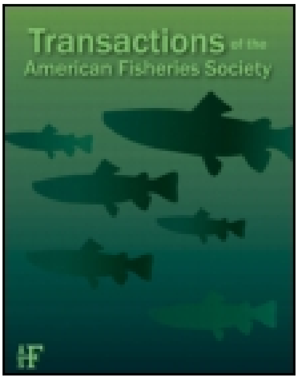

Transactions of the American Fisheries Society

Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/utaf20

Movement and Habitat Selection by Invasive Asian Carps in a Large River

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Version of record first published: 09 Jan 2011.

Transactions of the American Fisheries Society 137:45–56, 2008

DOI: 10.1577/T06-116.1

[Article]

Movement and Habitat Selection by Invasive Asian Carps in a Large River

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Abstract.—We evaluated the habitat use and movements of 50 adult bighead carp *Hypophthalmichthys nobilis* and 50 silver carp *H. molitrix* by means of ultrasonic telemetry during spring–summer 2004 and 2005 to gain insight into the conditions that facilitate their establishment, persistence, and dispersal in the lower Illinois River (river kilometer 0–130). Movement and habitat use were monitored with stationary receivers and boat-mounted tracking. The relative availability of four macrohabitat categories (main channel, island side channel, channel border, and connected backwater) was quantified to determine selection; discriminant function analysis was used to evaluate changes in physical characteristics within each category. A flood pulse occurred in spring through early summer of 2004 but not 2005. Movement rates (km/week) of both species were positively correlated with flow but not with temperature. Including data from stationary receivers greatly increased estimates of daily movement. During low summer flow, both species typically selected channel borders and avoided the main channel and backwaters. Both species rarely occupied depths over 4 m, regardless of abiotic conditions. Flood pulses appear to trigger dispersal, while habitat use is only specific during low summer flow. Thus, movement prevention efforts (e.g., dispersal barriers) will require particular vigilance during late-winter or spring flooding, and controlled removal (e.g., harvest) should be directed toward selected habitats during summer.

Many successful invading fishes possess life history traits of *r*-selected species, generally exhibiting rapid growth rates, short generation times, exceptional dispersal capabilities, high reproductive output early in life, high density in the native range, and broad environmental tolerance (Ehrlich 1984; Lodge 1993). These opportunistic characteristics allow populations to become dense soon after they become established (Lodge 1993; Williamson 1996; McMahon 2002). The ability of invasive exotics to disperse and then establish themselves in novel locations is particularly problematic in rivers owing to the broad range and high connectivity among these systems (Junk et al. 1989).

Two river-dwelling Asian fishes, the bighead carp *Hypophthalmichthys nobilis* and silver carp *H. molitrix*, became established in the Mississippi River basin in the early 1980s (Freeze and Henderson 1982; Costa-Pierce 1992). In the late 1990s, these species expanded into the connected Illinois River system and their density has since increased (Koel et al. 2000; Chick and Pegg 2001; Conover et al. 2007). Clearly, the connection between the Mississippi and Illinois rivers and the species' apparently high dispersal potential facilitate their expansion. Given that the Illinois River is connected to Lake Michigan via a shipping canal, there is great need to understand factors influencing the ability of these species to move into novel areas and become established.

Knowledge of movement and habitat selection by Asian carp adults should provide insight into the conditions that facilitate their establishment, persistence, and dispersal. We used ultrasonic telemetry to quantify the movement and habitat selection of bighead and silver carps within the well-established Asian carp assemblage of the lower Illinois River and a major backwater, 1,100-ha Swan Lake. We expected that habitat use in both the river and the adjacent backwater would be nonrandom, reflecting selection. Movement from selected areas would be seasonal and perhaps related to spawning. In their native waters, a sharp rise in stage and current velocity has been associated with spawning migrations, and shortly thereafter, spawning (Krykhtin and Gorbach 1981; Abdusamadov 1987). In the LaGrange Pool of the Illinois River, movement of bighead carp appeared to increase with increased flow (Peters et al. 2006). However, the relative contribution of river stage and temperature (or both) to movement and whether such effects differ between bighead and silver carps are unknown.

The objectives of our telemetry effort were to (1) determine whether temperature or flow was related to bighead and silver carp movement in the lower Illinois River (i.e., an index of dispersal potential), (2) identify gross habitat categories (hereafter, macrohabitats) that bighead and silver carps avoid or select, and (3)

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Received May 17, 2006; accepted August 16, 2007
Published online January 3, 2008

identify the abiotic characteristics at fish locations (i.e., microhabitats) within selected macrohabitats.

Methods

Study site.—The low-gradient lower Illinois River extends from La Grange Lock and Dam (river kilometer [rkm] 130) at Beardstown to the confluence with the Mississippi River (rkm 0) at Grafton. Despite a century of alterations by dredging, water diversion from Lake Michigan, channelization, and levee construction, the river retains an annual, albeit flashy, flood pulse (Karr et al. 1985; Sparks 1995).

Swan Lake is the major backwater of the Illinois–Mississippi River confluence and an important source of secondary fish production. To reduce sedimentation, this backwater was separated by levees into three management compartments: lower, middle, and upper Swan Lake (Figure 1). Lower Swan Lake encompasses nearly half the area and is the only compartment continuously connected with the Illinois River that subsequently allows access to Asian carps and other fishes. Middle Swan Lake becomes accessible to fishes during flooding.

We classified the lower 41 km of the Illinois River, including Swan Lake (Figure 1), into four macrohabitat categories: main channel, channel border, island side channel, and backwater (i.e., mostly Swan Lake). The proportion of available habitat was derived from digital raster graphic topographic maps obtained from the Illinois State Geological Survey (2006), ArcMap 9.2, and U.S. Army Corps of Engineers navigation maps (USACE 2006). Areas of the river with a depth less than 5.0 m at normal pool (NP) were classified as channel border; areas of 5.0 m or more at NP were classified as main channel; areas between the channel border and islands were classified as island side channel; and lower and middle Swan Lake constituted the backwater habitat.

