American Fisheries Society Symposium 77:495–509, 2011

Intra-Annual Movement and Migration of Flathead Catfish and Blue Catfish in the Lower Missouri River and Tributaries

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Abstract.—Flathead catfish *Pylodictis olivaris* and blue catfish *Ictalurus furcatus* thrive in large rivers and constitute large sport fisheries. Defining a spatial scale for new management strategies has become increasingly important due to rapid expansion of the sport fishery. To investigate life history characteristics, migratory pathways, and space use, we used telemetry to monitor the movement behavior of flathead catfish and blue catfish during two complete annual cycles. Individuals were sampled from a 97-km reach of the lower Missouri River and surgically implanted with transmitters during April 2006 (N = 77) and again in April and July of 2007 (N = 80). Acoustic tracking by boat and radio tracking by helicopter were used on the Missouri, Lamine, Chariton, Little Chariton, and Grand rivers during 2006–2008. The proportion of individuals that used a tributary during the putative spawning period (May 15–July 15) increased from 10% (8 of 77) in 2006 to 18% (14 of 80) in 2007. Flood conditions in May 2007 may have contributed to this increase. Between April 2006 and May 2007, the majority of flathead (51%) and blue catfishes (55%) moved less than 100 river kilometers from where they were tagged. The maximum linear range during 2006–2007 was 347.6 river kilometers for blue catfish and 751.9 river kilometers for flathead catfish. Seasonal structure to annual movements was evident with periods of both restricted movement (December–March; July–September) and migratory behavior (March–June; October–December). The variability in observed behaviors provides a substantial basis for managers to identify and protect distant habitats that are used by adult catfish for spawning, feeding and growth, and overwintering.

Introduction

Information on large-scale movement patterns of fishes has become increasingly important to biologists in the central United States. In a recent survey, anglers and biologists from the Mississippi River basin agreed that trophy catfishes, and in particular flathead catfish *Pylodictis olivaris* and blue catfish *Ictalurus furcatus*, are important angling resources worthy of more intensive management (Arterburn et al. 2002). In Missouri, the growing sport of catfish angling has elicited interest among state biologists to create special harvest regulations that would facilitate a trophy catfish fishery in an interior reach of the lower Missouri River. The effect of special regulations on the fishery inherently relies on spatial scale of the regulation coupled with relative mobility of these species. Individuals protected by special harvest restrictions that incorporate distant habitats to complete life history activities would inherently leave the area within which protections were in place. Thus, the Missouri Department of Conservation (MDC) helped to conceive this project to determine the scale at which adult catfish carry out their lives, from restricted-movement (i.e., nonmigratory) to migratory behavior.

Past research on blue catfish and flathead catfish has presented an incomplete and sometimes

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contradictory picture of life history characteristics. Although flathead catfish have been described as nonmigratory, exhibiting restricted-movement behavior (Funk 1957; Robinson 1977; Daugherty and Sutton 2005), they have been shown to migrate several hundred kilometers to complete life history requirements (Dames et al. 1989; Stauffer et al. 1996; Travnichek 2004). Restricted-movement or nonmigratory behavior has been considered prevalent in stream fishes since the influential writings of Gerking (1950, 1953, 1959). The "restricted-movement paradigm" states that adult fish in streams are sedentary and spend most of their lives in short (20–50 m) reaches of stream (Gerking 1959). This may be true for many temperate stream fishes (Scalet 1973; Mundahl and Ingersoll 1983; Hill and Grossman 1987), but nonmigratory movement does not always occur at small spatial scales, as supported by Gerking (1959). In the Grand and Cuivre rivers, Missouri, flathead catfish used seasonal habitats that varied in scale from 0.15 to 50.4 river kilometers during the summer/fall period, suggesting that fidelity to a home area may occur at multiple spatial scales (Vokoun and Rabeni 2005a). In a parallel study, Vokoun and Rabeni (2005b) showed that riverine habitats used by flathead catfish during summer/fall and overwintering periods may be located in the same section of river (<1 km) or separated by more than 40 river kilometers. Thus, behavioral deviations from restricted-movement to migratory behavior must be evaluated on an individual basis. In general, migrations occur over a shorter time period than restricted-movement behavior, are often timed with environmental triggers, and expand observed extent of annual space use.

Most movement studies on blue catfish have been conducted in lakes and reservoirs (Fischer et al. 1999; Graham and DeiSanti 1999; Timmons 1999; Grist 2002). Pugh and Schramm (1999) conducted a tag-recapture study on channel catfish *Ictalurus punctatus*, blue catfish, and flathead catfish in the lower Mississippi River (LMOR) and found that blue catfish moved 5–12 km from their release site after 363–635 d and were more mobile than flathead catfish. On Lake Norman, North Carolina, Grist (2002) found that blue catfish established a home range that varied by season and exhibited site fidelity, with a maximum distance traveled of 34 km in the spring. Because there is no information on the movement of blue catfish in the LMOR, it remains unclear what management actions, if any, are needed to address habitat quality and connectedness, what spatial scale is appropriate for management actions, and whether those should differ for flathead catfish.

Tributaries of the LMOR are used by catfish throughout the annual cycle (Dames et al. 1989; Vokoun and Rabeni 2005b), but extent of seasonal use by migrants from the main stem is unknown. Anecdotal evidence from 2007 sampling in the Lamine, Platte, and Grand rivers in Missouri suggests that abundance of adult catfish increases in tributaries of the LMOR during the spawning period (Z. Ford, Missouri Department of Conservation, personal communication). This may be attributed to potential spawning habitat that tributaries provide. Flathead catfish select protected nesting sites, such as hollow logs, excavated cavities in clay banks, and root masses from downed trees (Bobea 1989; Francis 1993). These habitats are generally more available in tributaries of large, channelized rivers where natural features have been removed. Blue catfish have been studied to a lesser degree but are believed to spawn around similar habitat features (Graham 1999). Given lack of empirical data, it remains unclear whether tributaries to large, turbid rivers play a major role in the life history of catfishes that reside primarily in the main stem. To address this information need, this study was designed in part to estimate the proportion of flathead and blue catfish that migrate up adjacent tributaries during the prespawn/spawning period. Given that three large (sixth to eighth order) tributaries flow into the 97-km study reach, we hypothesized that many, if not most, catfish would migrate up these tributaries in May and early June, presumably to find an undercut bank, log complex, or other feature to facilitate spawning and subsequent nest guarding. Information on how fish in the LMOR use adjacent tributaries during an annual cycle will allow managers to account for movement and migration when implementing special regulations that apply to specific rivers.

