

## ORIGINAL ARTICLE

# Migration, homing and spatial ecology of common carp in interconnected lakes

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**Abstract**

The common carp, *Cyprinus carpio*, is a large, long-lived, fecund and mobile cyprinid, which evolved in complex inter-braided Ponto-Caspian rivers that experience both springtime flooding and freezing winters. Studies suggest adults often move to productive, shallow lakes and floodplains to spawn because they often lack egg predators and then return to deeper normoxic waters to overwinter. Whether these movements involve individuals consistently selecting, or homing to, the same spawning and refuge lakes as part of a strategy benefiting their reproductive success is unknown. To address this question, we examined the movements of 67 radio-tagged adult carp for 3 years in a watershed with 11 interconnected lakes. Carp were tagged and released into a centrally located, normoxic deep lake in spring and fall. Each spring over 95% of its adults left via a single stream and swam into one of 5 shallow lakes, with most individuals (84%) selecting the same lake(s) in which to spawn each year (median Bhattacharyya affinity coefficient of similarity of 0.82). Young were later found in those lakes without egg predators, which cannot survive winter anoxia. After spawning, carp spent summers moving between productive lakes in an individualistic fashion, presumably foraging, with most (89%) eventually returning to the same deep lake to overwinter (median Bhattacharyya affinity of 1.0). These movements appear to reveal a life-history tactic involving seasonal homing migration, first to a spawning location and later to winter refuges, that is well adapted to productive but highly heterogeneous and interconnected freshwater environments.

**KEYWORDS**

foraging, homing, invasive species, refuge, spawning

## 1 | INTRODUCTION

The spatial ecology of many temperate freshwater fishes is complex, presumably because of the heterogeneous nature of their habitats, which can be spatially complex and experience erratic seasonal cycles of flooding and hypoxia. Indeed, dozens of species found in these temperate regions, and Europe in particular, have now been shown to exhibit migratory movements among weakly connected

waterbodies, often using adjoining shallow lakes and/ or seasonally available floodplains for spawning or refugia (Lindsey & Northcutt, 1963; Lucas & Baras, 2001; Tyus, 1991; Whelan, 1983). Generally, these movements involve entire populations, but in some instances, they may involve only parts of populations, a phenomenon known as partial migration (Chapman et al., 2011a, b). Both full and partial migrations can be highly prescribed and involve individuals traveling to specific locations, a phenomenon known as homing (Dingle,

1996). Presumably, homing is used to locate waterbodies of unique and predictable ecological significance in complex, large, and/or unpredictable environments, but this phenomenon is not well studied apart from the anadromous salmonids (Ueda, 2014). The spatial ecology of fishes appears to be especially complex in temperate rivers and interconnected lakes, which experience both spatial and temporal heterogeneity because of flooding, extreme temperatures and the presence of large flood plains and high productivity, and it has only been investigated a few times (Lucas & Baras, 2001).

The common carp, *Cyprinus carpio* (or “carp”), is a large river cyprinid from the Ponto-Caspian whose widespread distribution in extremely heterogeneous, yet productive temperate ecosystems, make it a good model to understand the ecology of freshwater fishes in these systems (Balon, 1995a, b; Sorensen & Bajer, 2011; <https://www.fishbase.in/search.php>). Results of studies from within its native range (Balon, 1995a, 2004; Ciolac, 2004), as well as ecosystems into which it has been introduced (Bajer & Sorensen, 2010; Hennen & Brown, 2014; Taylor et al., 2012; Watkinson et al., 2021), suggest that adults of this species employ a combination of both spawning and refuge movement patterns. However, there is little consensus as to how extensive or systematic these movements are, or their ecological significance (Bajer & Sorensen, 2010; Chizinski et al., 2016; Hennen & Brown, 2014; Penne & Pierce, 2008; Weber & Brown, 2009). In addition, there are observations of adults seeking overwintering refuges; however, this information is largely anecdotal and based on wintertime in-lake movements in North America (Bajer et al., 2011; Johnsen & Hasler, 1997; Watkinson et al., 2021).

The possibility that adult common carp perform regular movements benefitting reproductive success is intriguing. Unlike many fishes, its spawning habitat rarely seems to be limited, but its nursery habitat may be as female carp spawn only one—few times a year and onto common shallow aquatic plants (McCrimmon, 1968) where their eggs appear to be highly susceptible to predation as do their fry (Bajer et al., 2012; Silbernagel & Sorensen, 2013). In contrast, juvenile and adult carp are omnivorous and grow quickly to a large size so they seemingly face little predation pressure (Swee & McCrimmon, 1966). Although the carp tolerates a wide range of temperatures (2–30°C), it does not tolerate oxygen levels below 2 mg/L (Bauer & Schlott, 2006; Billard, 1999) that are also often observed in highly productive temperate ecosystems (Bajer et al., 2012; Bajer & Sorensen, 2010). These broad spawning and feeding requirements seemingly make the carp well suited to productive ecosystems with a wide variety of possible food items, but recruitment appears to be key to the life cycle because of egg/larval predators as does adult survival because of winter anoxia.

One ecoregion where the common carp thrives is the Upper Mississippi River Basin of North America, especially where it overlaps with the Great Plains Ecoregion (Bajer et al., 2015a). This region is characterised by interconnected lakes, wetlands and rivers. The summers and winters are harsh and unpredictable, and aquatic environments typically have high nutrient loads and productivity. Connections among waterbodies can be extremely complex, with dozens being linked via ephemeral waters and draining into rivers

that frequently flood. Depending on local weather, winter and summer hypoxia are commonplace but vary greatly among environments. Although the biomass of carp is high in the Great Plains Ecoregion, recruitment varies greatly by year and is restricted to a small percentage of the productive shallow lakes and wetlands (Bajer et al., 2012). This pattern has been attributed to a tendency of adult carp to overwinter in deeper lakes that rarely winterkill and then move each spring to spawn in connected shallower lakes and wetlands that do have winterkills and thus lack the fishes that prey on eggs and young (Bajer & Sorensen, 2010; Dauphinais et al., 2018). Studies of adult carp leaving deep lakes in the spring have shown that these fish appear to favour one outlet (or inlet) but offered no explanation as to why (Chizinski et al., 2016). In addition, these studies have also not yet provided any information on whether individual carp make the same choice(s) of migratory route every year, or whether/when these adults might return to the same deep lakes (Bajer et al., 2015b; Chizinski et al., 2016). One study using genetic markers suggested that adult carp leaving lakes might be homing, but data were limited to a single year (Dauphinais et al., 2018). Homing behaviour might be adaptive because different lakes experience winterkills with different frequencies and tend to have different populations of native fishes (Bajer et al., 2012; Tonn & Paszkowski, 1986) including the bluegill sunfish, *Lepomis macrochirus*, which is known to consume large numbers of carp eggs and larvae (Bajer & Sorensen, 2010; Silbernagel & Sorensen, 2013). Finally, although adult carp have been shown to aggregate in specific deep-water lakes during winter (Bajer et al., 2011), the reasons for and mechanisms of movements into these lakes from spawning lakes are unclear. In sum, information from prior research suggests carp have a remarkably adaptive life history involving migrations for spawning and winter refuge use, which is well suited to temperate ecosystems whose conditions vary over both space and time. However, whether these movements involve homing behaviour and how they might affect reproductive success and survival has not been elucidated.