Fish collection and transmitter implantation.—The fish used in telemetry were collected either from the lower Illinois River near Swan Lake ($N = 86$) or from lower Swan Lake ($N = 14$; typically rkm 0–10; Figure 1). Asian carps are notoriously difficult to sample (Williamson and Garvey 2005). Thus, a combination of gears was used. Drifting and dead-set trammel nets (experimental nets with 51-, 76-, 89-, and 102-mm bar mesh panels [3.7-, 4.0-, 4.0-, and 4.3-m outer walls, respectively] that were 91.4 m in length) were primarily used, but hoop nets (38-mm bar mesh, 1-m-diameter fiberglass hoops), trap nets, commercial fishers, electrofishing, and fish jumping into the boat were also capture sources (see Figure 1 for distribution of captures). During March–April 2004, 25 bighead carp and 25 silver carp were collected. During September 2004, an additional 15 fish/species were caught. During March 2005, another 10 fish/species were sampled (total = 50 fish/species).

After capture, surgery and transmitter implantation were conducted based on the guidelines of Summerfelt and Smith (1990). Each fish was placed in a holding tank with buffered (sodium bicarbonate) river water; carbon dioxide gas was diffused into the tank for anesthetization. Fish were measured (total length [TL]; mm) and weighed (kg). River water was circulated over the gills. Before surgical incision, scales were removed from the ventral left side of each fish posterior to the pelvic fin and anterior to the anus. After the removal of scales, the area was disinfected with betadine. In silver carp, the incision was made more dorsally than in bighead carp to account for displacement of the body cavity by the well-developed keel.

Ultrasonic transmitters (69 kHz, 10 g in water, 65 mm long; <2% body weight; Vemco Ltd., Halifax, Nova Scotia; Model V16) for remote individual identification were implanted during surgery. Each transmitter was pulse coded, which provided unique identification numbers. Transmitters implanted into fish during March–April 2004 had a minimum life expectancy of 570 d. The remaining 50 transmitters had a minimum life expectancy of 366 d. Each transmitter was tested for recognition before its use with a portable hydrophone and receiver (Vemco; Model VR60). Immediately after surgery and implantation, each fish was placed in a recovery tank supplemented with oxygen and was released at the capture site after regaining buoyancy and swimming independently (Figure 1). We allowed implanted fish 2 weeks at large to recover before logging their movements with telemetry (Winter 1996).

Mobile tracking.—To quantify movement and macro- and microhabitat selection within the lower 41 km of the river (see Figure 1), fish were tracked by boat with an omnidirectional portable hydrophone and receiver. During both years, tagged fish were tracked monthly during April–August (the period of purported spawning; but see DeGrandchamp et al. 2007) starting upstream at rkm 130 and progressing toward rkm 0 and the lower and middle compartments of Swan Lake.

When detected with the omnidirectional hydrophone, each fish location was determined by drifting the boat toward the fish until hydrophone signal strength was the same in all directions. Each fish location was georeferenced, and the following microhabitat variables were quantified: depth (m), water temperature (°C at 1-m depth; Yellow Springs Instruments [YSI], Yellow Springs, Ohio; Model 85), dissolved oxygen (DO; mg/L at 1-m depth; YSI Model 85), and water velocity (m/s at 1-m depth; Marsh-

