

Effects of common carp on phosphorus concentrations, water clarity, and vegetation density: a whole system experiment in a thermally stratified lake

Przemyslaw G. Bajer · Peter W. Sorensen

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Abstract Although numerous studies have investigated the impacts of common carp (*Cyprinus carpio*) on aquatic ecosystems, the effects of this species on nutrient cycling, water clarity, and vegetation density have rarely been addressed in whole lakes, especially in those that stratify. In this study, we documented changes in total phosphorus, water clarity, and aquatic vegetation density in a stratified eutrophic lake while we reduced carp biomass from 300 to 40 kg/ha. Carp removal was associated with an increase in vegetation density, an increase in springtime water clarity, a decline in early season chlorophyll *a*, and a decline in total suspended solids. However, neither clarity nor chlorophyll *a* improved during the summer months. Carp removal also had no apparent effect on total phosphorus, which increased rapidly in the summer both before and after carp removal, and was seemingly driven by abiotic internal loading. The lack of a decline in phosphorus following carp removal

suggests that despite their high biomass, carp may sometimes play a relatively minor role in nutrient transport from benthic sediments in stratified eutrophic lakes. Their removal is nonetheless beneficial for improving water clarity and restoring macrophyte communities in such systems.

Keywords *Cyprinus carpio* · Macrophytes · Phosphorus · Nutrient cycling · Invasive fish

Introduction

The common carp (*Cyprinus carpio* or “carp”) is one of the world’s most invasive fish (Kulhanek et al., 2011). It is often called an “ecological engineer” because of its ability to modify the habitat and biotic communities of the lakes it invades (Matsuzaki et al., 2009). Carp root in the bottom while searching for food and have been shown to drive rapid declines in aquatic vegetation and increases in water turbidity (Lougheed et al., 1998; Zambrano et al., 2001; Bajer et al., 2009; Matsuzaki et al., 2009). The carp has also been hypothesized to play an important role in nutrient transport from the sediments into the water column due to bioturbation and excretion (Lamarra Jr., 1975; Breukelaar et al., 1994; Parkos III et al., 2003; Morgan & Hicks, 2013). For all of these reasons, carp removal is often recommended as an important element of lake restoration (Meijer et al., 1990). However, although

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P. G. Bajer (✉) · P. W. Sorensen
Department of Fisheries, Wildlife, and Conservation
Biology, University of Minnesota, 1980 Folwell Ave,
St. Paul, MN 55108, USA
e-mail: bajer003@umn.edu

the effects of carp on lakes have been investigated in over 50 studies, some aspects of carp in lake ecology remain unclear. In particular, it is not clear what the precise effects of carp are on nutrient cycling and water clarity in whole lakes as most studies have used relatively small experimental arenas or theoretical calculations (Weber & Brown, 2009; Morgan & Hicks, 2013). The effects of carp on nutrients and water clarity are particularly poorly documented in thermally stratified lakes.

Although small-scale experiments have shown that carp usually cause an overall increase in nutrient concentrations in ponds or enclosures (Lamarra, 1975; Breukelaar et al., 1994; Parkos et al., 2003; Chumchal & Drenner, 2004; Morgan & Hicks, 2013), whole-lake experiments have shown mixed results. For example, some carp exclusion efforts in shallow lakes have shown only subtle or nonexistent effects on total phosphorus (Meijer et al., 1990; Thomsen & Chow-Fraser, 2011). Further, while declines in phosphorus have been documented in other lakes from which carp have been removed (Schrage & Downing, 2004), these studies used piscicides so the observed declines might have been attributable to a loss of fish in general, not just carp. Several small-scale experiments have also shown inconsistent relationships between carp biomass and nutrient concentrations (Lougheed et al., 1998; Matsuzaki et al., 2007, 2009). Together, these inconsistencies suggest that the effects of carp on whole-lake nutrient cycling might be more complex than presently realized.

