FACTORS AFFECTING PADDLEFISH

REPRODUCTIVE SUCCESS

IN THE LOWER OSAGE RIVER

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Doctor of Philosophy

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by

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

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FACTORS AFFECTING PADDLEFISH REPRODUCTIVE SUCCESS IN THE LOWER OSAGE RIVER

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ABSTRACT

Large rivers and their associated fish communities have undergone major alterations over the last century. Habitat fragmentation caused by both large and small dams, channelization to promote river transportation, and increased sedimentation from land use changes have all altered large river habitat and affected large-river fishes. Paddlefish are an archetypical large-river migrant that have experienced population declines as a result of overexploitation and large-river habitat alteration, so may serve as an indicator of habitat condition and connectivity. Paddlefish in the lower Osage River are believed to be a naturally self-sustaining population, yet may be vulnerable to interruptions in reproductive habitat and behavior caused by both a low-head dam and large hydroelectric facility. I developed a series of comprehensive research objectives to assess the critical components required for successful paddlefish reproduction in the lower Osage River and identify potential limiting factors. This information will help focus future management efforts to sustain natural reproduction of lithopelagophilic spawners in altered rivers.

Sex steroid information clearly identified gravid male and female paddlefish were present in the lower Osage River and provided a timeframe for physiological spawning readiness that occurred during a decrease in discharge release as opposed to a natural rise.

Over all three study years, 41 of 86 transmittered paddlefish moved upstream over Osage River Lock and Dam #1, allowing for the successful development of a discharge and temperature model to predict upstream passage. Historical analysis of discharge and temperature conditions during the spawning period (1 March – 31 May) from 1939-2009 indicate that upstream passage likely occurs in most years (69% of those studied) but may be restricted in low water years that occurred as frequently as 31% of the years studied. Movement and habitat use downstream of Bagnell Dam were affected by large decreases (> 550 cms) in river discharge that were a result of Missouri River flood mitigation. No spent females or eggs were collected below Bagnell Dam, and only one larval paddlefish was collected, suggesting that natural reproduction was limited in the three years studied.

Despite the presence of gravid fish and access to upstream spawning habitat, we observed a strong weight of evidence that suggests paddlefish reproduction downstream of Bagnell Dam is most likely limited by altered discharges, resulting in disrupted spawning behavior or insufficient environmental conditions for spawning. Altered flows are suspected in the decline of many riverine species, yet the effects of these flows are still poorly understood. Successful management of regulated river systems for societal and biological benefits requires a more comprehensive understanding of specific species life history traits that are vulnerable to alterations in natural flow regimes.

Chapter I

Paddlefish as an Indicator of Large River Status

Rivers have undergone significant anthropogenic alteration over the last century. Changes in land use have resulted in increased sedimentation, pollution, and water quality changes. Large-scale channelization and construction of low-head lock and dams for navigation in addition to the construction of large dams for flood control and hydroelectric power have significantly altered the habitat of the world's river systems. These alterations have resulted in significant declines in biodiversity, especially within river fishes (Dudgeon et al. 2006). Changes in land use have resulted in increased erosion and sediment inputs into river systems, changing water quality and increasing siltation of course substrates that many species rely upon for reproduction (Wood and Armatige 1997). Channelization and reduction of floods has reduced lateral access to floodplains, altering nutrient flow and reducing connectivity to floodplain rearing habitat (Jurajda 1995). Habitat fragmentation caused by large and low-head dams has inundated large reaches of river habitat and greatly reduced upriver habitat access for migratory species (Jager et al. 2001). Alteration of natural flow regime by large dams has altered river function and disrupts discharge cues riverine species use for critical behaviors (Poff et al. 1997).

The North American paddlefish (*Polyodon spathula*) is an archetypical large-river species native to rivers of the Central United States and several gulf coast drainages (Russell 1986). Paddlefish populations were once abundant throughout most of this range; however, large population declines have occurred over the last century due to past overharvest, restriction of spawning movements by dams, and alteration of spawning habitat by increased sedimentation. Paddlefish are an ideal indicator of large river status because populations track changes at multiple temporal and spatial scales, respond to major habitat alterations and stressors, and interact across ecological, economic, and social realms (Galat et al. 2005).

Temporally, paddlefish mature late, have low natural mortality, and typically spawn on a non-annual cycle. Males mature between 4-9 years of age and spawn every year or every other year. Females mature between 10-14 years of age and spawn every 2-4 years (Russell 1986). This strategy is similar to other large, long-lived river fishes and is believed to increase fitness over an entire lifetime despite potential reproductive failure during years with poor reproductive conditions (Sulak and Randall 2002). Additionally, females will forgo spawning and reabsorb eggs in years with poor spawning conditions, presumably as means of conserving energy and decreasing the development period to the next reproductive event (Russell 1986). Reabsorption may provide a proximate advantage for the reabsorption of energy reserves, but could lower overall reproductive fitness if eggs are reabsorbed continually in successive reproductive events.

Spatially, paddlefish use a wide variety of habitats that vary both seasonally and annually (Jennings and Zigler 2009). Optimal foraging habitat is longitudinally separated from optimal reproductive and overwintering habitat (Russell 1986). Paddlefish are lithopelagophilic spawners and make long distance migrations. These migrations occur seasonally between spring spawning habitat in moderate to fast velocities with coarse substrate, summer foraging habitat in slow velocity backwaters abundant in plankton, and overwintering habitat in deep slow velocity water (Jennings and Zigler 2009). Spawning migrations are dependent upon photoperiod, temperature, and discharge cues to synchronize arrival at spawning habitats under optimal environmental conditions and reproductive physiology (Russell 1986; Jennings and Zigler 2009).

The successful life-history strategy of longevity, non-annual reproduction, and long-distance migration in paddlefish also increases the vulnerability of populations to anthropogenic alteration of river habitats and overharvest (Gengerke 1986; Gerken and Paukert 2009). Increased siltation in rivers has resulted in a loss of coarse spawning substrates, which has been shown to reduce embryo survival in other river species (Unkenholz 1986; Gerken and Paukert 2009). Both large and low-head dams have restricted historical spawning migrations, further reducing access to upstream spawning habitat (Sparrowe 1986; Unkenholz 1986). Large-scale dams have altered the natural flow and temperature regimes that paddlefish use for migration and spawning cues (Paukert and Fisher 2001; Gerken and Paukert 2009). Channelization along with reduced spring floods has reduced mainstem connectivity to floodplain backwater areas, which are critical nursery areas for larval and juvenile paddlefish (Graham 1997). This vulnerability to multiple stressors makes paddlefish good indicators of complex alterations to riverine habitat.

Ecologically, paddlefish have a primitive morphology and are a unique member of large river fish communities, surviving relatively unchanged for the last 200 million years. Paddlefish are a member of the primitive order Acipenceriformes (sturgeon and paddlefish) and are only one of two extant species in the paddlefish family Polyodontidae. Very few live specimens of the Chinese paddlefish (*Psephurus gladius*) have been captured in the last decade, suggesting that the North American paddlefish may be the only species of paddlefish in the world (Fan et al. 2006).