In this study, we asked whether adult common carp perform systematic homing migrations to particular lakes to spawn each spring and then return to specific refuge lakes each summer/ fall to overwinter. In addition, we sought to characterise the nature of any movement patterns we might document and to consider their ecological and evolutionary significance, including any effect on reproductive success. To address these issues, we conducted a 3-year-long tracking study of adult common carp in a large and complex system of interconnected lakes while collecting information on carp distribution and ecology of the waters into which they moved.

## 2 | METHODS

### 2.1 | Study area

This study was conducted in the lower portion of the Rice Creek Watershed (Minnesota, USA), which contains 11 interconnected lakes along with a variety of smaller associated marshes and

wetlands (45.0536N, 93.1142W; Table 1; Figure 1). This watershed drains into the Mississippi River and is like many lake systems in the Upper Mississippi River Basin and other previously glaciated lake systems throughout the world (see Bajer & Sorensen, 2010; Dauphinais et al., 2018). Its shallow lakes and wetlands vary greatly in size, tendency to winterkill and productivity, although most are highly productive and eutrophic (total dissolved phosphorous often exceeds 100 µg/L) (Table 1; Figure 1). Long Lake is located near the geographic centre of this watershed and is the deepest lake (9 m). It has three inlets and a single outlet, is one of the least productive of the lakes and is not highly subject to winterkill. Rice Creek, the largest inlet (and outlet), flows through Long Lake and then west. Five, large but shallow (<3 m deep), lakes are located approximately 12 km upstream of Long Lake (Baldwin Lake, George Watch Lake, Marshan Lake, Reshanau Lake and Rice Lake). These shallow lakes have robust populations of submerged plants and extensive littoral zones. Several smaller lakes are located to the south and west of Long Lake. At the time of the study, Long Lake was known by commercial fishers (Jeff Riedemann, personal communication) to contain a large number of overwintering carp, which was later estimated to be ~20,000 adults (Bajer et al., 2018). In most years, connections between the 5 lakes are open year-round, although connections to the south of Long Lake are ephemeral. At the outlet of the watershed, and just upstream of its confluence with the Mississippi River, is a large dam that blocks upstream-swimming fish. In addition, four small dams also block upstream movements of common carp under most flow conditions. Temperatures in the summer exceed 30°C and in the winter can fall to -30°C.

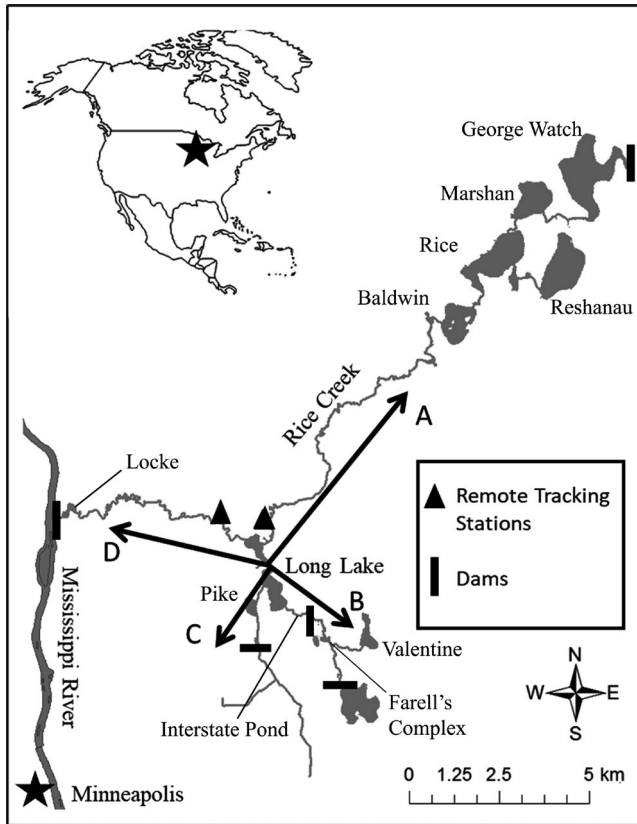
## 2.2 | Experimental design

Adult carp were captured in Long Lake, radio-tagged and then released on three occasions to minimise possible artefacts associated with date of capture: September 2013 (before ice formed), April 2014 (after ice thawed) and October 2014. We chose Long Lake because it was the only lake that did not experience winterkill and was known from commercial fishing to have many adult carp in the winter (see Section 2.1). We tagged as many carp as we could reasonably manage on each occasion (Table 2;  $N = 67$ ). After radio-tagging, we then attempted to locate all radio-tagged carp at least every other week throughout the entire study area using manual tracking (see below). Two continuously recording remote tracking stations were also positioned at the inlet and outlet to Long Lake in Rice Creek to determine the timing of carp movements out of Long Lake. Lake and stream temperatures were recorded using archival temperature loggers (HOBO UA-002-64 Pendant; Onset Computer Corporation) placed into Long Lake, Peltier Lake, Rice Creek and Rice Lakes. These loggers recorded water temperatures between April 21 and July 14, 2014; August 3 and December 29, 2014; March 16 and December 31, 2015; and January 1 and July 4, 2016. Dissolved oxygen levels were also measured several times in most lakes in the mid-winter of 2014–2015 and sporadically thereafter using an oxygen probe (YSI 85; Yellow Springs, OH, USA) after drilling holes in the ice. Data on winterkill, water clarity (Secchi depth), productivity (total dissolved phosphorous), and summertime juvenile fish communities were obtained from the Rice Creek Watershed District as part of their regular summertime sampling and research programmes.

