North American Journal of Fisheries Management

ISSN: 0275-5947 (Print) 1548-8675 (Online) Journal homepage: http://www.tandfonline.com/loi/ujfm20

Different Migratory Strategies of Invasive Common Carp and Native Northern Pike in the American Midwest Suggest an Opportunity for Selective Management Strategies

Christopher J. Chizinski, Przemyslaw G. Bajer, Mary E. Headrick & Peter W. Sorensen

To cite this article: Christopher J. Chizinski, Przemyslaw G. Bajer, Mary E. Headrick & Peter W. Sorensen (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, 36:4, 769-779, DOI: 10.1080/02755947.2016.1167141

To link to this article: http://dx.doi.org/10.1080/02755947.2016.1167141

Published online: 08 Jul 2016.

North American Journal of Fisheries Management 36:769–779, 2016

ISSN: 0275-5947 print / 1548-8675 online
DOI: 10.1080/02755947.2016.1167141

ARTICLE

Different Migratory Strategies of Invasive Common Carp and Native Northern Pike in the American Midwest Suggest an Opportunity for Selective Management Strategies

Christopher J. Chizinski,*[1] Przemyslaw G. Bajer, Mary E. Headrick, and Peter W. Sorensen
Department of Fisheries, Wildlife, and Conservation Biology, University of Minnesota, 1980 Folwell Avenue, St. Paul, Minnesota 55108, USA

Abstract
Inundated floodplains, backwaters, and wetlands are important spawning habitats for many freshwater fish. In Midwestern North America and areas of northern Europe, the Common Carp *Cyprinus carpio* and Northern Pike *Esox lucius* inhabit many of the same watersheds and perform migrations to interconnected wetlands during the spring to spawn. In this study, the movement patterns of adult Northern Pike and Common Carp from lakes into adjoining wetlands were assessed in Minnesota to determine how and when these species moved, and if Common Carp might be blocked or trapped without disrupting the Northern Pike. Adult Northern Pike migrated over an extended several-week period starting early each March, when temperatures were greater than 4ºC and when the fish were fully sexually mature (i.e., females were ovulated and running with eggs, and males were spermiating). In contrast, adult Common Carp migrated over relatively short time periods that lasted just a few days between April and June, and whose specific timing varied but always occurred after water temperatures rose to 10ºC and usually coincided with rain. Migrating Common Carp were in prespawning condition (i.e., females were not yet ovulated) and appeared to be homing as stream selection was very specific. Less than half of the Common Carp population migrated each year, reinforcing earlier observations that Common Carp likely conduct partial migrations. Overlap between Northern Pike and Common Carp was minimal, suggesting that management strategies using removable barriers, for example, could be used to control invasive Common Carp without affecting native Northern Pike populations.

Inundated floodplains, backwaters, marshes, and wetlands are important spawning habitats for many species of temperate freshwater fish. The use of such habitats by migrating fish in temperate latitudes is important because they can also serve as nursery areas (Copp 1989; Bénech and Penáz 1995; Poizat and Corivelli 1997; Górski et al. 2010). In seasonally flooded habitats, predator densities are often low (Moler and Franz 1987; Snodgrass et al. 1996), while invertebrate densities (i.e., food) are generally high (Neckles et al. 1990). Many lacustrine fish have evolved reproductive strategies to migrate from lakes into interconnected wetlands for spawning, taking advantage of environmental conditions that are favorable for larval and juvenile survival (i.e., successful recruitment; Casselman and Lewis 1996; Bajer and Sorensen 2010). Often, only a portion of the population will migrate into peripheral spawning habitats and then only when conditions are favorable. Such a strategy in which only a portion of a population moves is known as partial migration, and while it often is associated with reproduction, this is not always the case (Jonsson and Jonsson 1993). This type of migratory strategy may result in increased population stability and resilience in spatially diverse habitats (Kerr et al. 2010), and its importance among freshwater fishes is being recognized with increased frequency (Chapman et al. 2012; Brodersen et al. 2014). Nevertheless,

*Corresponding author: cchizinski2@unl.edu
[1]Present address: School of Natural Resources, University of Nebraska, 3310 Holdrege Avenue, Lincoln, Nebraska 68583, USA.
Received August 12, 2015; accepted March 11, 2016

while reproductive migrations have been reported among populations of invasive and native fish that inhabit the same geographic areas, it is unknown whether differences in migratory patterns exist to allow for selective management strategies for the former without disrupting the latter.

Over large areas of North America, the invasive Common Carp *Cyprinus carpio* and the native Northern Pike *Esox lucius* share the same watersheds and exhibit reproductive migrations to wetlands during the spring. In both species, shallow marshes and floodplains are thought to be critical nursery areas (Balon 1995; Vilizzi and Walker 1999; Craig 2008; Cucherousset et al. 2009; Bajer et al. 2012). The Common Carp, which was introduced to North America in the late 1800s (Sorensen and Bajer 2011), causes ecological damage to shallow lakes and wetlands (Weber and Brown 2009) and is a subject of frequent management efforts, whereas the Northern Pike is a top predator and a valuable sport fish (Paukert et al. 2001). Barriers have often been used to block Common Carp from entering wetlands to spawn (Verrill et al. 1995; Maceina et al. 1999), but these devices have not been used in a manner designed to minimize impacts on native fishes. This is largely due to insufficient information on the nature of Common Carp movement as compared with the movement of native fishes such as the Northern Pike (e.g., Miller et al. 2001; Craig 2008). Similarly, the movement patterns of Northern Pike are not well described (e.g., the role of environmental correlates), particularly with respect to other fishes like Common Carp. Better understanding of the timing and the degree of overlap of Common Carp and Northern Pike reproductive migrations is needed to realize the implications of the management of both species, including the possible use of barriers in North America. More generally, the management of other fishes in temperate North America might benefit from documenting the intricacies of migrations, especially in seasonally unstable regions such as the upper Midwest, where many lakes winterkill and are recolonized by migratory individuals.

In this study, springtime migrations of Northern Pike and Common Carp were assessed in two systems of lakes and associated wetlands from 2009 to 2012 in Minnesota. The main objectives of this study were to (1) identify the timing and describe the relationship of the migratory patterns of these fish to stream temperature, stream depth, and precipitation; and (2) determine periods of overlap that could be important to management (i.e., assess the feasibility of selective blocking or removal of Common Carp).