Paddlefish are a ram-suspension filter-feeding planktivore, having evolved a long paddle-shaped rostrum with hundreds of electrosensory organs to aid in the detection of plankton (Sanderson et al. 1994; Wilkens et al. 2001). Large zooplankton make up the majority of paddlefish's diet. Insects and small fish are occasionally found in paddlefish diets, yet these organisms likely are consumed incidentally during periods of high abundance (Hoopes 1960). Consequently, paddlefish require access to large schools of plankton, which often vary in space and time in large rivers and are sensitive to habitat changes (Basu and Pick 1995). Paddlefish play an important role in the trophic energy transfer in large rivers and represent an important part of large-river biodiversity, resulting in a loss of system stability and resilience if paddlefish are eliminated from their native large river communities (Gunderson 2000). Paddlefish may also be vulnerable to the recent invasion of the non-native planktivores, silver carp *Hypophthalmichthys molitrix*, and bighead carp, *Hypophthalmichthys nobilis*. Laboratory tests of age-0 paddlefish and bighead carp indicate a high diet overlap and the possibility of negative interaction if plankton resources are limiting in the wild (Schrank et al. 2003). Unfortunately, very little evidence is available on how increases of these invasive planktivores will affect native populations of paddlefish.

Economically and socially, paddlefish are highly desirable sport and commercial species (Russell 1986; Jennings and Zigler 2009). Currently, paddlefish populations support recreational or commercial harvest in fourteen states (AR, IL, IN, IA, KS, KY, MS, MO, MT, NE, ND, OK, SD, and TN). Commercial harvest is allowed in seven of these states (AR, IA, IL, IN, KY, MO, and TN) and is primarily a roe fishery targeted at gravid adult females, with peak catch estimates nearing 20 metric tonnes annually

(Pikitch et al. 2005; Quinn 2009). Sustainable paddlefish fisheries can attract significant social attention and provide economically valuable fisheries due to their unique morphology, large size, and desirable meat and roe (Russell 1986).

Overharvest combined with large scale habitat alteration has resulted in extirpation of paddlefish in four states (MD, NC, NY, and PA) and listing as a threatened or endangered species in eight states (AL, LA, MN, OH, TX, VA, WV, and WI) (Jennings and Zigler 2000). The International Union of the Conservation of Nature (IUCN) lists paddlefish as a vulnerable species and future population trends remain uncertain. Exploitation pressure will continue to increase as recreational fisheries increase in popularity and demand for commercially harvested caviar increases (Quinn 2009). Habitat alteration and disruption of natural flow regimes will continue to be a threat to paddlefish, especially in exploited populations. Maintaining sustainable paddlefish populations and the ecological integrity of large river communities requires specific information on species reproduction and the ability of these species to maintain sustainable populations in altered systems.

The goal of this research was to investigate a comprehensive suite of paddlefish reproductive requirements in an altered river environment to understand limitations to reproductive success (Figure 1). My specific objectives were to 1) determine sex, spawning condition, and timing of spawning, 2) model physical conditions that facilitate upstream passage over a low-head dam, 3) understand spawning movement and habitat use of paddlefish in a regulated river, and 4) evaluate reproductive success downstream of a large hydroelectric dam. Quantifying the relationships between river alteration and reproduction is critical for sustainably managing paddlefish populations, as well as other lithopelagophilic large-river migrants. Additionally, understanding reproductive requirements for one migratory river species can provide insight into connectivity, discharge, and habitat requirements needed for other river migrants; ultimately providing a broader perspective to sustainably manage fish communities in altered river systems.

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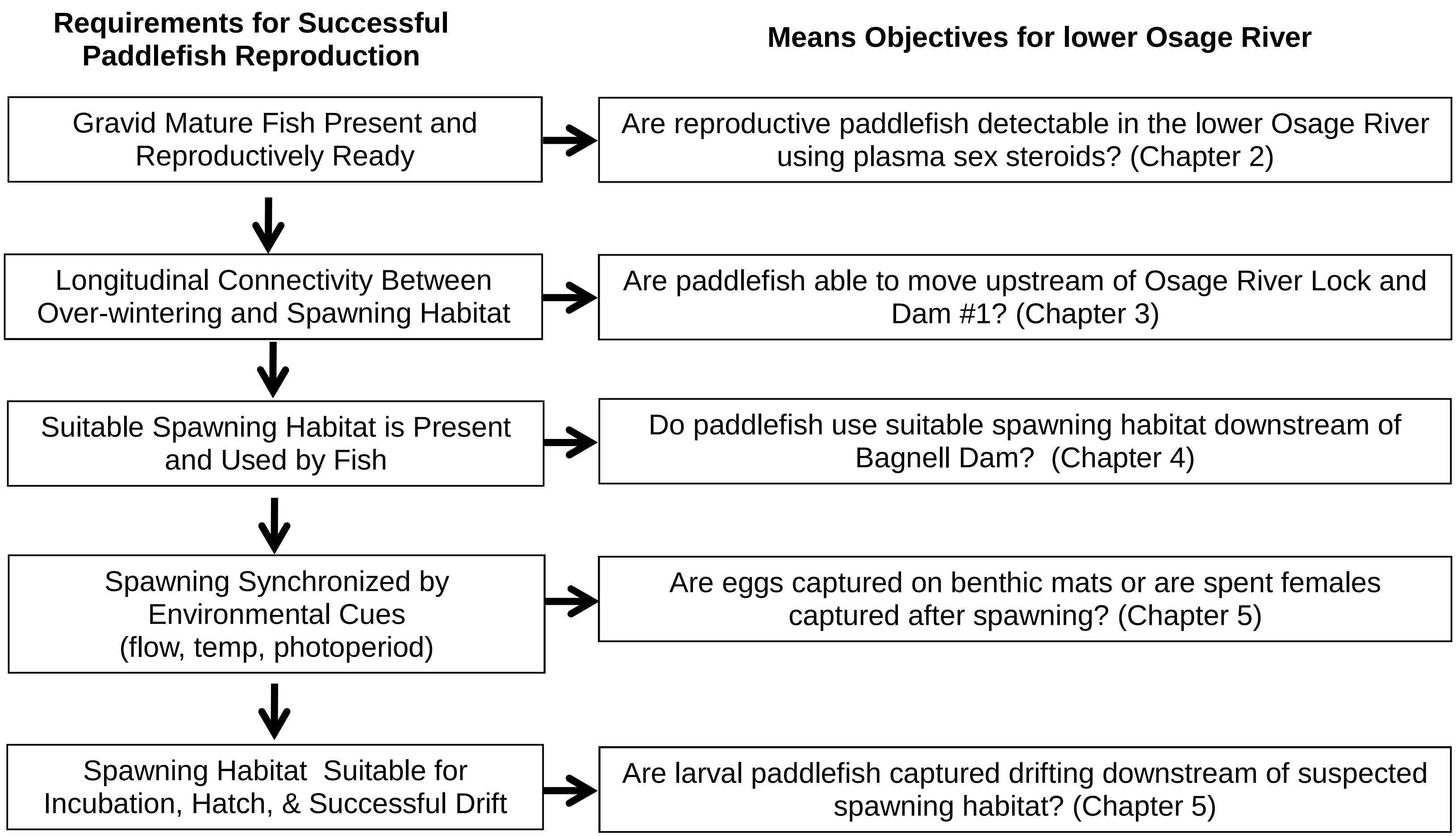

Figure 1. Conceptual diagram of paddlefish spawning requirements and means objectives of corresponding research chapters.

