MOVEMENT, HABITAT USE, AND SPAWNING CHARACTERISTICS OF FLATHEAD AND BLUE CATFISH ON THE LOWER MISSOURI RIVER AND TRIBUTARIES

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by
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The undersigned, appointed by the dean of the Graduate School, have examined the dissertation entitled

MOVEMENT, HABITAT USE, AND SPAWNING CHARACTERISTICS OF
FLATHEAD AND BLUE CATFISH ON THE
LOWER MISSOURI RIVER AND TRIBUTARIES

presented by Daniel L. Garrett,

a candidate for the degree of Doctor of Philosophy,

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Movement, Habitat Use, and Spawning Characteristics of Flathead and Blue Catfish in the Lower Missouri River and Tributaries

Daniel L. Garrett

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ABSTRACT

The movement and habitat use patterns of adult flathead and blue catfish were studied via acoustic and radio telemetry in the lower Missouri River and adjacent tributaries including the Grand, Lamine, Chariton, and Little Chariton Rivers. At the largest spatiotemporal scale, annual movement patterns varied greatly from restricted-movement behavior throughout the annual cycle to seasonal migrations commonly tens of kilometers between habitats used for spawning, feeding and growth, and overwintering. Fish moved the least during the overwintering period and the most during the prespawn/spawn period, followed by a third period of restricted movement during the summer and early fall. The diversity in life history strategies suggests that populations of large-river catfish use resources at multiple spatial scales, from the reach to the watershed, to meet life requisites.

Diurnal home range and resource selection was investigated during the summer/fall restricted-movement period; an ecologically relevant time frame with respect to feeding and growth. With the exception of few, both species established small home ranges (<10 km) with fidelity to one, two, or three discrete areas of high use (core areas). Resource selection analysis revealed that both species select deep habitats associated with anthropogenic structures (i.e., dike structures, revetment) that are spatially segregated along the river corridor. The spatial arrangement of selected habitats explains why multiple areas of high use were identified by home range estimates. The movement behavior of flathead and blue catfish during the summer/fall suggests that diurnal requisites for feeding and growth are primarily exploited in small (< 1 km) sections of river that include deep, low-velocity habitats associated with anthropogenic structures.

During the prespawn/spawning period, I monitored movement, body weight and physiological changes (i.e., levels of estradiol and testosterone) of flathead and blue catfish to identify potential spawning sites in the lower Missouri River. Indicative of spawning, most individuals demonstrated a loss in body weight and a drop in levels of sex steroids between prespawn and postspawn sampling. Telemetry data and field observations indicated that shallow, low-velocity areas downstream of wing- and L-dike structures are used by flathead catfish to complete spawning cycle.

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General Introduction and Study Design

Catfish species are becoming increasingly important to anglers in the USA (USDC/USDI 1996). A recent survey by Arterburn et al. (2002) shows anglers and biologists from the Mississippi River basin agree that trophy catfish, and in particular flathead catfish *Pylodictis olivaris* and blue catfish *Ictalurus furcatus*, are important angling resources worthy of more intensive management. For the last century, catfish management has sought to provide maximum sustained harvest and has generally not promoted high quality fishing, particularly in lotic systems (Pugh & Schramm 1999; Travnichek 2004). This historical management provides good fishing opportunities for many, but may not optimize maximum growth potential of catfish or desires of some anglers who seek large fish (Travnichek 2004).

Perhaps there are opportunities to better manage catfish in large and altered ecosystems such as the Missouri River. Ideally, an ecologically-based management strategy should include the restoration of specific habitat features that promote feeding, growth, or spawning coupled with larger-scale considerations of flow regime that influence behavior and abundance of catfishes and their food base. However, much of the basic ecological information of catfishes in large-river systems that could be relevant to management is unknown (Michaletz and Dillard 1999). This is partly because large rivers present formidable obstacles for studying fish. The large spatial extent of the supposed habitat, the deep and turbid conditions, and the often-changing flow regime all combine to hamper the examination of important population characteristics.

One common approach that researchers have used to infer basic ecological information in these complex systems is to track fish movement, either by tagging and recapture or by telemetry. Fish movement is important because all fishes move to satisfy life requisites including food, shelter, and spawning (Matthews 1998; Lucas and Baras 2001). Whether these movements are short term to meet daily energy requirements or long term to meet life-history requirements, the places we find fish tells us much about their biological needs and possibly whether those needs are being met by available habitat and environmental conditions (Northcote 1984; Lucas and Baras 2001). Since movement and habitat use data translates to behavioral attributes, the information we derive relies heavily on spatial and temporal resolution (Millspaugh and Marzluff 2001). At large temporal scales such as the annual cycle, movement data can be used to infer the full extent of resource exploitation (e.g., Vokoun and Rabeni 2005a), what resources may be limiting, and whether seasonal environmental shifts cue shifts in habitat use to meet life requisites (e.g., Garrett and Bennett 1995). Within behaviorally-defined seasons, habitat-use data may reveal important habitat requirements that promote specific activities such as feeding, growth, and spawning (e.g., Vokoun and Rabeni 2005b). If life requisites are not being met, particularly for large, mature adults, then a fishery may fail to sustain trophy-size fish that maximize population growth, regardless of the harvest restrictions imposed upon anglers.

The primary challenge in movement studies is relating observed behavioral patterns to ecological relationships that are relevant to population well-being. To achieve this, movement must be thought of in terms of biological and ecological function. In the simplest terms, all fishes move for purposes of reproduction, feeding, and growth (Matthews 1997).

Reproduction.—During the spring, many fish move to meet their habitat requirements for spawning since most fish spawn in shallower habitats than they normally reside (Lucas and Baras 2001). Movement related to spawning may consist of local movements to adjacent or nearby spawning habitat or seasonal migrations that incorporate distant habitats to complete the spawning cycle. Northcote (1984) defines migration as a cyclic movement between two or more habitats, most commonly between spawning and feeding sites. The diadromy (i.e., migration between freshwater and saltwater to complete life cycle) exhibited by salmonid species is the best known example. Long diadromous migrations of salmonids in clear rivers of the Pacific Northwest are conspicuous, and have historically provided important sources of food through interception fisheries sited in the lower reaches of rivers (Lucas and Baras 2001). However, the widespread potadromy (i.e., migration within freshwater) exhibited by many lotic fishes has received more attention in recent years (Lucas and Baras 2001). In the Amazon River, many catfishes make long-range spawning migrations exceeding 3000 km (Barthem and Goulding 1997). In eastern North America, spawning migrations of a variety of fishes; e.g., darters (Percidae), suckers (Catostomidae), and catfishes (Ictaluridae) have been described (Ingersoll et al. 1984; Matthews 1998; Vokoun and Rabeni 2005a). In western North America, minnows (squawfish, humpback chub) and suckers (razorback sucker) move to known spawning areas within the Colorado River system (Minckley 1991). Spawning migrations are necessary to reach suitable habitats where environmental conditions (e.g., temperature gradients, flow characteristics, substrate size, and cover) promote high egg survival (Northcote 1984). Upstream migration may also be an evolutionary adaptation to offset the downstream dispersal of eggs (e.g., Reynolds 1983).

Feeding and Growth.—Movement related to feeding and growth is largely dependent on life-history strategy. Fishes that actively search for food may 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 backwaters at night (Matheny and Rabeni 1995).

Many riverine fishes move to find the best-available physical habitats that minimize energy expenditure and maximize opportunities for food (Northcote 1984). To be successful, an organism must maintain a balance between the energy and materials acquired from the environment, and that required for metabolism, growth, and reproduction (Warren 1971; Fausch 1984). Known as optimal foraging theory (MacArthur and Pianka 1966), this idea is a major tenet of bioenergetic (Ware 1980) and optimal foraging models (Werner and Mittelbach 1981). During the warmest months of the summer when energy demands are highest, fishes tend to select physical habitats that maximize feeding rates. Optimal foraging models have been shown to accurately predict habitat use by bluegill *Lepomis macrochirus* (Werner et al. 1983) and drift-feeding stream minnows (Grossman et al. 2002).

During winter months when metabolic rates are reduced and prey items are scarce, stream fishes often move to deeper, lower-velocity habitats to reduce energy expenditure. For example, riffle-dwelling madtoms in the Cottonwood River, Kansas move to microhabitats with slower-velocity current in the winter (Fuselier and Edds 1994). Similarly, flathead catfish in the Grand and Cuivre River move to deeper holes with low-velocity current prior to winter (Vokoun and Rabeni 2005a). Fall movements of fishes seeking winter refuge have also been reported in northern pike *Esox lucius* (Derkson 1989), cutthroat trout *Oncorhynchus mykiss* (Brown and Mackay 1995) and brown trout *Salmo trutta* (Hesthagen 1988).

Similar to optimal foraging (MacArthur and Pianka 1966), fishes may also move across physicochemical gradients to maximize metabolic efficiency. For example, brown trout (*Salmo trutta*) move out of Box Canyon Reservoir, Washington in late June when water temperatures reach 19–20°C and inhabit tributary streams containing water below 16°C (Garrett and Bennett 1995). Similarly, red shiners *Cyprinella lutrensis* have distinct preferences in thermal and oxygen gradients that explain movement among microhabitats in the South Canadian River, Oklahoma (Matthews and Hill 1979).

Changing Movement Concepts.—Concepts of fish movement in interior, warmwater streams have changed over the past 50 years. Since the writings of Gerking (1950, 1953, 1959), restricted movement was considered prevalent in stream fishes and mark-recapture studies have demonstrated stream fishes as moving very little (<30 m) to meet life requisites (Scalet 1973; Mundahl and Ingersol 1983; Hill and Grossman 1987). However, better field techniques, especially telemetry, has shown that many stream fishes make substantial movements (Lucas and Baras 2001). Notably, Gowan et al. (1994) and Gowan and Fausch (1996) detected much greater movement of resident (nondiadromous) salmonid populations than previously recorded and proposed a re-evaluation of restricted movement in stream fishes. Similarly, recent work by Northcote (1997, 1998) and Welcomme (1979, 1985) has shown potadromy (i.e., migration within freshwater) to be more prevalent in streams and rivers than previously thought.

Flathead Catfish Movement.—Flathead catfish have been described as nonmigratory, exhibiting restricted-movement behavior (Funk 1957; Robinson 1977; Daugherty and Sutton 2005). In more recent studies, however, flathead catfish in the lower Missouri River (LMOR; downstream of Gavins Point Dam) have been shown to travel several hundred kilometers to complete life-history requirements (Dames et al. 1989; Travnichek 2004). Seasonal movements up to 105 km have been shown in the Minnesota River by Stauffer et al. (1996), with individuals moving between summer areas and overwintering pools. In the Grand and Cuivre River, Missouri, migratory behavior of flathead catfish consists of three main periods of restricted movement (summer/fall, overwintering, and prespawning/spawning) interrupted by brief migrations that can exceed 180 km. In light of recent findings, flathead catfish in large-rivers may have a more complex life-history strategy than previously thought.

Blue Catfish Movement.—Blue catfish have been described as the most migratory ictalurid (Graham 1999; Pugh and Schramm 1999), although most movement studies have been conducted in lakes and reservoirs (Fisher et al. 1999; Graham and DeiSanti 1999; Timmons 1999; Grist 2002). Pugh and Schramm (1999) conducted a tag-recapture study on channel, blue, and flathead catfish in the Lower Mississippi River (LMR) and found that blue catfish moved 5–12 km 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.

Ecological Role of Tributaries.—Tributaries of LMOR are used by catfish throughout the annual cycle (Dames et al. 1989; Vokoun and Rabeni 2005a), but the extent of seasonal use by migrants from the mainstem is unknown. Among LMOR and the Grand and Cuivre Rivers, Vokoun and Rabeni (2005a) identified three pathways through which flathead catfish complete an annual cycle. With the exception of a few residents of the Cuivre River, fish overwintered in LMOR until mid-March when temperatures rose above 10°C at which point they entered a tributary and moved upstream. The reproductive maturity of these fish coupled with the seasonality of movements suggests that flathead catfish spawn in tributaries of LMOR. However, these inferences were made from sample populations that were collected in the Grand and Cuivre River during June. Thus, the relative proportion of mainstem residents moving from LMOR to an adjacent tributary could not be estimated. Additionally, comparative data for blue catfish do not exist. Anecdotal evidence from 2007 sampling by state biologists in tributaries to LMOR (i.e., Lamine, Platte, and Grand Rivers) suggests that the abundance of adult catfish in tributaries increases during the spawning period (Zach Ford, MDC, pers. comm.). This may be attributed to the potential spawning habitat that tributaries provide during spring high flows. Flathead catfish select protected nesting sites such as hollow logs, excavated caves in clay banks, and root masses from downed trees (Bobea 1989; Francis 1993). These habitats are generally more available in tributaries to large, channelized rivers where natural features have been removed. Blue catfish have been studied to a lesser degree, but are believed to spawn near similar habitat features (Graham 1999). Thus, spawning requirements of these two species may necessitate seasonal migrations to and from tributaries.

Habitat Use in Regulated Rivers.—Active management of catfish at small spatial scales includes the restoration and protection of critical habitat features that are used and thus inferred as being important to growth and fitness (optimal foraging theory; MacArthur and Pianka 1966). However, the significance of anthropogenic changes on LMOR to flathead and blue catfish populations is unknown. Impoundment, water withdrawal, flow regulation, channelization, bank stabilization, and levee construction are activities that have modified natural physical habitat of LMOR (Galat et al. 2001). These physical changes parallel population declines of large river fishes and their food base (Galat et al. 2001). In the Mississippi and Missouri River, the channel has also been shown to be important to fluvial specialist/dependent fishes; not merely as a highway to move between more desirable habitats (Junk et al. 1989), but as important feeding and spawning habitat (Dettmers et al. 2001; Galat and Zweimueller 2001). Flathead and blue catfish in the lower Mississippi River (LMR) have been found to be more abundant in main channel habitats including wing dikes and revetment than in side channel habitats (Driscoll et al. 1999), whereas blue catfish tend to be found in swifter water within these main channel areas (Pflieger 1997). Barko et al. (2004) and Barko and Herzog (2003) suggested that fishes in the unimpounded Upper Mississippi River (UMR) use wing-dike scour holes and side channels as surrogate backwater habitat for flooded terrestrial areas that are now scarce. Depth and large woody debris complexes are important predictors of flathead catfish presence in stream pools (Minkley and Deacon 1959; Lee and Terrell 1987; Jackson 1999). In the Grand and Cuivre River, log complexes ranked highest among habitat variables used to construct *a priori* models of habitat use by flathead catfish (Vokoun 2004). Insaurralde (1992) demonstrated that the abundance of flathead catfish in four Mississippi streams was directly related to the proportion of the riparian zone in mature forest; whereas the proportional stock density of adults was described by the mean number of snags per 100 m. With the exception of Vokoun (2004), a quantitative approach relating habitat variables to observed use patterns has yet to be published. Further, information on habitat use by blue catfish is anecdotal, and of little use to managers.

Catfish Management in Missouri.**—**Flathead and blue catfish comprise large fisheries in LMOR and adjacent tributaries, and annual angler exploitation rates within many of these tributaries have been high (>30%) in recent years (Z. Ford, MDC, pers. comm.). Current management of catfish in Missouri is limited to statewide harvest restrictions (5 fish/day). However, state biologists have shown interest in creating special harvest regulations that would facilitate a trophy catfish fishery in an interior reach of LMOR. Knowledge of fish movement patterns can contribute to effective management in such cases. Fish exhibiting limited movement are more likely to respond positively to management strategies compared with more nomadic species (Travnichek 2004). To delineate boundaries to management that are population-based, movement data is needed to infer the spatial extent of interannual population dispersal.

Management and Scale Considerations in LMOR.**—**Managers use life-history information to evaluate factors affecting size structure and limiting population growth. If catfish in LMOR incorporate migration as part of a life-history strategy, then environmental factors at multiple spatial scales may affect the growth and spawning success of individuals. The timing of migration depends on the physiological state of the fish (levels of thyroid and corticosteroid hormones) and external triggering factors including flow, temperature, and photoperiod (Northcote 1984). Thus, hydrologic conditions at the watershed scale affect movement behavior of fishes at smaller spatial scales. River reaches used during periods of restricted movement (spawning period, postspawn/feeding period) can also be inferred as supporting population growth. Lastly, the identification of environmental variables (e.g., depth) associated with fish locations at smaller spatial scales (e.g., microhabitat characteristics) can be inferred as supporting individual efforts to spawn, feed, or rest.

I used telemetry in this study to examine migratory and restricted-movement behavior to evaluate the scope of life-history strategies used by flathead and blue catfish on the lower Missouri River. I isolated the summer-fall restricted-movement period (July 15 – November 15) to evaluate space use and habitat selection associated with feeding and growth. I collected physiological evidence of spawning to determine possible spawning sites on the lower Missouri River. Specific objectives and corresponding chapters are as follows:

(1) Estimate the proportion of individuals in LMOR that move into adjacent tributaries during the spawning period (Chapter Two).
(2) Describe migratory pathways used throughout the annual cycle (Chapter Two).
(3) Determine the size and internal structure of home range for flathead and blue catfish during the summer-fall restricted-movement period (Chapter Three).
(4) Determine habitats selected by flathead and blue catfish during the summer-fall period (Chapter Four).
(5) Describe diel movement behavior over a 24-hour period (Chapter Four).
(6) Determine where flathead and blue catfish spawn in LMOR (Chapter Five).

The following subsections describe the study sites and general methods common to chapters two through six.

Regional Information.— The Missouri River can be divided into three sections of approximate equal length. The upper 1241 km is the "least-impacted" section, despite containing seven small mainstem dams and reservoirs. Referred to as the "inter-reservoir" section, the 1233 km middle section was impounded between 1937 and 1963 by a series of six large mainstem reservoirs that regulate flows to the 1212 km LMOR (Galat and Lipkin 2000). Although not impounded, LMOR was highly altered by channelization, bank stabilization and levee construction to facilitate navigation and floodplain development (Galat et al. 1996). Specific anthropogenic habitat features include wing dikes, L-head dikes, and revetment that divert water to the channel for navigation while providing flood control and bank stabilization. Reservoir releases are presently managed to maintain minimum target flows in LMOR for the April-November navigation season and minimum flows for water quality, power production, and flood control (Hesse et al. 1989; Galat and Lipkin 2000).

Study Site.—My goal was to quantify movement between LMOR and adjacent tributaries in central Missouri. To accomplish this, I selected a 93-km reach (river mile 195 to 255) that includes the confluence of the Grand (eighth order), Chariton (sixth order), and Lamine (seventh order) rivers (Fig. 1.1). The spatial extent of tracking efforts (Figure 1.2) was exclusively based on tracking efficiency. Given the temporal resolution selected for this study (1 relocation/week), 97-km was the largest area of river I could effectively find fish over the course of a week.

Methods.—Flathead and blue catfish were obtained within the 93-km study reach (Figure 1.1). To obtain a spatially-unbiased sample, no more than 10 fish of each species were collected within a 24-km section. The resulting fish collection sites were spread throughout the reach in 2006 (N=77) and 2007 (N=80), with no bias towards proximity to adjacent tributaries (Figure 1.1). Individuals were surgically implanted with transmitters during April 2006 (Flathead: N = 37; Blue: N = 40) and again in April and July of 2007 (Flathead: N = 40; Blue: 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). Tagged flathead catfish had a mean total length of 80.7 cm and ranged from 594 to 1400 cm. 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 872.3 cm and ranged from 569 to 1260 cm. These 80 individuals weighed a mean 8.9 kg and ranged from 2.1 to 29.4 kg.

Transmitters were manufactured by Lotek Wireless, Inc. (Newmarket, Ontario). In 2006, combination acoustic-radio transmitters (CART; 480 day warranty life) were used which alternate between a radio burst (164.4 MHz) and an acoustic burst (76.8 KHz) at a pulse rate of 2.5 sec. These dual-transmission tags are particularly useful when tracking between shallow and deep water. The much higher radio frequencies (140-175 MHz) transmit well in air for shallow-water tracking, whereas acoustic signals (65-80 KHz) transmit well through the water column for monitoring deeper contacts. The success of acoustic tracking in 2006-2007 prompted the exclusive use of acoustic transmitters (CAFT; 504 day warranty life) in 2007-2008. These tags transmitted an acoustic signal every 4 sec 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 approximately half way 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 3–5 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 the location of capture. To allow for a recovery period, individuals were not relocated for two weeks following surgery.

Fish were relocated from a boat using a Lotek SRX_400A datalogging coded series receiver with W5XG firmware coupled with an ultra-sonic upconverter and omni-directional 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. In 2006, the Columbia Environmental Research Center (CERC)-United States Geologic Survey (USGS) began a long term tracking and monitoring program for pallid and shovelnose sturgeon in LMOR. Using compatible Lotek tracking equipment, they assisted with relocations outside of the 93-km sampling reach to monitor long range movements (>100 km) during the first year of tracking.

In 2006 and 2007, tracking efforts in 6th-8th order tributary streams were only conducted during the spawning period (May 15 – July 15) to address spawning-related tributary use (Chapter 3). In 2006, I investigated large scale movement patterns throughout LMOR (river mouth to Gavins Point Dam; river mile 0-811) with the help of CERC that included upstream movements as far north as Omaha, Nebraska (river mile 626). From May 2006 – July 2007, we relocated individuals on a weekly basis. In 2007, I obtained two relocations a week for each individual to address home range and habitat selection during the summer-fall restricted movement period. From July 2007 – March 2008, tracking was restricted to the sampling area shown in Figure 2.1 (river mile 195-255). Specific time periods of data collection and associated topics are shown in Table 1.1.

Table 1.1. Time periods of data collection used to address project objectives (April 2006-April 2008).

		2006									2007													2008				
Chapter	Broad Topic	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A
3	Migration	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
2	Home Range																■	■	■	■	■					
4	Habitat																■	■	■	■	■					
4	24-h Diel																		■		■					
3	Tributary Use		■	■	■	■									■	■	■	■								
5	Spawning														■	■	■									

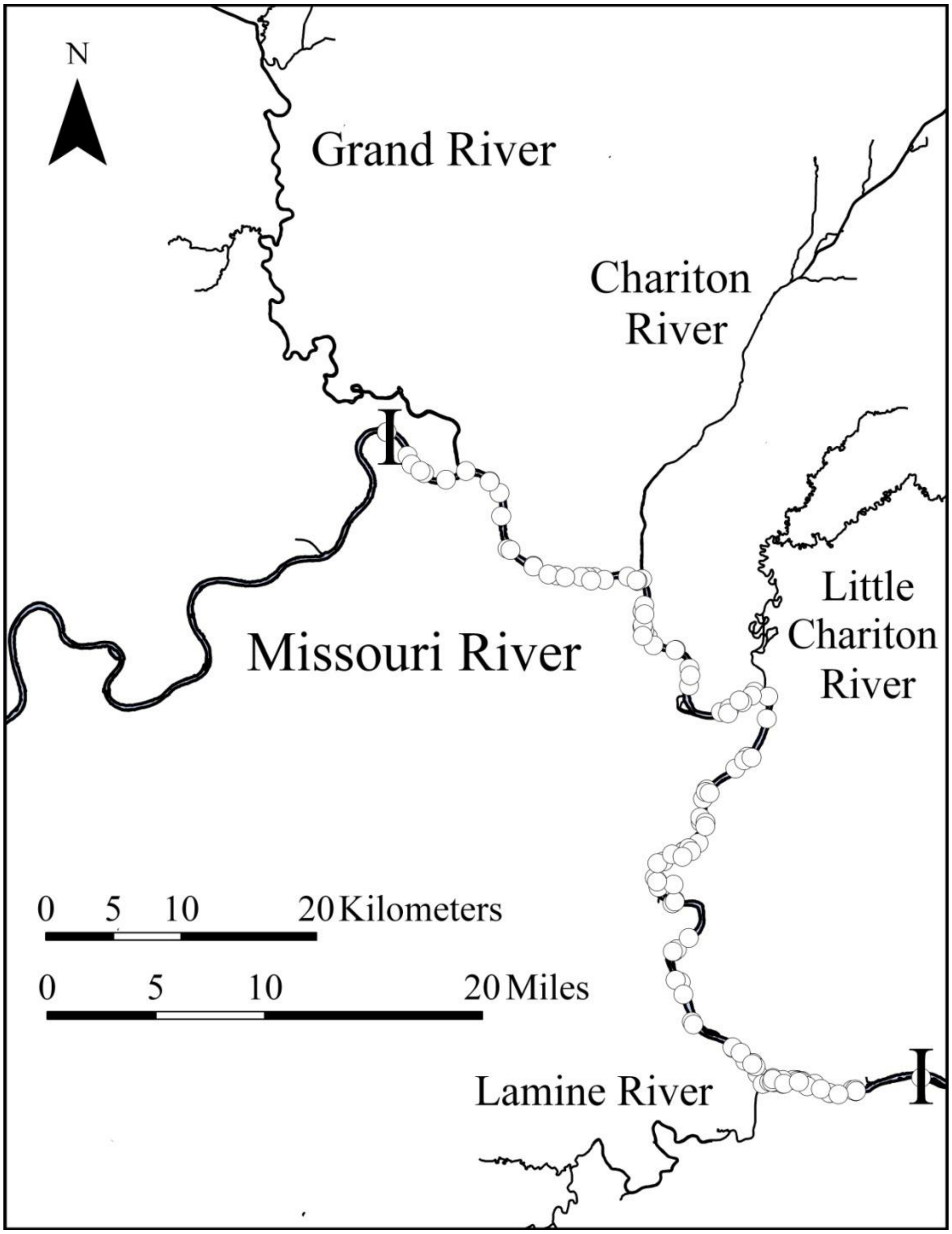

Figure 1.1. Catfish sampling reach on the lower Missouri River (LMOR) including the Lamine, Chariton, Little Chariton, and Grand Rivers. Hollow circles denote capture locations of individual flathead and blue catfish tagged in 2006 and 2007. Vertical bars delineate the upper and lower boundaries of catfish sampling on LMOR (river miles 195-255).

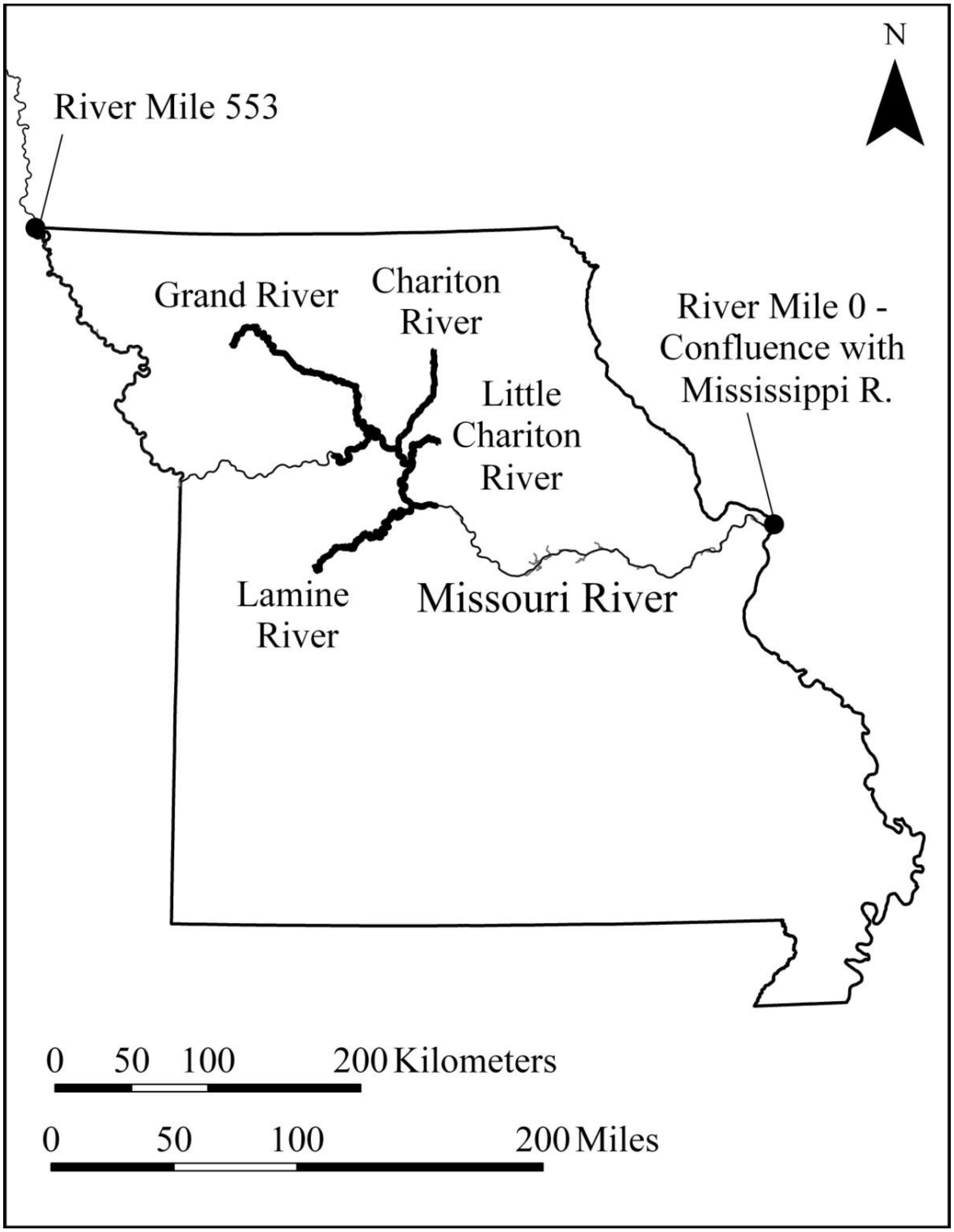

Figure 1.2. Spatial extent of flathead and blue catfish tracking efforts during 2006-2008. Bolded river reaches were monitored by University of Missouri tracking crews by boat and helicopter. USGS located individuals on the Missouri River downstream and upstream of our tracking extent beginning at the mouth (river mile 0) and extending upstream to Gavins Point Dam (river mile 811; not shown).

