Development and implementation of a sustainable strategy to control common carp in Riley Creek chain of lakes

A report to the managers of Riley Purgatory Bluff Creek Watershed District
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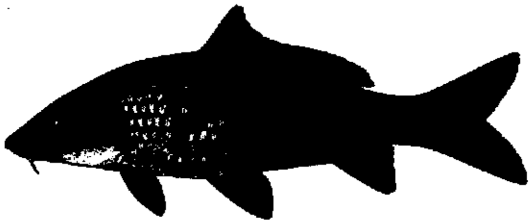

Summary

This document is comprised of two parts. The first part describes the research we conducted to determine several key elements needed to develop an integrated management strategy for common carp (*Cyprinus carpio*) in Riley Chain of Lakes (RCL). The second part presents a carp manual that the managers of Riley Purgatory Bluff Creek Watershed District (RPBCWD) might use to implement carp control in the RCL in the future.

We addressed five elements needed to develop a sustainable carp management program in the RCL. First, we determined that carp biomass needs to be maintained below 100 kg/ha to ensure that these invasive fish are not causing any significant damage to water quality. Second, we developed a rapid assessment protocol to estimate if carp biomass exceeds the management threshold by surveying lakes with an electrofishing boat. Third, we demonstrated that telemetry-guided winter seining can be used to remove excessive numbers of carp from lakes with high efficiency and without harming native fish populations. Forth, we determined that maintaining healthy populations of bluegill sunfish is sufficient to control carp's reproductive success as these native predator fish forage on carp eggs and larvae. Bluegill populations are healthy in lakes Lucy, Ann and Riley, but their numbers often decline in Susan and Rice Marsh as a result of winter hypoxia, which could potentially lead to outbursts of carp recruitment. We recommend that winter aeration be continued both in Lake Susan and Rice Marsh Lake to prevent winterkills. We also recommend that the velocity barrier (installed by MN DNR) below Lake Riley remain in place as it has played a key role in protecting the RCL from the population of carp in the Minnesota River.

Using our findings we developed a practical approach to assess and manage carp abundance in the RCL. The protocol involves annual lake surveys for adult and juvenile carp using boat electrofishing, winter aeration of lakes Rice Marsh and Susan if winterkill risk is high, and occasional (likely no more than once every 5 years) removal of adult carp using winter seining whenever their biomass builds to exceed 100 kg/ha. This effort represents the first integrated pest management approach to controlling common carp populations in an entire chain of lakes using approaches that target specific life stages. All of our findings have been published in peer-reviewed literature and are attached as appendices. More detailed description follows.

Part I: Developing an integrated common carp management strategy for Riley Creek chain of lakes

Introduction

Common carp (*Cyprinus carpio*, or 'carp') is one of the world's most widely distributed and damaging invasive fish (Weber and Brown 2009, Kulhanek et al. 2011). Carp evolved in large rivers of Eastern Europe but have been introduced worldwide as a sport or food fish over the last 150 years. Carp have established populations in many regions, but are especially abundant in North America and Australia. Ecological effects of carp on lake ecosystems have been documented for the past few decades, but nearly all research has focused on shallow lakes (lakes shallower than 10 feet, which do not stratify thermally in the summer), wetlands and waterfowl marshes. Much less it is known about the impacts of carp on deeper, thermally stratified lakes, such as those that are common in the Minneapolis-St. Paul metro area, and those that are present in the Riley Chain of Lakes (RCL). Those types of lakes provide important recreational and sport-fish opportunities and are heavily used by the public. Managing carp in those systems to improve water quality and fisheries is therefore of substantial interest.

Carp can impact lakes in several ways. They root in the bottom while looking for food thereby disturbing benthic sediments and uprooting aquatic vegetation. Carp are also believed to accelerate nutrient (mainly phosphorus) transport from the sediments into the water by disturbing sediments and through excretion (biological pump). Increased nutrient concentration in the water then drives excessive blooms of algae. Urban lakes with high carp densities have poor water clarity, often toxic algal blooms and near complete lack of aquatic vegetation (Appendix A). It is important to reduce excessive carp biomass in those systems to improve these conditions. However, while all of the effects described above have been documented with some detail in shallow lakes and wetlands, the effects of carp on vegetation, water clarity and nutrients have not been documented in thermally-stratified lakes, like those present in the RCL. Thus, our first study addresses this gap of knowledge by conducting carp removal experiments in lakes of the RCL (Appendix A, B). The specific goal of study 1 was to determine the impacts of carp on water quality of stratified lakes, and determine what biomass of carp is damaging. These data are essential to establish management goals.

Once a biomass threshold is established for carp management, strategies need to be developed to control the population below such threshold. In Minnesota, carp control has been attempted since 1930's using physical removal with nets or lake-wide chemical treatment with rotenone (a natural, non-selective fish toxin). These management strategies are often applied after a lake has been isolated from other systems using electric or velocity barriers. A combination of barriers and lake poisoning is often effective and justified in waterfowl lakes where maintaining fish populations is not considered to be important. However, such a strategy is not practical in metropolitan lakes that are heavily used by anglers and boaters. The concept of Integrated Pest Management (IPM) for controlling invasive species was coined in the 1950's. It stipulates that control of invasive species can be achieved using a combination of tools that are applied in a systematic and sustainable way to target specific life history attributes of the species. It emphasizes using natural biological mechanisms whenever possible. Our goal was to develop a carp IPM in RCL. This goal involved two sub-objectives: 1) develop methods to remove adult carp (study 2) and 2) develop strategies to control carp reproductive success (study 3).

Rapid carp population assessment methods are needed to determine whether management objectives are being met and also to detect sudden increases in carp population abundance that may require additional and timely management actions. Currently, no such approaches exist. To develop rapid assessment protocols we conducted a series of mark-recapture analyses in RCL that were accompanied by boat electrofishing surveys. This approach resulted in a simple equation which allows the managers to estimate carp abundance (carp/ha) and biomass (kg/ha or lbs/acre) from the number of carp that are being captured per one hour of electrofishing (Study 4). Such assessments can be conducted with a crew of two people in a course of 3 days.

The Study system

The Riley Creek Chain of lakes includes 5 lakes. The most upstream is Lake Lucy, followed by lakes Ann, Susan, Rice Marsh and Riley. Lake surface areas range from 87 (Lucy) to 297 (Riley) acres in size. With the exception of Rice Marsh Lake, which is only 3 m deep, all lakes in the chain are deep enough to develop thermal stratification in the summer. Lakes Lucy and Susan, which are approximately 5 m deep, can be considered polymictic as the epilimnion (top layer of water, usually 3-5 m deep) in these lakes mixes with upper portions of the hypolimnion (bottom layer of water, usually colder and having low oxygen concentration) on windy summer days. In addition, these lakes mix to the bottom in late fall and early spring. Lakes Ann and Riley, which are approximately 15 m deep are dimictic and mix only in late fall and early spring. All lakes in the system, with the exception of Lake Ann, can be considered eutrophic as their summertime total phosphorus (TP) concentrations exceed 50 – 100 µg/L. Lake Ann is mesotrophic with summertime TP below 40 µg/L. Lake Ann has the highest water clarity (~ 2 m in the summer) and the greatest diversity of native aquatic vegetation. Rice Marsh Lake is also densely vegetated and has high summertime water clarity (1.5-2 m). Water clarity in lakes Lucy, Susan and Riley typically declines below 1 m in the summer. The entire chain is located in an urban area.

All lakes in the chain have relatively similar native fish communities that are dominated by bluegill (*Lepomis macrochirus*), black crappie (*Pomoxis nigromaculatus*), largemouth bass (*Micropterus salmoides*), northern pike (*Esox lucius*), yellow perch (Perca flavescens), yellow bullheads (*Ameiurus natalis*), and black bullheads (*Ameiurus melas*). Common carp are present in all lakes, although their density has been historically highest in the three lower lakes (see below), two of which (Susan and Rice Marsh) historically had less stable native fish communities due to periodic winter hypoxia and winterkills. Winterkills have been occurring in Rice Marsh Lake every 2-5 years (Bajer and Sorensen 2010). In Lake Susan, the most recent winterkills occurred in late 1980's and early 1990's but ceased in 1993 after installation of a winter aeration system (Bajer and Sorensen 2010). No confirmed winterkills have occurred in Riley or Ann, and one suspected winterkill occurred in Lucy in 1989.

Fish, including carp, can move relatively freely among the two upper lakes (Lucy and Ann) and among the three lower lakes (Susan-Rice Marsh-Riley) but the connection between the upper lakes and the lower lakes is not easily passable, especially for fish attempting to move upstream. For example, radiotelemetry showed that no common carp moved between the lower and the upper lakes over a course of a 3-year period (Bajer and Sorensen 2010). A velocity barrier below Lake Riley prevents carp from moving into the lakes from the Minnesota River.

Study 1: Determining what constitutes a damaging carp biomass in Riley Creek Lakes

Eradication of carp is difficult, expensive, and often not necessary as carp do not cause ecological damage if their populations are kept at low densities. The main objective of sustainable carp management is thus to determine an acceptable carp biomass threshold and then manage the population below that level. Unfortunately, what constitutes tolerable carp biomass in lakes has not been well established. While experiments conducted in shallow (< 10 feet), well mixed lakes, suggest that carp populations need to be reduced to below 100 kg/ha to improve water quality (Schrage and Downing 2004; Bajer et al. 2009), published literature does not provide similar guidelines for thermally stratified lakes similar to those in the RCL. The goal of this study was to determine such a management threshold for the RCL.

Methods

To address this objective we first estimated the abundance and biomass of carp in four of the five lakes in the RCL. We did not perform this estimate for Rice Marsh Lake because the carp population varied from year-to-year as a result of seasonal migration and occasional winterkill. We used mark and recapture analyses to estimate the number and biomass of carp in lakes Lucy, Susan and Riley, and boat electrofishing (two surveys) to estimate the abundance and biomass of carp in Lake Ann following protocols described in Bajer and Sorensen (2012). Following these initial estimates, we reduced carp biomass by ~ 80% in lakes Lucy, Susan and Riley (Table 1) using telemetry-guided winter seining as described in Bajer et al. (2011). Carp biomass was not reduced in Lake Ann because it was already very low (Table 1). Concurrent to estimating and reducing carp biomass, we monitored the density and diversity of aquatic vegetation and measured improvements in water quality by measuring Secchi depth, total phosphorus (TP), chlorophyll a (Chl a), and total suspended solids (TSS) every two weeks during May-September of each year. We used t-tests to compare mean values of water quality parameters before and after carp removal (Appendix A). A more detailed analysis in Lake Susan (where carp biomass was highest) also investigated seasonal changes in water quality before and after carp removal (Appendix B).

In addition, in 2009, we began measuring hypolimnetic TP and lake mixing to determine if the increases in TP that we noted in each lake in the summer or fall were a result of internal loading. In lakes with internal loading, large quantities of phosphorus can be released from sediments when dissolved oxygen concentrations near the bottom of the lake (hypolimniom) decline (Liboriussen et al., 2009; Nürnberg, 2009). This can lead to epilimnetic phosphorus spikes and algae blooms when the lake mixes during windy days or during fall turn over. To quantify the role of internal loading on TP concentrations we began measuring TP 1 m below the thermocline during mid to late summer of 2009-2011. In July 2010 we also installed a vertical array of temperature dataloggers in Lake Susan (HOBO Pendant, Onset, Bourne, Massachusetts, 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 (Appendix B).

Results and discussion

Vegetation density in the RCL was strongly impacted by carp biomass (Fig. 1). The density of aquatic vegetation was very low (~ 5% cover) in Lake Susan prior to carp removal, however, it increased to ~ 50% cover after carp biomass was reduced from 300 to 40 kg/ha. In Lake Lucy, where the starting carp biomass was low (70 kg/ha), the density of aquatic vegetation was high even before carp removal. The density and diversity of aquatic vegetation was also high in lake Ann, which had a very low carp biomass (~ 30 kg/ha) and in which no removal was necessary. These results suggest that a carp biomass of 300 kg/ha is very damaging to aquatic vegetation, and that reducing it to below 100 kg/ha is sufficient to restore aquatic vegetation. The effects of carp removal on vegetation density could not be adequately addressed in Lake Riley because the plant community seems to be controlled by annual application of herbicides by individual homeowners. Natural healthy lakes are characterized by a diverse and abundant community of plants in the shallows and along the shoreline. Healthier plant communities are expected to improve water clarity by providing a refuge for water-filtering zooplankton. Stands of aquatic vegetation may also provide a better habitat for native fishes such as the northern pike. Thus increased density of aquatic vegetation following carp removal should be viewed as beneficial for restoring the RCL.

Carp removal was associated with a substantial increase in springtime water clarity in Lake Susan (Fig. 2, 3). Clarity more than doubled, and extended all the way to the bottom (5m) for the first time in nearly 40 years of collecting water quality samples in this lake. This increase was driven by reduced sediment re-suspension by carp (TSS) and reduced algal density (Chlorophyll a) (Fig. 2; Appendix A, B). The dramatic change in water clarity of lake Susan shows that removal of carp plays an important role in restoring metropolitan lakes. However, additional efforts are needed to further improve water clarity in those systems because carp removal was not sufficient to improve water clarity during the summer or fall. The removal of carp also had no perceptible effect on phosphorus concentrations, contrary to what might be expected based on previously published results (Fig. 2, 3; Appendix B). The phosphorus in Lake Susan increased rapidly in mid-summer, both before and after carp removal, and appeared to have been driven by abiotic internal loading rather than carp (Appendix B). Specifically, once the lake stratified in early summer we observed a buildup of TP in the bottom hypoxic layer of the lake (hypolimnion). This phosphorus-rich layer of water mixed with the surface layer (epilimnion) in mid-summer during a particularly windy day (Fig. 4). This mixing of lake layers caused a rapid spike in surface water TP, which then resulted in a heavy algal bloom (Fig. 4; Appendix A). A similar mechanism was also noted in Lake Riley, although there the mixing does not occur during late-fall lake turnover in November.

The improvements in water clarity were less pronounced in lakes Riley and Lucy where the initial carp biomass was substantially lower than in Lake Susan (Fig. 3). The effect of carp removal on water quality of Lake Riley cannot be addressed with a great deal of confidence because it is complicated by the frequent application of herbicides by lake residents, which prevents the establishment of a plant community. A poor plant community in Lake Riley may contribute to algal blooms and low water clarity in the summer because zooplankton that clears the water of the algae is unable to find a refuge from fish.

Overall, the results of our carp removal experiments suggest that excessive biomass of carp does play a significant role in reducing water clarity and vegetation density in the RCL. Differences observed in lakes Susan and Lucy before and after carp removal suggest that while the biomass of carp of 300 kg/ha is damaging to plants and water clarity, one of 70 kg/ha or less does not have any perceptible negative effects. In addition, the relationship between carp biomass and vegetation density plotted across lakes and years suggests that lakes with carp biomass below 100 kg/ha have relatively dense littoral aquatic plant community (50-100% cover; Fig. 1) while those in which carp biomass exceeds 300 kg/ha have very poor aquatic plant community (Fig. 1). Thus, we suggest that a biomass threshold of 100 kg/ha or less represents a reasonable management goal for lakes within the Riley chain, and likely similar metropolitan systems.

Table 1 Common carp abundance (N) and biomass, carp removal, and in-lake variables measured each year.

Lake	Year	Variables measured	Carp Removal	N Mean (95% CI)	Biomass (kg/ha)
Susan	2008	Secchi, TP, ChlA, TSS, Vegetation, Fish	Before	4,181 (3,292 – 5,069)	307.1
	2009	Secchi, TP, ChlA, TSS, Vegetation, Fish, Zooplankton	After	756	64.5
	2010	Secchi, TP, ChlA, TSS, Vegetation, Fish, Zooplankton	After	374	43.0
	2011	Secchi, TP, ChlA, TSS, Vegetation, Fish, Zooplankton	After	281	40.8
Riley	2008	Secchi, TP, ChlA, TSS, Vegetation, Fish	Before	6,419 (6,132 – 6,706)	176.1
	2009	Secchi, TP, ChlA, TSS, Vegetation, Fish, Zooplankton	After	3,025	90.0
	2010	Secchi, TP, ChlA, TSS, Vegetation, Fish, Zooplankton	After	376	10.5
	2011	Secchi, TP, ChlA, TSS, Vegetation, Fish, Zooplankton	After	320	10.5
Lucy	2010	Secchi, TP, ChlA, TSS, Vegetation, Fish, Zooplankton	Before	808 (768 - 851)	69.8
	2011	Secchi, TP, ChlA, TSS, Vegetation, Fish, Zooplankton	After	105	20.5
	2012	Secchi, TP, ChlA, TSS, Vegetation, Fish, Zooplankton	After	94	18.5
Ann	2009	Secchi, TP, ChlA, TSS, Vegetation, Fish, Zooplankton	Before	399	37.2

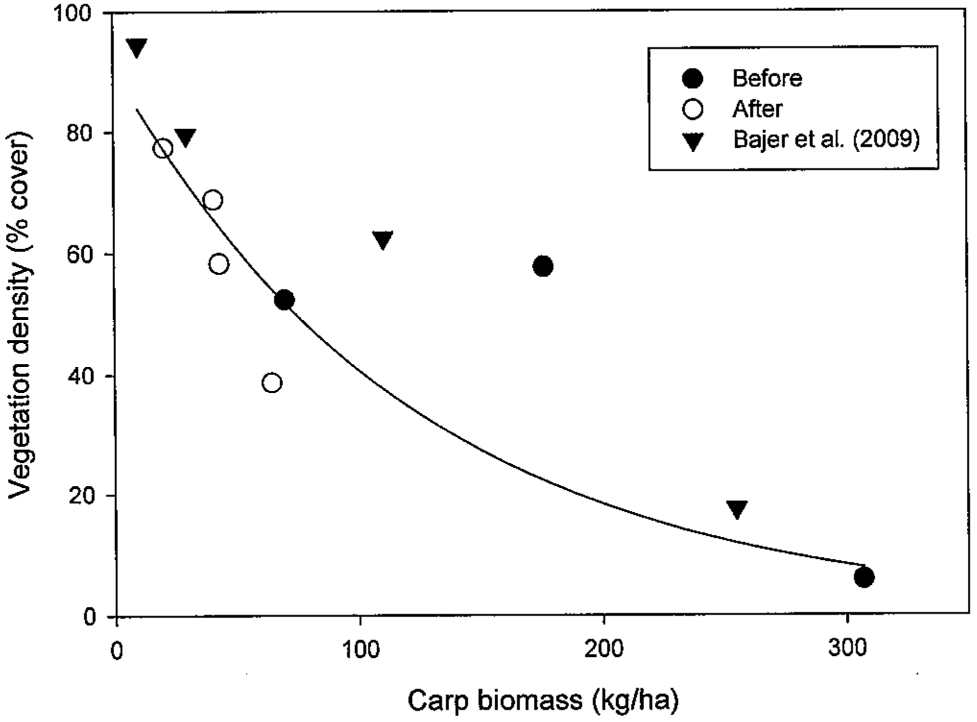

Fig. 1 The relationship between carp biomass and vegetation density. Circles represent vegetation density in each of the three study lakes before (black circles) and after (white circles) carp removal. Triangles show vegetation density documented by Bajer et al. (2009) in a shallow Midwestern lake and are used here for comparison.

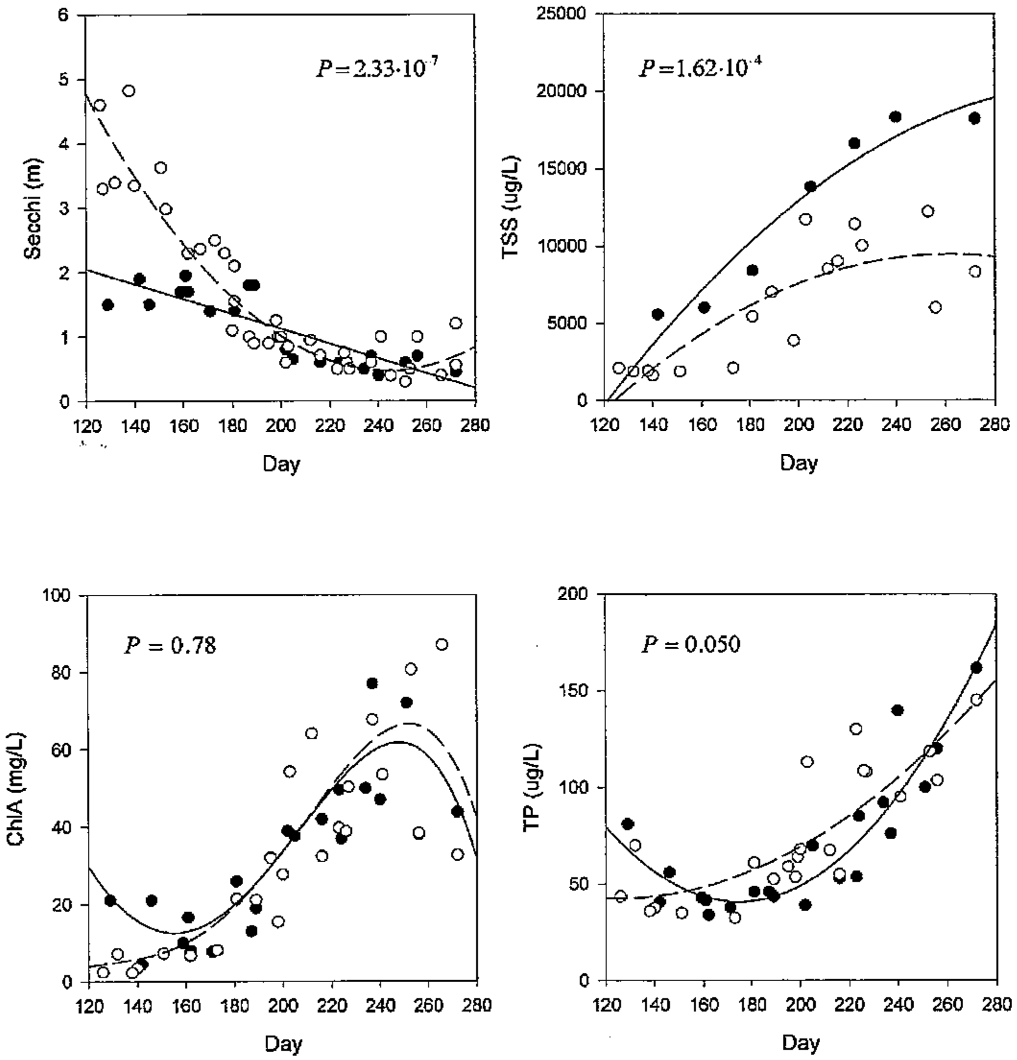

Fig. 2 Secchi depth, total suspended solids (TSS), chlorophyll a (ChlA), and total phosphorus (TP) before (filled circles) and after (open circles) carp removal in Lake Susan versus the ordinal day of year (May 1 – September 30, day 120 – 273, respectively). Solid line shows the ordinal day model fitted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

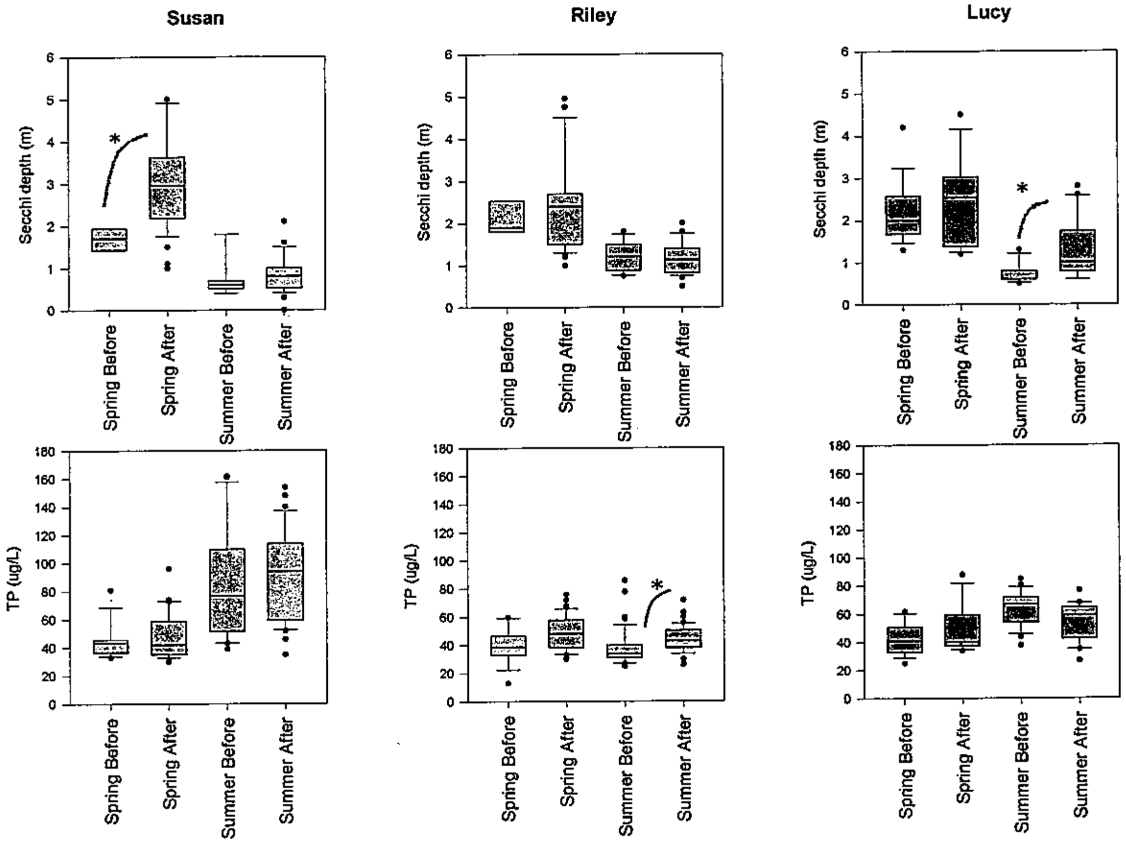

Fig. 3 Spring and summer water clarity (Secchi depth) and total phosphorus (TP) before and after carp removal in lakes Susan, Riley and Lucy. Asterisks indicate statistically significant differences (*t*-test; $P<0.05$).

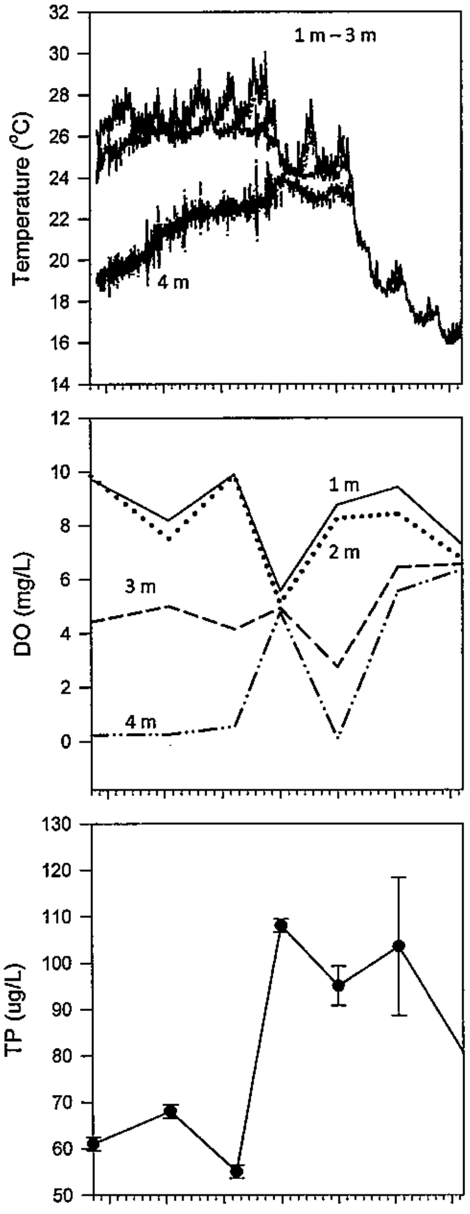

Fig. 4 Water temperature, dissolved oxygen and total phosphorus in Lake Susan during July 1 – October 4, 2010. Top panel: water temperatures recorded hourly by dataloggers at 1 m, 2 m, 3 m, and 4 m depths. Middle panel: Dissolved oxygen concentrations measured approximately every 2 weeks at 1 m, 2 m,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

Study 2: Developing effective removal methods for adult common carp

Because adult carp can live for decades, they need to be removed to accelerate lake restoration efforts. Common carp are highly social and are known for forming large wintertime aggregations in lakes (Johnsen and Hasler 1977). We tested whether these aggregations can be targeted for removal using the Judas technique in which few individuals are implanted with radiotags to locate and remove these aggregations using large seine nets.

Methods

We implanted ten to twenty carp with radiotransmitters in lakes Susan, Riley and Lucy and mapped their aggregations during two consecutive winters. Once located, these aggregations were targeted with a large seine net (1,500 feet in length) on one occasion in Lake Susan, two occasions in Lake Lucy and three occasions in Lake Riley. Captured carp were counted to determine what percentage of the population was removed. More details on the methods used in this experiment can be found in Bajer et al. 2011; Appendix C. In addition, in Lake Susan we conducted an experiment to determine if carp can be taught to aggregate in selected locations by baiting these locations with corn during summer months (peak of carp feeding activity). To do so, a location in Lake Susan was selected and baited with corn for twenty days during which time radiotagged carp in the lake were mapped during the day and night. More details on the methods used in this experiment can be found in (Bajer et al. 2010); Appendix D.

Results and Discussion

Radiotelemetry showed that carp would form aggregations during each winter in lakes Susan, Riley and Lucy. Using seine nets to target those aggregations was an effective removal technique. In Lake Susan, 78% of carp were removed in one seine haul. In lake Lucy, over 90% of carp were captured twice and in Riley, the highest catch was 68% (Appendix C). However, carp escaped the net on one occasion in lake Riley due to excessive noise and delayed net deployment (Bajer et al. 2011). Overall, more than 80% of adult carp were removed from each of the lakes as a result of one to three seine hauls. These results demonstrate that targeting winter aggregations of carp with seine nets is very effective and should be used in the RCL whenever excessive numbers of carp need to be removed. This approach is also selective as native fish can be released back into the lake unharmed.

The summertime baiting experiment in Lake Susan showed that carp can be trained to visit baited locations within approximately 10 days. But, this experiment also showed that carp aggregated at the bait only at night, suggesting that summertime removal efforts need to be conducted at night or early in the morning. While no radiotagged carp visited the baited site during the first night, by the fourth night, approximately 50% of the population were at the baited site. This proportion increased to 61% by the 10th night (Appendix D). This suggests that baiting should be continued for at least 10 days to capture and remove most carp.

