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Research Article

Low downstream dispersal of young-of-year common carp from marshes into lakes in the Upper Mississippi River region and its implications for integrated pest management strategies

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Abstract

In lakes of the Upper Mississippi River Basin (UMRB), invasive common carp (*Cyprinus carpio*) employ a reproductive strategy in which adults migrate out of lakes to spawn in seasonally unstable marshes that have few egg and larval predators. The rates with which the juveniles outmigrate from marshes into adjacent lakes have critical management implications but have not been quantified using direct approaches. We used passive integrated transponder (PIT) tags to quantify outmigration of young-of-year (YOY) carp from marshes into lakes in two systems in UMRB. In both cases, marshes were located upstream of lakes and PIT antennas continuously monitored the movement of carp. In the first system, which we monitored for three years, 0.2% to 5.5% of PIT-tagged YOY carp outmigrated to the lake each year; highest outmigration occurred during mid-summer periods of low water level in the marsh. In the second system, which comprised much more extensive area of deeper marshes, 0.2% of YOY carp outmigrated to the lake. Ageing and mark-recapture analyses confirmed that relatively few YOY carp recruited into the lake populations from the marshes each year (between 5 and 50 per hectare). Our results show that YOY carp outmigration rates are low (< 6%) but can vary an order of magnitude among years. These findings are important for removal-based management strategies for carp in lakes of UMRB by showing what adult removal rates are needed to compensate for juvenile recruitment from marshy nurseries.

Key words: invasive fish, biological invasions, *Cyprinus carpio*, outmigration, management, Minnesota

Introduction

Many invasive fish employ spatially complex life histories, in which adult individuals conduct seasonal migrations to outlying habitats to spawn. Such strategies have been shown for the common carp (*Cyprinus carpio* Linnaeus, 1758) in Minnesota, northern pike (*Esox lucius* Linnaeus, 1758) in Alaska, and the sea lamprey (*Petromyzon marinus* Linnaeus, 1758) in the Laurentian Great Lakes (Morman et al. 1980; Bajer and Sorensen 2010; Sepulveda et al. 2013). These migrations function to exploit peripheral areas that provide adequate spawning and nursery habitat, including shelter from predators, and/or more abundant food resources for the larvae and juveniles (Clark 1950; Bajer et al. 2012). Utilization of these nursery habitats can increase recruitment success of the invader (Bajer et al. 2015). For example, in species that employ partial migration strategies (where some but not all adults migrate into outlying habitats to spawn), adults that migrate can disproportionally drive population abundance due to a much higher reproductive success as compared to resident individuals (Jonsson and Jonsson 1993; Bajer et al. 2015). However, for this strategy to be successful, juveniles must outmigrate from the peripheral habitats in which they develop to join the adult population. Juvenile outmigration and cues that drive it remains one of the least understood elements of population dynamics of many invasive fish that employ spatially complex life histories.

The common carp (hereafter "carp") is among the most widespread invasive fishes worldwide and it has been shown to employ partial spawning migrations in some geographic regions (Bajer and Sorensen 2010). In interconnected lake-marsh complexes of Minnesota, or more broadly throughout the northern regions of the Upper Mississippi River Basin (UMRB), large numbers of adult carp migrate from lakes to outlying marshes to spawn (Bajer and Sorensen 2010; Chizinski et al. 2016). It is hypothesized that this behavior has evolved in response to heavy egg and larval predation in lakes and temporary lapses in predator abundance in marshes that winterkill (Bajer et al. 2012; Silbernagel and Sorensen 2013). In such systems, winterkill-prone marshes have been suggested to be the primary source of new carp recruits (Bajer et al. 2012; Osborne 2012; Koch 2014). However, it is generally not known how many young-of-year (YOY) carp move out of winterkill-prone marshes and migrate to adjacent lakes. Indirect evidence suggest that outmigration probabilities are relatively low, approximately 0.3% during the first year of life (Bajer et al. 2015). However, these estimates, which were derived from end-of-season trap net surveys, are relatively crude and of limited use in carp management. First, they do not provide lake mangers with a detailed picture of the outmigration process including times when outmigration occurs and environmental variables that might drive it. Perhaps even more important, these estimates do not allow for determining the actual numbers of carp that recruit from marshes into lakes (i.e. carp per hectare). More direct approaches, such as the use of passive integrated transponder (PIT) tags, are needed to document outmigration of juvenile carp on a continuous basis to describe outmigration probabilities, how they change over time, and what their environmental drivers might be. The use of PIT tags would be especially informative if supplemented by ageing and mark-recapture analyses in the receiving populations to estimate the actual numbers of juveniles that recruit into lakes from adjacent marshes.

Outmigration rates (i.e. numbers of fish that outmigrate) of juvenile carp from marshes into lakes have key management implications. Low outmigration rates would allow for management of carp populations in many lakes using simple removal strategies, such as winter seining (Bajer et al. 2011; Lechelt and Bajer 2016). This, in turn, would allow for improving water quality and increasing biodiversity in many such ecosystems (Bajer et al. 2016). However, much higher outmigration rates would likely require unrealistically high or frequent removal efforts (Lechelt and Bajer 2016), and therefore require additional management strategies, such as the use of outmigration deterrent systems (Zielinski and Sorensen 2015, 2016). Finally, more detailed information about the outmigration process might allow for developing new management strategies. For example, in regions where marshes winterkill with high frequency, outmigration deterrents could be used to increase residence in marshes and affect high mortality among carp during subsequent winters.

The goal of this study was to describe both the probability and rate for outmigration of YOY carp from hypoxia-prone marshes to adjacent lakes. We used passive integrated transponder (PIT) tags to estimate outmigration probabilities and determine how they change over time. We also estimated the overall number of YOY carp that outmigrated from marshes and recruited into lake populations using mark-recapture and age-structure analyses. The information from this study is important to inform sustainable management schemes and to increase the accuracy of existing models of carp populations in lake-marsh systems. Our results may also suggest which environmental cues drive YOY carp outmigration from marshes into lakes and what management strategies might be used to reduce outmigration.

