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Effects of a rapidly increasing population of common carp on vegetative cover and waterfowl in a recently restored Midwestern shallow lake

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Abstract Although the common carp (*Cyprinus carpio*), an invasive benthic fish from Eurasia, has long been strongly implicated in the disappearance of vegetative cover and reduced waterfowl abundance in North American shallow lakes, the details of this relationship are obscure. This study documented ecological changes in a recently restored shallow lake (Hennepin and Hopper Lakes, IL, USA) at a time that it was experiencing a large increase in its carp population. We estimated the abundance and biomass of carp 7 years after this lake had been restored and then back-calculated carp population size across time while examining changes in the lake's plant and waterfowl communities. We found that the biomass of carp remained below ~30 kg/ha for 5 years following restoration, but then increased to ~100 kg/ha in the sixth year following a strong recruitment event. Although a carp biomass of <30 kg/ha had no discernible effects on vegetative cover (which exceeded 90%) or waterfowl (which exceeded 150,000 individuals during fall censuses), the increase to 100 kg/ha was associated with a ~50% decrease in both vegetative cover and waterfowl. A further increase in carp biomass to over 250 kg/ha during the seventh year coincided with a decrease in the vegetative cover to 17% of the lake's surface and a decline in waterfowl use to ~10% of its original value. These data suggest that the common carp is extremely damaging to the ecological integrity of shallow lakes when its density exceeds ~100 kg/ha. Since the biomass of carp in Midwestern shallow lakes commonly exceeds this value by 3–4 times, it seems likely that carp are responsible for the large-scale habitat deterioration described in many of these ecosystems.

Keywords *Cyprinus carpio* · Biological invasion · Macrophytes · Ducks · Rotenone

Introduction

The common carp (*Cyprinus carpio*), a large cyprinid fish native to the Caspian Sea region, was introduced to North America in the late 1870s (Balon, 1995). Since then, it has spread widely and has currently reached very high densities in many regions in both the northern and southern hemispheres (Neess et al., 1957; Crivelli, 1983; Koehn, 2004; Schrage & Downing, 2004). Adult common carp (hereafter

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called ‘carp’) are benthivorous, and their foraging activity is commonly associated with uprooted aquatic vegetation and increased turbidity (Crivelli, 1983; Lougheed et al., 1998; Zambrano et al., 2001). Although many reports from the Midwestern region of North America have shown that shallow lakes with abundant carp have sparse aquatic macrophyte communities (Cahn, 1929; Cahoon, 1953; Verrill & Berry, 1995; Schrage & Downing, 2004) and attract few waterfowl (Bouffard & Hanson, 1997; Haas et al., 2007), quantitative relationships between carp biomass, vegetative cover, and waterfowl abundance have not been well documented in whole-lake ecosystems. Specific information on how the effects of carp on vegetation translate within whole ecosystems across time and at various levels of biomass are needed to understand the dynamics of these systems and manage carp populations effectively.

A variety of pond and enclosure experiments have established that carp are damaging to aquatic macrophyte communities and can also negatively impact waterfowl (Robel, 1961; Crivelli, 1983; Drenner et al., 1998; Sidorkewicj et al., 1998; Parkos et al., 2003; Chumchal & Drenner, 2004; Chumchal et al., 2005; Haas et al., 2007). Typically, deleterious effects have been noted within a few weeks of carp addition at densities ranging between 100 and 200 kg/ha. However, these relatively small-scale studies may not fully portray responses in whole lakes where free-ranging carp exhibit seasonal patterns in foraging activity and distribution, and their impacts will be affected by local fishes, invertebrates, wind mixing, sediment stability, and nutrient loading (Scheffer et al., 1993; Hanson & Butler, 1994; Zambrano et al., 2001; Schrage & Downing, 2004). That carp can severely impact vegetation and waterfowl in whole lakes, whereas removal of these fish reverses this process, has already been demonstrated (Cahn, 1929; Verrill & Berry, 1995; Lougheed et al., 2004; Schrage & Downing, 2004), but the specific effects of varying levels of carp biomass have not been described in enough detail to develop management targets for carp control in shallow lakes.

Two approaches might be employed to address the relationship between carp biomass and shallow lake ecosystem integrity: replicated whole-lake studies or case studies that describe the impacts of carp in specific locales. The latter is more practical and was pursued here. This article provides a detailed description of an increasing biomass of common carp in a recently restored, relatively representative shallow lake and changes in vegetative cover and waterfowl use that occurred in this system. It provides some of the first data on the population dynamics of carp in a shallow lake and suggests a value at which carp biomass appears to cause severe ecological problems within such systems.