We used temporal movement patterns to describe restricted-movement and migratory behaviors of flathead and blue catfish in the LMOR and adjacent tributaries in central Missouri. To assess how fish might benefit from migration, we used temporal overlap of general life history characteristics (i.e., spawning, feeding and growth, and overwintering) to present the life history context behind nonmigratory and migratory behaviors. Our primary objectives were to (1) estimate annual and seasonal ranges (farthest upstream and downstream extent of movement during 1 year) of blue and flathead catfish, (2) broadly define spatiotemporal dimensions of migration and restricted-movement periods based on animal behaviors, and (3) estimate the proportion of individuals that migrate up adjacent tributaries during the prespawn/spawning period.

Methods

Sampling and Design

Flathead and blue catfish were obtained from a 97-km reach of the LMOR (Figure 1). To obtain a spatially unbiased sample, no more than 10 fish of each species were collected within a 24-km section. The resulting sample in 2006 (*N* = 77) and 2007 (*N* = 80) was spread throughout the reach, with no bias towards proximity to adjacent tributaries. Individuals were surgically implanted with transmitters during April 2006 (flathead catfish *N* = 37; blue catfish *N* = 40) and again in April and July of 2007 (flathead catfish *N* = 40; blue catfish *N* = 40). Fish were collected primarily by low-frequency DC electrofishing (15–30 Hz), although some blue catfish were taken by gill nets in 2006 (*N* = 8) and hook and line during both sampling years (*N* = 10). To support high survival of released fish, no individual weighing less than 2.1 kg was tagged (i.e., transmitter constitutes <2% of the total body weight). To ensure sexual maturity of tagged fish, no individual measuring less than 560 mm total length (TL) was tagged. Blue catfish in Missouri are reported to reach sexual maturity at about 380 mm in the Mississippi River and 420 mm from the Lake of the Ozarks (Barnickol and Starrett 1951; Graham and DeiSanti 1999). Female flathead and blue catfishes greater than 426 and 508 mm TL, respectively, from the middle Mississippi

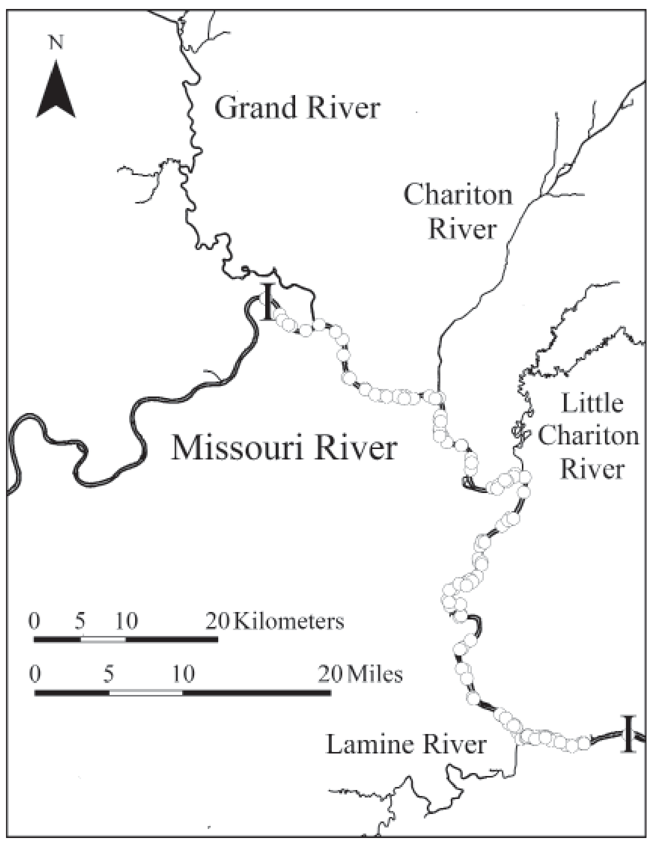

FIGURE 1. Sampling reach on the lower Missouri River (LMOR), including the Lamine, Chariton, Little Chariton, and Grand rivers. Hollow circles denote capture locations of individual flathead and blue catfishes tagged in 2006 and 2007. Vertical bars delineate the upper and lower boundaries of sampling and tracking in the LMOR (river kilometers 315–411). U.S. Geological Survey Columbia Environmental Research Center accounted for relocations in the LMOR beyond this study reach.

River (between Hannibal and Cape Girardeau, Missouri) had mature ovaries (Colehour 2009).

Transmitters were manufactured by Lotek Wireless, Inc. (Newmarket, Ontario). In 2006, combination acoustic-radio transmitters (CART; 480-d warranty life) were used and alternated between a radio burst (164.4 MHz) and an acoustic burst (76.8 KHz) at a pulse rate of 2.5 s. These dual-transmission tags are particularly useful when tracking between shallow and deep water. The success of acoustic tracking at all depths in 2006–2007 prompted the use of acoustic transmitters (CAFT; 504-d warranty life) in 2007–2008. These tags transmitted an acoustic signal every 4 s at 76.8 KHz. Based on one confirmed and several unconfirmed cases of transmitter expulsion by blue catfish in 2006, CAFT tags were coated in paraffin wax in 2007. Coating transmitters in wax has been shown to reduce the risk of expulsion by stimulating the growth of mesentery tissue around the transmitter (Hart and Summerfelt 1975; Sakaris et al. 2005).