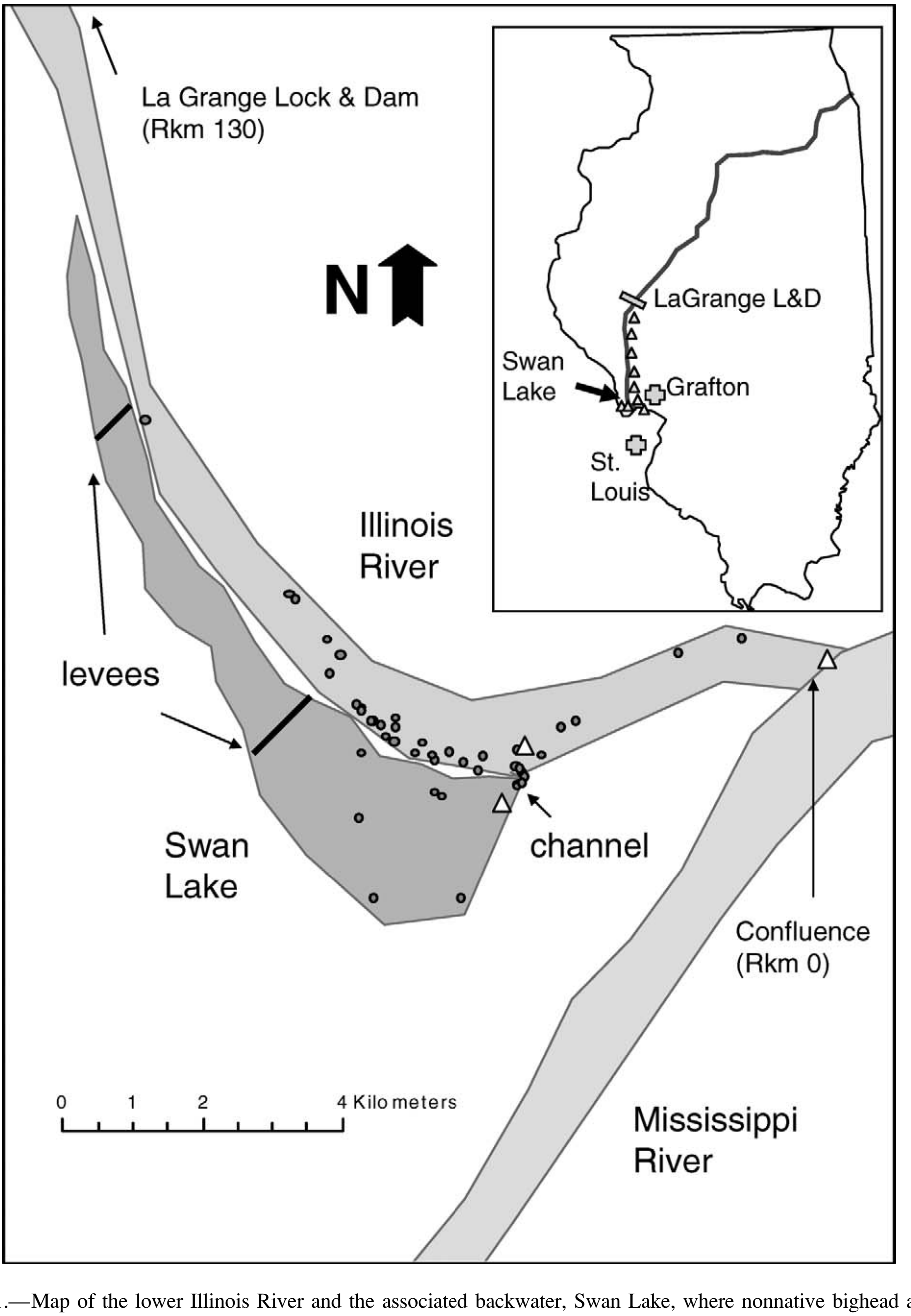

FIGURE 1.—Map of the lower Illinois River and the associated backwater, Swan Lake, where nonnative bighead and silver carps were captured, implanted with ultrasonic transmitters, released (overlapping points), and tracked during 2004 and 2005. Triangles denote the locations of stationary ultrasonic receivers.

McBirney, Inc., Fredrick, Maryland; Flo-Mate Model 2000). Sediment was sampled at each site using a petite ponar grab (2.4-L volume; Wildlife Supply Company, Buffalo, New York) and was classified as predominately clay, silt, sand, gravel, or organic material (see Bain 1999).

Stationary receivers.—To enhance our movement data, stationary receivers (Vemco; Model VR2) also logged fish movement. In March 2004, two stationary receivers were mounted underwater at each side of the lower Swan Lake channel (Figure 1), primarily to document movements in and out of Swan Lake. These receivers also continuously quantified main-channel passage past this location. In November 2004, additional receivers were affixed to navigation buoys and placed in the main channel of the Illinois River adjacent to the main navigation channel. Buoys were deployed at the following sites (approximately every 16 km): rkm 3.2, 22.7, 36.4, 50.7, 67.4, 84.5, and 100.4. All were checked and downloaded every 3 weeks.

Statistical analysis.—For all analyses, spring was defined as March–May and summer as June–August. All statistical analyses were conducted with SAS 9.1 (SAS Institute 1996). The significance level was set at 0.05 for all tests.

All geographic coordinates of fish locations were mapped in ArcMap 9.2; distances between successive individual fish locations were calculated. Fish that were detected either by mobile, boat-mounted tracking or by stationary receivers at least once during a season (about 90 d) were included in movement analysis. The distance between locations was measured as the shortest linear distance through water between successive fish locations; therefore, the actual distance traveled by individual fish was probably underestimated.

Daily rate of movement (km/d) was quantified for individual fish during the spring and summer of each year, and a mean daily rate of movement was quantified for each species. The deployment of additional stationary receivers in late 2004 increased our detection rate, which in turn increased the precision of weekly and daily movement estimates in 2005. We compared rates based on mobile tracking only with those based on mobile tracking plus stationary receivers. To further determine how augmentation of manual tracking with stationary receivers affected daily movement rates, a truncated, 32-km section of river encompassing the three stationary receivers in the lower river was selected to determine the movement rate in 2005. This fine-scale daily rate of movement was based on the passage of 20 fish (12 bighead carp and 8 silver carp) during April–June 2005. Directionality of movement was quantified by determining the proportion of each individual's locations occurring (1) in Swan Lake, (2) upstream of the release point, and (3) downstream of the release point.

To determine how river conditions affected bighead and silver carp movement, we quantified weekly rates of movement (i.e., mean km/week) for each species in the spring and summer of 2004 and 2005. Again, we did this with mobile tracking only and mobile tracking plus stationary receiver locations. Mean daily water temperature was obtained at rkm 34.6 with a submerged temperature logger (Vemco Minilog). Daily river stage was obtained from the U.S. Geological Survey river gauge at rkm 34.6. Pearson's product-moment correlation was used to test the linear relationship between mean weekly movement estimates and mean weekly river stage and temperature for both species during both years.

We calculated habitat selection in the lower 41 km using individual fish as the sampling unit (Otis and White 1999). Selection within each species, season (spring and summer), and year was quantified separately. To determine how fish were distributed among macrohabitat categories, a chi-square test was conducted to test two null hypotheses. The first was that fish locations of each species were uniformly distributed across habitats (e.g., if all four habitats contained equal abundances, each would have 25% of the fish). The second hypothesis was that the proportion of habitat used by individual fish was equal to the proportion of habitat available.

To test the first null hypothesis, we used the equation presented by Manly et al. (2002). If u_{ij} is the amount of habitat type i used by fish j; u_{i+} is the amount of type i used by all fish; u_{+j} is the total amount of habitat units used by fish j; and u_{++} is the total number of habitat units used by all fish, then the log-likelihood test statistic is

$$\chi^2 = 2\sum_{j=1}^{n}\sum_{i=1}^{I} u_{ij}\log_e[u_{ij}/E(u_{ij})],$$

where the expected value $E(u_{ij}) = u_{i+}u_{+j}u_{++}$. If the resulting value of χ^2 (with df $= [I-1][n-1]$, where I $=$ the number of habitat categories and $n =$ the number of fish) is large in comparison with the chi-square distribution, then a nonuniform distribution of fish across habitats is indicated (Manly et al. 2002).