METHODS

Sampling design and study area.—Our study sites included two chains of lakes and associated wetlands (marshes) in two watersheds (Riley Creek watershed and Kohlman Creek watershed) located in central Minnesota. The Riley Creek watershed (44°49.983′N, 93°31.514′W) is comprised of five water bodies that drain into the Minnesota River and then the Mississippi River (Figure 1). Three water bodies (two lakes and a marsh located between them) within the lower portion of this chain comprised our first study system (looking downstream):

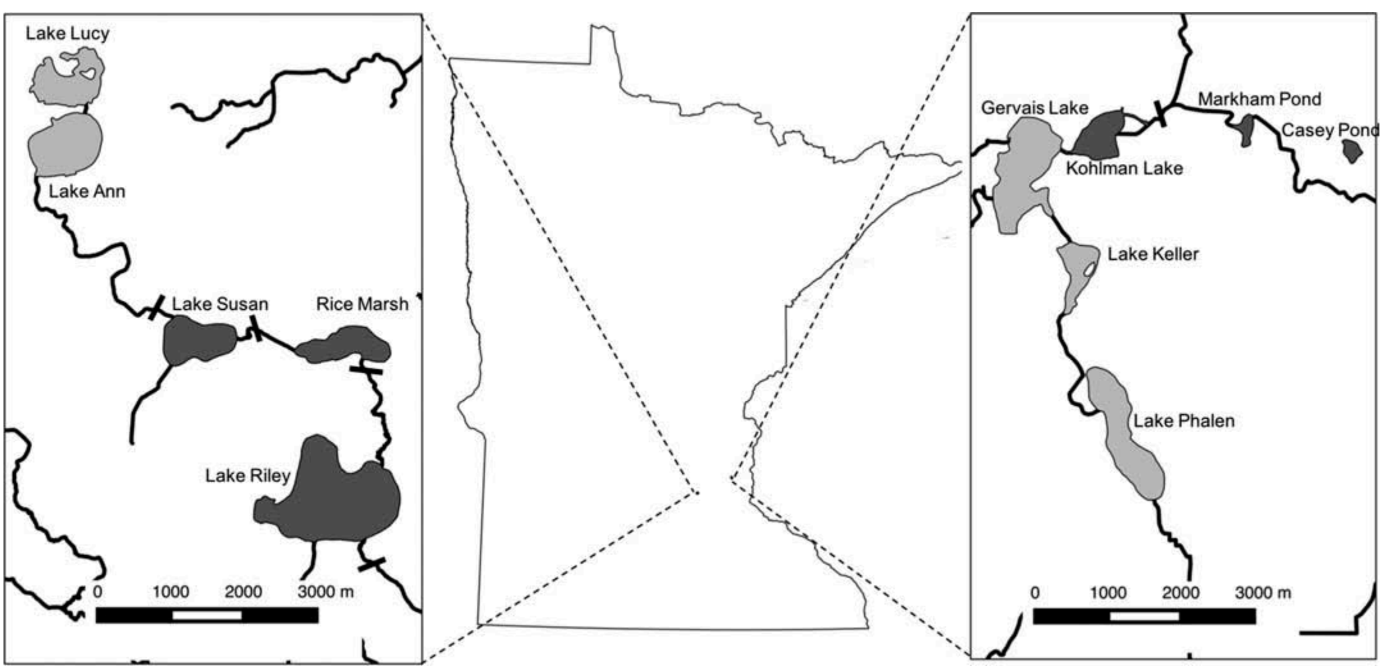

FIGURE 1. Map of the locations of fish sampling barriers in the Riley Creek watershed (left panel) and the Kohlman Creek watershed (right panel) in Minnesota. Barriers are indicated by the solid lines bisecting the streams.

Lake Susan (37.5 ha surface area; 5.1 m maximum depth), Rice Marsh (40.0 ha surface area; 3.0 m maximum depth), and finally Lake Riley (120 ha surface area; 14.9 m maximum depth). At the beginning of this study, Lake Riley contained approximately 2,600 adult Common Carp and Lake Susan contained approximately 800 adult Common Carp (Bajer and Sorensen 2012). The density of carp was further reduced in 2010 to approximately 400 carp in Lake Riley and 600 carp in Lake Susan using winter seining (Bajer et al. 2011; Bajer and Sorensen 2012). A mark–recapture study suggested that Lake Riley was inhabited by approximately 1,600 adult Northern Pike (P. G. Bajer, unpublished data). While Common Carp spawn throughout this system of lakes, only those that migrate to spawn in Rice Marsh Lake were thought to produce recruits because of abundant predator populations in Lakes Susan and Riley (Bajer and Sorensen 2010; Bajer et al. 2012). Likewise, while Northern Pike had not been studied in this system, it has been shown to spawn in a variety of habitats (Craig 2008), with the greatest contribution of young of year coming from seasonally flooded emergent vegetation in tributaries followed by submerged aquatic vegetation in shallow bays and almost no contribution from deep, littoral habitats (Farrell et al. 2006). The stream that connects these three water bodies, Riley Creek, is relatively narrow (width, 5–15 m), shallow (maximum depth, ~1 m) and often goes dry in the summer. No other major connections to other water bodies flow into or out of these lakes, and their inlets and outlets are similar in depth, flow, and bottom types. Severe winters characterize this region, and winter hypoxia commonly occurs in Rice Marsh where oxygen levels fall below 1 mg/L and fish mortality occurs (Bajer and Sorensen 2010). The waters went hypoxic in Rice Marsh in January 2009, and there was a large fish kill. The waters did not become hypoxic in 2010 or 2011, and no fish kill was observed.

The Kohlman Creek watershed (45°1.149′N, 93°3.268′W) is comprised of five water bodies that drain into the Mississippi River (Figure 1). At the upper portion of this watershed is Kohlman Lake (29.6 ha surface area; 3 m maximum depth), our second study system. Kohlman Lake connects to an upstream wetland (upper Kohlman basin) and two ponds (Markham and Casey ponds) via Kohlman Creek, which is relatively narrow (width, 5–10 m), shallow (maximum depth, ~1 m), and flows during April–July fed by snowmelts and spring rains, but goes nearly dry during late summer. Below Kohlman Lake, the connections between the lakes are large, with frequent motorboat traffic that prevented the construction of barriers to assess movement between lakes (but see Bajer et al. 2011 for movement of radio-tagged Common Carp among lakes in this watershed). Kohlman Lake contained approximately 800 adult Common Carp during the time of this study, while gill netting showed this system to contain relatively few Northern Pike (no pike were caught in a Minnesota Department of Natural Resources gill-net fish survey conducted in 2005).

Fish sampling.—Fish movement was documented during the springs and summers of 2009, 2010, and 2011 in the Riley Creek watershed, and in 2011 and 2012 in Kohlman Creek at five locations (four in Riley Creek and one in Kohlman Creek) where temporary barriers were constructed (Figure 1). In 2009, we commenced sampling in April (when we discovered Northern Pike migration was already ongoing), while the sampling commenced right after ice-out in all subsequent years in March, at which time streams also typically started thawing and flowing. In all instances, sampling continued until migrating fish had not been caught for at least 2 weeks (usually late June). All locations were sampled daily to create continuous data records for analysis. Fish movement was documented using temporary barriers at locations where fish could be easily counted visually, caught, and either released (Northern Pike) or removed (Common Carp). In the Riley Creek watershed, four temporary fish barriers were erected on April 7, 2009, at the inlet and outlet of Lake Susan, the inlet to Lake Riley, and downstream of Lake Riley (Figure 1). In Kohlman Creek, one barrier was erected on April 12, 2011, at the inlet to Lake Kohlman (Figure 1). Barriers spanned the entire width of each stream, extended approximately 0.5 m above the surface, and were constructed of horizontal PVC pipes spaced at 3-cm intervals on wooden posts to allow debris to pass (Figure 2). A mesh screen at the top of the barrier prevented fish from jumping over the barrier. Sandbags placed at the base of the fish barrier prevented scouring.