Almost all studies that have investigated the effects of carp have focused on shallow lakes (reviewed in Weber & Brown, 2009); i.e., lakes that rarely stratify and can be largely colonized by aquatic vegetation (Scheffer, 2005). However, carp can also be abundant in deeper, thermally stratified systems in which their presence is often associated with poor water clarity and high nutrient concentrations (O'Donnell, 1943; Ten Winkel & Meulemans, 1984; Jackson et al., 2010; Weber & Brown, 2011). To what extent carp drive water clarity and nutrient concentrations in such systems is poorly documented. Nutrient cycling in stratified lakes often is strongly affected by abiotic “internal loading” in which large quantities of phosphorus are released from sediments during hypolimnetic hypoxia in the summer (Liboriussen et al., 2009; Nürnberg, 2009), leading to epilimnetic phosphorus spikes as a consequence of thermocline erosion. While

internal loading might play an important role in nutrient cycling in stratified lakes, carp may substantially accelerate phosphorus transport from benthic sediments into the water column of such systems via excretion (Morgan & Hicks, 2013) and bioturbation (Zambrano et al., 2001). One might, therefore, expect elevated phosphorus concentrations and more severe algal blooms in stratified lakes with large carp populations as compared to lakes that lack carp. Stratified lakes with abundant carp are also likely to suffer from poor aquatic vegetation communities and increased loads of suspended sediments.

In this study, we selectively removed common carp from a stratified (polymictic), eutrophic lake in the North American Midwest to address the role of carp in water clarity, nutrient cycling, and vegetation density in such lakes. We reduced the biomass of carp from approximately 300 kg/ha to approximately 40 kg/ha using winter seining, while measuring changes in percent cover of aquatic vegetation, water clarity (Secchi depth), total phosphorus (TP), chlorophyll *a* (ChlA), and total suspended solids (TSS). We also collected information on thermocline stability and internal phosphorus loading to better explain the concentrations and seasonal TP patterns before and after carp removal. Additionally, changes in the native fish community were monitored. This study is relevant to the restoration of stratified lakes as well as to our understanding of the role of carp in nutrient cycling.

Methods

Study site

This study was conducted in Lake Susan, a small (35.1 ha), hyper-eutrophic (summer TP > 100 µg/L) lake in central Minnesota, USA, which appears to be representative of many lakes in this region. In spite of its shallow depth (max. depth 5.1 m), Lake Susan stratifies in early summer and hypolimnetic waters with dissolved oxygen concentrations of less than 0.1 mg/L cover approximately 50% of its bottom during July and August. Partial thermocline erosion occurs on windy days, but the lake does not mix to the bottom until autumn. At the beginning of this study, the lake contained a large population of common carp whose biomass exceeded 300 kg/ha (Bajer & Sorensen, 2010). Radio telemetry showed that carp in

this lake tend to occupy the littoral zone during the summer (Bajer et al., 2010; Bajer & Sorensen, 2010). The native fish community was dominated by several species of centrarchids including bluegill (*Lepomis macrochirus*), black crappie (*Pomoxis nigromaculatus*), and largemouth bass (*Micropterus salmoides*). Lake Susan is located in an urban setting and has historically suffered from high phosphorus concentrations, poor water clarity, and a poor aquatic plant community. Sediment cores showed high rates of internal phosphorous release, and alum was applied in 1998 to remediate these conditions, but it was underdosed and failed to reduce internal phosphorus loading or improve water clarity (Huser, 2012).

Experimental design

The abundance and biomass of carp in Lake Susan were estimated in 2008 (Bajer & Sorensen, 2010) at which time we also collected baseline (pre-removal) data on aquatic vegetation, Secchi, TP, ChlA, TSS, and native fish abundance. In addition, we retrieved two additional years of historical data (2004, 2005) on Secchi depth, TP, and ChlA collected by the local watershed district to better portray conditions in the lake prior to carp removal. Most carp were removed from the lake in March 2009 (see below), while our measurements of aquatic vegetation density, water quality, nutrients, and native fish continued for three additional years (2009–2011).

Carp biomass estimates and removal

Carp abundance and biomass were estimated in the summer of 2008 using mark-and-recapture analyses (Bajer & Sorensen, 2010) (Table 1). A large number of adult carp (approximately 80% of the population) were removed from the lake in March of 2009 using telemetry-guided seining under the ice that targeted carp aggregations (Table 1; Bajer et al., 2011). No other fishes were removed at that time. Approximately, 300 carp were also removed in the spring of 2010. Carp removed from the lake were subtracted from the initial population to generate post-removal estimates. We adjusted these post-removal estimates for natural mortality that we estimated to be 10% using the survival of radio-tagged carp in the lake. The lake inlet and outlet were blocked during the study to eliminate emigration and immigration. Finally, the