Chapter II

Reproductive Status and Spawning Times in Paddlefish using Plasma Sex Steroids and Vitellogenin

Abstract

Plasma sex steroids, such as estradiol, testosterone, and 11-ketotestosterone, regulate important physiological processes like spawning behavior and gonadal development. Concentrations of these sex steroids follow predictable cycles that have been used to accurately determine sex and reproductive status of many fish species. Our objectives were to 1) determine if estradiol, testosterone, 11-ketotestoreone, and vitellogenin could be used to determine sex and reproductive condition in paddlefish and 2) use temporal changes in sex steroid concentrations to identify potential spawning dates. Paddlefish from the lower Osage River were collected throughout the spawning season in 2007-2009. Approximately 5 ml of blood was drawn for plasma hormone analysis in the laboratory. Surgical incisions were made to validate sex and reproductive status of captured individuals. Overall differences in mean plasma hormone concentrations between sex and reproductive condition were tested using a 2-Factor ANOVA. A stepwise-discriminant function analysis was used to determine if sex and spawning condition could be correctly classified by hormone concentrations. Plasma sex steroids varied between individuals, but females had significantly higher concentrations of estradiol ($F_{df=2,73} = 30.144$, $p < 0.000$) and males had significantly higher concentrations of testosterone ($F_{df=2,73} = 81.269$, $p < 0.000$). Only estradiol was significantly higher in spawning individuals compared with non-spawning or post-spawning individuals ($F_{df=1,74} = 16.614$, $p <0.000$) . Concentration of 11-ketotestosterone was significantly higher in males than in females or juveniles ($F_{df=2,73} = 14.989$, $p <0.000$)

but not between spawning and non-spawning fish ($F_{df=1,74} = 0.099$, $p = 0.754$). The discriminant function analysis was able to correctly classify 96% of individuals as male or female and spawning or non-spawning based on estradiol and testosterone concentrations alone. Decreases in plasma steroid concentrations associated with spawning occurred during optimal reported spawning temperatures but did not occur during a peak in river discharge, suggesting that spawning may be occurring during sub-optimal discharge conditions for successful paddlefish spawning. Identification of spawning condition and physiological timing of spawning using plasma steroids can provide a valuable tool for monitoring reproductive condition and reproductive timing of fish populations with complex reproductive behavior.

Introduction

Sex specific data are a critical component of many management and recovery plans for imperiled species. Estimates of spawning populations based solely on the number of adults may greatly overestimate the true spawning potential if sex and reproductive condition are unknown (Rafetto et al. 1990). Sex information for heavily exploited or critically imperiled populations may be of special concern as these populations typically possess skewed sex ratios and may be reproductively or genetically limited by the number of one sex (Frankham 1995; Rowe and Hutchings 2003). Identifying sex and reproductive status of fishes is critical to accurately estimating effective spawning population sizes to make informed management decisions.

Paddlefish, like other Acipensiformes, mature late in life and typically spawn on a non-annual basis. Male paddlefish mature as early as age 4 and females as early as age 6 in the southern portion of their native range, whereas, average age of maturity exceeds age 14 in the northern portion of their range (Carlson and Bonislawsky 1981). Female spawning periodicity also ranges from 1-2 years in the south, compared to 2-5 years in the north (Jennings and Zigler 2009). This variability in reproductive strategy makes assessing sex and spawning condition a challenge, as the proportion of spawning adults and sex ratio may differ within and between populations.

Similar to many other freshwater fishes, paddlefish show little external sexual dimorphism or secondary sexual spawning characteristics. Male paddlefish commonly develop breeding tubercles on the head and rostrum during the spawning season. However, this is not a definitive characteristic as not all males develop tubercles and females may also develop breeding tubercles (Mims et al. 2009). A macroscopic examination of urogenital openings was used by Vescei et al. (2003) to determine sex of several North American sturgeon species, but this technique has never been applied or validated for paddlefish. Consequently, identification of sex and reproductive status for paddlefish based solely on external characteristics is difficult and may be highly inaccurate.

Sex determination in non-dimorphic species has traditionally relied on sacrificing fish to examine the gonads visually. Sacrificing individuals solely to identify sex may be detrimental to populations and also may have ethical implications. Non-lethal surgical methods have been used to examine the gonads and sex individual fish visually (Bruch et al. 2001), yet this technique is highly invasive and requires intensive handling, which may result in undesirable stress or mortality. Recently, ultrasonographic and endoscopic methods have been developed as non-invasive measures for determining both sex and reproductive condition. Both endoscopy and ultrasonography allow rapid identification in the field, but are not as accurate for species that do not spawn annually (Wildhaber et al. 2005). These non-invasive methods also require specific equipment, detailed training, and often are less accurate than direct visual examination of gonadal tissue (Wildhaber et al. 2005).

Plasma hormone analysis is a minimally invasive technique that has been used to assess sex accurately in numerous fish species, including several species of sturgeon (Doroshov et al. 1997; Webb et al. 2002; Feist et al. 2005; Wildhaber et al. 2007; Craig et al. 2009). Three hormones are primarily responsible for gonadal development and reproductive behavior in fish: estradiol (E), testosterone (T), and 11-ketotestosterone (11-KT). Testosterone and 11-KT in males regulate the maturation of the testes, initiate sperm production, and development of secondary sexual characteristics, such as breeding tubercles. Females typically possess lower concentrations of T and 11-KT but possess higher concentrations of estradiol, which regulates ovary maturation, egg production, and development of female secondary sexual characteristics, such as fat deposition (Doroshov 1997; Webb et al. 1999). In addition to these three sex steroids, the protein vitellogenin (VTG), a precursor of egg yolk protein, is found at high concentrations in females and is critical for egg development. Consequently, VTG can distinguish spawning females from males and non-spawning females even when female estradiol levels are low (Wildhaber et al. 2005).

Physiological cycles in plasma sex steroid concentrations have been used to determine sex and spawning condition in many fish species, especially within the sturgeon family, Acipenseridae (Doroshov et al. 1997; Webb et al. 2002; Feist et al.

2005; Wildhaber et al. 2007; Craig et al. 2009). Concentrations of sex steroids are typically low in immature individuals and begin to increase with the onset of maturity and gonadal development. These large differences in steroid concentrations allow for discrimination between immature and mature individuals. Steroid concentrations in mature individuals cycle with reproductive behavior, increasing during the initiation of spawning behavior, peaking just prior to spawning, and decreasing immediately after spawning (Doroshov et al. 1997; Wildhaber et al. 2007). These differences can also be used to identify individuals that are mature but not in spawning condition, which provides a powerful discriminatory tool for species like sturgeon and paddlefish that do not spawn annually upon reaching maturity (Doroshov et al. 1997).

The predictable changes in steroid concentration that occur with reproductive behavior also have been used to estimate the spawning dates of many fish species (Baynes and Scott 1985; Truscott et al. 1986; Norberg et al. 1989). Concentrations of sex steroids peak once gametes reach full development and the fish is ready to spawn. Sex steroid concentrations then drop precipitously just prior to the actual spawning event (Ceapa et al. 2002; Wildhaber et al. 2005). Sex steroid concentrations can be a powerful tool to identify potential spawning times because of the close link between physiological cycle and spawning behavior.