To standardize fish sampling, we marked transects that extended 25 m downstream and 25 m upstream of each barrier. These transects were sampled daily by walking along each transect to conduct visual fish counts, followed by surveying the entire transect using a backpack electrofisher. Because these surveys showed that visual counts could accurately determine the presence of pike or carp in the creek, we continued the daily visual checks throughout the rest of the season but conducted

FIGURE 2. Image of the fish barrier in Riley Creek.

electrofishing only if Common Carp or Northern Pike were seen. These counts also ensured that we did not miss fish that might have been returning to the lakes. All Common Carp and Northern Pike were netted, counted, measured for TL (nearest mm), and examined for gender and maturational status (spermiating, running eggs, swollen with nonovulated eggs, and unknown) by gently squeezing them. Northern Pike were released on the opposite side of the barrier from where they were captured while Common Carp were removed and euthanized using a lethal dose of MS-222 (tricaine methanesulfonate; Western Chemical, Ferndale, Washington; 1 g/L). Measurements of water temperature and water depth were also collected at each sampling site each day. Other fish species were also counted.

Data analysis.—We examined data by species by location by year. Counts of upstream- and downstream-moving Common Carp and Northern Pike were plotted by day and by location for all 4 years. Precipitation data collected from the National Climatic Data Center (ftp://ftp.ncdc.noaa.gov) from weather stations in Chanhassen, Minnesota (Riley Creek watershed), and Saint Paul, Minnesota (Kohlman Creek watershed); water depth; and temperature were plotted in relation to fish counts. To analyze the relationship between the number of Common Carp and Northern Pike moving toward the barriers with year and environmental variables, we used a binomial (logit link) generalized linear model in R (R Development Core Team 2015). Specifically, we modeled the probability of movement conditional on the number of fish still available to move as a function of precipitation, water temperature, year, and location (Riley Creek watershed only). The fish still available to move in the Riley and Kohlman Creek watersheds were calculated as the total number of fish observed moving towards the marshes minus the cumulative sum of the fish that had already moved by each species during a location and year. Day of year (DOY) was initially considered in the model but was highly collinear with the other independent variables of interest (e.g., temperature) and thus was not included in the final models.

RESULTS

Northern Pike

Northern Pike were captured migrating between Lake Susan and Rice Marsh as well as between Lake Riley and Rice Marsh each year. However, no Northern Pike were caught at any other location, including upstream of Lake Susan or downstream of Lake Riley. Only one Northern Pike was caught at Lake Kohlman for the 2 years assessed.

In 2009, sampling in Riley Creek began on April 9 (DOY 99), when water temperatures were 4°C and migrating Northern Pike were already in postspawning condition. Between April 9 and May 10 (DOY 99–130), we captured Northern Pike on 16 d, migrating from Rice Marsh to Lake Susan or from Rice Marsh to Lake Riley (Figures 3, 4). Captured Northern Pike had external signs of recent spawning (e.g., abraded fins, deflated abdomens). Only a few Northern Pike were captured migrating towards Rice Marsh during that time.

In 2010, sampling in Riley Creek began on March 10, when the lakes and creek were just starting to thaw. We first started capturing Northern Pike on March 17 (DOY 76), when they began their migration towards Rice Marsh from both Lake Susan and Lake Riley. Northern Pike migrating towards Rice Marsh were caught nearly every day for 3 weeks through early April, after which time no more Northern Pike were captured (Figures 3, 4). Water levels dropped during the migration while water temperatures rose from 3°C to 10°C (Figures 2, 3). Northern Pike that were migrating from Lake Riley to Rice Marsh had a median length of 618 mm (range, 166–950 mm TL) and a sex ratio of 33:28 (female : male), and although not systematically assessed, most were running with eggs and milt. After April 10 and through mid-May, our catches were dominated by Northern Pike in postspawning condition (no expressible gametes; thin, abraded fins) that were moving from Rice Marsh towards Lakes Susan and Riley.

In 2011, sampling started in early March, prior to the start of migration and before the systems were fully thawed. The migration to the marsh by Northern Pike from Lake Riley began March 25 (DOY 84), when stream temperatures were 2°C and stream depth was 58 cm, while Northern Pike movement from Lake Susan to Rice Marsh began just a few days earlier (DOY 77; Figures 3, 4). Migration to the marsh was observed on an almost daily basis and stopped by early May (DOY 128–132), when water temperatures were ~10°C. The sex ratio of Northern Pike moving to the marsh was 108:71 (female : male). Females had large vitellogenic ovaries, and a large number of them (38 of 108) were ovulated (i.e., running with eggs), while nearly all males (69 of 71) were spermiating (i.e., releasing large amounts of hydrated spermatozoa). After April 10 (DOY 100), migrating Northern Pike were dominated by postspawning individuals that were moving out of Rice Marsh and towards Lake Susan or Riley. This postspawning migration lasted through late May.

Analysis of the conditional movement of Northern Pike toward Rice Marsh from Lake Riley and Lake Susan indicated significant relationships to environmental variables (Table 1). The probability of Northern Pike to move to the marsh, conditional on the number of pike that were available to move, was positively related to temperature but negatively to precipitation. There was no significant difference ($P > 0.05$) between years, but there was a significant, lower probability of movement from Lake Susan relative to Lake Riley.

Common Carp

Adult Common Carp were captured migrating downstream from Lake Susan and upstream from Lake Riley each year. In late April 2009, 11 adult Common Carp (<1% of the population) were captured moving from Lake Riley to Rice Marsh, and 41 were caught moving from Lake Susan to Rice Marsh (about 5% of the population; Figures 3, 4). In both cases, the