To determine whether individual fish were selecting or avoiding specific habitat types (the second null hypothesis), we employed the same log-likelihood test statistic but with a different $E(u_{ij})$ calculation (Manly et al. 2002): $E(u_{ij}) = \pi_i u_{+j}$, where π_i is the proportion of available habitat units composed of habitat type i. In this case, selection or avoidance is established if the value of χ^2 is large (with df $= n[I-1]$). The P-value indicated whether each fish was selective in its habitat choice.

A selection ratio ($\hat{W}_i$) was used to determine the selected habitat type. Because we were interested in the population as a whole (i.e., the population was a species sampled in a given season in a single year), we used the Manly et al. (2002) estimation method, $\hat{W}_i = u_{i+}/\pi_j u_{++}$, which is a ratio of the proportion of habitat used to the proportion available ($\hat{W}_i > 1$ indicates selection; $\hat{W}_i < 1$ indicates avoidance; and $\hat{W}_i = 1$ indicates neutrality). We calculated Bonferroni 95% confidence intervals (CIs) around each mean selection

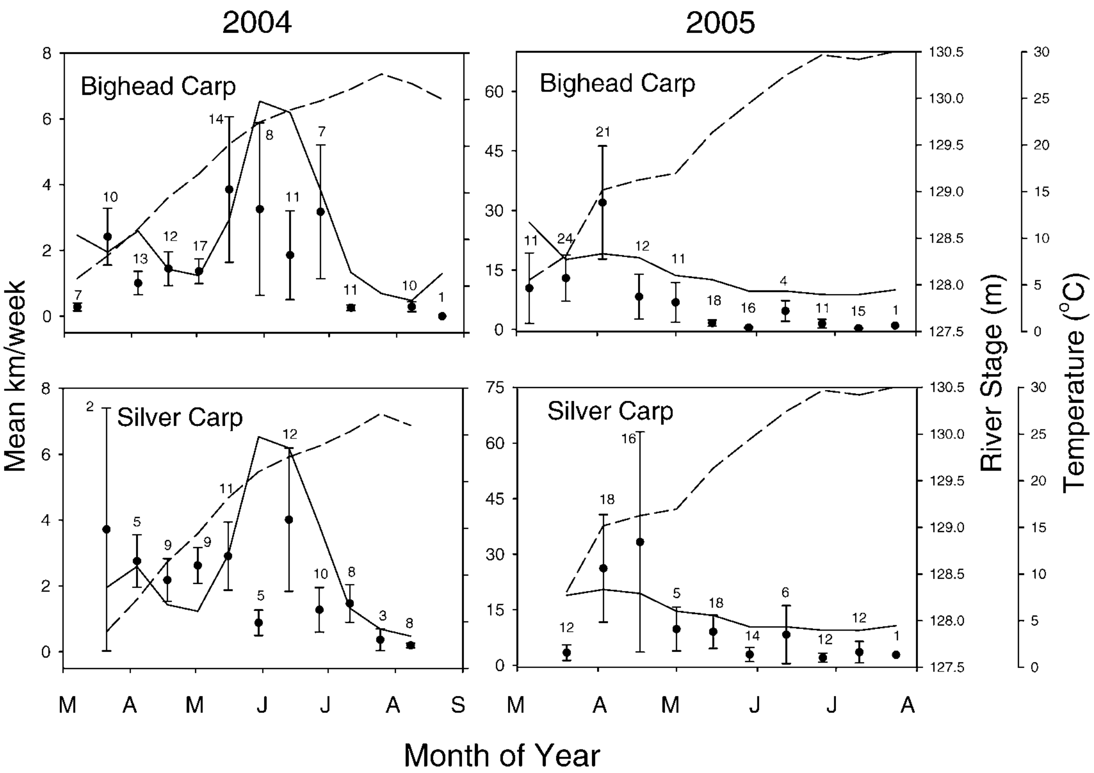

FIGURE 2.—Mean weekly river stage (m; solid lines), mean weekly water temperature (°C; dashed lines), and mean ± SE rates of movement (circles; the number of tagged fish is indicated above each data point) by bighead and silver carps in the lower Illinois River and Swan Lake during March–August or September 2004 and 2005.

ratio to determine whether it encompassed the neutral selection value of 1 (Thomas and Taylor 1990). Pearson's product-moment correlation tested whether bighead and silver carp habitat selection ratios were linearly correlated.

To determine how the microhabitat (i.e., point of fish location) characteristics chosen by fish within each of the four macrohabitats changed through time, discriminant function analysis (DFA) was conducted on four microhabitat variables (depth, velocity, temperature, and dissolved oxygen) for combined species data. The DFA was used to account for differences in river stage conditions between years; relatively high water was present in spring–summer 2004 (flood year), and relatively low water was present in 2005 during the same period. Only observations that included a value for all four macrohabitat variables were included in the analysis ($N = 386$ observations). Groups were defined by year (2004 or 2005), season (spring or summer), and macrohabitat type (backwater, main channel, channel border, or island side channel). Four discriminant functions (DFs) were generated for the DFA; the first two were retained in each analysis because they accounted for most of the variance. A structure matrix, where the correlation between each variable and each DF determined the differences between macrohabitat types, was used to rank habitat variables.