Whereas steroid regulation of spawning behavior may allow gross approximation of physiological readiness, actual spawning in paddlefish and sturgeon is believed to be triggered by two proximate environmental cues: suitable temperature and an increase in river discharge (Russell 1986). Numerous studies have observed paddlefish spawning occurring immediately after an increase or peak in river discharge (Purkett 1961;

Firehammer et al. 2006; O'Keefe et al. 2007). Use of this environmental cue could be a highly adaptive trait to synchronize spawning events with favorable river conditions for egg development and larval growth (Ovidio et al. 1998). Comparing physiological processes with environmental stimuli may provide a means of identifying or determining if environmental spawning cues are sufficient to trigger spawning.

Use of plasma steroids to identify sex and spawning condition of paddlefish can provide a minimally invasive and accurate assessment technique for collecting sex specific population information in this often imperiled species. Additionally, we sought to evaluate the use of temporal changes in steroid levels to identify dates of spawning readiness. By comparing physiological readiness to known environmental spawning conditions, such as temperature and river discharge, we can determine if adequate environmental conditions, such as temperature and river discharge, occur during the window of optimal physiological readiness.

Methods

Study Area

The Osage River is located in west-central Missouri and is the largest river within the state, excluding the Mississippi or Missouri rivers (Figure 1). The two upper reservoirs, Truman Reservoir and Lake of the Ozarks, support large recreational paddlefish fisheries that are maintained primarily through intensive stocking efforts (Gengerke 1986). The lower Osage River, defined as the 130-km stretch extending downstream from Bagnell Dam to the confluence with the Missouri River, supports a small fishery that is believed to have natural reproduction and does not receive supplemental stocking.   A spring spawning run of paddlefish begins entering the lower Osage River in early to late March and concentrates in the lower 20 rkm prior to migrating upstream (Lallaman Chapters 3,4). Paddlefish begin moving upstream in early to late April and concentrate in the lower 2 rkm downstream of Bagnell Dam during optimal spawning temperatures of 14-20^{o}C (Lallaman Chapter 4).

Data Collection

Paddlefish were captured by deploying monofilament gill and trammel nets set stationary or drifted in the current. Sampling was conducted 5-6 days per week from early March until middle June to capture fish throughout the entire spawning period in 2007, 2008, and 2009. Paddlefish were initially sampled near staging areas within the lower 20 km of the Osage River. As paddlefish began migrating upstream, sampling was conducted at upstream holding areas near potential spawning areas downstream of Bagnell Dam (Figure 1).

All paddlefish were measured for eye-to-fork length (EFL) to the nearest 0.5 cm and weight to the nearest 0.1 kg to estimate maturity qualitatively.   Fish under 60 cm were assumed to be immature, based on published length and age at maturity data (Reed et al. 1992; Lein and Devries 1998). Recapture information (weight, gonadal condition, sex steroid concentration) from individual paddlefish captured over the spawning period provided supportive evidence to verify spawning, so a uniquely numbered metal jaw tag was clamped around the lower jaw of all fish greater than 60 cm to identify recaptured individuals.

A macroscopic assessment of the gonads was performed on all individuals longer than 60 cm to validate sex and reproductive condition. A 4-8 cm incision was made in the ventral midline of the abdomen just anterior of the pelvic girdle to macroscopically examine the gonads and assess sex and reproductive condition. Sex and spawning condition were visually assessed using photos and criteria developed for lake sturgeon, which have similar gonadal development (Bruch et al. 2001). All fish were categorized as immature, male, or female using staging criteria of Bruch et al. (2001). Immature fish with poorly developed gonads were classified as juveniles of unknown sex (U). Males were assessed to be non-spawning or possessing underdeveloped testes (M1) or fully developed and enlarged testes ready to spawn (M2). Mature females were assessed to be in early gonadal development with no visible eggs (F1), intermediate stages of egg development with differentiated but not fully developed eggs (F2-F3), fully developed eggs and ready to spawn (F4), and post-spawning with a significant loss of egg mass or with eggs that are undergoing atresia and reabsorption (F6). Incisions were sutured using a monofilament absorbable suture and covered with surgical glue.

Approximately 5 ml of blood was drawn from all fish greater than 60 cm for sex steroid analysis. Blood was drawn from the dorsal aorta just posterior to the anal fin using a 10-cc syringe and 20-gauge needle. Extracted blood was immediately transferred to a 10-cc heparin-coated vaccutainer and stored on ice while in the field to prevent clotting. At the end of each collection day, plasma was separated from the whole blood by centrifuging the vaccutainers at 3500 rpm for 10 min. To minimize sample degradation, the decanted plasma was inserted into labeled 1-ml cryovials and placed on dry ice until samples could be stored in a -80 ^{o}C freezer.

Steroid Analysis

Sex steroids were extracted and analyzed using methods developed for shovelnose sturgeon, *Scaphirhynchus platorynchus* (Wildhaber et al. 2007). Preliminary analysis with differing extraction volumes (0.2 to 1.0 ml) indicated that extracting 1 ml of plasma for males and 0.35 ml of plasma for females resulted in the optimal analytical concentration for each of the steroids. Steroids were reconstituted with 1ml of phosphate buffered saline with 1% gelatin after extraction and stored at -20 ^{o}C until analyzed. A radioimmuno-assay (RIA) was used to determine concentrations of the three sex steroids: E, T, and 11-KT similar to the methods used by Craig et al. (2009) for lake sturgeon. Steroid concentrations were determined through a competitive antibody reaction with a radioactively labeled steroid. Calculation of steroid concentrations in the samples was determined using a standard curve of a known serial dilution for each hormone which was run along with the samples. All samples were analyzed in duplicate, and the averaged results were expressed as nanograms (ng) of steroid ⁄ml of blood plasma.

Assay validation procedures were assessed using a spiked recovery procedure, comparison of intra and inter assay variation, and comparison of slope parallelism between serial dilutions and the standard curve. Since no paddlefish standard was available, a known shovelnose sturgeon sample was run in all steroid assays and used for comparison of inter-assay variability.

Vitellogenin Analysis

VTG was analyzed using a sandwich Enzyme-Linked-Immuno-Sorbant-Assay (ELISA) similar to the method used by Folmar et al. (1996) and adapted by Wildhaber et al. (2007) for shovelnose sturgeon. Anti-paddlefish VTG was not commercially available, so a mouse derived anti-shovelnose sturgeon VTG protein (Abraxis LLC, Pennsylvania) was used as a surrogate. No independent validation of mouse derived shovelnose antibodies was conducted in this study, but preliminary analysis indicates that the surrogate functioned as expected. Microtiter plates were coated with the anti-protein and incubated overnight. Two dilutions of each sample were added to the plate in duplicate and a standard curve, created with serial dilutions of purified shovelnose sturgeon VTG, was also added to the plate. After adding all of the samples and standard, the plate was allowed to incubate at room temperature for 1 h. After incubation a secondary antibody, goat anti-rabbit horseradish peroxidase, was added and incubated for 1 h. Plates were read on spectrophotometer at 450 nm and absorbance values were recorded. Concentrations of VTG were determined by comparing absorbance values of the samples to a standard curve.

Temporal Evaluation

Potential associations between physiology and environmental variables that affect paddlefish spawning were evaluated by monitoring discharge and water temperature during the spring spawning period (March-June) in 2007-2009. Mean daily discharge data (cms) for the lower Osage River were obtained from U.S. Geological Survey (USGS) gauging station downstream of Bagnell Dam. The gauging station downstream of Bagnell Dam was selected because of the direct downstream effects on staging paddlefish and management implications to discharge regulation. Osage River temperature (^{o}C) was recorded hourly at all sampling locations using continuous recording data loggers (Onset Co., Pocasset, Ma, Model TBI32[1]).