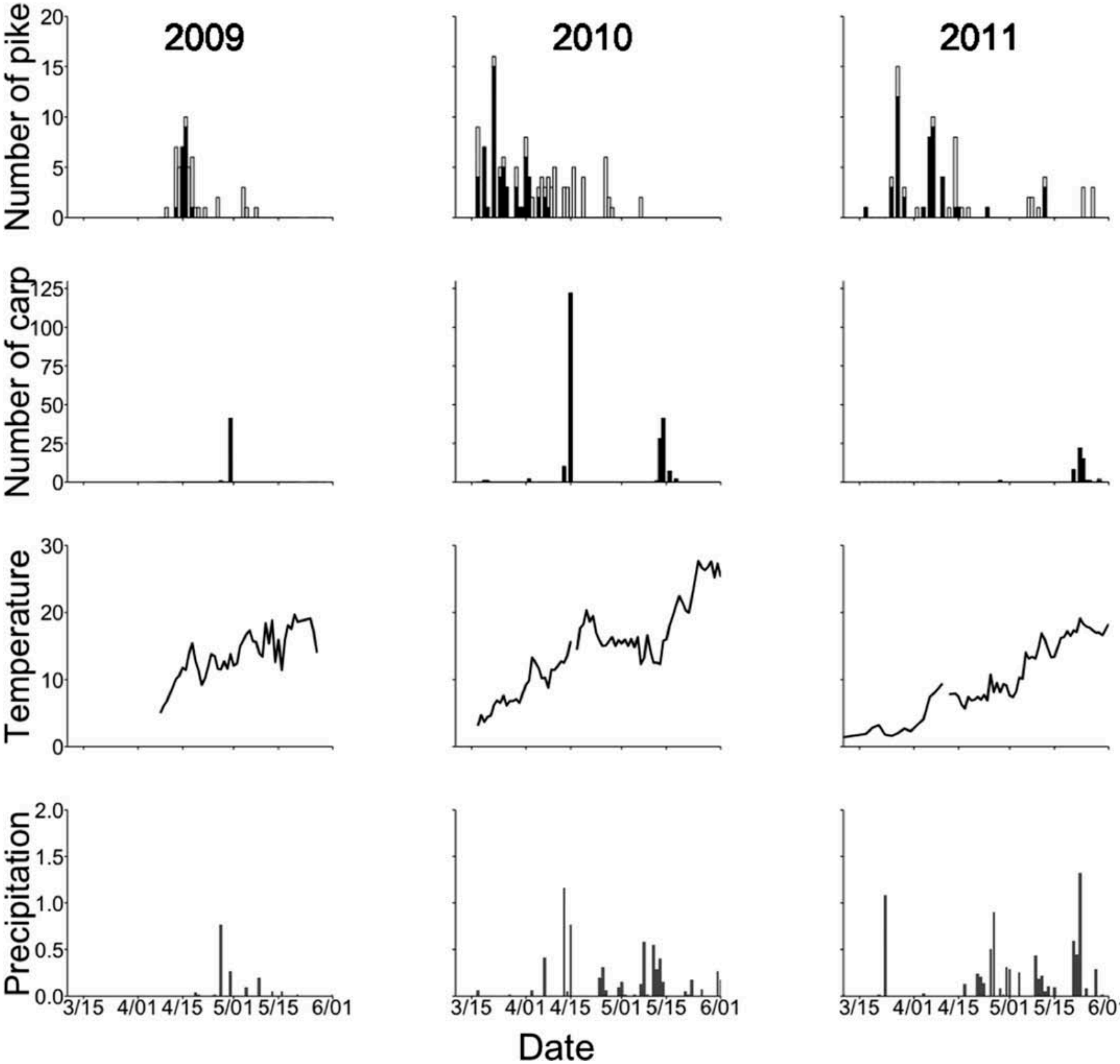

FIGURE 3. The number of Northern Pike and Common Carp and associated environmental variables at the outlet of Lake Susan in 2009, 2010, and 2011. Black bars indicate fish moving toward the marsh, and white bars indicate fish moving toward Lake Susan.

Common Carp moved en masse (i.e., as a single group) on a single day, although nearly a week separated the events (DOY 125 in Riley, DOY 102 in Susan). Movements coincided with rain events, but there was no increase in stream water depth, and temperatures were relatively constant at 13.8º and 13.0ºC, respectively. Common Carp movement occurred after approximately 90% of pike had moved back to Lake Susan and approximately 83% had moved back to Lake Riley. Common Carp leaving Lake Susan had a median length of 575 mm (range, 507–669 mm TL), and those leaving Lake Riley had a median length of 562 mm (range, 515–696 mm TL). The sex ratio and maturity status of these fish was not systematically assessed, but females did not appear to be ovulated (i.e., not running with eggs).

In 2010, a total of 201 adult Common Carp were captured moving from Lake Susan to Rice Marsh (33% of the population), and none were caught moving upstream of Lake Susan. Similar to 2009, the Common Carp moved en masse, but this

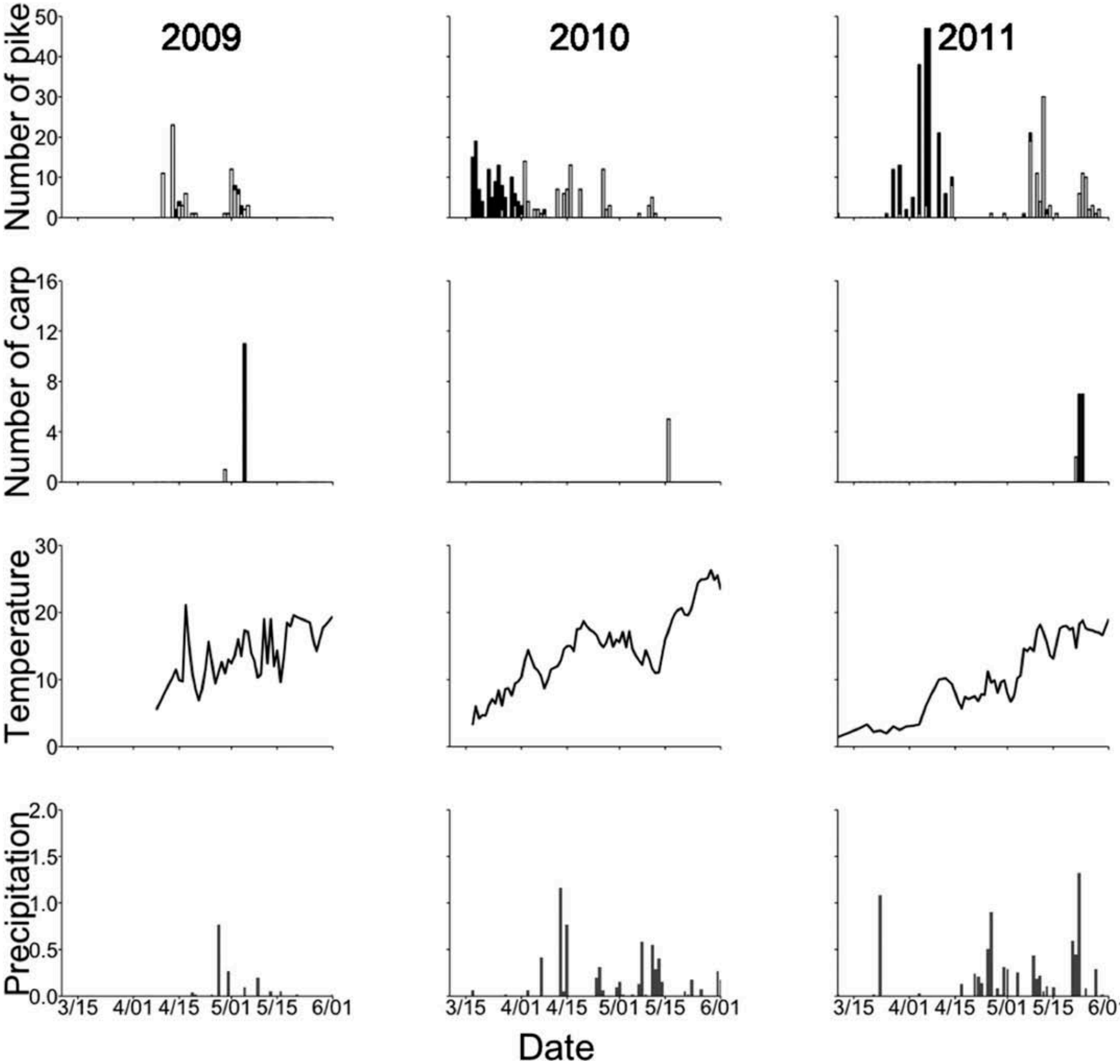

FIGURE 4. The number of Northern Pike and Common Carp and associated environmental variables at the inlet to Lake Riley in 2009, 2010, and 2011. Black bars indicate fish moving toward the marsh, and white bars indicate fish moving toward Lake Riley.

time during two events: mid-April (DOY 103, 105) and mid-May (DOY 135), following rain events when water temperatures had reached 16°C (Figure 3). Common Carp leaving Lake Susan had a median length of 514 mm (range, 515–669 mm TL). Common Carp were caught leaving Lake Riley and migrating towards Rice Marsh that year in two events in late April, but unfortunately our data were stolen from our field vehicle so they cannot be reported here. No Common Carp were captured moving from Rice Marsh toward the lakes in either stream. There was no overlap in the movement of Common Carp and Northern Pike for the Lake Riley location, but there was a slight overlap between carp that were moving towards the marsh and Northern Pike that were returning from the marsh for the Lake Susan location in 2010 (Figures 3, 4). In the latter case, the movement of carp occurred after 92% of Northern Pike movement had already occurred.