Study 3: Developing strategies to control carp reproductive success

Determining how to control the reproductive success of carp is arguably the most important element of a successful carp management strategy. Because carp are very fecund (a female can carry over 1 million eggs) and spawn annually it is important to determine processes that control the survival of their eggs and larvae. Carp spawn in May and June spreading their small (~ 1 mm diameter) and sticky eggs over beds of aquatic vegetation. The eggs stick to vegetation and hatch in 3-4 days. The larvae are small (~ 5 mm in length) but grow quickly, feeding first on zooplankton and then insect larvae. Juvenile carp grow fast, reaching 100-150 mm by late summer. The window of opportunity for native predators to control juvenile carp occurs within the first few weeks after spawning when eggs and larvae are small and vulnerable.

Successful survival of carp eggs and larvae of the critical developmental period is termed 'recruitment'. Prior to this study no clear evidence was presented to suggest that any control processes for carp recruitment may be present in Midwestern lakes. Carp recruitment is typically considered inevitable, and controlled mainly by the abundance of adult carp. However, fish surveys conducted in Minnesota lakes very rarely catch small carp while large individuals are commonly captured. This suggests that natural control mechanisms exist in Minnesota lakes. Most fishes found in lakes in Minnesota are highly predacious and we hypothesized that they play an important role in controlling carp recruitment.

We addressed this hypothesis by conducting a series of analyses during 2008-2014. Using historical data collected by the DNR we hypothesized that native fish can effectively control carp recruitment in most lakes and during most years but that this control mechanism deteriorates when native fish die off as a result of winterkills is shallow lakes and marshes, in which oxygen supplies are insufficient to last the entire winter. Adult carp are known for conducting springtime migrations into such marshes and their eggs and larvae can survive in large numbers in such predator-poor habitat (Appendix E).Young carp can then disperse out of such marshes and into the lakes driving excessive carp abundance throughout entire chains of lakes.

Methods:

To determine processes that regulate carp recruitment we conducted four analyses. First we implanted approximately 50 adult carp with radiotransmitters in lakes Susan, Rice Marsh and Riley to document their movement during spawning season of 2008 and 2009. We also surveyed all three lakes daily during 2009 and 2010 to document when and where carp spawn. Second, we aged a representative sample of carp to determine how often carp recruit and what conditions are associated with successful recruitment. The ageing analysis was conducted in lake Susan and another lake located in an independent watershed (Lake Echo in SW Minnesota, LCCMR funded) to achieve greater statistical power. In each case, age structures were analyzed against known winterkill records to test the hypothesis that carp recruit in lakes that winterkill and lack native predatory fishes. More details on the study design can be found in Bajer and Sorensen (2010); Appendix E.

In the third analysis we conducted trapnet surveys in all Riley Chain lakes and four other chains of lakes (LCCMR- funded research) to develop statistical associations between the age-0 carp catch rate and catch rates of native fish to determine which native fish might be playing the most important role in controlling carp recruitment. We used logistic regression to model carp recruitment (for details see Appendix F).

Last, we placed known numbers of carp eggs attached to artificial spawning substrate (green yarn) within carp spawning areas of a lake where winterkills did or did not occur (Lake Riley and three other lakes (funded by LCCMR). We examined the rate with which native fish were able to consume carp eggs in lakes that winterkill or not. We also collected a sample of fish in one lake to determine which species were consuming carp eggs. More details can be found in Bajer and Sorensen (2012); Appendix F.

Results and Discussion

Telemetry results showed that many adult carp (10 % to 40% of population) migrate each spring from lakes Susan and Riley to spawn in Rice Marsh Lake and then come back to their home lakes (Appendix E). Spawning occurred each year in Rice Marsh in May and approximately 2-3 weeks later in Susan and Riley. Despite intense (> 100 spawning sites per lake) spawning activity and despite the fact that eggs collected from lakes hatched successfully into larvae when transported to the laboratory, we found no young carp in any of the three lakes (Appendix E; Bajer and Sorensen 2010). This suggested that carp recruitment in lakes Susan, Riley and Rice Marsh is very effectively controlled by native fish during most years. This was corroborated by ageing analysis, which showed that carp recruit infrequently (last strong recruitment occurred in early 1990s) and then only in adjacent shallow marshes that winterkill and which lack native fish. Trapnet surveys, egg-predation experiments and fish diet analyses all suggested that bluegills are the dominant and effective predators of carp eggs and larvae. Apparently bluegills, augmented by other species of native fish, are able to completely suppress carp recruitment in most lakes, unless they perish in a winterkill.

We concluded that shallow marshes that periodically winterkill, such as Rice Marsh Lake, function as carp nurseries following winterkills. The young carp then spread from these marshes into adjacent lakes driving high carp biomass in entire chains of lakes. This process can be controlled by installing winter aeration systems that prevent winterkills in marshes and allow bluegills to survive winter. For example, a winter aeration system has been installed in Lake Susan since 1993 and our ageing analysis suggests that no major recruitment event occurred in that lake since, while numerous strong recruitment pulses occurred during 1989-1991. A winter aeration system was also installed in Rice Marsh Lake in 2012 in light of our research. While preventing winterkills in Rice Marsh is more challenging than in Susan (due to a shallower depth of Rice Marsh Lake), no winterkills have occurred since the system has been in place. We recommend that winter aeration in Rice Marsh Lake be used whenever there is a high chance of a winterkill occurring. Collecting systematic measurements of winter dissolved oxygen in Rice Marsh Lake during early winter could be conducted to assess the risk of a winterkill and manage the aeration system. In case the aeration fails and carp recruitment occurs, we recommend that boat electrofishing surveys be conducted in Rice Marsh, Susan and Riley to assess the abundance and spread of young carp (Study 4 below) and the Judas technique be used to remove excessive numbers of carp from those lakes if necessary (Study 2 above).

Study 4: Developing practical tools to assess carp biomass in lakes

To effectively manage carp populations, managers need to be able to assess if biomass exceeds the desired management threshold of 100 kg/ha (Study 1). Mark-recapture analyses allow for the most accurate estimates of carp density and biomass in lakes but are labor intensive and require statistical expertise. Thus, we developed a more practical method that the managers can use to estimate carp biomass by conducting lake surveys with an electrofishing boat.

Methods

We developed a low-effort approach to estimate the density and biomass of carp in a lake from the number of carp caught per one hour of boat electrofishing. To do so, we conducted three to four boat electrofishing surveys in lakes Susan, Riley and Lucy each year before and after carp removal and estimated the mean catch of carp per one hour of electrofishing for each lake and year. Because carp abundance (number per hectare) was known in each lake, since mark-recapture analyses were already conducted (Bajer and Sorensen 2012; Appendix C), we were able to develop a relationship between electrofishing catch rate and carp density in the lake. We gathered similar data from five other lakes outside Riley Creek Chain of Lakes (LCCMR funded) to increase sample size to eight lakes and achieve statistical power (Bajer and Sorensen 2012). All of these additional lakes were of similar size and depth to lakes in RCC. We then developed a linear regression between the mean carp catch rate per one hour of electrofishing and carp density in each lake. The regression was tested for robustness using a "leave one out" cross-validation approach (Bajer and Sorensen 2012). More details can be found in Appendix G.

Results and discussion

Our analysis suggested that the density of carp in RCC lakes can be predicted using the following equation:

Carp density per hectare = 4.71 * CPUE + 3.04;

where CPUE (catch per unit of effort) is the mean catch of common carp per one hour of electrofishing. Estimated carp density per hectare can then be multiplied by the mean weight of carp to obtain carp biomass per hectare. This approach can be used to determine if carp exceed the 100 kg/ha threshold and need to be removed. We recommend conducting at least three electrofishing surveys to get an accurate estimate of mean carp CPUE in each lake. These surveys should be conducted during July-September when the carp are more evenly distributed in the lakes. Each surveys should last approximately 1 h (ideally three 20 minute, non-overlapping transects) and cover most of the shoreline area of the lake. Only carp larger than 300 mm should be included in this analysis because that was the smallest size of carp that we encountered in the study lakes. More details of how to conduct the surveys can be found in (Bajer and Sorensen 2012) (Appendix G).

Part II: Implementing a sustainable carp management strategy in Riley Chain of lakes

Studies 1 through 4 described in the first part of this document demonstrated that 1) common carp populations need to be controlled at a density of 100 kg/ha or less to minimize their effects on aquatic vegetation and water clarity, 2) excessive numbers of carp can be effectively removed using telemetry-guided winter seining, and possibly also summer seining over baited areas, 3) preventing winterkills by aeration and maintaining healthy populations of bluegills can be used to control carp recruitment, and 4) boat electrofishing can be used to determine if carp management thresholds are met or if additional removal is needed. Given these results, a sustainable carp management program can be formed for the RCL. In addition, as a result of our work conducted to address studies 1-4, we removed most carp from the RCL and their biomass is currently below the damaging threshold throughout the entire chain (Table 1). Consequently, the management strategy that we propose places the main emphasis on preventing carp recruitment and conducting routine monitoring to assess population status. We expect that removal will only be needed on an occasional basis (every several years). We outline this program below.

Step 1: Preventing and monitoring carp recruitment

The cornerstone of the proposed carp management strategy is the prevention and monitoring of carp recruitment. Both Lake Susan and Rice Marsh Lake have functioned as productive carp nurseries in the past when they winterkilled. Thus, it is important to use winter aeration in those systems to ensure that winter dissolved oxygen concentrations remain above 1.5 mg/L. This oxygen level should allow for the survival of most native fish, including bluegills, which are the main predators of carp eggs and larvae. Aeration does not need to be used every winter in Lake Susan, but can be implemented if oxygen levels decline to approximately 5 mg/L and further decline is expected. The approach used by the city of Chanhassen has been very effective and should continue. A winter aeration system has also been installed in Rice Marsh Lake in 2012 in light of our findings. While it is difficult to determine with certainty the effectiveness of this system, no winterkills have occurred since it was put in place, although dissolved oxygen concentrations did decline to near-lethal levels. We recommend that this system remains in place and is evaluated during the next several winters by collecting bi-monthly (every 2 weeks) winter dissolved oxygen concentrations near the aerator as well as in other areas of the lake.

We recommend that trapnet surveys be conducted annually in Rice Marsh Lake and other lakes throughout the chain to verify the lack of carp recruitment and determine the status of bluegill population. Those surveys are particularly important following a suspected winterkill in any of the lakes.

Practical considerations:

- Five trapnets should be used in each lake.

- The trapnets need to be distributed in approximately equal distances along the shoreline.
- The trapnets are set, left in the lake overnight and removed the next day approximately 24 h later.
- These nets are constructed using a net material with a mesh size of 13 mm (bar) and consist of a lead line (length: 10 m), an entrance frame (rectangle: 1.8 m x 0.9 m), 5 hoops (diameter: 0.76 m) with 2 internal net funnels (.10 m). The lead line is anchored at the shoreline or close to the cattail edge using a metal stake and the rest of the net is then stretched into the lake perpendicular to the shoreline or cattail line. The back of the net should be tied shut and then pulled tight with an anchor attached to keep it in place. A float is attached to the anchor to mark the location of the net and allow for easy pick-up (Photo 1).
- The DNR needs to be consulted on using nets in lakes that are designated as infested with aquatic invasive species
- All fish need to be counted and measured. All carp < 150 mm should be assumed to be age-0 individuals and their presence will indicate that carp recruitment occurred. The carp may also be aged using otoliths.
- It is important to use small mesh trapnets (13 mm bar) to ensure that age-0 carp can be reliably captured.
- Trapnets should be set in August or September when age-0 carp are large enough to be captured but before water temperatures decline below 10C at which time carp move offshore.

Photo 1. A trapnet set in Lake Riley to assess presence of age-0 carp and abundance of native fish.

Step 2: Monitoring the abundance of adult carp in each lake to determine if removal is necessary

Current carp populations are low in the Riley Creek lakes. It is important, however, to monitor the abundance of adult carp so that they do not exceed the biomass of 100 kg/ha. Given the infrequent history of carp recruitment in Riley Creek Chain of Lakes we recommend that a series of electrofishing surveys be conducted in each lake every 2 years to assess adult carp abundance. The surveys should be conducted annually if recruitment occurs (see Step 1 above).

Practical considerations:

- At least three surveys should be conducted in each lake to obtain a robust mean estimate of adult carp catch rate. These surveys need to be spaced by at least one week.
- Each electrofishing survey should consist of three 20 min transects each conducted in a different area of the lake. Time needs to be recorded for each transect.
- Catch per unit of effort (CPUE) needs to be calculated for each transect as: CPUE = number of carp caught within a transect * 3600/time (seconds) in each transect
- The CPUEs for each transect need to be averaged to obtain mean daily CPUE. Three values of mean daily CPUEs are needed to estimate a mean CPUE for each lake
- The surveys need to be conducted in August and September when carp are near shore and are relatively equally distributed in lakes
- During the surveys the boat needs to be maneuvered along the shoreline in a leap-frog fashion targeting patches of vegetation and submersed trees.
- We recommend the following electric field settings: 10-15A, 100-150V, duty cycle 35%, pulsed DC current
- Follow DNR safety protocols
- All carp should be measured for length (mm) to obtain weight estimate: weight in kilograms = $6*10^{-8}*\text{Length}^{2.76}$
- The mean carp catch rate should be entered in Equation 1 to estimate mean carp density per hectare. Mean carp density should be multiplied by mean weight to obtain mean biomass per hectare

If the estimated carp biomass exceeds 100 kg/ha, carp need to be removed (Step 3).

Step 3: Removing excessive biomass of carp from Lakes

We recommend winter seining to remove carp from lakes. Carp density and biomass estimates (Step 2) should be used to determine how many carp are expected to be in the lake and how many need to be removed to bring the population down below 100 kg/ha. If removal is necessary, implant 15 carp with radiotransmitters in each lake. These fish should then be located once a week during January –March periods (whenever ice cover is safe) to determine aggregations. An aggregation is defined when distances between radiotagged carp are below 100 m (Bajer et al. 2011).

Number of radiotagged carp in one area can be used to estimate the proportion of the population in that location. We recommend hiring commercial fishermen to conduct the seining after informing them about the locations of the fish. Commercial fishing requires permitting process through the Minnesota DNR and we recommend that arrangements be made several months in advance.

Practical considerations:

- Commercial fishermen need to be contacted in early fall and informed about planned seining to apply for all necessary permits before winter. We recommend written agreements with the fishermen to specify general conditions and the number of carp that need to be removed.
- To maximize seining efficiency carp aggregations need to be mapped on the day of seining. Plastic cones should be placed on ice to mark the edges of the aggregation and provide a visual mark for the fisherman to deploy the net.
- All carp should be counted and measured to determine the number and biomass of carp removed from the lake.

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Appendix B: Bajer, P. G., and P. W. Sorensen. 2014. Effects of common carp on phosphorus concentrations, water clarity, and vegetation density: a whole system experiment in a thermally stratified lake. Hydrobiologia:1-9.

Appendix C: Bajer P., G., C. J. Chizinski, and P. W. Sorensen. 2011. Using the Judas technique to locate and remove wintertime aggregations of invasive common carp. Fisheries Management and Ecology. 18: 497-505

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Appendix F: Bajer, P. G., C. J. Chizinski, J. J. Silbernagel, and P. W. Sorensen. 2012. Variation in native micro-predator abundance explains recruitment of a mobile invasive fish, the common carp, in a naturally unstable environment. Biological Invasions 14:1919-1929.

Appendix G: Bajer, P. G. and P. W. Sorensen. 2012. Using Boat Electrofishing to Estimate the Abundance of Invasive Common Carp in Small Midwestern Lakes. North American Journal of Fisheries Management 32:817-822.

Appendix A

Effects of common carp on vegetative cover, total phosphorus and water clarity in thermally stratified eutrophic lakes

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Abstract – Although it has been demonstrated that the common carp (*Cyprinus carpio*) can negatively impact shallow lake ecosystems, the effects of this invasive species have not been addressed in thermally stratified lakes. In this study we estimated the biomass of carp in three stratified lakes and reduced it by ~ 80% while monitoring changes in aquatic vegetation density, water clarity and phosphorus. A mixed-effect model selection analysis showed that while carp had a strong effect on vegetation, which declined exponentially with increasing carp biomass, it had a less pronounced effect on water clarity or phosphorus. In the lake that initially had the highest biomass of carp (307 kg/ha), carp removal was associated with a rapid increase in vegetation density and a two-fold increase in springtime water clarity, but summertime clarity remained poor. No major increases in springtime or summertime clarity occurred in lakes that initially had a moderate (176 kg/ha) or low (70 kg/ha) biomass of carp. The removal of carp had no discernible effect on phosphorus concentrations in any of our study lakes. Our findings suggest that while carp severely impact aquatic vegetation, they may have only a moderate effect on phosphorus and water clarity in thermally stratified, eutrophic lakes.

Keywords: *Cyprinus carpio*; Macrophytes; Removal; Invasive fish

Introduction

The common carp (*Cyprinus carpio*) is one of the world's most widespread and abundant 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 lakes it invades (Matsuzaki et al., 2009). It has been demonstrated that carp can be damaging to shallow lakes, e.g. lakes that can be largely colonized by vegetation and that do not stratify for long periods in summer (Scheffer, 2005), but this species' impacts on deeper, thermally stratified lakes have not been addressed. This is perhaps a result of the notion that carp are not sufficiently abundant in thermally stratified lakes to cause ecological damage. However, recent studies show that carp biomass in stratified lakes can be similar to values reported from shallow systems (Bajer & Sorensen, 2012), and it can exceed levels that are considered ecologically damaging by several fold (Bajer et al., 2009). Furthermore, most biodiversity and ecological processes in thermally stratified lakes occurs in the littoral zone (Heino, 2008), directly overlapping habitats occupied by the carp (Bajer et al., 2010).

Over 40 studies have examined the impacts of common carp in shallow lakes (Matsuzaki et al., 2009; Weber &Brown, 2009). In shallow systems, carp have been shown to cause declines in vegetation density and water clarity and lead to increases in total suspended solids and chlorophyll a (Bajer et al., 2009; Lougheed et al., 1998; Schrage & Downing, 2004; Zambrano et al., 2001). Several studies also suggested that carp increase total phosphorus concentrations in shallow lakes due to sediment resuspension and excretion (Breukelaar et al., 1994; Lamarra Jr, 1975; Moss et al., 2002; Schrage & Downing, 2004). However, the knowledge of carp impacts on shallow lakes may not be directly applicable to predicting the effects of this species on thermally stratified systems because of differences in carp spatial distribution and unique physical processes that occur in stratified lakes.

In stratified lakes carp tend to occupy littoral zone (Bajer et al., 2010) as opposed to being more evenly distributed in shallow lakes (Penne & Pierce, 2008). The concentration of carp in the littoral zone is likely to accentuate the impacts on aquatic vegetation, while diminishing the impacts on suspended solids. Summer stratification can also profoundly affect phosphorus cycling independently of the effects of carp. Large quantities of phosphorus can be released from sediments when hypolimnetic dissolved oxygen concentrations decline to low levels (Liboriussen et al., 2009; Nürnberg, 2009). This 'internal loading' can lead to epilimnetic phosphorus spikes and algae blooms as a result of thermocline erosion and mixing. The phytoplankton blooms may in turn be controlled by the well-established interactions between filtering zooplankton, planktivorous fish and the vegetation that the zooplankton uses as a refuge from fish (Nicolle et al., 2010; Timms & Moss, 1984). Carp may play a role in these interactions via at least two possible mechanisms. First, they may reduce the density of aquatic macrophytes, thus eliminating the shelter for zooplankton. Second, they may elevate phosphorus concentrations above those associated with abiotic internal loading by bioturbation of littoral sediments and excretion. None of those questions have been addressed.

In this study we quantified the effects of common carp in three thermally stratified eutrophic lakes in the North American Midwest. We estimated the abundance and biomass of carp in these lakes while measuring the percent cover of aquatic vegetation, water clarity, total phosphorus (TP), chlorophyll a (ChlA), and total suspended solids (TSS). In each lake we also conducted a survey of the native fish community and filtering zooplankton. The biomass of carp was then reduced in each lake by approximately 80% and changes in vegetation density and water quality parameters were documented. The results of our study demonstrate that while the impacts of carp on aquatic vegetation are similar to those reported in shallow lakes, the impacts on water clarity and phosphorus are subtler. Our results are relevant to vegetation restoration and phosphorus-reduction efforts in stratified eutrophic lakes.

Methods

Study lakes

This study was conducted in three lakes in central Minnesota, USA. In the two smaller lakes, Susan (35.1 ha; max depth 5.1 m) and Lucy (34.6 ha, max depth 6.0 m), summer stratification sets at approximately 3m, and hypolimnetic waters with dissolved oxygen concentrations < 0.1 mg/L cover approximately 50% of each lakes' area during July - September. In the larger and deeper Lake Riley (118.8 ha, max depth 14.7 m), summer stratification sets at approximately 5 m and hypolimnetic waters with dissolved oxygen < 0.1 mg/L also cover approximately 50% of the lake. In each lake, aquatic vegetation is restricted to the littoral zone that extends approximately 50-100 m from the shore where water depths are less than 3 m. The native fish community in each lake is dominated by centrarchids including the bluegill sunfish (*Lepomis macrochirus*), black crappie (*Pomoxis nigromaculatus)* and largemouth bass (*Salmoides micropterus*). Radiotelemetry studies showed that carp in the study lakes tend to occupy the littoral zone during summers and are rarely found offshore (Bajer et al., 2010; Bajer & Sorensen 2010). Carp biomass at the onset of the study ranged from relatively low in Lake Lucy, to medium in Lake Riley, to high in Lake Susan (Table 1), resembling values published from other systems in the region and elsewhere (Crivelli, 1983; Bajer et al., 2012).

Experimental design

This study started in lakes Susan and Riley in which we estimated the biomass of carp in the summer of 2008 while concurrently collecting baseline data of vegetation density, water quality (Secchi, TP, ChlA, TSS), and native fish abundance. In March of 2009, a large number of the carp were removed from both lakes, while monitoring of vegetation, water quality and fish continued for two more years (2009 and 2010) and data collection was expanded to include zooplankton abundance (Table 1). We estimated the abundance of carp in Lake Lucy in 2010 as well as vegetation, water quality, native fish and zooplankton. The carp were then removed from Lake Lucy in early spring of 2011 while post-removal measurements continued through 2012. This resulted in one year of pre-removal data and 2-3 years of post-removal data in each lake (Table 1). This data was used in a multivariate analysis to test the effects of carp removal on vegetative cover and water quality parameters. The multivariate analysis was unbalanced because it included only one year of pre-removal data versus 2-3 years of post-removal data for each lake (Table 1). Thus, we conducted a companion analysis that included two additional years of pre-removal data (2004 and 2005; http://www.rileywd.org). This data set included only Secchi, TP and ChlA, but lacked vegetation, TSS, native fish and zooplankton, therefore, it could not be used in the multivariate analysis. Instead, we used it to conduct simple t-tests on Secchi, ChlA and TP before and after carp removal in each lake.

Carp biomass estimates and removal

Carp abundance and biomass in each study lakes were recently estimated using mark-and-recapture analyses (Bajer & Sorensen 2012) (Table 1). Following these initial estimates, carp were removed from each lake using telemetry-guided winter seining as described in Bajer et al. (2011). Carp removed from each lake were subtracted from the initial population estimate to generate a post-removal estimate. These post-removal estimates were adjusted for natural mortality that was estimated using the survival of radiotagged carp that were present in each lake as a part of a related study (natural annual mortality rates were approximately 10%; Bajer et al., 2012). Lake inlets and outlets were blocked to reduce emigration and immigration, and each lake was sampled annually to account for recruitment (no recruitment occurred throughout the study; Bajer & Sorensen, 2012).

Aquatic vegetation

Aquatic vegetation (both submersed and floating-leaf) was sampled annually in each lake in late June and early July (peak abundance) following procedures similar to Schrage & Downing (2004). Ten transects distributed approximately equidistance from each other were mapped in each lake using ArcGis. These transects were perpendicular to shore and vegetation was sampled at locations with water depths of 0.5 m, 1 m, 1.5 m and 2 m along each transect (the vegetation could not be seen at depths > 2 m due to poor water clarity). At each sampling location visual estimates of percent vegetative cover (nearest 10%) were recorded within a 2 m x 2 m area using the front of the boat (2 m long) as a visual reference. To validate that our visual assessments 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 assessments and rake biomass ($P<0.001$). The rake was also used to confirm that little vegetation occurred at depths exceeding 2 m. Visual estimates were averaged across transects and depths to represent a mean percent vegetative cover in the littoral zone (0.5 m to 2 m depth) of each lake.

Water clarity, total phosphorus, total suspended solids, and chlorophyll a

Water clarity (Secchi depth) total phosphorus, total suspended solids and chlorophyll a were sampled at two (lakes Lucy and Susan) or three (Lake Riley) offshore locations in each lake every two weeks between May and September. Secchi depth was measured from a boat using a standard 20 cm disc. To determine TP, TSS and ChlA we collected integrated epilimnetic samples following standard methods (APHA, 1998). At each of the sampling locations we first measured a temperature and DO 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 1m increments. The 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. In 2009–2012 we also collected hypolimnetic TP samples. All samples were stored in a cooler and delivered to an analytical laboratory within 24h. 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°C–105°C (SM 2540 D), and ChlA was analyzed using 10200 H method (APHA, 1998).

Zooplankton

Zooplankton samples were collected in 2009–2011 in all three lakes together with water samples. Zooplankton was collected using vertical tows (64 μm net, 0.2 m diameter) from the bottom of the epilimnion to the surface. Three tows were collected at each sampling location, and the total volume of filtered water was calculated using the depth of each tow and the diameter of the top ring of the plankton net. Zooplankton samples were preserved using ethyl alcohol and concentrated to 50 mL. In the laboratory, the samples were thoroughly mixed and 1 mL subsample was collected and organisms were counted under a microscope (Nikon Optiphot; Melville, NY, USA; 40 x power) using a 1 mL graduated counting well. Because we were interested in large filtering zooplankton, we focused on cladocera, which were identified to the genus level. The first 20 organisms of each genus were measured for length (nearest μm). The density of Daphnia sp. (individuals/L) was calculated for each sampling date and location to portray the abundance of large filtering zooplankton.

Native fish

The fish community in each lake was assessed in late summer using standard survey trapnets (single 12 m lead, single rectangular 0.6 m x 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 each lake for one 24 h period and all collected fish species were counted and first 30 of each species measured for length (nearest mm). The mean catch rate of bluegill sunfish (individuals/net), which comprised over 90% of all collected fish, was calculated to represent an index of planktivorous fish abundance.

Data analysis

We conducted two analyses. First, we conducted a series of multivariate mixed-effect model selection analyses to test the effect of carp removal on: 1) vegetation density, 2) water clarity, 3) ChlA (main driver of clarity), and 4) TP (main driver of ChlA). In each of those analyses we tested the support for several competing models that included or excluded carp removal as a categorical variable in combination with other relevant variables. For example, while testing models for vegetation density we used carp removal, parameters associated with water transparency (Secchi and TSS), trophic conditions (TP; some species of vegetation employ foliar uptake), or different combinations of all of the above. Similarly, while testing what explained water clarity (Secchi) we considered carp removal, TP, ChlA, TSS, abundance of planktivorous fish (bluegill sunfish), vegetation density, or their combinations. We did not test if Daphnia played a role in water clarity because we lacked zooplankton data for the pre-removal phase of the study (years 2008 and 2009) in lakes Susan and Riley. However, Daphnia was tested in a sub-analysis (years 2010–2012) that evaluated what explained ChlA concentrations. All models included a random year, lake, and sampling site effect to account for the repeated nature of our measurements. Also, because water clarity, TP and ChlA often show distinct seasonal patterns in eutrophic lakes (clear-water spring phase followed by poor quality summer phase; Scheffer, 2005), all models also included a fixed seasonal effect [spring (May and June) or summer (July-September)]. If necessary, the continuous variables were log-transformed to achieve co-linearity with the response variable. The support for each competing model within each model selection analysis was determined using the AICc scores and Akaike's weights (w_i) following Burnham & Anderson (2002). Model selection analysis was conducted using ModAvg package in R (R Development Core Team, 2012).

In addition to the model selection analysis, we conducted simple t-tests to determine if water clarity, TP or ChlA changed after carp removal in each lake. Separate t-tests were conducted for spring and summertime periods to account for observed seasonal patterns. Because this analysis did not require complete case data, we used supplementary data on TP, Secchi and ChlA collected by the local watershed district in each lake during 2004 and 2005. This allowed us to obtain three years of pre-removal data and three years of post removal data in each lake. Because this analysis did not include a sampling site effect, like the model selection analysis did, samples collected at different sites were averaged for each sampling date. The t-tests were conducted using R.

Results

The biomass of carp appeared to have a strong negative effect on vegetative cover (Fig. 1). This was corroborated both by the model selection analyses and the responses observed in individual lakes following carp removal. Model selection analysis showed that vegetation density was best explained by a single-variable model that included carp removal as the sole predictor variable (Table 2). Vegetation density declined exponentially with increasing carp biomass and was less than 20% in lakes with carp biomass greater than 200 kg/ha (Fig. 1). Following carp biomass reduction from 307 kg/ha to 60 kg/ha in Lake Susan, littoral vegetation density increased from 5% to nearly 70% (Figure 1). An increase also occurred in Lake Lucy in which carp biomass was reduced from 50 to 10 kg/ha. The effects of carp removal on vegetation density could not be evaluated in Lake Riley due to extensive herbicide application by lake residents.

Model selection analysis showed that water clarity was best explained by a model that included TP, ChlA, TSS, carp and season (Table 2). Model parameters showed that clarity declined with increasing TP, ChlA, and TSS, was lower before carp removal, and lower in the summer than in the spring (Table 3; Fig. 2). ChlA appeared to have the most direct effect on clarity (Fig. 2). This was corroborated by AIC scores which increased by ~ 80 units following the removal of ChlA from the best model. Removal of carp from the model resulted in an AIC score increase of less than 3 units (Table 2). Investigation of changes in water clarity before and after carp removal using t-tests showed that in Lake Susan, water clarity improved significantly in the spring (approximately a two-fold increase, $P=0.04$), but not in the summer (Fig. 3). No significant changes in springtime or summertime clarity occurred in Lake Riley (Fig. 3) and only a slight increase in summertime water clarity occurred in Lake Lucy (Fig 3).