Paddlefish plasma was collected throughout the potential spawning period. Large decreases in plasma steroid concentrations associated with spawning physiology were used to indicate the approximate dates of potential spawning. Daily discharge and temperature during the potential spawning period were examined and qualitatively compared to reported spawning conditions of 10-20 ^{o}C and an increase in river stage greater than 3 m (Purkett 1961; Russell 1986; O'Keefe et al. 2007).

Data Analysis

Differences in sex steroid and vitellogenin concentrations between sex (Male, Female, or Juvenile/Unknown) and reproductive status (Spawning or Non-Spawning) were assessed using a 2-Factor ANOVA for each steroid (E, T, 11-KT) and VTG. Multiple ANOVA comparisons were corrected using the Bonferroni correction factor (alpha = 0.0125).

Stepwise discriminant function analysis (DFA) was used to determine the accuracy of assigning sex and reproductive status based on sex-steroids concentrations, following methods used for white sturgeon by Webb et al. (2002). Paddlefish were separated into reproductive groups based upon differences in the three plasma steroid concentrations (E, T, and 11-KT). The accuracy of individuals placed into these groups was then validated using the known reproductive condition from the macroscopic examination. Small sample sizes within some of the macroscopically assigned reproductive groups were corrected by simplifying sex and spawning status into 3 major categories: non-spawning individuals (unknown/juveniles, non-spawning males, and non-spawning females), spawning females (F4), and spawning males (M2). Non-spawning individuals were grouped with immature individuals, because the low hormone concentrations in these groups should have resulted in similar grouping. Not all samples analyzed for plasma steroids were analyzed for VTG, due to insufficient plasma collection or sample loss. Vitellogenin was left-out of the discriminant analysis to maintain a larger sample size and consistency in the analysis.

Results

Plasma samples were collected and analyzed for 80 paddlefish collected over all three study years (Table 1). Vitellogenin was analyzed for 57 of these 80 samples, because 23 samples had insufficient plasma volume for both analyses. Spiked extraction efficiency was 95, 97, and 98% recovery efficiency for E, T, and 11-KT, respectively. Inter-assay variation was measured over all 5 assay trials, with intra-assay comparisons between 6 and 48 samples run per assay. Overall Estradiol intra-assay variation was 12%, and inter-assay variation was 3%. Testosterone intra-assay variation was 1%, and inter-assay variation was 16%. 11-KT intra-assay variation was 9%, and inter-assay variation was 19%. The measurement of E, T, and VTG by verifying that serial dilutions of sample were parallel to a standard curve. The slopes for assay validation were 0.97, 0.92, and 0.85 for E, T, and 11-KT, respectively. Serial dilution slopes to test accuracy for VTG were 0.94 for males and 0.67 for females.

Estradiol assay sensitivity was 895 pg/ml at 20% binding and 12 pg/ml at 80% binding. Testosterone assay sensitivity was 253 pg/ml at 20% binding and 6.5 pg/ml at 80% binding. Cross-reactivity of the antibodies used in these assays with other similar steroids are reportedly <10% according to the vendors.

Estradiol was significantly greater in females than in males and juveniles ($F_{df=2,73} = 30.144$, $p < 0.000$) and significantly higher in spawning fish than non-spawning fish ($F_{df=1,74} = 16.614$, $p < 0.000$). T and 11-KT concentrations were significantly greater in males than females and juveniles ($F_{df=2,73} = 81.269$, $p < 0.000$ and $F_{df=2,73} = 14.989$, $p <0.000$, respectively) but not significantly different between spawning and non-spawning fish ($F_{df=1,74} = 0.321$, $p = 0.573$ and $F_{df=1,74} = 0.099$, $p = 0.754$, respectively). Concentration of VTG, similar to E, was significantly greater in females compared to males and juveniles ($F_{df=2,73} = 45.619$, $p < 0.000$) and significantly higher in spawning fish compared to non-spawning fish ($F_{df=1,74} = 32.419$, $p < 0.000$). Both sex steroids and VTG showed distinct patterns between reproductive groups (Figure 2).

The stepwise DFA included both E and T, but did not include 11-KT in the final discriminant function. The overall accuracy of the discriminant function analysis was 96.2%. Accuracy within groups was best for spawning males (100%) and non-spawning fish (98.4%), but still relatively high for spawning females (81.8%) (Table 2). One non-spawning fish was incorrectly classified as a spawning female, and two spawning females were incorrectly classified as a non-spawning fish and a spawning male.

Despite considerable efforts to continually capture paddlefish and monitor steroid concentrations, no spawning paddlefish were captured during the period of heavy upstream movement that occurred in late March and early April in any study year.

Spawning paddlefish were successfully sampled in late April and early May as fish began concentrating downstream from Bagnell Dam, yet no females were collected later in the spawning season in 2007 and only two females were captured in 2008. Six females were captured downstream of Bagnell Dam in 2009 and temporal evaluation of steroid concentrations for the 19 female paddlefish captured over the 2009 spawning season showed an 10x decrease in testosterone and 5x decrease drop in estradiol concentrations occurring between 19 March and 28 April (Figure 3). Temperature during this period ranged between 9.5-14.4 ^{o}C. Discharge during this period initially climbed from 100 to 945 cms, peaked daily between 450 and 900 cms, then fell precipitously just prior to collecting individuals with low steroid concentrations (Figure 3).

Discussion

Analysis of plasma sex steroids provided a minimally invasive, yet highly accurate means of classifying both sex and reproductive condition of mature paddlefish, despite relatively small sample sizes. Analyzing a suite of sex steroids rather than just one steroid allowed for accurate (96.2%) overall differentiation of both sex and spawning condition in paddlefish, similar to the findings for sturgeon (Webb et al. 2002; Wildhaber et al 2007; Craig et al. 2009). Plasma steroid concentrations among individual paddlefish were variable, yet the pattern of elevated estradiol in spawning females and elevated testosterone in spawning males was consistent. The high accuracy for both males (100%) and non-spawning fish (98.4%), suggest good differentiation for spawning males based on elevated testosterone levels. The identification of spawning females had the lowest accuracy (81.4%), but accuracy would most likely improve with a sample size larger than 11 individuals. The high accuracy of the DFA based on E and T plasma concentrations may provide accurate differentiation using laboratory analysis of only these two variables. The larger variability and non-significant differences in 11-KT values between reproductive groups suggest that this measurement provides little explanatory power and may not justify the additional laboratory time required to measure 11-KT concentrations.

The use of plasma steroids for the lower Osage River paddlefish provided a valuable insight into population dynamics. We observed a large proportion of juveniles and individuals in non-spawning condition, despite targeting mature spawning adults. Additionally we observed a highly skewed sex ratio of spawning adults. Although skewed sex ratios are commonly observed in spawning populations of sturgeon and paddlefish (Lein and DeVries 1998; Scholten and Bettoli 2005), only 8% of all captured paddlefish were gravid females and we observed less than 19 spawning females (< 10% of the total number of fish caught) annually. Spawning population estimates lacking the information provided by steroid analysis and based solely on the number of paddlefish present would have severely overestimated the reproductive potential of this population.