**TABLE 1** Main lakes in the study area, their surface areas, maximum depths, mean Secchi depth (summer), mean phosphorus concentration (summer), dissolved oxygen in winter 2015, and average number of bluegill sunfish (carp egg predator) and YOY carp caught in fall 2015. Data were not available or collected for some of the smaller lakes and wetlands

Lake	Area (ha)	Max depth (m)	Secchi depth (m)	TP average (µg/L) <sup>A</sup>	DO mg/L <sup>B</sup>	BLG <sup>C</sup>	CRP <sup>C</sup>
Long	69	9.1	1.0	64	3.8	88	2.4
Baldwin <sup>W</sup>	76	1.5	-	-	2.11	14.4	8.2
Rice <sup>W</sup>	150	1.5	0.7	120	-	10.3	41.8
Marshan <sup>W</sup>	82	1.5	1.2	110	-	4.5	48.8
George Watch <sup>W</sup>	196	1.5	0.5	186	2.0	12.6	25.0
Reshanau <sup>W</sup>	136	3.0	0.8	94	1.9	5.2	0.4
Pike <sup>W</sup>	14	2.7	1.1	70	-	26.3	0
Locke	9	1.5	1.0	69	-	-	-
Valentine <sup>W</sup>	24	4	1.9	67	-	-	-
Interstate <sup>W</sup>	1	-	-	-	-	-	-
Farrel's C. <sup>W</sup>	25	-	-	-	-	-	-

A, total dissolved total phosphorous (TP) levels measured mid-summer as reported by the RCWD; B, average dissolved oxygen levels measured by us February 20, 2015 (1–5 points per lake); C, average number of bluegill sunfish (BLG) or YOY carp (CRP) captured per trap-net in sets of 5 standard survey trap-nets in late summer 2015 as reported by Bajer et al. (2018a); W, known to commonly winterkill as reported by the Rice Creek Watershed District (RCWD);



**FIGURE 1** The Rice Creek Chain of Lakes. Long Lake is close to its centre and has three inlets and one outlet that we characterise as movement paths (A, B, C and D) by which carp can move to other lakes. Remote tracking stations are represented as triangles. The system has one large dam at the outlet of the watershed that blocks fish passage under all conditions except for 500-yr flood events. The system also has several low-head dams that block fish migration during most flow levels (rectangles). During flood conditions, these low-head dams can be passable

### 2.3 | Fish collection and tagging

Adult carp (>300 mm TL) were captured using electrofishing by boat following established procedures (pulsed DC electric field, 5–12 A 80–150 V, 20% duty cycle, 120-pulse frequency; see Bajer & Sorensen, 2010). Carp were captured in shallow areas with vegetation or woody debris near the shoreline from all areas of this lake. Following established procedures (Bajer & Sorensen, 2010; Penne & Pierce, 2008), these carp were anaesthetised with eugenol (100 ml/L) and a small 3- to 4-cm incision was made on the ventral side of the fish between the pelvic and anal fins. Adult carp were then implanted with individually coded sterile radio-transmitters (model number F1850, pulse rate = 35 pulses per minute (ppm), pulse width = 16 ms, battery life = 1941 days and mortality option (signal) after 24 h of inactivity with a pulse rate of 70 ppm; Advanced Telemetry Systems Inc). We used the shielded needle technique to thread the external whip antenna through the abdominal cavity and musculature to the fish's exterior (Ross & Kleiner, 1982) and closed the wound with several absorbable sutures (Ethicon) every 0.5 cm

(Bajer & Sorensen, 2010; Penne & Pierce, 2008). Tags weighed 23 g and were <2% of the body weight of the fish. These tags were sensitive to movement and if inactive for more than 24 h, emitted a distinctive code (70 ppm) until their battery died. Following surgery, carp were held in a recovery tank refreshed with lake water and released after 30 minutes into a central location of Long Lake. Procedures were approved by the University of Minnesota IACUC (protocol 1201A08922).

### 2.4 | Locating tagged carp

We conducted manual telemetry surveys during daylight hours to locate radio-tagged carp weekly from October 2013 to November 2015, biweekly from January 2016 to March 2016, and weekly from May 2016 to June 2016. We started tracking fish one to two weeks after their being tagged and surveyed all lakes and streams on each occasion by walking the shore, using small boats, or walking on the ice in the winter. A survey usually took two 8-hour days. We searched for all radio-tag frequencies using a scanning receiver (model number R2000; Advanced Telemetry Systems Inc). When a fish was located, we used a GPS to determine location in Universal Transverse Mercator (UTM) coordinates and a compass to take a bearing to the signal, before moving to another location and recording its position at an angle approximately 90° from the first bearing. Computer software (LOAS® 4.0; Ecological Software Solutions) was later used to calculate the intersection of the two bearings and provide a location in UTM units, which could be plotted on ArcGIS Pro 2.2 (Redlands, CA: Environmental Systems Research Institute). When searching for fish, we also looked for spawning activity (e.g. groups of carp splashing at the surface in submersed plants).

During telemetry surveys, each tag's status was assigned one of three conditions: active, inactive or not present (i.e. "lost"). Tags initially found to signal inactivity were monitored at least twice for the next month to confirm the tag's location, while that area was carefully searched for dead fish and expelled tags (neither were ever found). After a month of signalling inactivity, these tags were no longer checked and assigned the status of being inactive (Table 2). We never stopped searching for lost tags whose fate might include the fish leaving the study area and/or tag failure (Table 2). We estimated the accuracy of our technique by calculating the average distance between estimated and true locations using two dummy tags and found it to be <20 m. The maximum detection range for radio-tags was approximately 1000 m across open water in shallow lakes (approximately 2.0 m in depth) but was reduced to 200 m when tags in deep water (9.0 m). During winter, detection range was approximately 400 m.

We supplemented manual tracking with two stationary continuously scanning remote receivers equipped with data-loggers (model number R4500SD; Advanced Telemetry Systems Inc). They were positioned at the inlet and outlet of Long Lake along Rice Creek and collected data on carp movement in and out of Long Lake. A control tag was located at each tracking station and monitored every

**TABLE 2** The number of fish captured, tagged and released during 2013–2014 in Long Lake, tag status at the end of the experiment, fork length, mean number of days tracked and location of last detection. Active = detected and emitting active signal for the entire experiment; Inactive = detected emitting inactive signal at some point before the end of the experiment; and Lost = tag could not be located at some point after release. Shallow lakes refer to 5 shallow lakes in the northeast region of the subwatershed

Tagging dates	Tag status	No.	Ave. Carp Fork length (mm; SD)	Mean days detected (SD)	Location last detected		
					Long Lake	Rice Creek	Shallow Lakes
9/19-9/26/2013	Active	2	534 (17)	1000 (7)	-	-	2
	Inactive	11	569 (46)	351 (330)	5	2	4
	Lost	2	570 (5)	302 (426)	-	1	1
4/21/2014	Active	3	543 (25)	791 (0)	3	-	-
	Inactive	7	566 (16)	149 (159)	3	-	4
	Lost	1	672	446	1	-	-
10/7-10/20/2014	Active	33	583 (45)	617 (5)	6	-	27
	Inactive	5	629 (63)	336 (162)	1	-	4
	Lost	3	597 (65)	461 (179)	-	-	3

hour to confirm proper operation and cycled continuously through all radio-tag frequencies between April and October 2014; March and November 2015; and March and June 2016. Stations were located on the bank of Rice Creek and had two antennas mounted 5 m above the ground and positioned 90° apart with one facing upstream and the other facing downstream. The 90° angle opened towards the creek along a linear reach. Detection range was estimated to be 400 m in both directions from the remote station and did not include Long Lake. When a tag was detected by a remote receiver, its data-logger recorded the frequency, signal strength, date, time, pulse rate (35 ppm for active tags and 70 ppm for inactive tags) and antenna number. This configuration allowed us to identify direction of movement to and from Long Lake using signal strength. The tracking station located downstream of Long Lake (Figure 1) also allowed us to monitor for fish leaving the study area via the Mississippi River. No fish tagged were found to have left the system.