Model selection analysis showed that ChlA (main driver of clarity, see above) was best explained by a model that included TP, Daphnia, carp, and season (Table 2). Model coefficient values suggested that ChlA increased with TP, decreased with Daphnia, was higher prior to carp removal and was higher during the summer than spring (Table 3). TP had the most direct effect on ChlA (Fig. 2) and removal of TP from the model caused an increase in AIC scores by 18 units (Table 2). Investigation of changes in ChlA before and after carp removal using t-tests showed that springtime ChlA declined three fold in the high carp biomass lake (Lake Susan; $P=0.08$) but no improvements in summertime ChlA were observed. No changes in springtime or summertime ChlA occurred in lakes Riley or Lucy.

Model selection analysis showed that TP (main driver of ChlA, see above) in our study lakes was best explained by a model that included the season and carp removal (Table 2). AIC scores suggested that the season had the main effect on TP concentrations as the removal of it from the model increased AIC scores by 30 units, and that carp had only a minor effect on TP (Table 2). Model coefficients showed that TP was substantially higher (~ 18 ug/L on average) during summer than spring and that it slightly (~ 1.5 ug/L on average) increased after carp removal (Table 3). T-tests showed no differences in springtime or summertime TP before vs. after carp removal in any of the study lakes, except for a slight increase in summertime TP in Lake Riley following carp removal (Fig. 3). Seasonal TP patterns also suggested that carp removal had no discernible effect on epilimnetic TP, which appeared to be driven instead by hypolimnetic loading (Fig. 4). For example, in lakes Susan and Lucy epilimnetic TP increased in mid-summer following the spike in hypolimnetic TP (Fig. 4); an erosion of thermal stratification occurred in both lakes during particularly windy summer days (data not shown). Internal loading was also evident in Lake Riley, although this lake had deeper and more stable epilimnion and did not mix until late fall (Fig. 4).

Discussion

This study provides the first account of the effects of common carp on the ecology of thermally stratified eutrophic lakes. We found that while the carp had a severe impact on the density of submersed vegetation, it appeared to have a relatively modest effect on water clarity and phosphorus. This suggests that carp play a different role in stratified than in shallow lakes.

Vegetated littoral zone provides key habitats for fish, amphibians and invertebrates, and a considerable effort is currently being expended in North America to restore aquatic vegetation in lakes by conducting transplants 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). These efforts appear to be unlikely to succeed in many areas unless the problem of excessive carp biomass is addressed first. The relationship between carp biomass and vegetation density reported in this study suggests that lakes with carp biomass that exceeds 100 kg/ha have less that 50% littoral vegetation density and those with >300 kg/ha have almost no littoral vegetation. This relationship closely matches one recently developed for a shallow Midwestern lake (Bajer et al., 2009) suggesting that the trends presented herein may have broader applicability across ecosystem types and geographic regions. Because carp biomass commonly exceeds 100 kg/ha in large regions of North America, Australia and Europe (Crivelli, 1983; Koehn, 2004; Bajer and Sorensen 2012), this species is expected to have broad impacts on aquatic vegetation.

It has been suggested that common carp can cause an increase in nutrients, particularly phosphorus, in shallow lakes due to sediment re-suspension and excretion (Lamarra Jr, 1975; Schrage & Downing, 2004; Morgan & Hicks, 2013). Our results suggest that in stratified, eutrophic lakes carp have less pronounced effects on phosphorus concentrations. Removal of carp from lakes Susan, Riley and Lucy was associated with no perceptible decline in phosphorus concentrations. This was especially surprising in Lake Susan in which the biomass of carp was particularly high. We speculate that generally high trophic levels and extensive internal loading that occurred in our lakes may have masked the effects of carp on phosphorus. While we cannot directly determine whether carp might have more pronounced effects in less eutrophic systems, our study provides additional evidence that increased biomass of carp is not always associated with increased phosphorus concentrations in lakes, as has been also suggested by others (Lougheed et al., 1998; Matsuzaki et al., 2009; Thomasen & Chow-Fraser, 2011). Despite much research over the last few decades, the effects of carp on phosphorus in lakes are not clear.

Although the removal of carp did not 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 reached the bottom of the lake, an unprecedented event in over 40 years of measurements collected in this lake. This increase was not driven by a decline in TP or TSS, which remained relatively unchanged, but was associated with a 3-fold decline in ChlA. This decline in ChlA despite no change in TP suggests an increase in filtering zooplankton following the removal of carp in Lake Susan. Such increase might have occurred for two reasons: carp might have exerted predatory pressure on large zooplankton prior to their removal, or, the increase in aquatic vegetation that occurred in Lake Susan after the removal of carp created refugia for the zooplankton. Unfortunately, these hypotheses could not be addressed as we collected no zooplankton data in Lake Susan prior to the removal of carp.

Although limited in scope, this study advances our understanding of carp's impacts on lakes. In addition to being perhaps the first study of such kind in thermally stratified lakes, it is also one of few whole-lake studies for which the estimates of carp biomass are available; usually only relative catch rates are reported. Absolute biomass estimates allow for developing more robust management thresholds and for more direct comparisons between studies. For example, both this study, and one recently published (Bajer et al., 2009) suggest that common carp biomass of 100 kg/ha comprises a level that is damaging to aquatic vegetation. The recently developed ability to determine whether carp are approaching such damaging biomass levels using low-effort sampling methods (Bajer & Sorensen, 2012) should allow for more targeted carp management schemes in lakes. Our study is also unique because we removed the carp in a selective manner, as opposed to using rotenone, which impacts the entire community. Future studies, both in shallow and deep lakes, should adopt selective carp removal methods to better determine the role of this species in lake ecology.

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Table 1 Common carp abundance (N) and biomass, carp removal, and in-lake variables measured each year

Lake	Year	Variables measured	Carp Removal	N Mean (95% CI)	Biomass (kg/ha)
Susan	2008	Secchi, TP, ChlA, TSS, Vegetation, Fish	Before	4,181 (3,292 – 5,069)	307.1
	2009	Secchi, TP, ChlA, TSS, Vegetation, Fish, Zooplankton	After	756	64.5
	2010	Secchi, TP, ChlA, TSS, Vegetation, Fish, Zooplankton	After	374	43.0
	2011	Secchi, TP, ChlA, TSS, Vegetation, Fish, Zooplankton	After	281	40.8
Riley	2008	Secchi, TP, ChlA, TSS, Vegetation, Fish	Before	6,419 (6,132 – 6,706)	176.1
	2009	Secchi, TP, ChlA, TSS, Vegetation, Fish, Zooplankton	After	3,025	90.0
	2010	Secchi, TP, ChlA, TSS, Vegetation, Fish, Zooplankton	After	376	10.5
	2011	Secchi, TP, ChlA, TSS, Vegetation, Fish, Zooplankton	After	320	10.5
Lucy	2010	Secchi, TP, ChlA, TSS, Vegetation, Fish, Zooplankton	Before	808 (768 - 851)	69.8
	2011	Secchi, TP, ChlA, TSS, Vegetation, Fish, Zooplankton	After	105	20.5
	2012	Secchi, TP, ChlA, TSS, Vegetation, Fish, Zooplankton	After	94	18.5

Table 2 Results of model selection analyses. Variables include: removal of carp (Carp), water clarity (Secchi, m), chlorophyll a (ChlA, ug/L), total suspended solids (TSS, mg/L), total phosphorus (TP, ug/L), vegetation density (Vegetation, % cover), Daphnia density (Daphnia, individuals/L), or bluegill sunfish density (Bluegill, individuals/trapnet). Global models show which variables were considered in each analysis. All models also included a fixed seasonal effect (Season, summer or spring) and random year, lake, and sampling site effect (not shown)

Response	Predictor variables	AICc	ΔAICc	*w*	Model
Vegetation	Carp	-798.33	0.00	1.00	Best model
	Secchi, TP, TSS, Carp	-625.86	172.47	0.00	Global
Secchi	ChlA, TSS, Carp, Season	96.73	0.00	0.62	Best model
	ChlA, TSS, Season	99.45	2.72	0.15	Best model minus Carp
	TSS, Carp, Season	176.22	79.50	0.00	Best model minus ChlA
	ChlA, TSS, Carp, Season, Vegetation, Bluegill	106.44	9.71	0.00	Global
ChlA	TP, Daphnia, Carp, Season	594.65	0.00	0.75	Best model
	TP, Daphnia, Season	601.01	6.33	0.01	Best model minus Carp
	Daphnia, Carp, Season	613.36	18.71	0.00	Best model without TP
	TP, Daphnia, Carp, Season, Vegetation	604.40	9.75	0.01	Global
TP	Season, Carp	1626.29	0.00	0.98	Best model
	Season	1634.30	8.01	0.02	Best model minus Carp
	Carp	1656.24	29.95	0.00	Best model minus Season
	Season, TSS, Carp	1643.64	17.35	0.00	Global

Table 3 Parameter coefficient values for the Secchi, ChLA, and TP models that were most supported by model selection analyses (Table 2). Each model also included a random year, lake and site effect that are not shown

Model	Parameter	Estimate	Std. Error	t value
Secchi	Intercept	3.25	0.29	11.05
	log(TP)	-0.30	0.067	-4.44
	Log(ChlA)	-0.26	0.033	-7.97
	Log(TSS)	-0.81	0.025	-3.21
	Season (summer)	-0.46	0.055	-8.45
	Carp (before)	-0.28	0.071	-3.87
ChlA	Intercept	-7.42	4.48	-1.73
	TP	0.41	0.07	5.66
	Daphnia	-1.39	0.73	-1.91
	Season (summer)	15.39	3.31	4.64
	Carp (before)	3.61	4.10	0.88
TP	Intercept	46.75	9.06	5.16
	Season (summer)	18.08	3.65	4.95
	Carp (before)	-1.41	6.23	-0.23

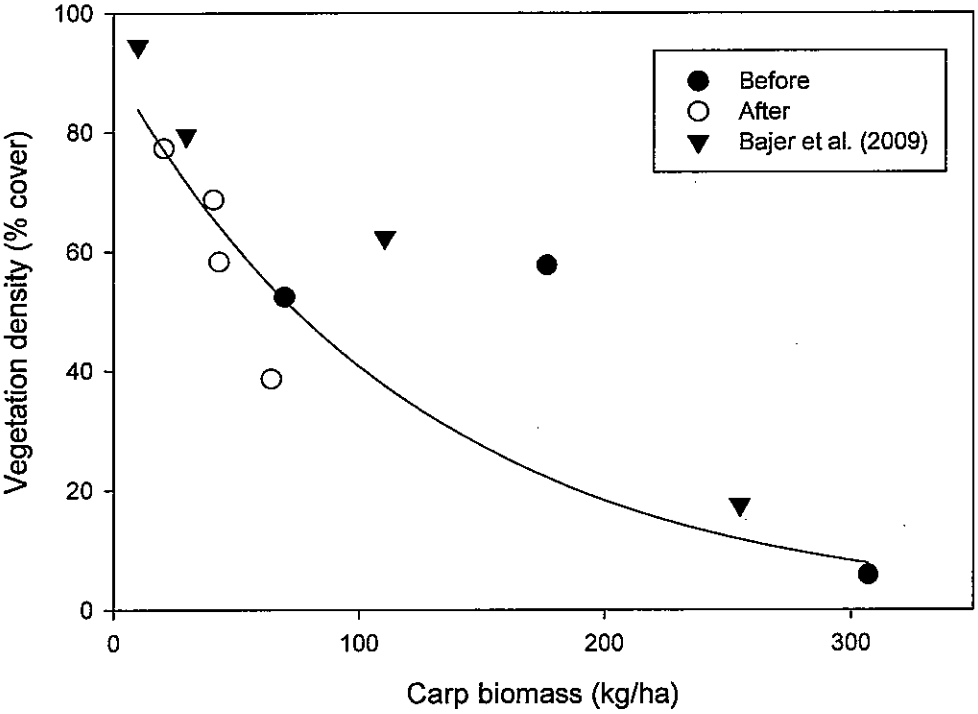

Fig. 1 Circles represent the relationship between carp biomass and vegetation density in each of the three study lakes before and after carp removal; an exponential relationship was fitted to these data (P=0.001). Triangles show vegetation density documented by Bajer et al. (2009) in a shallow Midwestern lake and are used here for comparison

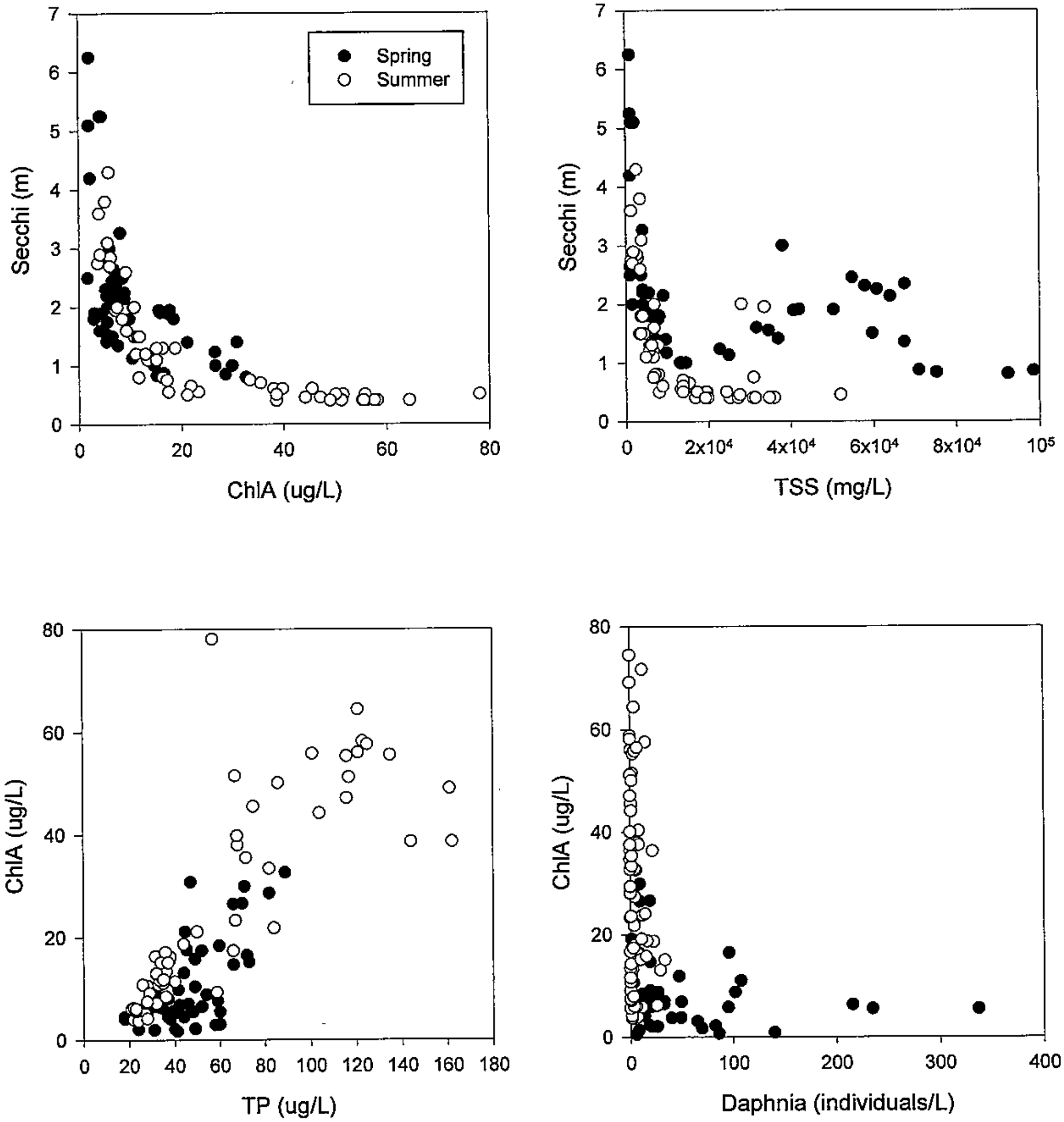

Fig. 2 Relationships between Secchi depth, Chlrophyll A (ChlA), total suspended solids (TSS), total phosphorus (TP) and Daphnia (individuals/L) during spring and summer in our study lakes

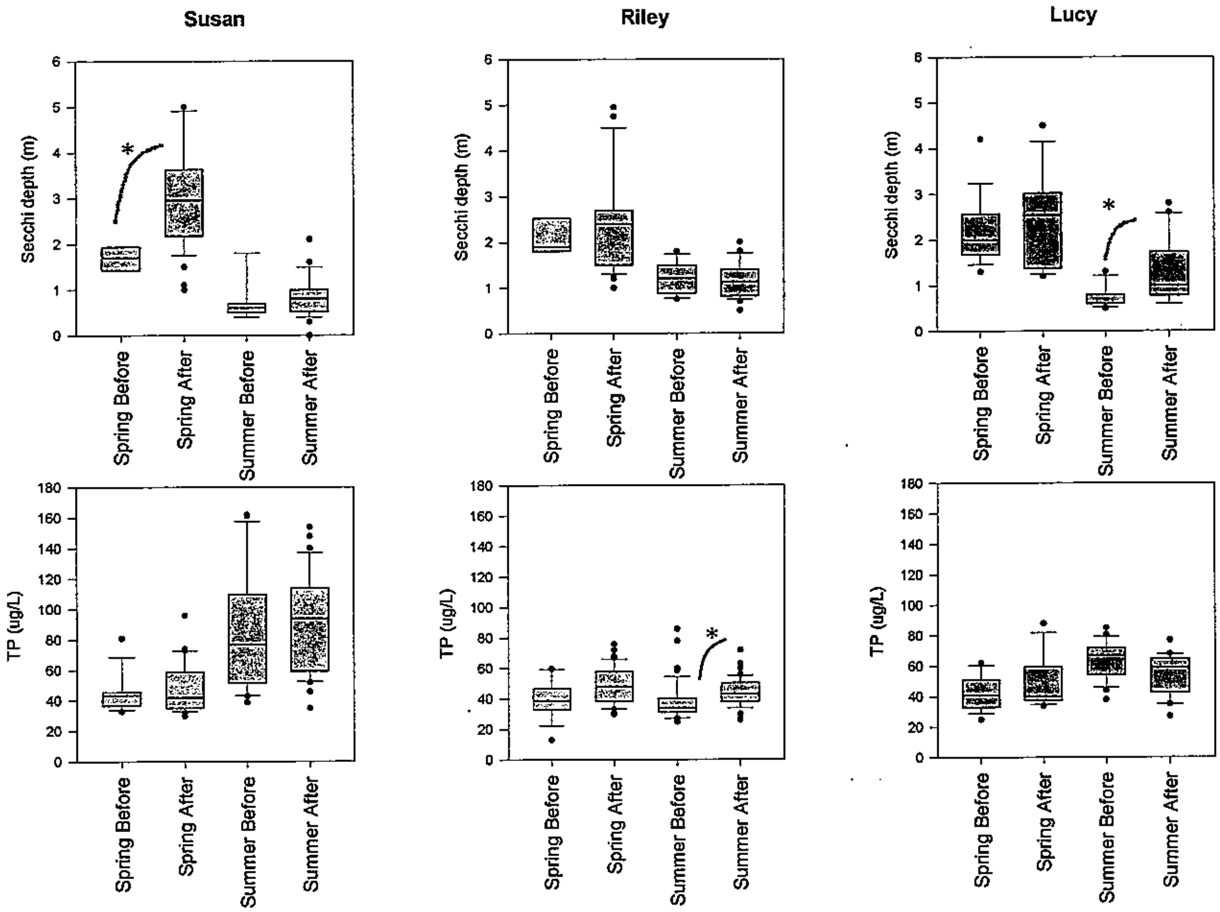

Fig. 3 Spring and summer water clarity (Secchi depth) and total phosphorus (TP) before and after carp removal in the three study lakes. Asterisks indicate statistically significant differences (*t*-test; $P<0.05$)

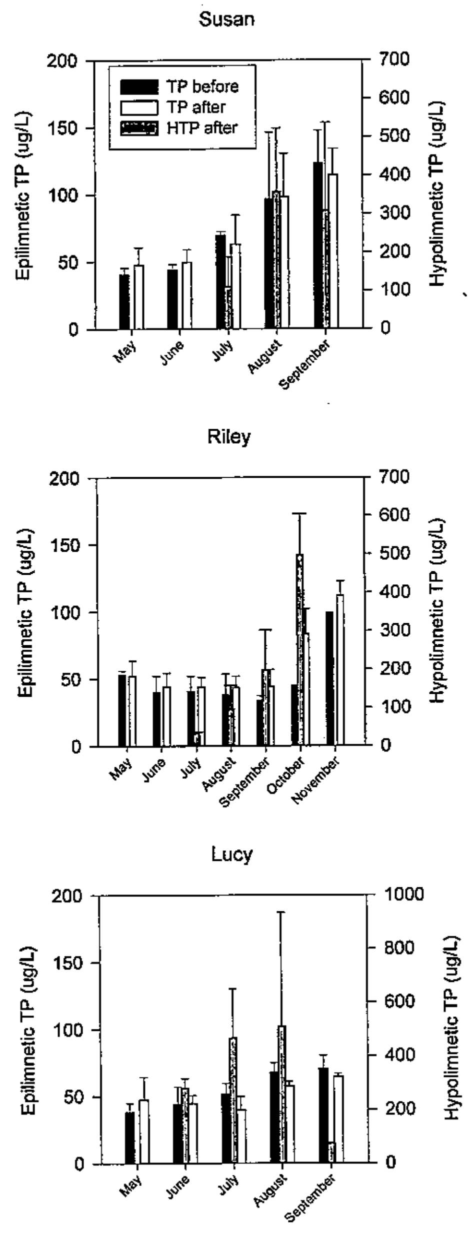

Fig. 4 Monthly epilimnetic (TP) and hypolimnetic (HTP) total phosphorus concentrations in lakes Susan, Riley and Lucy before and after carp removal. Hypolimnetic values were measured only after carp removal. Note different Y scales

Appendix B

Hydrobiologia
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INVASIVE SPECIES

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

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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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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; Thomasen & Chow-Fraser, 2011). Further, while declines in phosphorous 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, Chl*A*, TSS, and native fish abundance. In addition, we retrieved two additional years of historical data (2004, 2005) on Secchi depth, TP, and Chl*A* 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 lake was sampled annually to account for possible carp recruitment (no recruitment occurred throughout the study; Bajer et al., 2012).

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)

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 Chl*A*

Secchi depth, TP, TSS, and Chl*A* 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 Chl*A*, 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 Chl*A* 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). Chl*A* 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 Chl*A* 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, Chl*A*, 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, Chl*A*, 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 Chl*A* 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 x 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, $P = 1.62 \times 10^{-4}$; 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 Chl*A* relative to ordinal day were best depicted by a 4th degree polynomial model in which Chl*A* 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 Chl*A* followed the same seasonal pattern before and after carp removal. However, visual examination suggested that Chl*A* 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 × 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 μg/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 μg/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).

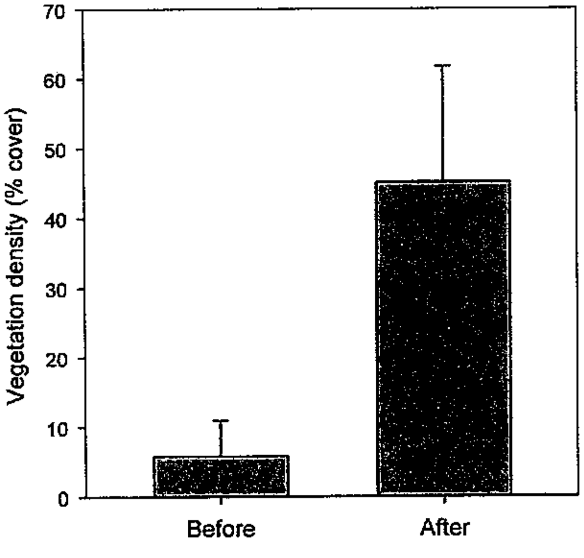

Fig. 1 Density of aquatic vegetation before and after carp removal in Lake Susan. The density is expressed as mean percent cover (±SE) in littoral areas between 0 and 2 m in depth. The increase after carp removal was statistically significant (t test; $P < 0.01$)

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

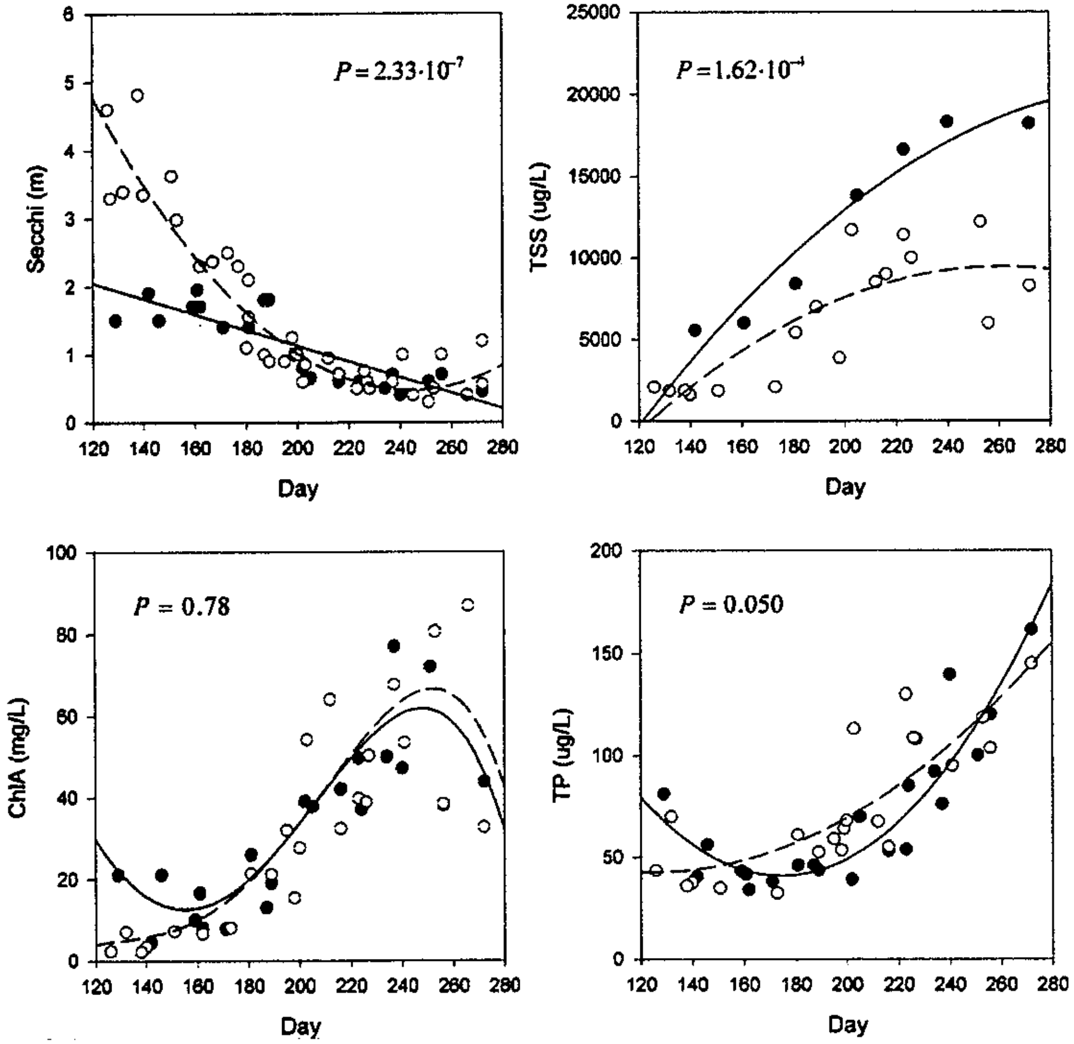

Fig. 2 Secchi depth, total suspended solids (TSS), chlorophyll *a* (ChlA), and total phosphorus (TP) before (*filled circles*) and after (*open circles*) carp removal in Lake Susan versus the ordinal day of year (May 1 to September 30, day 120–273, respectively). *Solid line* shows the ordinal day model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

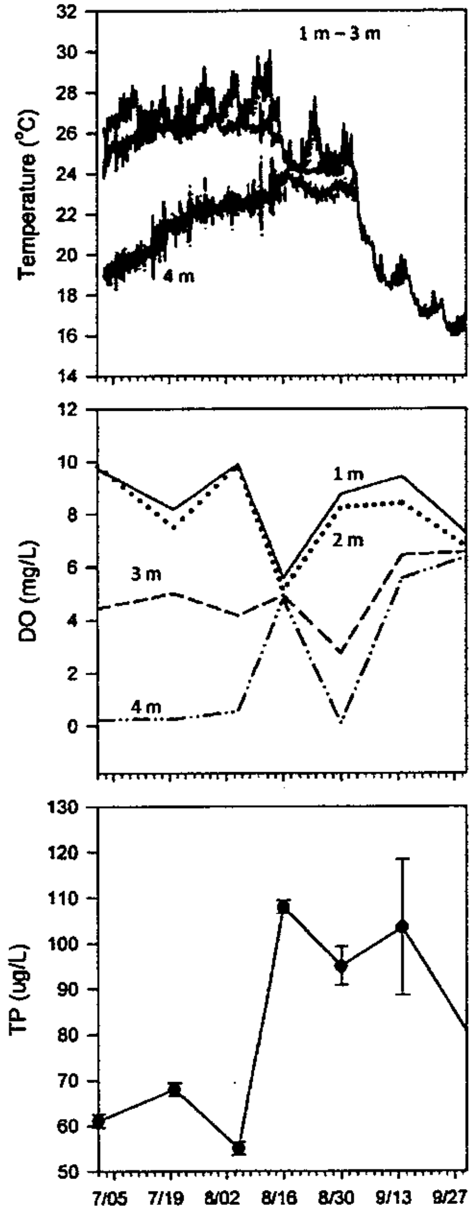

Fig. 3 Water temperature, dissolved oxygen, and total phosphorus in Lake Susan during July 1 to October 4, 2010. *Top* water temperatures recorded hourly by dataloggers at 1, 2, 3, and 4 m depths. *Middle* dissolved oxygen concentrations measured approximately every 2 weeks at 1, 2, 3, and 4 m depths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

observed mid-summer increases of ~1.5 μg 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 Chl*A* 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 Chl*A* 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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Appendix C

Fisheries Management
and Ecology

Fisheries Management and Ecology, 2011, 18, 497–505

Using the Judas technique to locate and remove wintertime aggregations of invasive common carp

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Abstract Radio- and acoustic telemetry in three Midwestern lakes demonstrated that common carp, *Cyprinus carpio* L., aggregate as water temperatures descend below 10 °C. Particularly dense aggregations formed at temperatures < 5 °C, and once located, these aggregations could be removed with an efficiency of up to 94% using seine nets. Carp aggregated just below the surface of the ice (approximately 1.5 m) and rarely descended to warmer waters, which extended down to 10 m. Although aggregations consistently formed close to shore, their locations could not be explained by temperature or dissolved oxygen. The aggregations also moved frequently, making radio-tagged fish invaluable to locate them. Coldwater aggregations of carp may reflect a type of shoaling behaviour and can be exploited with the aid of radio-tagged (Judas) fish to control this invasive fish effectively. Similar approaches might be developed for other gregarious invasive fishes.