Transmitters were implanted in the abdominal cavity through a ventral incision about halfway between the pectoral and pelvic fins. The whip antenna was fed through a shielded, 16-gauge needle posterior to the incision to ensure that once implanted, the transmitter would not rest directly on the incision, potentially hindering the healing process (CART tags only). The incision was closed with three to five interrupted stitches using absorbable, monofilament suture material. Surgeries were conducted onboard the tracking vessel and fish were held in an aerated tank for 20 min and then released at location of capture. To allow for a recovery period, individuals were not relocated for 2 weeks following surgery. Fish were relocated from a boat using a Lotek SRX_400A datalogging coded series receiver with W5XG firmware coupled with an ultrasonic upconverter and omnidirectional amplified hydrophone. For aerial tracking efforts, the SRX_400A receiver was coupled with onboard antennas mounted on a Bell 206 Jet Ranger owned and operated by MDC.

Telemetry Design

The tracking schedule was variable throughout the year, primarily due to ice flows in winter, high-water events in spring, and movement of individuals as the study progressed. We attempted to locate fish in a 97-km reach of the LMOR at least weekly throughout the annual cycle (April to March) from spring 2006 through spring 2008, with exception of the overwintering period when fish were relocated once every 2 weeks. Thus, time lapse between relocations was no less than 1 week. In 2006 and 2007, we conducted boat tracking efforts in the Grand, Chariton, Little Chariton, and Lamine rivers (sixth- to eighth-order tributary streams) every week during the spawning period (May 15–July 15) to address spawning-related tributary use. During 3 d in late July and early August 2006, radio tracking was conducted from a helicopter to account for any individuals that were missed by on-the-water acoustic tracking. Tributaries above and below our 97-km study reach could not be sampled with available resources, raising the potential for bias (see Discussion).

In 2006, the U.S. Geological Survey Columbia Environmental Research Center (USGS-CERC) began a long-term tracking and monitoring program for pallid sturgeon *Scaphirhynchus albus* and shovelnose sturgeon *S. platorynchus* in the LMOR. Using compatible Lotek tracking equipment, they assisted with relocations outside of the 97-km sampling reach to monitor long range movements (>100 km) during the first year of tracking.

The two monitoring efforts from 2006 and 2007 yielded very different data sets, in part due to differing environmental conditions between years, fewer resources in 2007, and a modified set of objectives. In 2007, 13 of 80 individuals could not be captured and tagged until July 5 due to a sustained high-flow event (>3,000 m^3/s) lasting from late April to late June. During this time period, few individuals were relocated due to high turbidity that increased attenuation of acoustic signals through the water column. Once effective tracking resumed in July, about half (33 of 67) of the individuals tagged in April could not be found within the 97-km study reach, and not having the assistance of USGS-CERC in 2007 to monitor long-ranging individuals, this apparent increase in mobility could not be recorded and described and should be considered when interpreting the results presented here. Given ideal acoustic-tracking conditions in 2006, individuals tagged in 2006 were monitored more consistently throughout the annual cycle and were subsequently used to define spatiotemporal dimensions of restricted-movement periods.

Data Analyses

Field-collected relocations were imported into ArcView geographic information systems (Environmental Systems Research Institute, Redlands, California). Relocations were overlaid on a spatial data layer of the Missouri, Grand, Chariton, Little Chariton, and Lamine rivers (Missouri Spatial Data

Service). The Missouri River data layer contained a thalweg line that was used to convert two-dimensional Universal Transverse Mercator coordinates into univariate positions along the river corridor to the nearest 10 m (kilimeters above the river mouth). Thalweg lines for the tributaries were estimated using aerial photographs (National Agricultural Imaging Program). Univariate data sets based on the thalweg in each river were used as the basis to calculate movement statistics. When fish entered a tributary, distances were measured individually using aerial photographs and the ArcView measuring tool. The same process was used to calculate distance to river mouths (km) for those individuals that migrated into a tributary.

General Movement Patterns

Linear movement was defined as the farthest upstream and farthest downstream position during a specified period. Mean linear movement (average linear movement among all individuals) coupled with spatial information from tracking revealed distinct periods of restricted movement punctuated by brief migrations. Means of individual movement were defined for 2-month periods because relocations were too sporadic during the overwintering period to make monthly or weekly comparisons. Data collected during 2007–2008 were only used to validate movement patterns recorded in 2006 and not for calculations of linear movement during 2-month periods.

We were able to reconstruct patterns of migration and movement exhibited by flathead and blue catfishes in the LMOR by using ArcView geographic information systems to examine relocations spatially and plotting distances from the river mouths against calendar dates. Harvest locations from anglers were used to supplement tracking data and allowed us to include long-range movements within the scope of the project. During the first year of tracking, the USGS-CERC aided our project in relocating individuals that traveled outside of our 97-km study reach in the LMOR. All movements greater than 100 km that we report were recorded by an angler or by USGS-CERC during 2006–2007. The data set during 2006–2007 was more complete than during 2007–2008, and a comparison between years was not appropriate.

Seasonal Periods

We used a three-period annual cycle framework similar to Vokoun and Rabeni (2005b) to describe intra-annual movement and migration in the LMOR. For the purposes of this study, restricted movement is synonymous with the home-range concept and is defined as fidelity to a commonly used area. Migration is defined as seasonal movement between discrete areas of river used to complete life history requirements (i.e., reproduction, feeding and growth, and overwintering (sensu Schlosser and Angermeier 1995; Fausch et al. 2002). Individuals monitored during the course of the study (April 2006–May 2008) displayed restricted-movement behavior during three seasonal periods: the prespawn/spawning period, summer/fall period, and overwintering period. While these periods were previously defined for flathead catfish (Vokoun and Rabeni 2005b), spatiotemporal dimensions presented in this study were not defined a priori. Seasonal movement behavior in the LMOR was assessed to broadly define timing and spatial extent of migration. One-way analysis of variance (ANOVA) was performed to test for differences in linear movement (distance between farthest upstream and farthest downstream movement) between species and behaviorally defined periods. Data were log transformed prior to analysis to achieve normality.