Results

Fish and Physical Conditions

The mean TL ± SE of tagged bighead carp was 774 ± 6 mm (range = 665–856 mm), and the wet weight was 5,657 ± 159 g (range = 3,200–9,500 g). For tagged silver carp, the mean TL was 740 ± 13 mm (range = 538–954 mm) and weight was 5,024 ± 264 g (range = 1,800–8,250 g). High river stages occurred during spring–summer 2004 (mean monthly temperatures were as follows: April = 12.3°C, May = 18.8°C, June = 23.5°C, July = 26.1°C, August = 26.5°C, and September = 24.7°C; Figure 2); low water occurred during this period in 2005 (mean monthly temperatures were as follows: April = 15.4°C, May = 19.4°C, June = 27.0°C, July = 29.6°C, August = 28.6°C, and September = 26.9°C; Figure 2). For those fish tagged in spring 2004, the median tag detection period was 11 months, and about 20% of the fish were detected

TABLE 1.—Daily movement rate and total movement range for bighead and silver carps tagged with ultrasonic transmitters in the lower Illinois River and Swan Lake during spring–summer 2004 and 2005. Movement was quantified by mobile tracking within a 130-km reach during both years (M) or by a combination of mobile tracking and stationary receivers (M + S). To determine the impact of stationary receivers on our estimates, we quantified movement in a 32-km reach of the lower Illinois River during 2005 with stationary receivers only (S).

Species	Year	Tracking method	Movement rate (km/d)		Maximum total range (km)
			Mean (SE)	Maximum	
Bighead carp	2004	M	0.21 (0.05)	4.3	89
		M + S	0.35 (0.07)	10.0	172
	2005	M	0.20 (0.05)	2.1	197
		M + S	3.60 (0.75)	64.0	462
		S	6.83 (1.75)	16.2	60
Silver carp	2004	M	0.27 (0.05)	3.3	105
		M + S	0.31 (0.05)	3.4	112
	2005	M	0.38 (0.15)	5.8	219
		M + S	3.18 (0.71)	64.0	411
		S	10.61 (2.65)	29.7	30

through the study period. The majority (80%) of fish tagged in fall 2004 or spring 2005 were detected throughout the remainder of our tracking effort.

Movement

In 2004, 25 bighead carp and 21 silver carp were located and used to generate movement data. In 2005, 35 bighead carp and 32 silver carp were used. In addition to mobile tracking, 733 locations logged by stationary receivers were used for analysis (2004: 235 bighead carp locations, 169 silver carp locations; 2005: 190 bighead carp locations, 139 silver carp locations).

Across all years and seasons, bighead and silver carps were more frequently located upstream of the release point than downstream of the release point or within Swan Lake (mean proportion of detections ± SD; bighead carp: upstream = 0.50 ± 0.40, downstream = 0.27 ± 0.35, Swan Lake = 0.23 ± 0.35; silver carp: upstream = 0.60 ± 0.37, downstream = 0.21 ± 0.29, Swan Lake = 0.18 ± 0.33); this result is not surprising given that a much greater distance of river was monitored upstream of releases (see Figure 1). For the entire 130-km study reach and mobile tracking only, the daily movement rates for bighead carp were similar between 2004 and 2005 (0.21 and 0.20 km/d, respectively; Table 1); because of the addition of reachwide stationary receivers in fall 2004, this estimate increased to 3.6 km/d in 2005 (Table 1). Based on mobile tracking only, silver carp moved at similar rates in 2004 and 2005 (0.27 and 0.38 km/d, respectively; Table 1). Again, use of stationary receiver data in combination with mobile tracking increased the movement rate estimate for this species (Table 1). The combination of stationary receivers and mobile tracking also increased our ability to detect total movement of both species; the maximum distance moved was 462 km for bighead carp and 411 km for silver carp (Table 1). Evaluating the performance of stationary receivers solely in the truncated 32-km section during April–June 2005 generated the highest estimates of daily movement (Table 1). Bighead carp in this partial stretch of river moved an average of 6.83 km/d, while silver carp moved 10.61 km/d (Table 1).

Using mobile tracking data only, we found no relationships between abiotic factors and weekly movement for either species. Combining stationary receiver data with mobile tracking revealed that weekly movement (km/week) of bighead carp in 2004 was positively, linearly correlated with river stage; such movement was highest in early summer ($r = 0.63$; $P = 0.02$; Figure 2) but was unrelated to temperature ($r = -0.074$; $P = 0.81$; Figure 2). In 2005, the movement of bighead carp was again positively correlated with river stage, was highest in April ($r = 0.62$; $P = 0.042$; Figure 2), and was negatively correlated with temperature ($r = -0.59$; $P = 0.06$; Figure 2). Weekly movement estimates for silver carp in 2004 were not correlated with river stage ($r = 0.28$; $P = 0.40$; Figure 2), but were negatively correlated with temperature ($r = -0.65$; $P = 0.030$; Figure 2). In 2005, silver carp movement was positively correlated with river stage, was highest in April ($r = 0.75$; $P = 0.013$; Figure 2), and was unrelated to temperature ($r = -0.47$; $P = 0.17$; Figure 2).

Habitat

In the lower 41-km reach, the macrohabitat composition was 28.7% main channel, 41.1% channel border, 7% island side channel, and 23% backwater. Data for 35 silver carp and 45 bighead carp were included in habitat use analyses. The remaining fish were never located with mobile tracking. Mobile tracking resulted in 538 locations used for analysis (2004: 179 bighead

TABLE 2.—Likelihood chi-square statistics testing (1) the distribution of bighead and silver carps tagged with ultrasonic transmitters across macrohabitat types and (2) selection or avoidance of a macrohabitat type by these species in the lower Illinois River (ns indicates nonsignificant [$P > 0.05$]). Macrohabitat types were main channel, channel border, island side channel, and backwater.

			Distribution			Selection		
Species	Year	Season	χ^2	df	P	χ^2	df	P
Bighead carp	2004	Spring	134.1	63	0.001	145.9	66	0.001
		Summer	72.2	39	0.001	106.5	42	0.001
	2005	Spring	121.4	66	0.001	163.5	69	0.001
		Summer	48.2	36	ns	101.5	39	0.001
Silver carp	2004	Spring	60.7	42	0.03	66.8	45	0.02
		Summer	49.5	33	0.03	51.5	36	0.04
	2005	Spring	49.1	45	ns	65.8	48	0.04
		Summer	51.8	33	0.02	109.8	36	0.001

carp locations, 109 silver carp locations; 2005: 142 bighead carp locations, 108 silver carp locations).

