 greater SRP release compared to undisturbed sediment; Sondergaard et al. 1992). Even if diffusive P release is small compared to the P transport associated with sediment resuspension, it still could play an important role in providing readily available P to the water column (Moore and Reddy 1994).

Nutrient uptake by macrophytes

The substantial increase in macrophyte coverage would have meant a substantial amount of nutrients being used for building plant biomass. Although data were not available on the mass of macrophytes in the lake, aquatic plants, in general, consist of ~0.1–1.2% P as dry matter (Thiébaut 2008). The timing of sampling (early May), however, meant that most macrophytes had not started to grow, and most, if not all, of the P contained in remaining organic matter would be contained in the sediment.

Summary

The removal of carp led to a drastic improvement in the ecological status of Pickerel Lake. All water quality-related variables improved after carp removal, macrophyte coverage increased from near 0% to 90%, and fish community structure was also improved (thanks in part to stocking efforts). A clear shift from an algal-dominated to a macrophyte-dominated state occurred, which was sustained through the end of this study in 2016. The decrease in water column P after carp removal was not significantly different compared to the increase in labile sediment P forms after treatment, indicating that carp were a key driver of P transport from sediment to water. The reestablishment of macrophytes across the lake, however, likely had an indirect, positive effect on sedimentation and retention of P in the sediment. The results of this study indicate that an ecological (i.e., both abiotic and biotic) perspective is needed when managing eutrophic lakes because management of nutrients alone will not likely be adequate to restore ecological quality in eutrophic lakes dominated by carp or other large benthic feeding fish.

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