Results

Tagged flathead catfish had a mean total length of 870 mm and ranged from 594 to 1,400 mm. The same 77 individuals had a mean weight of 7.67 kg and ranged from 2.2 to 37.8 kg. Tagged blue catfish had a mean total length of 872 mm and ranged from 569 to 1,260 mm. These 80 individuals had a mean weight of 8.9 kg and ranged from 2.1 to 29.4 kg. Descriptions of the annual movement cycle are based on recorded movements of 26 flathead catfish and 24 blue catfish that were implanted with transmitters in the LMOR (river kilometers 315–411) in April 2006 and in April and July 2007. During April 2006–July 2007, 12 of 37 flathead catfish and 12 of 40 blue catfish were monitored weekly during daylight hours and facilitated descriptions of large-scale movement patterns during a complete annual cycle. Ten (27%) flathead and 12 (30%) blue catfish were harvested during the first 15 months of tracking, most by trot line in the LMOR. Three blue catfish were caught by rod and reel and were released, allowing for continued monitoring. Fifteen flathead and 16 blue catfish were not relocated often enough to discern movement patterns. During April 2007–March 2008, 17 of 40 flathead catfish and 9 of 40 blue catfish implanted with transmitters were used to discern movement patterns during the summer/fall and overwintering periods. Five (13%) flathead and eight (20%) blue catfish were harvested during this time while three blue catfish were caught and released. Eighteen flathead and 23 blue catfish were not relocated often enough for inclusion in analyses. Postsurgery survival was assumed as only four individuals in 2006 (5%) and 10 individuals in 2007 (13%) were never relocated after they were released. Several high-water events during the spring, summer, and fall of 2007 created difficult tracking conditions and possibly stimulated greater movement of individuals. The mean number of relocations for individuals during 2006–2007 was 33 (range 18–43) and 35 (19–59) for flathead and blue catfishes, respectively. During 2007–2008, mean number of relocations per individual fish was 41 (range 15–49) and 32 (13–45) for flathead and blue catfishes, respectively.

General Movement Patterns

Variability of movement was greater during the first few months of tracking. Six flathead and three blue catfishes traveled more than 100 river kilometers; two individual flathead moved greater distances upstream than previously recorded for the species (668 and 752 km; Table 1). Flathead and blue catfish displayed similar patterns of monthly movement throughout the annual cycle (Figure 2). Measurements of mean linear movement during the first spring of tracking were influenced by highly mobile individuals, some of which were lost during the course of the study. As such, mean linear movement measured during the latter half of each tracking cycle (January–August) is biased in favor of restricted-movement that was more easily recorded (Figure 3).

Sufficient data were collected during 2006–2007 to reveal seasonal movement patterns covering 14 months and two spawning cycles for the same group of individuals. Both species incorporated migration as a life history strategy, though variation in migratory pathways was unexpected. Within the three-period annual cycle framework (Vokoun and Rabeni 2005b), individual fish displayed at least five variant pathways through an annual cycle (Figure 4). Of the 50 individuals used to define seasonal structure, 22 (44%) displayed restricted-movement behavior throughout the year. These individuals stayed within a 10-km stretch of river and showed no signs of migratory movement related to season. Fifteen individuals (30%) migrated to and from seasonal habitats within the LMOR. Within this group, three distinct pathways were revealed that incorporated downstream migration following the summer/fall restricted-movement period. Eleven flathead and 11 blue catfishes migrated up a tributary during the prespawn/spawning period, the fifth migratory pathway observed. Nine of these contacts were lost after leaving the tributary and were excluded from evaluations of intra-annual movement and seasonal structure.

Timing of migration was not synchronous among individuals, and there was no observed effect of period (ANOVA: $F_{2,71} = 1.04$, $P = 0.36$) or species (ANOVA: $F_{1,71} = 0.01$, $P = 0.91$) on linear ranges. Thus, dates selected to define restricted-movement periods are based on the majority of movement recorded and were not strictly adhered to by all indi-

TABLE 1. Tracking, biological, and movement data for individual flathead (FL) and blue (BL) catfish that traveled >100 km (farthest upstream and downstream movement). These individuals were not included in analyses of seasonal structure throughout the annual cycle due to insufficient number and frequency of relocations. We were also unable to calculate mean linear movement by months (Figures 2 and 3) for these individuals.

Code	Species	Relocations	Tracking days	Total length (mm)	Weight (kg)	Linear movement (km)
98	BL	23	185	685	4.1	275.2
108	BL	2	97	915	10.6	282.1
149	BL	2	95	845	6.3	347.6
172	FL	12	209	742	5.2	101.2
145	FL	9	484	1,025	14.6	177.0
137	FL	10	244	714	4.4	248.3
150	FL	3	40	765	5.8	267.5
208	FL	13	369	985	10.6	667.9
173	FL	15	463	1,110	19.8	751.9

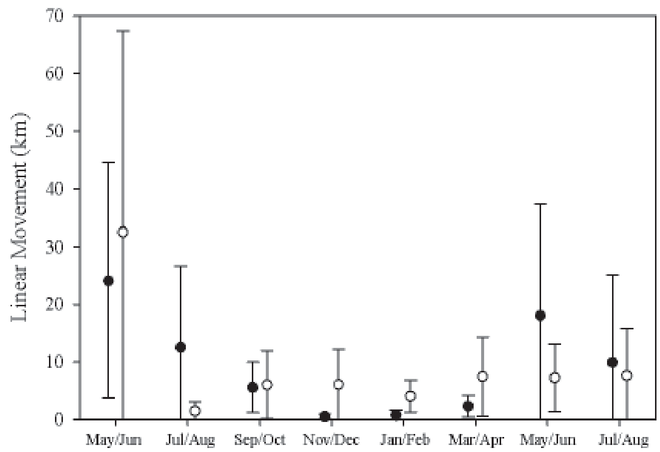

FIGURE 2. Mean and 95% confidence intervals of linear movements by blue (solid circles) and flathead catfish (hollow circles) from May 2006 to August 2007 in the lower Missouri River and adjacent tributaries.

viduals. Spawning-related migrations occurred from mid-March to the end of June, and overwintering migrations occurred from mid-October to the end of December. Given the temporal resolution of this study (weekly to bimonthly relocations), movement rates were not used to define migratory behavior, although they are likely highly variable among individuals given variability in life history strategies (Figure 4) and timing of directed movements (Figures 5 and 6). We examined spatial arrangement of relocations to differentiate between restricted-movement and migratory behavior. Directed movements that did not result in a new, spatially distinct home range were not included as evidence of migration. Thus, long-range movements of individuals that were not continuously monitored across restricted-movement periods were excluded as evidence of migratory behavior (Table 1). The intra-annual movements of 12 individuals were selected to illustrate the diversity of movement behavior recorded in this study (Figures 5 and 6).