## 2.5 | Data analysis

We identified each tag's status at the end of the experiment and compiled summaries for each carp's mean fork length, mean number of days tracked and location of last detection based on tag status (active, inactive or lost). Data were grouped by capture/tagging interval (9/19 – 9/26/2013; 4/21/2014; 10/7 – 10/20/2014; Table 2). We then plotted the distribution of all fish locations by month. Once we had an overall understanding of fish distributions, we proceeded with several analyses to evaluate the regularity of carp movement patterns as described below.

We began our numeric analysis by considering spring–summer–fall movements to and from Long Lake from the time when the first fish was observed to leave Long Lake in the spring until water temperatures fell below 10°C in the fall (when the carp's feeding rate decreases; Song-bo et al., 2012). Each year, we quantified how many adult carp left Long Lake, how many of these carp returned and the

timing of movements to determine their regularity. For annual summaries, we included all fish that were monitored for the full spring-to-fall time period. To be considered a departure from Long Lake, carp had to leave the lake for at least one day (24 h) as measured by either the stationary tracking station or the manual tracking. We also tabulated how many days individuals spent away from Long Lake (mean  $\pm$  standard deviation) and the number of complete out-and-back migrations originating from Long Lake (mean  $\pm$  standard deviation) by year. We defined spawning period using the first and last days that spawning was noted anywhere in the study area each year. We determined where carp were during these periods (if individual carp were found in more than one lake during this period, per cent time in each lake was calculated). Finally, we calculated the average daily water temperature when carp first moved out of Long Lake and the average daily temperature for each spawning period each year. We next characterised the paths that carp took when they left Long Lake each year. Long Lake is connected by four streams (routes) to the rest of the study system, including three inlets (A, B and C) and one outlet (D; Figure 1). In two instances, we observed fish using more than one stream (they returned) so we used their final path. We used a chi-square goodness-of-fit test to evaluate whether carp exhibited a preference for one of the four streams.

To characterise annual patterns of movement, we calculated net squared displacement (NSD), the square of the distance from a point of reference to subsequent locations in the movement path of an animal (Börger & Fryxell, 2012; Singh et al., 2012). The NSD is a well-established technique used to classify animal movement and it allowed us to describe the timing and duration of movements, as well as trends in distribution patterns in a highly quantifiable fashion that match known movement patterns (Spitz et al., 2017). The southernmost point of Long Lake was used as the reference location (i.e. NSD = 0). We calculated NSD for each carp using the actual distance from the reference point to the location of the fish (i.e. following the stream network) and recorded each fish's largest NSD value each week. The NSD statistic provided a relatively

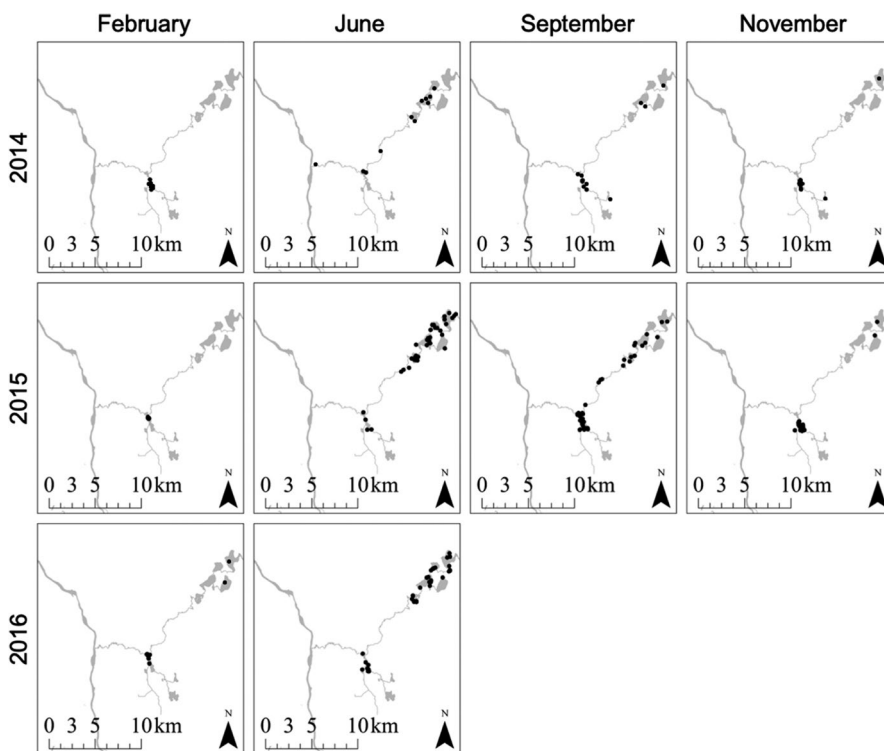


**TABLE 3** Characteristics of carp tagged in Long Lake that were monitored from April to October each year (Monitored No) including the following: the number of carp that moved out of Long Lake (no. Moved); the number that returned to Long Lake (Returned No.); date that migration started (Migrate Start Date); dates spawning were observed (Spawning Dates); water temperature when carp first moved out of Long Lake; average water temperature during spawning; average time away from Long Lake (mean number of days and standard deviation); and the average number of movements that carp performed to and from Long Lake each year

Year	Monitored	Moved	Returned	Migrate start	Spawning	Temp (°C)		Time away	
	No.	No.	No.	Date	Dates	Move	Spawn	No. of days	# Move
2014	12	10	8	4/15	5/22-6/20	7.1	22.6	107 ± 77	1.7 ± 0.7
2015	44	43	39	4/7	5/18-6/22	6.9	21.6	120 ± 61	1.9 ± 0.8
2016	36	35	- <sup>a</sup>	3/14 <sup>b</sup>	5/9-6/20	5.9	21.6	- <sup>a</sup>	- <sup>a</sup>

<sup>a</sup>Tracking ended in June 2016 so return movements and time spent away from Long Lake are unknown

<sup>b</sup>Movement determined using archival remote receiver station



**FIGURE 2** Locations of the Long Lake radio-tagged carp with active transmitters in a given year between February 2014 and June 2016. A total of 12, 44 and 36 carp were plotted in 2014, 2015 and 2016 respectively. Data are shown for February (mid-winter); June (spawning); September (late summer, feeding); and December (early winter) to show their distribution and movement at representative times

straightforward metric to gauge movements over time, especially because carp tended to leave Long Lake via a single route (see Section 3). We plotted average and median NSD values by week, highlighting the spawning period for each year. For 2014 and 2015, we again included all fish that were monitored for the complete spring-to-fall periods. For 2016, we included all fish that were followed from their first departure from Long Lake in the spring until the conclusion of the study. To characterise variability in individual movement patterns, we also plotted individual NSD values for radio-tagged carp monitored between 2014 and 2015, our most data-rich period.