KEYWORDS: acoustic telemetry, invasive species, mark–recapture, nearest neighbour, radiotelemetry, winter seining.

Introduction

Control of long-lived invasive species requires a removal component (Simberloff *et al.* 2005). This task is particularly challenging for fish that live in large volumes of water and are not easily located. However, selective removal approaches might be developed for species that aggregate if they could be effectively located. Biologists working with invasive goats, pigs and birds have solved the problem of locating their aggregations using the Judas technique (Taylor & Katahira 1988; Woolnough *et al.* 2006; Cruz *et al.* 2009; McCann & Garcelon 2009). In this technique, a few individuals are captured, radio-tagged and then followed as they relocate (and inadvertently betray) the groups in which they normally live and which can then be targeted and removed. Many fish aggregate or shoal (Pitcher & Parrish 1993), suggesting that they too might be controlled using the Judas technique. Common carp, *Cyprinus carpio* L., one of world's most invasive fish (Sorensen & Bajer 2011), forms aggregations during winter (Johnsen & Hasler 1977; Penne & Pierce 2008), and while few details are available about this behaviour, it appears to be a good model for developing Judas techniques for invasive fish that exhibit shoaling behaviours.

The common carp (hereafter carp) is a large, long-lived cyprinid native to parts of Eastern Europe and Western Asia that has been introduced worldwide during the last 150 years (Balon 1995). In many regions, especially North America and Australia, the carp is invasive and super-abundant (Bajer *et al.* 2009; Weber & Brown 2009; Bajer & Sorensen 2010). It is presently managed using whole-lake poisoning (Schrage & Downing 2004) and water drawdowns (Shields 1958; Koehn 2003), which are expensive and ecologically damaging. Although carp live in small, dispersed groups during the summer (Penne & Pierce 2008; Bajer *et al.* 2010), they have been reported to form large aggregations in ice-covered lakes of the North American Midwest and Eastern Europe (Johnsen & Hasler 1977; Osipova 1979; Penne & Pierce 2008). Historically, commercial fishermen have exploited this behaviour but their success has not been quantified. Also, although observations from ice-covered aquaculture ponds suggest that carp may be selecting relatively deep and warm refuges (Bauer & Schlott 2004, 2006), there have been no systematic studies of under-ice behaviour of free-ranging carp inhabiting larger, more natural systems.

In this study, radio and acoustic telemetry was used to evaluate the winter aggregation behaviour of

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common carp in three Midwestern lake systems, where carp population abundances were estimated using mark and recapture methods. The depths and temperatures selected by the carp were recorded using pressure-sensitive tags, while dissolved oxygen concentrations and temperatures measured throughout each lake were used to determine whether or not carp selected for specific areas. Finally, aggregations were targeted with seine nets using the locations of radio-tagged Judas fish to determine how effective this combination of techniques might be for removing this invasive species.

Materials and methods

The distribution of carp was studied in three lakes in south-central Minnesota USA. Two of these lakes, Lake Riley (area = 120 ha, max. depth = 14 m) and Lucy (area = 36 ha, max. depth = 6 m), are located within the same chain of lakes (44°50′08″N, 93°31′18″W); however, artificial and natural barriers block the movement of carp between them. The third lake, Lake Gervais (area = 95 ha, max. depth = 12 m), is located in another chain of lakes approximately 40 km to the east (45°01′13″N, 93°04′16″W). This lake is connected with two shallow basins, Lake Kohlman (area = 30 ha, max. depth = 3 m) and Lake Keller (area = 29 ha, max. depth = 3 m), which collectively form a relatively large and complex system. All study lakes are covered with approximately 30 cm of ice cover from December to March of each year.

Proceeding in a step-wise manner, the investigations began in the autumn of 2008 in Lake Riley in which a group of carp (Judas fish) was implanted with radio transmitters and tracked throughout the winter to determine whether or not the fish aggregated and therefore could be selectively captured using a seine net. A few Judas carp ($n = 2$) were also implanted with pressure-sensitive transmitters to determine depths at which they aggregated. This study of aggregation behaviour continued for an additional year during which captured and radio-tagged Judas carp were rereleased into lakes Lucy and Gervais as well. Distributions of Judas carp during the second year were monitored in all study lakes, and their winter aggregations were once again targeted with the seine. Population sizes and capture efficiencies were estimated throughout the study using mark and recapture analyses. During the second winter, temperature and dissolved oxygen profiles were measured in random locations within and outside areas in which carp aggregated to test whether they were selecting for warmer or more oxygen-rich areas in each lake. In addition, in the largest and more complex Lake Gervais, a group of carp was implanted with temperature- and depth-sensitive acoustic transmitters to determine habitats selected by carp under the ice. More detailed description of the data collected in each lake is presented below, followed by an analytical section that describes procedures common to all lakes.

Experiments in Lake Riley commenced in November 2008 by capturing 13 adult common carp (410–760 mm TL) using an electrofishing boat and implanting them with radio transmitters (F1850; Advanced Telemetry Systems; Isanti, Minnesota, USA) following established procedures (Penne & Pierce 2008; Bajer & Sorensen 2010). Two additional carp were implanted with archival radio transmitters (also Advanced Telemetry Systems), which recorded the depth of these fish at 5-min intervals. All carp survived the surgery and were located approximately every 3 weeks thereafter by following their radio signals until they were strong and unidirectional (an accuracy of 15 m determined in control trails). Their UTM coordinates (NAD 83) were recorded with a GPS unit (Garmin eTrex Vista). Once carp were determined to be aggregating (see statistics section), they were targeted with a 500-m seine net (3.5-cm square mesh size; 15 m deep). Seine netting followed procedures employed by local commercial fishermen and began by cutting a 5 × 5 m opening in the ice through which the net was deployed into the lake. A series of holes were drilled in a V-shaped pattern surrounding the aggregation, and ropes were stretched under the ice between them using remote-controlled submersibles. These ropes were used to pull both sides of the net with power winches. The net was then landed through a 5 × 5 m opening cut near shore so fish could be easily handled. Captured carp were counted, and two-thirds of them were removed from the lake (the objective of a parallel study that evaluated the effects of carp biomass on water quality), while the remaining carp were released after approximately 50% of them had been tagged with a numbered T-bar tag (TBF-1; Hallprint, Hindmarsh Valley, South Australia) inserted under the dorsal fin (Table 1).

Radio telemetry resumed in the summer in Lake Riley and continued throughout the next autumn and winter, when carp aggregations were once again located. Five dissolved oxygen and temperature profiles (YSI® 85; 0.5-m vertical resolution) were collected within and outside the aggregation using random point selection function in ArcMap (v9.3.1; Esri, Redlands, CA, USA) to test for differences. The area in which carp aggregated was then targeted with the seine net as before, but this time all carp were examined for T-bar

Table 1. The number of carp captured in different seine nettings and the percent of each lake's carp population that they represented along with population estimates (*n* and 95% CI) calculated from the number of carp that were marked (*M*) and subsequently examined for marks (*C*) and recaptured (*R*) in each lake

Lake	Date	Captured	% population	*n*	95% CI	*M*	*C*	*R*
Riley	19/1/09	4440	68	6499*	6177–6821	600	2303	388
Riley	3/3/10	2303	65	3559	–	–	–	–
Gervais	14/1/10	3537	52	6745	4953–8537	1035	292	44
Lucy	24/1/10	642	94	685	601–769	642	15	14

*Estimate includes 2940 carp that were removed from the lake on 19 January 2010.

Estimate was derived by subtracting 2940 carp that were removed from the lake on 19 January 2009 from the population of 6499 carp.

tags and fin clips and removed from the lake. Temperatures in the lake were monitored throughout the entire study by collecting bi-monthly vertical profiles.

Experiments in Lake Lucy began in September 2009 by implanting ten carp (400–700 mm TL) with radio transmitters. All survived the surgery. These fish were located monthly through January, and water temperatures were monitored with a similar frequency. Once the carp were found to be aggregating, five temperature and dissolved oxygen profiles were measured at randomly selected locations within and outside the aggregation. Then, the aggregation was targeted using seine nets (as in Lake Riley), and all carp were counted, measured, marked with T-bar tags and released. To estimate population size and capture efficiency, three 1-h electrofishing surveys were conducted the following summer and recapture rates determined.

Experiments in the Gervais system of lakes commenced in May 2009 by implanting 38 carp with radio transmitters (10 in Gervais, 10 in Kohlman and 18 in Keller). Within the first 2 months, two of the carp shed their tags or perished in Lake Gervais and six carp from Lake Keller emigrated downstream. One carp in Lake Kohlman was never found. The remaining fish were located approximately every 2 weeks throughout the next spring. In October 2009, an additional ten carp were captured in Lake Gervais and implanted with acoustic tags (V13 coded transmitter; Vemco, Halifax, NS, Canada) that transmitted their temperature and depth (accuracy ±0.1 °C and ±0.2 m) every 90 s. This information was automatically recorded by three receivers (VR2W, Vemco; approximately 150-m detection range) placed in different areas of the lake. Ten temperature and dissolved oxygen profiles were measured at randomly selected locations within and outside carp aggregations to define the available and used habitats. Winter aggregations were then targeted using seine netting. Approximately one-third of the captured carp were marked with numbered T-bar tags and released while others were released without marking (Table 1). As in Lake Lucy, the population was estimated by collecting several hundred carp from the entire system using an electric fishing boat during the following summer and determining recapture rates (Table 1).

For statistical analysis, locations of carp were plotted on bathymetric maps using ArcMap. The tendency of carp to aggregate was quantified by calculating nearest neighbour distances (NNDs; mean distance to five nearest neighbours; Penne & Pierce 2008) using Hawth's Tools (Beyer 2004). The NNDs were plotted against seasonal changes in water temperature in each study lake to discern seasonal patterns and determine when tightest aggregations occurred. Ultimately, data from all lakes were combined, and a single regression relationship between water temperature and NND was developed in SAS (v9.2; Carry. NC, USA). Statistical comparisons (Students' two-tailed *t*-test, using SAS) of mean temperature and dissolved oxygen concentrations within and outside carp aggregations were undertaken for the upper 2 m of the water column only (because carp rarely descended to greater depths). Petersen's equations (Krebs 1999) were used to estimate the mean and 95% CI of carp population in each lake from the number of individuals that were marked and released (*M*), examined for marks (*C*) and recaptured (*R*):

$$N = \frac{[(M+1)(C+1)]}{R+1};$$

$$95\%\ \mathrm{CI} = 1.96\sqrt{\frac{(M+1)(C+1)(M-R)(C-R)}{(R+1)^2(R+2)}}.$$

Results

Although radio-tagged carp in Lake Riley were dispersed relatively widely throughout the summer and autumn, they formed tight aggregations during both winters (Figs 1 & 2). During the first winter, carp started aggregating in mid-December, and by

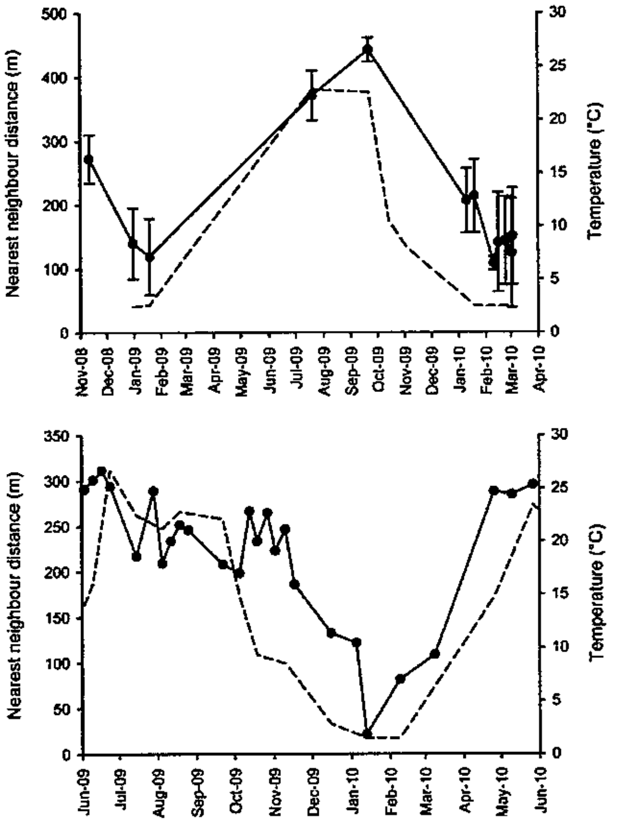

Figure 1. Top: Mean nearest neighbour distances (solid line) of radio-tagged carp in Lake Riley and mean water temperature in the lake (broken line). Bottom: the same relationship for carp in the Lake Gervais system of lakes.

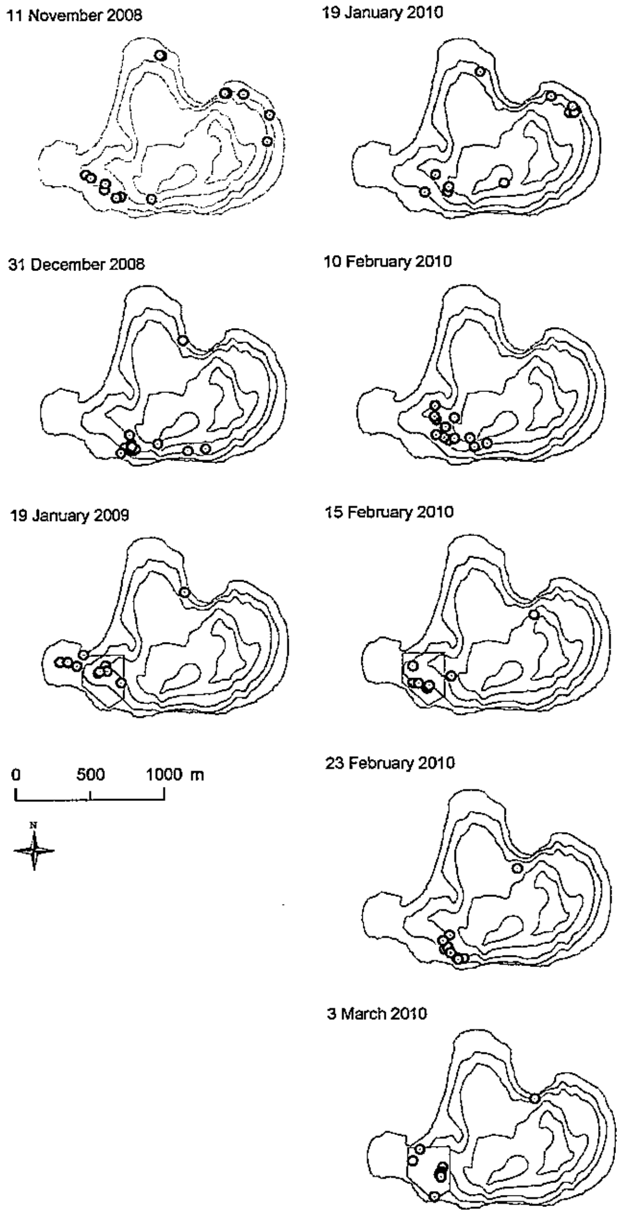

Figure 2. Locations of radio-tagged carp (circles) in Lake Riley during the winter of 2008–2009 (left) and 2009–2010 (right). Aggregations documented on 19 January 2009, 15 February 2010 and 3 March 2010 were targeted with a seine net. Shaded polygon represents the area seined. Bathymetric contours represent 3-m depth increments.

mid-January, all but one radio-tagged carp formed a dense aggregation in SW area of the lake with NND of approximately 100 m (Figs 1 & 2). The centre of aggregation was 100 m offshore, and the fish were found over an area that was relatively shallow (1–6 m) and had a gradually sloping bottom (Fig. 2). Seine netting was conducted, and a total of 4440 carp were captured (440–800 mm TL; 2940 carp were removed from the lake while the rest was released). As was later estimated, this catch comprised approximately 68% of the entire population (of the 600 carp that were marked and released, 388 were recaptured next winter among 2303 carp; Table 1). One of the two fish that carried archival transmitters was also captured, and archived data showed that between 31 December and 19 January, when the carp were aggregating, this individual spent most of the time approximately 1.5 m below the ice even though oxygenated and warmer waters extended to a depth of 10 m in adjacent areas of the lake (Fig. 3). During the winter of 2009–2010, two loose aggregations were noted in January, but a tight aggregation did not occur until mid-February (Fig. 2). On 15 February 2010, all but one radio-tagged carp were once again located in the SW area of the lake (Fig. 2). This time, the fish remained slightly further offshore (mean = 125 m) and over a slightly deeper area (3–9 m). There were no differences between water temperatures ($P = 0.09$) and dissolved oxygen ($P = 0.82$) inside vs outside the aggregation area. An

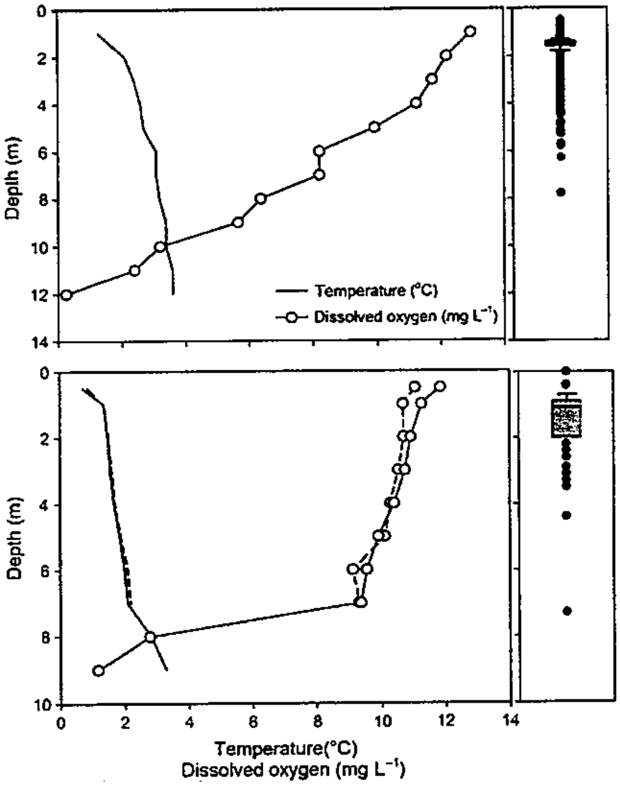

Figure 3. Top: Mean depth profiles of temperature and dissolved oxygen (DO) in Lake Riley in January 2009 (left panel) vs the depth selected by the carp implanted with pressure-sensitive radio transmitter during the same month (box and whisker plot to the right). Bottom: Mean depth profiles of temperature and dissolved oxygen measured within (broken lines) and outside (solid lines) the aggregation of carp in Lake Gervais in January 2010 vs the depths selected during the same period by carp carrying depth-sensitive acoustic transmitters (box whisker plot to the right).

attempt to net this aggregation was complicated by equipment problems (submersible malfunction), which substantially delayed the process, and only 376 carp were captured (radio-tracking showed that carp were able to swim around the net before it was closed). The aggregation reformed in approximately the same area in early March (Fig. 2), and this time 2303 carp were captured, which comprised of approximately 65% of the population (Table 1).

Radio-tagged carp in Lake Lucy were relatively evenly dispersed along the shoreline in the summer and fall of 2009 (NND = 146 m, SD = 28 m), but by January they were aggregated tightly in the SW area of the lake (NND = 29 m; SD = 3.9 m) (Fig. 4). This area was approximately 3 m deep and 140 m off the nearest shore and did not differ from other areas of the lake in terms of water temperature ($P = 0.34$) and dissolved oxygen ($P = 0.26$), which was relatively high (>7 mg L$^{)1}$). This aggregation was seine netted on 24 January, and 694 carp were captured (size range 300–777 mm TL), including all radio-tagged fish. Recapture rates determined during the following summer, which included 14 marked fish among 15 collected, suggested that this catch represented 94% of the population (Table 1).

Radio-tagged carp in the Gervais system of lakes were relatively dispersed in the summer and autumn, and most of them were found in shallow waters of lakes Kohlman and Keller. This pattern persisted until mid-December 2009 when NNDs declined to < 130 m, and the carp were gradually leaving the two shallow lakes and aggregating in the deeper Lake Gervais (Figs 1 & 5). By early January, all carp had moved to Lake Gervais and formed two tight aggregations, both of which were located 50–60 m offshore and occurred in areas in which the depth increased from approximately 3 to 6 m (Fig. 5). Although the areas in which carp aggregated had similar temperatures as other locations in the lake ($P = 0.19$), they had slightly lower oxygen concentrations ($P = 0.01$; Fig. 3). Data from acoustic tags showed that the carp stayed relatively close to the surface of the ice (median depth = 1.07 m) and experienced relatively cold temperatures despite warmer and oxygenated waters extending down to 8 m in areas located further offshore (Fig. 3). The larger of these two aggregations was targeted with the seine net on 14 January, and a total of 3537 carp were captured (size range 340–978 mm TL). Recapture rates documented during the following summer (44 marked fish among 292 examined) suggested that this catch represented 52% of the entire population of 6745 carp that inhabited this three-lake system (Table 1). Following their release, the carp re-aggregated in the western area of the lake in February. In March, approximately 50% of the fish moved to the south-eastern area of the lake, and by late April, the carp had dispersed into the two adjacent shallow lakes (Fig. 5).

When the results from all study lakes were combined, a strong relationship was found between mean water temperature and carp NNDs (Fig. 6). This relationship explained over 60% of the overall variance in carp NNDs and showed that carp exhibited a tendency to aggregate once water temperatures declined below 10 °C, with particularly strong aggregations occurring < 5 °C. The bycatch (of non-target native species) was < 10% of the total carp biomass.

Discussion

This study demonstrated that common carp inhabiting Midwestern lakes form tight winter-time aggregations

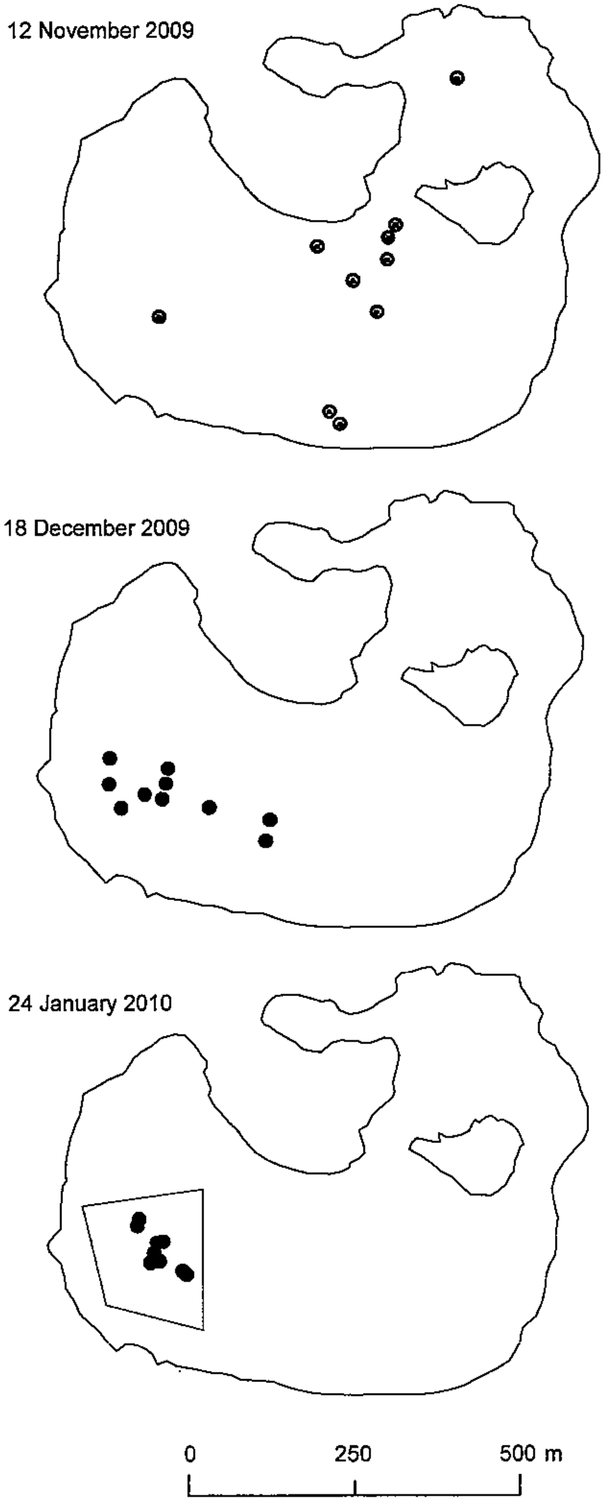

Figure 4. The distribution of radio-tagged carp in Lake Lucy in the winter of 2009–2010. The shaded polygon indicates the area seined.

that can be precisely tracked and removed using small numbers of radio-tagged Judas fish. Conventional commercial seining guided by Judas fish achieved high removal rates (52–94%), suggesting that the Judas technique could be very useful in carp control. It is especially intriguing that carp will move between lakes and aggregate at single locations, implying that entire systems of lakes might be controlled by targeting small focal areas. Although the experiments were conducted in relatively small lakes, similar approaches might also be used in large ecosystems where aggregations have also been demonstrated (Johnsen & Hasler 1977; Penne & Pierce 2008). This technique might also be useful in regions that do not experience ice cover because aggregations appear to correlate with declining temperature and not necessarily with ice formation.

Aggregations appear to represent a type of carp shoaling behaviour rather than strong attraction to specific areas or habitats. Shoals moved within each lake (especially in Lake Gervais) and did not occur in areas with measurable differences in temperature or dissolved oxygen. However, the fact that carp aggregated in the south-western area of Lake Riley during both years suggests that they may be cueing on less-conspicuous habitat features that were not evaluated. Further, all aggregations occurred relatively close (50–150 m) to shoreline vegetation, where water depths increased from approximately 1 to 6 m. This scenario matches sites of winter-time aggregations reported by Johnsen and Hasler (1977). Both this study and the study by Johnsen and Hasler (1977) indicated that deeper, open water sites were consistently avoided, but this does not appear to be the case in shallow systems in which deeper areas were preferred (Penne & Pierce 2008).

Carp appear to aggregate when water temperatures decline <10 °C, with particularly tight aggregations occurring below 5 °C. Contrary to expectations, there was no evidence that carp selected warmer, deeper waters, but instead tended to stay approximately 1 m below the ice experiencing relatively cold temperatures. This behaviour was not caused by dissolved oxygen deficiencies, which occurred only at depths exceeding 8–10 m. The tendency to aggregate as temperature decreases below 10 °C, at which point carp appear to stop foraging (Bauer & Schlott 2004), suggests a shift from foraging to a predator defence strategy. Although carp are large and have few fish predators, they are subject to winter predation by otters and possibly also seals in their native range (Adamek *et al.* 2003; Kortan *et al.* 2007). Thus, shoaling near the surface of the ice may represent an example of 'many eyes' visual

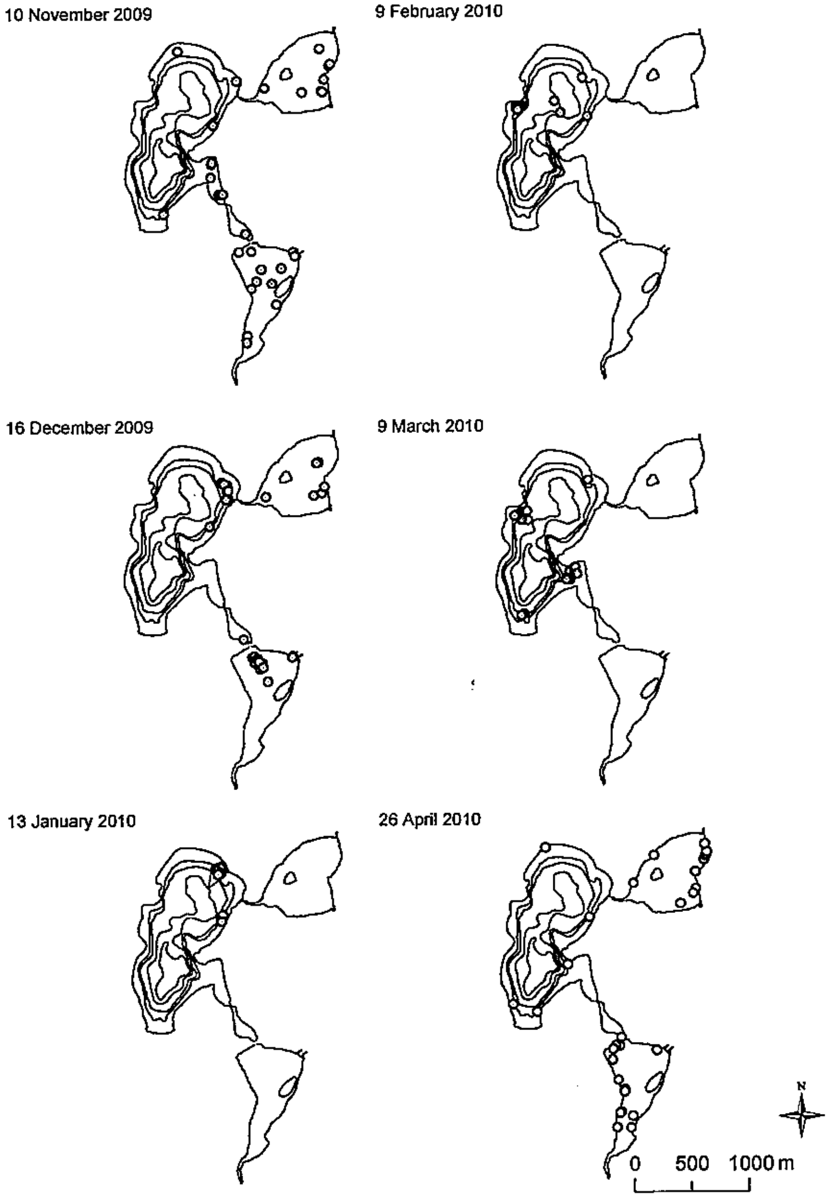

Figure 5. Locations of radio-tagged carp in Lake Gervais (the westernmost lake) and the two adjacent shallow basins: Lake Kohlman (upper right) and Keller (lower right) from November 2009 to April 2010. The larger of the two aggregations found on 13 January 2010 was targeted with a seine net. The shaded polygon indicates the area seined. Bathymetric contours represent 3-m depth increments.

defence mechanism against fast-moving predators (Pitcher & Parisch 1993). This hypothesis is partially supported by rapidly attenuating light conditions at depths >2 m in the study lakes. Similar light-mediated shoaling behaviours have been shown for coregonids (Gjelland *et al.* 2009). This hypothesis warrants further study.