Seasonal Periods

As water temperatures rose above 8–10°C in late March/early April, individuals began upstream migrations to areas used during the prespawn/spawning period (April 15–July 15). During this period,

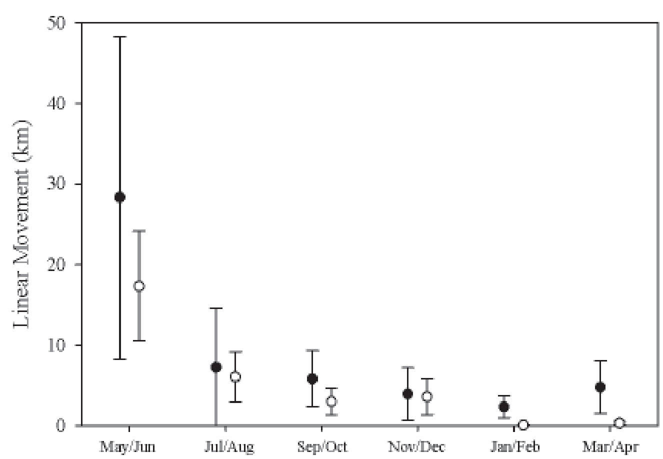

FIGURE 3. Mean and 95% confidence intervals of linear movements by flathead and blue catfish (pooled) during 2006 (solid circles) and 2007 (hollow circles) in the lower Missouri River and adjacent tributaries.

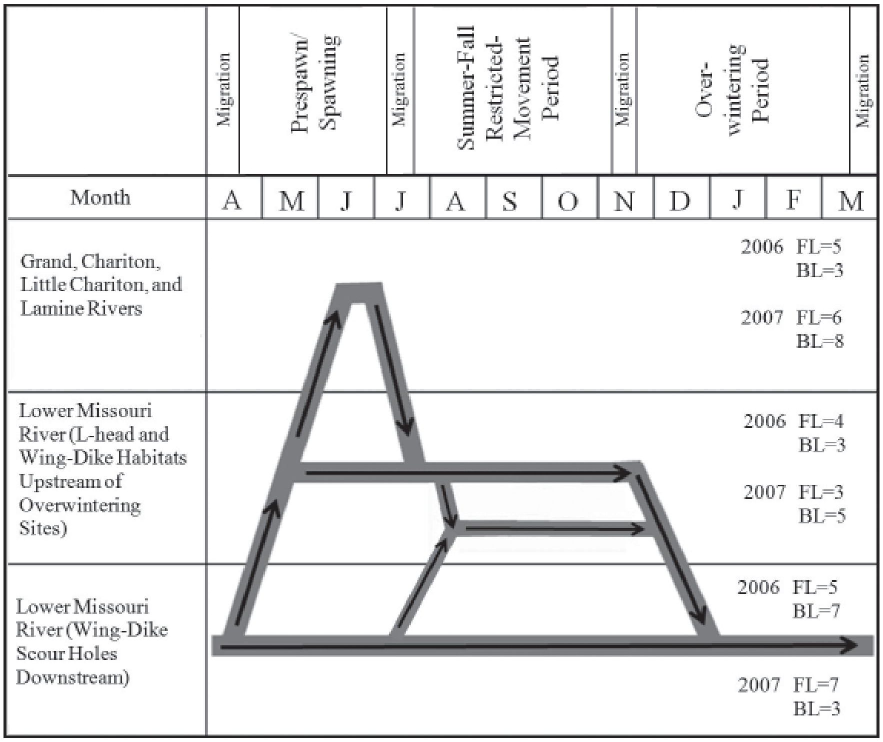

FIGURE 4. Spatial pathways used to complete an annual cycle (shown in gray) by acoustically tracked flathead (FL) and blue catfishes (BL) in the lower Missouri River (LMOR) and adjacent tributaries. Numbers of individuals that were documented for each tier are presented: restricted-movement behavior throughout the annual cycle (bottom tier), upstream migration in spring/summer and downstream migration in fall within the main-stem Missouri River (middle tier), and spawning migration incorporating one of three major tributaries to the LMOR (top tier).

movement distances were highly variable for both species (Table 2) though directed predominantly upstream (Figures 5 and 6). Linear range of movement (river kilometers) during this period was not significantly different from other periods (ANOVA: $F_{2,71}$ = 1.04, P = 0.36). Beginning in mid-July, fish migrated downstream and upstream towards areas where they spent the summer/fall period. During this space-use transition, all tributary migrants returned to the LMOR and traveled greater distances than those individuals that remained in the LMOR.

During the summer/fall period (July 15–November 15), individuals of both species displayed fidelity to a section of river that averaged 10–20 km in length (Table 2), though one blue catfish moved downstream more than 220 river kilometers. Three brief periods of intense flooding in 2007 were associated with both upstream and downstream movement of individuals traveling to and from high-use areas. However, 70% of individuals either remained in one high-use area (<1 km) or moved independent of river discharge (Figure 7). With few exceptions, fish that moved in relation to spates returned to their previous location after flood water receded (Figure 7). Exceptions to the trend appeared more mobile overall and expanded their home range as the season progressed. In late-November, fish began migrating towards overwintering areas. Migration during this period was directed downstream, although one individual moved a short distance upstream to the mouth of the Lamine River where it resided for most of the year (Figure 5).

Movement was relatively low during the overwintering period (November 15–March 15; Table 2), though not significantly different from other periods (ANOVA: $F_{2,71}$ = 1.04, P = 0.36). Most individuals traveled downstream in late November to deep scour holes (>7 m deep) associated with wing-dike structures, although a few individuals moved downstream as late as January. After a single directed movement downstream, most individuals remained stationary throughout the overwintering period until early March.