Table 1 The abundance (N), biomass, and length of common carp in Lake Susan for each year of the study

Year	Carp removal	N mean (95% CI)	Biomass (kg/ha)	Length (mm) mean (SE)
2008	Before	4,181 (3,292–5,069)	307.1	598 (67)
2009	After	756	64.5	609 (139)
2010	After	374	43.0	587 (129)
2011	After	281	40.8	677 (114)

Carp abundance was estimated in 2008 using mark and recapture and was originally reported by Bajer & Sorensen (2010)

lake was sampled annually to account for possible carp recruitment (no recruitment occurred throughout the study; Bajer et al., 2012).

Aquatic vegetation

Aquatic vegetation (both submersed and floating-leaf) was sampled annually during 2008–2011 in June (time of peak abundance) following procedures similar to those of Schrage & Downing (2004). Twenty transects distributed approximately equidistantly from each other were mapped in the lake using ArcGIS. These transects were perpendicular to the shoreline, and vegetation was sampled at locations with water depths of 0.5, 1, 1.5, and 2 m along each transect (the vegetation was generally not visible at depths >2 m). At each sampling location, visual estimates of percent vegetative cover (nearest 10%) were recorded within a 2 × 2 m area using the front of the boat (2 m long) as a reference. To confirm that our visual estimates were unbiased, a sampling rake was lowered to the bottom at every other transect, twisted three times, and the vegetation was pulled on the boat and weighed (nearest 10 g); we observed a linear relationship between visual estimates and rake biomass ($P < 0.001$). The rake was also used to confirm that little vegetation occurred at depths exceeding 2 m.

Secchi depth, TP, TSS, and ChlA

Secchi depth, TP, TSS, and ChlA were sampled at two offshore locations every 2 weeks between May and September of 2008–2011. Selecting only two locations was deemed sufficient due to the small size of the

lake, and the fact that both locations had nearly identical water quality parameters. Visual assessments also suggested that water quality was similar in inshore and offshore areas of the lake. Secchi depth was measured from a boat using a 20-cm disc. To determine TP, TSS, and ChlA, we collected integrated epilimnetic samples following standard methods (APHA, 1998). Specifically, at each of the sampling locations, we first measured the temperature and dissolved oxygen profile (1 m increments; YSI 55, Yellow Springs, Ohio, USA) to determine the depth of the epilimnion. Then, we used a stainless steel 2 L Van Dorn sampler to collect water samples from the surface of the lake to the bottom of the epilimnion at 1 m increments. Samples were poured into a clean plastic container and mixed. From this aggregate, we collected 200 ml samples for TP analysis, 500 ml for TSS analysis, and 500 ml for ChlA analysis. All samples were stored in a cooler and delivered to an analytical laboratory within 24 h. The TP samples were analyzed using the persulfate digestion method (SM 4500-P E-97). The TSS samples were dried to a constant weight at 103–105°C (SM 2540 D). ChlA was analyzed using 10200 H method (APHA, 1998). Because our sampling protocol included only one year of data prior to carp removal (2008), we used two additional years of data (2004 and 2005) of Secchi, TP, and ChlA collected by a local watershed district (<http://www.rileywd.org>) to better portray pre-removal conditions in the lake. These data were collected using similar methods but usually only once a month.

In 2009, we began measuring hypolimnetic TP by collecting samples of water approximately 1 m below the thermocline during mid to late summer when the lake was stratified. These measurements continued during 2010 and 2011 and were used to develop a better understanding of the role of abiotic internal loading in summertime increases in epilimnetic TP that we observed during each year of the study. In July 2010, we also installed a vertical array of temperature data loggers (HOBO Pendant, Onset, Bourne, MA, USA) spaced every 0.5 m from 1 m below the surface to the bottom of the lake to collect continuous data on the stability of summer stratification and determine if the summertime increases in epilimnetic TP were associated with erosion of thermocline and mixing with the phosphorus-rich hypolimnetic waters.

Native fish

The fish community was assessed in late summer of each year (2008–2011) using trapnets (single 12 m lead, single rectangular 0.6 × 1.2 m wire frame followed by four 0.6 m diameter hoops enclosed with 15 mm bar mesh; Bajer et al., 2012). Five nets were set along the entire perimeter of the lake for one 24-h period, all collected fish were counted, and the first 30 of each species were measured for length (nearest mm).