Materials and methods

Our study site: Hennepin and Hopper Lakes

This study was conducted in a relatively large (508 ha) and shallow (max depth 3.5 m) lake that is comprised of two conjoined basins, and is known as Hennepin and Hopper Lakes (HHL). This ecosystem is located within the historic floodplain of the Illinois River near Hennepin, IL, USA (Fig. 1), and is currently separated from the river and other bodies of water by an earthen dike and is fed by springs, seeps, and ground water infiltration. Water levels in HHL are presently controlled by outlet pumps that pump water to the Illinois River following a schedule

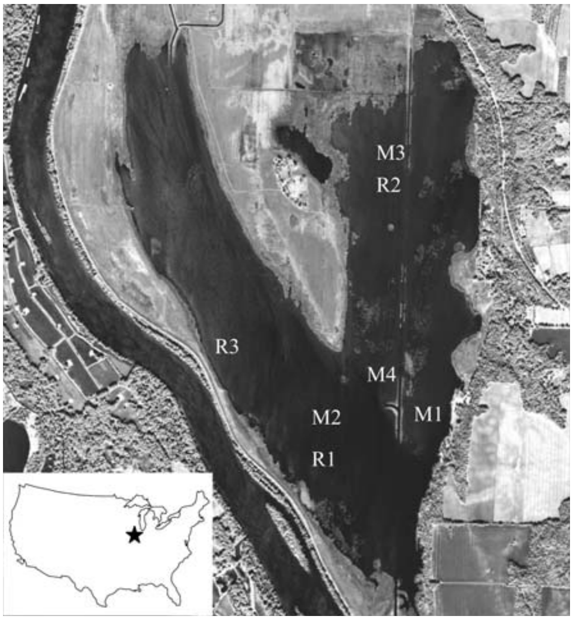

Fig. 1 Aerial photograph of the Hennepin and Hopper Lakes in 2007; M1–M4 are locations where carp were marked and released, while R1–R3 are locations where carp were recaptured

which mimics the historic hydrograph with moderate (<0.5 m) increases in each spring and declines in the late summer. Bottom substrate is composed of clay and silt with pockets of mud or sand found along nearly a quarter of the shoreline. Due to its shallow depth, HHL does not stratify in the summer. With respect to size, depth, bottom substrate, and productivity, HHL resembles over 40,000 ha of habitat in the Illinois River Valley (Havera & Bellrose, 1984; Stafford et al., 2007) as well as many other shallow lakes in the Midwest that have also seemingly been impacted by carp (Egertson & Downing, 2004; Schrage & Downing, 2004).

Historically, HHL served as an important nursery and foraging area for waterfowl migrating along the Mississippi Flyway until it was isolated from the river in 1912 and drained to serve as irrigated farmland (http://www.wetlands-initiative.org/HennHopper.html). Ninety years later, it was reclaimed. Lake restoration began in April 2001 when water in its irrigational channels was treated with rotenone to eradicate the numerous carp that inhabited these channels (Wayne Herndon, Illinois Department of Natural Resources [IL DNR], personal communication). Following successful rotenone application, the outlet pumps were shut off, and the water level was allowed to rise via groundwater seepage and precipitation to pre-settlement levels. Gillnet fish surveys conducted in September 2001 found no carp. However, seven carp were collected with gillnets in September 2002, indicating that a small number had survived rotenone treatment (Wayne Herndon; IL DNR, personal communication). Nevertheless, a relatively diverse native aquatic macrophyte community had become established by 2002, and by 2004, vegetative cover of the lake exceeded 90% and vegetation surveys commenced. In addition, during 2001 and 2002, HHL was stocked with over 2.8 million fry and 800 adult native fish including northern pike (*Esox lucius*), bluegill sunfish (*Lepomis macrochirus*), black crappie (*Pomoxis nigromaculatus*), walleye (*Sander vitreus*), largemouth bass (*Micropterus salmoides*), and channel catfish (*Ictalurus punctatus*). By 2004, fisheries surveys documented that the densities of these species had reached or surpassed densities commonly observed in healthy Midwestern shallow lakes (data reported herein). Numerous waterfowl were also observed in the lake, and HHL was included in routine state waterfowl surveys starting in 2003 (data reported herein).