Temporal analysis of steroid concentrations allowed us to identify the period of physiological spawning readiness and identify the potential spawning period for this population. The low number of females captured during and after the spawning season in 2007 and 2008, prevented detailed temporal analysis of hormone data. Sufficient numbers of females (n = 19) in 2009 allowed for an evaluation of hormone data over the spawning period, but the inability to capture females during the upstream migratory period resulted in a large gap between 19 March and 28 April (Figure 3). However, we observed significantly lower steroid concentrations in all fish captured on 28 April or later, indicating that spawning was occurring prior to this date. Based on fish behavior and reported spawning temperatures, spawning readiness was most likely occurring during the latter half of this window near the end of April. Additional study of sex steroids in a larger population would enhance the ability to capture females throughout the spawning period and increase sample sizes, allowing for a more detailed temporal analysis.

Despite the limited data, a coarse examination of temperature and flow cues during the period of spawning readiness was conducted for the lower Osage River. During the physiological spawning window, water temperatures were well within reported spawning temperatures, but we did not observe a characteristic rise in discharge associated with paddlefish spawning cues (Purkett 1961; Paukert and Fisher 2001, O'Keefe 2007). Papoulias et al. (2011) found very similar results for pallid sturgeon *Scaphirhyncus platorynchus* in the altered Missouri River, where photoperiod and temperature were believed to be important cues for overall gonadal development and hormone concentration, but that other short term cues like river discharge may be important to signal the release of gametes. Delonay et al. (2010) captured larval sturgeon and paddlefish in the Missouri River in 2010 without a large rise in discharge preceding the date of capture, suggesting that the complex nature of spawning cues is still poorly understood. In contrast to the Missouri River, regulated flow releases from Bagnell Dam produced sharper increases and decreases in river discharge that were interspersed with periods of peaking operation or relatively stable flood releases (Figure 3). Additionally, we did not observe females with substantial egg loss to indicate spawning occurred, despite observing a predictable drop in steroid concentrations that has been associated with spawning readiness in other species. We captured several females in 2009 that had not successfully spawned, but were captured at water temperatures reaching or exceeding reported spawning temperatures. The eggs in these females appeared atretic and were in the process of reabsorption. Russell (1986) noted that female paddlefish would reabsorb their eggs if spawning conditions (e.g. flow or temperature) were insufficient to cue spawning. The coupling of our physiological data with environmental data indicates the lack of an adequate flow cue as a possible limitation to paddlefish spawning in the lower Osage River.

Initial collection of blood samples required very little additional time or effort in the field. Optimal preservation of samples required separation and cold storage of plasma within 12 hrs of field collection. Immediate access to a centrifuge and storage on dry ice until transfer to a -80^{o}C freezer may be problematic if sampling in remote locations. Plasma analysis does not provide immediate field results like surgical examination, ultrasonography, or endoscopic techniques and also requires additional laboratory equipment and trained laboratory personnel to analyze the samples. Macroscopic examination with histological verification provides a rapid and reliable identification of both sex and spawning status, but requires invasive surgical incisions and suturing. Macroscopic examination is commonly used when surgical methods are required for other purposes, such as transmitter implantation, but still represents a significant risk to the stress and health of the individual. Direct comparison of ultrasonography and endoscopy with hormone analysis in sturgeon species have shown significantly lower accuracy using ultrasonography and endoscopy (Wildhaber et al. 2005). The higher accuracy of sex steroid classification and ability to analyze precise temporal changes may warrant the use of this technique in combination with other non-invasive methods.

Several studies have explored sex steroid applications in the aquaculture industry (Feist et al. 2005; Wilhelm 2006), yet few studies have used plasma steroids to identify sex and reproductive condition of wild paddlefish populations. Plasma steroids offer several advantages over other non-invasive methods, but does require additional training and complex laboratory analysis. The ability to identify physiological changes and temporal patterns associated with spawning behavior can provide managers and researchers an accurate tool for assessing sex, spawning condition, and timing of spawning. For species with complex reproductive behavior or skewed sex ratios this information may be used to identify potential reproductive bottlenecks.

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Table 1. Number of plasma samples analyzed for estradiol, testosterone, and 11-ketotestosterone along with spawning ratios for paddlefish collected in the lower Osage River during 2007-2009 spawning seasons.

Year	**Number of Samples**	**Spawning Ratio (spawners: non-spawners)**	**Sex Ratio (Female:Male)**
2007	9	2:7	1:8
2008	37	13:24	11:27
2009	34	15:19	19:16

Table 2. Percent correct classification (and number of observations) of non-spawning fish, reproductive males, and reproductive females using the step-wise discriminant function analysis.

Observed Sex & Spawning Status	Discriminant Function Classification		
	Non-Spawning	Spawning Male	Spawning Female
Non-Spawning	98.4% (n = 60)	-	1.6% (n = 1)
Spawning Male	-	100% (n = 8)	-
Spawning Female	9.1% (n = 1)	9.1% (n = 1)	81.8% (n = 9)