Chapter Two

Intraannual Movement of Flathead and Blue Catfish in the Lower Missouri River and Adjacent Tributaries

Early fish ecologists showed how movement patterns of fishes reveal life-history characteristics (Nikolsky 1963). Fish movement is important because all fishes move to satisfy life requisites including food, shelter, and spawning (Matthews 1998; Lucas and Baras 2001). Whether these movements are short term to meet daily energy requirements or long term to meet life-history requirements, the places we find fish tells us much about their biological needs and possibly whether those needs are being met by available habitat and environmental conditions (Northcote 1984; Lucas and Baras 2001). Since movement and habitat use data translates to behavioral attributes, the information we derive relies heavily on spatial and temporal resolution (Millspaugh and Marzluff 2001). At large temporal scales such as the annual cycle, movement data can be used to infer the full extent of resource exploitation to meet life requisites (e.g., Vokoun and Rabeni 2005a). Within behaviorally-defined seasons, habitat-use data may reveal important habitat requirements that promote specific activities such as feeding, growth, and spawning (e.g., Vokoun and Rabeni 2005b). If life requisites are not being met, particularly for large, mature adults, then a fishery may fail to sustain trophy-size fish that maximize population growth, regardless of the harvest restrictions imposed upon anglers. In this large-scale investigation, I attempted to characterize the full extent of variation in life-history strategies of large, adult catfishes in the lower Missouri River (LMOR). Rigorous telemetry studies that incorporate new technologies are increasingly yielding new data that improve our understanding of movement behavior and the ecological value of migration in large rivers (Northcote 1998).

Home range, as defined by Burt (1943) and Gerking (1953), is the area around a commonly-used site over which the animal normally travels. However, migratory animals may only display fidelity to home areas during seasonal periods such as spawning, feeding, and overwintering. Non-migratory animals fulfill all their life-history needs within a single area. In the Grand and Cuivre River, Missouri, seasonal migrations of flathead catfish among habitats were generally brief and cued by environmental triggers such as flow and temperature (Vokoun and Rabeni 2005a). However, long-ranging animals migrating hundreds of river kilometers may appear to be in a constant state of movement given the distances traveled to complete life-history requirements. Here, I collected a dataset over an entire annual cycle to reveal when and where restricted-movement behavior occurred including migrations between these sites. 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).

Information on large-scale movement patterns has become increasingly important to state biologists and resource scientists in the central United States. In a recent survey, anglers and biologists from the Mississippi River basin agreed that trophy catfish, and in particular flathead catfish *Pylodictis olivaris* and blue catfish *Ictalurus furcatus*, are important angling resources worthy of more intensive management (Arterburn et al. 2001). In Missouri, the growing sport of catfish angling has elicited interest among state biologists and resource scientists to create special harvest regulations that would facilitate a trophy catfish fishery in an interior reach of the LMOR. The effect of special regulations on the fishery inherently relies on the spatial scale of the regulation coupled with the relative mobility of the 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. Based on movement accounts in the literature (Dames et al. 1989; Stauffer et al. 1996; Timmons 1999; Grist 2002; Travnichek 2004), I hypothesized that both species would incorporate migration as a life-history strategy and that blue catfish would be more mobile than flathead catfish. If so, the appropriate spatial scale to management could vary among these large-river species.

Past research on blue and flathead catfish has presented an incomplete and sometimes 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 recently 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" (RMP) 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 temperature stream fishes (Scalet 1973; Mundahl and Ingersol 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 0.15–50.4 river kilometers during the summer/fall period, suggesting that fidelity to a home area may occur at multiple spatial scales (Vokoun and Rabeni 2005b). In a parallel study, Vokoun and Rabeni (2005a) showed that riverine habitats used by flathead catfish during the 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 the observed extent of annual space use. However, interindividual variation in life-history strategies can hinder efforts to generalize about a species group. In this study, I attempted to use intraannual movement patterns of individuals to describe the variation in life-history strategies.

Most movement studies on blue catfish have been conducted in lakes and reservoirs (Fisher et al. 1999; Graham and DeiSanti 1999; Timmons 1999; Grist 2002). Pugh and Schramm (1999) conducted a tag-recapture study on channel, blue, and flathead catfish in the Lower Mississippi River (LMR) 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. Since there is no information on the movement of blue catfish in 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 LMOR are used by catfish throughout the annual cycle (Dames et al. 1989; Vokoun and Rabeni 2005a), but the extent of seasonal use by migrants from the mainstem is unknown. Anecdotal evidence from 2007 sampling in the Lamine, Platte, and Grand River suggests that abundance of adult catfish increases in tributaries of LMOR during the spawning period (Zach Ford, MDC, pers. comm.). This may be attributed to the potential spawning habitat that tributaries provide. Flathead catfish select protected nesting sites such as hollow logs, excavated caves in clay banks, and root masses from downed trees (Bobea 1989; Francis 1993). These habitats are generally more available in tributaries to large, channelized rivers in which 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 the 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 mainstem. To address this information need, this study was designed to estimate the proportion of flathead and blue catfish that migrate up adjacent tributaries during the prespawn/spawning period. Given that three large (6-8 order) tributaries flow into the 97-km study reach, I 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 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.

The nature and extent of migration in freshwater may be influenced by a host of abiotic environmental factors and biotic factors that combine to define habitat and may prove critical for the completion of the life cycle. In this regard, migration categories (i.e., diadromy, potadromy) which reference the salinity through which fish swim are somewhat arbitrary, even though marine and freshwater represent very different environments. Large-river fishes respond to many variables, among which water velocity, temperature, and chemical cues are important (Lucas and Baras 2001). When an adaptive advantage exists, behavioral responses to environmental stimuli that improve fitness or survival odds are said to have adaptive value and are often population-specific (Northcote 1984). From an ecological and functional viewpoint, the adaptive value of such responses far outweighs the importance of scale, predictability, or synchronicity as they pertain to fish migration. If catfish migrate to an adjacent tributary to complete the spawning cycle, presumably to improve spawning success and survival odds of young, then the environmental conditions that cue and facilitate that behavior are important to the conservation of the species. To inform future decisions regarding water control and flow regime in the lower Missouri River, my goal was to characterize the flow and temperature conditions associated with catfish spawning migrations and examine the hypothesis that catfish migrate upstream during spring runoff as temperature and discharge increase in the lower Missouri River.

To achieve project objectives and examine related hypotheses, I used temporal movement patterns to describe restricted-movement and migratory behaviors of flathead and blue catfish on the lower Missouri River and adjacent tributaries in central Missouri. To assess how fish might benefit from migration, I 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. My primary objectives were to (1) estimate the annual range (farthest upstream and downstream extent of movement during one year) of blue and flathead catfish, (2) broadly define the spatiotemporal dimensions of migration and restricted-movement periods based on animal behaviors, (3) relate migration timing to environmental cues such as discharge, temperature, and time of year, and (4) 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 93-km reach of the lower Missouri River (river miles 195-255). 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: N = 37; Blue: N = 40) and again in April and July of 2007 (Flathead: N = 40; Blue: 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). Tagged flathead catfish had a mean total length of 80.7 cm and ranged from 594 to 1400 cm. 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 872.3 cm and ranged from 569 to 1260 cm. These 80 individuals weighed a mean 8.9 kg and ranged from 2.1 to 29.4 kg.

Telemetry Design.—The tracking schedule was variable throughout the year, primarily due to ice flows in the winter, high-water events in the spring, and movement of individuals as the study progressed. I attempted to locate fish in a 93-km reach of LMOR at least weekly throughout the annual cycle (April to March) in 2006 and 2007, with the exception of the overwintering period during which fish were relocated once every two weeks. Thus, time lapse between relocations was no less than one week. Individuals in the Grand, Chariton, Little Chariton, and Lamine Rivers were relocated every week during May-July 2006 and 2007. In 2006, the Columbia Environmental Research Center (CERC)-United States Geologic Survey (USGS) began a long term tracking and monitoring program for pallid and shovelnose sturgeon in LMOR. Using compatible Lotek tracking equipment, they assisted with relocations outside of the 93-km sampling reach to monitor long range movements (>100 km) during the first year of tracking.

The two samples from 2006 and 2007 yielded very different datasets, in part due to environmental conditions, fewer resources in 2007 and a modified set of objectives. In 2007, 13 of 80 individuals could not be captured and tagged until 5 July 2007 due to a sustained high-flow event (>100,000 ft^3/sec) lasting from late April to late June (Figure 2.5). During this time period, few individuals were relocated due to high turbidity that hampered 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. Without the assistance of USGS-CERC to monitor long-ranging individuals, this apparent increase in mobility could not be recorded and described. To maximize the information gathered during the second year of the study, I opted to intensify tracking efforts (2 relocations/week) within the 97-km reach during the summer/fall period to describe home range and habitat use patterns at a smaller spatial and temporal scale (see chapters 3 and 4). As a result, I obtained a larger dataset (~2 relocations/week) for a small subset of individuals (N=23) that remained within the 97-km reach during the summer/fall period (see chapters 3 and 4). Given the ideal acoustic-tracking conditions in 2006, individuals tagged in 2006 were monitored more consistently throughout the annual cycle and were subsequently used to define the spatiotemporal dimensions of restricted-movement periods. The tributary coverage in 2006 and 2007 allowed us to estimate the proportion of individuals that used a tributary during both years. The apparent increase in mobility during 2007 when high-flow events were frequent should be considered when interpreting the results presented here.

Data analyses.—Field-collected relocations were imported into ArcView GIS (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 UTM coordinates into univariate positions along the river corridor to the nearest 10 m (km above the river mouth). Thalweg lines for the tributaries were estimated using aerial photographs (National Agricultural Imaging Program). Univariate datasets 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 of time. 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 two-month periods since relocations were too sporadic during the overwintering period to make monthly or weekly comparisons. Data collected during 2007-2008 were only used to validate the movement patterns recorded in 2006, and not for calculations of linear movement during two-month periods.

Migratory pathways.—Using ArcView GIS to examine relocations spatially and plotting distances from the river mouths against calendar dates, I was able to reconstruct the patterns of migration and movement exhibited by flathead and blue catfish in LMOR. I included harvest locations from anglers to supplement tracking data and to include long-range movements within the scope of the project. During the first year of tracking, the Columbia Environmental Research Center (USGS-CERC) aided our project in relocating individuals that traveled outside of our 93-km study reach on LMOR. All movements >100 km we report were recorded by an angler or by USGS-CERC during 2006-2007. The dataset during 2006-2007 was more complete than during 2007-2008 (Table 2.1), and a comparison between years was not possible. The reported site fidelity refers only to individuals that returned to the same section of river (<10 km in length) during the prespawn/spawning period after a complete annual cycle (Table 2.1).

Spatiotemporal dimensions of restricted-movement periods.—I used a three-period annual cycle framework similar to Vokoun and Rabeni (2005a) to describe intraannual movement and migration in LMOR. Individuals monitored during the course of the study (April 2006 – May 2008) displayed restricted-movement behavior, i.e., homing behavior, during three seasonal periods that generally correspond to life-history activities demonstrated by all fishes living in temperate streams: reproduction, feeding and growth, and overwintering (Schlosser and Angermeier 1995; Fausch et al. 2002). Hereto after, I refer to these as the prespawn/spawning period, summer/fall period, and overwintering period. Whereas these periods were previously defined for flathead catfish (Vokoun and Rabeni 2005a), the spatiotemporal dimensions presented in this study were not defined *a priori*. Seasonal movement behavior in LMOR was assessed to broadly define the timing and spatial extent of migration. One-way analysis of variance 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.

Tributary Use during the Prespawn/Spawning Period.—Study design was largely dictated by the objective to estimate the proportion of adult catfish residing in LMOR that use an adjacent tributary to complete the spawning cycle. First, to insure that sampling was not biased in favor of proximity to tributary mouths, the 93-km reach was separated into four approximately 24-km sections within which no more than 10 individuals of each species were captured and tagged. Second, weekly tributary coverage during the prespawn/spawning period included both boat (acoustic) and helicopter (radio) tracking efforts to increase the probability that all individuals entering a tributary were found.

Results

Descriptions of the annual movement cycle are based on recorded movements of 26 flathead catfish and 24 blue catfish implanted in the lower Missouri River (river mile marker 195-255) 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 (Table 2.1). Ten flathead (27%) and 12 (30%) blue catfish were harvested during the first 15 months of tracking, most by trot line on LMOR. Three blue catfish were caught by rod and reel and 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 were used to discern movement patterns during the summer/fall and overwintering periods (Table 2.1). Five flathead (13%) and eight blue catfish (20%) were harvested within the first 15 months of tracking, and three blue catfish were caught and released. Eighteen flathead and 23 blue catfish were not relocated often enough for inclusion in analyses. Post-surgery 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.

Relocations per individual fish from Table 2.1 during 2006-2007 had mean values of 33 (range 18-43) and 35 (19-59) for flathead and blue catfish, respectively (Table 2.1). During 2007-2008, relocations per individual fish had mean values of 41 (range 15-49) and 32 (13-45) for flathead and blue catfish, respectively.

General movement patterns.— The variability of movement was higher during the first few months of tracking (Fig. 2.1). Six flathead and three blue catfish traveled >100 river km; two individual flathead moved greater distances upstream than previously recorded for the species (668 and 752 km; Table 2.2). Flathead and blue catfish displayed similar patterns of monthly movement throughout the annual cycle (Fig. 2.2). 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 (Jan-Aug) is biased in favor of restricted movement that was more easily recorded (Fig. 2.3).

Table 2.1. Tracking and behavioral information for individual flathead and blue catfish included in analyses of seasonal structure throughout two annual cycles (April-March 2006, 2007) in the lower Missouri River and adjacent tributaries. Site fidelity indicates a return to spawning area (<10 river km) after one full year of tracking.

Tracking Year	Species	Relocations	Tracking Days	Tributary Usage	Site Fidelity
2006-2007	Blue	59	479		
		22	338	Grand (2006; lost March 2007)	
		42	472	Grand (2007 only)	
		43	484	Grand (2007 only)	
		33	465		
		32	454		
		19	471	Grand (2006 and 2007)	
		28	336		
		31	481		
		34	376		
		37	484		
		39	471		
	Flathead	35	448	Lamine (2006 and 2007)	X
		31	338		
		18	356		
		43	471		X
		27	476		
		29	318		
		25	480		
		30	477	Chariton (2006 and 2007)	X
		40	466		X
		32	455	Lamine (2007 only)	X
		40	477		
		43	483		
2007-2008	Blue	27	350		
		21	343		X
		32	350		X
		13	350		X
		32	341		
		14	266		
		42	345		
		40	224		
		40	259		
		36	237		
		43	273		
		45	273		
	Flathead	44	229		
		15	315		
		39	347		
		45	347		
		49	347		
		40	250		
		49	346	Little Chariton (2007)	
		46	346		
		43	346		
		39	225	Chariton (2007)	
		44	345	Chariton (2007)	
		33	311		
		43	273		
		44	273		

Migratory pathways.—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. As hypothesized, both species incorporated migration as a life-history strategy, though the variation in migratory pathways was unexpected. Within the three-period annual cycle framework (Vokoun and Rabeni 2005a), individual fish displayed at least five variant pathways through an annual cycle (Figure 2.4). 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 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 catfish 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 intraannual movement and seasonal structure (Table 2.1). Fidelity could not be determined for 32% (16 of 50) of individuals that were lost after 8–11 months of tracking (Figure 2.1).

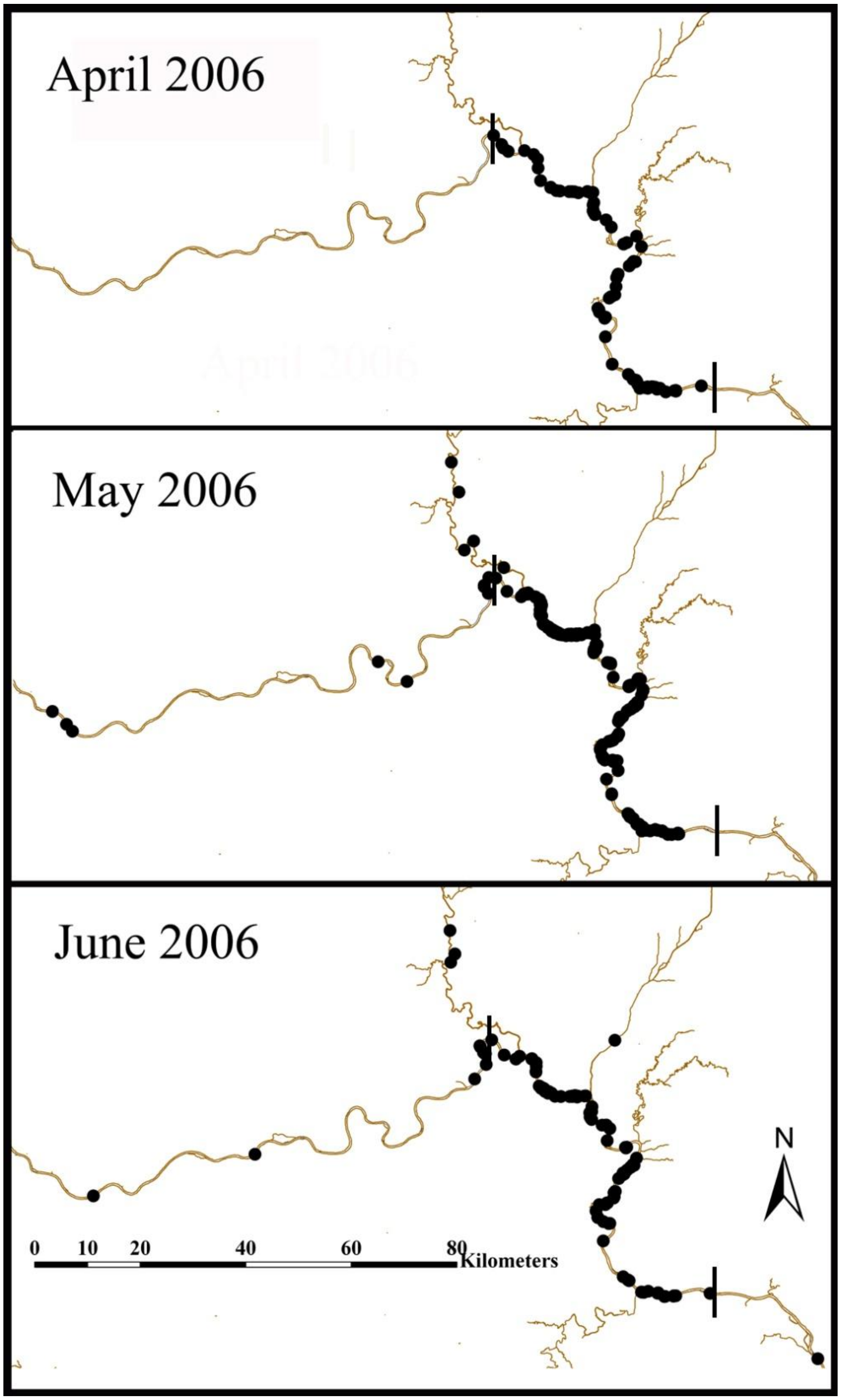

Figure 2.1. Spatial distribution of acoustically-tracked flathead and blue catfish in the lower Missouri River and adjacent tributaries during the prespawn/spawning period in 2006. Tributaries from north to south are the Grand, Chariton, Little Chariton, and Lamine Rivers. LMOR flows from left to right. Markers represent all relocations during each month: April N=86; May N=299; June N=187. Vertical bars denote the upper and lower extent of the 97-km study reach. USGS-CERC accounted for relocations in LMOR beyond this study reach.

Table 2.2. 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. I was also unable to calculate mean linear movement by months (Fig. 2.2 and 2.3) for these individuals.

Species	Relocations	Tracking Days	TL (mm)	Weight (kg)	Linear Movement (km)
BL	23	185	685	4.14	275.2
BL	2	97	915	10.64	282.1
BL	2	95	845	6.33	347.6
FL	12	209	742	5.2	101.2
FL	9	484	1025	14.64	177.0
FL	10	244	714	4.4	248.3
FL	3	40	765	5.82	267.5
FL	13	369	985	10.62	667.9
FL	15	463	1110	19.75	751.9

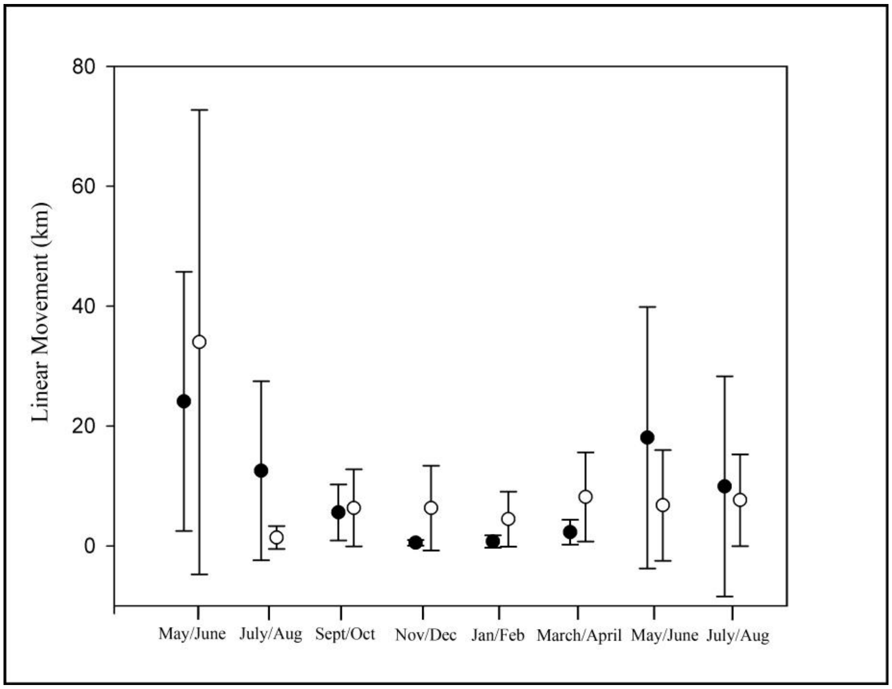

Figure 2.2. Mean and 95% confidence intervals of linear movements by blue (solid circles) and flathead catfish (hollow circles) from April 2006 to August 2007 in the lower Missouri River and adjacent tributaries.

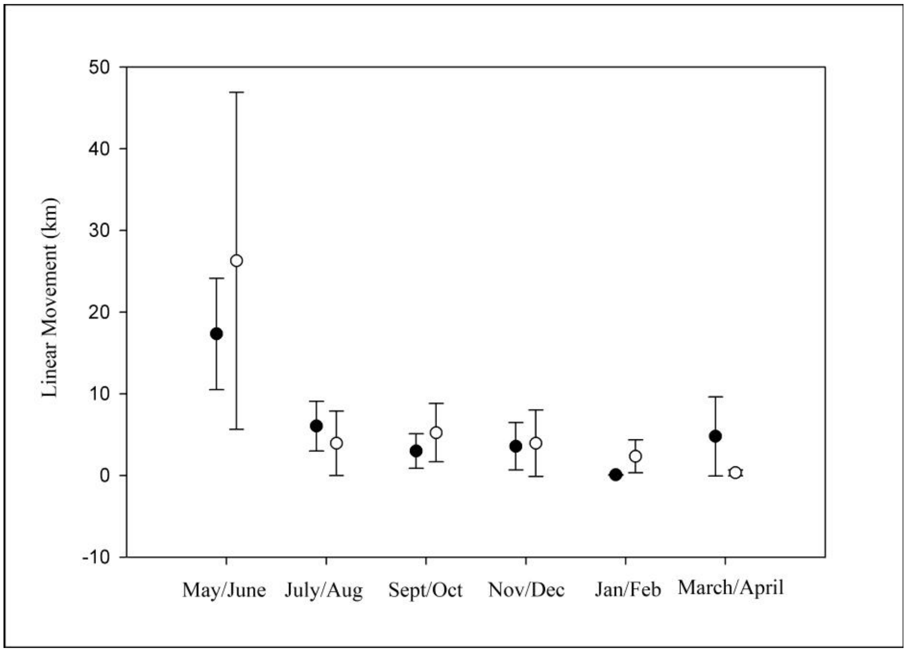

Figure 2.3. Mean and 95% confidence intervals of linear movements by flathead and blue catfish (pooled) during 2006 (solid circles) and 2007 (hollow circles) in the lower Missouri River and adjacent tributaries.

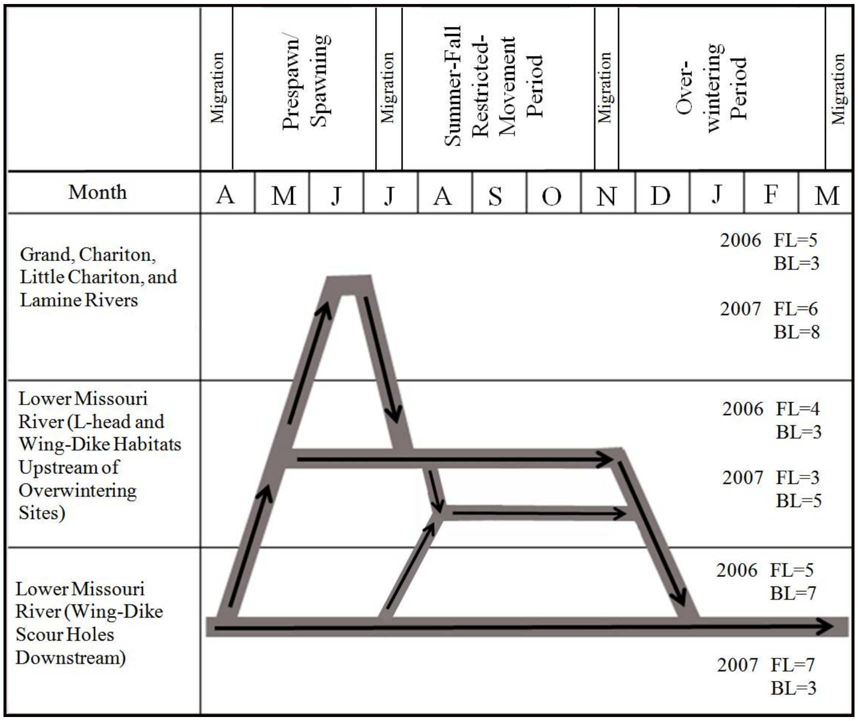

Figure 2.4. Spatial pathways used to complete an annual cycle (shown in gray) by acoustically-tracked flathead (FL) and blue catfish (BL) in the lower Missouri River and adjacent tributaries, Missouri, USA. Numbers of individuals that were documented for each tier are presented: restricted-movement behavior throughout the annual cycle (bottom tier); upstream migration in spring/summer and downstream migration in fall within the mainstem Missouri River (middle tier); spawning migration incorporating one of three major tributaries to LMOR (top tier).

Spatiotemporal dimensions of restricted-movement periods.—Timing of migration was not synchronous among individuals and there was no observed effect of period or species on linear ranges (Table 2.4). Thus, the dates selected to define restricted-movement periods are based on the majority of movement recorded, and were not strictly adhered to by all individuals. Spawning-related migrations occurred from mid-March to the end of June and overwintering migrations occurred from mid-October to the end of December (Figure 2.5). 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 the variability in life-history strategies (Figure 2.4) and timing of directed movements (Figure 2.6 and 2.7). I examined the 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 2.2). The intraannual movements of 12 individuals were selected to represent the diversity of movement behavior recorded (Figure 2.6 and 2.7).

As water temperatures rose above 8–10 °C in late March/early April (Figure 2.5), individuals began upstream migrations to areas used during the prespawn/spawning period (April 15 – July 15; Figure 2.6 and 2.7). During this period, movement distances were highly variable for both species (Table 2.3) though directed predominantly upstream (Fig. 2.6 and 2.7). Results from two-way ANOVA indicated that linear range of movement (river km) during this period was not significantly different from other periods (Table 2.4). Three individual flathead and nine individual blue catfish remained stationary for several weeks during the prespawn/spawning period; although physiological evidence of spawning was not collected until 2007 (see Chapter 5). Beginning in mid-July, fish migrated downstream and upstream towards areas where they spent the summer/fall period (Fig. 2.6 and 2.7). During this space-use transition, all tributary migrants returned to LMOR and traveled greater distances than those individuals that remained in 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 2.3), though one blue catfish moved downstream over 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 (Fig. 2.8). However, 70% of individuals either remained in one high-use area (< 1 km) or moved independent of river discharge. With few exceptions, fish that moved in relation to spates returned to their previous location after flood water receded (Figure 2.8). The 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 (Fig. 2.6). Additional information on space-use during the summer/fall period is covered in Chapter 3.

Movement was relatively low during the overwintering period (November 15 – March 15; Table 2.3), though not significantly different from other periods (Table 2.4). 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.