In spite of these initially promising results, symptoms of vegetation and waterfowl decline were noted by 2005 at which time common carp were also noted in shallow areas (G. Sullivan, personal observation). By 2006, vegetation and waterfowl had declined further, and carp had become very noticeable. In 2007, the manager of the lake (The Wetlands Initiative) decided to support a formal survey of the abundance and age structure of the carp population. This article uses carp population data collected as part of this 2007 survey as well as aquatic plant surveys conducted by The Wetlands Initiative, waterfowl census data collected by the Illinois Natural History Survey, and fish community surveys conducted by the IL DNR to document changes that occurred in HHL and develop correlations between carp biomass, vegetative cover, and waterfowl.

Aquatic vegetation surveys

Starting in 2004, a stratified random sampling design was used to assess percent vegetative cover and species identity in HHL. In order to accomplish this, a grid was superimposed over satellite imagery of HHL, and one hundred 200 m × 200 m grid cells were randomly selected using spatial analyst extension in Arc GIS (ArcMap Version 9.2; Environmental Systems Research Institute, Redlands, California). Next, a single pair of x–y coordinates was randomly selected within each of these cells to determine 100 sampling locations. These locations were sampled once a year in September. Sites were accessed by wading, a 1-m^2 plastic frame (quadrat) was placed on the water surface, and the percent area within the frame that was covered by vegetation was visually estimated to the nearest 10%. Species present were also noted at that time. If the bottom could not be seen (an infrequent occurrence), vegetation was brought to the surface by hand or rake for identification and to estimate percent coverage. The overall percent vegetative coverage in the lake was calculated as an arithmetic mean across all quadrats.

Waterfowl surveys

Waterfowl abundance in HHL was estimated from aerial surveys conducted by the Illinois Natural History Survey (Steven Forbes Biological Station) between 2003 and 2007. Counts were conducted approximately every 10 days during September–December of each year (data available at: http://dnr.state.il.us/admin/systems/duckgeese/). The accuracy of these surveys was validated by ground counts (Stafford et al., 2007). All the surveys were performed by an experienced observer who flew over the lake at an altitude of 60–130 m at 161–241 km/h (for detailed methodology see Stafford et al., 2007). For each survey, two passes were completed. During each pass, the observer counted the number of individual dabbling ducks and diving ducks, identifying species based on the body size and coloration patterns. Since the number of censuses conducted each year varied between 9 and 15, we standardized the data by summing the nine highest waterfowl censuses per year to develop an index of waterfowl abundance (cumulative waterfowl count).

Abundance and age structure of the common carp population

The size of the carp population was estimated in the spring of 2007 using a mark-and-recapture approach that we have employed successfully for several years in similar lakes (Bajer & Sorensen, in press). During March 29–31, we performed four seine hauls using an 800-m seine net (mesh size 3.75 cm) to capture, mark, and release known numbers of carp in four different locations (Fig. 1). By marking and releasing carp in different locations, we sought to randomize the distribution of marked individuals within the lake, thereby increasing the quality of the population estimate (Ricker, 1975). Carp from each capture location received a location-specific mark (different color plastic Floy-tag or a unique fin clip). Following the marking period, the sampling was halted for 9 days to allow marked individuals to mix with the rest of the population. Five seine hauls were then conducted to recapture carp during April 9–13 in three different areas. One of these locations was seined three times because recaptures showed that carp were gathering there from all the release points, thus enhancing the accuracy of our census. Independent population estimates (N) were then generated for each seine haul from the number of marked carp in the population at large (M), the number of carp captured in each haul (C), and the number of carp recaptured in each haul (R) using Petersen's method: $N = (M \cdot C)/R$ (Van Den Avyle & Hayward, 1999). These independent estimates were then averaged to calculate a mean (±standard deviation) carp population estimate for HHL. The number of marked, censused, and recaptured carp was designed to satisfy the sample-size requirements for this technique as described by Ricker (1975, p. 80, Fig. 3.1).

The first 1,000 carp we collected were measured to determine the length structure of the population. In addition, 150 carp were weighed and frozen for aging analysis. At a later date, their asterisci otoliths were removed, cleaned in tap water, dried, embedded in epoxy and sectioned transversely through the primordium region using a low speed saw. Three 300-micron sections were cut from each otolith and aged under a microscope using transmitted light (Brown et al., 2004). Each sample was aged by two readers, and only those samples for which both readers agreed were used in the analysis (both readers agreed in 79% of the samples and differed by ±1 year among the remaining samples). Following Campana et al. (1995), aging accuracy was independently validated a posteriori using historical records of age-1 carp reported by fish surveys conducted by the IL DNR (Wayne Herndon; IL DNR, unpublished data). Carp body-condition index, the relative weight (W_r), was also calculated using the standard weight equation for this species (Bister et al., 2000).