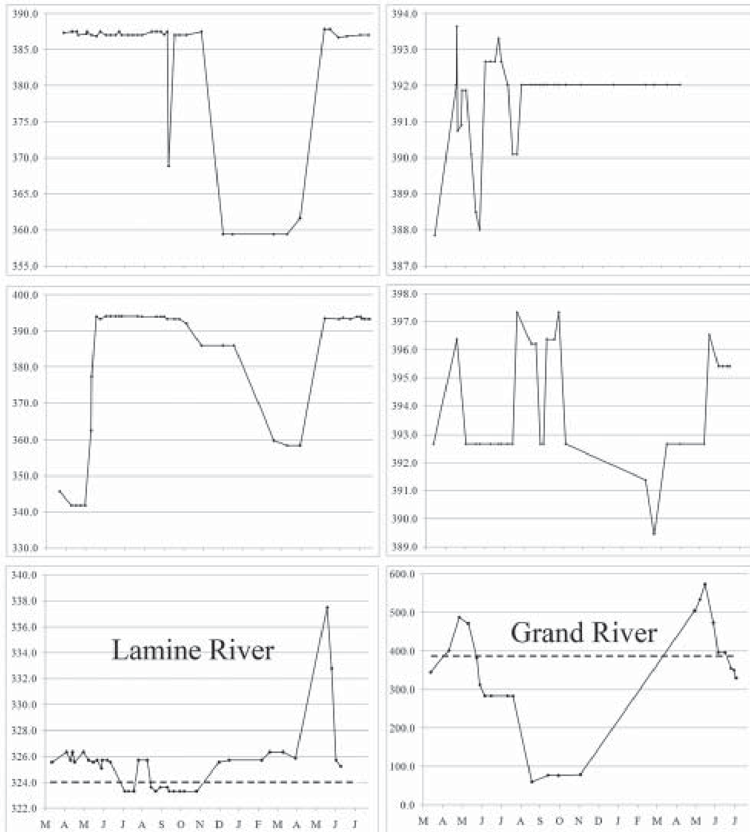

FIGURE 5. Examples of annual movement patterns from individual flathead catfish (left column) and blue catfish (right column) relocated between March 2006 and July 2007 in the lower Missouri River and adjacent tributaries. The *y*-axis represents river kilometers upstream from the mouth of the Missouri River. Dashed lines on bottom two panels denote confluence of tributary (labeled) and Missouri River. Note: scales on *y*-axis vary.

Tributary Use during the Prespawn/Spawning Period

Twenty-two of 50 individuals (44%) used one of four major tributaries (third to eighth order) that flow into the 97-km study reach of the LMOR (Figure 1). Twelve of these individuals were monitored infrequently following the prespawn/spawning period and were not included in analyses of intra-annual movement and seasonal structure. During May–June 2006, 5 of 37 flathead catfish and 3 of 40 blue catfish migrated upstream into an adjacent tributary (Figure 4). The proportion of individuals that used a tributary increased from 10% (8 of 77) in 2006 to 18% (14 of 80) in 2007, coinciding with high discharge associated with heavy rainfall in May and June 2007. Two individual blue catfish tagged in April 2006 did not use a tributary until the LMOR flooded in May 2007, although they quickly returned to the LMOR after flood water receded (Figure 7). Two individual flathead catfish displayed a similar response in the Lamine River, as depicted for one individual in Figure 5.

Discussion

In North America, many ictalurid catfishes are regarded as sedentary (Lucas and Baras 2001), yet considerable evidence suggests that channel catfish, flathead catfish, and blue catfish display migratory behavior (Dames et al. 1989; Newcomb 1989; Smith and Hubert 1989; Vokoun and Rabeni 2005b). In this study, annual movement patterns of 18 (60%) flathead and 19 (66%) blue catfishes supported the hypothesis that these species migrate to and from seasonal habitats in the LMOR and adjacent tributaries. However, variability observed in movement

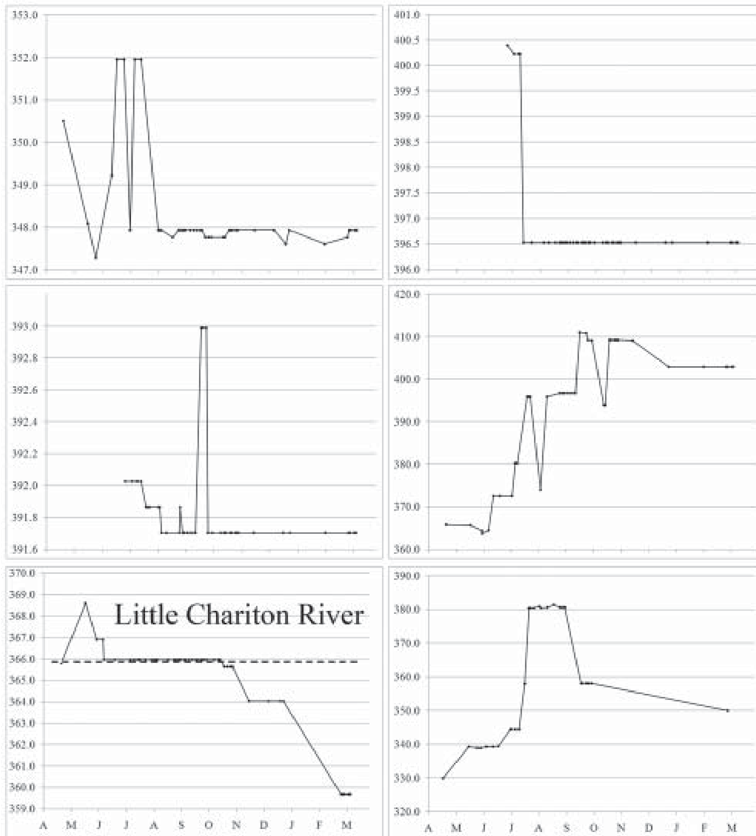

FIGURE 6. Examples of annual movement patterns from individual flathead catfish (left column) and blue catfish (right column) relocated between April 2007 and March 2008 in the lower Missouri River and adjacent tributaries. The *y*-axis represents river kilometers upstream from the mouth of the Missouri River. Dashed line on bottom left panel denotes confluence of tributary (labeled) and Missouri River. Note: scales on *y*-axis vary.