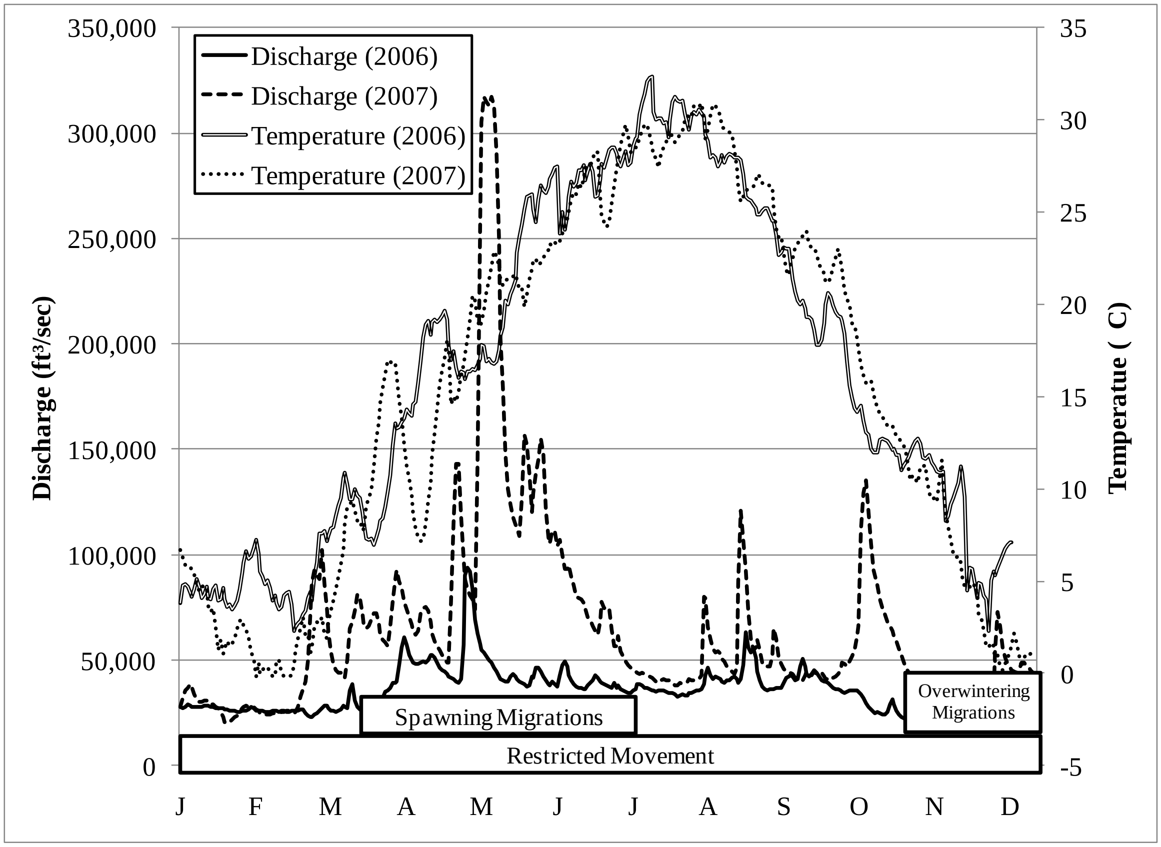

Figure 2.5. General periods of restricted-movement and migration by flathead and blue catfish coupled with environmental conditions (i.e., discharge, temperature) during 2006 and 2007 in the lower Missouri River. Temperature and discharge was measured at USGS gauge 06906500 at Glasgow, MO.

Environmental Cues.—Timing of migrations was variable (Figure 2.5). Whereas 62% (21 of 34) of individuals migrating upstream in spring did so in May, the remaining migrations were as early as mid-March and as late as early-July. During the first couple weeks in May when the majority of migrations took place, temperatures ranged from 15 °C to 20 °C during both years. The annual peak discharge for 2006 (94,000 ft³/sec) and 2007 (317,000 ft³/sec) occurred on May 4 and May 11. Overwintering migrations were equally variable beginning in mid-October and occurring as late as December, although the majority (67%; 10 of 15) migrated in mid-November. Water temperatures in mid-November ranged between 10 and

12 °C during both years, and rapidly dropped to around 5 °C in early December. In 2006, the lowest discharge recorded for the year was on November 15th (20,900 ft^3/sec); water levels remained low until February 2007. In 2007, daily discharges during November were low relative to other periods (30,000–60,000 ft^3/sec), but considerably higher than comparable discharges in 2006.

Tributary Usage during the Prespawn/Spawning Period.—Twenty-two of 50 individuals (44%) used one of four major tributaries (3–8th order) that flow into the 93-km study reach on LMOR. Twelve of these individuals were monitored infrequently following the prespawn/spawning period, and were not included in analyses of intraannual movement and seasonal structure (Table 2.1). During May-June 2006, five of 37 flathead and three of 40 blue catfish migrated upstream into an adjacent tributary (Figure 2.4). 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 (Figure 2.5). Two individual blue catfish tagged in April 2006 did not use a tributary until LMOR flooded in May 2007, although they quickly returned to LMOR after flood water receded (Fig. 2.8). Two individual flathead displayed a similar response in the Lamine River as depicted for one individual in Figure 2.6.

Table 2.3. 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		St. Deviation		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	2.1	0	13.2	63.9	0	0	31.9	223

Table 2.4. Summary of results from two-way analysis of variance for the linear seasonal range of flathead and blue catfish in the lower Missouri River and adjacent tributaries (April 2006 – March 2007). Seasonal period values were log-transformed to achieve normality; untransformed means and variances are presented in Table 2.3.

Main Effect -Class Level	*F*	df	*P*
Period	1.04	2	0.3597
-Prespawn/spawn			
-Summer/fall			
-Overwintering			
Species	0.01	1	0.9145
-Flathead			
-Blue			
Species X Period	0.06	2	0.9397

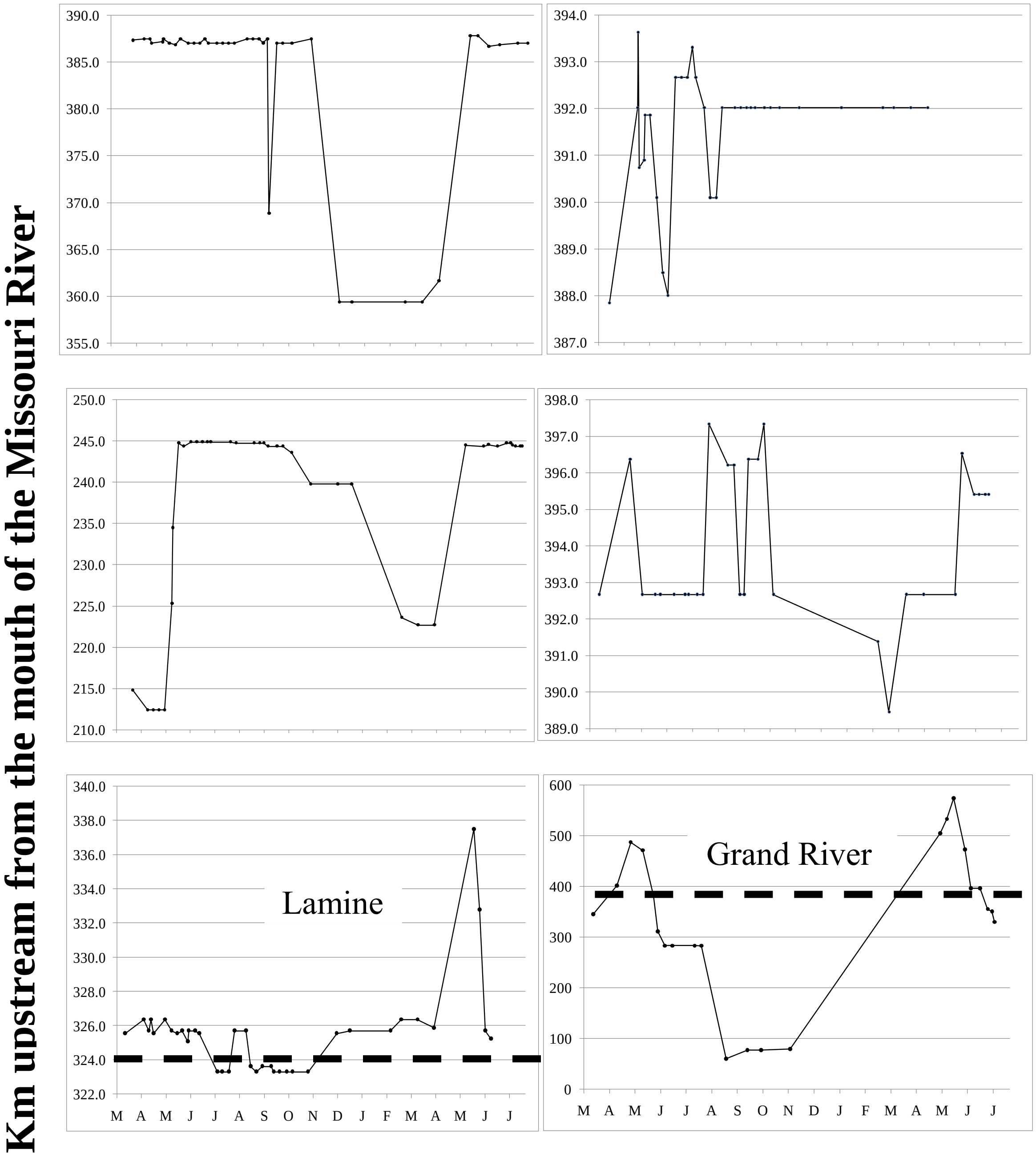

Figure 2.6. Examples of annual movement patterns from individual flathead catfish (left column) and blue catfish (right column) relocated between March 2006 and July 2007 in the lower Missouri River and adjacent tributaries. Dashed lines on bottom two panels denote confluence of tributary (labeled) and Missouri River. Note: Scales on y-axis vary.

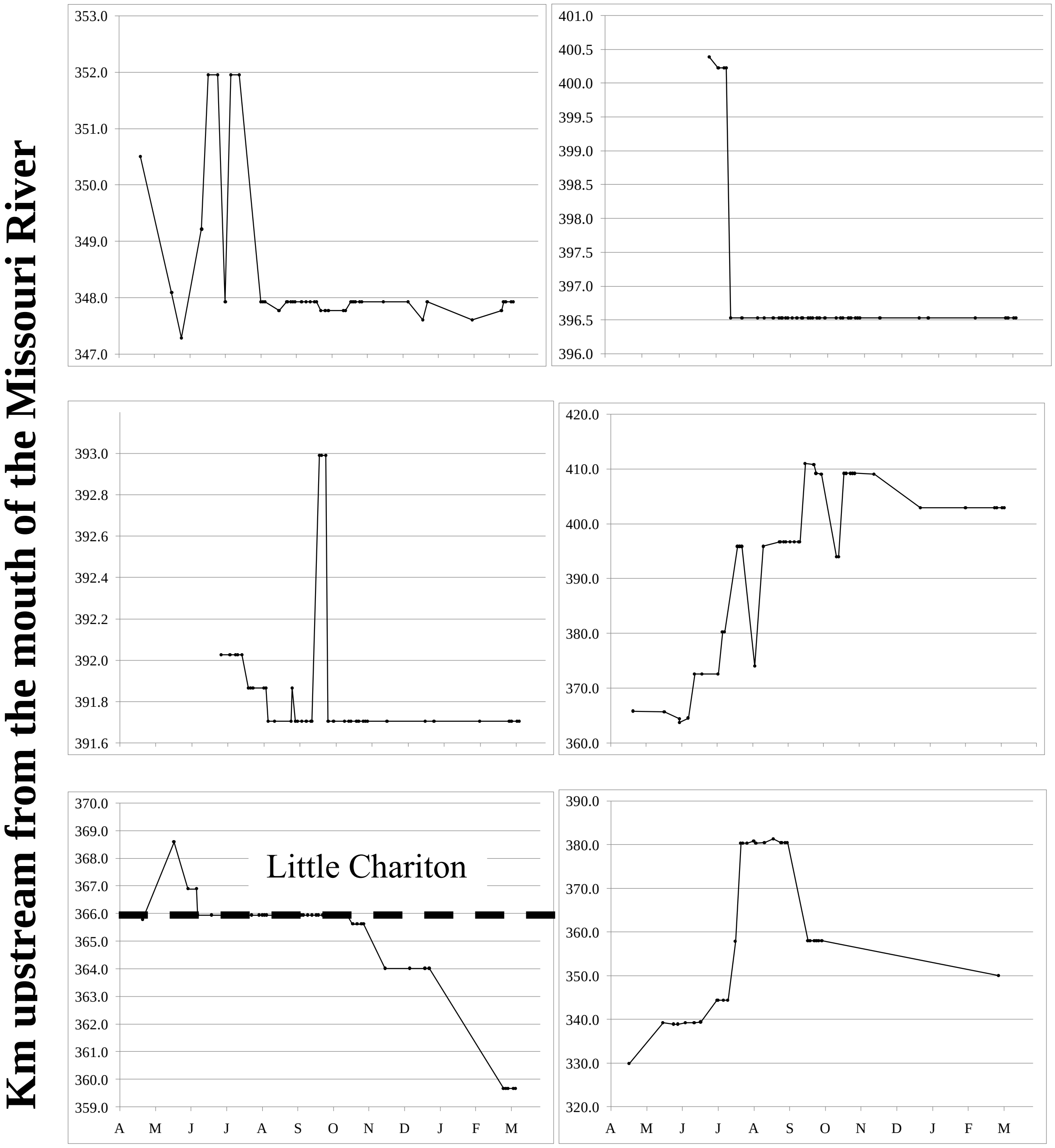

Figure 2.7. Examples of annual movement patterns from individual flathead catfish (left column) and blue catfish (right column) relocated between April 2007 and March 2008 in the lower Missouri River and adjacent tributaries. Dashed line on bottom left panel denotes confluence of tributary (labeled) and Missouri River. Note: Scales on y-axis vary.

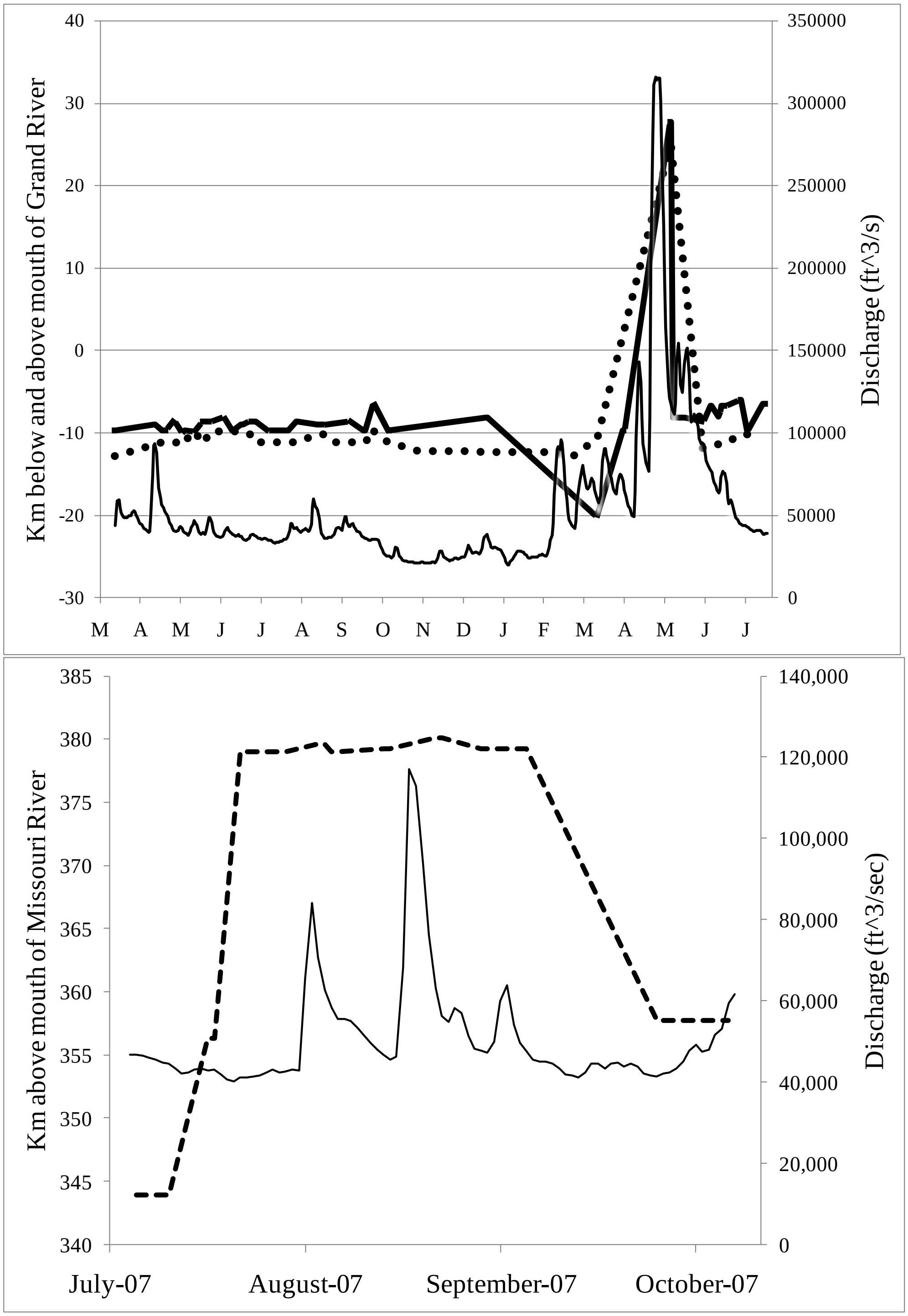

Figure 2.8. Example of linear movements of two blue catfish (upper panel) relocated between March 2006 and July 2007 and one flathead catfish (lower panel) relocated during the summer/fall period. Dashed lines denote linear movement along the river corridor in relation to river mouths. Solid lines denote discharge of the lower Missouri River measured at USGS gauge 06906500 at Glasgow, MO.

Discussion

In North America, many ictalurid catfishes are regarded as sedentary (Lucas and Baras 2001) yet considerable evidence suggests that many channel catfish, flathead catfish, and blue catfish display migratory behavior (Dames et al. 1989; Newcomb 1989; Smith and Hubert 1989; Vokoun and Rabeni 2005a). In this study, annual movement patterns of 18 (60%) flathead and 19 (66%) blue catfish supported the hypothesis that these species migrate to and from seasonal habitats in LMOR and adjacent tributaries. However, the variability in movement 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 that traveled greater than 600 river kilometers during the prespawn/spawning period in 2006 (Figure 2.2). These long-range movements represent approximately 10% of the fish we tagged during both years, and likely explain why 50% of the fish we tagged in 2007 were lost during the first few months of tracking. Spawning migrations temporally overlapped with peak spring discharges during 2006 and 2007 (Fig. 2.5). I speculate that high spring discharges during the spring of 2007 may have caused an increase in movement. Without the additional tracking coverage by USGS-CERC in 2007, movement beyond the 97-km study reach was not recorded. Given the diversity of migratory pathways displayed during both tracking years and the long-range movements recorded in 2006, the evidence suggests that both species exhibit a diverse array of life-history strategies to spawn, feed, and grow in large rivers. Hypothetically, special harvest restrictions applied to a 50–100 km reach of 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 2005a), individual fish displayed at least five variant pathways through an annual cycle (Figure 2.4). Of the 50 individuals used to define seasonal structure, 22 displayed restricted-movement behavior, 15 individuals migrated to and from seasonal habitats within LMOR, and 13 migrated up a tributary during the prespawn/spawning period. Based on the literature (Graham 1999; Pugh and Schramm 1999), I expected blue catfish to exhibit much greater mobility than flathead catfish. However, both species incorporated migration as a life history strategy (Figure 2.4) and displayed a propensity for long-range upstream movement (Table 2.2). Further, individuals of both species used the Grand, Chariton, and Lamine Rivers during the prespawn/spawning period (Figure 2.4). During restricted-movement periods, seasonal ranges were not statistically different (Table 2.4). Thus, I 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 LMOR (Vokoun and Rabeni 2005a). Thus, a diversity of ecologically-distinct groups converges in the mainstem 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. Since both species are nest-guarders and are thought to spawn primarily in cavities (Bobea 1989; Francis 1993;

Graham 1999), multiple life histories may help to exploit optimal spawning locations. Further, upstream migrations may also facilitate the dispersal of larvae and juveniles to suitable rearing habitat. Following the spawn, many catfish remain in the tributaries for the summer/fall and establish a home range around log complexes or other optimal feeding sites (Vokoun and Rabeni 2005b). Others migrate downstream to spend the summer/fall around dike structures in LMOR. Thus, flathead and blue catfish migrate among habitats throughout the mainstem Missouri River and major tributaries for feeding and growth. Therefore, longitudinal connectedness between mainstem and tributary habitats is important for flathead and blue catfish to reach (1) overwintering habitat in LMOR in late fall, (2) spawning habitat in adjacent tributaries in early spring, and (3) feeding habitat in LMOR in early summer.

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, aerial radiotracking support during July and August 2006 suggested that individuals in tributaries were not missed by acoustic-tracking efforts. Thus, the proportion of fish tagged on 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 (2005a) showed that some residents of the Grand and Cuirvre River (most overwinter in LMOR) move up tributaries as early as March. Since my tagging efforts on LMOR were unsuccessful until April, my sample is somewhat biased in favor of those individuals that remain in LMOR throughout the annual cycle. Nevertheless, the weight of the evidence leads me to reject my initial hypothesis that most adult catfish in LMOR use tributary habitats to complete the spawning cycle. My data suggest that the mainstem Missouri provides spawning habitat for both species of catfish and warrants further investigation. During the putative spawning period in 2006 (May 15 – July 15), three flathead and nine blue catfish took up residence in low-velocity, shallow (<2 m) areas downstream of L-head dike structures. Although I cannot conclude spawning activity without physical evidence, the stationary behavior coupled with field observations led me to hypothesize that the mainstem Missouri provides shallow-water spawning habitat for adult catfish. To examine this hypothesis further, I collected physiological evidence of spawning activity during the spawning period in 2007 (see Chapter 5).

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 LMOR throughout an annual cycle (April 2006 – April 2007) moved up the Grand River for only one week during the annual peak discharge in May 2007 (Figure 2.8). 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 chub *Leuciscus 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 backwaters at night (Matheny and Rabeni 1995). In 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, the migratory movement of stream fishes at different spatial scales has become better understood with the 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 catfish in 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. The river segments that were used for the prespawn/spawning, summer/fall, and overwintering periods did not vary significantly in size (Table 2.4). 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 (2005a) provide empirical support for the riverscape framework with flathead catfish moving among seasonal habitats. Two-thirds of the flathead and blue catfish I monitored in LMOR support this hypothesis, although the stationary behavior we recorded for many individuals suggest that LMOR provides more suitable habitat year around than adjacent tributaries, particularly during the overwintering period.

Intraannual movement patterns of 56% (38 of 50 catfish tracked for one complete year) supported the hypothesis that flathead and blue catfish migrate upstream during spring runoff as temperature and discharge increase in the lower Missouri River. However, this observational study was not designed to address the causal relationship between flow, temperature, and movement (Figure 2.5). Further, pinpointing the day or week of departure for migrating individuals was not possible given the temporal resolution of this study (i.e., 2-4 relocations/month). Ovidio et al. (1998) found that the spawning migration of brown trout (*Salmo trutta*) took place when both flow and temperature varied considerably between consecutive days within a restricted thermal range (10–12 ºC). The reliance on a multitude of stimuli is a more efficient strategy than responding to a single cue which could occur on several occasions outside of the spawning period, and lead to decreased fitness (Ovidio et al. 1998). In this study, the spawning migrations of flathead and blue catfish occurred over a protracted period (mid-March to early July), but the majority of upstream migrations occurred during annual peak discharges (varied considerably between years) and increasing water temperatures (15–20 ºC) in May. Although flow conditions varied considerably among years, the temporal overlap of spawning migrations with annual peak discharges provides some evidence that spring runoff is important to catfish reproduction and thus species management. The variation in the timing of migration is not surprising given the diversity of life-history strategies. Individuals that migrate great distances (>100 km) or use adjacent tributaries to spawn must leave overwintering habitats earlier in the year to reach available spawning habitat during ideal spawning conditions. Thus, individual fish are likely triggered at different times to move, depending on the migratory pathway used to complete an annual cycle (Figure 2.4).

The variation in intraannual movement patterns I documented for catfishes resemble other large-river archetypes that have responded adversely to anthropogenic change. The Colorado pikeminnow (*Ptychocheilus lucius*), a large, endangered cyprinid endemic to the Colorado River basin, is known to migrate to restricted spawning sites in the Yampa and Green Rivers and display fidelity to distant (>100 km) home feeding areas in deep pools and runs (Tyus 1985, 1990; Irving and Modde 2000). The recent decline in distribution has been attributed primarily to river regulation, loss of habitat, and dams that interrupt cyclical movements to preferred habitat (Tyus 1986). Similarly, dams and weirs that block historic migratory routes are thought to be the greatest factor preventing the recovery of potadromous paddlefish and sturgeon species (Auer 1996; Lucas and Baras 2001). In the Missouri River, impoundment, water withdrawal, flow regulation, channelization, bank stabilization, and levee construction are activities that have modified natural physical habitat (Galat et al. 2001). Historic information suggests that the Missouri River channel once had a high density of large woody debris (LWD; Funk and Robinson 1974; Mestle and Hesse 1993; Hanson 2003). In the now highly-regulated Missouri River, delivery of LWD to the channel and establishment of new riparian forest stands are both greatly reduced because the river and its floodplain are ecologically uncoupled (NRC 2002; Angradi et al. 2004). Although flathead catfish have been shown to select natural features such as log jams in tributaries to LMOR (Vokoun 2003), it remains unclear how impactful these habitat alterations are to catfish populations in LMOR. At small spatial scales, I investigated habitat selection in LMOR by flathead and blue catfish (see Chapter 4). With regard to large-scale migrations (hundreds of kilometers), I speculate that connectivity of the free-flowing, 1305-km lower Missouri River (downstream of Gavins Point dam) is ecologically beneficial to adult catfish. When maintained over time, longitudinal connectivity allows highly migratory individuals to exploit distant habitats to meet life-history requirements.

Although genetic data is lacking for these populations of catfish, the variation in life history strategies I 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 at multiple spatial scales.

Chapter Three

Diurnal Home Range and Space-Use Patterns of Flathead and Blue Catfish During the Summer/Fall Period in the Lower Missouri River

Flathead and blue catfish are important game fish in all medium to large rivers of Missouri, and annual angler exploitation rates within many of these tributaries have been high (>30%) in recent years (Z. Ford, MDC, pers. comm.). In general, catfish management over the last century has sought to provide maximum sustained harvest and generally not promoted high quality fishing, particularly in lotic systems (Pugh & Schramm 1999; Travnichek 2004). This historical management approach may not optimize longevity and maximum growth potential of catfish or desires of some anglers who seek large fish (Travnichek 2004). Managers are increasingly turning to ecological research to better understand the space requirements of large, adult catfish.

Understanding space-use requirements is an important component of managing large-river fishes because the extent to which fishes display territorial behavior reveals space requirements of a species. Large-river fishes such as the flathead and blue catfish are presented with an almost unlimited set of possibilities for use in their riverine environment. The pattern of space use exhibited by individuals is likely related to its life-history strategy. During seasonal periods, fishes may display fidelity to restricted areas that provide the best-available conditions for spawning, feeding and growth, or refuge. By studying and understanding space-use patterns of a population we gain insights into the ecological requirements of the species.

Space use occurs at multiple spatial and temporal scales from annual migrations to more restricted movements within a home range. The original home-range concept was developed by Burt (1943) as the area, usually around a commonly-used site, over which the animal normally travels in search of food. Gerking (1953) contended that this definition overemphasized feeding, and refined the definition to "the area over which the animal normally travels." Others have since criticized these two definitions (Mohr 1947; Hansteen et al. 1997), specifically the use of the term "normal" and the inadequacy of defining a temporal component (White and Garrott 1990; Kernohan et al. 2001). A more useful definition includes a temporal component that is defined by life-history characteristics. In this study, I focus on home range during the summer/fall period (July 15 – November 15; see Chapter 2), a limited time period but functionally relevant with regard to feeding and growth of adult catfish. Following the spawning period (May 15 – July 15), rates of metabolic processes (e.g., heart rate, digestion) and energy requirements increase as water temperature rises and intake of calories becomes important to growth and condition. Somatic growth during the summer/fall period also affects fitness traits during the following spawning period (greater body size = greater fecundity) and body condition may ultimately influence spawning success. Thus, this period is ecologically relevant with respect to feeding and growth and should be related to food density and metabolic needs (Schoener 1981).

During a parallel study in 2006, a majority of flathead and blue catfish displayed nonmigratory behavior during this 4-month period and moved between 0.1–57.5 linear river-kilometers. Similar findings have been reported by Vokoun and Rabeni (2005a) for flathead catfish in the Grand River (tributary to LMOR). Thus, I hypothesized that flathead and blue catfish during the summer/fall period in 2007 would display fidelity to one section of river and that blue catfish would exhibit greater mobility overall. Blue catfish have been described as the most migratory ictalurid (Graham 1999; Pugh and Schramm 1999), although most movement studies have been conducted in lakes and reservoirs (Fisher et al. 1999; Graham and DeiSanti 1999; Timmons 1999; Grist 2002).

Many novel techniques for estimating home range are now available that address previous methodological limitations. Traditional linear home-range estimates are defined as the distance between the most upstream and farthest downstream relocations of an individual fish. These estimates do not account for variable space use within the outer extent of travel or identify fidelity to discrete areas within the home range (Kernohan et al. 2001; Vokoun 2003). The kernel density estimator (Worton 1989) calculates home range as the extent of an area with a defined probability of occurrence of an animal during a specified period of time. The 50%, 90%, and 95% kernels are commonly reported distinguishing areas within the home range with a 50%, 90%, and 95% probability of occurrence. The 50% kernel estimate is commonly referred to as the "core area," an area within which the probability of fish presence is 50%. With increasing sensitivity of analysis, researchers are increasingly aware that many organisms display fidelity to discrete areas within the home range. Among lotic fishes, kernel density estimation was not applied until recently (Vokoun and Rabeni 2005b; Hodder et al. 2007), although we will undoubtedly see increased use in years to come.

To examine the home range of flathead and blue catfish, I gathered telemetry data during the summer/fall period (July 15, 2007 – November 15, 2007). Specific objectives were to 1) calculate traditional home-range estimates; 2) use kernel density estimation to create estimates of home range that describe the internal structure of the home range within a probabilistic framework; 3) compare home-range estimates between species, sexes, and among size classes; and 4) examine relationship between linear movements and river discharge within home ranges.