Methods

Study system

This study took place from 2013–2016 in two lake-marsh systems in Minnesota, USA (Figure 1), both located within the UMRB. The first system was comprised of a marsh, the Purgatory Creek Conservation Area (hereafter PCCA; 60 ha, max depth 1.0 m), positioned approximately 1 km upstream of a similarly sized Lake Staring (65 ha; max depth 4.9 m). These two water bodies are connected by Purgatory Creek, a relatively small (10 m wide, 0.5 m deep) stream. Carp can move freely between Staring and PCCA but are unable to move upstream of PCCA or downstream of Staring due to man-made barriers. Each year, large numbers of adult carp, up to 90% of adults, migrate from Staring to PCCA in the spring to spawn, and return to the lake in late spring (Bajer et al. 2015; J. Lechelt unpublished data). Both PCCA and Staring are hypereutrophic (total phosphorus > 100 ug/L). Due to frequent winter hypoxia, PCCA has unstable native fish community and is a carp nursery with recruitment occurring approximately every other year (Bajer et al. 2012).

The second system was comprised of a complex of five marshes (max depth 2.5 m) collectively called

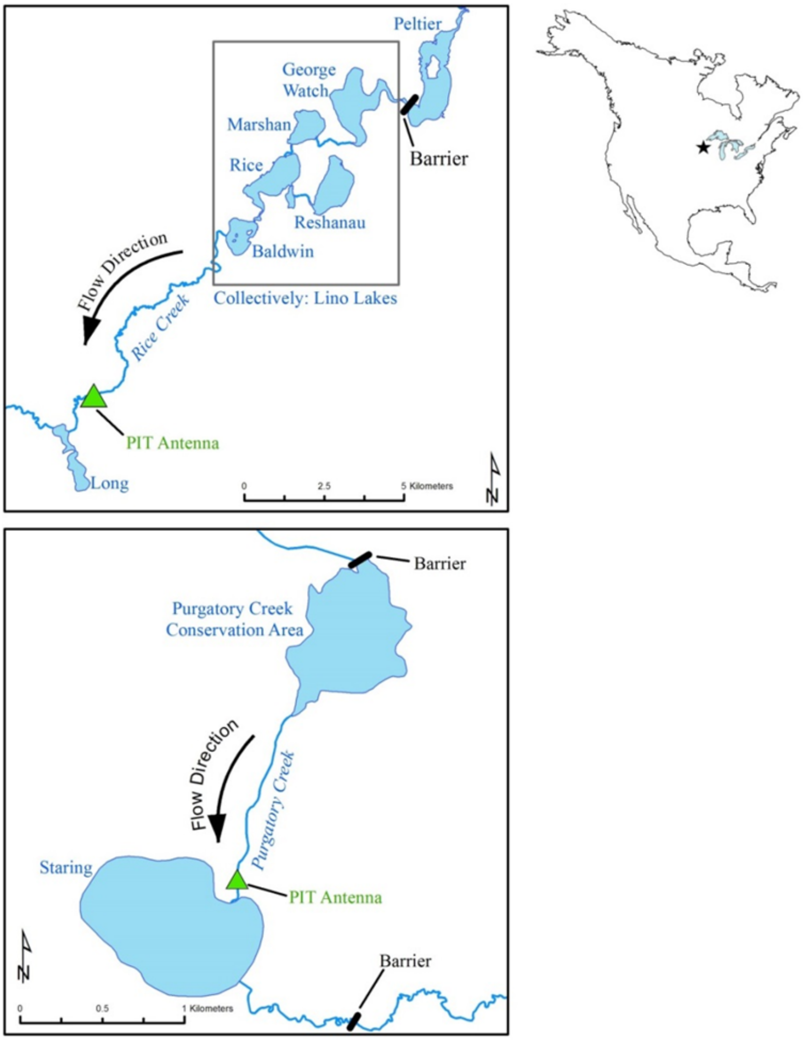

Figure 1. Map of the Staring – Purgatory Creek Conservation Area (PCCA) system (top) and the Long Lake – Lino Lakes system (bottom). Star shows our study region.

"Lino Lakes", with a combined area of 641 ha, that are located approximately 14 km upstream of Long Lake (68.8 ha; max depth 8 m; Figure 1). Long Lake and Lino Lakes are connected by Rice Creek (~ 12 m width, 0.5 m deep). As in the first system, adult carp employ spawning migrations from Long Lake into Lino Lakes (Banet 2016). Lino Lakes, which become hypoxic during most winters, have unstable populations of native predators allowing carp to produce strong year classes on a quasi-annual basis (M. Kocian, unpublished data).

Study design

This study was designed to estimate three different aspects of the outmigration of YOY carp from marshes into downstream lakes: 1) the overall percentage of tagged YOY carp that outmigrated each year, 2) the daily probability of outmigration and how it was related to water temperature or water level, and 3) the overall number of YOY carp that migrated out of the marshes and recruited into the two lake populations each year. These analyses were conducted using a combination of trap net surveys, PIT tags, and ageing and mark-recapture analyses. We will describe procedures used at each study site separately. Although this analysis focuses on YOY carp, the possibility that carp may survive winters and outmigrate at age 1 or 2 is also assessed because PIT antennas were monitored for multiple years at each site.

PCCA – Staring system

In the PCCA-Staring system, trap net surveys were conducted annually for three consecutive years

(2013–2015) to determine the presence of YOY carp and estimate their relative abundance (catch per unit of effort; CPUE). Small mesh (see below) trap nets that had been previously used to sample YOY carp (Bajer et al. 2012) were set at five locations for a 24-hour period in PCCA and in Lake Staring equidistant along the shoreline, with the exception of the western side of PCCA, which was inaccessible. Initial surveys were conducted in July of each year, when carp grew large enough to be captured and implanted with PIT tags. In years when YOY carp were found in PCCA (2013 and 2015), surveys were repeated at approximately monthly intervals to estimate YOY carp natural mortality, which was needed to calculate daily outmigration probabilities (see below). The trap nets were comprised of a 10 m lead followed by 1.8 m × 0.9 m metal frame followed by three hoops. The nets were constructed using a small mesh (13 mm bar). They were set in late morning and retrieved the next day. All carp were counted and measured to the nearest millimeter. YOYs were identified based on their total length (< 200 mm), which was verified by ageing using otoliths following methods in Bajer and Sorensen (2010). All carp captured in PCCA that were longer than 65 mm were tagged with 12 mm-HDX PIT tags (Oregon RFID©, Portland, OR, USA) and released. Because trap net catch rates were relatively low, we conducted supplementary beach seining and backpack electrofishing to capture and tag additional carp in PCCA so that at least 400 were tagged each year. Mortality due to tagging was assessed by placing 20 tagged and untagged (control) carp in a 2 m × 2 m net pen for 48 hours. Shortly before PIT tagging began, two PIT tag antennas were placed in Purgatory Creek, approximately 1 km downstream of PCCA (Figure 1).