We developed the age structure of the carp population in HHL using established protocols for fish populations (Isley & Grabowski, 2007). In brief, we first determined the relationship between fish length and age (age–length key). Then, we applied this key to the length structure (numbers of fish in 20-mm length intervals) to calculate numbers at age. The numbers at age in the spring of 2007 were used to back-calculate numbers at age during years 2001–2006 using an estimate of natural mortality rate which we developed by applying data on carp longevity collected in other Midwestern lakes (Bajer & Sorensen, in press) to the linear equation described by Hewitt & Hoenig (2005). The biomass of carp in the lake each spring was then estimated by multiplying the back-calculated numbers at age by age-specific average weight, which was determined by fitting a von Bertalanffy equation to weight versus age data, using a commonly accepted protocol (see Van Den Avyle & Hayward, 1999). The sensitivity of our biomass estimate to mortality rate was evaluated by recalculating biomass using mortality values that were two times higher or two times lower than the 12% nominal value. Least-squares linear regressions between the back-calculated biomass of carp, percent vegetative cover, and the waterfowl count were developed in SAS (Version 9.1; SAS Institute Inc., Cary, North Carolina).

Fish community surveys

The fish community in HHL was surveyed annually using 10 large trap nets (mesh size 3.75 cm, two metal frames 1.2-m wide and 1.2-m high with eight hoops 0.9 m in diameter, and a 17-m lead attached to the front of the net) which were set along an 800-m transect at the eastern shoreline of the lake where water depth is approximately 1 m. Nets were set in late March of each year for one 24-h period except for 2002 when the nets were set in September. Due to their mesh size, these nets only captured fish larger than ~10 cm. All fish caught were identified, measured (nearest millimeter), and counted.

Results

We marked and released 2,261 carp in HHL, of which 190 were recaptured among a total of 6,784 that were captured and examined for marks (Table 1). Catch rates in different areas within the lake were more uniform during the mark-and-release period, suggesting a relatively dispersed carp distribution (Table 1). During the recapture period, catch rates increased substantially in the central, deepest area of the lake (area R1), while they declined to near zero in the other two shallower areas (Table 1). Seine hauls collected in area R1 included large numbers of carp from all locations within the lake, suggesting that carp were aggregating there (Table 1). This behavior coincided with a sudden drop in air temperature to below freezing. The three seine hauls collected in area R1 captured sufficient numbers of marked individuals (between 15 and 122 individuals) to permit population estimates that ranged from 61,444 to 84,923 individuals. Based on these values, we estimated that 75,989 ± 12,706 (mean ± standard deviation) common carp inhabited HHL in April 2007 (Table 1).

Table 1 The number of carp captured, marked and released, and recaptured during each seine haul

Date	Area	Captured (C)	Total marked at large (M)	Mark type					Population (N)
				FC	Yellow	Blue	Red	Green	
Phase I—mark and release									
3/29	M1	238	238	0	0	0	238	0	
3/30	M2	1,522	1,760	1,492	0	0	0	128	
3/31	M3	360	2,120	0	360	0	0	0	
3/31	M4	141	2,261	0	0	67	0	74	
Phase II—recapture marked individuals and estimate the population									
4/9	R1	4,250	2,261	85	11	7	6	13	81,600
4/10	R2	27	2,139	0	0	0	0	0	–
4/11	R1	381	2,139	14	0	0	1	0	61,444
4/13	R1	2,005	2,124	39	2	3	7	4	84,923
4/13	R3	121	2,069	0	1	0	0	0	–
Average population estimate									75,989
Standard deviation									12,706

The population abundance of carp (N) was estimated for each seine haul during the recapture period from the number of marked carp in the population (M), the total number of carp collected in each seine haul (C), and the number of recaptured carp in each seine haul (R): $N = (M \cdot C)/R$, the recapture samples which included <150 carp and only one marked individual were omitted from the analysis. Sampling locations are shown on Fig. 1