Methods

Field Sampling.—Forty blue catfish and 40 flathead catfish were tagged in April and July 2007 to investigate patterns of movement and habitat use. Of these, 23 were monitored frequently enough to facilitate home-range analysis. Five individuals were relocated infrequently (<5 relocations/month) and the remainder moved outside of the 97-km sampling reach of the lower Missouri River (Figure 3.1). Sixteen flathead and seven blue catfish were relocated twice a week during daylight hours (0900 – 1700 hours) during the 4-month summer/fall period (July 15, 2007 – November 15, 2007). I attempted to obtain 30 relocations per individual while minimizing the potential for autocorrelated data. Thirty relocations were set as a target for kernel calculations based on simulation work conducted by Vokoun (2003). Given the hazards of nighttime telemetry work on LMOR, I opted not to stagger the schedule to achieve even diel coverage. Although catfish are presumed to be nocturnal, a parallel study of 24-hour movement conducted during this same time period (September and November 2007) yielded little support for this hypothesis (see Chapter 4). However, the diurnal dataset we present here cannot be used to infer nocturnal movement behavior.

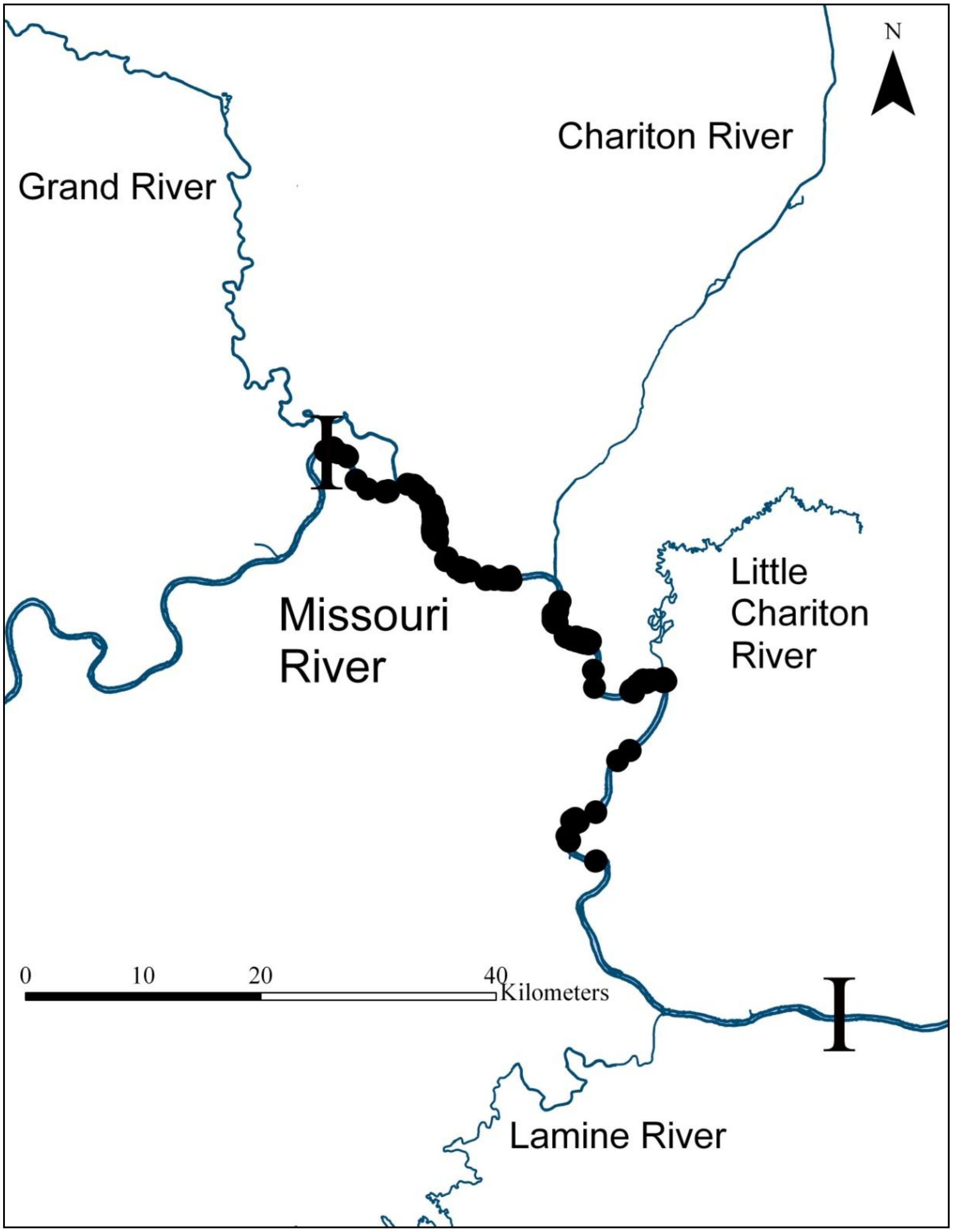

Figure 3.1. Distribution and spatial extent of movement data used to define homes range characteristics of flathead and blue catfish on the lower Missouri River during the summer/fall period (July 15, 2007 – November 15, 2007). Vertical bars indicate upper and lower extent of the 97-km study reach.

Home-range estimation.—Home-range estimates for individual blue and flathead catfish during the summer/fall period were calculated using two methods. Traditional home range, defined as the distance between the furthest upstream and furthest downstream movement, is reported to show the farthest extent of travel for each individual. The second method, kernel density estimation, provides the internal structure of the home range, with areas of higher and lower use (Vokoun 2003). To analyze data points one-dimensionally along the river corridor, I assigned fish relocations to the nearest 1–m point along a thalweg line beginning with zero at the furthest downstream point in the 97-km sampling reach. I used the univariate distribution of relocation data points along the thalweg line to calculate a fixed univariate kernel density estimate. Kernels were calculated in Statistical Analysis Software Version 9.1 (SAS) using PROC KDE (SAS Institute, Inc. 2000). Bandwidth selection was by the Sheather-Jones plug in method (Jones et al. 1996). Kernel density estimates of home range are an integrated function that sums to 1, allowing the estimate to be interpreted as a utilization distribution (van Winkle 1975). A utilization distribution estimates the percentage of time an individual spent in a given location within the home range (Worton 1989). I calculated the 95%, 90%, and 50% kernel estimate. The 95% and 90% level-of-use kernel estimates delineate larger portions of home range in which the fish was located throughout almost all of the study period (this includes the 50% use area). The 50% kernel estimate or “core area” (Rodríguez-Robles 2003) represents the length of river wherein there is a 50% probability of occurrence; multiple core areas exist when an individual splits its time between two or more discrete areas with little movement in between.

Home-range Comparisons.—Home-range estimates for blue and flathead catfish were compared using three-way analysis of variance (ANOVA) with main effects of species, sex, and size class. Sex was determined by comparing levels of estradiol and testosterone measured from blood samples using the radioimmunoassay method (RIA; McMaster et al. 1992). Since little is known with regard to these species, an E2/T ratio of 1.0 was used as the threshold between males and females, with females predicted to have an E2/T ratio greater than 1.0 (see also Craig et al. 2009). I evaluated three size classes based on relative stock density lengths evaluated by Quinn (1991), these included 510-709 mm (quality size), 710-859 mm (preferred size), and >859 mm (trophy size; Table 3.1). ANOVA models were run separately for the linear range, 95% kernel, 90% kernel, and 50% kernel estimates of home range. The three-way interaction term was not computed due to insufficient degrees of freedom. Home-range data were log transformed to achieve a normal distribution prior to analysis.

River Discharge.**—**Discharge (ft^3/sec) was recorded by a USGS gauge station in Glasgow, Missouri and plotted with catfish locations (km above mouth of Missouri) to examine potential behavioral responses to high flow events. Three periods of increased flow occurred during the study period including peak discharges of 85,000 ft^3/sec (August 12), 117,000 ft^3/sec (August 27), and 138,000 ft^3/sec (October 19). Individuals were relocated before and after high flow events, although few fish were relocated during the week of peak flows given the high turbidity which interferes with acoustic signals.

Results

Sample Size and Tracking.—During the first week of this study (July 15–21, 2007), 19 individual blue catfish and 26 flathead catfish were relocated within the 97-km study reach (Fig. 3.1). By the end of the 4-month summer/fall period, 12 of 19 (63%) blue catfish and 10 of 26 (38%) flathead catfish were lost, likely due to movement outside of the study reach. The remaining 23 individuals in the study reach were subsequently used to estimate home range.

Home-range estimation.—During the summer/fall period (July 15 – November 15, 2007), I achieved a mean of 29.5 relocations per individual with a range of 21–34. No fish was relocated with an elapsed time less than 48 h. Kernel-density estimates of diurnal home range revealed attributes of the internal structure of utilization distributions during the summer/fall period (Figure 3.2). Three of seven (43%) blue catfish and four of sixteen (25%) flathead catfish established more than one core area of use (Table 3.1), although only three individuals established multiple core areas that were greater than 500 m apart. Among all individuals, core areas were positioned equally in the downstream (35%), center (30%), and upstream (35%) portions of the 95% and 90% kernel estimate. No individual used in this analysis was harvested during the course of the study, although 5 of 40 (13%) flathead catfish and 8 of 40 (20%) blue catfish were harvested since they were implanted in April and July 2007.

Home-range Comparisons.—Home-range size (95% kernel estimate) varied greatly among individuals of both flathead catfish (43–7305 m) and blue catfish (19-18322 m;

Table 3.2). The mean traditional linear range was greater for blue catfish (12034 m) than flathead catfish (3814 m; Table 3.2), though I found no statistical difference between blue and flathead catfish (Table 3.3). Comparisons of home-range sizes by sex demonstrated a significant difference between males and females for kernel density estimates, but not traditional linear calculations (three-way ANOVA, $\alpha = 0.05$; Table 3.3). Mean 95%, 90%, and 50% kernel density estimates were greater for males than females (species combined) although ranges overlapped (Table 3.2). Other main effects (species, size class) and two-way interactions were not significant.

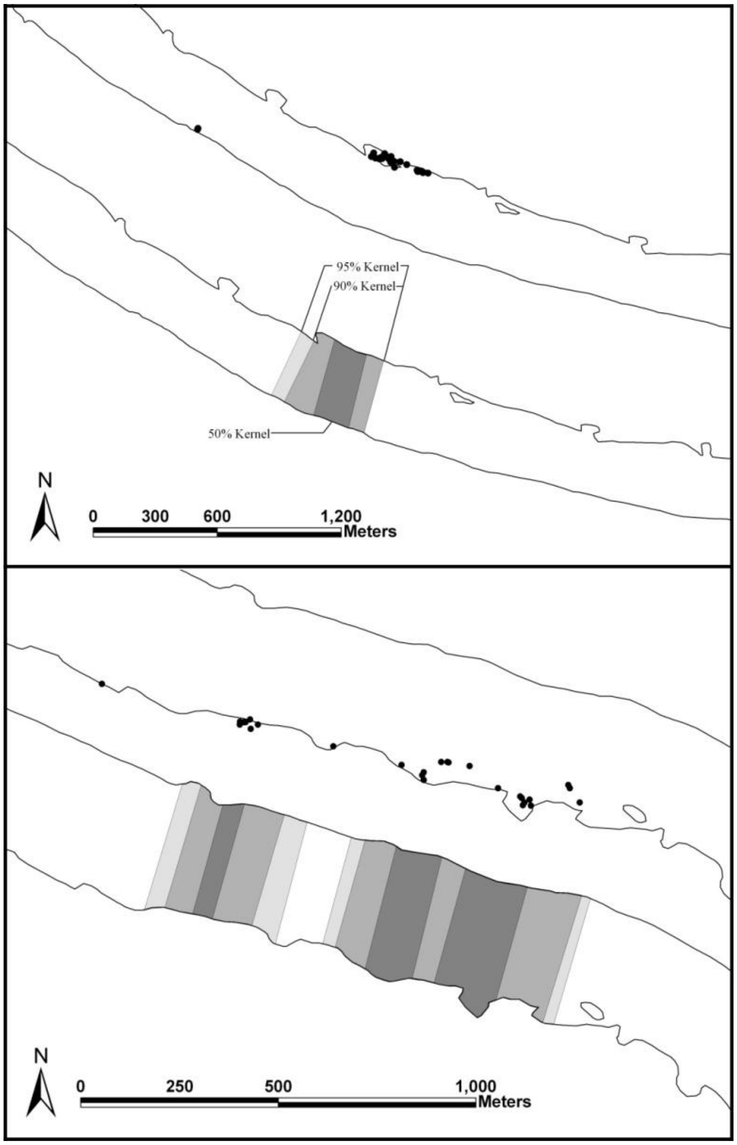

Figure 3.2. Plan view of the distribution of relocation points and the calculated 50%, 90%, and 95% kernel density estimates for two female flathead catfish (see Table 3.1 for details). Core areas (50%) are shaded darker gray. Upper panel displays a continuous home range, while the fish shown in the bottom panel had three core areas that were used during the study period. Note: kernel density estimates were univariate, calculated along the thalweg. River flow is from left to right.

Directed Movements and River Discharge.**—**The relation between linear movement within the home range and river discharge varied greatly among individuals. Seven of 23 (30%) individuals made at least one directed movement upstream or downstream that expanded their home range during one or more peaks in river discharge (e.g., Figure 3.3). Nine of 23 (39%) displayed at least one directed movement during the study period that occurred independent of peak discharges (Figure 3.4). The remainder (N=7) concentrated their movements within a smaller home range (<300 m) with no directed movements upstream or downstream.

Table 3.1. Species, sex, total length, number of relocations, number of core areas used during the study period, and individual estimates of linear range, and the 95%, 90%, and 50% kernel density estimates of home range for seven blue catfish and 16 flathead catfish (BL=blue; FL=flathead). Single asterisks denote individuals shown in Figure 3.2. Double asterisks denote individuals shown in Figures 3.3 and 3.4. Fish are ordered by increasing total length within each sex; relative stock density length groups (Quinn 1991) are shown.

Size Class	Species	Sex	Total length (mm)	Reloc-ations	No. Core Areas	Home Range (m)			
						Linear	95% Kernel	90% Kernel	50% Kernel
Quality	FL	M	577	31	1	183	58	41	6
	FL	M	584	31	2	618	298	209	60
	BL**	F	594	21	3	36191	13572	11310	3348
	FL	F	610	26	1	702	407	298	90
	BL	F	617	30	1	3675	2885	2398	937
	FL	F	622	33	2	348	123	108	44
	BL	M	625	30	1	3946	3186	2693	1036
	FL**	F	625	34	1	1008	307	275	66
	BL	F	658	34	1	23	19	17	3
	BL	M	709	27	2	37974	18322	15000	4177
Preferred	BL	F	711	29	1	844	91	74	30
	FL	F	714	34	1	98	43	33	13
	FL	F	726	24	2	1586	813	654	198
	BL	F	747	31	2	1587	694	536	135
	FL	F	749	32	1	3751	1988	1604	319
	FL	F	762	25	1	473	441	414	220
	FL*	F	841	30	3	1350	948	800	327
Trophy	FL	M	899	27	1	4000	2000	1460	990
	FL*	F	917	33	1	1135	463	386	173
	FL	M	917	30	1	43611	7305	5342	1090
	FL	F	953	33	1	132	27	23	9
	FL	F	968	24	1	712	255	196	50
	FL	M	1062	30	1	1318	540	418	115

Table 3.2. Median and range of estimated linear diurnal home-range sizes for flathead and blue catfish tracked in the lower Missouri River arranged by species, sex, and size class. Linear range is defined as the distance between the most upstream and most downstream relocations. Kernel estimates are the 95%, 90%, and 50% levels of use produced by a univariate fixed kernel density estimate (see text for details).

	N	**Linear Range (m)**	**95% Kernel Estimate (m)**	**90% Kernel Estimate (m)**	**50% Kernel Estimate (m)**
		Mean (Range)	**Mean (Range)**	**Mean (Range)**	**Mean (Range)**
Blue	**7**	12034 (23-37974)	5538 (19-18322)	4575 (17-15000)	1380 (3-4177)
Flathead	**16**	3814 (98-43611)	1000 (43-7305)	766 (33-5342)	236 (13-1090)
Male	**7**	13093 (183-43611)	4530 (58-18322)	3594 (41-1500)	1067 (6-4177)
Female	**16**	3351 (23-36191)	1442 (19-13572)	1195 (17-11310)	372 (3-3348)
510-709 mm	**9**	8467 (23-36191)	3917 (19-13572)	3234 (17-11310)	977 (3-3348)
710-859 mm	**8**	1384 (98-37974)	716 (43-18322)	588 (33-15000)	177 (13-4177)
>859 mm	**6**	8485 (132-43611)	1765 (27-7305)	1304 (23-5342)	405 (9-1090)
All Fish	**23**	6316 (23-43611)	2382 (19-7305)	1925 (17-5342)	584 (3-1090)

Table 3.3. Summary of results from two-way analysis of variance for linear range, 95%, 90%, and 50% kernel estimates of home-range distances. Home-range data were log-transformed to achieve normal distribution. Bolded text denotes statistical significance ($P<0.05$).

Home Range Estimate	**Effect**	***F***	**df**	***P***
Linear Range	Sex	3.8	1,23	0.071
	Size	0.92	2,23	0.422
	Species	1.32	1,23	0.270
	Sex*Size	1.34	2,23	0.293
	Species*Sex	0.36	1,23	0.556
	Species*Size	0.05	1,23	0.820
95% Kernel	Sex	5.41	1,23	**0.036**
	Size	0.47	2,23	0.633
	Species	1.34	1,23	0.266
	Sex*Size	1.63	2,23	0.231
	Species*Sex	0.52	1,23	0.481
	Species*Size	0.91	1,23	0.357
90% Kernel	Sex	5.23	1,23	**0.038**
	Size	0.47	2,23	0.635
	Species	1.49	1,23	0.242
	Sex*Size	1.72	2,23	0.215
	Species*Sex	0.63	1,23	0.441
	Species*Size	0.97	1,23	0.340
50% Kernel	Sex	5.02	1,23	**0.042**
	Size	0.59	2,23	0.565
	Species	1.33	1,23	0.268
	Sex*Size	1.63	2,23	0.231
	Species*Sex	1.09	1,23	0.314
	Species*Size	0.8	1,23	0.386

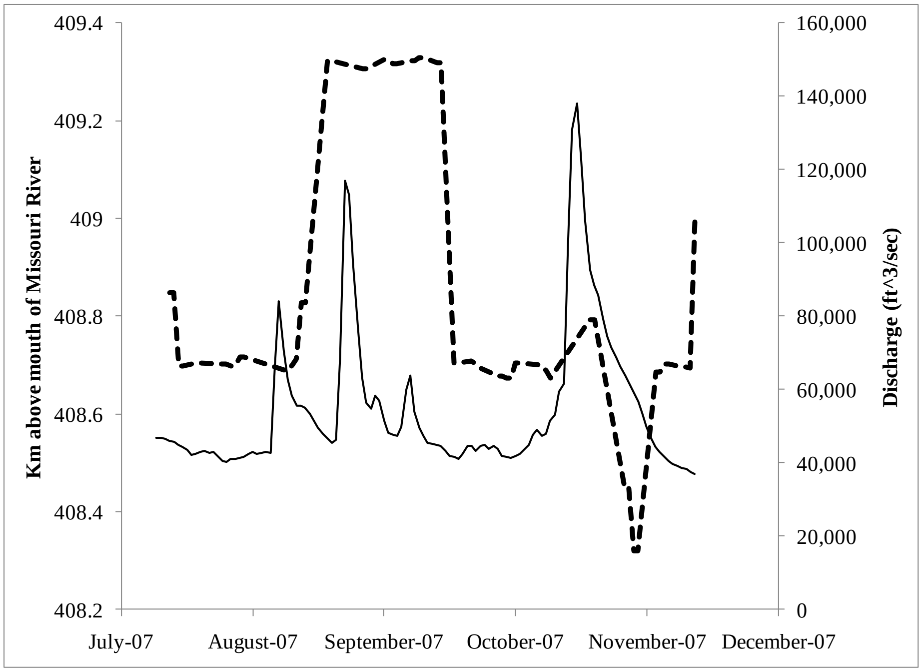

Figure 3.3. Relationship between the linear movements of one female, flathead catfish (625 mm TL) monitored during the summer/fall period and discharge of LMOR as measured by the USGS gauge in Glasgow, Missouri. Dashed line represents linear movements; solid line represents discharge. Home-range data are shown in Table 3.1.

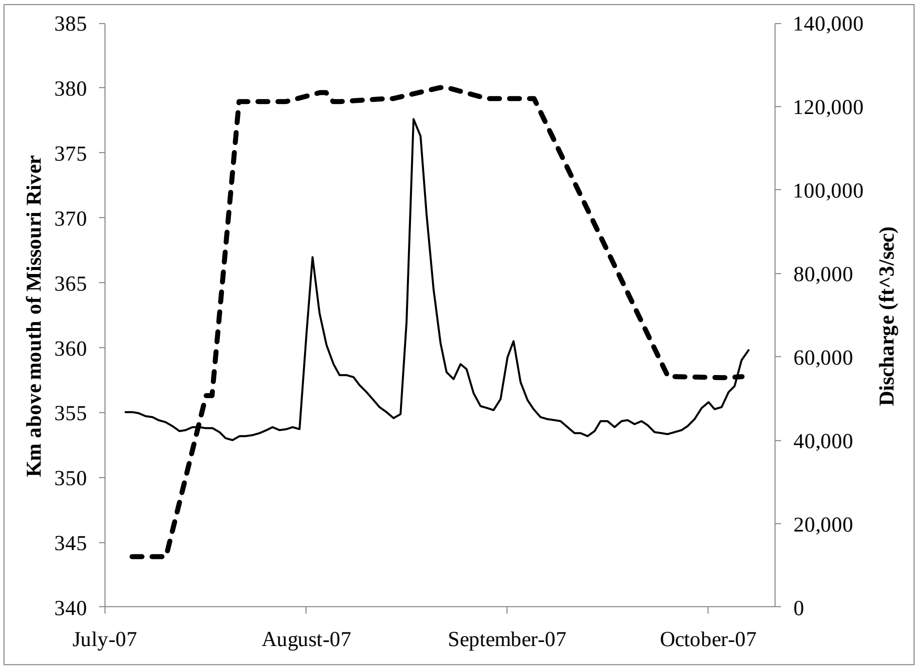

Figure 3.4. Relationship between the linear movements of one female, blue catfish (594 mm TL) monitored during the summer/fall period and discharge of LMOR as measured by the USGS gauge in Glasgow, Missouri. Dashed line represents linear movements; solid line represents discharge. Home-range data are shown in Table 3.1.

Discussion

Kernel density estimates of home range showed that most catfish (87% of individuals included in study) established relatively small home ranges (<10 km) during the summer/fall period, though three individuals expanded their ranges beyond 30 km (Table 3.1). Thus, the movement results from my sample of 23 individuals support the hypothesis that catfish display fidelity to a relatively small section of river.

When evaluating the results of mark-recapture and telemetry studies, it is likely that bias exists against the detection of movement outside of the study reach (Gowan et al. 1994). Often, a high proportion of fish are relocated or found in a described area where they were originally tagged, but another subset is never found (Rodríguez 2002). An example of such discrepancies in movement data for flathead catfish is described by Daugherty and Sutton (2005), where 16 of 39 (41%) individuals were lost during a 2-year period of monitoring. This is not uncommon in telemetry studies, and may explain why the "restricted-movement paradigm" (Gerking 1959) was not relinquished for many riverine species until recently (Gowan et al. 1994; Rodríguez 2002). During this 4-month investigation, 22 of 45 (49%) individuals were lost and presumably left the 97-km study reach (Fig. 3.1). Thus, my results are biased in favor of space use that did not exceed the boundaries I created on the basis of tracking efficiency and sample size requirements.

Perhaps the presumption of movement outside of the study reach can be related to high-flow events. The summer/fall period in 2007 experienced high precipitation in the Midwest, and three periods of increased flow occurred including peak discharges of 85,000 ft^3/sec (August 12), 117,000 ft^3/sec (August 27), and 138,000 ft^3/sec (October 19). Similar to flathead catfish radiotracked by Vokoun and Rabeni (2005b), some individual blue and flathead catfish (30% of sample) responded to these conditions by moving upstream or downstream to another discrete area within their home range, and remained there until the next period of high discharge (Figure 3.3). However, 70% of individuals either remained in one high-use area (< 1 km) or moved independent of river discharge (Figure 3.4).

During a parallel study in 2006, 5 of 39 (13%) blue catfish and 6 of 32 (19%) flathead catfish moved greater than 100 km from where they were originally tagged with a maximum distance recorded of 377 km and 752 km, respectfully (see Chapter 2). These individuals were monitored exclusively by Columbia Environmental Research Center (USGS) personnel who aided our project while tracking pallid sturgeon with compatible tracking equipment. Whereas these individuals are the exception and not the rule, they represent a significant portion of the total individuals we tagged. Highly mobile individuals that migrate great distances (>100 km) are not represented by the individuals in this home-range study. Further, individuals that migrate great distances may not restrict their movements during seasonal periods given the distances needed to reach seasonal habitats.

The 4-month summer/fall period (July 15 – November 15) was behaviorally defined by flathead and blue catfish that displayed nonmigratory behavior during this period in 2006 (see Chapter 2 for more details). Based on the variability in movement we recorded, however, this period is clearly not rigidly defined by all flathead and blue catfish. For example, while most of the individuals I monitored in 2006 and 2007 began a downstream migration in mid-November, a few did not move downstream until December (see Chapter 2 for details). Because these behaviorally-defined seasons are not strictly adhered to by all individuals, I was not surprised that home-range estimates were highly variable among individuals.

The calculated 95%, 90%, and 50% kernels revealed the structure of space use within the outer extent of travel (traditional home range) during the summer/fall period. The mean 95% kernel estimate (3.4 km; Table 3.2) represented only 38% of the mean traditional home-range estimate (6.3 km; Table 3.2) indicating that the traditional method overestimates the size of these individuals' home range with respect to 95% of the movement we recorded. Traditional home-range estimates overemphasized the peripheral movements that define the home-range boundary, and did not characterize fidelity to discrete areas. The individuals in this study displayed site fidelity to anthropogenic structures that are spatially segregated by several hundred meters and evenly spaced along the river corridor. Thirty percent of individuals split their time between multiple high-use areas (Table 3.1) with little movement in between. Thus, the 50% kernel proved useful for identifying these high-use areas (<1 km) within the outer extent of travel.

Individuals were positioned downstream of anthropogenic structures, i.e., wing dikes, L-head dikes, almost exclusively throughout the study period (see Chapter 4). Thus, habitats adjacent to dike-structures appeared to be selected and were subsequently identified as "core areas" in the kernel density estimate. Anthropogenic structures in LMOR are separated by largely uniform, main channel habitats that were not used frequently in this study. Vokoun and Rabeni (2005b) found that flathead catfish in the Grand and Cuivre Rivers used discrete areas that were characterized by a log complex, clay point, or other habitat feature that provides refuge and opportunistic feeding. In

LMOR, anthropogenic structures may act as surrogate habitat for natural features that were removed during channelization. During this same 4-month period, I conducted a parallel study of habitat selection to examine this hypothesis further (see Chapter 4).

The internal structure of home ranges was different than previous findings for flathead catfish. Vokoun and Rabeni (2005b) reported that 50% kernel estimates (core areas) were most often found in the middle of the 90% estimate suggesting that departures from the core area were split between upstream and downstream movement. Other studies have also reported a similar finding (Robinson 1977; Grace 1985; Skains 1992). Among individuals in this study, however, core areas were positioned equally in the downstream (35%), center (30%), and upstream (35%) portions of the 95% and 90% kernel estimate. Thus, directionality of movement was more variable than previously reported.

Blue catfish are reportedly the most mobile ictalurid catfish (Ladler 1961; Graham 1999), yet only tag-recapture data supports this contention (Graham and DeiSanti 1999; Pugh and Schramm 1999; Timmons 1999). Mean traditional home ranges and kernel density estimates were not significantly different between blue and flathead catfish for the samples in this study (Table 3.3). Despite their evolutionary and taxonomic differences, the blue and flathead catfish we monitored behaved similar at the home-range scale suggesting that both species respond similarly to selective environmental pressures (e.g., availability of food and cover) during this time period.

I isolated the summer/fall period (July 15- Nov 15) on the basis of nonmigratory movement that was demonstrated by 2006 tracking data and the ecological relevancy of this period with respect to feeding and growth. The home ranges I estimated in 2007 suggest that the best-available conditions for feeding and growth are available in small, discrete sections of river that are characterized by habitat heterogeneity associated with dike structures. Given that both species display a diversity of life-history characteristics that include long-range migrations (see Chapter 2), connectivity of distant habitats and large-scale environmental processes such as flow regime likely influence catfish populations in large rivers. However, managers seeking to enhance growth of adult catfish may look to small (< 1 km) sections of river that offer energetically-profitable stream positions for these top predators.

Chapter Four

Habitat Selection and 24-Hour Diel Movement of Flathead and Blue Catfish During the Summer/Fall Period

Though flathead and blue catfish are thought to have evolved as fluvial species that use flowing water during their life cycle (Becker 1983; Pflieger 1997; Galat et al. 2005), they may adapt well to lentic environments as evidenced by successful introductions throughout the central and southeastern United States (Graham 1999; Jackson 1999). Catfishes appear more resilient to impoundment and anthropogenic disturbance in the Missouri River than other native species experiencing population declines (i.e., pallid sturgeon, flathead chub; Galat et al. 2005; Ridenour et al. 2009). The decline of native fish populations in highly regulated rivers has been linked to the degradation of habitat required to complete life-history cycles (Ward et al. 1999; Humphries et al. 2002; Aarts et al. 2004; Hirzinger et al. 2004). Over the course of several seasons, flathead and blue catfish are known to migrate to and from discrete areas of habitat in response to changing environmental conditions (Grist 2002; Vokoun and Rabeni 2005a). If discrete areas of use are associated with smaller-scale environmental variables advantageous to growth and fitness, then the identification of these areas may be important to population management and species conservation.