Finally, to determine whether/how individual carp might be homing to specific spawning and/or refuge lake(s), Bhattacharyya's affinity analysis was used (BA; Fieberg & Kochanny, 2005; see

below). First, we plotted distributions of the five fish that had active tags, which also could be tracked across over three years to visually evaluate consistency of lake choice across years. Next, we examined our complete data set (all fish that survived and had active tags for at least two consecutive spawning and/or overwintering periods). First, we tabulated the lake(s) used by all carp for spawning and overwintering across all years. Then, we used the Bhattacharyya's affinity coefficient (BA), a common measure of similarity (Fieberg & Kochanny, 2005), to quantify the degree of consistency (similarity) in the carps' choice of habitat/ lake(s) ( $i$ ) in successive years ( $t$  and  $t+1$ ):

$$BA_i = \sum_{j=1}^{L_i} \sqrt{p_{ij,t}} \sqrt{p_{ij,t+1}}$$

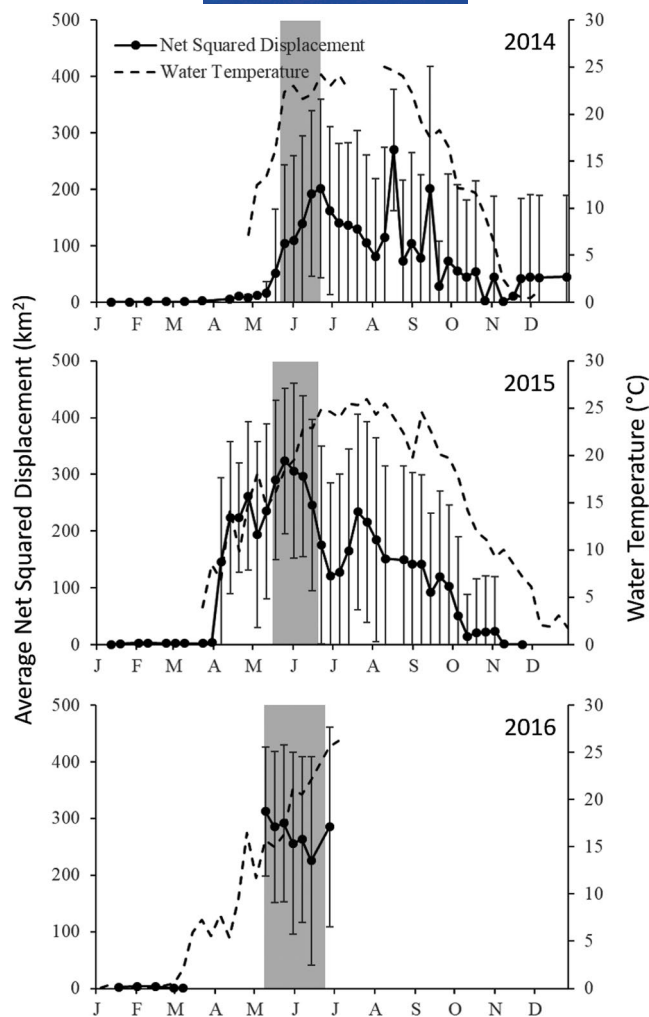
where the sum is over all ( $L_j$ ) lakes visited by carp  $i$  during either the spawning or the overwintering period,  $p_{i,j,t}$  is the proportion of time individual  $i$  spent in lake  $j$  during either the spawning or the overwintering period of year  $t$ , and  $p_{i,j,t+1}$  is the proportion of time individual  $i$  spent in lake  $j$  during either the spawning or overwintering period of year  $t + 1$ . This index assumes a value between 0.0 and 1.0, with a value of 1.0 indicating the carp spent exactly the same amount of time in each of the same lake(s) in consecutive years (perfect overlap), whereas a value of 0.0 indicates the carp was found in an entirely different set of lakes during the years examined. We calculated BAs for all fish that were observed for at least two complete spawning/overwintering periods. We calculated median BA values during the spawning and overwintering periods and plotted their frequency distributions. Median values were calculated because the data were not normally distributed. We used program R (version 1.3.959-1) to calculate and plot BA statistics (R Core Team, 2020). Finally, the total number carp found in each lake during each spawning period each year was tabulated.

### 3 | RESULTS

Sixty-seven carp ( $582 \pm 47$  mm SD) were captured, tagged and released in Long Lake, of which 38 retained their tags and survived (57%) through the end of the study (Table 2; Figure S1). Of the remaining tagged fish, 23 had tags that went inactive at some time during the study (11 during the first year) and 6 were lost and never located again (Table 2). Those carp that survived and retained their tags did not differ in size or gender ( $p > .05$ ) from those whose tags went inactive or were lost. None of the inactive or lost tags were located.

Each year, nearly all fish left Long Lake by June and returned before winter (10 of 12 fish in 2014, 43 of 44 in 2015 and 35 of 36 in 2016; Table 3; Figure 2). Nevertheless, one-to-two fish did not leave Long Lake each year by June, and several also stayed behind in Reshanau, George Watch, and Valentine lakes in November 2014 and 2015 (Figure 2). Of the carp that moved out of Long Lake each year, almost all (97%) used the inlet of Rice Creek to Long Lake (path A) ( $\chi^2$  goodness-of fit test,  $p < .05$ ) with a total of 8, 43 and 35 individuals moving via movement path A in 2014, 2015 and 2016 respectively. In 2014, a high-water year, two carp chose a path other than A, with one fish choosing path B and another choosing path D.