Bighead carp were not uniformly distributed across macrohabitats (test of the first null hypothesis) except during summer 2005. The second null hypothesis was rejected; bighead carp did exhibit selection of macrohabitat (Table 2). The Bonferroni 95% CIs around the selection ratios for bighead carp in spring 2004 reflected neutral selection among habitats (Figure 3). Conversely, during summer 2004, bighead carp avoided backwater and main-channel habitat (Figure 3). Bighead carp also avoided main-channel habitat in spring 2005 (Figure 3). Bighead carp selected for channel border habitat and avoided backwater and main-channel habitat in summer 2005 (Figure 3).

Silver carp were not uniformly distributed among habitats across all seasons except for spring 2005 (first null hypothesis). Fish selected macrohabitats differently among seasons (second null hypothesis; Table 2). The Bonferroni 95% CIs around the selection ratios for spring and summer 2004 did not indicate true selection for or avoidance of any habitat type (Figure 3). Silver carp avoided main-channel habitat and selected for channel border habitat in spring 2005 (Figure 3). Silver carp avoided both backwater and main-channel habitat in summer 2005 (Figure 3).

Macrohabitat selection was similar between species; habitat selection ratios were positively correlated between the species ($r = 0.60$, $P = 0.01$). Consequently, DFA that combined data from both species within each macrohabitat type was justified. The point-of-location microhabitats selected by both species were correctly classified by the DFA 89.5% of the time within backwater habitat, 76.2% within main-channel habitat, 75.1% within channel border habitat, and 82.0% within island side channel habitat. The first discriminant function (DF1) ranked depth and velocity as explaining 45.9% of the variance; DF2 ranked temperature and dissolved oxygen as explaining 38.3% of the variance (cumulative variance = 84.2%). Summer habitat types were associated with higher temperatures and lower DO concentrations, while spring microhabitat types were associated with cooler temperatures and higher DO concentrations (Figure 4; Table 3). Microhabitat within backwaters was shallow and velocities were low in both years. Channel border and island side channel habitat types in each season were clustered, indicating that characteristics of these macrohabitat types were similar. Selected microhabitats within channel borders were slightly shallower and had lower velocities than island side channels during spring and summer of both years. Main-channel microhabitat was consistently deeper and had higher water velocities than other habitat types in both years. The proximity of centroids for each group (macrohabitat type, season, and year; Figure 4) indicates that similar microhabitats within each macrohabitat type were used despite the marked difference in river stage between 2004 and 2005 (Figure 2).

Discussion

Water levels approximated historical Illinois River conditions more closely during spring–summer 2004 than during 2005. In 2005, flooding occurred in late winter (DeGrandchamp et al. 2007) and was subsiding by the time we began sampling. These conditions allowed us to bracket the movement and habitat selection by both Asian carp species under two different environmental scenarios that are probably important to their life histories.

Movement

Movement has two components: directed movement away from the point of capture (i.e., dispersal) and active movement within the area of release. Both kinds of movement varied in intensity among seasons. We captured and tagged the majority of silver and bighead carps near Swan Lake. However, individuals moved at