The lower Missouri River (LMOR; downstream of Gavins Point Dam) is significantly altered by channelization, bank stabilization and levee construction to regulate flows for barge traffic navigation and flood protection. Channel modifying structures (CMS; i.e., wing dikes, L-dikes, revetment) redirect flow towards the thalweg (i.e., wing-dikes and L-dikes) and reduce bank erosions (i.e., revetment) thus inhibiting fluvial processes that create and maintain natural fish habitat (Figure 4.1; Nestler and Sutton 2000; Galat et al. 2005; Ridenour et al. 2009). More specific, a wing-dike is a straight dike that is perpendicular to the main channel current (Figure 4.1). An L-dike is shaped like an L with the shorter arm extending to the bank and the longer arm parallel with the thalweg. Revetment, also referred to as riprap, is an artificial shoreline structure comprised of rocks of various sizes (Eitzmann et al. 2007).

Although CMS are related to the deleterious impacts of river modification, they also provide low-velocity habitat that was removed during channelization. Barko and Herzog (2003) and Barko et al. (2004) suggested that fishes use wing-dike scour holes and side channels as surrogate low-velocity habitat where other types of backwater habitat (e.g., flooded terrestrial) are scarce. In LMOR, Jennings (1979) found 42 different species of fish using backwater habitat associated with dike structures. When comparing among L-dikes, wing-dikes in secondary chutes, and enclosed pools (i.e., backwater created by an engineered false bank), enclosed pools with a larger area of low-velocity habitat showed higher chlorophyll-a content, larger average standing crops of zooplankton, higher average diversity of zooplankton, and a greater number of zooplankton species. In addition, enclosed pools showed a higher abundance of juvenile gizzard shad, channel catfish, drum, and centrarchid *spp*. Thus, artificially-created backwaters may be associated with an increase in productivity that could have bottom-up effects on the food web.

In highly modified systems such as LMOR, the identification of CMS used by fishes is most applicable to current river management. The U.S. Army Corps of

Engineers implements habitat improvement projects for fish on CMS to affect proximate environmental factors (e.g., flow, depth, and substrate) on the Missouri River (US Army Corps of Engineers 2006). Small-scale habitats (i.e., scour holes, large woody debris, and velocity fences) associated with CMS comprise the majority of aquatic habitat in LMOR outside of the thalweg (Ridenour et al. 2009). Further, CMS maintain habitats at adjacent smaller spatial scales (Frissell et al. 1986; Tonn 1990; Poff 1997) by affecting flow velocity and water depth.

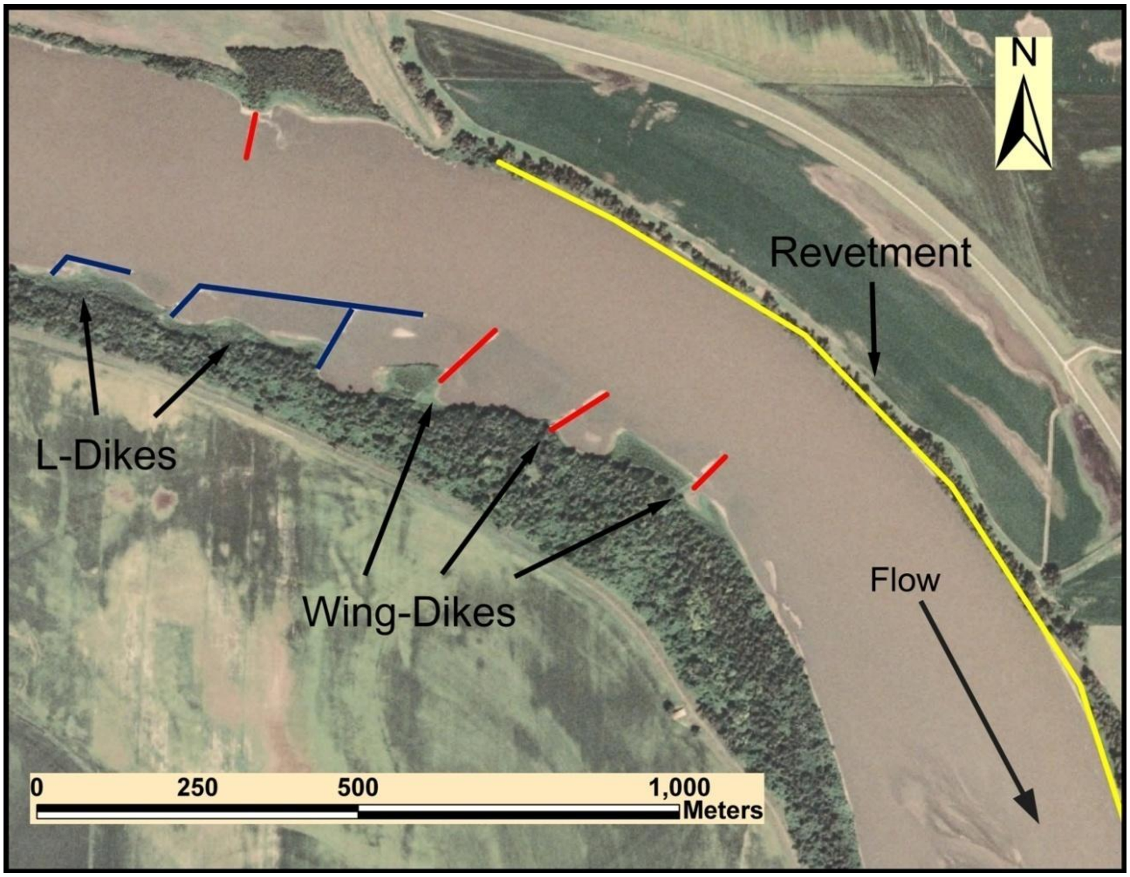

Figure 4.1. Channel-modifying structures on the lower Missouri River incorporated as habitat variables to model habitat selection by flathead and blue catfish.

Evaluating habitat selection by lotic fishes presents unique challenges given the dynamic nature of rivers. Natural habitat features deemed as available in habitat selection analyses are often moved or modified by high-flow events. Natural habitats are also removed or degraded by anthropogenic disturbance, limiting our ability to distinguish between habitat use and habitat preference. Although CMS may not be preferred by fishes, they are easily classified, static structures that are available to fishes regardless of time of year or discharge. However, smaller-scale proximate environmental factors (e.g., depth, flow velocity, substrate) associated with each may vary at different river stages.

The summer/fall period (July 15 – November 15; see Chapter 2) is a limited time frame but functionally relevant with regard to feeding and growth of adult catfish. Following the spawning period (May 15 – July 15), rates of metabolic processes (e.g., heart rate, digestion) and energy requirements increase as water temperature rises and intake of calories becomes important to growth and condition. Somatic growth during the summer/fall period also affects fitness traits during the following spawning period (greater body size = greater fecundity) and body condition may ultimately influence spawning success. Thus, this period is ecologically relevant with respect to feeding and growth and in theory, should be related to food density and metabolic needs (Schoener 1981).

During the summer/fall period in 2007, I conducted a parallel study of home range and space use. Kernel density estimates of home range showed that most catfish (87% of individuals included in study) established relatively small home ranges (<10 km) during the summer/fall period, though three individuals expanded their ranges beyond 30 km (Table 3.1). Thus, the movement results from my sample of 23 individuals support the hypothesis that catfish display fidelity to a relatively small section of river. This study focuses on habitat use within the summer/fall home range of each individual. Habitat use information collected within an individual's home range may help explain the patterns of space use I observed at the home-range scale (see Chapter 3).

Catfish behavior and habitat use may be variable among different river systems that have different composition of habitats and varying degrees of anthropogenic disturbance. Whereas adult flathead catfish in the St. Joseph River, Michigan predominately used large woody debris and riprap (Daugherty and Sutton 2005), flathead and blue catfish were found in higher abundance around wing-dike structures in the unimpounded upper Mississippi River (Barko et al. 2004). Since information from the upper Mississippi River is the closest spatial reference point to catfish in LMOR (Barko et al. 2004), I hypothesized that adult catfish would select habitats adjacent to CMS. To examine this hypothesis, I developed a discrete choice model (Cooper and Millspaugh 1999) to evaluate habitat variables selected by flathead and blue catfish in LMOR. Since habitats adjacent to CMS are difficult to define spatially, I selected distance-to measurements that relate catfish locations to their proximity to CMS. During high-flow events, flushing through dike notches and the redirection of flow around these structures maintains deep scour holes (5–10 m) directly downstream of CMS. Thus, depth is an environmental variable that is related to proximity to CMS, and may be an important predictor of site selection. I included depth (m) as a habitat variable in the model to examine the hypothesis that adult catfish select deep-water habitats in LMOR. Last, I monitored the movements of eight flathead and five blue catfish during a 24-hour diel period to evaluate potential shifts in movement and habitat use related to nocturnal feeding behavior.

Methods

Sampling.—Forty blue catfish and 40 flathead catfish were tagged in April and July 2007 to investigate patterns of movement and habitat use. Of these, only 23 individuals were monitored frequently enough to examine home range (Chapter 3) and habitat use during the summer/fall period. Five individuals were relocated infrequently (<5 relocations/month) and the remainder presumably moved outside of the 97-km sampling reach of the lower Missouri River (Figure 4.2). I attempted to obtain 30 relocations per individual while minimizing the potential for autocorrelated data.

The 4-month summer/fall period (July 15 – November 15) was chosen as the temporal scale to use and availability in this investigation. This time period was chosen for home range (see Chapter 3) and habitat use analyses based on the predominance of nonmigratory behavior exhibited by flathead and blue catfish during this period in 2006 (see Chapter 2). Further, the home ranges I estimated during the summer/fall period showed that the majority of catfish (89%) in the 97-km study reach used discrete areas of river (<10 river-kilometers). This study focuses on habitat use within the summer/fall home range of each individual.

Sixteen flathead (range 577-1062 mm TL) and seven blue catfish (range 594-747 mm TL) were relocated twice a week during daylight hours (0900 – 1700 hours) during the 4-month summer/fall period (July 15, 2007 – November 15, 2007). Descriptive statistics for these individuals are provided in Table 4.1. Three periods of increased flow occurred during the study period including peak discharges of 85,000 ft^3/sec (August 12), 117,000 ft^3/sec (August 27), and 138,000 ft^3/sec (October 19). Individuals were relocated before and after high flow events, although few fish were relocated during the week of peak flows given the high turbidity which interferes with acoustic signals. However, I achieved a mean of 29.5 relocations per individual with a range of 21–34 (Table 4.1). No fish were relocated with an elapsed time less than 48 hours. Fish were surgically implanted with acoustic transmitters from 10 to 75 days prior to the start of tracking (15 July 2007). Thus, effects of stress and recuperation associated with capture and implantation should be negligible (Summerfelt 1972).

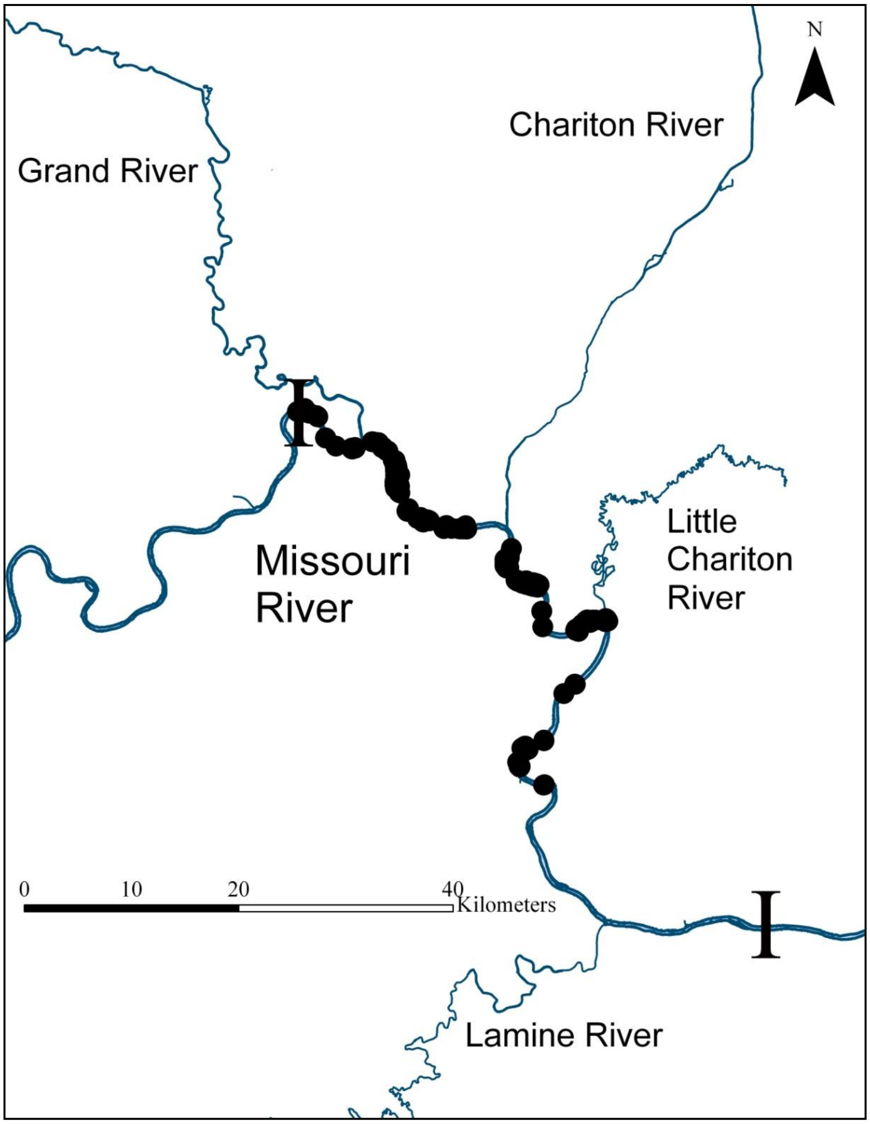

Figure 4.2. Distribution and spatial extent of movement data used to examine habitat use by flathead and blue catfish on the lower Missouri River during the summer/fall period (July 15, 2007 – November 15, 2007). Vertical bars indicate upper and lower extent of the 97-km study reach.

24-hour Diel Sampling.—Eight flathead (577–917 mm TL) and five blue catfish (617–1156 mm TL) were relocated during a 24-hour period with a sampling interval of two to three hours. Sampling interval was largely based on the spatial orientation and movement of individuals, coupled with nighttime tracking efficiency. Thus, I chose individuals in close proximity to one another (< 1 km). Four of thirteen individuals sampled (ID 2, 3, 4, 126; Table 4.4) were relocated too infrequently (<5 relocations/4-month period) to include in habitat selection analysis; further, calculations of home range were not obtained for these individuals. Mid-September was selected for 24-hour sampling since this is the approximate midpoint of the summer/fall period. Five flathead catfish were monitored on 18 September 2007 and two flathead catfish and three blue catfish were monitored on 26 September 2007. On 1 November 2007, I relocated the same three blue catfish as 26 September 2007 to examine potential shifts in movement patterns related to time of year. Two additional blue catfish and one flathead catfish that had not been monitored previously were also included. These fish were surgically implanted with acoustic transmitters from 60 to 205 days prior to the dates of diel tracking.

Model parameters.— Habitat variables were selected on the basis of (1) information of habitat use by adult catfish in the upper Mississippi River (Barko et al. 2004) and (2) the availability of variables that could be incorporated in a GIS framework. Since habitats adjacent to CMS are difficult to define spatially, I selected distance-to measurements that relate catfish locations to their proximity to CMS (i.e., distance to wing-dike (m), distance to L-dike (m), and distance to revetment (m). I included depth (m) as a habitat variable in the model to examine the hypothesis that adult catfish select deep-water habitats in LMOR.

Data analysis.—Relocations, aerial photographs, and pertinent data layers were imported into ArcView GIS 9.1 (Environmental Systems Research Institute, Redlands, California).

For every point of use, I generated five random points (available sites) within the home range of the individual (95% kernel density estimate; Chapter 2). NAIP (National Agricultural Innovation Project) aerial photographs of the Missouri River (Missouri Spatial Data Service) were used to create shapefiles of wing dike, L-dike, and revetment structures. The Near Tool was used to calculate the distances between used/available sites and CMS. A bathymetry profile of the lower Missouri River (U. S. Corps of Engineers 2007) was used identify points of elevation (measured in meters above sea level). To calculate depth on the day the fish were observed, I measured the difference in elevation between each used/available data point and the USGS gauge at Glasgow, Missouri. The difference was then used to correct the daily river stage (m) measurement at Glasgow, Missouri to calculate approximate depths of used and available sites. The Join Tool was used to join used/available point locations to the nearest depth measurement.

Table 4.1. Descriptive statistics for individuals monitored during the summer/fall period (BL=Blue; FL=Flathead).

ID	Species	Total Length (mm)	Relocations	# Available Sites	Linear Home Range (m)	95% Kernel Density Estimate (m)	Dates of 24-Hour Study
13	BL	594	21	105	36191	13572	
145	BL	617	30	150	3675	2885	9/26/2007 11/1/2007
162	BL	658	34	170	23	19	
61	BL	711	29	145	844	91	
57	BL	747	31	155	1587	694	
128	BL	625	30	150	3946	3186	
49	BL	709	27	135	37974	18322	9/26/2007 11/1/2007
54	FL	610	26	130	702	407	9/18/2007
196	FL	622	33	165	348	123	
7	FL	625	34	170	1008	307	
71	FL	714	34	170	98	43	
70	FL	726	24	120	1586	813	9/26/2007
151	FL	749	32	160	3751	1988	
37	FL	762	25	125	473	441	
44	FL	841	30	150	1350	948	
69	FL	917	33	165	1135	463	9/26/2007
65	FL	953	33	165	132	27	
66	FL	968	24	120	712	255	
53	FL	577	31	155	183	58	9/18/2007
62	FL	584	31	155	618	298	9/18/2007
40	FL	899	26	130	4000	2000	
43	FL	917	30	150	43611	7305	9/18/2007
58	FL	1062	30	150	1318	540	9/18/2007

Estimating the discrete choice model.—The discrete choice model used to predict habitat selection by flathead and blue catfish was based upon depth, distance to wing-dike, distance to L-dike, and distance to revetment. Discrete choice models (Cooper and Millspaugh 1999) are appropriate for examining habitat selection at the population level when available habitats are measured uniquely for each individual; that is, each choice set is distinct. I generated five random samples of available choices within each choice set, defined as habitat (distance to CMS, depth) available within an individual's home range. Classic discrete choice models assume that when a choice is made from each of several sets of units, a new random sample of available units is taken (Manly et al. 2002). Using home range to define my choice set, I assume that habitats found within the home range of an individual are available to that individual at every point of use.

I used a manual, forward selection procedure to determine which independent variables to include in the main-effects model. I used Akaike's Information Criteria (AIC; Burnham and Anderson 2002) to rank models, retained the model with the lowest AIC at each step, and continued adding variables provided each additional variable ranked $\Delta AIC_c > 3.0$ higher than the model without the added variable. I stopped adding variables when $\Delta AIC_c < 3.0$. Lastly, I calculated selection probabilities associated with a range of values for each parameter included in the main-effects model.

I evaluated the predictive ability of habitat selection models using a k-fold cross-validation design (Boyce et al. 2002). With discrete choice models, the probability of a site's selection is conditional on the available choice set (Cooper and Millspaugh 1999). I divided the data into 5 random subsets, each comprising approximately 20% of the choice sets, maintaining the used and available sites for each choice set. I successively removed one subset (the testing set) and refit the model using the remaining data. Validation was based on the testing set, where I fit selection probabilities to all sites in each individual's choice set. Predicted sites were identified as having the highest relative probability of those within the choice set. I assessed the model's performance by determining the percentage of used sites in the testing set that were correctly predicted.

24-hour Diel Movement Analysis.—The 24-hour datasets were analyzed in a GIS framework similar to the summer/fall dataset. Six descriptive statistics were computed for each individual including length of movement path, linear distance traversed, percent of linear home range traversed, and mean distance to habitat variables included in the discrete choice model (Table 4.4). Linear distance traversed was defined as the distance between the farthest upstream and farthest downstream movement. I compared this measurement to the linear home range of each individual (Table 4.1) to estimate the percentage of home range used during a 24-hour period.

Results

The final model's coefficients, along with their respective standard errors, *t* statistics, and *P* values, are in Table 4.2 (flathead catfish) and Table 4.3 (blue catfish). Depth (m), distance to wing dike (m), distance to L-dike (m), and distance to revetment (m) all had significant effects on the probability of selecting a site for both species. However, coefficients associated with wing-dike, L-dike, and revetment structures indicate that habitat selection varied between species.

Depth was the most significant parameter included in the main-effects model of flathead catfish habitat selection (Table 4.2). Positive coefficient values indicate that as the parameter values increases (e.g., depth), the probability of selection increases. Compared to random locations, used telemetry locations were found in areas with greater depth and closer to wing-dike and L-dike structures. Thus, the model predicts greater probability of selection with increasing depth and decreasing distance to these structures (Figure 4.3). Conversely, few individuals were relocated near revetment structure. The model predicts a lower probability of selection with decreasing distance to revetment.

Similar to flathead catfish, the blue catfish model predicts greater probability of selection with increasing depth (Table 4.3). However, used telemetry locations were found in areas closer to L-dike and revetment, as opposed to wing-dike and L-dike structures. Thus, the model predicts greater probability of selection by blue catfish with increasing depth and decreasing distance to L-dikes and revetment (Figure 4.4). Conversely, the model predicts a lower probability of selection with decreasing distance to wing-dike structures.

With regard to model validation, the flathead catfish and blue catfish model of habitat use had fair predictive ability, correctly classifying 74% and 62% of the used territories, respectively.

Table 4.2. Parameterization and output for the final discrete choice model for site selection by flathead catfish.

Variable	DF	Coefficient	SE	*t* value	*P*
Depth	1	0.4153 ± 0.058	0.0291	14.28	<0.0001
Distance to					
Wing Dike	1	-0.003 ± 0.001	0.0005	-6.44	<0.0001
L-Head Dike	1	-0.001 ± 0.0004	0.0002	-5.63	<0.0001
Revetment	1	0.0015 ± 0.0006	0.0003	5.01	<0.0001

Table 4.3. Parameterization and output for the final discrete choice model for site selection by blue catfish.

Variable	DF	Coefficient	SE	*t* value	*P*
Depth	1	0.4978 ± 0.095	0.0473	10.52	<0.0001
Distance to					
Wing Dike	1	0.0034 ± 0.001	0.0006	5.46	<0.0001
L-Head Dike	1	-0.001 ± 0.0006	0.0003	-3.68	0.0002
Revetment	1	-0.002 ± 0.001	0.0005	-3.9	<0.0001

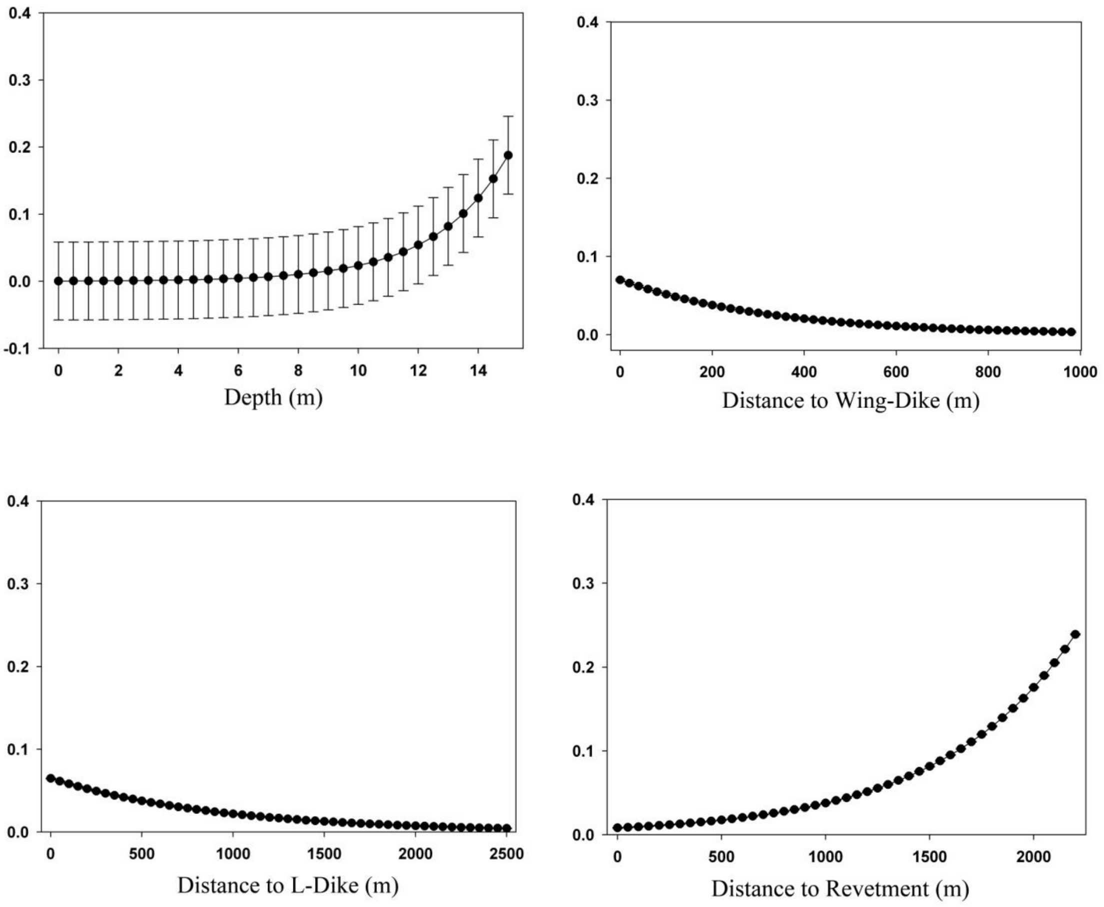

Figure 4.3. Selection probabilities associated with habitat variables for flathead catfish. The Y-axes represent selection probabilities that range between 0 and 1.0. Scale was standardized with the exception of distance to revetment (right side); here, selection probabilities were much higher than all others. Error bars represent two times the standard error; these cannot be viewed in many graphs since error was extremely low (<0.001).

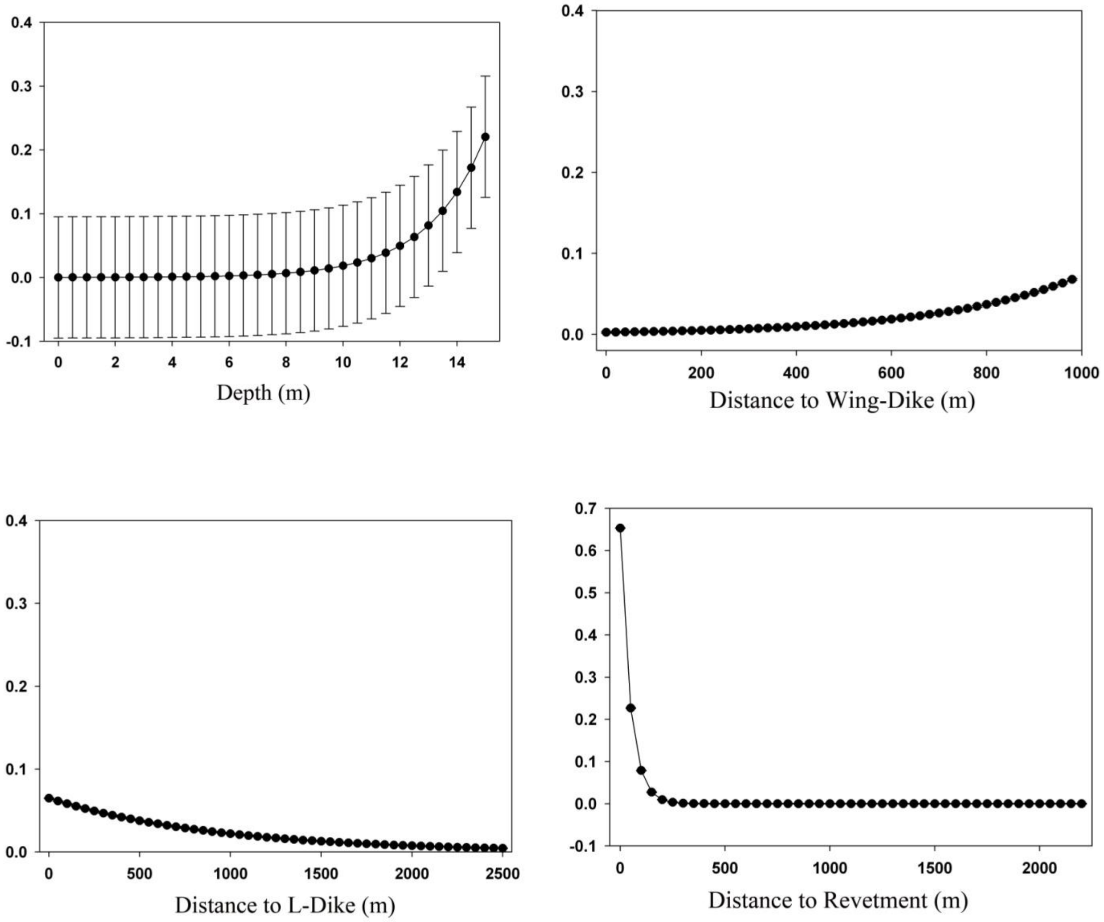

Figure 4.4. Selection probabilities associated with habitat variables for blue catfish. The Y-axes represent selection probabilities that range between 0 and 1.0. Scale was standardized with the exception of distance to revetment (right side); here, selection probabilities were much higher than all others. Error bars represent two times the standard error; these cannot be viewed in many graphs since error was extremely low (<0.001).