FC fin-clipped

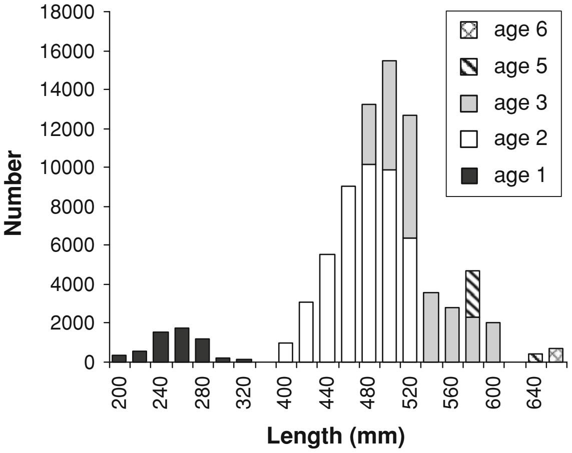

Fig. 2 Abundance, age structure, and length structure of the common carp population in the Hennepin and Hopper Lakes. No age-4 carp were found

Aging analysis indicated that the population of carp in HHL was dominated by age-2 individuals (60% of the population) and age-3 individuals (22%); only a few age-1 (13%), age-5 (3%), and age-6 (2%) fish were present (Fig. 2). No carp older than 6 (e.g., fish which predated rotenone treatment) was encountered. The high abundance of age-2 and age-3 carp indicated a strong carp recruitment event in 2005, and a moderate one in 2004. Back-calculations indicated that 60 and 140 age-1 carp per hectare were produced in HHL as a result of successful carp recruitment in 2004 and 2005, respectively. Recruitment rates during other years remained below 5 individuals per ha. The growth rate of carp in HHL was very rapid $\left(\text{Length} = 677.5 \times \left[1 - \mathrm{e}^{-0.619\times(\text{age}-0.009)}\right]\right)$, and on average, carp reached 253, 449, and 555 mm in TL by the end of the first, second, and third growth seasons, respectively. The average value of the body-condition index was also high ($W_{\mathrm{r}} = 108$), indicating that the carp were well nourished.

Our calculations suggest that the biomass of carp during 2001–2004 was <10 kg/ha, but that a small increase to ~30 kg/ha occurred by the spring of 2005. By the spring of 2006, the biomass of carp had reached 110 kg/ha following a recruitment pulse in 2004. A second recruitment event in 2005 caused the biomass of carp to increase to 255 kg/ha by the spring of 2007 (Fig. 3). These estimates changed by <15 kg/ha when mortality was either doubled or halved in tests of model sensitivity.

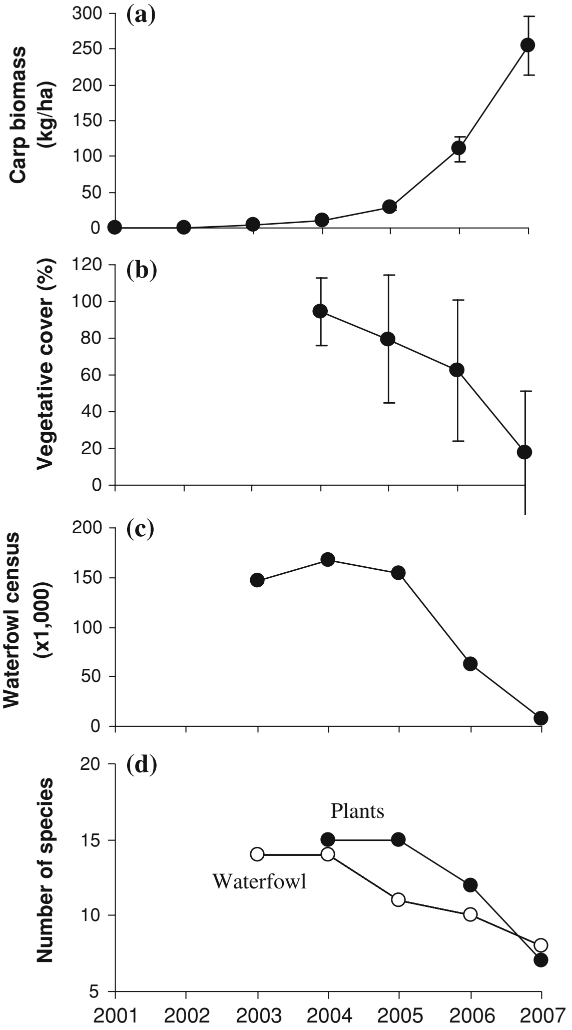

Fig. 3 **a** Biomass of carp in the Hennepin and Hopper Lakes during 2001–2007 (mean ± 1 SD); **b** percent vegetative cover (mean ± 1 SD); **c** cumulative waterfowl (dabbling and diving ducks) count; **d** number of aquatic plant and duck species