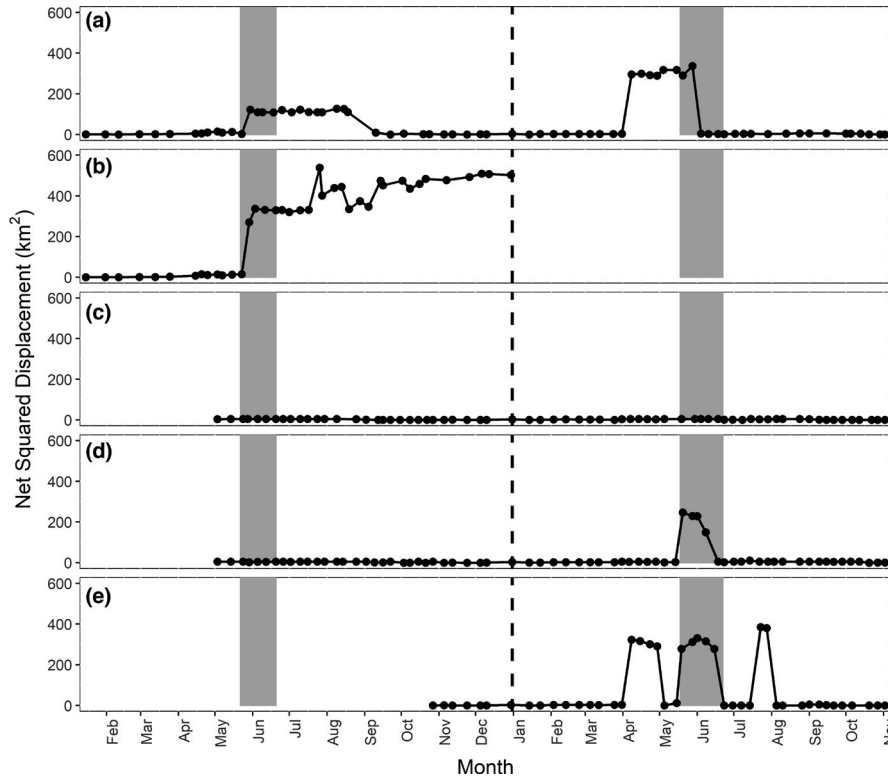
As described above, nearly all tagged carp (83% in 2014; 98% in 2015; and 97% in 2016) left Long Lake each spring between mid-March and mid-April, during which time the temperature of that lake was between 5.9°C and 7.1°C and increasing (Table 3, Figure 3). Carp were first observed to leave Long Lake on April 15 in 2014, April 7 in 2015 and March 14 in 2016 (Table 3). After leaving this lake, carp moved an average of ~15–20 km upstream in 3–6 weeks (average NSD values between 137 km<sup>2</sup> and 273 km<sup>2</sup> during spawning; Figure 3), but there was considerable individual variation with weekly NSD values having a large standard deviation. In all three years, spawning was noted between mid-May and mid-June in all lakes (including Long Lake) when the average temperature of



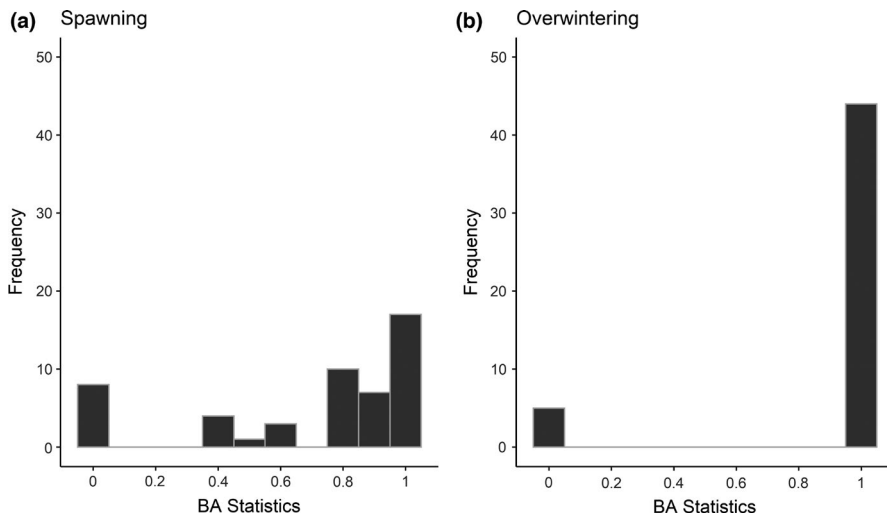
**FIGURE 3** Weekly mean net squared displacement (NSD, the square of the distance from southern end of Long Lake to individual carp locations;  $n = 12$  in 2014;  $n = 44$  in 2015; and  $n = 36$  in 2016). Water temperature is indicated by the orange dashed line, right axis. Bars above and below NSD indicate mean  $\pm$  standard deviation (SD). The dates across which spawning was noted each year are noted. Tracking ceased late spring in 2016 and then resumed later after the ice was completely out before ending early summer in 2016 at project end

all lakes with spawning activity ranged between 21°C and 23°C (Table 3). After spawning, some, but not all, carp showed a tendency to return to Long Lake as weekly mean NSD values dropped (see below). However, most carp returned to Long Lake by October in 2014 and 2015 (no data on return migration were collected in 2016 as the study concluded in June). Separate analyses of the NSD values of carp tagged in the spring versus the fall, and of carp whose tags were active for the entire study ( $n = 38$ ), failed to show any notable differences, suggesting that these results were robust to our choice of inclusion criteria (Figures S2 and S3).

The high variance in the NSD values was attributable to large variation in individual summer movement patterns (Figures 4 and S4). Individual NSD plots for fish that were followed for at least one complete spring-to-fall period demonstrated that although some



**FIGURE 4** Individual net squared displacement values of 5 individual carp that exemplified the 5 types of annual movement patterns we observed. Vertical dashed lines separate year 2014 (left) and year 2015 (right). Shaded grey bars represent observed spawning dates each year. Each point represents when an individual carp was located and lines connect dates. Data for each individual start on the date that their tag was implanted. Five types of movements were seen and are exemplified by the following tracks: (a) an out-and-back movement from Long Lake each year; (b) a movement out of Long Lake in the spring without a return to Long Lake in the winter; (c) a year-long resident in Long Lake; (d) a movement out of Long Lake in the spring with several out-and-back trips before overwintering in Long Lake; and (e) a combination of the aforementioned movement strategies over multiple years (resident in 2014 and out-and-back migrant in 2015). NSD values for all 49 individuals tracked and quantified in this manner are shown in Figure S4



**FIGURE 5** Distribution of Bhattacharyya's affinity (BA) values, an index of similarity, for 45 carp with active transmitters for two consecutive spawning seasons (a) and 46 carp with active transmitters for two consecutive overwintering seasons (b)

fish stayed in spawning lakes most of the summer, nearly all moved, and then in a number of ways (see below). Most fish visited at least 2 lakes each summer (including one or more spawning lakes), but others visited four with nearly a third of all carp returning to Long Lake at least once during that time (Table 3, Figure S4). Movement patterns of carp also varied by year. In 2014, 10 carp spent an

average of 107 days away from Long Lake and made on average 1.7 out-and-back movements to Long Lake during this time. In 2015, 43 carp spent an average of 120 days away from Long Lake, during which time they averaged 2.0 out-and-back movements before returning for the winter (Table 3, Figure S4). We noted five movement patterns among the 49 individuals monitored for at least one



complete spring-to-fall period: (1) 25 individuals (51%) migrated out of Long Lake in the spring with multiple out-and-back trips before overwintering in Long Lake; (2) 16 individuals (33%) completed one annual out-and-back migration originating from Long Lake; (3) four (8%) individuals migrated out of Long Lake in the spring and did not return; (4) 3 individuals (6%) exhibited multiple movement strategies (e.g. one fish was resident in Long Lake one year and then performed one complete out-and-back migration the following year; and (5) one individual (2%) never left Long Lake (Figure 4).