The antennas were placed 5 m apart to detect movement direction. The antennas were constructed of one loop of 8-gauge wire and one loop of 12-gauge wire attached to a tuning module connected to a multi-antenna HDX reader and datalogger (Oregon RFID). Detection efficiency of each antenna ranged between 85% and 100% and was assessed by tethering a tagged YOY carp to a fishing line and allowing it to swim through the antennas twenty times both up- and downstream. Antennas were maintained from July 2013 to December 2015 (the stream was frozen to the bottom between January and March of each year). A temperature data logger (Onset® HOBO® Pendent UV-002-08) was placed near the antenna to collect water temperature at 3 hour intervals. A meter stick was placed in the stream near the antenna to record water level at least once a week, and after precipitation events.

To estimate daily outmigration probabilities, we first estimated the number of PIT tagged carp present in PCCA on each day of the study by applying a daily mortality rate to carp tagged on previous occasions, adding newly tagged carp, and subtracting carp that have moved (crossed the antennas). The daily mortality rate in PCCA was calculated by analyzing trap net catch rates (CPUE) over time. Catch rates were $\ln(y + 1)$ transformed (to account for zeros), a linear model was fit to the data, and the negative value of the slope coefficient was used as the estimate of mortality (Chapman and Robson 1960). The daily outmigration probability of YOY carp was calculated by dividing the number of PIT tagged carp detected by the antenna by the number of PIT tagged carp remaining in PCCA.

To estimate the overall number of carp that outmigrated from PCCA and recruited into the population in Lake Staring from the year class of 2013 and 2015, we conducted mark-recapture and ageing analyses in Lake Staring. We conducted a boat electrofishing survey in the summer of 2014 marking and releasing all captured carp (N = 56); all captured carp were larger than 400 mm (i.e. adult carp). While conducting these surveys, we followed established protocols to sample carp populations (Bajer and Sorensen 2010; Bajer et al. 2012). In January 2015, we pulled a large (550 m long) seine in Lake Staring targeting an aggregation of carp to collect a large sample of the population, documented recapture rates, and estimated the population using Chapman's equation (modified Lincoln-Peterson estimator; Chapman 1954). To estimate the proportion of the population that was comprised by the carp that outmigrated from PCCA (year classes 2013 and 2015), we conducted another boat electrofishing survey in Lake Staring in October 2015 and developed a length and age structure of the population; carp were aged using asterisci otoliths (Bajer and Sorensen 2010).

Lino Lakes – Long Lake system

Similar procedures were used in the Lino Lakes system from July 2015 to December 2016. First, trap nets were set (five per lake as above) in each of the Lino Lakes and in Long Lake in July 2015 to determine presence of YOY carp. Carp larger than 65 mm were PIT tagged and released. These surveys continued throughout September to tag and release YOY carp in Lino Lakes. A final survey was conducted one year later in July 2016 to estimate the annual mortality rate of YOY carp. In addition to tagging YOY carp, we also tagged a small number of adult (> 400 mm) carp (N = 29). Because adult carp travel extensively and repeatedly between Long and Lino Lakes each year, as shown by an ongoing radiotelemetry study (Nathan Banet, University of Minnesota, unpublished data), we used these adult carp as a "positive control" to verify that the antenna was functioning properly. A PIT antenna (similar design as in Purgatory Creek, except that only one loop of wire was used) was placed in Rice Creek before carp were PIT tagged, approximately 12 km downstream of Lino Lakes and 2 km upstream of Long Lake. The antenna monitored the passage of PIT-tagged carp on a continuous basis between July 2015 and December 2016 and was tested on a weekly basis using a dummy reference tag; the antenna performed without a fault. Water level in Rice Creek was monitored continuously by a United States Geological Survey water gage (05288580). Non-continuous (approximately once a week) water temperature data were also collected in Rice Lake and in Rice Creek. Finally, we also conducted weekly backpack electrofishing surveys in Rice Creek to determine presence of YOY carp in the stream. Nine of such surveys were conducted in 2015 between August 8 and November 3. These surveys were conducted on the upstream and downstream side of the antenna (50 m transects). All YOY carp captured in those surveys were also implanted with PIT tags and released within the transects they were captured in. Ten of such surveys were also conducted in 2016 between June 6 and September 7.

To estimate the overall number of YOY carp that migrated to Long Lake we estimated the abundance, length- and age-structure of carp in Long Lake in the fall of 2015 and in the summer of 2016. To facilitate these estimates, seven hundred adult carp were captured in Long Lake using baited traps (box nets with 10 m by 10 m mesh bottom and four mesh sides that initially lay flat on the bottom, but which are quickly lifted above the surface of the water once the carp aggregate inside the net near the bait) in the fall of 2015, marked with fin clips and released. These fish were marked and released in two different areas of the lake to increase random distribution of marked individuals. In February 2016, a large (500 m) winter seine was pulled in Long Lake targeting an area where carp aggregated. All carp captured during fall trapping and winter seining were measured for length and a sample of 100 carp were aged to determine the proportion of the population that was comprised by YOY. Sides (wings) of the seine net were constructed using 6.2 cm (bar) mesh, while the middle portion on the net was constructed using 3.5 cm (bar) mesh. Thus, the middle portion of the net was capable of catching carp > 150 mm, but some YOY carp might have escaped through the sides of the net, which potentially biased the length structure. To ameliorate those potential concerns, another population survey was conducted in July 2016 at which point the lake was surveyed using an electrofishing boat on two separate occasions (July 20 and 29). In total, 15 20-min electrofishing transects were conducted targeting all littoral areas on the lake. All carp were measured and a sample of 25 carp < 400 mm were collected for aging, focusing on individuals that were either age-0, age-1 and age-2. In addition to providing a less-biased length structure of the population, these electrofishing surveys provided another population estimate using an equation that relates the observed catch rate per hour and the density of carp per hectare (Bajer and Sorensen 2012).