Correlations between carp biomass, vegetation, and waterfowl

Dramatic reductions in vegetative cover occurred when carp biomass increased (Fig. 3). In 2004, when carp biomass was only ~10 kg/ha, the percent vegetative cover was 94%. A small decline to 80% was observed in 2005, by which time carp biomass was estimated to have increased to ~30 kg/ha. Notably, percent vegetative cover declined precipitously to 62% in 2006 (with 20% of all quadrats having no vegetation) at which time carp biomass was calculated to have reached 110 kg/ha. Finally, by 2007, when carp biomass had increased to 255 kg/ha, 80% of the quadrats had no vegetation, and the overall vegetative cover was only 17% (Fig. 3). This increase in carp biomass was strongly correlated with the decline in percent vegetative cover from 2004 to 2007 (Percent vegetative cover $= 93.5 - 0.297 \cdot$ carp biomass in kg/ha; $r^2 = 0.98$; $P < 0.001$). The number of macrophyte species declined from 15 in 2004, to 7 in 2007 (Table 2). Qualitative assessments of the plant community found that only white water lily (*Nymphaea odorata*) and American lotus (*Nelumbo lutea*) (despite its presence in the lake, lotus was not found within the sampling quadrats) remained relatively unaffected by the increase in carp biomass.

Waterfowl abundance also decreased dramatically at the time that increases in carp biomass were noted. During 2003–2005, between 144,000 and 166,000 dabbling and diving ducks representing 15 species were counted during fall censuses (Fig. 3; Table 3). Dabbling ducks comprised 92% of the waterfowl during that period. However, when the carp population reached 110 kg/ha in 2006, the number of waterfowl declined to 77,995 individuals. This decline was even more severe in 2007, when only 13,695 waterfowl, including only 100 diving ducks, were counted (Fig. 3). Only 9 waterfowl species were present in 2007 (Table 3). Overall, the increase in carp biomass could explain 93% of the variation in waterfowl abundance decline during 2003–2007 (waterfowl in 1,000s of individuals $= 159.5 - 0.502 \cdot$ carp biomass in kg/ha; $r^2 = 0.93$; $P < 0.001$).

Table 3 Species of waterfowl found (designated by '+') in Hennepin and Hopper Lakes in 2004 and 2007

Species	2004	2007
Dabbling ducks		
Mallard (*Anas platyrhynchos*)	+	+
American black duck (*A. rubripes*)	+	+
Northern pintail (*A. acuta*)	+	+
Blue-winged teal (*A. discors*)	+	+
Green-winged teal (*A. crecca*)	+	+
American wigeon (*A. americana*)	+	+
Gadwall (*A. strepera*)	+	+
Northern shoveler (*A. clypeata*)	+	+
Diving ducks		
Lesser scaup (*Aythya affinis*)	+	
Ring-necked duck (*A. collaris*)	+	+
Canvasback (*A. valisineria*)	+	
Redhead duck (*A. americana*)	+	
Ruddy duck (*Oxyura jamaicensis*),	+	
Common goldeneye (*Bucephala clangula*)	+	
Bufflehead duck (*B. albeola*)	+	

Table 2 Aquatic macrophyte species found (designated by a '+') in Hennepin and Hopper Lakes during 2004–2007

Species	Common Name	2004	2005	2006	2007
Alisma subcordatum	Water plantain		+		
Azolla caroliniana	Mosquito fern	+			
Ceratophyllum demersum	Coontail	+	+	+	+
Chara spp.	Musk grass	+			
Elodea nutallii	Nutall's elodea	+	+	+	
Myriophyllum spicatum	Eurasian watermilfoil	+	+	+	
Najas guadalupensis	Southern naiad	+	+	+	+
Najas minor	Brittle naiad	+	+		+
Nymphaea odorata	White water lily	+	+	+	+
Polygonum amphibium	Water knotweed	+	+	+	
Potamogeton crispus	Curly leaf pondweed		+	+	
Potamogeton foliosus	Leafy pondweed	+	+	+	
Potamogeton nodosus	Nodding longleaf	+	+	+	+
Potamogeton pusillus	Narrow leaf pondweed	+	+	+	
Sagittaria latifolia	Arrow head; duck potato	+	+		
Stuckenia pectinata	Sago pondweed	+	+	+	+
Typha latifolia × *angustifolia*	Hybrid cattail	+	+	+	+