Plots of the 5 carp that survived the entire 3-year study period showed that 4 of these 5 carp selected the same spawning and winter refuge lake each of the 3 years (one never leaving Long Lake), and a fifth changing behaviours in 2016 (Figure S5). Subsequent analyses of the carp for which we had two years of data showed the same phenomenon in which carp repeatedly returned to the same lake(s) during spawning; the median BA coefficient for spawning site selection for the 45 tagged adult carp that survived at least 2 years was 0.82 with just a few individual BA values being less than 0.5 (Figure 5), suggesting a very high level of consistency in spawning lake selection. Nearly 84% of all carp (when averaged across all 3 years) were found in the same lake(s) each year during the spawning period, with 66% using a single lake for spawning, 21% using 2 lakes, and the remaining 13% more than two lakes. Although, on average, less than 10% of all adult carp observed during all spawning periods (2014, 2015 and 2016) were seen in Long Lake during this time, nearly a third (32%) were seen in Rice Lake, 22% in Baldwin, 8% in Marshan, 6% in George Watch and only 2% in Reshanau Lake (Table S1). We only had one complete year of lake sampling data, 2015. It showed that Rice, Marshan, George Watch and Baldwin lakes all had relatively large numbers of young-of-year (YOY) carp (52, 48, 25 and 8 YOY/ trap-net), as well as low numbers of bluegill sunfish (<15 fish/ trap-net) and low (<2 mg/L) mid-winter dissolved oxygen, whereas Long Lake had few YOY carp (2/ trap-net), many bluegill sunfish (88/ trap-net) and mid-winter oxygen levels of nearly 4 mg/L (Table 1).

Remarkably, nearly all carp (89%) returned to Long Lake in the winter during all three years; the median BA coefficient for overwintering site selection for 46 carp was 1.0 (Figure 5). Only 6 of the carp tagged in Long Lake never returned to overwinter in Long Lake after they left. Among the carp with active tags for three consecutive years, all overwintered in Long Lake in all three years (Figure S5). Interestingly, some variation was nevertheless evident. For example, two fish that overwintered in Long Lake one winter returned to Long Lake in the fall before later moving to Pike Lake to overwinter (they were assigned a BA coefficient of 0). Another three fish overwintered in Long Lake their first year, but in subsequent years in a shallow lake (BA = 0.0; Table 3).

## 4 | DISCUSSION

Our study of the movement patterns of 67 adult common carp in a complex heterogeneous ecosystem provides the first data in support

of the hypothesis that this species' life history includes homing as part of regular springtime spawning migrations and autumnal migrations to winter refugia, apparently benefitting reproduction and recruitment. We demonstrated that individual adult carp perform regular springtime spawning migrations to particular outlying shallow lakes and wetland environments (e.g. Rice Lake), which often winterkill and lack piscine micro-predators and where their fry then survive in abundance. Spawning stream choice is highly consistent, presumably because of homing. The extensive postspawning, individualistic movements we observed during the summer months might reflect a foraging strategy and/or tendency to avoid eating their own eggs. Remarkably, not all individuals showed the same behaviours and choices, which varied with year and seemingly reflects partial migration that may be evolutionarily favoured in unstable environments (Bajer et al., 2015b). The longevity and fecundity of this species compliment these flexible yet adaptive movement patterns, which appear well suited to the ecologies of many heterogeneous temperate freshwater ecosystems. Other large river cyprinids may also show similar suites of behaviours in their life histories, which also appear to typify a "periodic" life-history strategy (Winnemiller, 1992).

Our most novel and important finding is likely that adult carp home to shallow lakes to spawn. The median BA values for spawning lake choice was 0.82, showing that nearly all carp used the same lakes to spawn each year. By choosing specific lakes in which to spawn, individual carp are choosing specific streams for migration and therefore selecting between lakes/locations in this highly interconnected system. Remarkably, over half of all adult carp observations during the spawning period occurred in just two lakes, Rice Lake and Baldwin Lake, of the 11 lakes found in this subwatershed. Homing preference appears to correlate with reproductive success; both Rice and Baldwin lakes were later reported to support very high levels of carp recruitment in 2015 (Table 1, below), especially Rice Lake, with 4 of the remaining 5 shallow lakes (including Baldwin Lake) also supporting high numbers of YOY carp but very few YOY were found in Long Lake. Notably, all lakes that supported large number of YOY carp also lacked bluegill sunfish, had suffered winterkills and had high total dissolved phosphorous. Although a relationship between the number of spawning adults and the production of young is to be expected, the magnitude of the relationship we saw was not: Rice Lake produced 20 times the number of young with 3 times the number of adults in 2015, suggesting lakes selected by adult carp function as exceptional nurseries. This observation supports previous suggestions that this species uses source-sink population dynamics (Dauphinais et al., 2018; Sorensen & Bajer, 2020). Although our finding of homing supports previous trapping (Chizinski et al., 2016), genetic studies (Dauphinais et al., 2018) and tracking studies (Watkinson et al., 2021), we had not expected to see carp homing preferences to be so strong or precise. The precision with which individual adult carp choose lakes (and the streams connecting them) to spawn appears to approach that of Pacific salmonids, *Oncorhynchus* sp. (Stewart et al., 2003). That individuals from one population of overwintering carp should select several different

lakes is remarkable, although it may be adaptive given the unpredictability of winterkill in individual lakes (Bajer et al., 2012). This is so because individual carp cannot know or predict whether a particular lake has winter-killed; by spawning in two or more lakes, they may increase their chances of doing so and producing young in any particular year. Homing in carp likely reflects an ability to learn, remember and relocate natal habitat, which could be beneficial in an extremely heterogeneous and changing environment in which particular lakes tend to be more likely on average to serve as suitable spawning and nursery habitats than others (Bajer et al., 2012; Sorensen & Bajer, 2020). Previous studies have shown that juvenile common carp leave shallow nursery/spawning lakes after 1–2 years, presumably to avoid winterkill (Dauphinais et al., 2018; Lechelt et al., 2017).

The timing and manner with which carp performed spawning migrations appears adaptive. Almost all (90–95%) adult carp left Long Lake between March and April each year as water temperatures rose above 5°C, suggesting rising temperature is the trigger. These values are consistent with those noted by others (Chizinski et al., 2016; Watkinson et al., 2021). Rising temperature likely correlates with plant growth and thus spawning site suitability as carp spawn on plants (Bolduan et al., 1994; Brodersen et al., 2011; McCrimmon, 1968). Migratory and sex pheromones may synchronise these events (Sorensen & Baker, 2015; Stacey, 2015). Mass migration and synchronised spawning may reflect a predator-swamping strategy (Sorensen & Bajer, 2020).