Results

PCCA – Staring

Trap net surveys showed that YOY carp were present in PCCA in large numbers during 2013 and 2015, but not in 2014 (no YOY carp were captured in 2014). In 2013, mean trap net catch rates in PCCA ranged between 5.4 YOY carp/net and 23.5 YOY carp/net in July and August and decreased to zero in late September (Figure 2). In 2015, mean trap net catch rates were higher than in 2013, but also decreased from 79.4 in July to 0.8 in early October (Figure 2). YOY carp were not captured in Lake Staring, except in August 2015 when < 1 YOY carp were captured per net (Figure 2). The daily natural instantaneous mortality rate was 0.041 in 2013 and 0.044 in 2015 (Figure 2), indicating that the PCCA population of YOY carp declined by approximately 97% over a four-month period (July–October).

A total of 468 carp were tagged in 2013 in PCCA. Mortality due to tagging was negligible, as two out of 20 carp perished for both tagged and control carp over the 48-hour period. In 2013, only one YOY carp was detected by the antenna (0.2% of all tagged carp). This detection occurred in early August during a period of decreasing water level and when temperature was stable ~ 25 °C (Figure 3). The mean daily outmigration probability for a PIT tagged carp was $4.5 \cdot 10^{-5}$. We did not detect any carp tagged in 2013 that outmigrated at age-1 (in 2014), or age-2 (in 2015). A total of 663 carp were tagged in 2015 in PCCA, of which 37 were detected by the antenna (5.5%; Figure 3). The majority of detections occurred in August during a period of decreasing water levels and when the number of PIT tagged carp in PCCA was near its peak (Figure 3). The mean daily outmigration probability for a single tagged carp was $1.3 \cdot 10^{-3}$. Outmigration probabilities spiked between 8/13/2015 and 8/23/2015 and reached a maximum of $6.3 \cdot 10^{-2}$ on 8/16/2015, at

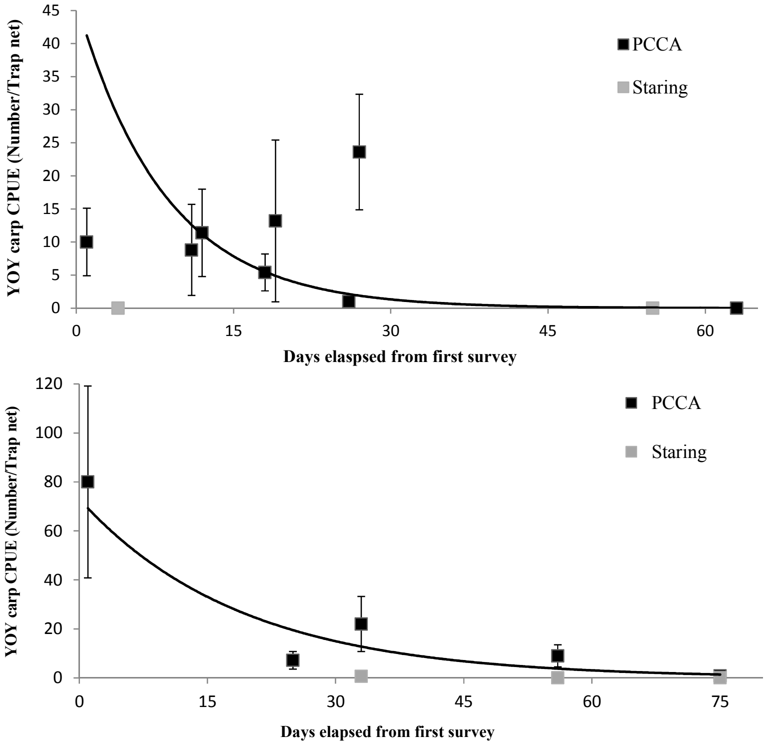

Figure 2. The mean (± SE) trap net catch rate (CPUE) of young of year common carp in PCCA (black squares) and Lake Staring (gray squares) in 2013 (top panel) and 2015 (bottom panel). The x-axis represents the number of days that elapsed from the first trap net survey. The CPUE values for PCCA were ln(y+1) transformed and fit with a linear model (2013: $y = -0.041 \cdot x + 2.86$; $r2 = 0.51$; $P = 0.048$ and 2015: $y = -0.044 \cdot x + 4.17$; $r2 = 0.79$; $P = 0.042$) to estimate daily mortality rate: 0.041/day in 2013 and 0.044/day in 2015.

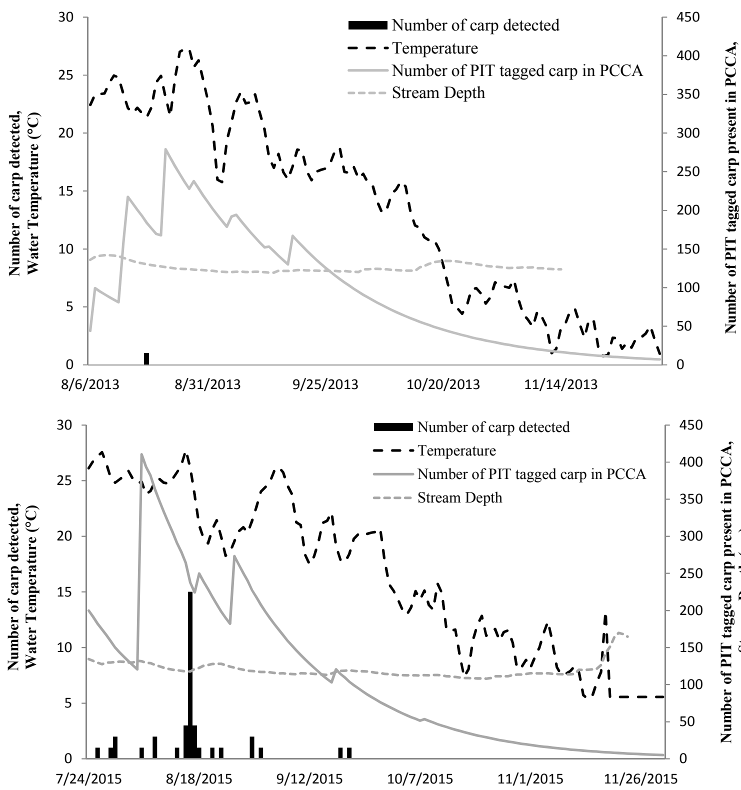

Figure 3. The number of PIT tagged carp present in PCCA (gray line; secondary y-axis) and number of carp detected by the antenna (black bars; primary y-axis) located downstream of PCCA in 2013 (top panel) and 2015 (bottom panel). The dashed lines represent water depth in cm (gray; short dash; secondary y-axis) and water temperature in °C (black, long dash).