24-hour Diel Movements.—Data collected on eight flathead and five blue catfish during a 24-hour period are presented in Table 4.4. During 18 and 26 September 2007, individuals of both species remained around habitat types (i.e., wing-dike, L-dike, revetment) where they were relocated during the summer/fall period (weekly/daytime relocations). During both periods, overall movement was low (mean length of movement path - 180 m). Three flathead catfish and two blue catfish (ID 43, 58, 70; Table 4.4) traversed a small portion of their summer/fall home range (0.1–4.6%). Four flathead catfish (ID 53, 54, 62, 69) traversed a much greater portion of their home range (11.5–45.5%), although their home ranges were more restricted (183–1135 m; Table 4.1). During 11 November 2007, overall movement was 23 times greater than during September sampling (mean length of movement path – 4165 m). One blue catfish (ID 145) remained in the same area where it was monitored during 26 September, and showed no increase in movement. Movement of another blue catfish (ID 4) was 100-times greater in November than September. Another blue catfish (ID 49) traversed 15% of its summer/fall linear home range (37974 m). Between 1900 and 1000 hours, this individual moved 5545 m upstream, leaving one of two core areas (50% kernel estimate; see Chapter 2) established during the summer/fall period. At 0822 and 0943 hours (end of 24-hour tracking cycle), this individual was relocated adjacent to revetment structure in a location not previously recorded. Comparing the 24-hour to the summer/fall dataset, only one individual (ID 49) differed between daytime and nighttime movement behavior.

Table 4.4. Descriptive statistics for flathead and blue catfish monitored during a 24-hour diel period. Shaded data is from individuals that were monitored during two 24-hour periods. Asterisk denotes individuals that were not included in the summer/fall dataset.

Date	ID	Species	Total Length (mm)	Length of Movement Path (m)	Linear Distance Traversed (m)	% of Linear Home Range Traversed	Mean Distance to Wing Dike (m)	Mean Distance to L-Dike (m)	Mean Distance to Revetment (m)
9/18/2007	53	FL	577	83	21	11.5	74	14	176
	62	FL	584	289	281	45.5	176	244	210
	54	FL	610	183	142	20.2	318	16	258
	58	FL	744	204	61	4.6	26	332	244
	43	FL	917	278	172	0.4	268	20	1120
9/26/2007	145	BL	617	71	24	0.7	19	354	363
	4*	BL	692	142	75	Insuff. Data	328	17	217
	49	BL	709	71	26	0.1	262	11	16
	70	FL	726	86	24	1.5	228	402	398
	69	FL	917	392	185	16.3	221	435	355
11/1/2007	145	BL	617	73	24	0.7	24	360	370
	4*	BL	692	6703	7590	Insuff. Data	228	186	701
	49	BL	709	5887	5545	14.6	229	471	1415
	3*	BL	921	4143	3701	Insuff. Data	382	586	873
	2*	BL	1156	172	48	Insuff. Data	345	33	515
	126*	FL	747	3845	3566	Insuff. Data	157	850	324

Discussion

Historic information suggests that the Missouri River channel once had a high density of large woody debris (LWD; Funk and Robinson 1974; Mestle and Hesse 1993; Hanson 2003). In the now highly-regulated Missouri River, delivery of LWD to the channel and establishment of new riparian forest stands are both greatly reduced because the river and its floodplain are ecologically uncoupled (NRC 2002; Angradi et al. 2004). Past research in the Mississippi and Missouri Rivers suggests that anthropogenic structures may act as surrogate habitat for natural features that were removed during channelization (Barko and Herzog 2003; Barko et al. 2004). In this study, the final habitat selection models for flathead and blue catfish support the hypothesis that adult catfish select habitats adjacent to CMS during the summer/fall period. The final models for flathead and blue catfish demonstrate depth as an important variable related to site selection. Individuals of both species were found adjacent to CMS, often in deep scour holes associated with wing-dike/L-dike features and in deeper areas of main-channel habitat associated with revetment along outside bends. In the lower Mississippi River, algal blooms and thermal stratification occur in lentic dike pools during warmer months with associated changes in water quality: oxygen supersaturation occurs in surface waters with anoxia in deeper regions (Beckett and Pennington 1986; Baker et al. 1991). In such cases, catfish may seek out a thermal regime ideal for growth and fitness. However, such areas are uncommon in LMOR; CMS used by individuals in this study are broadly connected to the main channel and adjacent waters are not thermally stratified.

With regard to model validation, the flathead catfish and blue catfish model of habitat use had fair predictive ability, correctly classifying 74% and 62% of the used territories, respectively. I speculate that the performance of these models may improve with the inclusion of other habitat variables that covary with depth and proximity to CMS. Deep scour holes (>5 m) downstream of dike structures provide refuge from flow which minimizes energy expenditure while at rest. Backwater habitat downstream of dike structures may also provide a high abundance of potential prey items. Slower-velocity habitats associated with wing-dikes promote benthos production and create microhabitats suitable for early life stages of some species in the unimpounded upper Mississippi River (Barko et al. 2004). In LMOR, Jennings (1979) showed an increase in benthos production related to low-velocity backwaters and documented more than 40 species of fish in backwater habitat associated with dike structures. Thus, substantial evidence supports the hypothesis that CMS provide a potential food base for adult catfish. Since the post-spawn period is a time when energy is devoted to feeding and growth, I speculate that CMS may provide ideal foraging sites which maximize the opportunity for food and provide low-velocity habitat to minimize energy expenditure. Though the utility of CMS to adult catfish remains speculative in this study, the model is informative to the degree that habitats associated with CMS are selected by adult catfish during a time period of increased feeding activity and growth.

The discrete model for flathead catfish predicts that selection probabilities increase around wing-dikes and L-dikes and decrease around revetment (Figure 4.3). One individual flathead (968 mm TL) spent approximately 80% the summer/fall period (20 of 24 relocations) around revetment structure and the remaining 15 individuals frequented habitat associated with dike structures. These results are consistent with Pflieger (1997), who suggested that flatheads occur more frequently in backwater habitats than those associated with swifter water. Others have shown habitat selection for natural features such as log jams (Vokoun 2003), which are also associated with low-velocity current. Log jams and woody debris are common features associated with wing-dikes and L-dikes in LMOR; thus, smaller-scale habitat features associated with CMS that I did not measure may be partially responsible for the selection of these sites.

The discrete model for blue catfish predicts that selection probabilities increase around L-dikes and revetment and decrease around wing-dikes. Blue catfish showed strong selection for revetment structure as evidenced by the selection probabilities plotted in Figure 4.4. With respect to habitat use, revetment is synonymous with the main channel when fishes use the deepest water at the base of revetment structure (outside edge of thalweg). Jenkins and Burkhead (1994) suggest that blue catfish prefer swift channels and flowing pools and Mettee et al. (1996) reported large specimens in swift, tailwater current below dams. In this study, blue catfish were typically found closer to the thalweg and in swifter current than flathead catfish occupying the same habitat type.

The spatial orientation of CMS is an important consideration with regards to methods. I used distance-to measurements rather than categorical habitat variables given that the area around CMS does not have discrete boundaries suitable for classifying habitat patches. In LMOR, wing-dike structures are traditionally built opposite to L-head and revetment structure that work cooperatively to divert water to the thalweg. Therefore, an individual selecting a wing-dike is often the maximum distance from other available structures. This may partially explain why the model for both species indicated negative selection for structures that were clearly selected by a few individuals. This same scenario would occur in a wildlife habitat selection study if individuals selected two discrete habitat types that were separated by a large area of available habitat that was rarely used.

An important consideration of any study is the potential bias imposed by sampling coupled with animal behavior. A high proportion of flathead catfish (24 of 40) and blue catfish (33 of 40) tagged in 2007 were not incorporated in this study; I only included individuals that were monitored on a biweekly basis within my 93-km sampling reach. Thus, my habitat use data is biased in favor of individuals that display restricted, nonmigratory behavior. During a study of seasonal movement and migration patterns in 2006, 5 of 39 (13%) blue catfish and 6 of 32 (19%) flathead catfish moved greater than 100 km from where they were originally tagged with a maximum distance recorded of 377 km and 752 km, respectfully (see Chapter 2). Individuals in this study displayed nonmigratory behavior during the summer/fall period in 2007 and established home range that did not exceed 40 km. However, the long-range movements occurred primarily in May and June prior to the summer/fall period; thus, I view these movements as migratory and not necessarily related to habitat selection at smaller spatial scales.

Given the hazards of nighttime telemetry work on LMOR, I was unable to incorporate even coverage of the 24-hour clock in the summer/fall dataset. This is particularly important to this study since flathead and blue catfish are presumed to be nocturnal (Pflieger 1997) with the majority of feeding activity occurring at night (Skains 1992). However, diel movement patterns have only been documented for flathead catfish in the Grand and Cuivre River (Vokoun and Rabeni 2006). I documented a 20-fold increase in diel movement between September (mean length of movement path - 180 m) and November (mean length of movement path – 4165 m). This may partially be explained by the inclusion three individuals (ID 2, 3, 126; Table 4.4) that were not monitored frequently during the summer/fall period (< 5 relocations), likely due to high mobility. However, two blue catfish (ID 4, 49) showed dramatic increases in movement between 26 September and 1 November (over 100 times greater length of movement path). Water temperature recorded during these periods indicated a large decrease between September (20.6–24.3 °C) and November (12.8–13.3 °C) sampling. Seasonal shifts in movement behavior are likely cued by decreases in food availability. The fall season in temperate rivers is characterized by a decrease in primary productivity related to photoperiod and a decrease in abundance of young-of-the-year (Matthews 1997). As food becomes scarce, catfish may have to travel greater distances to meet biological requirements prior to seeking winter refuge.

The effects of habitat alteration on riverine fishes may be scale dependent (White et al. 2009). At larger spatial scales such as river reaches and watersheds, habitat alteration lowers biodiversity (Karr et al. 1985; Wang et al. 2001), decreases habitat availability through backwater and floodplain sedimentation (Gore and Shields 1995; Shields et al. 1995) and is associated with reduced growth and abundance of fishes (Hesse and Mestl 1993; Galat et al. 2005; Paukert and Makinster 2009). At smaller spatial scales, engineered structures may be associated with increased abundance and biomass of riverine fishes and provide habitat that is similar to natural habitats such as woody debris (Shields et al. 1995; Barko et al. 2004; White et al. 2009).

This study adds to a growing body of evidence that suggests that habitats associated with CMS act as surrogate habitat for natural features that were removed by river modifications and channel maintenance. To examine this hypothesis further, future research may seek to incorporate additional environmental and biological variables (e.g., flow velocity, turbidity, substrate, species composition and abundance) that provide a better linkage between habitat-use patterns and ecological value. Without a better understanding of the utility of CMS and associated environmental variables, modifications to existing structures may fail to improve conditions that promote feeding and growth of adult catfish.

Chapter 5

Physiological Evidence of Spawning of Flathead and Blue Catfish in the Lower Missouri River

Dryland, alluvial rivers in the Midwest are characterized by low water clarity which precludes direct observations of spawning activity. Researchers are increasingly incorporating physiological information to indirectly assess spawning. Seasonal levels of sex steroids such as testosterone and estradiol are correlated with growth of testes and ovaries, respectively. Peak hormone concentrations generally occur just before the spawning season (Simpson and Wright 1977; Wingfield and Grimm 1977; Campbell et al. 1980). By coupling physiological indicators of spawning with telemetry data, potential spawning sites can be determined in lieu of direct observation. Spawning of *Scaphirhynchus* sturgeon was recently evaluated in the lower Missouri River using this approach (Delonay et al. 2007; Wildhaber et al. 2007). In this study, I used movement data and physiological indicators to identify discrete locations in the lower Missouri River (LMOR; downstream of Gavins Point Dam) that are likely used by flathead and blue catfish to complete the spawning cycle.

Common among organisms, fishes have evolved internal rhythms (e.g., circadian, circannual, and circalunar) that regulate the timing of physiological changes related to reproduction (Pflieger 1997; Randall et al. 1997). Environmental factors such as photoperiod, water temperature, and discharge are known to entrain these internal rhythms in fishes, including the pattern of hormone release which controls the timing of reproduction (Orlando et al. 2003). Further, environmental factors serve as cues to fish and enable the synchronization of gametogenesis, mating, and, in some species, parental care (Sumpter 1990). Interpretation of these environmental cues and control of reproductive timing is mediated by the nervous and endocrine systems (Sumpter 1990).

Flathead and blue catfish are known to spawn during summer months when stream flows have stabilized within main channels (Pflieger 1997) and temperatures reach 19–24 °C (Henderson 1965; Henderson 1972; Turner and Summerfelt 1971; Pflieger 1997). Thus, anthropogenic activities that alter the timing and duration of spring flood pulses may have direct impacts on fish spawning. Intensive management of the Missouri River for purposes of navigation, flood control, and power generation has resulted in dramatic physical changes to the river corridor and flow regime (Galat and Lipkin 2000). The lower Missouri river (LMOR; downstream of Gavins Point Dam) has been modified from a braided channel to a low-sinuosity meandering channel, and water surface has been reduced by 50–70% (Hallberg et al. 1979; Shields 1995; Galat and Lipkin 2000). These activities have been associated with changes in the native fish assemblage, most notably a decline of native sturgeon and chub species (Cross and Moss 1987; Funk and Robinson 1974; Hesse and Sheets 1993 Galat et al. 2005). Research from several large, regulated rivers suggests that decline of native fishes may be due to (1) altered flow regime which alters the timing of cues and reproduction; (2) loss of connectivity between the floodplain and the main channel; (3) a reduction of suitable spawning areas or flows for adults; (4) a reduction of suitable nursery areas for recruitment of young (Gehrke et al. 1995; Jurajda 1995; Humphries and Lake 2000; Aarts et al. 2004).

Spawning in freshwater fishes occurs over a relatively limited portion of the year and requires aggregation of adults of both sexes. Freshwater fishes exhibit spawning movements to reach suitable habitats where environmental conditions such as temperature, current velocity, substrate type, and cover promote high survival of eggs and newly-hatched young (Northcote 1984). Upstream migrations are most common, and may help to offset the downstream drift or translocation of young life-stage fishes, or enhance their dispersal over a range of appropriate habitats (Reynolds 1983; Northcote 1984; Lucas and Baras 2001). Ultimately, movement behavior during this period relates to the spatial distribution of appropriate spawning habitat, relative to feeding and refuge areas for adults (Lucas and Baras 2001). In large-river systems, the range of appropriate spawning habitats for adult catfish remains unclear. Movement data from the Grand River, Missouri suggests that many flathead catfish migrate from LMOR (mainstem) to tributary habitats to complete the spawning cycle (Vokoun and Rabeni 2005a). However, sampled individuals in this study remained in LMOR throughout the spawning period. The variation in movement behavior suggests that catfish spawning may be associated with large-river habitats that have not been previously examined.

Flathead and blue catfish are best described as K-selected equilibrium strategists having relatively modest numbers of large eggs (<150,000; Colehour 2009) and parental care to insure high survival during the first couple weeks of development. After spawning, males remain on the nest and use fin movements to keep eggs oxygenated and free of sediment (Pflieger 1997). Males also aggressively defend the eggs (Cross 1967) and guard the newly hatched young for a few days before vacating the nest (Pflieger 1997). Both species are known to select protected nesting sites such as hollow logs, excavated caves in clay banks, and root masses from downed trees which enhance their ability to provide parental care (Bobea 1989; Francis 1993; Graham 1999). In large reservoirs, flathead catfish may also select nest sites in secluded rock outcroppings or submerged timber (Turner and Summerfelt 1971).

Historic information suggests that the Missouri River channel once had a high density of large woody debris (LWD; Funk and Robinson 1974; Mestle and Hesse 1993; Hanson 2003). In the now highly-regulated Missouri River, delivery of LWD to the channel and establishment of new riparian forest stands are both greatly reduced because the river and its floodplain are ecologically uncoupled (NRC 2002; Angradi et al. 2004). Likely spawning sites for flathead and blue catfish, such as cavities in undercut banks and large woody debris, are available in tributaries to large, channelized rivers such as LMOR in which natural features have largely been removed. Not surprisingly, many catfish that reside in LMOR travel to and from tributaries, presumably to complete the spawning cycle (Dames et al. 1989; Vokoun and Rabeni 2005a). Among the Missouri, Grand, and Cuivre Rivers, Vokoun and Rabeni (2005a) identified three pathways through which flathead catfish complete an annual cycle. Fish overwintered in LMOR until mid-March when temperatures rose above 10°C at which point they entered a tributary and moved upstream. The reproductive maturity of these fish coupled with the seasonality of movements suggests that flathead catfish spawn in tributaries of LMOR. Anecdotal evidence from 2007 sampling in the Lamine, Platte, and Grand River suggests that abundance of adult catfish increases in tributaries of LMOR during the spawning period (Zach Ford, MDC, pers. comm.).

This study is a component of a larger investigation of catfish movement, migration, and habitat use that spanned two annual cycles from April 2006 to March 2008. During the spawning periods in these years (May 15–July 15), 22 of the 157 individuals tagged in a 97-km reach of LMOR (river miles 195–255) migrated up one of four major tributaries (3–8th order) that flow into the 93-km sampling reach. Although the proportion of individuals that used a tributary increased from 10% (8 of 77) in 2006 to 18% (14 of 80) in 2007, the majority of individuals remained in LMOR throughout the spawning period during both years. Given that only sexually mature individuals were tagged, I hypothesized from the movement data that individuals seek habitats within the mainstem Missouri River, rather than tributaries, to spawn (see Chapter 2).

To examine this hypothesis, I monitored movement and physiological changes of flathead and blue catfish to determine if spawning took place in LMOR. In female teleosts, growth of oocytes is principally dependent on the accumulation of yolk which is a function of estrogen-dependent vitellogenin synthesis by the liver (Korgaard and Peterson 1979). Thus, estrogen levels generally peak just before the spawning season as oocytes develop, and drop significantly prior to spawning. In male teleosts, seasonal testosterone levels parallel changes in the testicular cycle and GSI (gonadal-somatic index) values with increases in testosterone levels coinciding with active spermatogenesis. Since testosterone is an intermediate product in the synthesis of 11-ketotestosterone, levels of testosterone peak before levels of 11-ketotestosterone (Matty 1985). Similar to estrogen levels in females, hormone concentrations in males peak prior to spawning (Simpson and Wright 1977; Wingfield and Grimm 1977; Campbell et al. 1980) and drop significantly after. By comparing hormone levels of individuals between initial capture and recapture, I was able to determine whether spawning took place during this time period. Specific objectives were to (1) evaluate changes in sex steroids related to gonad development, (2) evaluate weight losses to provide additional evidence of spawning, and (3) use movement data of designated “spawners” to determine potential spawning sites in LMOR.

Methods

Forty flathead and 40 blue catfish were tagged in a 97-km reach of the lower Missouri River (river miles 195-255) in April and July 2007 as part of a 2-year investigation examining movement patterns and habitat selection (see Chapter 1 for details). No fish < 560 mm total length was implanted with transmitters to insure that all fish sampled were sexually mature. Blue catfish in Missouri are reported to reach sexual maturity at about 380 and 420 mm in the Mississippi River and Lake of the Ozarks, respectively (Barnickol and Starrett 1951; Graham and DeiSanti 1999). Female flathead and blue catfish from the middle Mississippi River (between Hannibal and Cape Girardeau) greater than 426 and 508 mm TL, respectively, had mature ovaries with egg production (Colehour 2009).

Upon initial capture of all individuals in April and early July, a blood sample was taken and stored for hormone comparisons. During eight days in July (12, 17, 20, 21, 26) and August (2, 8, 15), attempts were made to recapture individuals that remained within the 97-km sampling reach and resample blood of each to compare pre- and postspawn levels of sex steroids. After an individual was relocated to the nearest 5 m via acoustic telemetry, a low-frequency DC electrofishing (15-30 Hz) boat was positioned over the tagged fish. A second chase boat was used to aid with netting efforts. Recapture success via this method averaged 23% over 8 days of sampling, with a total of eight flathead and four blue catfish recaptured and sampled. One flathead and one blue catfish were recaptured twice (Table 5.1).

Blood extraction.— A 6 mL blood sample was collected from the caudal vein using a 20 gauge needle and a 10-cc syringe coated with heparin to prevent clotting. Blood was transferred into a 10 mL vaccutainer (coated with heparin) for short-term cold storage. At the end of each sampling day (1600–1800 hours), blood samples were centrifuged at 3500 RPM for 10 minutes to separate plasma from red blood cells. Blood plasma was transferred into three cryovials using a disposable pipet and placed into a cooler with dry ice and later stored in a –80°C freezer at the USGS Columbia Environmental Research Center (CERC) laboratory in Columbia, Missouri.

Extraction and analyses of Estradiol (E2) and Testosterone (T).—Laboratory analyses were conducted at CERC following protocols outlined by Craig et al. (2009). Plasma samples for steroid analyses were extracted using diethyl ether to separate steroids bound to proteins. The steroid-containing ether phase was quick-frozen on dry ice, and the resulting supernatant was placed in a 30 °C water bath and evaporated under nitrogen. The steroid residues were then reconstituted in phosphate buffered saline with 1% gelatin (PBSG, pH 7.0) and stored at –20 °C until assayed.

E2 and T were assayed using the RIA method (McMaster et al. 1992). Steroid concentrations were determined through competition of the standard or extracted sample and a constant amount of radiolabeled steroid using a fixed antibody titer. Extracted samples were incubated with the antibodies and radiolabeled steroid overnight at 4 °C. The following day, a chilled solution of dextran-coated activated charcoal in PBSG (0.4% dextran, 0.625% charcoal) was added and allowed to incubate before centrifugation at 0 °C for 20 min at 2800 rpm. A portion of the resulting supernatant was added to a scintillation vial containing 5 mL of scintillation cocktail (EcoLume®; Fisher Scientific, Pittsburgh, PA, USA). A scintillation count was performed, with the resulting values showing the amount of antibody bound to labeled steroid, which is inversely proportional to the amount of free steroid in the sample. A standard curve of a known serial dilution of each hormone was used to calculate steroid concentrations in the unknown samples. Results are expressed as picograms (pg) of steroid ⁄ mL of blood plasma.

Extraction and analyses of 11-Ketotestosterone (KT).—KT was assayed similar to E2 and KT using the radioimmunoassay method (McMaster et al. 1992) following protocols outlined by Wildhaber et al. (2007). Steroid concentration was determined through competition of the standard or sample KT and a constant volume of radiolabeled steroid for a fixed titer of antibody. Extracted samples were incubated with radiolabeled steroid (Amersham Biosciences) overnight at 4 °C. The following day a chilled solution of dextran-coated activated charcoal in PBSG (0.4% dextran, 0.625% charcoal) was added and allowed to incubate before centrifugation at 0 °C for 20 min at 1600 g. A 500-µL portion of the resulting supernatant was added to a scintillation vial containing 5 mL of scintillation cocktail (Ecolume®). Radioactivity was determined by scintillation spectroscopy with the resulting values showing the amount of antibody bound to labeled steroid, which is inversely proportional to the amount of free steroid in the sample. A standard curve of a serial dilution of KT standard (Sigma-Aldrich, MO, USA) was used to allow calculation of steroid concentrations in the unknown samples.

Sex Determination.—A ratio of E2 to T is commonly used to evaluate sex steroid data (Folmar et al. 1996; Goodbred et al. 1997; Ceapa et al. 2002) given that females typically have more E2 than T (i.e., E2 ⁄ T > 1.0) and males typically have more T than E2 (i.e., E2 ⁄ T < 1.0). However, the range of this value for an individual can vary widely depending on reproductive condition (Craig et al. 2009). In this study, an individual was determined male or female according to concentrations of plasma and the E2/T ratio. Since little is known with regard to these species, an E2/T ratio of 1.0 was used as the threshold between males and females, with females predicted to have an E2/T ratio greater than 1.0 (see also Craig et al. 2009). When capture and recapture E2/T ratios contradicted one another, the individual sex is reported as unknown (Figure 5.1).

Determinants of Reproduction.—To assess spawning activity during the spawning period (May 15 – July 15, 2007), I compared prespawn (sample from initial capture) and postspawn (recapture) levels of sex steroids (Table 5.1). Females that demonstrated a drop in estradiol concentration between initial capture and recapture were designated as putative spawners (Figure 5.1; see also Manosroi et al. 2003; Wildhaber et al. 2007). I measured both T and KT levels in males to evaluate their utility in determinations of spawning condition. Both have been used to monitor seasonal hormonal changes that correlate with reproductive condition in males (Stoekel and Burr 1999). A measurable drop in T between prespawn and postspawn samples was used as evidence of spawning in the individual males I sampled (see also Manosroi et al. 2003; Wildhaber et al. 2007).

To provide additional confirmation that spawning occurred, weights of individuals were compared between initial capture and recapture times (Table 5.2). Colehour (2009) reports the gonadosomatic index (GSI = ovary weight / body weight * 100) of female flathead and blue catfish from the Mississippi River between Hannibal and Cape Girardeau, Missouri. Using this regional GSI information, I plugged in the weights of individuals I sampled and solved for the expected ovary weight. Based on this calculation, I expected to see weight losses resulting from egg release of 0.25–0.45 kg for females weighing <10 kg and 0.74–0.98 kg for females weighing >10 kg. Further weight loss and poor body condition may also result from a lack of feeding during the spawning period (Matthews 1998).

I recorded water depth (m) at each fish relocation using onboard sonar equipment by Lowrance®. If an individual was found in close proximity (< 3 m) to a specific habitat feature (e.g., log jam, secondary channel, dike structure) I recorded field observations to provide some basic information about the habitat used by catfish during this time period.

Results

Sex Determination.—Sex assignments based on plasma indicator criteria were made for nine of the 12 individuals assayed (Table 5.1). The remaining three individuals could not be confidently sexed based on the plasma criteria. Transmitters were implanted in the abdominal cavity through a small ventral incision (35–40 mm) approximately half way between the pectoral and pelvic fins. Thus, the accuracy of laboratory-identified sex assignment was not scrutinized because gonads could not be inspected in the field. However, sex determination of putative spawners was made with high confidence given that E/T ratios of assigned females exceeded 5.0 upon initial capture (Table 5.1).

Assessment of Putative Spawning between Captures.—Measured concentrations of KT were low relative to E2 and T and showed little change between initial captures (April 20 – July 5, 2007) and recaptures (July 12 – August 8, 2007; Table 5.3). Thus, T was chosen as the androgen to evaluate hormonal changes in male and females. Eight of 12 individuals sampled showed a measurable drop in levels of E2 and T between initial capture and recapture and were designated as putative spawners (Table 5.1). The remaining four individuals did not show a measurable drop in both hormones, and were designated as putative non-spawners. All individuals weighing >10 kg demonstrated a loss of weight (0.49–2.71 kg) between capture and recapture (N=4; Table 5.2). One individual flathead weighing <10 kg (6.03 kg) also lost weight (0.45 kg; ID 37). The remaining three putative spawners weighing 2–4 kg at initial capture gained weight (0.07–0.67 kg) between capture and recapture. The four putative non-spawners weighing 2–6 kg also gained weight (0.29–0.76 kg) between capture and recapture (Table 5.2).

Two individuals were recaptured twice in July and August, allowing for an additional blood sample of each to be included in analyses (Table 5.1). Hormone levels dropped between April and July sampling but increased between July and August.

However, hormone levels in August remained well below hormone levels recorded before the spawn in April (Table 5.1).

Table 5.1. Species, identification number, sex (M=male, F=female, U=unknown), number of relocations, sampling dates, and sex steroid concentrations for flathead and blue catfish monitored via acoustic telemetry in a 97-km reach of the lower Missouri River.

Species	ID	Sex	Total Length (mm)	Number of Relo-cations	Sampling Date	Estradiol (pg/mL)	Testosterone (pg/mL)	Habitat Features At Shallow-Water Relocation Sites (<3 m)
Putative Spawners								
Flathead	19	F	584	10	4/20/2007	765.3	397.0	Flooded grass behind rock L-head dike
					7/17/2007	239.5	179.0	
Flathead	66	F	968	9	4/24/2007	8747.6	1193.4	Clay bank behind L-head dike
					7/20/2007	209.3	62.2	
Flathead	69	F	917	8	7/5/2007	97073.9	4669.3	Seconary channel behind rock wing-dike
					8/2/2007	130.7	67.2	
Flathead	58	U	1062	2	4/24/2007	227.1	229.7	Log jam in secondary channel behind rock wing-dike
					7/26/2007	131.6	102.0	
Flathead	37	F	762	3	4/23/2007	1908.2	359.6	Relocations around deep habitat (>3 m) associated with rock-wing dikes, rock L-head dikes, and revetment
					7/12/2007	112.4	70.2	
					8/8/2007	249.3	213.1	
Flathead	65	F	1191	9	4/24/2007	34409.0	623.6	
					8/2/2007	163.4	82.3	
Blue	49	M	709	8	4/24/2007	187.5	837.2	
					7/12/2007	187.8	228.5	
					8/2/2007	250.2	476.6	
Blue	128	U	625	4	7/5/2007	230.6	287.6	
					7/21/2007	192.8	114.9	
Putative Non-Spawners								
Flathead	53	M	577	11	4/24/2007	117.5	185.8	
					7/26/2007	192.0	228.1	
Flathead	54	F	610	8	4/24/2007	282.7	85.7	
					7/12/2007	295.2	78.0	
Blue	34	F	808	9	4/23/2007	245.0	140.2	
					7/12/2007	293.3	181.1	
Blue	13	U	594	10	4/20/2008	392.4	187.7	
					7/12/2007	187.7	548.6	

Table 5.2. Weights (kg) of flathead and blue catfish captured, tagged (April 20 – July 12, 2007) and recaptured (July 12 – August 8, 2007) in the lower Missouri River.

Species	ID	Sex	Tagged Weight (kg)	Recapture Weight (kg)	Weight Difference (kg)
Putative Spawners					
Flathead	58	Unknown	16.85	14.14	-2.71
Flathead	66	Female	12.35	11.86	-0.49
Flathead	65	Female	12.28	10.55	-1.73
Flathead	69	Female	10.38	9.7	-0.68
Flathead	37	Female	6.03	5.58	-0.45
Flathead	19	Female	2.4	2.63	+0.23
Blue	49	Male	3.61	4.28	+0.67
Blue	128	Unknown	2.39	2.46	+0.07
Putative Non-Spawners					
Flathead	54	Female	2.61	2.9	+0.29
Flathead	53	Male	2.11	2.87	+0.76
Blue	34	Female	5.11	5.76	+0.65
Blue	13	Unknown	2.12	1.83	-0.29

Table 5.3. Changes in concentrations of sex steroids between initial capture (April 20 – July 5, 2007) and recapture (July 12 – August 8, 2007) of flathead and blue catfish in a 97-km reach of the lower Missouri River. Data represent mean and standard errors.