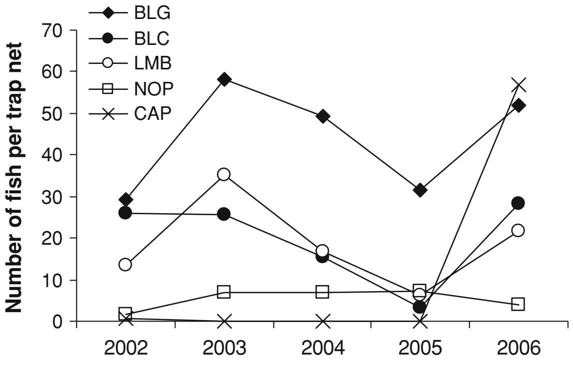

Fig. 4 Results of annual fish community surveys in Hennepin and Hopper Lakes. Numbers represent average catch rates per one trap net of the five fish species that comprised over 99% of all captured individuals: *BLG* bluegill sunfish, *BLC* black crappie, *LMB* largemouth bass, *NOP* northern pike, and *CAP* common carp

Except for the rapid increase in carp numbers and biomass, the fish community in HHL remained relatively stable during 2002–2006. The number of bluegill sunfish, black crappie, largemouth bass, and northern pike, which accounted for more than 95% of all the sampled individuals (excluding carp), did not change significantly during this period (Fig. 4). Linear regressions of their abundance over time were not statistically significant; $P > 0.05$.

Discussion

This study provides one of the most complete descriptions of the relationships between the biomass of free-ranging carp population, vegetative cover, and waterfowl abundance in a whole-lake ecosystem, and suggests a threshold biomass at which carp are particularly damaging. Our results largely confirm the effects of carp biomass measured in ponds and enclosures, at a larger scale (Crivelli, 1983; Drenner et al., 1998; Parkos et al., 2003; Haas et al., 2007). The supposition of carp removal studies (Lougheed et al., 2004; Schrage & Downing, 2004) that this species causes dramatic declines in aquatic vegetation and waterfowl in shallow lakes is also supported. We provide new and important evidence that populations of free-ranging carp may increase rapidly in shallow lakes and that carp densities of ~100 kg/ha may represent a threshold for damage in whole shallow lakes. Since the biomass of carp in shallow ecosystems across Midwestern North America appears to commonly approach 300–400 kg/ha (Neess et al., 1957; Crivelli, 1983; Panek, 1987; Bajer & Sorensen, in press), it is reasonable to suggest that carp pose a severe and wide-spread threat to habitat quality and function of these ecosystems.

Several lines of evidence suggest that carp were directly responsible for the dramatic declines in vegetative cover and waterfowl in Hennepin and Hopper Lakes. First, the declines in vegetation and waterfowl during 2002–2007 precisely coincided with the increase in this lake's carp population. Second, no abiotic or biotic disturbances were noted at this time, and the hydrologic regime of HHL was stable. Third, the native fish community remained relatively stable throughout the study, and did not include benthivorous species such as bullhead catfishes (Ictaluridae) which can also contribute to vegetation declines in Midwestern shallow lakes (Hanson & Butler, 1994; Braig & Johnson, 2003). Fourth, results of this study are consistent with those of both pond and enclosure experiments as well as various carp removal experiments (described above).

Our data suggests that a carp biomass of ~100 kg/ha may represent a threshold for vegetation disappearance in shallow lakes such as HHL. This conclusion is consistent with pond studies that document severe reductions in vegetation density at similar carp abundance (Parkos et al., 2003; Haas et al., 2007) but somewhat inconsistent with lake enclosure experiments which indicate that a biomass of >500 kg/ha may be required to cause a 50% loss in vegetation (Robel, 1961; Crivelli, 1983; Miller & Crowl, 2006). This disparity could be explained by the fact that processes which exacerbate the impacts of carp on vegetation, including the effects of wind on sediment stability and turbidity, can be reduced in enclosures. Additionally, clearer water can enter enclosures from the outside. No correlations between carp biomass and turbidity have been reported in enclosures (Robel, 1961; Crivelli, 1983; Miller & Crowl, 2006), while they are commonly observed in ponds and lakes (Sidorkewicj et al., 1998; Parkos et al., 2003; Schrage & Downing, 2004). Dramatic water turbidity increases were also observed in HHL during 2006 and 2007 (G. Sullivan, personal observation).