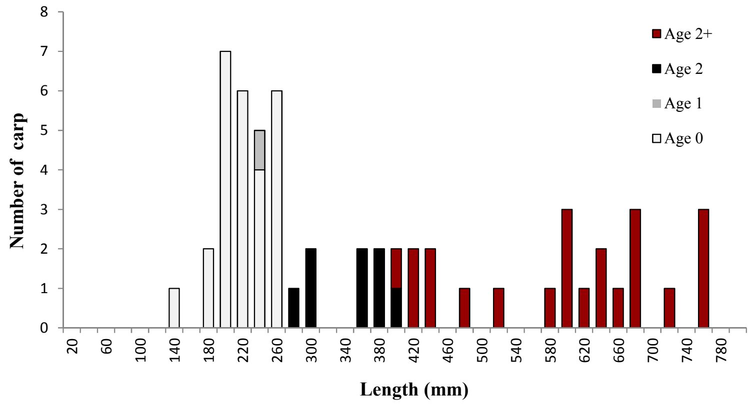

Figure 4. Length and age structure of common carp in Lake Staring in the fall 2015. Carp population estimates (N) for each age class is Age-0: 3,367; Age-1: 135; Age-2: 1,077; Age-2+: 2,963.

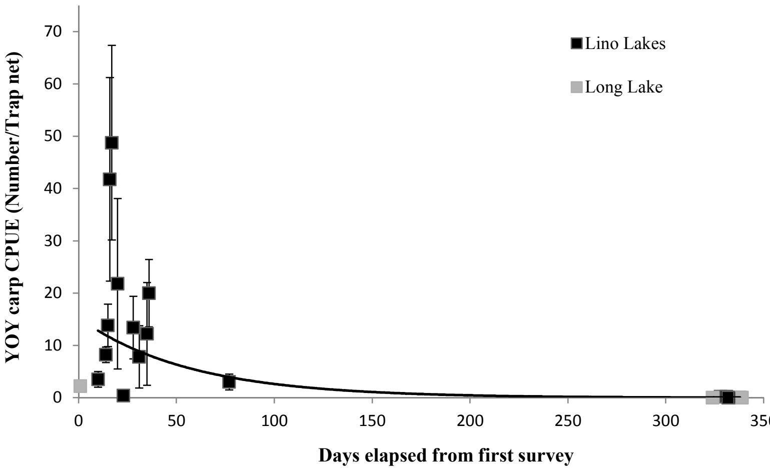

Figure 5. The mean trap net catch rate (CPUE) of young of year common carp in Lino Lakes (black squares) and Long Lake (gray squares). The x-axis represents the number of days that elapsed from the first trap net survey. The CPUE values for Lino Lakes were ln(y+1) transformed and fit with a linear model ($y = -0.0078 \cdot x + 2.60$; $r^2 = 0.62$; $P = 0.00031$) to estimate daily mortality rate: 0.0078/day.

other times outmigration probabilities were very low or zero. The January 2015 seining in Lake Staring yielded 834 carp. Of the 56 carp marked in Lake Staring in the summer 2014, eight were recaptured. This suggested that in the summer of 2014 (time of marking), Lake Staring was inhabited by 5,288 adult carp ± 1,295 (400 mm to 700 mm total length). 2,325 carp were removed during the winter and summer of 2015, thus reducing the population to ~2,963 individuals in the fall of 2015 (Figure 4). Electrofishing surveys in Lake Staring showed three distinct modes in carp length structure in fall of 2015: the first comprised of carp that ranged from 150 to 310 mm, another from 370 to 460 mm, and a third from 580 to 760 mm (Figure 4). Ageing analyses showed that the first and second modes were comprised primarily of YOY and age-2 carp corresponding to recruitment events in PCCA in 2015 and 2013, respectively, while the third mode represented adult carp (Figure 4). Assuming equal capture probabilities across carp of various length classes, and knowing that the last mode was comprised of ~2,963 carp (above), we estimated that 3,367 YOY carp (52 carp/ha) and 1,077 age-2 carp (17 carp/ha) were present in Lake Staring in the fall of 2015 (Figure 4). The probability of catching a carp via boat electrofishing shows a unimodal response with carp length, with the highest catch probability occurring at approximately 300 mm (Bayley and Austen 2002). Thus, our estimate of juvenile carp outmigration might be somewhat inflated.

Lino Lakes – Long Lake system

Trap net CPUE of YOY carp ranged between 10 and 49 in all of the Lino Lakes in July 2015, except for Reshanau Lake where CPUE was only 0.4 (Figure 5). CPUEs declined through late summer and declined below 1 carp/net in all Lino Lakes by July of 2016 (Figure 5; at this point the carp were age-1). Observed catch rates suggested a daily natural instantaneous mortality rate of $7.89 \cdot 10^{-3}$ (Figure 6). A total of 872 YOY carp were tagged with PIT tags in Lino Lakes between August and October 2015; 489 in Marshan, 322 in Rice, 58 in George Watch, 3 in Baldwin and 0

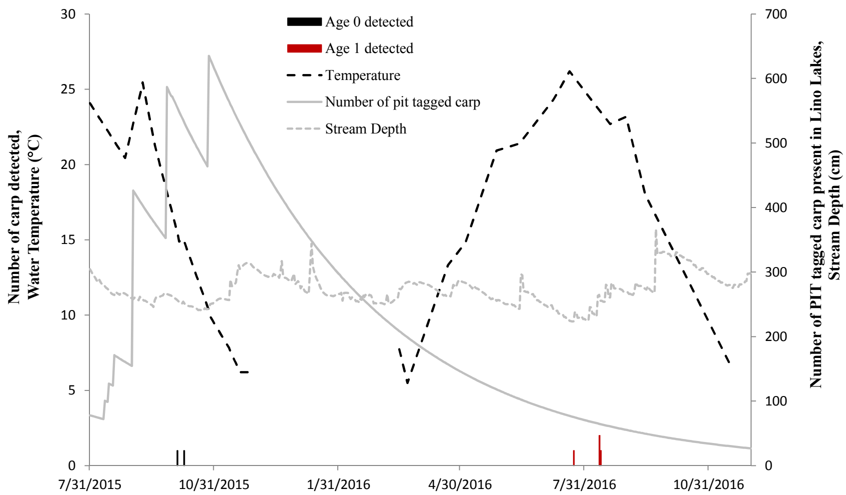

Figure 6. The number of PIT tagged carp present in Lino Lakes (gray line; secondary y-axis). The number of age-0 carp detected (black bars; primary y-axis) and age-1 carp (red bars; primary y-axis) detected by the antenna located downstream of Lino Lakes. The dashed lines represent water depth in cm (gray; short dash; secondary y-axis) and water temperature in °C (black, long dash).