Data analysis

We conducted separate analyses to assess if carp removal had an effect on vegetation density and water quality parameters. Because vegetation density was measured only once each year, we conducted a *t*-test using mean values of vegetation density within each sampling transect before and after carp removal. However, because water quality parameters were measured repeatedly throughout the season (i.e., data were dependent), we began the water quality analysis by fitting ordinal day (days 121–273; May 1 to September 30) models for Secchi, TSS, ChlA, and TP. While fitting these models, we considered exponential, quadratic, and 4th degree polynomial models and used ANOVA and AICc scores to test which ones provided the best fit for each variable. Once the ordinal day models were fitted, we tested if adding carp removal as a categorical variable significantly increased model fit (i.e., whether reduction in the residual sum of squares was statistically significant by ANOVA). Carp removal was evaluated both as an additive effect and as an interaction term with the ordinal day. A significant improvement in model fit would suggest that the seasonal patterns of Secchi, ChlA, TSS, and TP were different before versus after carp removal. Because water quality measurements collected on the same day tend to be similar in small lakes, we averaged them to represent daily means before we fitted the models to avoid pseudo-replication. Data collected during individual years were lumped into either before removal or after removal category as among year variation was low. All models were examined for linearity and homogeneity of residuals. All statistical analyses were conducted using R (R Development Core Team, 2012).

Results

Following carp removal, vegetation density increased from approximately 5% cover to over 45% cover (t test; $t = 10.13$; $df = 38$; $P < 0.01$) (Fig. 1). Most of this increase occurred during the first spring following carp removal but increases continued throughout the study; percent cover in 2009, 2010, and 2011 was 37, 54, and 63%, respectively. The number of aquatic plant species increased from four in 2008 to ten in 2011 (Online Resource 1).

Carp removal had a positive effect on water clarity, especially in the spring, and TSS but the effects on ChlA and TP were more subtle. Changes in Secchi depth in relation to ordinal day were best described by a quadratic model whose fit increased significantly after the addition of carp removal and the carp removal \times ordinal day interaction term ($F = 19.5$, $df = 3$, $P = 2.33 \times 10^{-7}$; Fig. 2). The model showed that the removal of carp caused an increase in water clarity during May and June (days 120–180) but not during July through September (days 180–280; Fig. 2). Changes in TSS in relation to ordinal day were also best described by a quadratic model whose fit improved after adding carp removal as both an additive and interaction term ($F = 11.84$, $df = 3$,

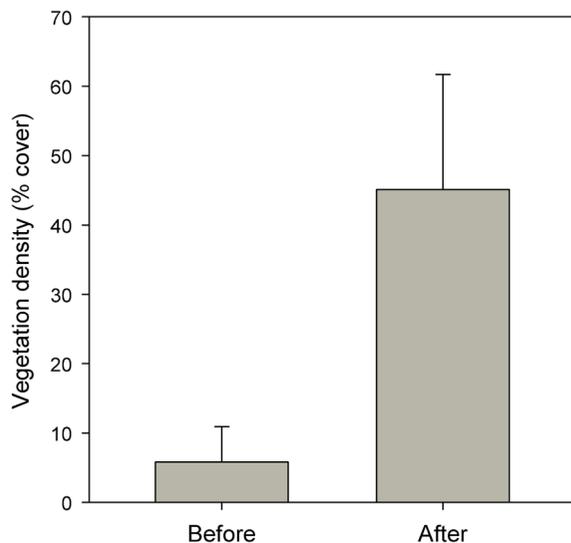


Fig. 1 Density of aquatic vegetation before and after carp removal in Lake Susan. The density is expressed as mean percent cover (\pm SE) in littoral areas between 0 and 2 m in depth. The increase after carp removal was statistically significant (t test; $P < 0.01$)