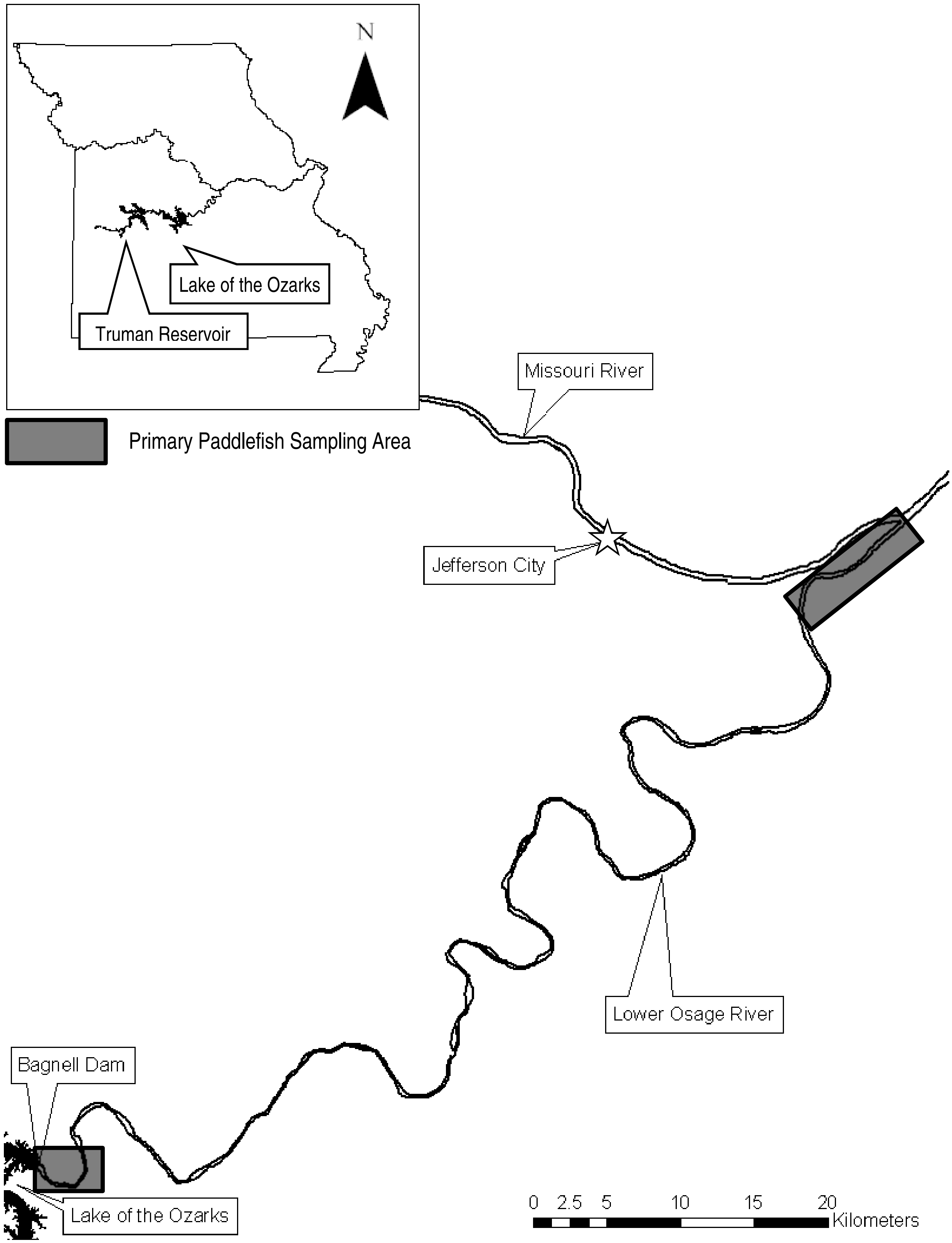

Figure 1. Map of the lower Osage River extending upstream of the Missouri River confluence to Bagnell Dam. Inset shows location of the Osage River in relation to the State of Missouri.

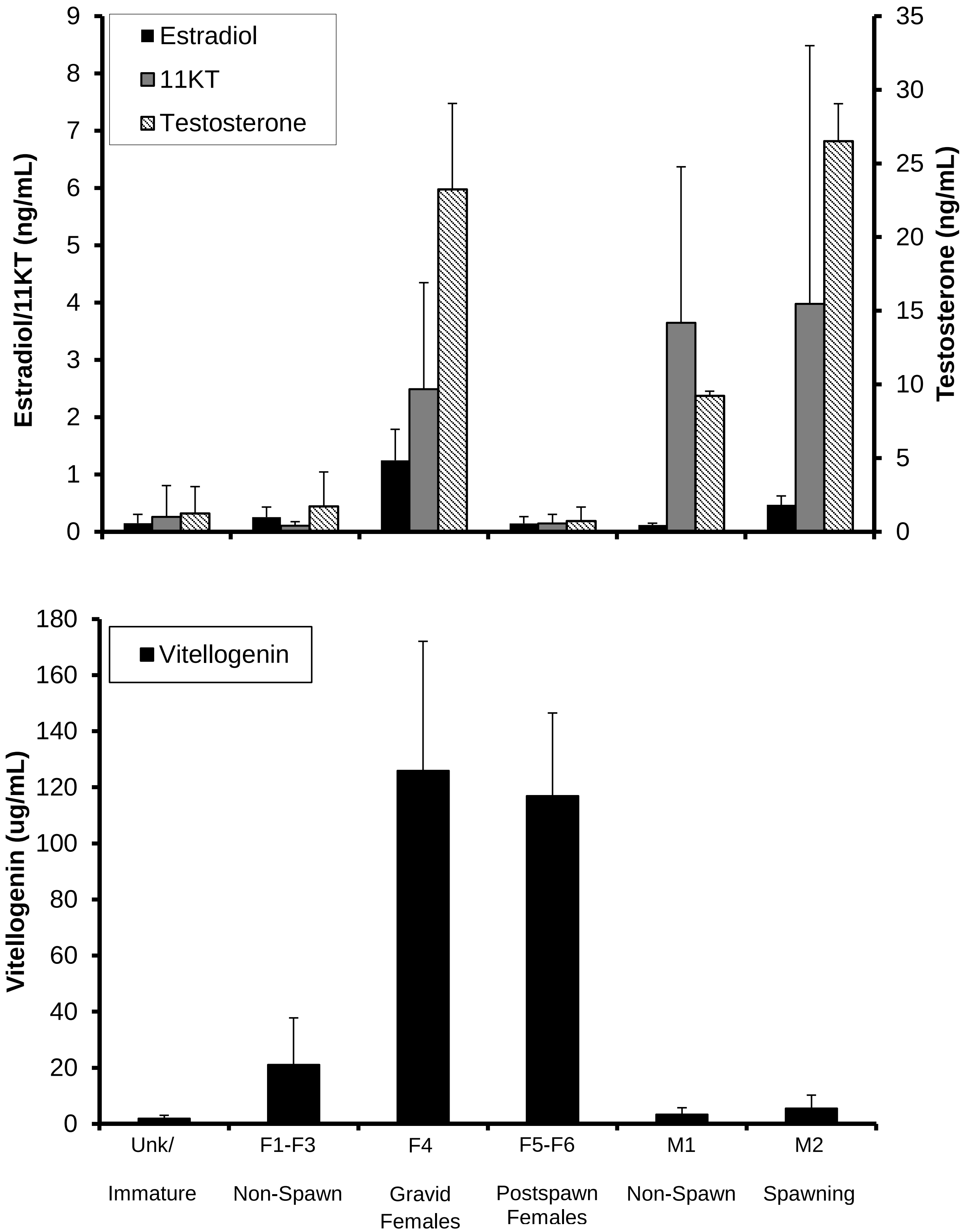

Figure 2. Estradiol, testosterone, 11-ketotestosterone, and vitellogenin levels for different macroscopically-assessed reproductive stages of paddlefish collected in the lower Osage River.