In 2011, adult Common Carp were captured moving downstream from Lake Susan and upstream from Lake Riley

TABLE 1. Coefficient estimates, SEs, *z*-value, and associated *p*-value for binomial generalized linear models predicting the conditional movement of Northern Pike and Common Carp toward the marsh in association with stream temperature, precipitation, year, and location in the Riley Creek watershed. For Riley Creek watershed Northern Pike, the reference level for year was 2010 and the reference level for location was Lake Riley. For Riley Creek watershed Common Carp, the reference level for year was 2009 and the reference level for location was Lake Riley. For Lake Kohlman Common Carp, the reference level for year was 2011.

Coefficient	Estimate	SE	*z*-value	*p*-value
Riley Creek watershed Northern Pike				
Intercept	–3.541	0.150	–23.666	<0.001
Temperature	0.267	0.019	14.129	<0.001
Precipitation	–2.178	0.602	–3.619	<0.001
Year (2011)	0.015	0.113	0.134	0.894
Location	–0.333	0.126	–2.645	0.008
Riley Creek watershed Common Carp				
Intercept	–17.655	1.156	–15.270	<0.001
Temperature	0.869	0.060	14.469	<0.001
Precipitation	0.485	0.086	5.630	<0.001
Year (2010)	2.310	0.538	4.296	<0.001
Year (2011)	–0.675	0.477	–1.416	0.157
Location	0.068	0.319	0.214	0.831
Lake Kohlman Common Carp				
Intercept	–6.957	0.130	–53.330	<0.001
Temperature	0.189	0.007	27.150	<0.001
Precipitation	0.933	0.026	35.430	<0.001
Year (2012)	–1.147	0.085	–13.560	<0.001

again as well as upstream from Lake Kohlman, which was sampled for the first time. Similar to previous years, Common Carp moved in well-defined groups and only for 1–2 d. In the case of Lake Susan, this was a single group ($N = 7$) on May 21 (DOY 141), when temperature was 17ºC and following precipitation events. Common Carp ($N = 14$) left Lake Riley on May 23–24 (DOY 143–144), when stream temperature was 20ºC. The Common Carp from Lakes Susan and Riley were examined and found to have a sex ratio of 2:1 (female : male), and while all males were spermiating, no ovulated females were captured (females had large, vitellogenic ovaries that had not yet undergone final oocyte maturation and ovulation). The movement of Common Carp occurred after 96% of Northern Pike had already moved back to Lake Susan and 93% had moved back to Lake Riley (Figures 3, 4). Three distinct groups of adult Common Carp were captured moving up Kohlman Creek on May 9–11 ($N = 62$), May 21–24 ($N = 259$), and June 21–24 ($N = 44$; Figure 5). This number represented nearly 45% of the total number of adult Common Carp thought to be present in Lake Kohlman that year. Each time, the Common Carp were moving during a rain event (although many days with rain did not have carp movements), and water temperatures were 13, 16, and 20°C, respectively. The largest of the three movements coincided with an increase in stream water level.

In 2012, only Kohlman Creek was sampled, and a total of 396 adult Common Carp (nearly 50% of the population) were caught moving toward the wetland north of Kohlman Lake (Figure 5). Common Carp moved en masse over the course of three different discrete periods: DOY 126–129 ($N = 176$), DOY 145–151 ($N = 154$), and DOY 170–172 ($N = 66$). Each time, Common Carp were captured following a rain event (but rain occurred on more than 50% of all days that spring) and a sharp increase in stream depth. Water temperatures during the three movements were 17, 17, and 20°C, respectively.

Analysis of the conditional number of Common Carp moving toward the marsh from Lake Riley, Lake Susan, and Lake Kohlman indicated very similar relationships for each of the environmental variables assessed (Table 1). At all locations, precipitation and temperature were significantly related to the conditional probability of Common Carp movement to the associated marsh. At the Riley Creek watershed, there was a significant increase in the probability of movement in 2010 relative to 2009 but not in 2011, and no difference between Lake Susan and Lake Riley. In Lake Kohlman, there was a significant decrease in the probability of movement in 2012 relative to 2011.

Other Fish

In addition to Northern Pike and Common Carp, nine other species of native fish were caught, some of which appeared to be migrating both upstream and downstream (Table 2). Bluegills were the most abundant of these, followed by Black Crappies and then an unidentified species of minnow (Table 2).

DISCUSSION

Our results suggest that Northern Pike and Common Carp exhibit different migration strategies. Although both species moved from lakes to wetlands to spawn each spring, the timing, ecological correlates, and physiological underpinnings of their behaviors were different. While adult Northern Pike consistently started to move towards the marsh in mid-March, when temperature reached about 3°C, and continued to migrate for several weeks, adult Common Carp moved as brief, but intense pulses that lasted only a few days between early April and late June. There was relatively little (<20%) overlap between adult Common Carp and Northern Pike migrations, although both selected the same wetlands. These differences in the timing of the movement patterns suggest that temporary barriers could be used to exclude Common Carp in North America from wetlands used for spawning while permitting most Northern Pike to pass.

The timing and duration of Northern Pike spawning migrations were remarkably consistent across years and lakes, and always started in mid-March. In our study design, we set up the barriers at ice-out and generally did not see Northern Pike moving to the barriers until March, when stream temperatures