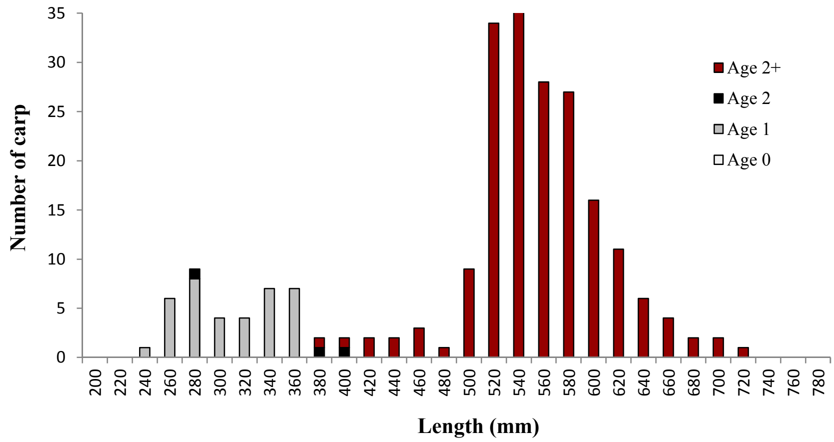

Figure 7. Length and age structure of common carp in Long Lake in July 2016. Carp population estimates (N) for each age class is Age-0: 0; Age-1: 2,862; Age-2: 228; Age-2+: 14,470.

in Reshanau. Only two (~ 0.2%) of these fish were detected by the antenna through the end of December 2015 (Figure 6). These fish crossed the antenna during early to mid-October (Figure 6). In addition, four carp from the same cohort passed the antenna in July and August of 2016 (Figure 6; those fish were age-1 at that point). The mean daily outmigration probability for an age-0 carp in 2015 was $2.9 \cdot 10^{-5}$ and the daily outmigration probability for an age-1 carp in 2016 was $4.3 \cdot 10^{-4}$. Backpack electrofishing surveys conducted on nine occasions between 8/20/15 and 11/3/15 in Rice Creek captured only 35 YOY carp total, of which most were captured during multiple surveys suggesting that these fish were residing in the same pools for weeks rather than moving quickly to Long Lake. This was confirmed by the PIT antenna that recorded the presence of the same carp near the antenna for many consecutive days or even weeks (227 detections of 35 fish in total). Backpack electrofishing surveys conducted on ten occasions between 6/2/16 and 9/7/16 in Rice Creek captured only five age-1 carp (272 mm to 313 mm in length). Meanwhile, the adult carp were moving much more frequently, crossing the antenna on multiple occasions. For example, of the 29 adult carp tagged in 2015, 12 were detected by the antenna, many on multiple occasions in the same year. Similarly, of the 511 adult carp tagged in 2016, 127 were detected by the antenna in the same year (Supplementary material Figure S1).

As a result of winter seining, 340 carp were captured in Long Lake in February 2016, including 11 marked individuals. This suggested that the lake was inhabited by approximately 20,600 carp. Length and age analyses showed that no age-0 carp (which at the time of winter seining were age-1) were present among the captured fish. Boat electrofishing surveys conducted in July 2016 resulted in capturing 201 carp. The mean catch per hour (53.5) suggested that the lake was inhabited by approximately 17,560 carp at that time. Length and age of captured carp showed that approximately 16.3% of the population (2,862 carp) was comprised of age-1 carp (the 2015 year class; Figure 7). This suggested that approximately 41 carp per hectare recruited into Long Lake between July 2015 and July 2016 from the 2015 year class produced in Lino Lakes.

Discussion

The goal of this study was to estimate the outmigration of YOY carp from two seasonally-unstable marshes to downstream lakes in the northern temperate region of North America. Our results suggest that the outmigration rate of YOY carp is low, but can vary substantially from year to year. Between 0.2% and 5.5% of PIT tagged carp were detected moving from the marshes to lakes, and the mean daily outmigration probabilities ranged between $4.5 \cdot 10^{-5}$ and $1.3 \cdot 10^{-3}$. These values encompass a previous estimate from trap net catch rates, which suggested that 0.3% of YOY carp outmigrate in the first year (Bajer et al. 2015). Nevertheless, while only a low percentage of YOY carp outmigrate, the number of migrants can still be significant because densities of YOYs in nursery lakes can be very high (often 2,000–6,000 per hectare; Bajer et al. 2015). This was illustrated by Lake Staring, where approximately 4,500 carp recruited into the lake as a result of recruitment events that occurred in the upstream marsh in 2013 and 2015. This caused the population of carp in Lake Staring to more than double. A significant number of carp (~ 2,800) also recruited into Long Lake from Lino Lakes.

Documenting outmigration of YOY carp from marshes into lakes is of critical importance for carp management schemes that utilize integrated pest management strategies. Such strategies target multiple weaknesses in pest's life history and need to be guided by robust data to be cost effective. For example, targeting winter aggregations of adult carp using the "Judas fish" is often used to affect removal (Bajer et al. 2011). However, estimates of the immigration of recruits from marshes, such as those provided in this study (~ 20 to 50 carp/ha), are needed to inform frequency and intensity of such removal strategies so that the biomass of managed populations does not exceed a management threshold, which is often defined as one hundred kilograms per hectare (Bajer et al. 2009). Such direct estimates of recruitment are also needed to ground truth existing models that are used to guide carp management schemes (Bajer et al. 2015; Lechelt and Bajer 2016). In situations where simple removal schemes, such as the "Judas fish", are unlikely to compensate for juvenile immigration, which might occur when multiple large marshes are adjacent to a lake, outmigration deterrents, such as acoustic curtains (Zielinski and Sorensen 2016), could be used to slow down outmigration. Our data suggest that such systems should be particularly important during warm months of the year when most outmigration occurred. Finally, aerating marshes could reduce the risk of winterkills and curb carp recruitment by supporting native predators (Bajer et al. 2012). Multiple alternative strategies could be crafted to manage carp populations in lake-marsh systems; however, robust information on juvenile immigration into lakes from adjacent marshes is important to maximize cost-effectiveness of such strategies.