Although our study was restricted to a single lake, the findings are likely relevant to many shallow lake ecosystems. First, HHL is similar to tens of thousands of hectares of shallow lakes within the Illinois and Upper Mississippi River Valleys (Havera & Bellrose, 1984; Stafford et al., 2007) in terms of its size, depth, productivity, and geology. The aquatic vegetation in HHL is also common to the region (Muencher, 1944; Mohlenbrock & Ladd, 1978; Nichols, 1997). Second, many prominent shallow waterfowl lakes in the Midwest that are also known to be severely impacted by common carp are similar in size (>300 ha), depth (<5 m), and productivity to HHL (Hanson & Butler, 1994; Verrill & Berry, 1995; Lougheed et al., 2004; Schrage & Downing, 2004). The dynamics of shallow lake ecosystems are complex, and additional studies are needed to more precisely address the effects of lake size and depth, sediment type, nutrient levels, and local fish community on the severity of the ecological impacts of carp.

The seemingly dramatic effects of carp on plants appeared to vary by species. We observed that all species of macrophytes declined from 2002 to 2007 in HHL, except for a floating-leaved species, the white water lily, and the emergent American lotus. Unlike submersed species, these species are characterized by massive rhizomes and substantial overwintering carbohydrate reserves (Sculthorpe, 1967; Wetzel, 1983). These reserves can fuel shoot growth to the surface each year, despite the low light conditions promoted by carp foraging. The rhizomes also provide the structural integrity to withstand uprooting by carp (Crivelli, 1983). Drenner et al. (1998) also observed that while several submersed species declined in ponds with carp, species such as American lotus increased. It is likely, therefore, that aquatic macrophyte communities in systems with high carp biomass will be sparse and dominated by species less sensitive to uprooting and poor light penetration.

The changes in the plant community associated with increasing carp biomass most likely drove dramatic decreases in migratory waterfowl abundance. This was exemplified by the >90% decrease in dabbling and diving ducks in HHL between 2004 and 2007 during which time the biomass of carp was estimated to have increased from 10 to 255 kg/ha. Similar effects of carp on waterfowl abundance have been recently quantified in ponds (Haas et al., 2007) and shallow lake systems (Hanson & Butler, 1994; Bouffard & Hanson, 1997). While the decline in dabbling ducks and some species of diving ducks (i.e. canvasback and redhead duck) which forage on vegetation and associated invertebrates is intuitive (Hargeby et al., 1994), the reduction in other species of diving ducks suggests more complex interactions, including depletion of benthic invertebrates by carp (Stewart & Downing, 2008). Notably, HHL was also an important breeding area for many waterfowl species (including rare and listed species) in this region during 2004–2005 (Kleen, 2005, 2006). However, this function diminished greatly following the carp invasion and disappearance of aquatic vegetation (Kleen, 2007).

Finally, our study provides the first detailed assessment of the age structure and recruitment dynamics of carp in a recently restored shallow lake ecosystem. We demonstrate that carp number and biomass can remain low for several years, and then increase to over 250 kg/ha in only 2 years following successful recruitment events. In addition, we show that the annual recruitment success of carp can be highly variable and does not appear to be tightly controlled by the abundance of adults which only increased in 2006. Although the processes which control recruitment success of common carp are obscure, it is interesting that pools of standing water which might have supported larval carp while excluding their predators were noted in the spring of 2005 (Wayne Herndon, IL DNR, personal communication). Although our mark-and-recapture analysis was restricted to a single type of gear and a short period, we believe it provided an accurate estimate of carp population because individuals that were marked in different areas mixed within the lake and aggregated in one area, which we were able to effectively census collecting large numbers of recaptures. Further, sampling methodology employed in HHL has been shown to provide accurate estimates of carp abundance in other Midwestern lakes (Bajer & Sorensen, in press).

In conclusion, while supporting numerous studies that document the link between carp and vegetation, our results suggest that free-ranging populations of carp may cause large-scale declines in vegetation in shallow lakes at densities exceeding 100 kg/ha. We also expect that increased internal phosphorous loading will occur at similar carp densities, as these processes are commonly linked (Moss et al., 2002; Parkos et al., 2003; Schrage & Downing, 2004). A better understanding of the factors that determine carp recruitment success, and how to control it, are now needed to develop sustainable and ecologically sensible management plans for this species in shallow lakes.

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