and spatial extent of annual ranges was unexpected. At the smallest spatial scale, 22 individuals (14% of the total fish tagged during both years) used relatively small sections of river (<30 km) for the entire year. At the largest spatial scale, three blue catfish and six flathead catfish moved greater than 100 river kilometers, including two individual flathead catfish that traveled greater than 600 river kilometers during the prespawn/spawning period in 2006 (Table 1). Without the additional tracking coverage by USGS-CERC in 2007, movement beyond the 97-km study reach was not recorded during the second year of the tracking. Long-range movements recorded in 2006 (Table 1) suggests that individuals lost during both tracking years was likely due to high mobility. Without a more complete data set of long-range movement behavior, we must submit that our results are biased in favor of movement within the 97-km search area. Special harvest restrictions applied to a 50–100-km reach of the LMOR may fail to produce expected results if highly mobile individuals leave the management area, particularly during the prespawn/spawn period when adults are more susceptible to harvest.

Within the three-period annual cycle framework (Vokoun and Rabeni 2005b), individual fish displayed at least five variant pathways through an annual cycle (Figure 4). Of the 50 individuals used to define seasonal structure, 22 displayed restricted-movement behavior, 15 individuals migrated to and from seasonal habitats within the LMOR, and 13 migrated up a tributary during the prespawn/spawning period. Based on the literature (Graham 1999; Pugh and Schramm 1999), we expected blue catfish to exhibit much greater mobility than flathead catfish. However, both species incorporated migration

TABLE 2. Descriptive statistics for annual and seasonal movement of flathead (FL; $N = 12$) and blue (BL; $N = 12$) catfish in the lower Missouri River and adjacent tributaries. Individuals that were not monitored continuously throughout the annual cycle were excluded from calculations. Asterisk denotes data from second year of tracking that were collected to facilitate comparisons of prespawn/spawning ranges for the same individuals across successive years.

	Mean		Median		SD		Min.		Max.	
	FL	BL	FL	BL	FL	BL	FL	BL	FL	BL
Annual range (km)	24.0	52.0	15.0	7.2	25.0	112.4	0.6	1.6	58.6	392.5
Prespawn/spawning period range (km) —2006	16.7	26.4	4.6	4.1	21.8	47.5	0.2	1.5	58.6	143.0
Prespawn/spawning period range (km) —2007*	17.9	34.1	15.3	18.5	11.9	52.2	0.3	0.1	35.3	158.3
Summer–fall restricted-movement period (km)	9.3	21.3	2.2	2.0	16.8	63.5	0.4	0.1	57.5	222.9
Overwintering period (km)	4.2	2.3	0.6	1.9	8.8	2.4	0.0	0.0	27.0	7.3
Distance between overwintering area and summer–fall area (km)	10.2	20.0	2.1	0.0	13.2	63.9	0.0	0.0	31.9	222.9

as a life history strategy (Figure 4) and displayed a propensity for long-range upstream movement (Table 1). Further, individuals of both species used the Grand, Chariton, Little Chariton, and Lamine rivers during the prespawn/spawning period (Figure 4). During restricted-movement periods, seasonal ranges were not statistically different. Thus, we observed little difference between these species with respect to life history strategies, migratory patterns, and within-season mobility.

Flathead catfish in the Grand River display several different life history patterns, all of which incorporate an overwintering migration to the LMOR (Vokoun and Rabeni 2005b). Thus, a diversity of ecologically distinct groups converges in the main-stem Missouri River during winter months. Increased movement occurs in spring as individuals migrate to available spawning habitat, although migrations may occur at multiple spatial scales from tens to hundreds of kilometers. Because both species are nest guarders and are thought to spawn primarily in cavities (Bobea 1989; Francis 1993; Graham 1999), multiple life history strategies may help to exploit optimal spawning locations. Following the spawn, many catfish remain in tributaries for the summer/fall and establish a home range around log complexes or other optimal feeding sites (Vokoun and Rabeni 2005a). Others migrate downstream to spend the summer/fall around dike structures in the LMOR. Thus, flathead and blue catfish migrate among habitats throughout the main-stem Missouri River and major tributaries for feeding and growth. Therefore, longitudinal connectedness between main-stem and tributary habitats is important for flathead and blue catfishes to reach (1) overwintering habitat in the LMOR in late fall, (2) spawning habitat in adjacent tributaries in early spring, and (3) feeding habitat in the LMOR in early summer.

Boat tracking efforts in the Grand, Chariton, Little Chariton, and Lamine rivers were extensive and covered all navigable waters on a weekly basis throughout the prespawn/spawning period. Further, helicopter radio-tracking during July and August 2006 suggested that individuals in tributaries were not missed by acoustic-tracking efforts. Thus, the proportion of fish tagged on the LMOR that used a tributary (10% and 21% in 2006 and 2007, respectively) is likely a reasonable estimate of seasonal use. However, Vokoun and Rabeni (2005b) showed that some residents of the Grand and Cuirvre rivers (most overwinter in the LMOR) move up tributaries as early as March. Because our tagging efforts in the LMOR