$P = 1.62 \times 10^{-4}$; Fig. 2). This model suggested that carp removal caused a decrease in TSS throughout the entire season, but particularly in the summer (Fig. 2). Changes in ChlA relative to ordinal day were best depicted by a 4th degree polynomial model in which ChlA was low in the spring and increased rapidly in the summer. Adding carp removal as an additive term or an interaction term did not improve model fit ($F = 0.48$, $df = 5$, $P = 0.78$; Fig. 2) suggesting that ChlA followed the same seasonal pattern before and after carp removal. However, visual examination suggested that ChlA was consistently lower during May and early June (days 120–160) following carp removal (Fig. 2). Changes in TP relative to ordinal day were best described by a quadratic model whose fit improved only marginally after the inclusion of carp removal and carp removal \times day interaction ($F = 2.85$, $df = 3$, $P = 0.050$; Fig. 2). TP increased each summer both before and after carp removal (Fig. 2). Mean TP concentrations before and after carp removal were 69.4 and 75.3 $\mu\text{g/L}$, respectively. Measurements of thermal stratification and hypolimnetic TP concentrations showed that stratification typically occurred by mid-June and that hypolimnetic TP concentrations increased rapidly in July and remained high through August and September. Vertical array of temperature loggers deployed in the summer of 2010 showed that although the lake remained stratified during July, mixing with hypoxic waters occurred in mid-August (Fig. 3), when hypolimnetic TP concentrations exceeded 1,000 $\mu\text{g/L}$. This partial thermocline erosion was associated with a near doubling of the epilimnetic TP (Fig. 3). Annual trapnet surveys suggested that no major changes in the native fish community occurred after carp removal (Online Resource 2).

Discussion

This study selectively removed carp from a small stratified eutrophic lake to better understand this species' effects on phosphorus, water clarity, and vegetation density in such systems. We found that while carp removal had a positive effect on the density of aquatic vegetation and early season water clarity, it seemingly had little or no effect on phosphorus concentration. Our results suggest that in thermally stratified eutrophic lakes, the role of carp in structuring