Relatively low outmigration rates of YOY carp (< 6% of tagged carp) from marshes in Minnesota may be a result of the absence of important environmental cues that drive outmigration in native habitats. In their native range, carp spawn in seasonally inundated floodplains, from which the juveniles might be forced out by rapidly receding water levels (Balon 2004). A similar pattern was also documented in the Murray Darling River in Australia, where most carp recruitment occurred within inundated floodplains and where YOY outmigration into the main channel of the river was driven by receding water levels and summer hypoxia in the stagnant pools of residual floodplain habitats (King et al. 2003; Stuart and Jones 2006). Environmental cues, such as receding water levels, might be subtler or absent in marshes in Minnesota where water levels are more stable. Nevertheless, the "reluctance" of YOY carp to migrate downstream may also suggest that there is a strong evolutionary disadvantage to leaving nursery habitats. In carp's native habitat (large lowland rivers), juveniles cyprinids that leave floodplain habitats too early are likely to have a lower chance of survival due to predation and lack of shelter in the main river channel (Staas and Neumann 1994; Grift et al. 2003; Janáč et al. 2010). YOY carp might have evolved a tendency to remain in sheltered floodplain habitat by employing positive rheotaxis to avoid being swept downstream into the main channel of the river. We did observe some evidence of positive rheotaxis in PCCA, where YOY carp often aggregated at and attempted to jump over a lowhead dam at the inlet. Positive rheotaxis is poorly documented in YOY carp, but might be important in situations where lakes are located upstream of nursery marshes (e.g. Bajer and Sorensen 2010).

The highest number of outmigrating YOY carp occurred in PCCA in August 2015 when the water level declined by approximately 15 cm over a two-week period at a time when abundance of YOY carp in PCCA was high. During that time, large areas of PCCA were shallower than 20 cm and piscivorous birds such as American pelicans (*Pelecanus erythrorhynchos* Gmelin, 1789), double-crested cormorants (*Phalacrocorax auritus* Lesson, 1831), egrets (*Ardea alba* Linnaeus, 1758), and blue herons (*Ardea herodias* Linnaeus, 1758) were seen foraging on juvenile fishes. The threat of avian predation has been shown to force other fish species to occupy deeper or more sheltered environments (Power et al. 1989; Tabor and Wurtsbaugh 1991; Gregory 1993; Allouche and Gaudin 2001) and might have contributed to higher outmigration of YOY carp. Although we observed avian predators in 2013, equally severe declines in water level were not observed in PCCA, which perhaps explains lower outmigration rates during that year. Declines in water level in PCCA in the fall (October–November) of either 2013 or 2015 did not coincide with outmigration events, possibly because the abundance of YOY was greatly reduced by then (4% daily mortality rate). Water levels were not monitored with high scrutiny in Lino Lakes, however, these systems are generally deeper than PCCA, and have much more stable water levels due to larger, more hydrologically stable watershed (lower percentage of impervious surface). Overall, our findings suggest that most YOY outmigration might occur in the summer (July–September) when the abundance of YOY carp in nursery areas is high and when water levels decline. However, the hypothesis that low water levels in the summer might increase the outmigration of age-0 carp needs to be verified by future studies. If this hypothesis is supported by future data, artificially increasing or stabilizing water levels using simple mechanical structures (e.g. stop logs) might be beneficial in reducing YOY carp outmigration from marshes into lakes. Future studies should also address if such management strategies might have inadvertent impacts on outmigration behavior of native species.

This study shows that carp have low tendencies to migrate out of marshes and into lakes in the first and second year of life, but it is not clear if the tendencies to outmigrate might increase in subsequent years of life. Drawing conclusions about outmigration tendencies of age-1 and age-2 carp was complicated in this study by the high mortality rates in the marshes (especially PCCA). Had the overwinter survival been higher, perhaps more carp would be seen outmigrating at age 1 or 2. Using largely anecdotal data, Bajer et al. (2015) suggested that outmigration rates remain low during the second year of life (age-1) but might increase in the third year (age-2) possibly in association with sexual maturation. It has also been shown that adult carp that migrate into marshes from lakes to spawn readily leave those systems after spawning (Bajer and Sorensen 2010; Bajer et al. 2015, Chizinski et al. 2016). It therefore appears that the tendency of carp to migrate out of marshes and into lakes increases at some point between YOY and adulthood. We suggest that future studies address this phenomenon in detail to inform more effective management strategies. Finally, it is worth pointing out that the decision not to outmigrate at YOY is maladaptive in many marsh-lake systems in northern temperate regions, such as Minnesota, where many shallow marshes experience severe winterkills that are likely to cause very high mortality rates among carp that overwinter there. In support of this argument, no age-1 carp were captured in trap net surveys in PCCA in 2014 (after the strong 2013 year class), and only 4 were captured in Lino Lakes in 2016 (after the strong 2015 year class). Because outmigration tendencies of juvenile carp are an important driver of carp abundance in lake-marsh systems (Lechelt and Bajer 2016), we suggest that this poorly-understood phenomenon is addressed in greater detail in future studies.

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References

Allouche S, Gaudin P (2001) Effects of avian predation threat, water flow and cover on growth and habitat use by chub, *Leuciscus cephalus*, in an experimental stream. *Oikos* 94: 481–492, https://doi.org/10.1034/j.1600-0706.2001.940310.x

Bajer PG, Beck MW, Cross TK, Koch JD, Bartodziej WM, Sorensen PW (2016) Biological invasion by a benthivorous fish reduced the cover and species richness of aquatic plants in most lakes of a large North American ecoregion. *Global Change Biology* 22: 3937–3947, https://doi.org/10.1111/gcb.13377

Bajer PG, Chizinski CJ, Silbernagel JJ, Sorensen PW (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, https://doi.org/10.1007/s10530-012-0203-3

Bajer PG, Chizinski CJ, Sorensen PW (2011) Using the Judas technique to locate and remove wintertime aggregations of invasive common carp. *Fisheries Management and Ecology* 18: 497–505, https://doi.org/10.1111/j.1365-2400.2011.00805.x