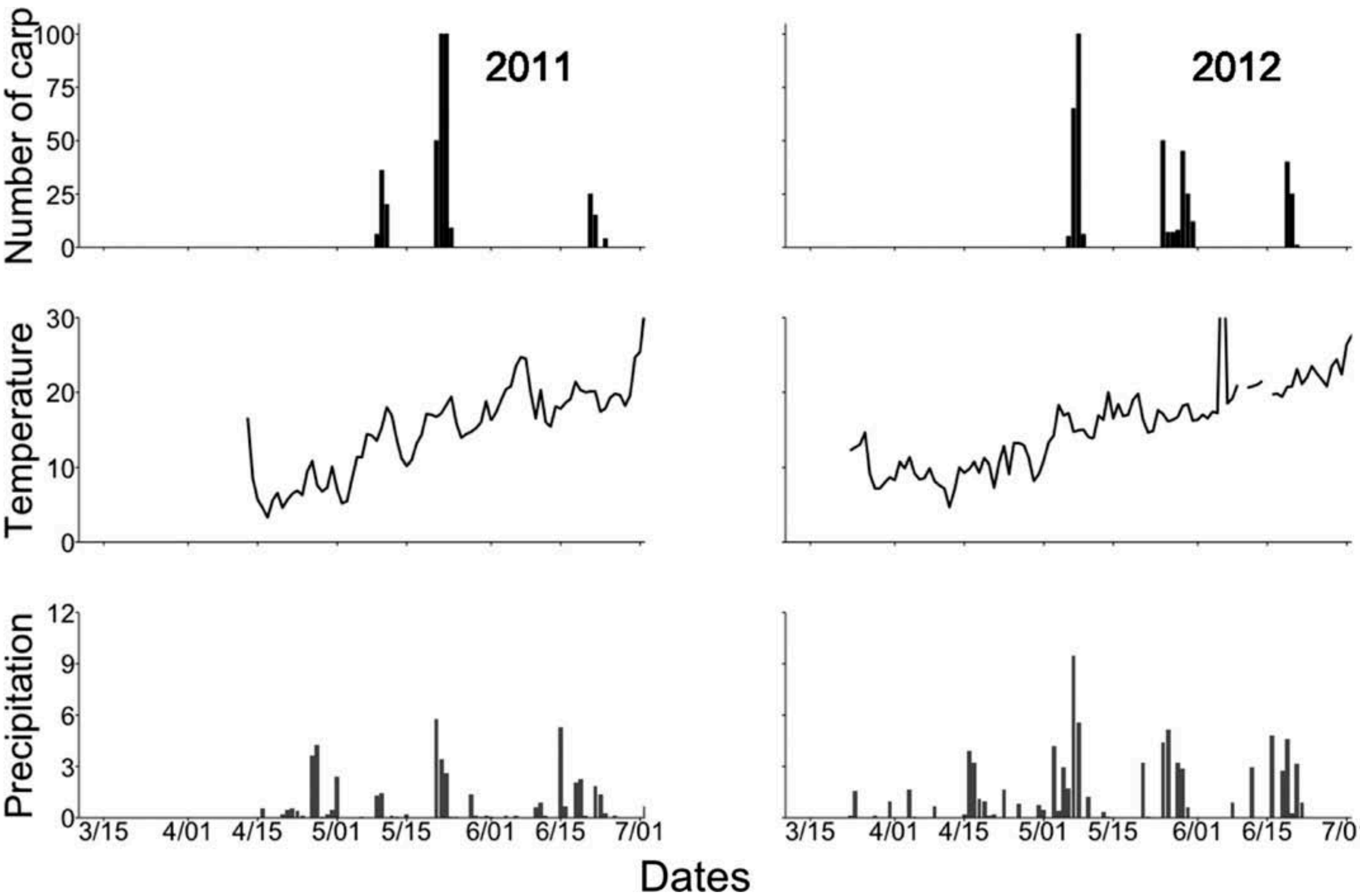

FIGURE 5. The number of Common Carp and associated environmental variables at the inlet to Lake Kohlman in 2011 and 2012. Black bars indicate fish moving toward the marsh, and white bars indicate the number of fish moving toward Lake Kohlman.

gradually increased from 2ºC to 10ºC, although it was possible we missed some Northern Pike moving below the ice. Franklin and Smith (1963) and Priegel and Krohn (1975) found that migrations began under the ice in Minnesota and Wisconsin. Forney (1968) reported that Northern Pike started spawning migrations from Oneida Lake, New York, to adjacent marshes when the lake was still covered in ice. Although our results suggest that the conditional probability of movement of Northern Pike toward the marsh increased with increasing stream temperatures, it is likely that seasonal changes in photoperiod, as noted for Pacific salmonids, could have been the trigger (i.e., zeitgeber; Hodgson et al. 2006; Quinn and Adams 1996). Although we do not have accurate population estimates of Northern Pike in our system, gill-net captures of tagged pike suggested a population of approximately 1,600 in Lake Riley (Bajer, unpublished data), further suggesting that 10–20% of the Northern Pike population migrated each year. Interestingly, female Northern Pike migrating towards the marsh were fully vitellogenic and ovulatory, with many already releasing ovulated eggs, suggesting that their migration is directly associated with spawning. Presumably, these fish spawned soon after entering Rice Marsh Lake, where we have confirmed recruitment of young (P. G. Bajer and P. W. Sorensen, unpublished data). Interestingly, Northern Pike only chose two of four stream inlets or outlets to enter in the Riley Chain, consistent with the genetic data, suggesting that they are homing to natal regions (Miller et al. 2001). While olfactory cues could have a role in this process, other cues must be involved in the case of Lake Susan, where they migrated downstream.

In contrast to Northern Pike, the timing of Common Carp spawning migrations was discrete and, in some situations, restricted to large, single-day movements between mid-April and late June (i.e., punctuated movement). Observations from other locations suggest an even broader window of time exists at other Midwestern locations, but that movement is always brief and can vary by many weeks (Swee and McCrimmon 1966; Bajer and Sorensen 2010), suggesting that photoperiod may not be critical. However, while the timing of adult Common Carp migratory movements was variable, it consistently occurred after temperatures were above 10°C and after most of the adult Northern

TABLE 2. Counts of fish other than Northern Pike and Common Carp caught at sampling locations. NS indicates that the site was not sampled (other than for Northern Pike or Common Carp). Sampling locations can be found in Figure 1.

Location	Species[a]										
	BHD	BLG	BLC	BUF	GSF	LMB	PKS	WAE	WSF	YEP	Other
2009											
Susan inlet	1	592	1	1	0	8	0	0	12	4	213
Susan outlet	563	239	72	0	0	61	0	0	3	20	1,409
Riley inlet	0	133	0	0	0	0	0	0	0	0	42
Riley outlet	0	0	0	0	0	0	0	0	0	0	0
Kohlman inlet	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
2010											
Susan inlet	8	31	56	0	0	1	0	0	5	0	269
Susan outlet	563	198	408	0	0	0	8	2	15	37	1,015
Riley inlet	4	130	2	0	2	2	3	0	0	0	14
Riley outlet	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Kohlman inlet	0	0	0	0	0	0	0	0	0	0	0
2011											
Susan inlet	0	319	4	0	0	11	0	0	28	0	20
Susan outlet	219	349	104	0	1	28	0	3	7	22	175
Riley inlet	13	317	0	0	0	26	4	0	1	1	13
Riley outlet	0	0	0	0	0	0	0	0	0	0	0
Kohlman inlet	0	0	0	0	0	0	0	0	0	0	20
2012											
Kohlman inlet	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS

[a] Species abbreviations: BHD = Black Bullhead *Ameiurus melas*, BLC = Black Crappie *Pomoxis nigromaculatus*, BLG = Bluegill *Lepomis macrochirus*, BUF = Bigmouth Buffalo *Ictiobus cyprinellus*, GSF = Green Sunfish *L. cyanellus*, LMB = Largemouth Bass *Micropterus salmoides*, PKS = Pumpkinseed *L. gibbosus*, WAE = Walleye *Sander vitreus*, WSF = White Sucker *Catostomus commersonii*, YEP = Yellow Perch *Perca flavescens*; "Other" includes unidentified species of small minnows.