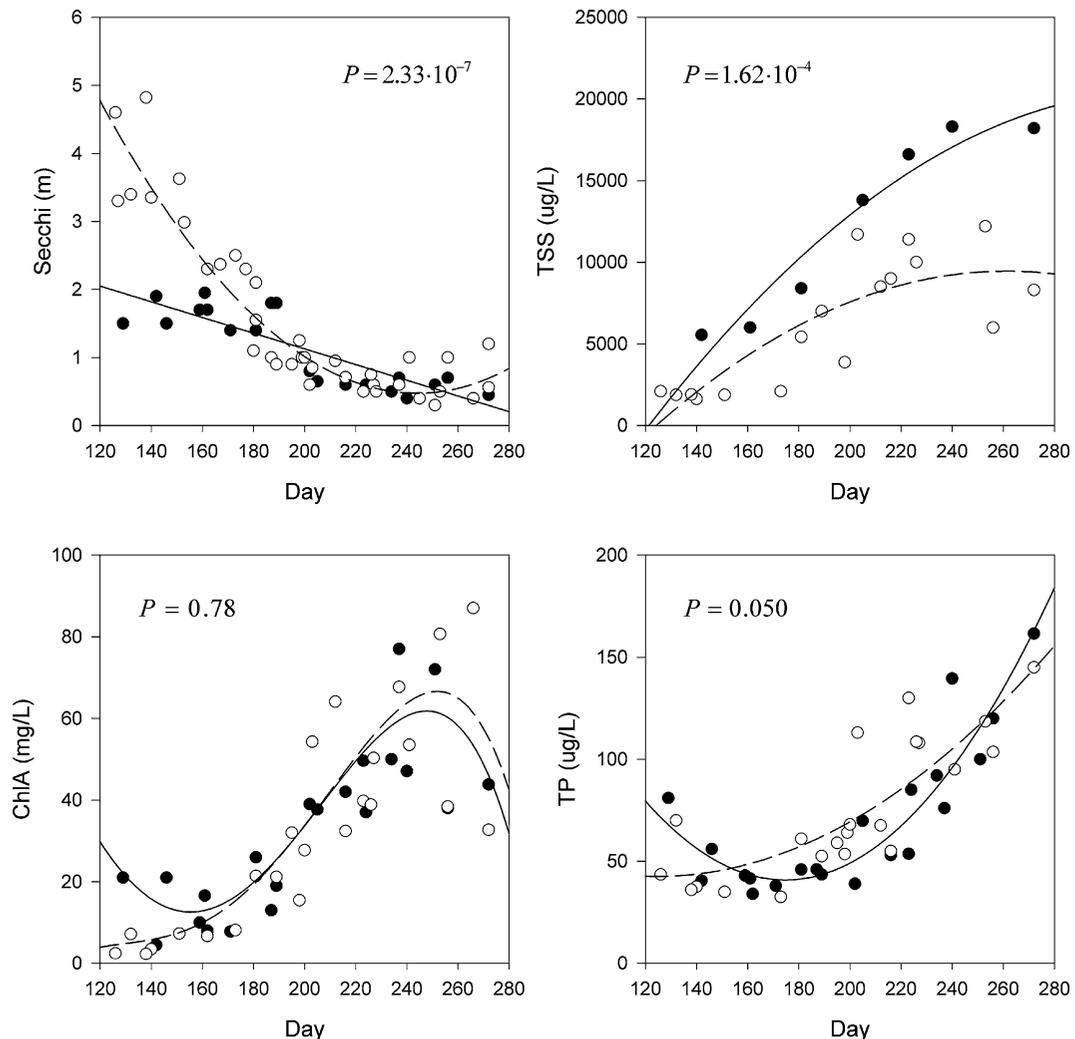


Fig. 2 Secchi depth, total suspended solids (TSS), chlorophyll *a* (ChlA), and total phosphorus (TP) before (filled circles) and after (open circles) carp removal in Lake Susan versus the ordinal day of year (May 1 to September 30, day 120–273,

respectively). *Solid line* shows the ordinal day model fitted before carp removal, while *dashed line* shows the ordinal day model fitted after carp removal. *P* values show whether the two models were significantly different

phosphorus budgets may be relatively minor as compared to that of abiotic internal loading. Nonetheless, carp removal should be viewed as an important element of efforts aiming to improve water clarity and restore aquatic macrophytes in stratified lakes.

It has been suggested that common carp and benthivorous fishes in general can cause a significant transfer of nutrients from benthic sediments into the water column due to sediment bioturbation and excretion (Lamarra Jr., 1975; Breukelaar et al., 1994; Morgan & Hicks, 2013). However, the lack of a decrease in phosphorus concentrations following carp

removal in Lake Susan suggests that neither bioturbation nor excretion played a significant role in phosphorus budget in this stratified lake. Theoretical calculations support this conclusion. Using available phosphorus budgets for benthivorous fishes (Schindler & Eby, 1997; Vanni et al., 2013), a reasonable daily food consumption rate by carp (3% body mass) and the known density of carp in Lake Susan (~100 3-kg carp per hectare), we estimated a daily carp excretion rate of approximately 0.4 mg P/m²/d or 0.2 µg P/L/d assuming a 2-m average depth. Such an excretion rate could account for only a relatively small fraction of the