Bajer PG, Parker JE, Cross TK, Venturelli PA, Sorensen PW (2015) Partial migration to seasonally-unstable habitat facilitates biological invasions in a predator-dominated system. *Oikos* 124: 1520–1526, https://doi.org/10.1111/oik.01795
Bajer PG, Sorensen PW (2010) 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. *Biological Invasions* 12: 1101–1112, https://doi.org/10.1007/s10530-009-9528-y
Bajer PG, Sorensen PW (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, https://doi.org/10.1080/02755947.2012.690822
Bajer PG, Sullivan G, Sorensen PW (2009) Effects of a rapidly increasing population of common carp on vegetative cover and waterfowl in a recently restored Midwestern shallow lake. *Hydrobiologia* 632: 235–245, https://doi.org/10.1007/s10750-009-9844-3
Balon EK (2004) About the oldest domesticates among fishes. *Journal of Fish Biology* 65: 1–27, https://doi.org/10.1111/j.0022-1112.2004.00563.x
Banet NV (2016) Partial migration, homing, diel activity, and distribution of adult common carp across a large, model watershed in the North American Midwest. Master's thesis. University of Minnesota, Minnesota, United States, 139 pp
Bayley PB, Austen DJ (2002) Capture efficiency of a boat electrofisher. *Transactions of the American Fisheries Society* 131: 435–451, https://doi.org/10.1577/1548-8659(2002)131<0435:CEOABE>2.0.CO;2
Chapman DG (1954) The estimation of biological populations. *Annals of Mathimatical and Statistics* 25: 1–15
Chapman DG, Robson DS (1960) The analysis of a catch curve. *Biometrics* 16: 354–368
Chizinski CJ, Bajer PG, Headrick ME, Sorensen PW (2016) Different Migratory Strategies of Invasive Common Carp and Native Northern Pike in the American Midwest Suggest an Opportunity for Selective Management Strategies. *North American Journal of Fisheries Management* 36: 769–779, https://doi.org/10.1080/02755947.2016.1167141
Clark CF (1950) Observations on the spawning habits of the northern pike, *Esox lucius*, in northwestern Ohio. *Copeia* 1950: 285–288, https://doi.org/10.2307/1437909
Gregory RS (1993) Effect of turbidity on the predator avoidance behaviour of juvenile chinook salmon (*Oncorhynchus tshawytscha*). *Canadian Journal of Fisheries and Aquatic Sciences* 50: 241–246, https://doi.org/10.1139/f93-027
Grift RE, Buijse AD, Van Densen WLT, Machiels MAM, Kranenbarg J, Klein Breteler, JGP, Backx JJGM (2003) Suitable habitats for 0-group fish in rehabilitated floodplains along the lower River Rhine. *River Research and Applications* 19: 353–374, https://doi.org/10.1002/rra.711
Janáč M, Ondračková M, Jurajda P, Valová Z, Reichard M (2010) Flood duration determines the reproduction success of fish in artificial oxbows in a floodplain of a potamal river. *Ecology of Freshwater Fish* 19: 644–655, https://doi.org/10.1111/j.1600-0633.2010.00449.x
Jonsson B, Jonsson N (1993) Partial migration: niche shift versus sexual maturation in fishes. *Reviews in Fish Biology and Fisheries* 3: 348–365, https://doi.org/10.1007/BF00043384
King AJ, Humphries P, Lake PS (2003) Fish recruitment on floodplains: the roles of patterns of flooding and life history characteristics. *Canadian Journal of Fisheries and Aquatic Sciences* 60: 773–786, https://doi.org/10.1139/f03-057
Koch JD (2014) Source-sink population structure of invasive common carp in a model Midwestern watershed: empirical evidence and notes on management. Master's thesis. University of Minnesota, Minnesota, United States, 105 pp
Lechelt JD, Bajer PG (2016) Modeling the potential for managing invasive common carp in temperate lakes by targeting their winter aggregations. *Biological Invasions* 18: 831–839, https://doi.org/10.1007/s10530-016-1054-0
Morman RH, Cuddy DW, Rugen PC (1980) Factors influencing the distribution of sea lamprey (*Petromyzon marinus*) in the Great Lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 37: 1811–1826, https://doi.org/10.1139/f80-224
Osborne JB (2012) Distribution, abundance and overwinter survival of young-of-the-year common carp in a Midwestern watershed. Master's Thesis. University of Minnesota, Minnesota, United States, 132 pp
Power ME, Dudley TL, Cooper SD (1989) Grazing catfish, fishing birds, and attached algae in a Panamanian stream. *Environmental Biology of Fishes* 26: 285–294, https://doi.org/10.1007/BF00002465
Sepulveda AJ, Rutz DS, Ivey SS, Dunker KJ, Gross JA (2013) Introduced northern pike predation on salmonids in southcentral Alaska. *Ecology of Freshwater Fish* 22: 268–279, https://doi.org/10.1111/eff.12024
Silbernagel JJ, Sorensen PW (2013) Direct field and laboratory evidence that a combination of egg and larval predation controls recruitment of invasive common carp in many lakes of the Upper Mississippi River Basin. *Transactions of the American Fisheries Society* 142: 1134–1140, https://doi.org/10.1080/00028487.2013.788889
Staas S, Neumann D (1994) Reproduction of fish in the lower river Rhine and connected gravel-pit lakes. *Water Sciences and Technology* 29: 311–313
Stuart IG, Jones M (2006) Large, regulated forest floodplain is an ideal recruitment zone for non-native common carp (*Cyprinus carpio* L.). *Marine and Freshwater Research* 57: 333–347, https://doi.org/10.1071/MF05035
Tabor RA, Wurtsbaugh WA (1991) Predation risk and the importance of cover for juvenile rainbow trout in lentic systems. *Transactions of the American Fisheries Society* 120: 728–738, https://doi.org/10.1577/1548-8659(1991)120<0728:PRATIO>2.3.CO;2
Zielinski DP, Sorensen PW (2015) Field test of a bubble curtain deterrent system for common carp. *Fisheries Management and Ecology* 22: 181–184, https://doi.org/10.1111/fme.12108
Zielinski DP, Sorensen PW (2016) Bubble Curtain Deflection Screen Diverts the Movement of both Asian and Common Carp. *North American Journal of Fisheries Management* 36: 267–276, https://doi.org/10.1080/02755947.2015.1120834

Supplementary material

The following supplementary material is available for this article:

Figure S1. The number adult carp detected by the antenna located downstream of Lino Lakes.

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