Sample	N	Estradiol (pg/mL)	Testosterone (pg/mL)	11-ketotestosterone (pg/mL)
Flathead Catfish (Prespawn Capture)	8	17941 ± 34044	968 ± 1535	43 ± 37
Flathead Catfish (Recapture July-Aug)		184 ± 62	108 ± 61	55 ± 109
Blue Catfish (Prespawn Capture)	4	263 ± 89	363 ± 321	401 ± 621
Blue Catfish (Recapture July-Aug)		215 ± 52	268 ± 192	281 ± 246

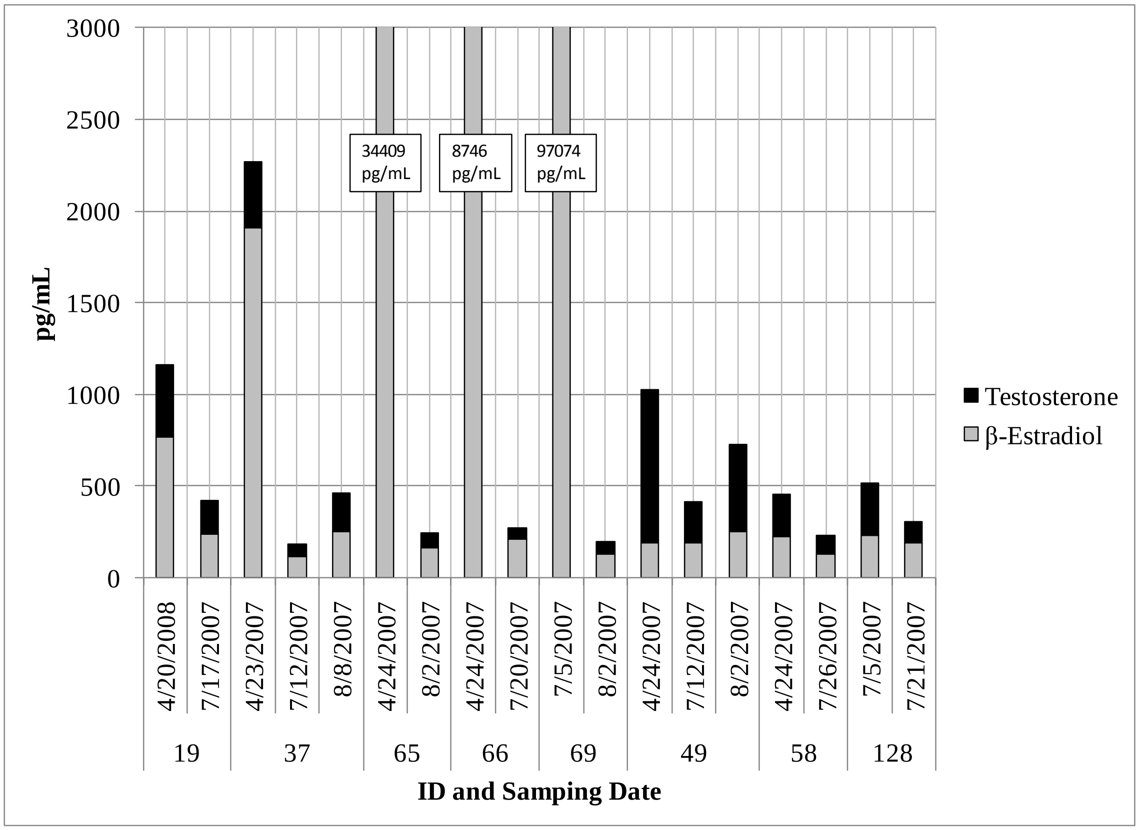

Figure 5.1. Concentrations of testosterone (pg/mL) and estradiol (pg/mL) for spawning flathead and blue catfish in a 97-km reach of the lower Missouri River.

Discussion

The flathead and blue catfish I sampled appear to support the hypothesis that catfish use the mainstem Missouri River to spawn. Substantial decreases in body weight and levels of sex steroids between initial capture and recapture indicated that eight of 12 individuals spawned. Further, the seasonal tributary use I recorded during a parallel study in 2006 (10%; 8 of 77) and 2007 (18%; 14 of 80) suggests that a large majority of catfish may remain in the mainstem Missouri River throughout the spawning cycle (see Chapter 2).

Although I cannot determine the specific time and place of spawning, the shallow-water relocations (<3 m) I recorded provide some basic information about where catfish were relocated in LMOR (Table 5.1). Two locations were downstream of wing-dike structures and two were downstream of L-dike structures. L-dikes generally provide greater flow refuge than straight-arm wing-dikes because their trailing downstream arm deflects river flows from outside the structure back towards the thalweg and protects the low-flow area inside the structure. In turn, L-dikes are characterized by slower current velocities and smaller substrate particles than wing-dikes (Ridenour et al. 2009). I cannot speculate about the utility and function of dike structures without direct observation of spawning.

Individuals were primarily captured in April because sampling efforts in the mainstem Missouri River proved ineffective until water temperatures rose to 10–15 °C and catfish became more mobile and susceptible to capture. Thus, flathead catfish that migrate up adjacent tributaries as early as March (i.e., Vokoun and Rabeni 2005a) were not sampled using this design. If the life-history strategies I documented represent evolutionary strategies (see Chapter 2), then the individuals I tagged may represent multiple subpopulations that rely on different areas of the watershed to complete the spawning cycle. The eight putative spawners I identified displayed restricted-movement behavior in LMOR throughout the prespawn/spawning period (see Chapter 2). Thus, these results only address spawning characteristics of nonmigratory catfishes in the Missouri River.

Hormone profiles of catfish are difficult to interpret given their protracted spawning season that varies by latitude. Both species spawn when water temperatures reach 19–24 °C and river flows stabilize (Henderson 1965; Henderson 1972; Turner and Summerfelt 1971; Pflieger 1997). For blue catfish, ideal spawning conditions may occur as early as April in Louisiana (Perry and Carver 1973) and as late as July in Iowa (Harlan et al. 1987). Consequently, levels of sex steroids associated with spawning condition have been shown to vary greatly within and among ictalurid species (Stoeckel and Burr 1999). In Missouri, both species are thought to spawn primarily in June and early July (Pflieger 1997). During the spring of 2007, ideal spawning temperatures (19–24 °C) were reached in May 2007, although river flows did not stabilize until June (Figure 5.2). In April 2007, I recorded high variability in prespawn levels of estradiol and testosterone in putative spawners (Table 5.3). Thus, gonadal development was likely variable at the time of capture and anecdotally suggests that spawning of individual fish occurred at different times between capture (April-early July) and recapture (early July-early August).

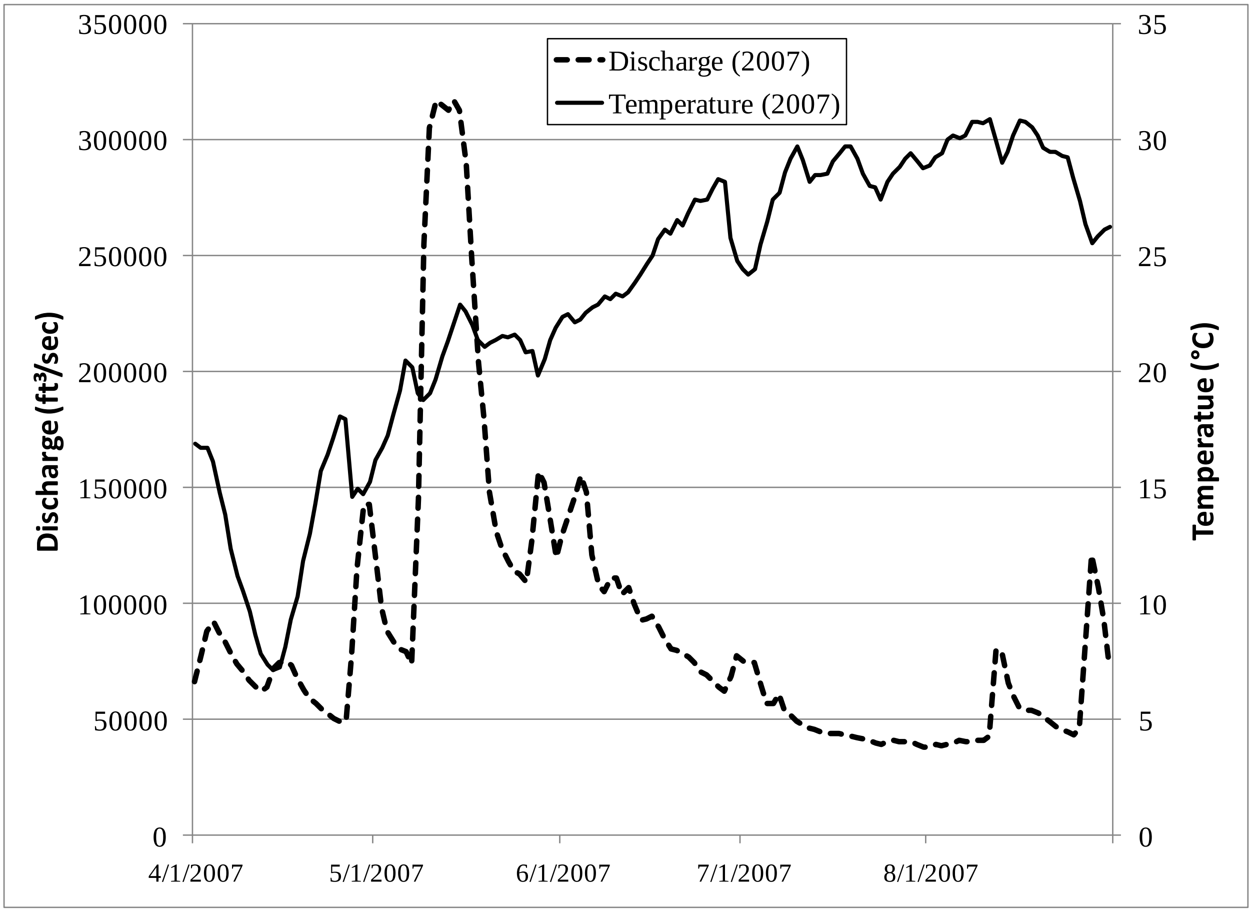

Figure 5.2. Discharge and temperature measured between April and August 2007 in the lower Missouri River. Measured at USGS gauge 06906500 at Glasgow, Missouri.

Past research has emphasized the importance of tributaries to adult catfish (Dames et al. 1989; Vokoun and Rabeni 2005a). Though some catfish populations may rely on tributaries to spawn, other populations may rely on mainstem habitats to spawn. The individuals I studied in 2006 and 2007 displayed a diversity of life-history characteristics that included upstream migrations to four adjacent tributaries (see Chapter 2). However, a large majority (80–90%) displayed both migratory and nonmigratory behaviors within the mainstem Missouri River. By showing that a portion of these individuals spawned, I must conclude that a closer examination of catfish spawning is needed. Without a better understanding of how large-river habitats are used during the spawning period, it is difficult to predict how current and future alterations to the lower Missouri River will affect catfish reproduction.

APPENDIX ONE

Capture Data for Individual Flathead and Blue Catfish

Tagged in the Lower Missouri River in 2006 and 2007

Date	ID	Species	TL (mm)	FL (mm)	Weight (kg)	Gear
4/3/2006	96	Blue	631	544	2.22	Gillnet
4/3/2006	97	Blue	905	815	9.03	Electrofishing
4/3/2006	98	Blue	685	630	4.14	Electrofishing
4/3/2006	99	Blue	665	605	2.79	Electrofishing
4/3/2006	103	Blue	680	615	3.07	Gillnet
4/3/2006	104	Blue	905	838	9.73	Electrofishing
4/3/2006	106	Blue	928	867	10.77	Electrofishing
4/3/2006	107	Blue	680	625	3.62	Gillnet
4/12/2006	168	Blue	770	705	4.53	Electrofishing
4/12/2006	171	Blue	667	605	3.03	Electrofishing
4/5/2006	127	Blue	606	536	2.82	Electrofishing
4/4/2006	132	Blue	825	758	7.27	Hook and Line
4/5/2006	134	Blue	844	795	7.5	Hook and Line
4/5/2006	135	Blue	859	769	6.95	Electrofishing
4/5/2006	139	Blue	707	635	3.22	Electrofishing
4/13/2006	188	Blue	675	605	2.72	Electrofishing
4/13/2006	192	Blue	870	785	8.77	Electrofishing
4/13/2006	195	Blue	793	704	4.73	Electrofishing
4/13/2006	196	Blue	669	608	3.04	Electrofishing
4/13/2006	198	Blue	715	650	3.82	Electrofishing
4/6/2006	140	Blue	910	845	8.2	Hook and Line
4/6/2006	141	Blue	724	660	3.83	Hook and Line
4/6/2006	142	Blue	865	800	7.02	Electrofishing
4/6/2006	147	Blue	740	685	3.88	Electrofishing
4/6/2006	149	Blue	845	765	6.33	Electrofishing
4/6/2006	151	Blue	968	895	11.6	Electrofishing
4/6/2006	153	Blue	660	590	2.7	Electrofishing
4/6/2006	155	Blue	920	835	8.75	Electrofishing
4/6/2006	158	Blue	710	635	3.65	Electrofishing
4/6/2006	160	Blue	815	735	5.3	Electrofishing
4/4/2006	108	Blue	915	825	10.64	Gillnet
4/4/2006	112	Blue	816	750	5.8	Gillnet
4/4/2006	113	Blue	950	864	11.33	Gillnet
4/4/2006	118	Blue	713	635	3.53	Gillnet
4/4/2006	119	Blue	865	785	6.4	Gillnet
4/4/2006	122	Blue	1075	975	14.21	Electrofishing
4/4/2006	123	Blue	672	614	3.1	Electrofishing
4/4/2006	124	Blue	823	750	6.32	Electrofishing
4/4/2006	125	Blue	1037	950	11.95	Electrofishing
4/4/2006	126	Blue	660	599	2.73	Electrofishing

Date	Species	ID	TL (mm)	Weight (kg)	Gear
4/3/2006	Flathead	95	1090	15.37	Electrofishing
4/3/2006	Flathead	105	1075	15.9	Electrofishing
4/12/2006	Flathead	172	742	5.2	Electrofishing
4/12/2006	Flathead	173	1110	19.75	Electrofishing
4/12/2006	Flathead	174	818	6.52	Electrofishing
4/12/2006	Flathead	175	715	4.45	Electrofishing
4/12/2006	Flathead	176	945	10.44	Electrofishing
4/12/2006	Flathead	179	1107	20.07	Electrofishing
4/12/2006	Flathead	181	887	10.19	Electrofishing
4/12/2006	Flathead	182	770	5.09	Electrofishing
4/5/2006	Flathead	136	811	5.69	Electrofishing
4/5/2006	Flathead	137	714	4.4	Electrofishing
4/13/2006	Flathead	184	695	3.71	Electrofishing
4/13/2006	Flathead	185	1059	16.64	Electrofishing
4/13/2006	Flathead	189	960	13.04	Electrofishing
4/13/2006	Flathead	190	905	9.15	Electrofishing
4/13/2006	Flathead	191	623	2.71	Electrofishing
4/13/2006	Flathead	194	803	5.51	Electrofishing
4/13/2006	Flathead	197	1095	19	Electrofishing
4/13/2006	Flathead	199	650	3.1	Electrofishing
4/6/2006	Flathead	145	1025	14.64	Electrofishing
4/6/2006	Flathead	148	1120	20.75	Electrofishing
4/6/2006	Flathead	150	765	5.82	Electrofishing
4/10/2006	Flathead	161	827	6.3	Electrofishing
4/10/2006	Flathead	162	642	2.7	Electrofishing
4/10/2006	Flathead	164	704	4.14	Electrofishing
4/10/2006	Flathead	165	865	8.25	Electrofishing
4/19/2006	Flathead	146	658	3.45	Electrofishing
4/19/2006	Flathead	201	955	10.92	Electrofishing
4/19/2006	Flathead	202	1117	20.68	Electrofishing
4/4/2006	Flathead	117	870	7.95	Electrofishing
4/11/2006	Flathead	166	616	2.91	Electrofishing
4/11/2006	Flathead	167	793	6.47	Electrofishing
4/21/2006	Flathead	206	740	4.68	Electrofishing
4/21/2006	Flathead	207	955	11.24	Electrofishing
4/21/2006	Flathead	208	985	10.62	Electrofishing
4/21/2006	Flathead	209	1260	29.4	Electrofishing

Date	ID	Species	TL(mm)	FL (mm)	Weight (kg)	Gear
4/19/2007	2	Blue	1156		20.3	Hook and Line
4/19/2007	3	Blue	921		9.0	Hook and Line
4/19/2007	4	Blue	692		3.2	Hook and Line
4/19/2007	8	Blue	665	597	2.4	Electrofishing
4/20/2007	9	Blue	1400	1321	37.8	Hook and Line
4/20/2007	10	Blue	998	902	13.4	Hook and Line
4/20/2007	11	Blue	785	688	5.8	Hook and Line
4/20/2007	13	Blue	594	533	2.1	Electrofishing
4/20/2007	14	Blue	711	648	3.5	Electrofishing
4/20/2007	17	Blue	617	554	2.3	Electrofishing
4/20/2007	18	Blue	820	749	5.7	Electrofishing
4/20/2007	21	Blue	693	635	3.6	Electrofishing
4/20/2007	22	Blue	790	729	5.1	Electrofishing
4/20/2007	24	Blue	719	643	3.6	Electrofishing
4/20/2007	25	Blue	963	884	9.7	Electrofishing
4/20/2007	26	Blue	871	803	8.8	Electrofishing
4/21/2007	27	Blue	777	719	4.8	Hook and Line
4/23/2007	28	Blue	864	792	7.1	Electrofishing
4/23/2007	29	Blue	1021	932	17.4	Electrofishing
4/23/2007	34	Blue	808	726	5.1	Electrofishing
4/23/2007	36	Blue	1097	1001	14.9	Electrofishing
4/23/2007	41	Blue	1049	970	15.7	Electrofishing
4/23/2007	45	Blue	1123	1044	17.5	Electrofishing
4/23/2007	46	Blue	940	874	10.6	Electrofishing
4/24/2007	49	Blue	709	643	3.6	Electrofishing
4/24/2007	50	Blue	696	625	3.8	Electrofishing
4/24/2007	51	Blue	602	536	2.4	Electrofishing
4/24/2007	55	Blue	732	655	4.5	Electrofishing
4/24/2007	56	Blue	744	640	3.7	Electrofishing
4/24/2007	57	Blue	747	673	5.8	Electrofishing
4/24/2007	59	Blue	699	630	3.8	Electrofishing
4/24/2007	60	Blue	767	686	4.8	Electrofishing
4/24/2007	61	Blue	711	620	3.5	Electrofishing
4/24/2007	64	Blue	1191	1115	28.5	Electrofishing
7/5/2007	127	Blue	681	617	3.1	Electrofishing
7/5/2007	128	Blue	625	561	2.4	Electrofishing
7/5/2007	145	Blue	617	554	2.0	Electrofishing
7/5/2007	162	Blue	658	594	3.0	Electrofishing
7/5/2007	181	Blue	686	617	3.2	Electrofishing
7/5/2007	206	Blue	607	549	2.1	Electrofishing

Date	ID	Species	TL(mm)	Weight (kg)	Gear
4/19/2007	5	FL	678	3.7	Electrofishing
4/19/2007	6	FL	605	2.6	Electrofishing
4/19/2007	7	FL	625	2.8	Electrofishing
4/20/2007	12	FL	625	2.7	Electrofishing
4/20/2007	15	FL	577	2.3	Electrofishing
4/20/2007	16	FL	1118	21.2	Electrofishing
4/20/2007	19	FL	584	2.4	Electrofishing
4/20/2007	20	FL	711	4.1	Electrofishing
4/20/2007	23	FL	620	2.8	Electrofishing
4/23/2007	30	FL	1105	9.4	Electrofishing
4/23/2007	31	FL	815	6.7	Electrofishing
4/23/2007	32	FL	798	6.6	Electrofishing
4/23/2007	33	FL	917	9.3	Electrofishing
4/23/2007	35	FL	1113	24.1	Electrofishing
4/23/2007	37	FL	762	6.0	Electrofishing
4/23/2007	38	FL	610	2.7	Electrofishing
4/23/2007	39	FL	980	12.8	Electrofishing
4/23/2007	40	FL	899	9.5	Electrofishing
4/23/2007	42	FL	1166	23.1	Electrofishing
4/23/2007	43	FL	917	12.5	Electrofishing
4/23/2007	44	FL	841	9.6	Electrofishing
4/23/2007	47	FL	912	9.8	Electrofishing
4/23/2007	48	FL	841	8.9	Electrofishing
4/24/2007	52	FL	569	2.3	Electrofishing
4/24/2007	53	FL	577	2.1	Electrofishing
4/24/2007	54	FL	610	2.6	Electrofishing
4/24/2007	58	FL	1062	16.9	Electrofishing
4/24/2007	62	FL	584	2.4	Electrofishing
4/24/2007	63	FL	1128	17.2	Electrofishing
4/24/2007	65	FL	953	12.3	Electrofishing
4/24/2007	66	FL	968	12.4	Electrofishing
4/24/2007	67	FL	986	12.3	Electrofishing
4/24/2007	68	FL	665	3.6	Electrofishing
7/5/2007	69	FL	917	10.4	Electrofishing
7/5/2007	70	FL	726	3.9	Electrofishing
7/5/2007	71	FL	714	4.8	Electrofishing
7/5/2007	126	FL	747	4.9	Electrofishing
7/5/2007	151	FL	749	5.2	Electrofishing
7/5/2007	195	FL	886	9.7	Electrofishing
7/5/2007	196	FL	622	2.9	Electrofishing

REFERENCES

Aarts, B. G. W, F. W. B. Van Den Brink, P. H. Nienhuis. 2004. Habitat loss as the main cause of the slow recovery of fish faunas of regulated rivers in Europe: the transversal floodplain gradient. River Research and Applications 20: 3–23.

Arterburn, J. E., Kirby, D. J. and C. R. Berry Jr. 2002. A survey of angler attitudes and biologist opinions regarding trophy catfish and their management. Fisheries 27(5):10–21.

Arthington, A. H., and R. L. Welcomme. 1995. The condition of large river systems of the world. Pages 44–75 in N. B. Armantrout and R. J. Wolotira, Jr.,editors. Condition of the world's aquatic habitats. Proceedings of the World Fisheries Congress, Theme 1.

Baker, J. A., K. J. Kilgore, and R. L. Kasul. 1991. Aquatic habitats and fish communities in the lower Mississippi River. Aquatic Sciences 3:313–356.

Baras, E. 1992. Étude des stratégies d'occupation du temps et de l'espace chez le barbeau fluviatile, *Barbus barbus* L. Cahiers d'Ethologie 12:125–412.

Barko, V. A., and D. P. Herzog. 2003. Relationships among side channels, fish assemblages, and environmental gradients in the unimpounded Upper Mississippi River. Journal of Freshwater Ecology 18:377–382.

Barko, V. A., D. P. Herzog, R. A. Hrabik, and J. S. Scheibe. 2004. Relationships among fish assemblages and main channel border physical habitats in the unimpounded Upper Mississippi River. Transactions of the American Fisheries Society 133:371–384.

Barnickol, P. G. and W. C. Starrett. 1951. Commercial and sport fishes of the Mississippi River between Caruthersville, Missouri, and Dubuque, Iowa. Bulletin of the Illinois Natural History Survey 25(5):267–350.

Barthem, R., and M. Goulding. 1997. The Catfish Connection: Ecology, Migration, and Conservation of Amazon Predators. Columbia University Press, New York.

Barnickol, P. G., and W. C. Starrett. 1951. Commercial and sport fishes of the Mississippi River between Caruthersville, Missouri, and Dubuque, Iowa. Bulletin of the Illinois Natural History Survey 25(5):267-350.

Becker, G. C. 1983. Fishes of Wisconsin. University of Wisconsin Press, Madison, Wisconsin.

Beckett, D. C., and C. H. Pennington. 1986. Water Quality, Macroinvertebrates, Larval Fishes, and Fishes of the Lower Mississippi River-A Synthesis, Technical Report E-86-12, US Army Corps of Engineers, Waterways Experiment Station, Vicksburg, Mississippi.

Benke, A. C. 1990. A perspective on America's vanishing streams. Journal of the North American Benthological Society 9:77–88.

Bobea, E. E. P. 1989. Distribution patterns and population structure of flathead catfish, *Pylodictis olivaris*, in the upper Noxubee River (Noxubee National Wildlife Refuge). Master's thesis. Mississippi State University, Mississippi State.

Brown, R. S., and W. C. Mackay. 1995. Fall and winter movements of and habitat use by cutthroat trout in the Ram River, Alberta. Transactions of the American Fisheries Society 124:873–885.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd Edition. Springer-Verlag, New York, USA.

Burt, W. H. 1943. Territoriality and home range concepts as applied to mammals. Journal of Mammalogy 24:346–352.

Campbell, C. M., A. Fostier, B. Jalabert, and B. Truscott. 1980. Identification and quantification of steroids in the serum of rainbow trout during spermiation and oocyte maturation. Journal of Endocrinology 85:371–378.

Ceapa, C., P. Williot, F. Le Menn, and B. Davail-Cuisset. 2002. Plasma sex steroids and vitellogenin levels in stellate turgeon (*Acipenser stellatus* Pallas) during spawning migration in the Danube River. Journal of Applied Ichthyology 18:391–396.

Colehour, J. D. 2009. Fecundity of flathead catfish from Mississippi River between Hannibal and Cape Girardeau, Missouri. Master's Thesis. University of Central Missouri, Kansas City, Missouri.

Cooper, A. B., and J. J. Millspaugh. 1999. The application of discrete choice models to wildlife resource selection studies. Ecology 80:566–575.

Cornelius, R. R., and T. L. Margenau. 1999. Effects of length limits on muskellunge in Bone Lake, Wisconsin. North American Journal of Fisheries Management 19:300–308.

Craig, J. M., D. M. Papoulias, M. V. Thomas, M. L. Annis, and J. Boase. 2009. Sex assignment of lake sturgeon (*Acipenser fluvescens*) based on plasma sex hormone and vitellogenin levels. Journal of Applied Ichthyology 25(Suppl. 2):60–67.

Cross, F. B., and R. E. Moss. 1987. Historic changes in fish communities and aquatic habitats in plains streams of Kansas. Pages 155–165 in W. J. Matthews, and D. C. Heins, editors. Community and Evolutionary Ecology of North American Stream Fishes, University of Oklahoma Press, Norman, Oklahoma.

Dames, H. R., T. G. Coon, and J. W. Robinson. 1989. Movements of channel and flathead catfish between the Missouri River and a tributary, Perche Creek. Transactions of the American Fisheries Society 118:670–679.

Daugherty, J., and T. M. Sutton. 2005. Diel movement patterns and habitat use of flathead catfish in the lower St. Joseph River, Michigan. Journal of Freshwater Ecology 20:1–8.

Delonay, A. J., D. M. Papoulias, M. L. Wildhaber, M. L. Annis, J. L. Bryan, S. A. Griffith, S. H. Holan, and D. E. Tillitt. 2007. Use of behavioral and physiological indicators to evaluate *Scaphirhynchus* sturgeon spawning success. Journal of Applied Ichthyology 23(4):428–435.

Derkson, A. J. 1989. Autumn movements of underyearling northern pike, *Esox lucius*, from a large Manitoba marsh. Canadian Field Naturalist 103:429–431.

Dettmers, J. M., S. Gutreuter, D. H. Wahl, and D. A. Soluk. 2001. Patterns in abundance of fishes in main channels of the upper Mississippi River system. Canadian Journal of Fisheries and Aquatic Sciences 58:933–942.

Driscoll M. T., Schramm H. L. Jr. and W. R. Davis. 1999. Relative abundance of catfishes in main channel and secondary channel habitats in the lower Mississippi River. Pages 231–237 in E.R. Irwin, W. A. Hubert, C. F. Rabeni, H. L. Schramm

Jr. and T. Coon, editors. Catfish 2000: Proceedings of the International Ictalurid Symposium. Bethesda, Maryland, American Fisheries Society.

Eitzmann, J. L., A. S. Makinster, and C. P. Paukert. 2007. Distribution and growth of blue sucker in a Great Plains USA river. Fisheries Management and Ecology 14:255–262.

Fausch, K. D. 1984. Profitable stream positions for salmonids: relating specific growth rate to net energy gain. Canadian Journal of Zoology 62:441–451.

Fausch, K. D., C. E. Torgersen, C. V. Baxter, and H. W. Li. 2002. Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes. Bioscience 52:483–498.

Fischer, S. A., S. Eder, and E. D. Aragon. 1999. Movements and habitat use of channel catfish and blue catfish in a small impoundment in Missouri. Pages 239–255 in E. R. Irwin, W. A. Hubert, C. F. Rabeni, H. L. Schramm Jr., and T. Coon, editors. Catfish 2000: proceedings of the international ictalurid symposium. Amer. Fish. Soc., Symp. 24, Bethesda, Maryland.

Folmar, L. C., N. D. Denslow, V. Rao, M. Chow, D. A. Crain, J. Enblom, J. Marcino, and L. J. Guillette, Jr. 1996. Vitellogenin induction and reduced serum testosterone concentrations in feral male carp (*Cyprinus carpio*) captured near a major metropolitan sewage treatment plant. Environmental Health Perspectives 104:1096–1101.