Because carp do not aggregate over areas that we can predict with confidence, and then move between locations during the course of the winter, Judas fish are needed to target them effectively for removal. Being able to locate these aggregations precisely is critical to seine netting success, as even large nets can only cover a small fraction of most lakes (mean seined area was approximately 8 ha) and seining can only be conducted in areas that are free of obstacles. Further, carp are very sensitive to sound and can easily avoid nets if targeting is imprecise and/or noisy, as was the case of the second haul in Lake Riley. To reduce this risk, preparatory work (drilling pilot holes, using submers-

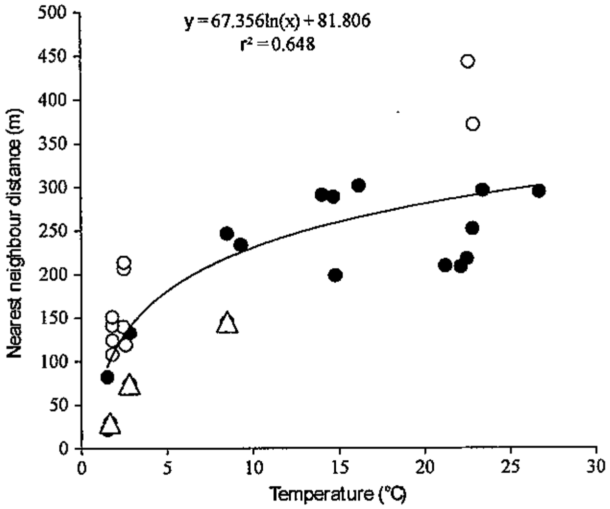

Figure 6. Relationship between nearest neighbour distance and water temperature in lakes Riley (open circles), Gervais (filled circles) and Lucy (triangles). A logarithmic relationship was fitted to data combined across lakes ($P < 0.05$).

ibles to stretch ropes under the ice) can be performed 1 day in advance and the locations of carp can then be verified before the net is deployed. Finally, targeting aggregations of carp using the Judas technique may not only improve capture efficiencies of carp, but also reduce the bycatch of native fish (see Results).

The Judas technique has previously been used successfully to remove invasive mammals and birds from islands (Simberloff *et al.* 2005). Recent reports also suggest that Judas male carp can be used to locate and target aggregations of pre-spawning female carp (Inland Fisheries Service, Tasmania 2009). Judas techniques may be useful for other species. For example, spawning aggregations of lake trout *Salvelinus namaycush* (Walbaum) (Warner *et al.* 2009) might be located and targeted using Judas fish to control these invasive fish in western lakes (Ruzycki *et al.* 2003). Similar techniques might be also explored for the Asian carp *Hypophthalmichthys* sp., which also appear to shoal (D. Chapman, US Geological Survey, personal communication). The Judas technique could be further enhanced by exploiting cognitive abilities of fish by enticing and training them to aggregate in locations suitable for capture using targetable cues such as food or pheromones (Sorensen & Stacey 2004; Bajer *et al.* 2010).

Acknowledgments

This research was funded by the Riley Purgatory Bluff Creek Watershed District (RPBCWD), the Ramsey-Washington Metro Watershed District (RWMWD), the Minnesota Environment and Natural Resources Trust Fund, and the Minnesota Agricultural Experiment Station. We thank K. Seemann and J. Riedemann for conducting the winter seining and the staff of RPBCWD and RWMWD for assistance with fish counting and tagging, as well as D. Ellison and G. Johnson (Minnesota Department of Natural Resources) for technical support and fish collection permits. We thank two anonymous reviewers for helpful comments on the manuscript.

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Appendix D

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Cognitive aspects of food searching behavior in free-ranging wild Common Carp

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Abstract Although laboratory experiments have shown that many fishes, Goldfish (*Carassius auratus*) in particular, employ relatively sophisticated orientation strategies to learn the location of food in laboratory arenas, this ability has not been rigorously tested in the natural environment. In this study we documented the ability of Common Carp (*Cyprinus carpio*), a close relative of Goldfish, to learn the location of newly introduced food in a lake. Two experiments were conducted, the first of which determined that carp feed largely at night. The second used this information and tracked the day- and night-time locations of 34 radio-tagged carp before and then while a food reward was introduced at a specific location in the lake for 10 days. Before the introduction of the reward, carp maintained small (~100 m× 70 m), isolated home ranges which expanded slightly at night. This movement pattern changed after the reward was added when on the fourth night six radiotagged carp visited and exploited the reward and then returned to their home areas after sunrise. This pattern persisted for the rest of the experiment with increasing numbers of carp visiting the reward each night (21 of 34 carp visited on the tenth night) and returning to their home ranges each day. The speed and precision with which wild carp learned to exploit this reward is consistent with the social learning and spatial memory skills that they and their relatives have shown in laboratory arenas. This is particularly impressive given the turbid conditions in the lake and the lack of obvious visual landmarks.

Keywords *Cyprinus carpio* · Learning · Telemetry · Reward · Home range · Movement

Introduction

The ability to quickly locate food is of high adaptive significance to fishes and ways in which they can learn to locate food and remember its location has been the subject of several recent laboratory studies (Braithwaite and de Perera 2006). These experiments have demonstrated that many teleost fish use learning-based strategies to locate food and possess brain regions homologous to higher vertebrates for processing spatial information derived from multiple sensory systems (Broglio et al. 2003; Odling-Smee and Braithwaite 2003; Vargas et al. 2009). The goldfish (*Carassius auratus*) has been an important model in the study of cognition and this species has been shown to use both visual landmarks and body-centered strategies to locate and remember the locations of food rewards in laboratory arenas (Rodriguez et al. 1994; Braithwaite and de Perera

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2006). Other studies have suggested that groups of foraging Goldfish learn from each other's behavior (social facilitation; Pitcher and House 1987). Tests of this species' cognitive abilities in a more complex natural environment do not appear to have been conducted.

In this study we used radiotelemetry to describe and test the ability of free-ranging Common Carp (*Cyprinus carpio*; hereafter 'carp'), a close relative of Goldfish, to learn and remember the location of a food reward in a turbid lake. The Common Carp is a member of the same clade as Goldfish (with which it will hybridize) and shares the same benthic feeding habits, reproductive behaviors, chemical cues, and neuroanatomy (Cunha et al. 2002; Sisler and Sorensen 2008). The Carp is a common inhabitant of many North American lakes (Bajer and Sorensen 2009), and being larger, its behavior in these ecosystems can be closely monitored using radiotelemetry. In this study, we assessed the learning ability of wild, free-ranging carps in a turbid lake by measuring changes in their spatial distribution in response to the systematic addition of a food reward to this system. An initial experiment determined the diel foraging activity of carp to define the periods of day that they should be tracked. This study increases our understanding of fish cognitive abilities in the natural environment and suggests how these abilities might be exploited in fish management.

Methods

Study site

This study was conducted in a 40 ha Midwestern lake (Lake Susan; Minnesota, USA; Lat 44.851384° Long −93.541428°) that was known to contain ~4,000 adult Common Carp (Bajer and Sorensen 2009). Habitat conditions in the lake were relatively uniform; its bottom was dominated by sand and mud, and patches of floating-leaved macrophytes occurred along ~50% of its shoreline. Although this lake has a maximum depth of 5 m, summer stratification and hypoxic conditions below 2 m restrict the distribution of fish to the shallow (<2 m) littoral zone during summer and fall. Water clarity in the lake was very low (Secchi disc <0.5 m) at the time of this experiment.

Experiment 1: Determining daily feeding patterns of carp

First, we determined whether the carp in our study lake had a diel feeding pattern which needed to be considered in future learning experiments (Experiment 2). This experiment was conducted in September 2007 when water temperatures were relatively warm (15°C) and carp were still actively feeding. Cracked corn, a favorite food of this omnivorous species (Hernandez et al. 1994) but not of other fish native to the lake, was weighed and placed into mesh bags (which carp could pull corn out of). These bags were then placed into the lake at a location along the shoreline that a pilot study had found to be frequented by carp. On the first day of this experiment a single 50 kg bag of corn was placed on the bottom and attached to an anchored float. It was lifted after 2-h, weighed (using a portable balance), re-filled with a known amount of fresh corn, and then re-positioned; in this way a surplus of food was always available and its consumption could be quantified. This cycle was repeated every 2-h for the next 5 days. Three low-light cameras (Scout XL; Aqua View®, MN, USA) were placed 1 m away from the bait to confirm the identities of the fish visiting the bait during 5-min intervals at the beginning of each hour. Feeding activity was determined by measuring the amount of corn consumed, average consumption calculated per 2-h interval, and plotted against time-of-day along with incident solar radiation at this location[1].

Experiment 2: Spatial memory and learning

This experiment was conducted in June-July of 2008 after carp had finished spawning and were once again actively foraging. It proceeded in two steps. The goals of the first step were to map the pre-baiting distribution of carp, determine whether individual fish maintained specific home ranges, and select a location that was rarely used by carp so we could use it to add food reward in the second step. We captured 14 adult carp (400–700 mm TL) using an electrofishing boat and implanted them with radiotransmitters (F1850, Advanced Telemetry Systems®, MN, USA) following established procedures (Penne and Pierce 2008). Carp were collected, implanted and immedi-

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[1] http://climate.umn.edu/doc/about_us.htm

ately released in patches of vegetation near their capture sites along the western, southern and eastern shores of the lake. Following a 1-week recovery period, we mapped the locations of these fish over the course of three 24-h cycles between June 30 and July 3. During each cycle, carp were located every 4-h (starting at 10:00) from a small boat using a loop antenna. Their locations were bi-angulated by measuring two bearings that were evaluated using computer software (LOAS® 4.0; Ecological Software Solutions, CA, USA).

The second step of this experiment determined whether and how carp might learn the location of an introduced food reward. It began 10 days after step one and employed an additional 20 carp (thus increasing the total sample size to 34 fish) which were captured, implanted with radiotransmitters and released (as described above) 3 days after step 1 was completed. One week later we introduced a food reward (mesh bags filled with corn as described above) at a location that had been rarely used by carp during the pre-baiting period. Corn was added for 10 consecutive days in the same manner as in Experiment 1 except that it was replaced twice a day (09:00 and 21:00). Also, the amount added was always twice the amount consumed to ensure that corn was always available as a reward. Every other day (i.e., days 2, 4, 6, and 10), the locations of all 34 radio-tagged carp were determined every 4-h for a 24-h period starting at 10:00. In the morning that followed the last day of the experiment, a seine net was passed through the reward area to determine if carp might be captured and assess which species were consuming corn. Water temperature was monitored throughout the experiment using an automated data logger (Model UA-002-64; Onset Computer Corporation, MA, USA) placed near the baited site.

The locations of carp were analyzed using common procedures in ArcGIS (ESRI®; CA, USA) to determine shifts in the overall distribution of carp when the reward was present (the rate of learning) and changes in individual movement patterns (spatial memory). For the first analysis, we determined the core areas of spatial distribution of carp prior to baiting (the first three telemetry cycles which employed 14 carp) and then while the bait was being added (the final five telemetry cycles using all 34 fish). This was accomplished by measuring 75% kernel density estimates (Spatial Analyst extension; 100 m bandwidth; Penne and Pierce 2008). Separate estimates of core areas of distribution (CADs) were constructed for day- (06:00, 10:00, 14:00, and 18:00) and night-time periods (22:00, 02:00) because Experiment 1 found carp to forage almost exclusively at night. Next, we measured the size of each day- and night-time CAD, the overlap between them, and the extent that each overlapped with the reward area. The reward area was defined *a posteriori* based on the distribution of radio-tagged carp as a circular area with a 100 m radius around the reward. To test for shifts in carp distribution (evidence of learning), we fit logistic regressions (Nlin procedure in SAS 9.1; SAS Institute Inc., NC, USA) to determine if the day- and night-time overlap between the CADs and the reward area increased over time.

In the second analysis we evaluated the locations of individual carp before and after the addition of the reward to assess movement patterns, orientation skills and spatial memory. This analysis was restricted to the 14 carp for which we had continuous records. First, we determined if individual carp maintained well-defined home ranges (Kernohan et al. 2001) during both the day- and night-time periods prior to the baiting period. This was accomplished for each fish by pooling day- and night-time data for the three pre-baiting periods and calculating day-time and night-time minimum convex polygons (MCP; Kerhonan et al. 2001) and their centroids using Hawth's tools in ArcGIS (Beyer 2004). Because MCPs are sensitive to outliers, we deleted the single most outlying location for each fish and time-period combination. Finally, to assess the spatial memory of carp we determined the frequency with which individual fish returned from the reward area to within 50 m of the centroids of their day-time home-ranges. A 50 m area around the centroid was selected because it approximated the average size of the typical carp's home range.

Results

Experiment 1

Carp showed a distinct diel pattern in corn consumption which increased sharply after sunset, peaked in the middle of the night and declined after sunrise (Fig. 1). Consumption was inversely related to the

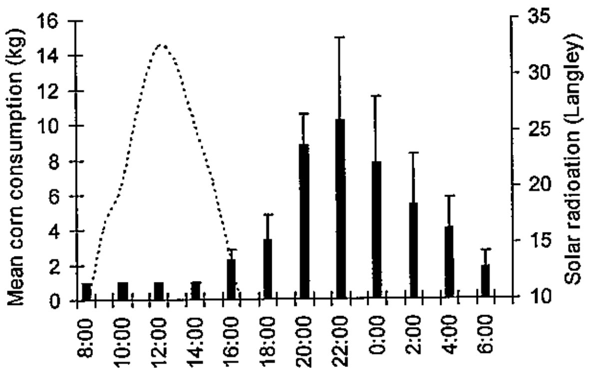

Fig. 1 Diel pattern in corn consumption exhibited by Common Carp. *Bars* indicate the average amount of corn consumed by the carp every 2-h averaged over the 5 day experimental period (mean ± SD). The *broken line* indicates the average intensity of solar radiation (*Langleys*) during this period

intensity of solar radiation and was consistently low (<1 kg/2 h^{-1}) during daylight hours. A total of 1,389 fish were observed using the cameras of which more than 99% were deemed to be carp.

Experiment 2

Analysis of core areas of distribution determined that before the reward was added, carp were broadly dispersed within the lake both during the day and at night. The daytime CADs measured during the three initial pre-baiting telemetry cycles averaged 67,891 m^2 (SD=19,880 m^2), whereas the size of the average nighttime CAD was slightly larger (70,614 m^2, SD=19,236 m^2). These patterns were relatively stable over time as percent overlap between the CADs measured on consecutive days and nights ranged from 53 to 92%. During both the day- and night-time, carp were found mostly along the western, southern and eastern shores of the lake so we selected a northern location to add the reward. Although less than 20% of the day and night-time CADs overlapped with the reward area prior to baiting, this changed a few days after the reward was added. In particular, on the fourth night of baiting, six radiotagged carp visited and exploited the reward after sunset but vacated the site after sunrise. This pattern persisted for the rest of the experiment with increasing numbers of radiotagged carp returning to the reward site each night (13, 19, and 21 radiotagged carp were found at the reward on sixth, eighth, and tenth night, respectively) and leaving it during the day (no more than five carp were ever recorded at the bait during the day). This pattern was evident in the CADs; while both the day- and night-time CADs overlapped less than 10% with the baited area during the first four 24-h periods of adding the reward, the night-time CAD shifted during the sixth night and came to overlap nearly entirely with the reward site (Fig. 2). The relationship between the nightly percent overlap versus the night of baiting was depicted by a logistic regression $\left(\%\ \text{overlap} = 100 \Big/ \left(1 + \left((100 - 8.24)/8.24\right)e^{-0.262(\text{night of baiting})}\right);\ P = 0.001\right)$. Strikingly, day-time CADs remained virtually unchanged during this period and overlapped with the reward site by less than 20% (Fig. 2). Three hundred ninety four carp and just a few other species of fish were captured by seining on the last day of the experiment, of which only the carp had corn in their intestines. Water temperature changed little during the course of the experiment (ranging between 23 to 27°C), and there were no storms or other significant weather changes.

Analysis of specific locations of the initial 14 carp demonstrated that individual carp occupied small home ranges during the pre-baiting period, particularly during daytime when the average MCP was only 6,921 m^2 (<3% of lake's surface) (Fig. 3a). At night, the average MCP increased 2.1 times (average MCP=14,759 m^2), suggesting that carp were more mobile after sunset.

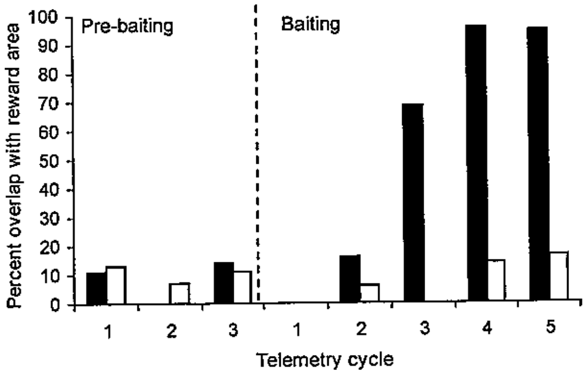

Fig. 2 Percent overlap between the core area of carp distribution and the reward area measured during the day (*clear bars*) and night (*filled bars*) of the three telemetry cycles conducted before the reward was added (*pre-baiting*) and five telemetry cycles after the reward was added (*baiting*). The three pre-baiting telemetry cycles were conducted 14, 12, and 11 days before the reward was added. The five baiting telemetry cycles were conducted on the second, fourth, sixth, eighth and tenth (*final*) day of baiting. Percent overlap was not measured during daylight hours of the third baiting cycle

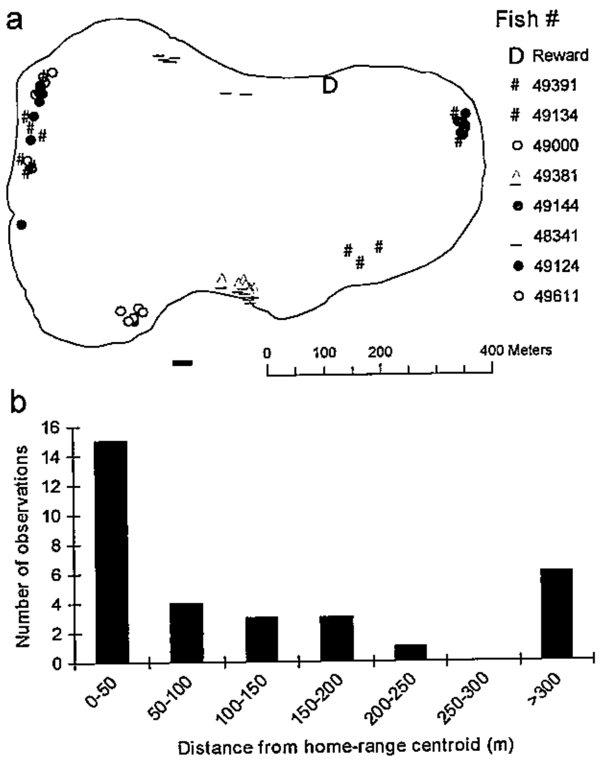

Fig. 3 **a**: Pre-baiting, daytime distributions of 8 radiotagged carp which later repeatedly visited the reward area. Out of 14 carp which were tracked during the pre-baiting and then the baiting phase, 10 found the reward but only 8 are shown here for clarity (the other two fish had a more dispersed distribution). "*X*" marks the location of the reward. **b**: Frequency histogram illustrating the tendency of carp which visited the reward site at night to return to their day-time home ranges (distance from centroids) during the day (n=32)

Prior to baiting, centroids of the day- and night-time MCPs were located on average, 441 m and 326 m, from the eventual baiting site. After baiting commenced, 10 of the 14 carp visited the reward on at least one night (two visited the reward once, three twice, three three times, and two four times). We were able to measure a total of 32 daytime locations of these fish, after they vacated the reward area, of which 47% were within 50 m of the centroids of their pre-baiting daytime MCPs with 60% being within 100 m (Fig. 3b).

Discussion

This study demonstrated that free-ranging Common Carp can quickly learn and remember the location of a food reward in the natural environment, supporting the results of earlier laboratory studies which demonstrated that carp and their close relatives possess well-developed cognitive abilities (Rodriguez et al. 1994; Braithwaite and de Perera 2006). The consistency and precision with which individual carp visited the reward site each night and then returned to their small home ranges during the day suggests both that wild carp employ cognitive strategies to find and learn the location of food and that they have an excellent spatial memory. The speed with which carp learned the location of the reward (6 days) also resembles that observed in laboratory arenas (Rodriguez et al. 1994; Zion et al. 2007). The learning abilities and spatial memory demonstrated by carp in the study lake are particularly impressive given the seemingly featureless, large, and turbid nature of this environment that precluded the use of visual landmarks which these fish often rely on in experimental arenas (Rodriguez et al. 1994; Braithwaite and de Perera 2006).

Our results demonstrate that free-ranging carp can learn the location of a food reward in a relatively large lake within only 6 days as evidenced by a sudden change in their spatial distribution. This shift cannot be explained by chance encounters with the bait as their numbers followed a rapidly increasing trend and individual fish exhibited a nearly perfect tendency to return to the reward site each night (only one fish did not return to the reward during one night). Environmental factors also seem unlikely explanations of the sudden change in carp behavior, as temperature and weather conditions were stable throughout the experiment. The speed with which carp learned to find the food was likely facilitated by social learning as carp and Goldfish have been shown to learn from shoaling conspecifics in laboratory tanks (Warren et al. 1975; Pitcher and House 1987; Zion et al. 2007). However, the nocturnal movement and foraging strategy exhibited by carp in our study lake suggests that these fish employed different learning mechanisms than those that have been previously tested in laboratory arenas. While laboratory studies of carp and Goldfish have focused on visual cues and short-range spatial orientation (Warburton 1990; Rodriguez et al. 1994; Vargas et al. 2004), it is likely that wild carp were using olfactory cues because water clarity was poor and all key movements occurred at night. The carp has an acute sense of smell and well developed regions of brain which are associated with

olfaction and cognitive functions (Irvine and Sorensen 1993; Broglio et al. 2003; Sorensen and Stacey 2004; Vargas et al. 2009). This hypothesis warrants testing.

The cognitive abilities of carp demonstrated by this study undoubtedly have important life history implications. Carp are known to inhabit large spatially-interconnected ecosystems in which they undergo extensive movements, often in excess of 100 km (Koblitskaya 1977). For instance, a recent study suggested that the carp's reproductive success hinges on its ability to move into and then spawn in outlying shallow areas that periodically experience severe instability and, as a result, lack predators that forage on carp larvae and eggs (Bajer and Sorensen 2009). Because such areas are often restricted to specific and distant regions, an ability to remember these locations would be highly adaptive. Common Carp are also among the most invasive and damaging fish worldwide (Koehn 2004; Bajer et al. 2009) and are currently managed using non-specific toxins and barriers (Marking 1992). This study suggests that novel management schemes which train fish to come to certain areas where they might be netted could be developed for this species by exploiting their cognitive abilities. Depending on geographic regions, these schemes might involve species-specific food rewards or other odors (Sorensen and Stacey 2004) to facilitate aggregation and thus enable selective removal.

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Appendix E

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ORIGINAL PAPER

Recruitment and abundance of an invasive fish, the common carp, is driven by its propensity to invade and reproduce in basins that experience winter-time hypoxia in interconnected lakes

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Abstract Although the common carp is globally distributed, it only reaches extreme densities in certain regions. We hypothesized that this phenomenon might be linked to recruitment bottlenecks which carp overcome where environmental conditions create unstable peripheral areas that it can access for spawning and nursery habitat. To test this hypothesis, the abundance, movement and reproductive success of carp was determined in two systems of inter-connected lakes in the North American Midwest whose shallow basins frequently experience winter-hypoxia ('winterkill'). Radio-tracking demonstrated that while adult carp overwinter in deep lakes that do not winterkill, they aggressively move into winterkill-prone shallow regions in the spring to spawn. The significance of this behavior was demonstrated by ageing analyses which found that carp recruit only in interconnected shallow lakes and then only in years following severe winter hypoxia. Presumably this strategy allows carp to exploit nursery habitat that is relatively free of predators. It likely evolved in response to seasonally variable conditions in the carp's native habitat in the Ponto-Caspian region. This life history may also explain the carp's abundance in other unstable regions such as southern Australia and could potentially be exploited to control this damaging invasive.

Keywords Invasiveness · Life history · Movement · Instability · Winterkill · Propagule pressure · Predatory release

Introduction

Among the hundreds of invasive species of fish that have been described (Lever 1996), the common carp, *Cyprinus carpio*, is one of the most pervasive and destructive (Zambrano et al. 2006). Native to the Ponto-Caspian region (Balon 1995), this large benthivorous cyprinid is now well established in Europe, North and South America, Australia, and Africa (Lever 1996). In many, but not all, of these locations it has either caused, or been associated with, large-scale and significant reductions in water quality and ecosystem health as a consequence of its habit of benthic feeding which uproots plants and liberates sediments as well as nutrients (Crivelli 1983; Parkos et al. 2003; Bajer et al. 2009). Although the spatial pattern of the abundance of common carp has not been systematically studied, reports of especially high, damaging densities appear restricted to Midwestern North America and south-central Australia where densities of up to 1,000 kg/ha are have been described (Neess et al. 1957; Panek 1987; Koehn 2004). Common carp (hereafter 'carp') may constitute the

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majority of the fish biomass in these systems. In contrast, densities of common carp in Europe, where it was introduced nearly 2000 years ago, typically appear to be only about one tenth of their density in North America and Australia (Crivelli 1983). Why this species should be especially abundant and damaging in some geographic regions versus others has long puzzled those seeking to understand and control this at times highly invasive fish (Crivelli 1983).

Although the carp possesses many attributes that can explain its ability to spread and survive in new habitats, no study has identified processes that might explain its restricted pattern of superabundance. For example, this species is well known for its tolerance of a wide range of temperatures, salinities, and oxygen (Opuszynski et al. 1989; Stecyk and Farrell 2007), mobility (Koblitskaya 1977; Brown et al. 2005), omnivorous diet (Crivelli 1981), and extreme fecundity (Sivakumaran et al. 2003). However, these life history characteristics are constant and cannot explain why carp should be extremely abundant in some locations and not in others. Clearly, carp abundance must be linked to local environmental conditions that favor as yet unidentified life history traits. No study that we know of has yet addressed how local environmental conditions and life history might interact to jointly determine the abundance of an invasive fish.

Regions of North America and Australia that suffer from a superabundance of carp are characterized by large, spatially connected aquatic habitats, and environmental instability which severely impacts ecological integrity of their shallow basins. In particular, the upper Midwest in North America is characterized by networks of interconnected rivers and lakes whose shallow basins frequently experience severe winter hypoxia and fish mortality ('winterkill') as a consequence of prolonged snow cover (Magnuson et al. 1985). Although not subject to winter-time hypoxia, the Murray-Darling River Basin in south-central Australia is also comprised of unstable habitats which include floodplain lakes that experience severe droughts and floods and summer hypoxia on a quasi-annual basis (Gehrke et al. 1995; Puckridge et al. 1998 Lake 2003; McNeil and Closs 2007). In the Ponto-Caspian region, the carp's native habitat and a place where severe winters and spring flooding are common, this species spawns and reproduces in floodplains and ephemeral marshes (Koblitskaya 1977). We hypothesize that the common carp has evolved a life history in which highly fecund adults seek access to unstable outlying habitats where their young have higher chances of survival. Specifically, we hypothesize that the carp has become superabundant and invasive in geographic regions outside of their native range which contain large areas of unstable habitats that can function as carp nursery areas.

To test this hypothesis, a study of carp abundance, movement, and reproductive success was conducted in the northern region of the North American Midwest (Minnesota) in two interconnected systems of lakes. Carp abundance was estimated and samples collected to describe basic population attributes. Then, we tracked carp movement and reproductive activity to determine if adults routinely move into peripheral, winterkill-prone regions to spawn. Female fecundity and egg viability was also measured to estimate reproductive output (propagule pressure). Finally, the age structures of both populations were determined and compared to records of winter hypoxia in interconnected shallow regions to see if years with exceptionally high carp reproductive success (recruitment) coincided with winterkills in shallow habitats. This is the first study we know of that evaluates the relationship between common carp movement, fecundity, recruitment and environmental instability.