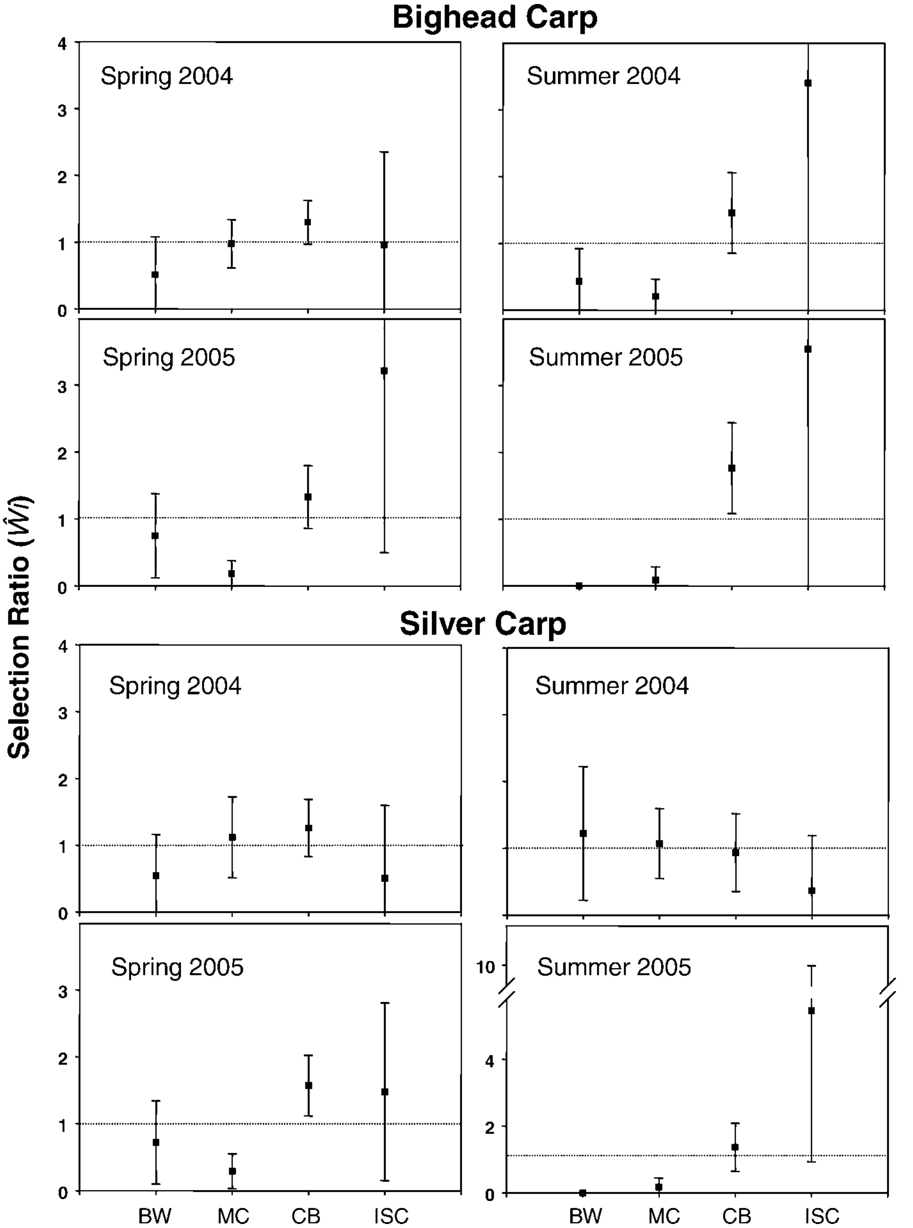

FIGURE 3.—Mean ratios of macrohabitat selection (BW = backwater, MC = main channel, CB = channel border, and ISC = island side channel) by bighead and silver carps in the lower Illinois River during 2004 and 2005. The thin vertical lines denote Bonferroni 95% confidence intervals. Points above the horizontal lines (where selection ratios = 1) indicate selection for a habitat type, points below the line avoidance of that habitat type.

least 130 km upstream to LaGrange Lock and Dam and as far as 80 km downstream into the Mississippi River (Garvey and DeGrandchamp, unpublished data). The total extent and rates of movement were similar to those of bighead carp in LaGrange Pool, where the movement of 23 individuals averaged 1.7 km/d (Peters et al. 2006). The dispersal rate and capacity of bighead and silver carps are comparable to the range and rates of movement by native Mississippi River species, including paddlefish *Polyodon spathula* (Zigler et al. 2003), lake sturgeon *Acipenser fulvescens* (Knights et al. 2002), and pallid sturgeon *Scaphirhynchus albus*

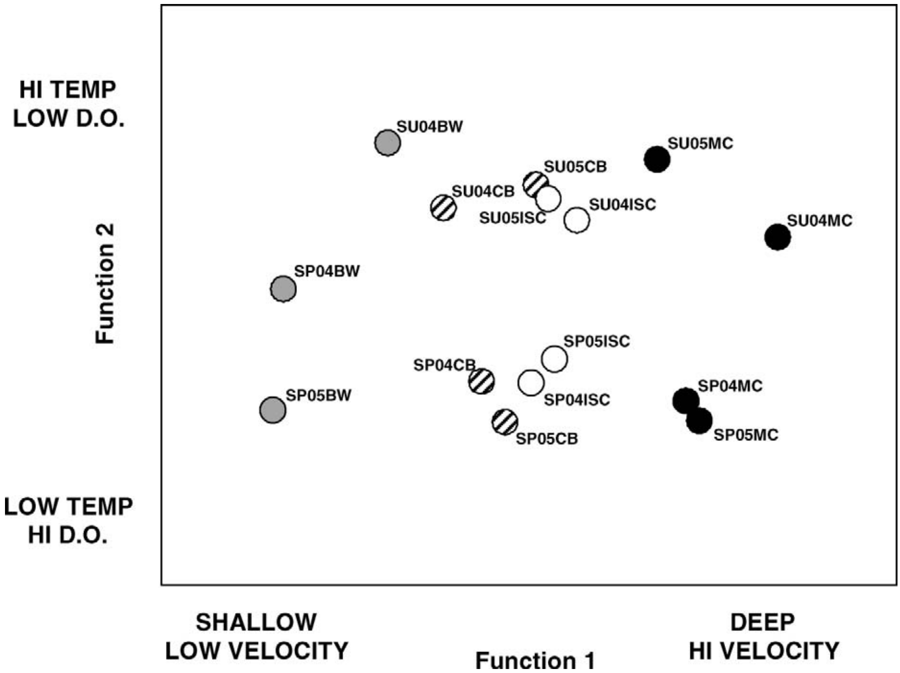

FIGURE 4.—Discriminant function ordination of bighead and silver carp microhabitat selection within four macrohabitat types in the lower Illinois River during spring (SP) and summer (SU) of 2004 (04) and 2005 (05): backwater (BW; gray circles), channel border (CB; striped circles), island side channel (ISC; white circles), and main channel (MC; black circles); HI = high. Each point indicates a group centroid (mean $N = 26$ observations/centroid; total $N = 386$ observations). Ranges of temperature, dissolved oxygen (D.O.), depth, and velocity are given in Table 3.

(Hurley et al. 1987; Garvey et al. 2007), leading to comparable North American distributions.

River stage should play an important role in the life history of bighead and silver carps. We predicted that movement would peak when river stage was rising. Despite the high water during late spring and early summer of 2004 and the low water during the same period in 2005, movement was positively correlated with relatively high river stage within each year. Peak movement was earlier in 2005, when temperatures were still cool in April as an early winter flood receded (see DeGrandchamp et al. 2007 for hydrographs).

TABLE 3.—Microhabitat (i.e., point-of-location) attributes (depth [m], velocity [m/s], temperature [°C], and dissolved oxygen [DO; mg/L]) used by bighead and silver carps tagged with ultrasonic transmitters in the lower Illinois River and Swan Lake across all fish locations during spring and summer 2004 and 2005.