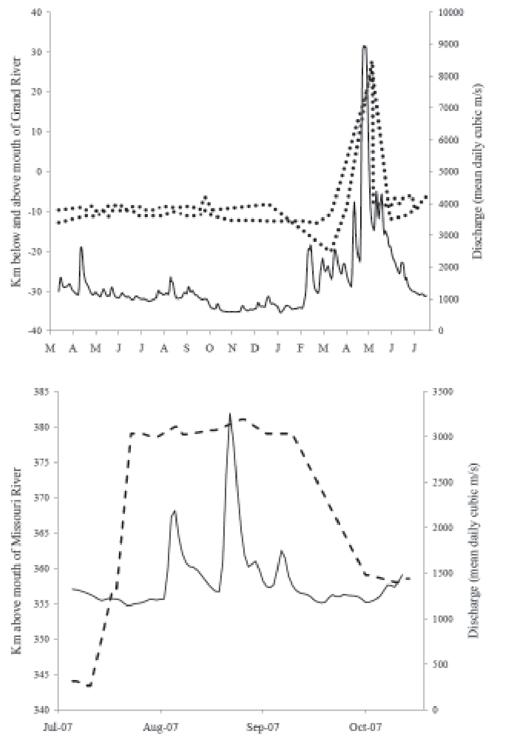

FIGURE 7. Example of linear movements of two blue catfish (upper panel) relocated between March 2006 and July 2007 and one flathead catfish (lower panel) relocated during the summer/fall period. Dashed lines denote linear movement along the river corridor in relation to river mouths. Solid lines denote discharge of the lower Missouri River measured at U.S. Geological Survey gauge 06906500 at Glasgow, Missouri.

were unsuccessful until April, our sample may be biased in favor of those individuals that remain in the LMOR throughout the annual cycle. Another source of bias is created by those individuals that were lost during this period, presumably due to high mobility. During the first 4 months of tracking (April–July), 17 of 77 (22%) and 33 of 80 (41%) fish were lost in 2006 and 2007, respectively. Thus, we may have underestimated the proportion of tributary spawners if long-ranging individuals used a distant tributary to spawn. Accounting for all possible biases, we conclude the following: (1) most individuals remained in the main-stem Missouri during the spawning period in 2006 and 2007, (2) the estimated proportion of tributary spawners is likely an underestimate of overall tributary usage in the watershed, and (3) the main-stem Missouri provides spawning habitat for both species of catfish and warrants further investigation.

Catfish migrations related to spawning, feeding, and overwintering are clearly related to seasonal changes that occur on an annual cycle. However, brief refuge migrations may also occur in response to environmental disturbances (e.g., high flow) that do not occur seasonally (Northcote 1984). Two individual blue catfish that remained in the LMOR throughout an annual cycle (April 2006–April 2007) moved up the Grand River for only 1 week during the annual peak discharge in May 2007 (Figure 7). Migration to tributaries during peak flows may conserve somatic energy reserves, which later enhance growth and reproductive output until more favorable conditions return (Lucas and Baras 2001). Refuge-seeking behavior has been shown for a variety of other riverine fish species. Radio-tracked barbel *Barbus barbus* and European chub *Squalius cephalus* were found to enter small tributaries during temporary floods in the spring (Baras 1992). Fishes that actively search for food may also be signaled to move by changing environmental conditions that allow newly available resources to be exploited (Lucas and Baras 2001). For example, fishes in Mississippi streams move into inundated floodplains to feed and benefit from improved physical condition and growth (Ross and Baker 1983). Other fishes such as northern hogsuckers *Hypentelium nigricans* move into feeding habitat during the day and into resting habitat at night (Matheney and Rabeni 1995). In the LMOR, levees reduce channel-floodplain connectivity (Nestler and Sutton 2000; Galat et al. 2005; Ridenour et al. 2009). Thus, tributaries may compensate for feeding and refuge habitat for floodplain backwaters that were historically more available.

In recent years, migratory movement of stream fishes at different spatial scales has become better understood with synthesis of data and utility of large-scale models (Northcote 1984; Schlosser and Angermeier 1995). Fausch et al. (2002) suggested that some stream fishes move through a "riverscape" at an intermediate spatial scale ranging from1 to 100 km in absolute length and possibly including different sizes of river segments for different life cycle purposes. Generally, flathead and blue catfishes in the LMOR were characterized by the intermediate spatial scale (1–100 km), although movement distances were highly variable and nine individuals moved greater than 100 km. River segments that were used for the prespawn/spawning, summer/fall, and overwintering periods did not vary significantly in size. The underlying hypothesis to the riverscape framework is that intermediate scales include discrete, often-separated habitats that are linked to life history strategies of stream fishes (Fausch et al. 2002). Kwak et al. (2004) and Vokoun and Rabeni (2005b) provide empirical support for the riverscape framework, with flathead catfish moving among seasonal habitats. Two-thirds of the flathead and blue catfishes we monitored in the LMOR support this hypothesis, although stationary behavior we recorded for many individuals suggest that the LMOR provides more suitable habitat year around than adjacent tributaries, particularly during the overwintering period.

Although genetic data are lacking for these populations of catfish, variation in life history strategies we documented provides a sufficient basis for managers to provide protection for each life history unit (sensu Gresswell et al. 1994). Regardless of the source of genotypic or phenotypic variation, observed behavioral differences are linked to reproduction, growth, and survival and are therefore valuable to preserve (Meka et al. 2003). Ideal conditions for reproduction, feeding and growth, and survival are exploited at distant locations, which may be separated by tens or hundreds of kilometers, suggesting that large, adult catfish would benefit from long-term maintenance of habitat quality and connectedness at multiple spatial scales.

Acknowledgments

This research is a contribution of the Missouri Cooperative Fish and Wildlife Research Unit (U.S. Geological Survey, Missouri Department of Conservation, University of Missouri, and Wildlife Management Institute cooperating). Major funding was provided by the Missouri Department of Conservation. We thank Ron Dent, Kevin Sullivan, Zach Ford, Craig Gemming, Greg Pitchford, Jake Allman, Mike Wallendorf, and many others from the Missouri Department of Conservation who contributed to the success of this project. From the University of Missouri, we thank Brook Kruz, Larry Lawson, Chris McLeland, Ryan Lueckenhoff, Matt Mullens, Joe Clayton, Benedict Nagy, Sander Jones, and Josh Willison for their tireless efforts collecting data. We are indebted to David Galat, Ray Semlitsch, and Josh Millspaugh from the University of Missouri who reviewed the manuscript. We benefitted enormously from the tracking efforts of Aaron Delonay, Emily Tracy, Emily Kunz, and other crew members from USGS-CERC and Nebraska Game and Parks Commission.

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