Materials and methods

Study lakes

This study took place in south-central Minnesota, USA (Fig. 1) a region with especially complex networks of interconnected lakes that frequently experience winter hypoxia and where carp is excessively abundant. We selected two seemingly representative lake systems that were moderate in size (30–100 ha), amenable to study, and whose oxygen levels have been monitored for the past 20 winters. The Riley Creek Watershed (Fig. 1) is comprised of five interconnected lakes, three of which we studied to document movement, propagule pressure, and the relationship between recruitment and winterkill occurrence. Lake Susan (30 ha) has a maximum depth of 6 m, a history of winterkills prior to 1993 (when a winter aeration system was installed) and connects downstream to Rice Marsh Lake (40 ha)

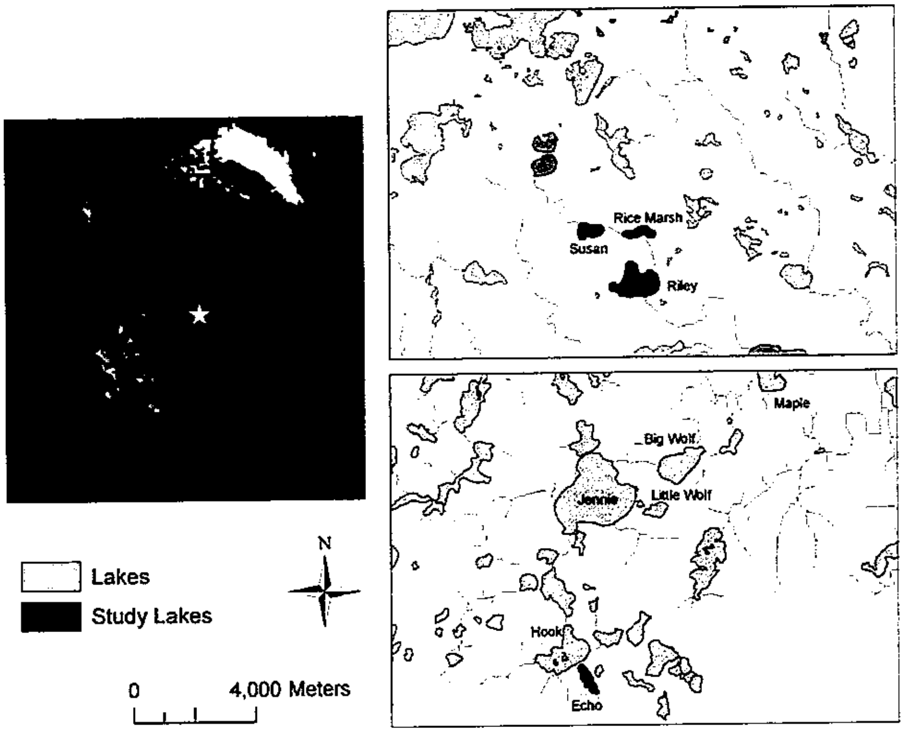

Fig. 1 The two interconnected systems of lakes that we studied. The *top panel* shows the Riley Creek chain of lakes where we studied carp in lakes Susan, Rice Marsh, and Riley. Winter dissolved oxygen was measured in lakes Susan and Rice Marsh. The *bottom panel* shows the upper portion of the Big Swan Lake Watershed where we studied carp in Lake Echo, and where winter dissolved oxygen was measured in lakes Maple, Big Wolf, Little Wolf, Jennie, and Hook, as well as eight other lakes positioned within 30 km radius (not shown). The panel to the left shows the study area (star) on a satellite photograph of North America (NASA)

which is shallow (max depth 3 m) and often winterkills. Rice Marsh Lake then drains downstream to Lake Riley which is relatively large (100 ha) and deep (max depth 18 m), and does not winterkill. Lake Riley finally drains into the Minnesota River. A velocity barrier has blocked fish movement from the river into the Riley Creek watershed for the past 50 years.

The second system selected for this study was the Big Swan Lake Watershed (Fig. 1). It is comprised of over 20 interconnected lakes which eventually flow into the North Fork of the Crow River. The Big Swan Lake Watershed includes lakes that are deeper than 5 m and do not winterkill (e.g. lakes Hook, Jennie, Collinwood, Big Swan) and lakes that are shallower than 3 m and which periodically develop severe winter hypoxia (e.g. lakes Echo, Maple, Big Wolf, Little Wolf, and others; Fig. 1). We selected one of these shallow lakes, Lake Echo (33 ha, max depth 2.5 m), to estimate carp abundance and age-structure and to determine if they can be explained by winterkill occurrence in this watershed. Because carp have been seen to migrate between Lake Echo and other lakes in the watershed (Lee Sundmark; Minnesota Department of Natural Resources, Hutchinson, MN; personal communication) we assumed that the carp population in Lake Echo reflects that in the watershed as a whole.

Determining the abundance and fecundity of carp in the study lakes

We estimated the abundance of carp in Lake Susan and Lake Echo during the late summer and fall of 2006 when their inlets and outlets were either dry (Lake Susan) or blocked using a wire grate (Lake Echo). Each population was sampled at least five times using a large seine (400 m long, 7 m deep, mesh size 3.5 cm) that was pulled across two areas, and boat electrofishing (Smith-Root model SR-16H) conducted along the entire shoreline of each lake. Length structure comparisons showed that both techniques sampled all size classes of carp equally well. During each census, all captured carp were counted, measured (total length), injected with numbered tags (model TBA-1; Hallprint Australia), fin-clipped (to monitor for tag loss), and released. At least 1 week was allowed to transpire between each sampling to allow the marked fish to intersperse within each population. Populations were estimated using Schnabel's equations for multiple mark-and-recapture censuses from

the numbers of marked and unmarked carp in each census and also the numbers of marked carp in each population (Van Den Avyle and Hayward 1999).

Two groups of 100 pre-spawning carp (May 2006) were selected from Lake Susan and Lake Echo to evaluate gender ratios and fecundity. These fish were weighed (nearest g), measured (nearest mm), and a 0.1 g samples of their ovaries were preserved. Oocytes were subsequently counted and measured under a microscope to determine the number of mature eggs (vitellogenic eggs 0.7–1.2 mm in diameter) (Gupta 1975; Linhart et al. 1995; Sivakumaran et al. 2003) and estimate fecundity.

Documenting movement patterns and spawning activity of adult carp

Although anecdotal reports describe sexually active carp moving into shallow outlying areas in the spring (Swee and McCrimmon 1966), the significance of these movements has not been studied. Accordingly, we documented the movement and spawning activity of adult common carp in lakes Susan, Rice Marsh, and Riley in 2006 and 2007 to determine the extent to which carp from the two deeper lakes (Riley and Susan) might use shallow, winterkill-prone Rice Marsh Lake as a spawning area. Prior to carp spawning season in 2006 (April), 16 adult carp (six females and ten males; total length 400–650 mm) were captured in Lake Susan, and 19 adult carp (nine females and ten males) were captured in Lake Riley by electrofishing and implanted with individually coded radio-transmitters (model F1850; Advanced Telemetry Systems; Isanti, MN, USA). An additional 12 adult carp (six males and six females) were surgically implanted with radio-transmitters in April 2007 in Lake Riley and also Lake Susan.

The distribution of radio-tagged carp in lakes Susan, Rice Marsh, and Riley was monitored during 2006 and 2007 by surveying the entire system using a small boat equipped with a portable Yagi antenna. Fish were located using signal directionality and their locations (UTM NAD83) were mapped using a GPS unit. Telemetry surveys were conducted weekly from ice out (April) until we observed carp spawning (vigorously splashing adult carp and presence of their eggs on vegetation). During the spawning season (mid May–June) we surveyed each lake daily to map the location of carp spawning sites. At the conclusion of spawning (July), telemetry surveys were conducted on a quasi-monthly basis until ice-up to document if carp returned to their lakes of origin.

Determining egg viability, survival and propagule pressure

Approximately 1,000 carp eggs were collected from vegetation mats located in three carp spawning locations in Rice Marsh Lake in May 2006 and transported to the laboratory. Randomly selected samples of 50 eggs were then placed into four 20-l aquaria where water temperature was maintained at 18 ± 2°C, the temperature in the lake at the time when eggs were collected. Aquaria were aerated while fresh well water was introduced at 100 ml/min. Once the eggs hatched, *Artemia* naupli, a food item for larval carp (Schlechtriem et al. 2004), was supplied to each aquarium on a daily basis. Egg viability was estimated by counting the number of eggs that hatched into larvae, while larval survival was determined by counting the number of surviving larvae 2 weeks later. Propagule pressure of carp on Rice Marsh Lake was estimated by multiplying female fecundity and egg viability by the number of females observed to migrate from Lake Susan to spawn in this lake.

Determining the relationship between age structure and winterkill

The age-structures of carp populations in lakes Susan and Echo were determined using established procedures (Isely and Grabowski 2007). First, we developed the relationships between carp age and length (age-length key) using 100 carp from each population that were selected so that entire length distribution was represented and then aged following established protocols for this species (Brown et al. 2004). Each fish was measured (nearest mm), weighed (nearest g), sexed, and its asterisci otoliths removed, cleaned in tap water, dried, embedded in epoxy and sectioned transversely through the primordium region using a low speed Isomet saw. Three 300-micron sections were then cut from each otolith and aged under a microscope using transmitted light (Brown et al. 2004). The number of annuli (visible as distinct opaque bands) was then counted along the main ventral plane to estimate age. Accuracy was validated

by examining the location of the first two annuli using fish of known age (a known cohort of carp from another lake system was collected and aged one and two years after hatching). Each otolith was aged by three readers and modal age (the age for which at least two of the three readers agreed) was used to develop an age-length key for each population. These keys were then used to estimate age structure of each population using unbiased length structures which were determined by measuring [500 individuals from each population.

Past winterkill events in our watersheds were determined using records of winter dissolved oxygen collected by state fishery biologists (Mr. Daryl Ellison Eden Prairie, MN; Mr. Lee Sundmark, Hutchinson, MN; and Mr. Paul Diedrich, Montrose, MN). These routine measurements had been collected annually to assess the likelihood of native sport-fish mortality due to winter hypoxia in shallow lakes. Dissolved oxygen was typically measured at depths of 0 and 1 m from several locations in each lake using electronic meters (YSI, Colorado). These measurements were conducted on a quasi-monthly basis between January and March but more frequently if the oxygen declined to\ 5 mg/l. We used these archived records to determine the winter minimum of dissolved oxygen (the highest reading on the day when oxygen declined to its annual low) in each lake. In the Riley Creek Watershed, measurements were collected annually in Lake Susan but only periodically in Rice Marsh Lake (a less valued fishery) (Table 2). No measurements were made in Lake Riley because this deep lake has had no history of winter hypoxia in the past 50 years (Mr. Daryl Ellison, Minnesota Department of Natural Resources; personal communication). In the larger and more complex Big Swan Lake Watershed, winter dissolved oxygen was measured in lakes Hook, Jennie, Maple, Big Wolf, and Little Wolf (Fig. 1b), although not all lakes were monitored annually. To supplement this data set and better portray annual trends in winter dissolved oxygen in this watershed, we used historic dissolved oxygen measurements from eight lakes of similar size and depth located within a 30 km radius from the Big Swan Lake Watershed (lakes Millstone, Melrose, Emma, Crawford, Ann, Sommers, Otter and Mink (Table 2). We interpreted oxygen concentrations of 2.0 mg/l and less as indicative of at least a partial winterkill and below 1 mg/l of certain winterkill, because these oxygen levels are known to cause mortality of fishes (Rahel 1984; Petrosky and Magnuson 1973).

To analyze the relationship between winterkill and carp reproductive success in the smaller and more isolated Lake Riley Watershed we plotted the age structure of carp in Lake Susan versus the winter minima of dissolved oxygen collected in lakes Susan and Rice Marsh. We expected that winterkill in either of these lakes would be associated with an increased year-class abundance of carp in Lake Susan because carp spawn in both lakes and move between them. To analyze the relationship between winterkill and carp recruitment success in the Big Swan Lake Watershed, we plotted the age structure of carp from Lake Echo versus the averaged minima of winter dissolved oxygen measured in lakes shallower than 3 m in both this watershed and the neighboring watersheds. Again, we assumed that the carp population in Lake Echo was representative of carp in the Big Swan Lake Watershed as these lakes are highly interconnected and carp are reported to move between them.

Results

Carp abundance and reproductive condition

Lake Susan contained * 4,048 carp (90% CI = 3,312–5,223) at a density of 307 kg/ha. Lake Echo contained * 5,666 carp (90% CI = 4,605–7,361) at a density of 327 kg/ha (Table 1). Carp lengths were normally distributed in Lake Susan with the average carp measuring 591 mm (2.84 kg). In Lake Echo, carp ranged from 340 to 820 mm, although two distinct size modes were observed: 420–520 mm (1.05–1.95 kg), and 560–720 mm (2.43–5.06 kg). Fifty-one and 32% of the carp populations in Lakes Susan and Echo, respectively, were females and all were sexually mature. The fecundity of these females increased with length [Fecundity (millions of eggs) = 0.0028 body length (mm)—0.9044; $r^2 = 0.73$; $P\backslash\ 0.05$], and exceeded one million mature eggs for females larger than 700 mm. The average female in Lake Susan carried 750,000 mature eggs while the average female in Lake Echo carried 560,000 mature eggs.

Table 1 Carp population estimates (N) and their 90% confidence intervals (CI) in lakes Susan and Echo using multiple-census mark and recapture approach

Date	Gear	Total captured (C_i)	Unmarked	Recaptured (R_i)	Marked in the population (M_i)
Lake Susan					
9/7/06	Seine	50	50	0	0
9/21/06	Seine	43	43	0	50
10/3/06	EF	27	27	0	93
10/10/06	EF	39	37	2	120
10/16/06	EF	33	30	3	157
10/23–30/06	EF	32	29	3	187
11/13/06	Seine	137	130	7	216
4/23/07	Seine	488	449	39	346
$\sum_{i=1}^{8} C_i \cdot M_i = 218{,}946; \sum_{i=1}^{8} R_i = 54; N = \frac{218{,}946}{54} = 4{,}054; 90\%\mathrm{CI} = 3{,}312 - 5{,}223$					
Lake Echo					
8/18–21/06	Seine	320	278	0	0
8/28–31/06	EF	106	96	10	278
9/20/06	Seine	301	268	18	374
9/26/06	EF	92	84	8	642
10/9–26/06	EF	121	38	15	726
$\sum_{i=1}^{5} C_i \cdot M_i = 288{,}952; \sum_{i=1}^{5} R_i = 51; N = \frac{288{,}952}{51} = 5{,}666; 90\%\mathrm{CI} = 4{,}605 - 7{,}361$					

EF electrofishing

Movement patterns and spawning activity of adult carp in lakes which winterkill

Radiotelemetry showed that adult carp from both lakes Susan and Riley aggressively moved into Rice Marsh Lake each spring, and that most of them returned late each summer or fall. For example, during April 26–May 7 of 2006, 6 out of the 16 radio-tagged carp (e.g. * 37% of the population) moved from Lake Susan to Rice Marsh Lake, and 2 out of 19 (11% of this population) moved from Lake Riley to Rice Marsh Lake (Fig. 2a). This movement was followed by intense spawning activity in Rice Marsh Lake on May 5 and May 18 (64 spawning sites were noted). By May 22, all of these radio-tagged carp had returned to their lakes of origin, except for two individuals who remained until the next year. In 2007 another movement of carp from Lakes Susan and Riley to Rice Marsh Lake occurred (Fig. 2b). During May 1–8, 7 out of the 31 carp that carried radio-transmitters in Lake Riley moved to Rice Marsh Lake. That movement was followed by carp spawning in Rice Marsh Lake on May 9–11 (85 spawning sites observed). Also, out of the 31 radio-tagged carp in Lake Susan, seven moved to Rice Marsh Lake on June 1, where another period of spawning was observed during June 2–8 (57 spawning sites). Both male and female carp moved in similar numbers. In Lake Susan, 48 and 187 spawning sites were mapped in 2006 and 2007, respectively, while in Lake Riley 290 and 305 sites were mapped during these years.

Egg fertility, larval survival, and propagule pressure

Laboratory tests of carp eggs collected from the spawning habitats in Rice Marsh Lake showed that 49% of the eggs hatched into larvae, from which 95% survived 2 weeks and were able to convert to exogenous food. Based on a 50% fertilization rate, fecundity, the abundance of carp in Lake Susan and the proportion of carp that migrated to Rice Marsh Lake for spawning, we conservatively estimate that at least 610 million fertilized eggs were deposited in Rice Marsh Lake during 2006 and then again in 2007. This estimate did not include the number of females which moved into the marsh from Lake Riley, which was not known, as the carp population in Lake Riley was not estimated.

Relationship between age structure and winterkill

At least two of the three otolith readers provided identical age estimates for 94% of the otoliths, while age bias graphs showed there to be no bias between

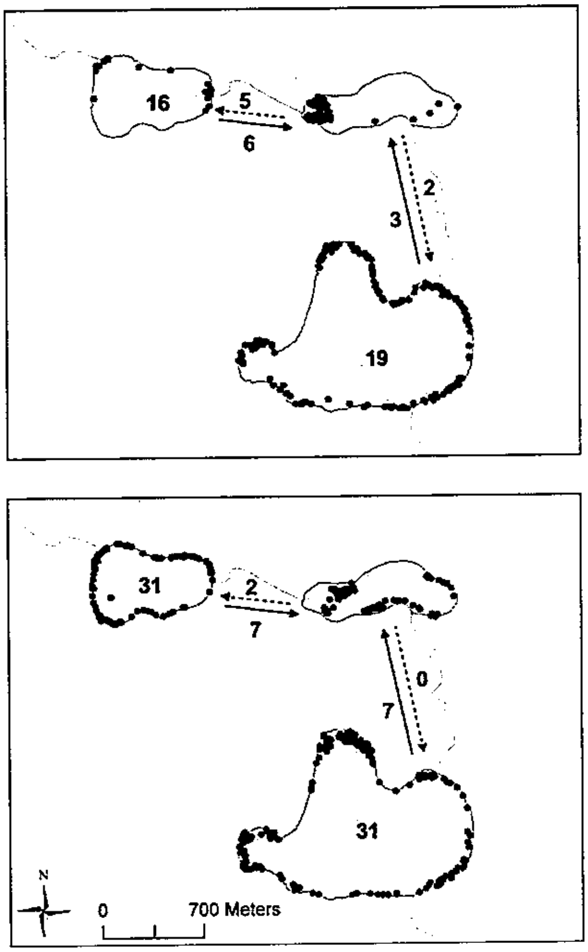

Fig. 2 Maps showing the movement of radio-tagged adult carp from lakes Susan and Riley into Rice Marsh Lake in 2006 (*top panel*) and 2007 (*lower panel*). The *numbers* in each lake show how many radiotagged adult carp inhabited lakes Susan and Riley before the spawning season, while numbers next to the *solid arrows* show how many of these carp moved to Rice Marsh Lake shortly before spawning and then returned (*dashed arrows*) to their lakes of origin after the spawning. *Black dots* indicate carp spawning sites

readers (data not shown). Evaluating the age structure of Lake Susan carp, we discovered evidence of recruitment for only 10 of the past 18 years, and that six of these (1990, 1991, 1996, 1997, 2003, 2004) accounted for over 90% of the carp in the lake (Fig. 3). Winter oxygen levels dipped below 1 mg/l in Lake Susan and/or Rice Marsh Lake for 4 of these 6 years (1990, 1991, 1997, 2004). For both of the other years (1996, 2003) no oxygen data were available for Rice Marsh Lake while winter oxygen levels in Lake Susan were high (Table 2; Fig. 3). By

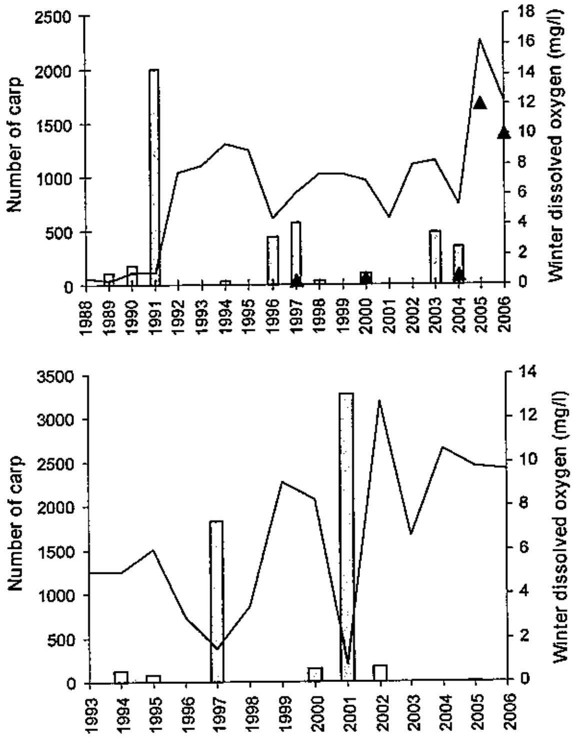

Fig. 3 *Top panel* the age structure (numbers of fish in each age class; *columns*) of carp in Lake Susan and winter-minima of dissolved oxygen measured in Lake Susan (*line*). *Triangles* show years when winter-minima of dissolved oxygen were also measured in the adjacent Rice Marsh Lake. *Bottom panel* the age structure of carp in Lake Echo (*columns*) and the average winter-minima of dissolved oxygen in lakes shallower than 3 m in the same watershed

far the highest recruitment event, which comprised over 40% of the population, occurred in 1991 following the fourth consecutive winter with oxygen minima below 1 mg/l in Lake Susan. On all 6 occasions when either Lake Susan and/or Rice Marsh experienced winter oxygen below 1 mg/l (1998, 1989, 1991, 1997, 2000, 2004), recruitment was observed. Conversely, recruitment was not observed for the 2 years when dissolved oxygen levels in both systems were high (2005, 2006).

In Lake Echo nearly 95% of the population was comprised of only two age classes (1997, 2001), both of which followed the two most recent winters when oxygen in many shallow lakes in the Big Swan and adjoining watersheds fell below 2 mg/l with some going below 1 mg/l (Fig. 3; Table 2). Accounts of large-scale fish mortality following both of these winters were also reported by state biologists. However, during each year, at least some lakes within this

Table 2 Winter dissolved oxygen minima recorded in the Big Swan Lake Watershed and adjacent watersheds (within 30 km)

Lake (depth; m)	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006
Big Swan Lake Watershed														
Little Wolf (3)				2.6	*1.5*	*1.3*			*1.7*			3.3	7.1	
Big Wolf (3)	6.0	5.0	8.3	*1.9*	*0.8*	3.9		9.8	*1.2*			13.3	10.1	13.0
Maple (3)	4.1		3.8	*1.7*	*1.4*				*0.6*			20.0	11.0	6.3
Jennie (5)	5.7	8.5	14.8	7.7	2.2			12.0	7.5				16.1	
Hook (5.8)	2.8	6.5	7.0	*1.3*	*1.4*	6.8		12.0	5.4			11.4	15.4	11.4
Neighbouring Watersheds														
Millstone (2.1)									*0.3*	17.4		14.4		
Melrose (2.1)				2.4	2.1	5.6	11.7	6.5	*0.5*	12.4			11.04	
Emma (3)				6.3	*1.8*	3.9		10.6	*0.4*	15.0	7.8	5.5		
Crawford (3.3)						2.5	6.5	6.2	*0.8*	6.3	5.5	7.1		
Sommers (5.5)				6.8	*1.4*	8.8		14.5	*0.8*		10.7	17.2	11.4	
Ann (5.8)				9.0	4.3	9.2	10.7	13.7			7.9	5.6		
Otter (6.3)				*1.4*	*0.4*				*0.5*					
Mink (10.3)	10.2	8.9		*1.6*	*1.5*	5.7	9.3	15.0	5.9	12.9	10.5	14.5		
Average (B3 m)	5.1	5.0	6.0	2.9	*1.5*	3.4	9.1	8.3	*0.8*	12.7	6.6	10.6	9.8	9.6

Records with oxygen values below 2 mg/l are indicated in italics. Lakes within each watershed are sorted by their maximum depths which are shown in parenthesis. Records date back to 1 year prior to the first measured recruitment event

watershed maintained oxygen concentrations substantially above 2 mg/l showing that a refuge was present (Table 2).

While most of the carp in Lakes Susan and Echo were between 5- and 16-years-old, each population included a small number of individuals that were considerably older. The oldest carp in Lake Echo was 17, and the oldest carp in Lake Susan was 34. These individuals appeared reproductively active, demonstrating that carp are long-lived and can exert propagule pressure on unstable habitats for many decades.

Discussion

This study describes new evidence from Midwestern North America which suggests that the superabundance of the common carp is driven by a complex interplay between its life history, local habitat characteristics, and environmental instability, all of which appear to be equally important. Our findings suggest that the success of the common carp is attributable to their longevity, mobility, and propensity to exploit peripheral unstable areas as spawning/nursery habitat. The significance of this life-history strategy and its dependence upon environmental instability was exemplified by aging analysis strongly suggesting that carp reproduced successfully only in outlying habitats that had experienced recent, severe winter hypoxia. Carp may maximize their reproductive success by exploiting severely disturbed (in our case winterkilled) peripheral habitats because such areas likely have reduced densities of native egg and/or larval predators. Such a strategy might also function effectively for carp in more temperate locations such as the Murray Darling Basin in south-central Australia where erratic flooding and/or summer hypoxia may periodically reduce predatory pressure and relax recruitment bottlenecks (King et al. 2003; McNeil and Closs 2007). Overcoming recruitment bottlenecks by reproducing in unstable regions may reflect the carp's evolutionary origins in the Ponto-Caspian region which also experiences severe winters and floods (Koblitskaya 1977).

Our study suggests that the reproductive success of carp is intimately linked with its strong migratory drive to gain access to the outlying shallow spawning habitats. Through the use of radiotelemetry during two consecutive spawning seasons in an interconnected

system of lakes we clearly demonstrate the strategic and synchronized nature of pre-spawning movements of adult carp. Each spring, nearly a third of the adult carp population left the two deeper lakes within a * 2 week period, and migrated (upstream or downstream depending on location) to the much shallower Rice Marsh Lake for spawning, even though their own lakes offered spawning habitat. Further, many carp returned to their original lake for the winter each year. The systematic and synchronized nature of this movement strongly suggests that it represents an adaptive behavior which is integral to carp life history. This conclusion is reinforced by numerous accounts of adult carp moving though small passages of water in early spring throughout the American Midwest, Australia, and Ponto-Caspian regions (Koblitskaya 1977; Swee and McCrimmon 1966; King et al. 2003; Crook and Gillanders 2006).

Perhaps our most significant finding is that the reproductive success of carp in Midwestern shallow lakes seems to be driven by environmental instability, winter hypoxia in particular. This conclusion is supported by our aging study which showed that carp recruited in significant numbers only in years when shallow spawning habitats experienced severe winter hypoxia. It was most clearly illustrated in Lake Echo, where the entire population could be attributed to just two recruitment events, both of which followed the only two winters when multiple shallow basins experienced oxygen levels below 1 mg/l. Similarly, by far the largest carp recruitment event in Lake Susan (1991) followed 4 years of severe winter hypoxia in that system. The Lake Susan example suggests that effects of consecutive winterkills can cancel each other out, as carp also perish in hypoxic lakes and only the last winterkill will have a lasting effect on population age structure. The same scenario may explain why only the 1997 year class was obvious in the Big Swan Lake Watershed which had severe winters in 1996 and 1997. We know of no other published data to document carp reproductive success in response to environmental instability, except for a single study from South Dakota which describes sporadic and synchronized carp recruitment among populations but does not explicitly examine winterkill or other instability process (Phelps et al. 2008). Although many questions remain to be answered about the association between carp recruitment and environmental instability, that these events can play a key role in driving carp population abundance seems clear.

Our study also identifies several other specialized biological attributes of the common carp that likely contribute to this species' ecological success in locations such as Minnesota which experience seasonal extremes. We found that carp in Minnesota mature at a very young age (3–4 years) and are extremely fecund, with many females carrying over a million mature eggs each spring. Similarly high fecundities have been noted in Australia and Canada (Swee and McCrimmon 1966; Sivakumaran et al. 2003; Brown et al. 2005). The enormous fecundity is responsible for an equally high propagule pressure, which we conservatively estimated to range upwards of 500 million fertile eggs per lake. If realized, such pressure can produce enormous recruitment events as illustrated by carp in Lake Echo, where over 95% of this very dense carp population was comprised of only two recruitment pulses. Finally, we find that carp in Minnesota lakes are very long-lived (maximum age 34) giving them ability to exert consistent propagule pressure for many years and produce offspring even if instability events occur infrequently.

We hypothesize that the association between winterkill and carp recruitment success is likely driven by predator-release mechanisms during early development of carp eggs. Although carp develop rapidly and grow quickly, their larvae are likely extremely vulnerable to predation as they are small, free-swimming and not protected by parental care (King et al. 2003). Notably, the fish community in normoxic Midwestern lakes is dominated by several predatory species of centrarchids, percids and esocids which are not resistant to hypoxia and are often absent from lakes that winterkill (Rahel 1984; Tonn and Paszkowski 1986). Bluegill sunfish (*Lepomis macrochirus*), a small predator that dominates the fish community in this region and is capable of consuming fish larvae (Drake and Pereira 2002; Carpenter and Mueller 2008), is known to be particularly sensitive to hypoxia (Petrosky and Magnuson 1973; Farwell et al. 2007). The alternative hypothesis that competition for food amongst larval fishes may be responsible for carp recruitment failures during non-winterkill years seems unlikely because larval carp are tolerant of starvation (Geurden et al. 1999). The biology of carp larvae and juveniles in systems that

do and do not experience winterkill needs to be studied to test these hypotheses.

Fragmentary information about carp biology in their native habitats suggests an evolutionary basis for the carp's reproductive strategy. In the delta of the Volga River, a complex ecosystem that covers over 3,000 km^2, carp are known to undertake extensive upstream spawning migrations from the estuary in the Caspian Sea (where they overwinter) during annual flooding events in April–June, to access shallow interconnected lakes and floodplains where they spawn (Koblitskaya 1977). Interestingly, the recent reduction of the Danube's floodplain by hydro-engineering has coincided with the near-extinction of the 'wild' form of carp in this region (Balon 1995).

Fundamental similarities in the biology of carp in their native habitats, Australia, and the Midwest allow us to suggest a more general hypothesis to explain carp abundance in these locations. In all of those regions carp have been shown to reproduce in outlying habitats subject to environmental instability. While in Minnesota, carp appear to reproduce successfully in lakes that experience winter hypoxia, in Australia and the Caspian region, carp use periodically inundated floodplain habitats as spawning sites and nurseries (Koblitskaya 1977; Balon 1995; King et al. 2003; Stuart and Jones 2006). These freshly inundated habitats might also be expected to have very low densities of egg and larval predators due to their rapidly expanding areas and shallow depth. Floodplain habitats in the Murray-Darling Basin of Australia may serve as particularly good nurseries for carp, because they frequently experience severe hypoxia during hot and dry periods and flooding during wet seasons (King et al. 2003; Stuart and Jones 2006; McNeil and Closs 2007). Some locations, such as New Zealand, may simply be prone to invasion by the carp because they have few native egg predators. Although additional processes likely influence carp abundance, we expect that, in general, carp will be superabundant in regions where extensive areas of occasionally unstable nursery habitats are frequently available along with refuges from which the highly mobile, long-lived and fecund adults can initiate their annual spawning migrations.

There is a genuine need for more detailed studies of carp abundance, recruitment and local environmental conditions across the globe to fully explain invasiveness of this species. The carp is not invasive in all locations that experience winter hypoxia or flooding such as large tropical river systems in South America and the lakes of northern Europe (Welcomme 1995; Chippari-Gomes et al. 2005; Öhman et al. 2006). Local habitat conditions such as connectivity, hypoxia, and flooding patterns, as well as the characteristics of local fish communities and their adaptations, are all likely to be important. Studies of whether and how predatory fishes feed on carp eggs and larvae do not appear to have been performed at any location and are needed both in the Caspian region and where carp invasiveness has been documented. Of special relevance to Midwestern North America is the fact that the native fish community is dominated by numerous species of small predators which are not particularly well adapted to survive severe winter hypoxia (Rahel 1984; Tonn 1990; Tonn et al. 1990; McNeil and Closs 2007).