Species	Season	Habitat variable	Minimum	Maximum	Mean
Bighead carp	Spring	Depth	0.5	13.7	4.0
		Velocity	0.0	0.7	0.2
		Temperature	5.6	25.7	16.1
		DO	3.4	19.1	9.9
	Summer	Depth	0.9	8.5	4.1
		Velocity	0.0	1.0	0.2
		Temperature	22.8	31.6	27.0
		DO	2.3	13.5	6.0
Silver carp	Spring	Depth	0.5	8.3	3.8
		Velocity	0.0	0.6	0.2
		Temperature	5.9	26.5	17.7
		DO	3.4	18.5	9.0
	Summer	Depth	0.8	9.1	3.9
		Velocity	0.0	1.2	0.2
		Temperature	21.7	32.0	27.1
		DO	2.2	13.5	6.4

Thus, an annual rise in river stage may serve as a cue for movement, which is consistent with reports from these species' native waters in Asia (Krykhtin and Gorbach 1981; Abdusamadov 1987).

The effect of temperature on both short- and long-range movement was less clear. Temperature was negatively correlated with movement for bighead carp in 2004 and silver carp in 2005, suggesting that both species move less when their growth optimum of 26°C is exceeded during summer (Verigin et al. 1978; Krykhtin and Gorbach 1981; Abdusamadov 1987; Jennings 1988). These species are warmwater spawners (≥17°C). Because fish moved long distances early and at cool (<17°C) temperatures several months before the purported spawning period in 2005, it appears that peak movement is more closely linked to river stage, regardless of temperature and its importance to reproduction. Indeed, spawning was not evident during 2005, probably because of a lack of congruence between the flood pulse and warm temperature (DeGrandchamp et al. 2007).

Habitat Selection

The similarity in habitat selection between bighead and silver carps in the lower reach of the Illinois River suggests that they co-exist by partitioning resources other than space. Both species seem to have similar reproductive requirements in rivers (e.g., high flow, unimpeded river; see DeGrandchamp et al. 2007), and their offspring probably share similar zooplankton resources (J.E.G. and A. Lohmeyer, Southern Illinois University–Carbondale, unpublished data). However, the adults occupy different ecological feeding niches; bighead carp are zooplanktivorous, whereas silver carp consume smaller particles such as phytoplankton and fine particulate organic matter (Fuller et al. 1999; Sampson 2005; Williamson and Garvey 2005). Thus, these two fishes may coexist spatially by consuming different prey.

Tracking demonstrated that adults of both species have specific habitat requirements; individuals did not distribute themselves uniformly across macrohabitats and actively selected or avoided particular macrohabitats during different seasons. Both species typically avoided the main channel and only used it in proportion to its abundance during high flow (e.g., the spring–summer 2004 flood), when occupation of the channel may be energetically expensive because of swimming costs. One hypothesis for this pattern revolves around food availability, because the main channel has especially high densities of zooplankton and probably particulate organic matter during high flow (Goodrich 1999; Dettmers et al. 2001; Csoboth 2006). Also, given that adults were moving long distances during high flow, presence in the main channel may have been related to increased local movements among macrohabitats and dispersal from the reach.

During low water, the avoidance of the main channel by adults may have resulted from low food availability and the presence of frequent barge traffic, which can induce mortality through propeller injuries when water levels are low. Avoidance of backwater macrohabitat by both species, notably during the drought in summer 2005, may have been related to poor food availability and low water. Also, the dominant backwater, Swan Lake, was over 5°C warmer than the river during this time and may have exceeded the temperatures that are ideal for growth (Schultz 2006).

Differences in river conditions between years produced a wide range of point-of-location microhabitat conditions within each predefined macrohabitat type, yet both species occupied the same specific microhabitats (i.e., physical conditions) each year. Thus, identifying the particular suite of physical conditions (e.g., low flow, shallow water, and proximity to shore) may also be useful for directing sampling and control efforts within the larger macrohabitat categories (e.g., side channel borders during summer).

Management Implications

Combining the fixed receivers with our manual mobile tracking greatly improved our understanding of the great distances that were rapidly traveled by bighead and silver carps during both years, particularly when flow increased. If managers want to improve detection rates (i.e., increase precision) and better predict dispersal potential, then maintaining the existing stationary receivers and installing additional receivers within uninvaded river reaches would be judicious. Because individuals are capable of extensive long-range movement, strategies for impeding their upstream dispersal, such as the Chicago Sanitary and Ship Canal electrified barrier (Moy 2005), may be justified. Bubble and sound barriers also may deter these fishes from moving further north in the river system (FishPro, Inc. 2004). The risk of barrier breech would be greatest during high flow in spring regardless of temperature; thus, these barriers would require high vigilance during such periods.

Although our research suggests that stationary receivers are necessary for assessing long-range movements as a function of environmental conditions, mobile tracking is necessary for understanding habitat selection and patterns of activity at local scales (e.g., movement among habitats). Quantifying habitat selection is critical for predicting the impact and spread of these and other aquatic invasive species. Targeting Asian carps for harvest within selected macrohabitats at selected areas of establishment, such as the lower Illinois River and Swan Lake (e.g., near the channel border in depths <4 m during low summer flow), may aid in greatly decreasing the biomass of these species and subsequently inhibiting their population growth and dispersal potential.

Currently, management efforts have been aimed at containing Asian carps and preventing further dispersal by means of barriers (Kolar et al. 2005; Conover et al. 2007). Although our research supports the idea that dispersal is not random through time and might be effectively stopped by barriers during spring flooding, it also suggests that management efforts designed to target adults for removal from specific locations also is a viable option that requires further exploration.

Acknowledgments

We thank the many undergraduate and graduate student workers at Southern Illinois University–Carbondale that assisted with this project, specifically Laura Csoboth and Doug Schultz. Three anonymous reviewers and Duane Chapman provided helpful comments on a previous draft of the manuscript. We also thank the Two Rivers National Wildlife Refuge (U.S. Fish and Wildlife Service) for lodging resources and field assistance. The U.S. Army Corps of Engineers St. Louis District provided partial support for K.L.D.'s assistantship and this research through the Environmental Management Program.

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