After spawning, we found that most adult carp ranged across the watershed, exhibiting one of 5 types of behaviours, three of which involved out-and-back movements to Long Lake as exhibited by specific type of NSD patterns across time. This type of active movement has not been described previously and may reflect a foraging strategy to find the locations with the highest concentrations of food while avoiding their own eggs. Indeed, for a generalist, these areas are likely to coincide with dissolved nutrient levels and vary by lake and shifting carp densities. A numeric model of carp abundance in the Great Plains Ecoregion shows that a combination of water productivity (as measured by clarity), the presence of piscine micro-predators (bluegill sunfish, *Lepomis macrochirus*) and adult propagule pressure can explain their numbers (Bajer et al., 2015a). Adult carp have no known predators of significance, so such movements would have little risk and might also reduce chances of their being stranded in low or hypoxic waters. They likely are not energetically costly, at least compared with movements of large long-lived river species such as shortnose sturgeon (*Acipenser brevirostrum*; Dionne et al., 2013). The tendency of carp to leave spawning lakes could also reflect a tendency to leave areas that might contain their own young, which they could otherwise eat.

The nearly unanimous choice of a single refuge lake, Long Lake, to overwinter (BA coefficient of 1.0) was just as remarkable as the highly targeted and individualistic choice of shallow lakes for spawning. This trait would also appear to be adaptive because Long Lake is the only lake in the watershed that has little chance of winterkilling. Unlike for spawning migration, the timing of the refuge migration was relatively unsynchronised and variable, perhaps because it was

influenced by food availability and declining food drive with dropping temperature. Thus, carp appear to anticipate winter conditions and to leave these regions before winter freeze-up and possible anoxia. Occasional failures to return to Long Lake (e.g. a few fish overwintered in shallow lakes and adult carp mortalities were seen in Reshanau Lake; Banet, 2016) may reflect an inability to gauge the onset of winter freeze-up in temperate lakes, which can be very rapid. Environmental conditions in shallow freshwater lake systems in northern temperate regions are likely different from European rivers and their associated floodplain where carp evolved.

Spawning and refuge migrations involved a variable majority of the population in Rice Creek Watershed, seemingly confirming that the carp's life-history strategy includes partial migration (Bajer et al., 2015b; Chizinski et al., 2016). Bajer et al., (2015b) present models supporting the hypothesis that partial migration is favoured in unstable environments where there is risk of carp being trapped by early freeze-up or choosing unfavourable lakes to spawn. Nearly 90% of the carp we studied in Long Lake migrated to spawn, a number more than twice that seen elsewhere in interconnected lakes (Chizinski et al., 2016) but similar that seen in a very large lake (983,000 h Lake Winnipeg; Watkinson et al., 2021). Variation in the numbers of adults migrating is to be expected with partial migration, depending on local conditions and how reliably they promote individual reproductive success. The large number of shallow lakes in the Rice Creek watershed may have provided a nearly constant and unusually high chance to reproduce; most adults therefore migrate, as has been observed in large lakes (Watkinson et al., 2021). Finally, although several studies show that partial migration can reflect a trade-off between reducing predation pressure on adults and allowing for growth (Brönmark et al., 2008), in common carp it appears to reflect a trade-off between reducing predation risk on eggs and larvae and the risk of anoxia to overwintering adults. Whether native fish species in the Upper Mississippi River basin or Great Plains Ecoregion (or elsewhere) also employ this strategy is an interesting question. One candidate native species is the northern pike, *Esox lucius*, which also migrates each spring (Chizinski et al., 2016).

Our study extended across 3 years and included a high sampling rate, providing a high level of resolution. Forty-nine carp with active transmitters were tracked for at least one out-and-back migratory cycle. The complex, but not atypical, watershed we studied offered carp many stream and lake choices across three years, supporting the conclusion of adaptive behaviour; however, more data would be very helpful especially when considering recruitment for a species with such a complex life history. Our observations confirm trends described in other lake systems (Chizinski et al., 2016), as well as Locke Lake within Rice Creek Watershed where a small number of adult carp were also tagged and tracked and seen to show the same migratory patterns (Banet, 2016). Despite these strengths, our study was complicated by some tags signalling inactivity. This rate was higher than the 5%–10% rate we have seen before (Bajer & Sorensen, 2010). We believe that tag loss, or perhaps dysfunction, was the likely explanation for most reports of tag inactivity because we never found dead fish despite great efforts made to find them.

Nevertheless, tag loss is expected in a three-year study in unstable habitats and has also been described by others for common carp for reasons that are also not clear (Daniel et al., 2009; Watkinson et al., 2021). In any case, inactive tags apparently did not bias our findings because our examinations of the NSD values of the 38 carp whose tags were active the entire study showed their NSD values did not differ from the NSD values of all tagged carp (Figure S3). We also recognise that tagging fish in Long Lake during the spring and fall could have influenced the composition of the study population and subsequent summaries of movement patterns (Fieberg & Conn, 2014; Fieberg et al., 2008). For example, our tagging efforts in September 2013 would have missed fish that were still in shallow spawning lakes in late fall. Nonetheless, most of the fish in our study (41 out of 67) were tagged in October 2014, at a time when nearly all fish had returned to Long Lake to overwinter; and comparisons of the NSD values of spring- and fall-tagged carp showed no indication that their behaviours differed (Figure S2). Thus, we assume our study accurately documented the life-history strategy of this species.

In conclusion, our finding that common carp perform both spawning and refuge migrations, which involve only part of the population and include homing, appears to represent a seemingly undescribed life-history strategy that is adapted to highly heterogeneous temperate ecosystems. This life-history strategy also appears to be related to this species' invasiveness in many disrupted and fragmented temperate ecosystems across the planet (Sorensen & Bajer, 2011; Weber & Brown, 2009; Yick et al., 2021). Our results suggest that these populations of carp might be controlled by blocking homing migrations and removing nurseries (Sorensen & Bajer, 2020). Indeed, since this study, common carp number in Rice Creek and have been reduced by placing a barrier with a trap into single location in Rice Creek (Bajer et al., 2018b). Moreover, our results suggest the common carp might be restored in areas of Europe (where native) by opening migratory pathways that have been blocked by dams and restoring the connected ephemeral wetlands on which they presumably depend as nurseries. We expect future research will show the carp's life-history strategy involving homing and partial migration to vary among different temperate freshwater ecosystems across the globe, including large shallow lakes with extensive wetlands (Bajer et al., 2015a; Hennen & Brown, 2014; Yick et al., 2021). The spatial ecology of other riverine fishes, especially cyprinids, might also be studied to see whether they too employ a similar combination of adaptive life-history traits in productive, unstable temperate ecosystems that experience extreme spatial and temporal variability.

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## DATA AVAILABILITY STATEMENT

Data are available from the first author upon reasonable request.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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