Our hypothesis that carp's reproductive success can be linked to instability processes suggests that future efforts to control the abundance of this species must focus on developing means to hinder the ability of migratory adults to access unstable habitats and/or reduce the severity of instability processes. The factors which cause development of hypoxia in lakes need to be better understood, as must be the mechanisms which enhance carp reproductive success following hypoxic events. Several approaches are possible. For example, in the North American Midwest, carp nursery habitat could either be identified and blocked using fish barriers, or winterkill effects could be controlled using aeration. Importantly, our results suggest that recruitment is not density-dependent so adults could be removed with little concern about triggering recruitment events. We advocate developing a holistic and integrated carp management program that focuses on carp recruitment and dispersal that perfects existing methods (e.g. seining) to remove the long-lived and damaging adults. Such an approach will require a much more thorough understanding of the basic biology and ecology of this enigmatic species.

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Appendix F

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ORIGINAL PAPER

Variation in native micro-predator abundance explains recruitment of a mobile invasive fish, the common carp, in a naturally unstable environment

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Abstract Why certain species of fish become invasive is poorly understood and a key obstacle to restoring many of the world's ecosystems. In this study we tested whether variation in biotic resistance exerted by native predators might explain the reproductive success of the common carp, a large and fecund invasive species that typically spawns in outlying and unstable shallow habitat. An initial three-year study of the relative abundance of young-of-year (YOY) carp in interconnected lakes in the Upper Mississippi River Basin discovered that YOY carp are only found in shallow waters that experience winter hypoxia (winterkill) and have low densities of the native egg-predators that otherwise dominate these locales. A follow-up experiment tested if native fish predation on carp eggs could explain this distribution. It found that while carp eggs survived in winterkill lakes, they only survived in non-winterkill lakes when protected by a mesh that excluded fish. Large numbers of carp eggs were found in the stomachs of native fish inhabiting lakes that did not winterkill. We conclude that common carp, and likely many other highly mobile and fecund invasive fish, have evolved life histories to avoid egg predators and can become invasive when they are absent.

Keywords Biological invasion · Common carp · *Cyprinus carpio* · Biotic resistance · Egg predation · Bluegill sunfish · *Lepomis macrochirus* · Winterkill · Hypoxia · Integrated pest management

Introduction

Dramatic increases in both the number and abundance of invasive fishes over the past few decades have caused precipitous declines in the biotic integrity of many aquatic ecosystems across the globe (Mack et al. 2000; Britton et al. 2010). While it is recognized that invasiveness in fish is often linked to complex combinations of local abiotic conditions and biotic resistance exerted by native competitors and predators, the precise nature of these relationships is poorly understood. Of special interest to aquatic ecologists and fisheries managers is whether native predators might control the abundance of invasive fish in natural ecosystems (Moyle and Light 1996a, b; Marchetti et al. 2004; Moyle and Marchetti 2006). Although it has been demonstrated that native predators can

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control invasive aquatic invertebrates and amphibians (Hill and Lodge 1999; DeRivera et al. 2005; Ward-Fear et al. 2010), no studies we know of provide direct (experimental) support for this possibility in fish. We speculate that one reason for this may simply be that the high mobility of many fishes coupled with the complexity of their life histories has made them difficult to study, which has precluded the development of meaningful biological control schemes.

The possibility that biotic resistance may often take the form of predatory pressure on eggs and larvae of invasive fishes (and thus impose a recruitment bottleneck) is compelling. First, although most invasive fishes are extremely fecund (Kolar and Lodge 2002), their eggs and larvae tend to be small and defenseless, suggesting that they are susceptible to predation. Second, the vulnerability of early life stages is suggested by the life histories of many invasive fishes, which often appear to employ predator-avoidance/swamping strategies (Ims 1990). In particular, many highly fecund invasive fishes have adult phases that are mobile and spawn in a synchronous fashion in unstable and peripheral areas that presumably have fewer predators. The common carp (*Cyprinus carpio*), Asian carps (*Hypophthalmichthys sp.*), sea lamprey (*Petromyzon marinus*), and northern pike (*Esox lucius*) are all invasive fish species in which highly fecund adults migrate long distances to disperse their gametes in seasonally-unstable peripheral habitats (Potter 1980; Koed et al. 2006; Lohmeyer and Garvey 2009; Bajer and Sorensen 2010). Whether this suite of life history characteristics evolved to reduce exposure to egg and/or larval predators does not appear to have been explicitly considered, nor does the possibility that differences in predator abundance might explain the success of invasive fishes in non-native habitats. Examples from the marine environment suggest that recruitment of fecund fishes (ex. cod [*Gadus morhua*]) can be controlled by egg and larval predators (Koster and Mollmann 2000).

The common carp (hereafter 'carp') is one of world's most invasive fish (Britton et al. 2010) and a good model to address the role of egg predation and its role in invasiveness. This species evolved in large and seasonally unstable rivers of Eastern Europe, is extremely fecund (up to 3 million eggs/female), and performs annual spawning migrations into peripheral floodplains and marshes (Balon 1995; Barus et al. 2001). Over the course of the past century it has been introduced worldwide and reaches extreme densities in temperate regions of North and South America and south-central Australia (Sorensen and Bajer 2011) where it is also extremely damaging to ecosystems (Weber and Brown 2009). These regions are both large and characterized by seasonal environmental extremes that include winter and summer hypoxia and spring flooding (King et al. 2003; Stuart and Jones 2006; Bajer and Sorensen 2010). Population-ageing studies conducted in the Upper Mississippi River Basin demonstrate that invasiveness of carp in this region can be attributed to punctuated and sporadic recruitment events (Phelps et al. 2008) that precisely coincide with severe winter hypoxia in peripheral shallow areas (Bajer and Sorensen 2010). Although several factors could explain this relationship, we have hypothesized that temporary reductions in biotic resistance triggered by winter hypoxia (winterkill) are the cause (Bajer and Sorensen 2010). In support of this possibility, we have described regular spawning movements of adult carp to and from seasonally-hypoxic areas (Bajer and Sorensen 2010). Furthermore, and most importantly, these areas are normally dominated by numerous species of centrarchids (sunfishes), which are voracious micro-predators (i.e. specialize in foraging on small particles; Gross and MacMillan 1981), but which are also sensitive to hypoxia and decline in abundance following winterkills (Rahel 1984).

In the present study we employed a combination of correlative observations and controlled experiments to test the hypothesis that recruitment (and invasiveness) of the common carp can be explained by localized reductions in biotic resistance associated with seasonal declines in native micro-predators in unstable spawning habitat (Bajer and Sorensen 2010; Sorensen and Bajer 2011). We found strong evidence that native micro-predators and bluegill sunfish (*Lepomis macrochirus*) in particular, are able to control carp recruitment by exerting strong predatory pressure on carp eggs. We also found no evidence that high propagule pressure that the carp exert on ecosystems can overwhelm this biotic resistance, unless the densities of native predators are reduced because of instability events (in this case winterkills). Our results appear to provide the first direct evidence that ecosystem invasions by the common carp, and possibly other species of mobile and highly fecund invasive fish, are fundamentally attributable to localized declines in biotic resistance.

Materials and methods

The study region and its fish

This study was conducted in the lake systems of the Upper Mississippi River Basin. This region is characterized by a dense network of lakes, marshes, and interconnecting streams, which drain into larger rivers and eventually the Mississippi River (Fig. 1). Adult carp inhabiting these systems typically overwinter in deeper lakes that have high oxygen concentrations but migrate in large numbers into shallow interconnected basins to spawn their adhesive eggs on floating vegetation in the spring (Bajer and Sorensen 2010; Fig. 1). Those carp that do not (or cannot) migrate, spawn at the edges of deeper lakes and propagule pressure is extremely high across entire watersheds (Bajer and Sorensen 2010; Fig. 1). Severe winters characterize this region and winter hypoxia commonly occurs in outlying shallow basins where oxygen levels often fall below 1.5–2 mg/L (Tonn et al. 1990). This level of oxygen is lethal to many native fish including the bluegill sunfish, which otherwise dominate these watersheds (Petrosky and Magnuson 1973; Rahel 1984). The bluegill is a relatively small (* 15 cm TL) micro-predator that forages on invertebrates, zooplankton, fish eggs and larvae and typically comprises 50–70 % of the native fish biomass (Gross and MacMillan 1981; Roth et al. 2007; Spotte 2007). Other abundant species include the black crappie (*Pomoxis nigromaculatus*), green sunfish (*Lepomis cyanellus*), pumpkinseed (*L. gibbosus*), yellow perch (*Perca flavescens*) and black bullhead (*Ictalurus melas*), all of which have larger mouths and tend to forage on larger prey items and are also relatively tolerant of hypoxia (Spotte 2007).

Study 1: Reproductive success of carp in stable and unstable habitats with different densities of native micro-predators

Winter dissolved-oxygen (DO) levels, the relative abundance of native fishes, and the relative abundance of young-of -year (YOY) carp were measured in 19 lakes in five chains of interconnected lakes for three consecutive years (2008–2010). Not all lakes were sampled each year (Table 1). These chains are representative of the region and each included 2–7 lakes, approximately half of which are shallower than 5 m and frequently experienced winter hypoxia while the other half were deeper and did not (Table 1). Our study had three steps. First, we monitored oxygen levels in each lake each winter. Then we confirmed that adult carp were present in each lake each spring and estimated their abundance and fecundity (propagule pressure). Finally, we sampled each lake for YOY carp and native fish at each summer's end.

Dissolved oxygen (DO) was measured 1–2 times a month in each lake between December and March. Holes were drilled through the ice at two locations of each lake and oxygen measured using an electronic meter (YSI 85, Yellow Springs, Ohio, USA) from the surface to the bottom of the lake at 0.5 m intervals. These values were then used to calculate winter DO minima following established protocols (Rahel 1984; Bajer and Sorensen 2010).

To estimate propagule pressure exerted by adult carp, we estimated the abundance of adult (sexually mature) carp in each lake. Precise population estimates of adult carp were available for ten of the study lakes from ongoing mark-recapture studies (Bajer and Sorensen 2010; Bajer et al. 2011; Osborne 2012; Table 1). In lakes for which mark-recapture data were not available, the abundance of carp was estimated using boat electrofishing in April-June and a regression relationship we developed using 4 years of census data [Density (carp/ha) = - 0.48 ? 4.93 9 electrofishing catch rate (carp/h); P. G. Bajer; unpublished data]. We assumed that females comprised 50 % of each population and estimated the fecundity of females from their body lengths. To develop the length-fecundity relationship we collected 30 prespawning females of various lengths and counted mature (stage [3) eggs in 1 g samples of their ovaries [Fecundity (millions of eggs) = - 0.90 ? 0.0028 9 length (mm); r^2 = 0.73; *N* = 30; *P*\ 0.01]. Our estimates of fecundity were in line with those previously reported for this region (Swee and McCrimmon 1966). We assumed that our calculations of propagule pressure are unbiased estimates of the actual propagule pressure (eggs spawned in each lake) because spawning and fertilization rates were unlikely to be influenced by winter DO.

Lastly, to estimate carp recruitment and native fish abundance, each lake was sampled in late summer using standard fish survey traps (9 mm bar mesh trapnets with a 10 m lead; Rahel 1984). These traps catch fish larger than approximately 40 mm in total length,

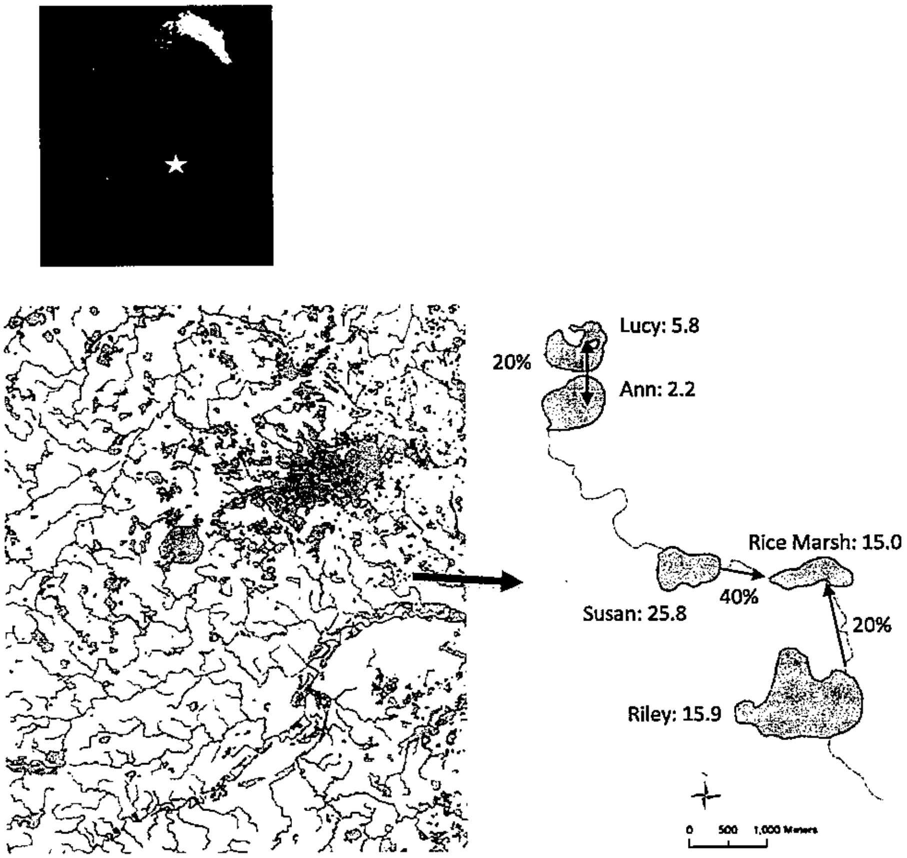


Fig. 1 Hydrography of the study region showing a network of interconnected lakes. The insert to the *right* shows Riley Creek chain of lakes, one of the five chains that we studied. Each year, between 20 and 40 % of adult carp move from lakes Susan and Riley, in which they overwinter, to spawn in the shallow, seasonally-hypoxic Rice Marsh Lake (*arrows*). The carp that do not move spawn along the edges of lakes Susan and Riley. The two upper lakes are isolated and inhabited by a smaller number of adult carp some of which also move between the two basins during spawning season. Propagule pressure (numbers next to lake names) ranges from 2.2 to 25.8 million eggs per ha. Numbers of adult carp in each lake and lake depths are presented in Table 1. For more details see Bajer and Sorensen (2010)

a size that carp typically surpass within 2 months in the region. Five traps were set at evenly spaced intervals around the entire perimeter of each lake for a 24-h period. Five traps per lake were deemed sufficient to collect representative samples of each lake's fish community as the study lakes were relatively small and catch rates were consistent between traps within each lake. Captured fish were identified to the species level, counted and measured. Catch rates of each species were averaged among the traps within each lake. Although 14 species of native fish were collected, four were included in the analysis (see below) because they comprised over 95 % of all fish collected. These species were the bluegill sunfish, black crappie, black bullhead and green sunfish. Native fish less than a year old (identified by length; Weaver et al. 1997; Pope and Willis 1998; Wolfe et al. 2009) were excluded from our analysis because they hatch after carp and thus could not have been foraging on carp eggs or larvae.

To analyze our data we produced scatter plots to examine possible relationships between YOY carp, native fish, winter DO, and propagule pressure. Because these plots revealed that YOY carp catch rates were highly dispersed and included many zeros, we used logistic regression analysis to model the presence of YOY carp (i.e. recruitment). Single and multiple logistic regressions were developed to determine which combinations of explanatory variables were most robust in predicting the recruitment of carp. These logistic regressions were ranked using Akaike's Information Criterion (AIC) and Akaike's weights following Burnham and Anderson (2002). The best model had the lowest AIC score and the highest weight, but other models with scores within two AIC units were considered to have equal data support (Burnham and Anderson 2002). All model fitting was done in R (R Development Core Team 2011) using AICcmodavg (Mazerolle 2011). Although the data collection design suggested including random lake and year within lake effects, we did not include these effects in our analysis because the dominant ecological variables of winter oxygen and its effects on native fish were highly collinear with the lake and year

Table 1 Size, maximum depth, and adult carp abundance (mean estimate) in each study lake

Chain	Lake	Area (ha)	Depth (m)	Adult carp abundance		
				2008	2009	2010
Riley Creek	Lucy	35.0	6.1	NS	642	105
	Ann	44.4	13.7	NS	662	662
	Susan	37.5	5.1	2,611	911	606
	Rice Marsh	40.0	3.0	2,065	178	178
	Riley	120.0	14.9	5,870	3,559	443
Carver Creek	Goose	159.2	3.05	*708*	10,707	9,239
	Hydes	89.7	5.5	28,037	9,332	*9,332*
	Reitz	31.9	11.0	9,184	6,904	8,044
	Rice	50.0	2.5	*7,962*	*2,342*	*5,152*
Sandy Creek	St. Catherine	38.0	3.0	*169*	4,712	*2,342*
	Cynthia	80.0	3.1	45,588	24,381	*23,330*
Purgatory Creek	Wetland	70.0	1.5	NS	NS	*5,301*
	Staring	66.2	4.9	NS	NS	*26,228*
Phalen Creek	Casey	4.7	1.1	NS	NS	*2,585*
	Markham	7.0	2.0	NS	NS	*211*
	Kohlman	29.9	2.7	NS	1,314	827
	Gervais	94.5	12.5	NS	4,115	2,613
	Keller	29.0	2.4	NS	1,275	802
	Phalen	79.6	27.8	NS	2,316	2,316

The abundance of adult carp was estimated using mark-recapture (underlined values) or boat electrofishing; for details on mark-recapture estimates see Bajer and Sorensen (2010) and Bajer et al. (2011). *NS* indicates lakes that were not sampled. Italicized values denote lakes in which carp recruitment was observed

effects. Instead, we included only the ecologically meaningful variables. To corroborate that our analysis was not biased by sampling some lakes multiple times, we conducted a separate model selection analysis in which only a single data point from each lake was used (see online Resource 1).

Study 2: Testing predation by native fish on carp eggs in stable versus unstable habitats

This experiment tested whether the presence (or absence) of YOY carp in lakes that winterkill (or not) could be explained by native fish predation on carp eggs. It was conducted in two hypoxic lakes (winter DO \ 1.5 mg/L; lakes Markham and Casey; Table 1) and two normoxic lakes (winter DO [1.5 mg/L; lakes Keller and Riley; Table 1). These lakes were selected from the systems included in Study 1. We first confirmed that these lakes contained native fish communities representative of hypoxic and normoxic systems by collecting five * 100 m^2 littoral seine hauls in each lake approximately 2 weeks before carp spawning season began (Table 2). The experiment then began in early May 2010 by monitoring daily carp spawning activity in each lake. When carp were observed spawning they were captured using an electrofishing boat and their eggs stripped into plastic containers and mixed with sperm (Billard 1999). Fertilized eggs, which are adhesive, were then placed onto 30-cm long pieces of artificial vegetation (green yarn) tied in loose clumps. Carp eggs were added to create densities similar to those found on natural vegetation (one per * 1 cm). Clumps of yarn with 200 (± 20) eggs were then attached to anchored lines with small floats to mimic floating plants on which carp typically spawn. Each clump included several empty strings of yarn to control for the possibility that spawning carp might deposit new eggs on our clamps, which did not occur. Eight clumps were placed (* 10 m apart) into each of two areas of each lake where spawning had recently been observed, while another set of 8 was inserted into either coarse- mesh bags to exclude fish (3 mm bar mesh, 4 per site), or fine-mesh bags to also exclude macroinvertebrates (0.5 mm mesh, 4 per site) and also placed in the spawning sites. These clumps were then examined on a daily basis and the number of attached eggs was counted before the clumps were placed back in the water (eggs that fell off

Table 2 Species composition and biomass (g/m^2) of native fish in the two hypoxic and two normoxic lakes used in Experiment 2 estimated using beach seines

Fish species	Hypoxic		Normoxic	
	Casey	Markham	Riley	Keller
Bluegill sunfish	0.0	0.0	9.81	23.66
Black crappie	0.0	0.0	0.0	0.18
Yellow perch	0.0	0.0	0.20	0.68
Largemouth bass	0.0	0.0	0.64	0.36
Northern pike	0.0	0.0	0.68	0.0
Pumpkinseed	0.06	0.0	0.05	0.18
Green sunfish	0.42	0.0	0.0	0.05
Black bullhead	3.18	0.0	0.0	0.0
Other native fish	0.0	0.09	0.0	0.0

Lake characteristics are presented in Table 1

the yarn were also counted for the fine mesh controls). This procedure continued until larvae were noted in the fine-mesh controls.

For data analysis, survival to hatch date was calculated as the proportion of eggs that were still found on the yarn on the last day before larvae were observed. Egg survival was then analyzed using a nested ANOVA (SAS 9.2) to test for lake-type effects (hypoxic vs normoxic), treatment type (open, coarse-mesh, fine-mesh), and interactions. In additon to monitoring egg survival, we monitored the feeding habits of local fishes. Fish were collected from carp spawning sites in one of the normoxic lakes using an electrofishing boat and their stomach contents examined for carp eggs using gastric lavage. Finally, each lake was surveyed for YOY carp in late summer to confirm that the egg predation we observed could explain the presence or absence of YOY carp.

Results

Study 1

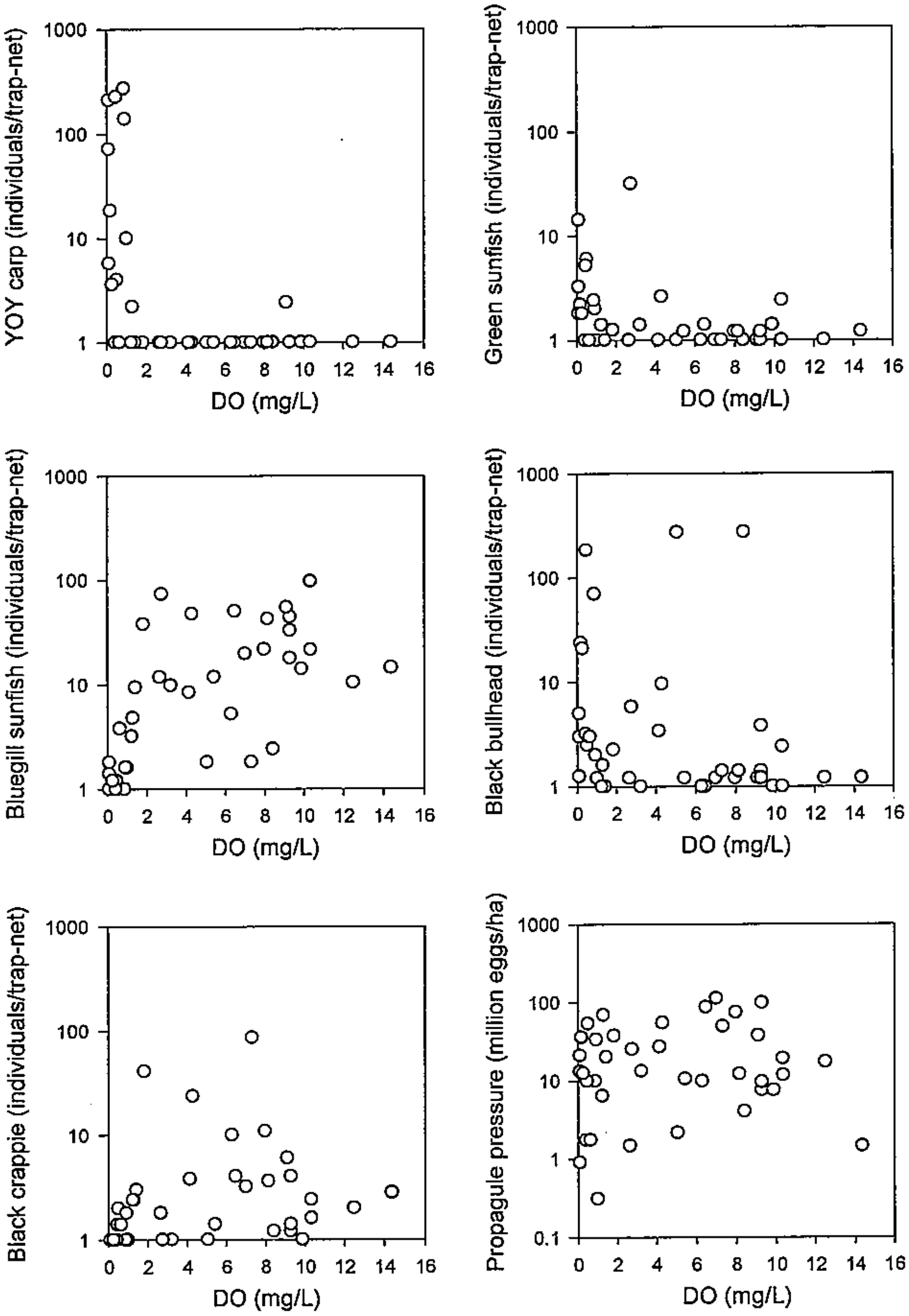
Winter DO appeared to have a strong influence on both YOY carp and native fish; with one exception, YOY carp were found only in lakes in which winter DO fell below * 1.5 mg/L (Fig. 2). The opposite trend was observed for bluegill sunfish, the dominant native species; while bluegill sunfish comprised 65 % of the median fish catch in lakes with oxygen levels [1.5 mg/L they were largely absent from lakes with DO\ 1.5 mg/L (6 % of median catch) (Fig. 2). As a result, a strong reciprocal relationship was observed between bluegill sunfish and YOY carp (Fig. 3). Other species of native fish were captured in lower abundance (typically\ 10 per trap-net); black crappie tended to be absent in lakes with DO\ 1.5 mg/L while green sunfish tended to be more abundant in those systems (Fig. 2). Overall, the median number of native fish was 2.5 times higher in lakes with DO[1.5 mg/L. Propagule pressure varied between 10 and 100 million eggs per ha (Fig. 2) but there was no clear evidence that carp recruitment was attributable to higher propagule pressure (Fig. 3).

The AIC model selection analysis indicated that five logistic regression models had relatively strong support (DAIC\ 2.0) and all of these included bluegill sunfish (Table 3). In contrast, all models that excluded bluegill sunfish had very little support (DAIC[6.3; w_i\ 0.02). The simple model that included bluegill sunfish as the sole predictor variable was able to correctly classify 87 % of all recruitment events (Table 3). The model that fit best included bluegill sunfish and green sunfish and indicated that carp recruitment was negatively related to bluegill sunfish and positively related to green sunfish, both of which were attributable to the effect of winter hypoxia on native fish. This model correctly classified 91 % of all recruitment events (Table 3).

Study 2

While 47 % of unprotected eggs survived to hatching in hypoxic lakes, only 0.8 % of unprotected eggs survived in normoxic lakes and over 90 % of these disappeared within the first 24-h (Fig. 3, P\ 0.05). In contrast, nearly 70 % of the eggs placed into either fine-mesh or coarse-mesh bags survived to hatching (4 days) in both the hypoxic and normoxic lakes (Fig. 4). Nested ANOVA showed that survivorship was highest among eggs placed in coarse or fine mesh bags, followed by unprotected eggs in hypoxic lakes, followed by unprotected lakes in normoxic lakes (Fig. 4). Carp larvae were observed in the fine-mesh bags after 4 days and we estimated that no more than 5 % of eggs fell off the yarn. Electrofishing surveys of carp spawning habitats in the normoxic lake captured 74 native fish including 45 bluegill sunfish. Thirty five of the bluegills were large enough for their diets to be examined and 29 of these had carp eggs in their

Fig. 2 Trap-net catch rates of young-of-the-year (YOY) carp, trap-net catch rates of native fish species, and propagule pressure versus winter dissolved oxygen minima in the study lakes. All *Y* axis variables, except for propagule pressure, were log ? 1 transformed



stomachs (on average 71 eggs per bluegill). We also captured 8 yellow perch of which 6 were found to have consumed carp eggs (an average of 118 eggs per fish). Late summer trap-net surveys caught an average of 3.0 (SE = 1.58) and 4.75 (SE = 2.86) YOY carp per trap-net in both of the hypoxic lakes, but no YOY carp were sampled in the two normoxic lakes.

Discussion

Although it has been previously demonstrated that native predators can control invasive invertebrates and amphibians (Hill and Lodge 1999; deRivera et al. 2005; Ward-Fear et al. 2010), our study appears to provide the first direct evidence for a fish. Using both

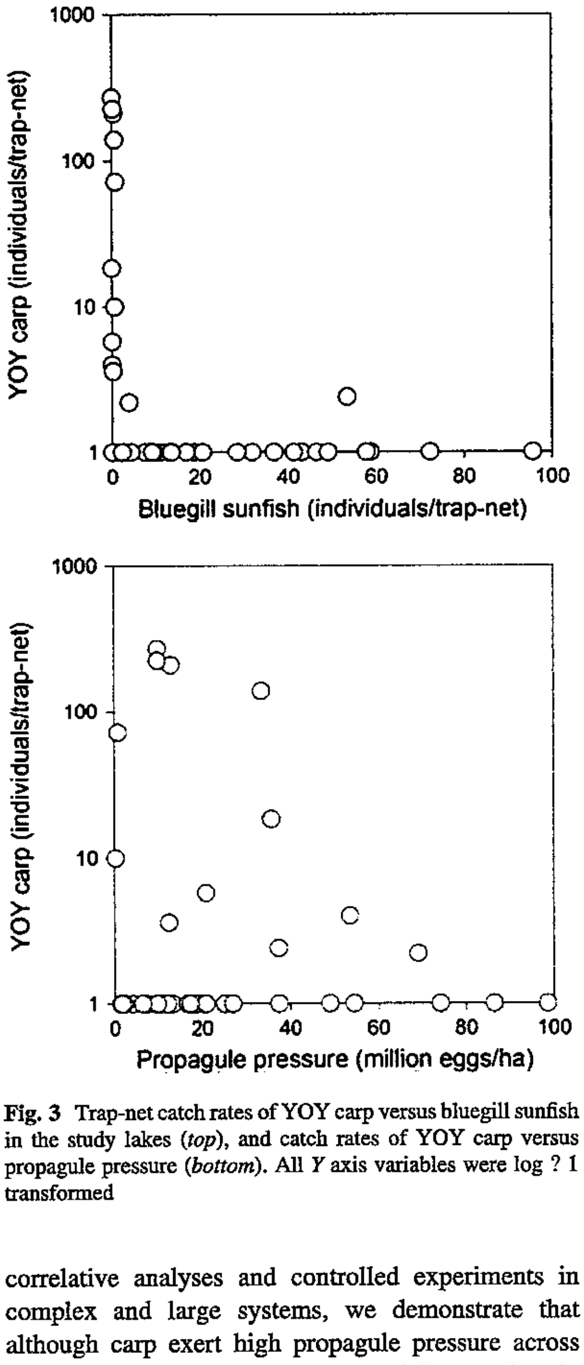


Fig. 3 Trap-net catch rates of YOY carp versus bluegill sunfish in the study lakes (*top*), and catch rates of YOY carp versus propagule pressure (*bottom*). All *Y* axis variables were log ? 1 transformed

correlative analyses and controlled experiments in complex and large systems, we demonstrate that although carp exert high propagule pressure across wide range of habitats, they successfully recruit only in lakes that experience severe instability events (in this case winterkills). This appears to be caused by reduced densities of native predators, and bluegill sunfish in particular, in winterkill lakes. Seemingly, the inability of carp to recruit in more stable and predator-rich communities is attributable to the fact that bluegill sunfish (and possibly also other native fish) exert very high predatory pressure on carp eggs. This scenario appears to explain the invasiveness of carp in large portions of the Upper Mississippi River Basin and possibly other regions, such as the Murray Darling Basin (Australia) that are also characterized by expansive and highly interconnected watersheds which have seasonal extremes such as floods, droughts and summer hypoxia, and likely extreme spatial variation in predator abundance (King et al. 2003). We speculate that the carp evolved to grow large and migrate into outlying shallow floodplains of the Ponto-Caspian region to escape predation by cyprinids native to this region whose proclivity for carp eggs has already been noted (Koblitskaya 1977; Barus et al. 2001).