Ford, Z. L., and K. Sullivan. 2006. Population dynamics, movement and nesting success of flathead catfish and blue catfish in selected Missouri Rivers with an emphasis on the effects of liberal and restrictive harvest regulations. Internal Progress Report 2005–2006. Missouri Department of Conservation, Jefferson City. 20 pp.

Francis, J. M. 1993. Recreational handgrabbing as a factor influencing flathead catfish stock characteristics in two Mississippi streams. Master's thesis. Mississippi State University, Mississippi State.

Frissell, C. A., W. J. Liss, C. E. Warren, and M. D. Hurley. 1986. A hierarchical framework for stream habitat classification: viewing streams in a watershed context. Environmental Management 10:199–214.

Funk, J. L. 1957. Movement of stream fishes in Missouri. Transactions of the American Fisheries Society 85:39–57.

Funk, J. L., and J. W. Robinson. 1974. Changes in the channel of the lower Missouri River and effects on fish and wildlife. Missouri Department of Conservation, Jefferson City, MO.

Fuselier, L., and D. Edds. 1994. Seasonal variation in habitat use by the Neosho madtom (Teleostei: Ictaluridae: *Noturus placidus*). Southwestern Naturalist 39:217–223.

Galat, D. L. and R. Lipkin. 2000. Restoring ecological integrity of great rivers: historical hydrographs aid in defining reference conditions for the Missouri River. Hydrobiologia 422/423:29–48.

Galat, D. L., and I. Zweimüller. 2001. Conserving large-river fishes: is the "highway analogy" an appropriate paradigm? Journal of the North American Benthological Society 20: 266–279.

Galat, D. L., J. W. Robinson and L. W. Hesse. 1996. Restoring aquatic resources to the lower Missouri River: issues and initiatives. Pages 49–72 in D. L. Galat and A. G.

Frazier, editors. Overview of river floodplain ecology in the upper Mississippi River basin. Volume 3 of J. A. Kelmelis, editor. Science for Floodplain Management into the 21st Century. U.S. Government Printing Office, Washington, DC.

Galat, D. L., M. L. Wildhaber, and D. J. Dieterman. 2001. Spatial patterns of physical habitat. Volume 2. Population structure and habitat use of benthic fishes along the Missouri and lower Yellowstone rivers. U. S. Geological Survey Cooperative Research Units, University of Missouri.

Galat, D. L., C. R. Berry, W. M. Gardner, J. C. Hendrickson, G. E. Mestl, G. J. Power, C. Stone, and M. R. Winston. 2005. Spatiotemporal patterns and changes in Missouri River fishes. Pages 249–291 in J. N. Rinne, R. M. Hughes, and R. Calamusso, editors. Historical Changes in Fish Assemblages of Large American Rivers, Symposium 45, American Fisheries Society: Bethesda, Maryland.

Garner, P. 1996. Microhabitat use and diet of 0+ year cyprinid fishes in a lentic, regulated reach of the river Great Ouse, England. Journal of Fish Biology 48:367–382.

Garrett, J. W., and D. H. Bennett. 1995. Seasonal movements of adult brown trout relative to temperature in a coolwater reservoir. North American Journal of Fisheries Management 15:480–487.

Gehrke, P. C., P. Brown, C. B. Schiller, D. B. Moffatt, and A. M. Bruce. 1995. River regulation and fish communities in the Murray-Darling river system, Australia. Regulated Rivers: Research and Management 11:363–375.

Gerking, S. D. 1950. Stability of a stream fish population. Journal of Wildlife Management 14:193–202.

Gerking, S. D. 1953. Evidence for the concepts of home range and territory of stream fishes. Ecology 34:347–365.

Gerking, S. D. 1959. The restricted movement of fish populations. Biological Reviews 34:221–242.

Goodbred, S. L., R. J. Gilliom, T. S. Gross, N. D. Denslow, W. B. Bryant, and T. R. Schoeb. 1997. Reconnaissance of 17β-estradiol, 11-ketotestosterone, vitellogenin, and gonad histopathology in common carp of United States stream: potential for contaminant induced endocrine disruption. U.S Geological Survey Open-File Report 96–627.

Gore, J. A., and F. D. Shields. 1995. Can large rivers be restored? BioScience 45:142–152.

Gowan, C. and K. D. Fausch. 1996. Mobile brook trout in two high-elevation Colorado streams: re-evaluating the concept of restricted movement. Canadian Journal of Fisheries and Aquatic Sciences 53:1370–1381.

Gowan, C., M. K. Young, K. D. Fausch, and S. C. Riley. 1994. Restricted movement in resident stream salmonids: a paradigm lost? Canadian Journal of Fisheries and Aquatic Sciences 51:2626–2637.

Grace, T. B. 1985. The status and distribution of commercial and forage fish in the Missouri River and their utilization of selected habitats. National Marine Fisheries Service, Program 2-363-R, Project 4, Job 3. Missouri Department of Conservation, Jefferson City.

Graham, K. 1999. Review of the biology and management of blue catfish. Pages 37–49 in E. R. Irwin, W. A. Hubert, C. F. Rabeni, H. L. Schramm Jr., and T. Coon, editors. Catfish 2000: proceedings of the international ictalurid symposium. American Fisheries Society, Symposium 24, Bethesda, Maryland.

Graham, K., and K. DeiSanti. 1999. The population and fishery of the blue catfish and channel catfish in the Harry S Truman Dam tailwater, Missouri. Pages 361–376 in E. R. Irwin, W. A. Hubert, C. F. Rabeni, H. L. Schramm, Jr., and T. Coon, editors. Catfish 2000: Proceedings of the international ictalurid symposium. American Fisheries Society, Symposium 24, Bethesda, Maryland.

Gresswell, R. E., W. J. Liss, and G. L. Larson. 1994. Life-history organization of Yellowstone cutthroat trout (*Oncorhynchus clarki bouvieri*) in Yellowstone Lake. Canadian Journal of Fisheries and Aquatic Sciences 51(1):298–309.

Grift, R. E., A. D. Buijse, W. L. T. Van Densen, M. A. M. Machiels, J. Dranenbarg, J. G. P. Klein Breteler, and J. J. G. M. Backx. 2003. Suitable habitats for 0-group fish in rehabilitated floodplains along the lower River Rhine. River Research and Applications 19: 353–374.

Grist, J. D. 2002. Analysis of a blue catfish population in a southeastern reservoir: Lake Norman, North Carolina. M. S. Thesis, Virginia Polytechnical Institute State University.

Grossman, G. D., P. A. Rincon, M. D. Farr, and R. E. Ratajczak, Jr. 2002. A new optimal foraging model predicts habitat use by drift-feeding stream minnows. Ecology of Freshwater Fish 11:2–10.

Hallberg, G. R., J. M. Harbaugh, and P. M. Witinok. 1979. Changes in the channel area of the Missouri River in Iowa 1879-1976. Iowa Geological Survey Special Report Series 1. Iowa City, Iowa.

Hansteen, T. L., H. P. Andreassen, and R. A. Ims. 1997. Effects of spatiotemporal scale on autocorrelation and home range estimators. Journal of Wildlife Biology 61:280–290.

Harlan, J. R., E. B. Speaker, and J. Mayhew. 1987. Iowa fish and fishing. Iowa Department of Natural Resources, Des Moines.

Hart, L. G., and R. C. Summerfelt. 1975. Surgical procedures for implanting ultrasonic transmitters into flathead catfish (*Pylodictis olivaris*). Transactions of the American Fisheries Society 104:56–59.

Hill, J., and G. D. Grossman. 1987. Home range estimates for three North American stream fishes. Copiea 2:379–380.

Hesse, L. W., and W. Sheets. 1993. The Missouri River hydrosystem. Fisheries 18:5–14.

Hesthagen, T. 1988. Movement of brown trout, *Salmo trutta*, and juvenile Atlantic Salmon, *Salmo salar*, in a coastal stream in northern Norway. Journal of Fish Biology 32:639–653.

Hesse, L. W., and G. E. Mestl. 1993. An alternative hydrograph for the Missouri River based on the precontrol condition. North American Journal of Fisheries Management 13:360–366.

Hesse, L. W., J. C. Schmulbach, J. M. Carr, K. D. Keenlyne, D. G. Unkenholz, J. W. Robinson, and G. E. Mestl. 1989. Missouri River fishery resources in relation to past, present and future stresses. Canadian Special Publications in Fisheries and Aquatic Sciences 106:352–371.

Hirzinger, V., H. Keckeis, H. L. Nemeschkal, and F. Schiemer. 2004. The importance of inshore areas for adult fish distribution along a free-flowing section of the Danube, Austria. River Research and Applications 20: 137–149.

Hodder, K. H., J. E. G. Masters, W. R. C. Beaumont, R. E. Gozlan, A. C. Pinder, and C. M. Knight. 2007. Techniques for evaluating the spatial behaviour of river fish. Hydrobiologia 582:257–269.

Henderson, H. 1965. Observations on the propagation of flathead catfish in the San Marcos State Fish Hatchery, Texas. Proceedings of the Annual Conference of the Southeastern Association of Game and Fish Commissioners 17(1963):173–177.

Henderson, G. G. 1972. Rio Grande blue catfish study. Texas Parks and Wildlife Department, Federal Aid and Fisheries Restoration Project F-18-R-7, Job 11, Progress Report, Austin.

Humphries, P. and P. S. Lake. 2000. Fish larvae and the management of regulated rivers. Regulated Rivers: Research and Management 16:421–432.

Humphries, P., L. G. Serafini, and A. J. King. 2002. River regulation and fish larvae: variation through space and time. Freshwater Biology 47:1307–1331.

Karr, J. R., L. A. Toth, and D. R. Dudley. 1985. Fish communities of midwestern rivers: a history of degradation. BioScience 35:90–95.

Kenward, R. E., C. G. Ingersoll, I. Hlohowskyj, and N. D. Mundahl. 1984. Movements and densities of the darters *Etheostoma flabellare, E. spectabile,* and *E. nigrum* during spring spawning. Journal of Freshwater Ecology 2:345–354.

Ingersoll, C. G., I Hlohowskyj, and N. D. Mundahl. 1984. Movements and densities of the darters *Etheostoma flabellare, E. spectabile,* and *E. nigrum* during spring spawning. Journal of Freshwater Ecology 2:345–351.

Insaurralde, M. S. 1992. Environmental characteristics associated with flathead catfish in four Mississippi streams. Ph. D. Dissertation. Mississippi State University, Mississippi State.

Irving, D. B. and T. Modde. 2000. Home-range fidelity and use of historic habitat by adult Colorado pikeminnow (*Ptychocheilus lucius*) in the White River, Colorado and Utah. Western North American Naturalist 60(1):16–25.

Jackson, D. C. 2001. Flathead Catfish: Biology, Fisheries, and Management. Pages 23–36 in E. R. Irwin, W. A. Hubert, C. F. Rabeni, H. L. Schramm Jr., and T. Coon, editors. Catfish 2000: proceedings of the international ictalurid symposium. American Fisheries Society, Symposium 24, Bethesda, Maryland.

Jenkins, R. E., and N. M. Burkhead. 1994. Freshwater fishes of Virginia. American Fisheries Society, Bethesda, Maryland.

Jennings, D. K. 1979. An evaluation of aquatic habitat associated with notched dikes on the Missouri River, Missouri. M.S. Thesis, University of Missouri-Columbia. 262 pp.

Jones, M. C., J. S. Marron, and S. J. Sheather. 1996. A brief survey of bandwidth selection for density estimation. Journal of the American Statistical Association 91:401–407.

Jungwirth, M., S. Muhar and S. Schmutz. 2000. Fundamentals of fish ecological integrity and their relation to the extended serial discontinuity concept. Hydrobiologia 422/423:85–97.

Jurajda, P. 1995. Effect of channelization and regulation on fish recruitment in a flood plain river. Regulated Rivers: Research and Management 10:207–215.

Kernohan, B. J., R. A. Gitzen, and J. J. Millspaugh. 2001. Analysis of animal space use and movements. Pages 125–166 *in* J. J. Millspaugh, and J. M. Marzluff, editors. Radio tracking and animal populations. Academic Press, San Diego, California.

Korsgaard, B., and I. Peterson. 1979. Vitellogenin, lipid, and carbohydrate metabolism during vitellogenesis and pregnancy, and after hormonal induction in the blenny, *Zoarces viviparous* (L.). Comparative Biochemistry and Physiology 63B:245–251.

Kwak, T. J., W. E. Pine, D. S. Waters, J. A. Rice, J. E. Hightower, and R. L. Noble. 2004. Population dynamics and ecology of introduced flathead catfish. U.S. Geological Survey, North Carolina Cooperative Fish and Wildlife Research Unit and Department of Zoology, North Carolina State University, Federal Aid in Sport Fish Restoration, Project F-68, Study 1, Phase 1, Final Report. Raleigh.

Lagler, K. F. 1961. Freshwater fishery biology. William C. Brown Company, Dubuque, Iowa.

Lee, L. A. and J. W. Terrell. 1987. Habitat suitability index models: flathead catfish. Biological Report 82 (10.152). U.S. Department of the Interior, Fish and Wildlife Service, Research and Development, Washington, D.C.

Lucas, M. C. and E. Baras. 2001. Migration of freshwater fishes. Blackwell Science, Oxford.

MacArthur, R. H., and E. R. Pianka. 1966. On the optimal use of a patchy environment. American Naturalist 100:603–609.

Manly, B., L. McDonald, and D. Thomas. 1993. Resource selection by animals, statistical design, and analysis for field studies. Chapman and Hall, London.

Manosroi, A., K. Meng-Umphan, and J. Manosroi. 2003. Annual sex hormonal profiles, gonad development and age determination of the Mekong giant catfish (*Pangasianodon gigas*, Chevey). Aquaculture Research 34:1379–1385.

Matheney, M. P., and C. F. Rabeni. 1995. Patterns of movement and habitat use by northern hog suckers in an Ozark stream. Transactions of the American Fisheries Society 124:886–897.

Matthews, W. J. 1998. Patterns in Freshwater Fish Ecology. Chapman and Hall, New York.

Matthews, W. J., and L. G. Hill. 1979. Influence of physico-chemical factors on habitat selection by red shiners, *Notropis lutrensis* (Pisces: Cyprinidae). Copeia 1979:70–81.

Matty, A. J. 1985. Fish endocrinology. Timber Press, Portland, Oregon.

McDowall, R. M. 1997. The evolution of diadromy in fishes (revisited) and its place in phylogenetic analysis. Reviews in Fish Biology and Fisheries 7:443–462.

McMaster, M. E., K. R. Munkittrick, G. J. Van Der Kraak. 1992. Protocol for measuring circulation levels of gonadal sex steroids in fish. Canadian Technical Report Fisheries and Aquatic Sciences 1836.

Meka, J. M., E. E. Knudsen, D. C. Douglas, and R. B. Benter. 2003. Variable migratory patterns of different adult rainbow trout life history types in a southwest Alaska watershed. Transactions of the American Fisheries Society 132:717–732.

Michaletz, P. H., and J. G. Dillard. 1999. A survey of catfish management in the United States and Canada. Fisheries 24:6–11.

Millspaugh, J. J., and J. M. Marzluff. 2001. Radio tracking and animal populations. Academic Press, San Diego, California.

Minckley, W. L. 1991. Native fishes of the Grand Canyon region: an obituary, in Colorado River Ecology and Dam Management. National Academy Press, Washington D.C.

Minckley, W. L., and J. E. Deacon. 1959. Biology of the flathead catfish in Kansas. Transactions of the American Fisheries Society 88:344–355.

Mitson, R. B. 1978. A review of biotelemetry techniques using acoustic tags. Pages 269–283 in J. E. Thorpe, editor. Rhythmic activities of fishes. Academic Press, New York.

Mohr, C. O. 1947. Table of equivalent populations of North American small mammals. American Midland Naturalist 37:223–449.

Muhar, S. M., S. Schwarz, S. Schmutz and M. Jungwirth. 2000. Identification of rivers with high and good habitat quality: methodological approach and applications in Austria. Hydrobiologia 422/423:343–358.

Mundahl, N. D., and C. G. Ingersoll. 1983. Early autumn movements and densities of johnny (*Etheostoma nigrum*) and fantail (*E. flabellare*) darters in a southwestern Ohio stream. Ohio Academy of Science 83:103–108.

Munger, C. R., G. R. Wilde, and B. J. Follis. 1994. Flathead catfish age and size at maturation in Texas. North American Journal of Fisheries Management 14:403–408.

Nestler, J., and V. K. Sutton. 2000. Describing scales of features in river channels using fractal geometry concepts. Regulated Rivers: Research and Management 16:1–22.

Newcomb, B. A. 1989. Winter abundance of channel catfish in the channelized Missouri River, Nebraska. North American Journal of Fisheries Management 9:195–202.

Nikolsky, G. V. 1963. The ecology of fishes. Academic Press, London.

Northcote, T. G. 1984. Mechanisms of fish migrations in rivers. Pages 317–355 in J. G. McCleave, J. J. Dodson, and W. H. Neill, editors. Plenum, New York.

Northcote, T. G. 1997. Potadromy in Salmonidae: living and moving in the fast lane. North American Journal of Fisheries Management 17:1029–1045.

Northcote, T. G. 1998. Migratory behavior of fish and its significance to movement through riverine fish passage facilities. Pages 3–18 in M. Jungwirth, S. Schmutz, and S. Weiss, editors. Fish Migration and Fish Passages. Fishing News Books, Blackwell Science Ltd, Oxford.

Northcote, T. G., and S. G. Hinch. 2004. Fish migration and passage in watersheds. Pages 123–142 in T. G. Northcote and G. F. Hartman, editors. Fishes and Forestry: Worldwide Watershed Interactions and Management. Blackwell Science, Oxford.

Nunn, A. D., J. P. Harvey, and I. G. Cowx. 2007. The food and feeding relationships of larval and 0+ juvenile fishes in lowland rivers and connected waterbodies. I.

Ontogenetic shifts and interspecific diet similarity. Journal of Fish Biology 7 0:726–742.

Orlando, E. F., G. A. Binczik, P. Thomas, L. J. Guillette Jr. 2003. Reproductive seasonality of the male Florida gar, *Lepisosteus platyrhincus*. General and Comparative Endocrinology 131:365–371.

Ovidio, M., E. Baras., D. Goffaux, C. Birtles, and J. C. Philippart. 1998. Environmental unpredictability rules the autumn migration of the brook trout (*Salmo trutta* L.) in the Belgian Ardennes. Hydrobiologia 371/372:263–274.

Paukert, C. P., and A. S. Makinster. 2009. Longitudinal patterns in flathead catfish relative abundance and length at age within a large river: effects of an urban gradient. River Research and Applications 25(7):861–873.

Perry, Jr., W. G., and D. C. Carver. 1973. Length at maturity and total length-collarbone length conversions for channel catfish, *Ictalurus punctatus*, and blue catfish, *Ictalurus furcatus*, collected from the marshes of southwest Louisiana. Proceedings of the Annual Conference of the Southwestern Association of Game and Fish Commissioners 26(1972):541–553.

Pflieger, W. L. 1997. The fishes of Missouri, revised edition. Missouri Department of Conservation, Jefferson City.

Poff, L. N. 1997. Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. Journal of the North American Benthological Society 16:391–409.

Pracheil, B. M., M. A. Pegg, and G. E. Mestl. 2009. Tributaries influence recruitment of fish in large rivers. Ecology of Freshwater Fish 18:603–609.

Pugh, L. L., and H. L. Schramm, Jr. 1999. Movement of tagged catfishes in the lower Mississippi River. Pages 193–197 in E. R. Irwin, W. A. Hubert, C. F. Rabeni, H. L. Schramm Jr., and T. Coon, editors. Catfish 2000: proceedings of the international ictalurid symposium. American Fisheries Society, Symposium 24, Bethesda, Maryland.

Quinn, S. P. 1991. Evaluation of a length-categorization system for flathead catfish. Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies 43(1989):146–152.

Reynolds, L. F. 1983. Migration patterns of five species in the Murray-Darling River system. Australian Journal of Marine and Freshwater Research 34:857–871.

Ridenour, C. J., A. B. Starostka, W. J. Doyle, and T. D. Hill. 2009. Habitat used by *Macrhybopsis* chubs associated with channel modifying structures in a large regulated river: implications for river modification. River Research Applications 25:472–485.

Robinson, J. W. 1977. The utilization of dikes by certain fishes in the Missouri River. Missouri Department of Conservation, Federal Aid in Sport Fish Restoration, Project 2.199R. Jefferson City.

Rodríguez, M. A. 2002. Restricted movement in stream fish: the paradigm is incomplete, not lost. Ecology 83(1):1–13.

Rodríguez -Robles, J. A. 2003. Home ranges of gopher snakes (*Pituophis catenifer*, Colubridae) in central California. Copeia 2003:391–396.

Ross, S. T., and J. A. Baker. 1983. The response of fishes to periodic spring floods in a southeastern stream. American Midland Naturalist 109(1):1–14.

Sakaris, P. C., R. V. Jesien, and A. E. Pinkley. 2005. Retention of surgically implanted ultrasonic transmitters in the brown bullhead catfish. North American Journal of Fisheries Management 25:822–826.

Scalet, C. G. 1973. Stream movements and population density of the orangebelly darter, *Etheostoma radiosum cyanorum* (Osteichthyes: Percidae). Southwestern Naturalist 17:381–387.

Schoener, T. W. 1981. An empirically based estimate of home range. Theoretical Population Biology 20:281–325.

Schlosser, I. J., and P. L. Angermeier. 1995. Spatial variation in demographic processes in lotic fishes: conceptual models, empirical evidence, and implications for conservation. Pages 392–401 in J. L. Neilsen, editor. Evolution and the aquatic ecosystem: defining unique units in population conservation. American Fisheries Society Symposium 17, Bethesda, Maryland.

Shetter, D. S., and G. R. Alexander. 1965. Results of angling under special and normal trout fishing regulations in a Michigan trout stream. Transactions of the American Fisheries Society 94:219–226.

Shields Jr., F. D., C. M. Commer, and S. Testa III. 1995. Toward greener riprap: environmental considerations from microscale to macroscale. Pages 557–574 in C. R. Thorne et al., editors. River, Coastal and Shoreline Protection: Erosion Control Using Riprap and Armourstone. JohnWiley and Sons, Chichester, New Hampshire.

Simpson, T. H., and R. S. Wright. 1977. A radioimmunoassay for 11-oxytestosterone; its application in the measurements of levels in blood serum of rainbow trout *Salmo gairdneri*. Steroids 29:383–398.

Skains, J. A. 1992. Linear home range and movements of flathead catfish (*Pylodictis olivaris*) in two Mississippi Streams. Master's thesis, Mississippi State University, Mississippi State.

Smith, J. B., and W. A. Hubert. 1989. Use of a tributary by fishes in a great plains river system. Prairie Naturalist 21:27–38.

So, N., G. E. Maes, and F. A. M Volckaert. 2006. High genetic diversity in cryptic populations of the migratory sutchi catfish *Pangasianodon hypophthalmus* in the Mekong River. Heredity 96:166–174.

Stauffer, K. W. 1991. Habitat use and growth of juvenile catfish (*Ictalurus punctatus* and *Pylodictus olivaris*) in the Missouri River and a tributary, the Lamine River. MS Thesis, University of Missouri-Columbia. 155pp.

Stauffer, K. W., R. C. Binder, B. C. Chapman and B. D. Koenen. 1996. Population characteristics and sampling methods of flathead catfish *Pylodictis olivaris* in the Minnesota River. Minn. Dept. Nat. Res., Div. Fish Wild., Sec. Fish., Study IV, Job 389, Final Report, St. Paul.

Stoeckel, J. N., and B. M. Burr. 1999. A review of key reproductive traits and methods used to spawn ictalurids. Pages 141–159 in E. R. Irwin, W. A. Hubert, C. F. Rabeni, H. L. Schramm Jr., and T. Coon, editors. Catfish 2000: proceedings of the international ictalurid symposium. American Fisheries Society, Symposium 24, Bethesda, Maryland.

Summerfelt, R. C. 1972. Flathead catfish movements. Completion Report, Oklahoma Project 4-60-R. National Marine Fisheries Service, National Oceanic and Atmospheric Administration, United States Department of Commerce, Washington, D.C.

Sumpter, J. P. 1990. General Concepts of Seasonal Reproduction. Pages 13–31 in A. D. Munro, A. P. Scott, and T. J. Lam, editors. Reproductive Seasonality in Teleosts: Environmental Influences. CRC, Press, Boca Raton.

Timmons, T. J. 1999. Movement and exploitation of blue and channel catfish in Kentucky Lake. Pages 187–191 in E. R. Irwin, W. A. Hubert, C. F. Rabeni, H. L. Schramm Jr., and T. Coon, editors. Catfish 2000: proceedings of the international ictalurid symposium. Amer. Fish. Soc., Symp. 24, Bethesda, MD.

Thompson, D. H. 1933. The Migration of Illinois Fishes, Biology Notes 1. Illinois Natural History Survey, Urbana, Illinois.

Travnichek, V. H. 2004. Movement of flathead catfish in the Missouri River: examining opportunities for managing river segments for different fishery goals. Fisheries Managament and Ecology 11:89-96.

Tonn, W. M. 1990. Climate change and fish communities: a conceptual framework. Transactions of the American Fisheries Society 119:337–352.

Turner, P.R., and R.C. Summerfelt. 1971. Reproductive biology of the flathead catfish, *Pylodictus olivais* (Rafinesque), in a turbid Oklahoma Reservoir. Pages 107–119 in G. E. Hall, editor. Reservoir Fisheries and Limnology American Fisheries Society Special Publication No. 8.

Tyus, H. M. 1985. Homing behavior noted for Colorado squawfish. Copeia 1985:213–215.

Tyus, H. M. 1986. Life strategies in the evolution of the Colorado squawfish (*Ptychocheilus lucius*). Great Basin Naturalist 46:656–661.

Tyus, H. M. 1990. Potamodromy and reproduction of Colorado squawfish *Ptychocheilus lucius*. Transactions of the American Fisheries Society 119:1035–1047.

U.S. Army Corps of Engineers. 2006. Missouri River bank stabilization and navigation project, fish and wildlife mitigation project: annual implementation report FY05 and FY06 http://www.nwk.usace.army.mil/projects/mitigation/. [15 October 2007].

USDI/USDC. 1996. National Survey of Fishing, Hunting, and Wildlife Associated Recreation. U.S. Department of Interior, Fish and Wildlife Service and U.S. Department of Commerce, Bureau of Census (USDC/USDI), Washington DC: U.S. Government Printing Office, 115 pp.

van Winkle, W. 1975. Comparison of several probabilistic home-range models. Journal of Wildlife Management 39:118–123.

Vokoun, J. C. 2003. Movement and habitat use of flathead catfish (*Pylodictis olivaris*) in two Missouri interior streams. Doctoral dissertation. University of Missouri, Columbia.

Vokoun, J. C. 2004. Movement and habitat use of flathead catfish (*Pylodictis olivaris*) in two Missouri interior streams. Ph. D. Dissertation, University of Missouri, Columbia, Missouri.

Vokoun, J. C., and C. F. Rabeni. 2005a. Variation in an annual movement cycle of flathead catfish within and between two Missouri watersheds. North American Journal of Fisheries Management 25:563–572.

Vokoun, J. C., and C. F. Rabeni. 2005b. Home range and space use patterns of flathead catfish during the summer-fall period in two Missouri streams. Transactions of the American Fisheries Society 134:509-517.

Vokoun, J. C., and C. F. Rabeni. 2006. Summer diel activity and movement paths of flathead catfish (*Pylodictis olivaris*) in two Missouri streams. American Midland Naturalist 155:113–122.

Ward J. V., K. Tockner, and F. Schiemer. 1999. Biodiversity of floodplain river ecosystems: ecotones and connectivity. Regulated Rivers: Research and Management 15:125–139.

Ware, D. M. 1980. Bioenergetics of stock and recruitment. Canadian Journal of Fisheries and Aquatic Sciences 37:1012–1024.

Warren, C. E. 1971. Biology and water pollution control. W. B. Saunders Company, Philadelphia.

Wang, L., J. Lyons, and P. Kanehl. 2001. Impacts of urbanization on stream habitat and fish across multiple spatial scales. Environmental Management 28:255–266.

Weithman, A. S., and R. O. Anderson. 1977. Catch-and-release fishing for largemouth bass on Hunter’s Lake – 1963 to 1967. Pages 109–118 in R. A. Barnhart and T. D. Roelofs, editors. Catch and Release Fishing as a Management Tool. Humboldt State University, Arcada, California.

Welcomme, R. L. 1979. Fisheries Ecology of Floodplain Rivers. Longman Press, New York.

Welcomme, R. L. 1985. River fisheries. FAO Fisheries Technical Paper 262.

Werner, E. E., and G. G. Mittelbach. 1981. Optimal foraging: field tests of diet choice and habitat switching. American Zoologists 21:813–829.

White, G. C., and R. A. Garrott. 1990. Analysis of wildlife radio-tracking data. Academic Press, San Diego, California, USA.

White, K., J. Gerken, C. Paukert, and A. Makinster. 2009. Fish community structure in natural and engineered habitats in the Kansas River. River Research and Applications. Published online in Wiley InterScience (www.interscience.wiley.com). DOI: 10.1002/rra.1287.

Wildhaber, M. L., D. M. Papoulias, A. J. DeLonay, D. E. Tillitt, J. L. Bryan, M. L. Annis, and J. A. Albert. 2005. Gender identification of shovelnose sturgeon using ultrasonic and endoscopic imagery and the application of the method to the pallid sturgeon. Journal of Fish Biology 67:114–132.

Wildhaber, M. L., D. M. Papoulias, A. J. DeLonay, D. E. Tillitt, J. L. Bryan and M. L. Annis. 2007. Physical and hormonal examination of Missouri River shovelnose sturgeon reproductive stage: a reference guide. Journal Applied Ichthyology 23:382–401.

Wingfield, J. C., and A. S. Grimm. 1977. Seasonal changes in plasma cortisol, testosterone, and estradiol-17β in the plaice, *Pleuronectes platessa* L. General and Comparative Endocrinology 31:1–11.

Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164–168.

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