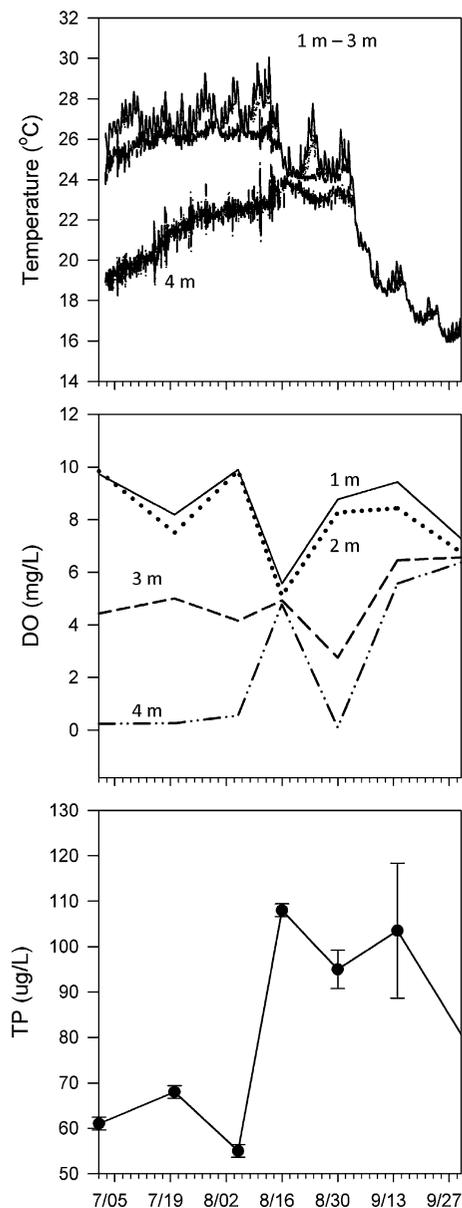


Fig. 3 Water temperature, dissolved oxygen, and total phosphorus in Lake Susan during July 1 to October 4, 2010. *Top* water temperatures recorded hourly by dataloggers at 1, 2, 3, and 4 m depths. *Middle* dissolved oxygen concentrations measured approximately every 2 weeks at 1, 2, 3, and 4 m depths (profiles at 1, 2, and 3 m overlap). *Bottom* total epilimnetic phosphorus (TP) measured concurrently with dissolved oxygen measurements

observed mid-summer increases of $\sim 1.5 \mu\text{g TP/L/d}$. Similarly, although the effect of carp bioturbation on phosphorus cycling is difficult to quantify because it is influenced by sediment properties, fish size, and food

availability (Zambrano et al., 2001; Driver et al., 2005), our results suggest that it was also relatively insignificant. This conclusion supports findings from enclosure experiments where the effects of carp bioturbation were similar in magnitude to those of excretion (Driver et al., 2005; Matsuzaki et al., 2007). Several factors, including a larger volume of water, might explain why the role of carp in phosphorus cycling appeared lower in Lake Susan than in shallow lakes (Schrage & Downing, 2004) but we suggest that more whole-lake experiments be conducted to better understand this process using ecologically-relevant scales.

Although carp removal did not seemingly have a strong effect on phosphorus, a significant improvement in springtime clarity occurred in Lake Susan following the removal of carp. In fact, springtime water clarity in 2009, 2010, and 2011 extended to the bottom of the lake, an unprecedented event in over 40 years of measurements from this lake. This increase was associated with a decline in TSS and a decline in ChlA in the early spring. The decline in TSS following carp removal was most likely caused by reduced sediment re-suspension due to benthic feeding and is consistent with other studies (Lougheed et al., 1998; Zambrano et al., 2001). The decline in ChlA despite no change in TP suggests an increase in filtering zooplankton following the removal of carp in Lake Susan. Such an increase might have occurred for two reasons: carp might have exerted predatory pressure on large zooplankton prior to their removal, and/or the increase in aquatic vegetation after carp removal might have created refugia for zooplankton. Unfortunately, these hypotheses cannot be addressed as we did not collect zooplankton data in Lake Susan prior to the removal of carp.

The vegetated littoral zone provides key habitats for fish, amphibians, and invertebrates, and considerable effort is currently being spent in North America to restore aquatic vegetation in lakes by transplantation and establishing littoral buffering zones (Radomski et al., 2010). Similarly, freshwater protected areas are being established in Europe to restore aquatic vegetation for migratory waterfowl and increase biodiversity (Williams et al., 2002). This study demonstrates that these efforts may not always succeed, unless carp biomass is reduced. The relationship between carp biomass and vegetation density reported in this study supports our previous findings from a shallow

Midwestern lake which showed that carp biomass in excess of 300 kg/ha is damaging to aquatic vegetation, but relatively little damage occurs in lakes with carp biomass of less than 100 kg/ha (Bajer et al., 2009). Because carp biomass often exceeds 300 kg/ha in aquatic ecosystems across large regions of North America, Australia, and Europe (Crivelli, 1983; Koehn, 2004; Bajer & Sorensen, 2012), this species is expected to have broad and negative impacts on aquatic vegetation.

Although limited in scope, this study advances our understanding of the carp's impacts on lake ecosystems in several ways. In addition to signaling that the effects of carp on nutrient cycling may be more subtle and complex than previously suggested, it appears to be the first study to employ whole-lake carp biomass manipulation in a thermally stratified lake. It is also one of few whole-lake manipulations that selectively removed carp without impacting the native fish community, thereby isolating the effects of carp. This study is also one of few for which mark-and-recapture estimates of carp biomass are available, advancing robust management thresholds. The recently developed ability to determine whether carp are approaching such thresholds using boat electrofishing (Bajer & Sorensen, 2012) should allow for more proactive and targeted carp management schemes in lakes to restore aquatic vegetation and improve water clarity.

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