Although we have not examined the effects of all native predators on all developmental stages of carp, our data strongly suggest that predation by native fish, and bluegill sunfish in particular, on carp eggs largely explains the invasiveness of carp in the Upper Mississippi River Basin. Bluegills are typically very abundant in this region, specialize in foraging on small prey in vegetated habitats (Keenleyside 1972; Werner and Hall 1974), and have been previously shown to be voracious egg predators (Gross and MacMillan 1981). We do not propose that bluegills necessarily consume all carp eggs, but rather that the extremely high predatory pressure they typically exert on eggs allows other sympatric predators to control the remaining eggs, larvae and fry. Laboratory experiments also show that bluegills are very effective predators on larval carp (Silbernagel 2011). The specific role of bluegill sunfish versus other native predators in controlling the survival of carp eggs and larvae needs to be further addressed. However, while sympatric predators (including larger piscivores) may have additive effects, the strong reciprocal relationship between bluegill sunfish and YOY carp in our study lakes and the results of model selection analysis suggest that the bluegill sunfish is the keystone element of biotic resistance in lakes of the Upper Mississippi region. This hypothesis is also supported by our carp aging studies (Bajer and Sorensen 2010). Interestingly, bluegill sunfish have also been shown to play a role in controlling the early life stages of the invasive rusty crayfish (*Orconectis rusticus*) (Roth et al. 2007).

As demonstrated by this study, explaining invasiveness of fish in specific locales may often not be

Table 3 Results of the logistic regression model selection analysis

Variables in the model	AIC	DAIC	w_i	% Concordant
BGS, GSF	45.36	0	0.19	90.1
BGS, BCP, GSF	46.21	0.85	0.12	91.1
BGS, BCP	46.25	0.89	0.12	87.1
BGS	46.40	1.03	0.11	87.1
BGS, PCP, Propagule	46.84	1.48	0.09	91.1
Best model without BGS as a predictor variable				
BCP, GSF	51.75	6.39	0.02	77.7

Predictor variables are: bluegill sunfish (BGS), black crappie (BCP), green sunfish (GSF), and propagule pressure (Propagule). The five best models (DAIC \ 2.0) among a total of 28 possible models are shown along with the best model that did not include bluegill sunfish as a predictor variable. Percent concordant shows the percentage of carp recruitment events correctly classified by each model. Each model was fitted using the same 42 data points (different combinations of lakes and years)

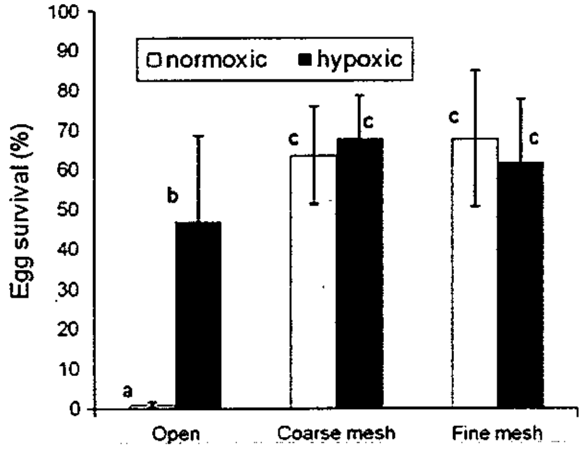


Fig. 4 Number of carp eggs that survived to hatching in normoxic and hypoxic lakes. Eggs were subjected to one of three treatments: (1) eggs placed into open water within carp spawning areas without any protection, (2) eggs placed into coarse-mesh bags that excluded fish, (3) eggs placed into fine-mesh bags that excluded both fish and invertebrates. Vertical bars represent standard deviation. *Letters* indicate statistical differences (nested ANOVA; $p = 0.05$)

possible without considering specific life history requirements and behaviors exhibited by invaders in local habitats (Korsu et al. 2007). Key to the success of the carp is its propensity to move into shallow unstable areas to spawn (King et al. 2003; Bajer and Sorensen 2010). However, this strategy may only be effective in ecosystems where unstable nurseries that lack predators are at least periodically connected with stable overwintering/foraging habitats. Adaptations of native predators to instability events in shallow waters may also help explain the success of carp in different areas of the world. In our study region, the success of carp appears to be explained by high sensitivity of the dominant egg predators to hypoxia. On the other hand, the fact that carp are typically not invasive in large tropical rivers in which summer hypoxia commonly occurs, may be explained by unique adaptations of native species in these systems to survive hypoxia (Welcomme 1995; Chippari-Gomes et al. 2005). Notably, although hypoxia has previously been shown to play a major role in structuring native fish assemblages in North America (Tonn and Magnuson 1982; Rahel 1984; Tonn et al. 1990), it seemingly has not been considered as an explanation for the success of invasive fishes.

Many of the world's most invasive fish are mobile and complete their life cycles over large areas using specialized nursery habitats. Of special interest are the silver (*Hypophthalmichthys molitrix*) and bighead carp (*H. nobilis*), which invaded the Mississippi River Basin and now threaten the Laurentian Great Lakes. These species employ long upstream migrations to spawn in open river habitat during spring floods, and their larvae drift into backwater flooded habitats located up to 200 km downstream (Lohmeyer and Garvey 2009). Flooded backwaters would be expected to have fewer predators. Another example is the northern pike, which is highly invasive in western North America and has a life history similar to that of the common carp as it also migrates to shallow peripheral regions to spawn after winterkill (Koed et al. 2006). Similarly, invasive salmonids and land-locked sea lamprey migrate into shallow streams to spawn (Potter 1980). Whether these behaviors function to protect their young from predators has not been explicitly studied, although it has been suggested for the lamprey (Potter 1980). Our study shows that this possibility needs to be examined to explain invasiveness of these fish in different regions of the world.

Propagule pressure has been shown to play an important role in explaining biological invasions in terrestrial and marine ecosystems. In these ecosystems it has been shown that high propagule pressure can overwhelm even highly resistant communities (Von Holle and Simberloff 2005; Hollebone and Hay 2007). Although our study was not designed to explicitly test this hypothesis, observed trends and logistic regression analysis suggest that propagule pressure plays only a relatively minor role in explaining the recruitment of carp (also see Bajer and Sorensen 2010). Alternative explanations for the lack of carp recruitment in normoxic systems are not apparent as lake productivity (total phosphorus) and habitat characteristics (water clarity and vegetation density) changed little from year to year in our systems, and YOY carp were only present following hypoxic events. Lakes that had YOY carp also typically had high densities of YOY of native species suggesting that competition for planktonic food plays a relatively minor role in the survival of YOY carp. In fact, a post hoc analysis showed that the densities of YOY of native fish species were, on average, 3.5 times higher in hypoxic lakes (*t* test; $P\backslash$ 0.001). Low abundance of YOYs of native fish in normoxic lakes further suggests that extremely high predation rates on fish eggs and larvae exist in these ecosystems.

Finally, this study suggests new and sustainable paths to control the common carp, which to date have been controlled using nonspecific toxins, barriers and water draw-downs (Marking 1992; Wiley 2008). While poisons, barriers and drawdowns may on occasion provide short-term improvements in carp numbers and water quality, they may also reduce biotic resistance and enhance the need for continuing intensive management. The present study suggests that the common carp, and possibly other invaders that employ similar life histories, could instead be controlled using approaches that strengthen native fish communities.

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Appendix G

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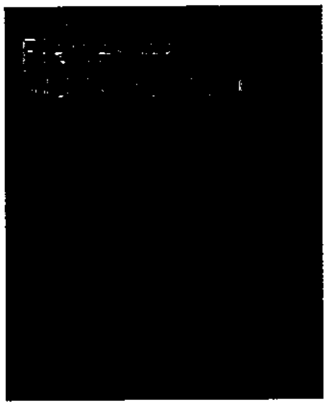

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Using Boat Electrofishing to Estimate the Abundance of Invasive Common Carp in Small Midwestern Lakes

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MANAGEMENT BRIEF

Using Boat Electrofishing to Estimate the Abundance of Invasive Common Carp in Small Midwestern Lakes

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Abstract

The common carp *Cyprinus carpio* is among the most invasive fish worldwide, but practical methods for estimating its abundance have not yet been developed. Particularly needed are methods that can accurately assess low densities of common carp to enact proactive management strategies before populations reach damaging levels. In this study we tested whether the density of adult common carp in small Minnesota lakes could be accurately predicted from their catch rates using boat electrofishing. We used mark and recapture to estimate the abundance of common carp in eight Midwestern lakes with a wide range of common carp densities (13–400 carp/ha), while also surveying each lake using boat electrofishing. In addition, we reduced common carp abundance by up to 90% in two lakes to test whether this was accompanied by a similar drop in electrofishing catch rates. A regression analysis showed that electrofishing catch rates increased linearly with increasing densities of common carp. A cross-validation procedure showed that boat electrofishing can accurately estimate common carp densities; however, we observed a tendency to overestimate low densities and underestimate high densities. Our results suggest that electrofishing surveys can be routinely employed to estimate common carp densities in small lakes.

Common carp *Cyprinus carpio* is among the most widespread and damaging invasive fish worldwide (Weber and Brown 2009), but practical methods for assessing its abundance have not been developed. Native to the Ponto-Caspian region, the carp is particularly damaging in temperate regions of North America and Australia (Lougheed et al. 1998; Parkos III et al. 2003; Koehn 2004; Lougheed et al. 2004; Schrage and Downing 2004; Bajer et al. 2009). Because introductions of carp have been associated with dramatic declines in vegetation, water quality, and native fauna (Haas et al. 2007; Kloskowski 2011), this species has been aggressively managed using toxins, barriers, and mechanical removal (Marking 1992; Schrage and Downing 2004; Bajer et al. 2009). However, carp management has largely been reactive, usually being conducted only after ecological damage has already been done. A proactive management approach in which the biomass of carp is suppressed before it reaches an ecologically damaging threshold would be useful. Such an approach may be practical in some regions because thresholds for damage have recently been developed (Bajer et al. 2009) and selective means to remove adult biomass also now exist (Bajer et al. 2010, 2011). However, for this combination of strategies to be practical, methods to accurately assess carp abundance are needed. Having the ability to accurately and rapidly estimate carp abundance would also aid studies of the invasiveness of carp and its ecological impacts (Kulhanek et al. 2011).

Although the densities of common carp can be estimated using mark-and-recapture approaches (Bajer and Sorensen 2010; Bajer et al. 2011), these methods require substantial effort and cannot be easily employed in large numbers of lakes. Alternatively, carp densities could also be estimated using catch-per-unit-effort (CPUE) data collected from common survey techniques such as trap nets, gill nets, and boat electrofishing. However, while age-0 carp appear to be captured relatively easily using these techniques (Barko et al. 2006; Phelps et al. 2008; Bajer et al., in press), older carp appear to be more "gear-shy" to passive capture techniques, especially trap nets (Clark et al. 1991). A study of common carp catchability by a boat electrofisher in enclosures and ponds showed that although catch rates were influenced by fish size and habitat characteristics, carp are relatively vulnerable to electrofishing (Bayley and Austen 2002), suggesting that this technique might also be effective in natural systems.

In this study we tested whether densities of adult common carp in small lakes can be accurately predicted from boat electrofishing catch rates. This was accomplished by estimating the abundance of carp using mark-and-recapture techniques in eight lakes having a wide range of carp densities, while sampling each lake on several occasions with a boat electrofisher to estimate

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TABLE 1. Sampling protocols and common carp population estimates in study lakes; lake size and maximum depth, mark-and-recapture type (simple, S; multiple, MT), sampling used to conduct mark and recapture (SS, summer seining; WS, winter seining; EF, electrofishing; BT, baited trap; numbers indicate how many samples were collected), numbers of marked (M) and recaptured (R) carp, carp population estimate (*N*); carp length, density, and biomass; and electrofishing CPUE (carp/h). Carp abundances in Lake Susan in 2009 and Lake Riley in 2010 were reduced (see Methods for details).

	Lake characteristics			Mark-and-recapture techniques				Estimated carp population and characteristics				
Name	Year sampled	Size (ha)	Depth (m)	Type	Sampling	M	R	*N*, mean (95% CI)	Length, mean (SD) (mm)	Density mean (carp/ha)	Biomass mean (kg/ha)	CPUE, mean (SE)
Echo	2006	33.2	3.0	MT	2SS, 4EF	726	37	6,213 (4,891–8,516)	521 (76)	187.1	326.8	32 (28.90)
Dutch	2006	64.4	6.3	MT	3SS, 4EF	1,444	66	15,550 (12,528–20,495)	524 (83)	241.5	494.81	64.4 (38.61)
Dog	2007	38.4	7.5	MT	4EF, 1SS	59	3	514 (263–1,022)	699 (51)	13.4	69.6	2.98 (4.30)
Susan	2008	35.1	5.1	S	1SS, 1WS	101	79	4,181 (3,292–5,069)	598 (67)	119.1	307.1	17.26 (9.28)
	2009	35.1	5.1	S	Reduced			756	609 (139)	21.5	64.5	8.52 (0.52)
Riley	2009	118.8	14.7	S	1WS, 1WS	600	462	6,419 (6,132–6,706)	585 (74)	54.0	176.1	12.16 (9.55)
	2010	118.8	14.7	S	Reduced			3,025	612 (84)	25.6	90.0	4.66 (2.82)
Lucy	2010	34.6	6.0	S	1WS, 1WS	642	282	808 (768–851)	670 (116)	23.3	69.8	8.15 (5.22)
Gervais	2010	152.0	5.8	S	1WS, 1WS	1,035	200	9,864 (8,538–11,144)	622 (52)	64.9	145.9	11.03 (6.85)
Staring	2011	65.7	4.8	S	1BT, 1WS	331	71	26,228 (20,938–31,472)	444 (69)	399.3	489.3	58.54 (11.85)

CPUEs. In addition, carp densities in two lakes were experimentally manipulated to test whether CPUEs would decline in a predictable manner. Our results have implications for basic and applied studies of carp in lake ecosystems.

STUDY LAKES

We conducted this study in eight lakes in the upper Mississippi River basin (south-central Minnesota) in which common carp populations have been studied over the past several years (Bajer and Sorensen 2010; Bajer et al. 2010, 2011; Table 1). These systems, which range in size from 33 to 152 ha, have maximum depths of 3–15 m and water conductivities between 300 and 600 µS/cm (Table 1), typical of small lakes in this region (Downing et al. 2006). The bottom substrate in these lakes varies from sandy to soft, and vegetative coverage and water clarity vary from relatively high in lakes with carp density below 100 kg/ha to extremely low in lakes with higher biomasses of carp (P. G. Bajer, unpublished data).

METHODS

Estimating common carp abundance.—We estimated the population abundance of common carp in all study lakes using either multiple or simple mark-and-recapture analyses in which we employed summer seining (400-m-long net with 35-mm-bar mesh-size pulled across obstacle-free areas; Bajer and Sorensen 2010), telemetry-guided winter seining (400-m-long net with 35-mm-bar mesh-size that targeted under-ice carp aggregations; Bajer et al. 2011), baited traps (20 m × 20 m box trap baited with corn), and boat electrofishing (described in detail below; Table 1). Estimates for five of our study lakes (Lakes Echo, Susan, Riley, Lucy, and Gervais) were recently published (Bajer and Sorensen 2010; Bajer et al. 2011), but were revised for the purpose of this analysis to achieve statistical independence between population estimates and CPUE estimates. Specifically, in Lake Echo, in which the population had previously been estimated using both summer seining and boat electrofishing (Bajer and Sorensen 2010), four electrofishing surveys were randomly excluded and used exclusively to calculate CPUEs in this study. In Lakes Susan, Riley, Lucy, and Gervais, in which carp populations had previously been estimated using a combination of winter seining and boat electrofishing, population estimates are now revised by excluding all summertime electrofishing surveys (now used to calculate CPUEs) and incorporating new winter seining data. Estimates for Lakes Dog, Dutch, and Staring have not been previously reported. Sampling methodologies employed in each lake are presented in Table 1 and described in detail in the following paragraphs.

In Lakes Echo, Dutch, and Dog, we estimated common carp populations using a multiple mark-and-recapture approach that involved repeated summer seinings and boat electrofishing surveys (Table 1). All carp captured on each sampling occasion were counted, measured, tagged with an individually numbered plastic tag (model TBA-1; Hallprint, Australia), fin clipped to take into account possible tag loss, and released. All carp were also examined for marks from previous surveys. These data were then used to calculate the mean and 95% confidence interval (CI; 1.96 · SE) of carp population in each lake using Schnabel's equations (Ricker 1975). We sought to randomize spatial distribution of marked individuals by seining in two different areas of each lake and electrofishing along at least 50% of the shoreline. All sampling was conducted during a relatively narrow time window (3 months) to minimize the effects of mortality rates on population estimates. In cases where the lakes were connected with other water bodies (Lake Echo), these connections were blocked with a metal grate to prevent immigration and emigration (Bajer and Sorensen 2010).

Common carp populations in Lakes Susan, Riley, Lucy, Staring, and Gervais were estimated using simple mark-and-recapture approaches (Table 1). We accomplished this in Lakes Susan and Staring by employing open-water seining or baited traps, respectively, to mark and release carp, and conducted winter seining approximately 3 months later to estimate recapture rates. In Lakes Riley, Lucy, and Gervais, we employed two winter seinings: carp caught in the first seining were marked and released, and recapture rates were determined a year later when the second seining was conducted. The adjusted Petersen's formula was used to calculate mean population estimates and 95% CIs (Ricker 1975). To randomize distribution of marked individuals within the population, we seined when carp from different areas aggregated in common locations (Bajer et al. 2011). We blocked the inlets and/or outlets of Lakes Susan, Riley, Lucy, and Gervais with horizontal PVC pipes spaced every 20 mm (Lake Staring had a natural barrier at the outflow) to minimize carp immigration and emigration; to verify that no recruitment occurred throughout the study, we surveyed each lake for age-0 carp using small-mesh trap nets (Bajer et al., in press). In addition to calculating initial population estimates, we reduced populations in Lakes Susan and Riley by removing carp caught in the second winter seining (Table 1). We included these data in this analysis because we were particularly interested in whether electrofishing could predict low carp densities in lakes and because we wanted to verify, to some extent, that our population estimates were unbiased; i.e., unexpectedly low postremoval electrofishing CPUEs would indicate that marked carp avoided second capture and that our initial population estimates were inflated (Beukema and de Vos 1974). The postremoval estimates were adjusted for mortality rates estimated from the survival of radiotagged carp by using Mayfield's equation (Winterstein et al. 2001); of 25 and 15 radiotagged carp present in Lakes Susan and Riley, respectively, 3 in each lake perished during the study, which suggested finite annual mortality rates of 14% and 17%, respectively.

Estimating electrofishing CPUEs.—In each study lake, three to four electrofishing surveys (each on separate dates) were conducted to calculate mean CPUE values. All surveys were conducted between August and October when water temperature ranged between approximately 25°C and 15°C, respectively, and common carp were relatively evenly dispersed throughout the lakes (Bajer et al. 2010, 2011). In Lakes Echo, Dutch, and Dog, electrofishing surveys were conducted concurrently with mark–recapture sampling. In Lakes Susan, Riley, Gervais, Lucy, and Staring, electrofishing surveys were conducted during the summer/fall between the winter seinings and additionally after the second seining in Lakes Susan and Riley to calculate the postremoval estimates. The same protocols were followed in each lake. Each electrofishing survey consisted of three transects lasting approximately 20 min each. These transects were conducted in three different areas of each lake and collectively covered 50% to 100% of the shoreline. Surveys were confined to the littoral zone because carp could not be effectively captured in waters deeper than approximately 1.5 m. We used a 5.4-m-long flat-bottom aluminum boat (Midwest Lake Management, Missouri) 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, each consisting of five stainless steel pipes 25 mm in diameter and 260 mm long. The anodes were located approximately 3 m in front of the boat and spaced 1.5 m apart. Only 10–20 cm of the electrodes was submersed in the water during electrofishing. The boat was maneuvered at a slow speed (~0.5 to 1 m/s) in a zigzagging fashion along the shore while two netters collected stunned carp and placed them in a live well. Although habitat characteristics differed among study lakes, we aimed at standardizing our surveys by maximizing carp catch rates within each transect. To do this, we briefly increased boat speed to capture carp that were observed escaping in front of the boat, electrofished around downed trees that carp were using for shelter, and made an additional pass through vegetation patches if we observed signs of carp (movement of vegetation) after the first pass. For each transect, electrofishing time was recorded and CPUE (carp/ha) calculated. Catch-per-unit-effort values were then averaged among transects and among sampling dates in each lake.

Statistical analyses.—To analyze the data, we calculated common carp density in each lake by dividing the population estimate by the lake area and developed a linear regression between carp density and mean electrofishing CPUE in each lake. To cross-validate this relationship, we used the "leave-one-out" approach. A single data point (lake) was removed from the data set and the regression was re-fitted and used to predict the density of carp in that lake by using the CPUE value. This was repeated for all study lakes and resulted in two sets of carp densities: those predicted with the regression analysis and those estimated with mark and recapture for each study lake. The predicted densities were regressed against those estimated by mark and recapture, and the 95% CIs for the intercept and slope estimates were calculated to determining whether they overlapped with zero and one, respectively. All analytical procedures were conducted in SAS 9.2 (SAS Institute, Cary, North Carolina).

RESULTS

Common carp populations in the study lakes ranged from approximately 500 to 26,000 individuals, or 13 to 400 carp/ha, and were mainly comprised of individuals that were 400 to 700 mm in length (Table 1; Figure 1A). Electrofishing CPUEs increased linearly with increasing carp densities ($r^2 = 0.83$; $P < 0.001$) and a particularly good fit occurred at densities below 200 carp/ha (Figure 1A). Postremoval CPUEs for Lakes Susan and Riley clustered tightly with the other data, suggesting that our population estimates were unbiased (Figure 1A). Cross validation demonstrated that carp densities in lakes can be reasonably accurately predicted from electrofishing CPUEs (Figure 1B) as

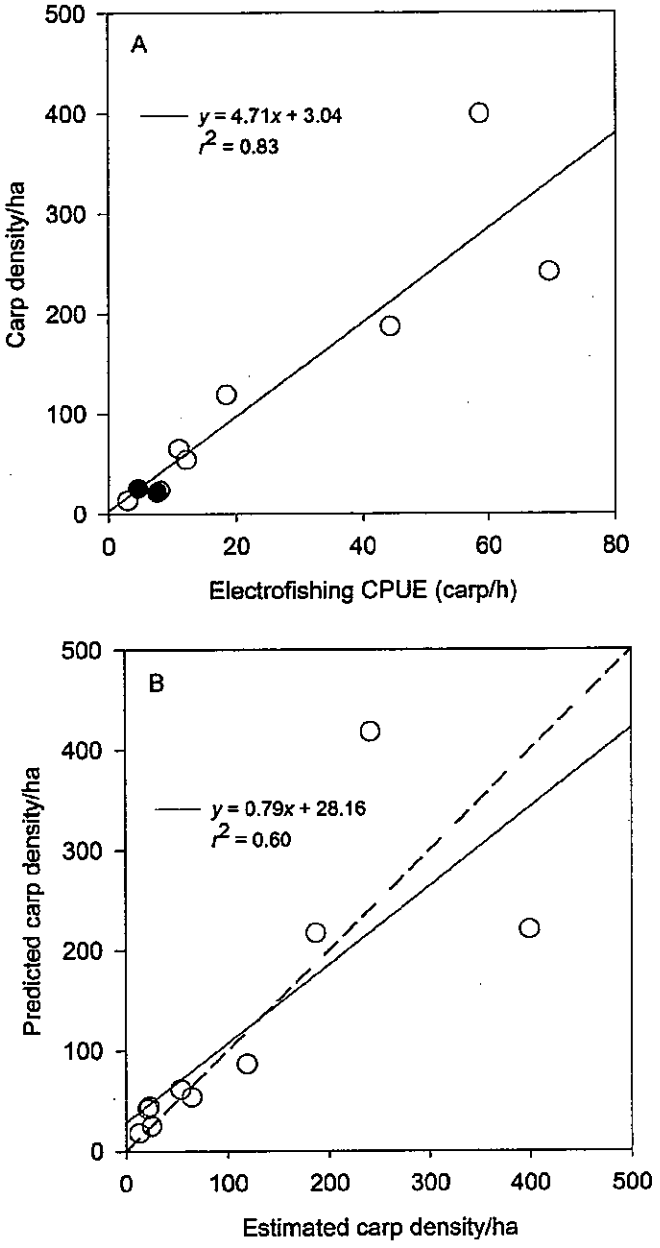

FIGURE 1. (A) Linear regression between common carp densities estimated using mark-and-recapture approaches and electrofishing CPUE values in study lakes. The regression line was fitted to all data; shaded circles indicate postremoval estimates in Lakes Susan and Riley. (B) Relationship between common carp densities predicted using electrofishing CPUE values and those estimated using mark-and-recapture approaches in study lakes. Predicted densities were calculated using model cross-validation approach. The dashed line is a 1:1 reference line and the solid line is a regression line fitted to the data.

the slope (0.73 ± 0.43 [mean ± SE]) and intercept (22 ± 73.3) of the regression between carp densities predicted from CPUEs and those estimated by using mark and recapture were not significantly different from one and zero ($P > 0.05$), respectively (Figure 1B). However, a slight bias toward overestimating low carp densities and underestimating high densities was observed (Figure 1B).

DISCUSSION

This study demonstrates that densities of adult common carp in small Midwestern lakes can be predicted from boat electrofishing catch rates. This technique appears to be especially accurate at low and moderate densities, which is particularly desirable when developing proactive management schemes. The relationship between electrofishing CPUE and carp density we present should aid lake managers in assessing carp abundance and determining if and how many carp need to be removed from ecosystems to prevent excessive biomass build-up and ecological damage (Bajer et al. 2009). This management tool may be particularly effective in conjunction with targeting winter aggregations of carp by using the "Judas" technique (Johnsen and Hasler 1977; Penne and Pierce 2008), which employs radiotelemetry to locate carp aggregations and which can be highly selective and efficient (Bajer et al. 2011). Ecological studies of carp abundance, distribution, niche requirements, invasiveness, and ecological damage also require practical and accurate tools for assessing their abundance (Egertson and Downing 2004; Barko et al. 2006; Zambrano et al. 2006; Jackson et al. 2010; Weber et al. 2010; Kulhanek et al. 2011) and may benefit from incorporating electrofishing surveys as standard survey methods.

Electrofishing catch rates of fish have been shown to be influenced by seasonal patterns and habitat conditions (McInerny and Cross 2000; Bayley and Austen 2002). Seasonal effects were minimized in this study by sampling during late summer and fall, when common carp were not spawning and were relatively uniformly distributed in lakes (Penne and Pierce 2008; Bajer et al. 2010), but the effect of habitat was not controlled. Bayley and Austen (2002) suggested that common carp electrofishing catch rates decline with increasing lake size and increasing vegetation density. The relationship between estimated carp densities and electrofishing CPUE presented in this study was surprisingly tight despite the fact that lakes varied both in size and vegetative cover (> 60% in Lakes Lucy and Dog to < 10% in Lakes Susan, Echo, and Staring; P. G. Bajer, unpublished data). The fact that habitat conditions had only a relatively minor effect on capture rates in our study lakes might be attributable to our sampling approach in which we aimed at maximizing common carp catch rates within each transect by targeting visible signs of their presence. This more aggressive sampling strategy probably reduced the effect of habitat complexity on catch rates. Also, although detailed, the study of Bayley and Austen (2002) was conducted in relatively small enclosed areas (0.1 to 5 ha) and may not be directly comparable with our study.

The effects of learning and gear avoidance on common carp mark-and-recapture experiments have not been studied in detail, but a pond study in which carp were repeatedly (multiple times per day) sampled with a seine suggested that carp can learn how to avoid repeatedly used gear, thus leading to biased population estimates (Beukema and de Vos 1974). Several pieces of evidence suggest that the single-gear mark-and-recapture population estimates we conducted in some of the study lakes were accurate. First, estimates generated by using either single or multiple gears clustered together and could be equally well predicted from observed CPUEs. Second, single-gear population estimates for Lakes Riley and Lucy reported in this study differ only slightly (3–15%) from those previously published for use of multiple-gear types (Bajer and Sorensen 2010; Bajer et al. 2011). Third, postremoval CPUEs in Lakes Riley and Susan, which declined in a predictable manner, suggested that the initial population estimates in those lakes were unbiased.

While our study shows that boat electrofishing is sensitive and accurate enough to estimate even low densities of common carp in lakes, the applicability of this technique to other geographic regions and ecosystem types needs to be examined. In particular, our study systems did not include large lakes, shallow marshes, or rivers, and so our regression relationship should be applied with caution in those systems. Independent tests of our regression relationship are especially important because the small sample size precluded thorough cross-validation analyses. Our sampling protocols should also be mimicked to reduce bias. Nonetheless, given the current lack of practical tools for assessing carp densities in lakes, the relationship presented in this study should be useful in many ecosystems in which the carp are currently excessively abundant and damaging, especially when mark and recapture is not practical or feasible. The regression relationship presented in this paper would be also useful in regional studies in which it is necessary to rapidly obtain estimates of carp abundance in a large numbers of lakes (e.g., Egertson and Downing 2004; Jackson et al. 2010).

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