Pike had moved. Generally, but not always, Common Carp moved during or just after precipitation events when stream water levels were rising. While it is possible that other variables that we did not measure might explain the precise time of their movements, we hypothesize that the movements may have been associated with the social dynamics of Common Carp (Levesque et al. 2011; Lim and Sorensen 2011). This would be flexible and adaptive. Notably, unlike Northern Pike, the Common Carp were not in spawning condition when they migrated (i.e., females were not ovulated and were not freely releasing eggs); thus, their migration is one that prepares them to spawn but not for spawning itself. We hypothesize that the Common Carp form prespawning aggregations outside of river mouths, which they enter depending on daily group dynamics that may be influenced by many environmental and social cues, including pheromone release (Sorensen and Stacey 2004; Lim and Sorensen 2011). Carp are known to release a sex pheromone that likely is estrogen based and stimulates behavioral activity (Kobayashi et al. 2002). Likely, Common Carp ovulate and spawn en masse within days to weeks of entering warming wetlands in a strategy that attempts to swamp predators (Sorensen and Stacey 2004; Bajer and Sorensen 2010; Bajer et al. 2012; Silbernagel and Sorensen 2013). Common Carp that did not migrate were seen spawning in the lakes each year, suggesting that the propensity to migrate is variable, not under strict genetic control, and not a prerequisite for spawning. Balon (1995) observed that Common Carp spawning occurred when water temperatures reached 18°C, and large schools of Common Carp entered freshly flooded grass flats within the inundation areas of the Danube and Volga rivers. In Minnesota, spawning typically occurs when water temperatures exceed 16–20°C, usually within a few days after the Common Carp are seen migrating in streams (Bajer and Sorensen 2010). Telemetry studies suggest that adult Common Carp return from wetlands after spawning over the course of the summer (Bajer and Sorensen 2010), while the young may take up to 2 years (Bajer et al. 2015b). Because we removed carp, the downstream movements of postspawning adults were not enumerated in this study. Interestingly, like Northern Pike and other species (Brodersen et al. 2014), adult Common Carp appear to be highly selective in their choices of stream inlets and outlets, selecting those that lead to the marsh and ignoring others irrespective of whether they were inflowing or outflowing. We speculate that this may reflect homing to nursery habitats as winterkill-prone marshes have been shown to be important Common Carp nurseries in the region (Bajer et al. 2015a).

Partial migration is employed by many taxa for reasons that often, but not always, include reproduction (Chapman et al. 2012). Several observations from our study suggest that Common Carp also exhibit a type of partial migration that is associated with reproduction but not the act of spawning. First, our population estimates suggest that only between 10% and 50% of the adult Common Carp moved from lakes and were observed at the barriers each year. Although it is possible that the entire population attempted the migration and that some fish returned to the lakes after encountering the barriers before we could count them, this seems highly unlikely because when observed, we found that Common Carp stayed at the barriers for several hours unless they were physically removed. Further, no fish were observed leaving our sample area while we made visual counts. Additionally, earlier telemetry studies conducted in the Riley Chain of lakes when no barriers were present in the streams (2006–2007) indicated that less than 50% of Common Carp migrated to the marsh (Bajer and Sorensen 2010). Our study suggests that Northern Pike may also be employing partial migrations, as apparently less than 20% of pike that inhabited our study lakes were observed at the barriers. However, this conclusion needs to be verified through further study.

The migratory strategies of Common Carp and Northern Pike are relevant to their management in several ways. First, the differing timing of their movement might allow for the selective management of adults that could include trapping systems that allow most Northern Pike to pass while stopping invasive Common Carp. Second, the brief duration of Common Carp movement suggests that temporary barrier and trap structures could be used effectively to remove Common Carp while reducing the need and costs of constructing permanent structures. In most situations, Common Carp barriers would only need to be in place during mid-April through the end of June. Third, we show that some connections between lakes may be much more important to Common Carp (e.g., carp in the Riley Creek watershed primarily moved between Lakes Susan and Riley to the wetland and were never observed moving to Lake Ann or Lake Lucy), and thus focusing management on those would be more important than others. Last, this study shows that to be effective in Common Carp control, stream trapping must be repeated for many years and include population estimates. We encourage the use of existing population dynamics models (e.g., Bajer et al. 2015b) to determine how trapping strategies in streams might be optimized given local recruitment dynamics to provide lasting benefits for overall population control.

An ancillary finding of this study was that in addition to Northern Pike and Common Carp, many other species of native fishes use connections between lakes to migrate in the spring. While we were unable to discern if this was a directed migration, the large numbers of Bluegills and other species captured suggested that they were actively moving between lakes. Movement between interconnected lakes by Black Crappies and Bluegills has been described (Parsons and Reed 2005) but not systematically studied.

We have shown that in a northern temperate climate, adult Northern Pike move into wetlands earlier than Common Carp, such that more than 90% of Northern Pike migration is completed before Common Carp migration begins. The Northern Pike move in a protracted fashion, with a few fish per day for a few weeks in early spring, while the Common Carp move in a punctuated fashion, with large numbers in later spring. Finally, while many Northern Pike females are in spawning condition (ovulated and spermiating) when they migrate, migrating Common Carp females are nonovulated, suggesting that they might not spawn for at least several days after moving to the marsh. Both strategies function well for both species throughout the Northern Hemisphere, but their differences also could be exploited by fisheries managers to promote one species at the expense of the other.

ACKNOWLEDGMENTS

This work was funded by the Minnesota Environmental and Natural Resources Trust Fund (P.W.S.), the Riley Purgatory Bluff Creek Watershed District (P.W.S.), and the Ramsey Washington Metro Watershed District (P.W.S.). Brett Miller, Tracy Szela, Robert Mullenhauer, Justine Koch, and Reid Swanson helped with collecting field samples.

REFERENCES

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

Bajer, P., C. J. Chizinski, and P. W. Sorensen. 2011. Using the Judas technique to locate and remove wintertime aggregations of invasive Common Carp. Fisheries Management and Ecology 18:497–505.

Bajer, P. G., T. K. Cross, J. D. Lechelt, C. J. Chizinski, M. J. Weber, and P. W. Sorensen. 2015a. Across-ecoregion analysis suggests a hierarchy of ecological filters that regulate recruitment of a globally invasive fish. Diversity and Distributions, 21:500–510.

Bajer, P. G., J. E. Parker, T. K. Cross, P. A. Venturelli, and P. W. Sorensen. 2015b. Partial migration to seasonally-unstable habitat facilitates biological invasions in a predator-dominated system. Oikos 124:1520–1526.

Bajer, P. G., and P. W. Sorensen. 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.

Bajer, P. G., and P. W. Sorensen. 2012. Using boat electrofishing to estimate the abundance of invasive Common Carp in small Midwestern lakes. North American Journal of Fisheries Management 32:817–822.

Balon, E. K. 1995. Origin and domestication of the wild Carp, *Cyprinus carpio*: from Roman gourmets to the swimming flowers. Aquaculture 129:3–48.

Bénech, V., and M. Penáz. 1995. An outline on lateral fish migrations within the central delta of the Niger River, Mali. Hydrobiologia 303:149–157.

Brodersen, J., B. B. Chapman, P. A. Nilsson, C. Skov, L.-A. Hansson, and C. Brönmark. 2014. Fixed and flexible: coexistence of obligate and facultative migratory strategies in a freshwater fish. PLoS (Public Library of Science) One [online serial] 9(3):e90294.

Casselman, J. M., and C. A. Lewis. 1996. Habitat requirements of Northern Pike (*Esox lucius*). Canadian Journal of Fisheries and Aquatic Sciences 53:161–174.

Chapman, B., C. Skov, K. Hulthén, J. Brodersen, P. Nilsson, L. Ä. Hansson, and C. Brönmark. 2012. Partial migration in fishes: causes and consequences. Journal of Fish Biology 81:456–478.

Copp, G. H. 1989. The habitat diversity and fish reproductive function of floodplain ecosystems. Environmental Biology of Fishes 26:1–27.

Craig, J. 2008. A short review of pike ecology. Hydrobiologia 601:5–16.

Cucherousset, J., J.-M. Paillisson, A. Cuzol, and J.-M. Roussel. 2009. Spatial behaviour of young-of-the-year Northern Pike (*Esox lucius* L.) in a temporarily flooded nursery area. Ecology of Freshwater Fish 18:314–322.

Farrell, J., J. Mead, and B. Murry. 2006. Protracted spawning of St Lawrence River Northern Pike (*Esox lucius*): simulated effects on survival, growth, and production. Ecology of Freshwater Fish 15:169–179.

Forney, J. L. 1968. Production of young Northern Pike in a regulated marsh. New York Fish and Game Journal 15:143–154.

Franklin, D. R., and L. L. Smith Jr. 1963. Early life history of the Northern Pike, *Esox lucius* L., with special reference to the factors influencing the numerical strength of year classes. Transactions of the American Fisheries Society 92:91–110.

Górski, K., H. Winter, J. De Leeuw, A. Minin, and L. Nagelkerke. 2010. Fish spawning in a large temperate floodplain: the role of flooding and temperature. Freshwater Biology 55:1509–1519.

Hodgson, S., T. P. Quinn, R. Hilborn, R., R. C. Francis, and D. E. Rogers. 2006. Marine and freshwater climatic factors affecting interannual variation in the timing of return migration to fresh water of Sockeye Salmon (*Oncorhynchus nerka*). Fisheries Oceanography 15:1–24.

Jonsson, B., and N. Jonsson. 1993. Partial migration: niche shift versus sexual maturation in fishes. Reviews in Fish Biology and Fisheries 3:348–365.

Kerr, L., S. Cadrin, and D. Secor. 2010. The role of spatial dynamics in the stability, resilience, and productivity of an estuarine fish population. Ecological Applications 20:497–507.

Kobayashi, M., P. W. Sorensen, and N. E. Stacey. 2002. Hormonal and pheromonal control of spawning behavior in the Goldfish. Fish Physiology and Biochemistry 26:71–84.

Levesque, H. M., D. Scaffidi, C. N. Polkinghorne, and P. W. Sorensen. 2011. A multi-component species identifying pheromone in the Goldfish. Journal of Chemical Ecology 37:219–227.

Lim, H., and P. W. Sorensen. 2011. Polar metabolites synergize the activity of prostaglandin $F_{2\alpha}$ in a species-specific hormonal sex pheromone released by ovulated Common Carp. Journal of Chemical Ecology 37:695–704.

Maceina, M. J., J. W. Slipke, and J. M. Grizzle. 1999. Effectiveness of three barrier types for confining Grass Carp in embayments of Lake Seminole, Georgia. North American Journal of Fisheries Management 19:968–976.

Miller, L. M., L. Kallemeyn, and W. Senanan. 2001. Spawning-site and natal-site fidelity by Northern Pike in a large lake: mark–recapture and genetic evidence. Transactions of the American Fisheries Society 130:307–316.

Moler, P. E., and R. Franz. 1987. Wildlife values of small, isolated wetlands in the southeastern coastal plain. Pages 234–241 *in* R. R. Odum, K. A. Riddleberger, and J. C. Ozier, editors. Proceedings of the third southeastern nongame and endangered wildlife symposium. Georgia Department of Natural Resources, Atlanta.

Neckles, H. A., H. R. Murkin, and J. A. Cooper. 1990. Influences of seasonal flooding on macroinvertebrate abundance in wetland habitats. Freshwater Biology 23:311–322.

Parsons, B. G., and J. R. Reed. 2005. Movement of Black Crappies and Bluegills among interconnected lakes in Minnesota. North American Journal of Fisheries Management 25:689–695.

Paukert, C. P., J. A. Klammer, R. B. Pierce, and T. D. Simonson. 2001. An overview of Northern Pike regulations in North America. Fisheries 26(6):6–13.

Poizat, G., and A. Corivelli. 1997. Use of seasonally flooded marshes by fish in a Mediterranean wetland: timing and demographic consequences. Journal of Fish Biology 51:106–119.

Priegel, G. R., and D. C. Krohn. 1975. Characteristics of a Northern Pike spawning population. Wisconsin Department of Natural Resources, Madison.

Quinn, T. P., and D. J. Adams. 1996. Environmental changes affecting the migratory timing of American Shad and Sockeye Salmon. Ecology 77:1151–1162.

R Development Core Team. 2015. R: a language and environment for statistical computing. R Foundation, Vienna.

Silbernagel, J. J., and P. W. Sorensen. 2013. Direct field and laboratory evidence that a combination of egg and larval predation controls recruitment of Common Carp in many lakes of the upper Mississippi basin. Transactions of the American Fisheries Society 142:1134–1140.

Snodgrass, J. W., A. L. Bryan Jr., R. F. Lide, and G. M. Smith. 1996. Factors affecting the occurrence and structure of fish assemblages in isolated wetlands of the upper coastal plain, USA. Canadian Journal of Fisheries and Aquatic Sciences 53:443–454.

Sorensen, P. W., and P. G. Bajer. 2011. The Common Carp. Pages 100–104 *in* D. Simberloff and M. Rejmanek, editors. Encyclopedia of invasive introduced species. University of California Press, Berkeley.

Sorensen, P. W., and N. E. Stacey. 2004. Brief review of fish pheromones and discussion of their possible uses in the control of non-indigenous teleost fishes. New Zealand Journal of Marine and Freshwater Research 38:399–417.

Swee, U. B., and H. R. McCrimmon. 1966. Reproductive biology of the carp, *Cyprinus carpio* L., in Lake St. Lawrence, Ontario. Transactions of the American Fisheries Society 95:372–380.

Verrill, D. D., and C. R. Berry Jr. 1995. Effectiveness of an electrical barrier and lake drawdown for reducing Common Carp and Bigmouth Buffalo abundances. North American Journal of Fisheries Management 15:137–141.

Vilizzi, L., and K. F. Walker. 1999. The onset of the juvenile period in Carp, *Cyprinus carpio*: a literature survey. Environmental Biology of Fishes 56:93–102.

Weber, M. J., and M. L. Brown. 2009. Effects of Common Carp on aquatic ecosystems 80 years after "carp as a dominant": ecological insights for fisheries management. Reviews in Fisheries Science 17:524–537.