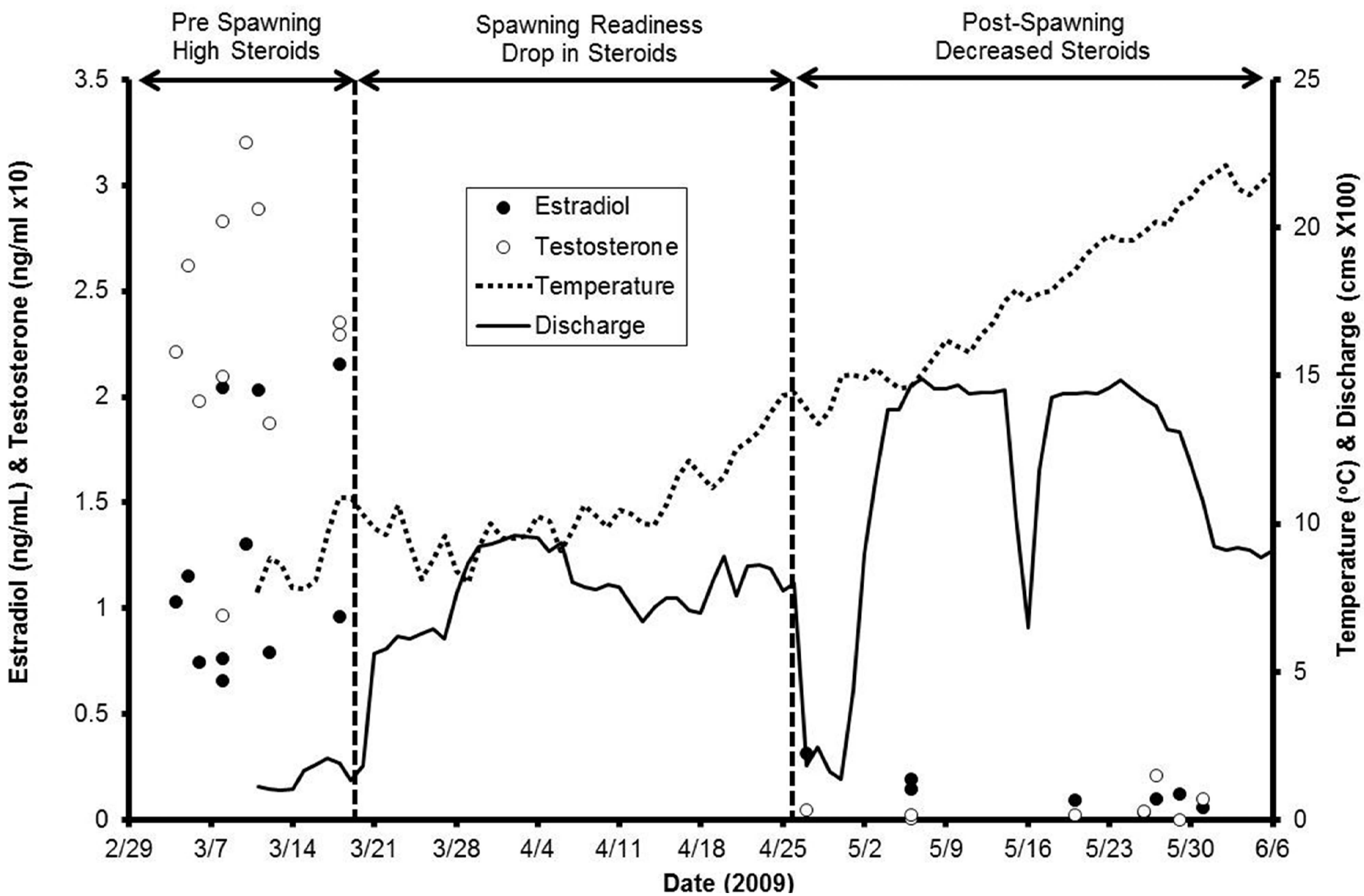

Figure 3. Estradiol and testoterone levels in spawning female paddlefish captured in the lower Osage River over the 2009 spawning season. The sharp drop in steroid levels indicate that spawning is likely occuring toward the end of April. Water temperatures and mean daily discharge are plotted for comparion with physiological data.

Chapter III

Predicting Physical Factors That Provide Upstream Passage Opportunities for Paddlefish over a Low-Head Lock and Dam

Abstract

Restriction of longitudinal migration is a major cause of population declines in river fishes. Effects of low-head and navigational dams that allow intermittent fish passage are poorly understood relative to the effect of large dams on fish passage and movement. Osage River Lock and Dam#1 is a 100-yr old navigational structure that restricts upstream fish movement during periods of low river discharge and provides an opportunity to study intermittent passage at a small scale in a regulated river system controlled by releases from a large hydroelectric facility, Bagnell Dam. We used logistic regression and AIC model selection procedures to predict upstream paddlefish passage through the lock and dam in relation to photoperiod, temperature, and discharge during the spring of 2007-2009. Over all three study years, we observed a total of 41 upstream passage events occurring between March 9th and May 15th. Mean daily temperatures during upstream passage events ranged from 8 to 16.8 ^{o}C. Osage and Missouri River discharge varied between passage events but all passages occurred at combined river discharge greater than 2,975 cms. The overall best fit model included a quadratic cumulative temperature function and an interaction term between mainstem (Missouri River) and tributary (Osage River) discharge, but did not include photoperiod (ΔAIC_c = 96.615, w_i = 09219). Retrospective application of our model showed passage probabilities greater than 50% occurring in 69% of the years analyzed between 1939-2009, however, nearly half (48%) of the years examined had 5 or fewer days exceeding the 50% passage probability. The ability to model and predict passage based on

environmental variables provides managers the ability to retrospectively analyze frequency of passage and better assess the need for structure modification and flow regulation. Additionally, predicting future flow patterns provides managers information to cooperate with large dam operators when determining minimal flow requirements needed for upstream fish passage.

Introduction

Fish behavior, including migration, is governed by an endogenous cycle which is adjusted and synchronized by environmental cues (Lam 1983; Rakowitz et al. 2008). Spawning migrations in many riverine fishes are thought to be triggered by three primary environmental cues: photoperiod, temperature, and flow regime characteristics (Northcote 1984). Photoperiod and temperature provide predictable annual cues for synchronizing reproductive cycles and regulating metabolic processes, including gonadal development and initiation of spawning migrations (Lam 1983). Predictable seasonal changes in water temperature and photoperiod synchronize fish behavior such as spawning, embryo development, and larval growth (Northcote 1998). In temperate regions, high spring discharges associated with snow-melt and increased spring precipitation result in consistent flow pulses which allow fish to capitalize on resultant conditioning of spawning substrate and inundation of flood plain habitat for larval rearing (Poff et al. 1997). Natural selection would likely favor integration of multiple environmental cues to stimulate spawning behavior under optimal conditions (Ovidio et al. 1998). Disruption or temporal decoupling of these cues therefore can alter behavior and ultimately reduce fitness.

Large dams (>15 m in height) are capable of altering riverine habitats on a greater scale compared to small dams (< 5m), yet small dams represent nearly 97% of the 75,000 dams in the continental United States (Graf 1999). Small dams can still result in significant ecological alterations, such as restricting longitudinal movement, fragmenting habitat, disrupting behavioral cues, and altering natural food webs, especially at the reach scale (Benstead et al. 1999). In contrast to large dams without fish passage structures, low-head and navigation dams may allow periodic passage of fishes, but these low-head dams are less commonly studied and information on the effects of intermittent passage on fish communities is therefore lacking (Zigler et al. 2004, Harford and McLaughlin 2007). Low-head structures may allow upstream passage during periods of high river discharge, yet delayed spawning migration during low river discharges can cause increased energy expenditures and cause fish to reach spawning grounds under sub-optimal spawning conditions (Sykes et al. 2009).

Paddlefish are a stereotypical large-river migratory species native to the large rivers and major tributaries of the Central United States. Paddlefish make long-distance spawning migrations associated with warming water temperatures and high spring river discharges. Paddlefish spawning has been recorded at temperatures ranging from 10-20^{o}C, although most observations are made near temperatures between 14-16^{o}C (Purkette 1961; Pasch et al. 1980; Russell 1986; Lein and Devries 1998; O'Keefe et al. 2007; Jennings and Zigler 2009). Most documented paddlefish spawning migrations have been observed during a rise in river discharge when water temperatures reached or exceed 8 to 10^{o}C (Purkette 1961, Paukert and Fisher 2001, O'Keefe et al. 2007). Dam construction has played a critical role in paddlefish population declines by restricting historical spawning migrations and decreasing available spawning habitat (Carlson and Bonislawsky 1981; Graham 1997; Gerken and Paukert 2009). Due to their migratory nature and historical abundance, paddlefish are an ideal study organism for understanding effects of low-head dams on intermittent passage within large river systems.

Despite potential impediments to fish passage and an altered flow regime, the Osage River (Figure 1) supports one of the largest paddlefish populations in Missouri. Two large mainstem impoundments, Truman Reservoir and Lake of the Ozarks, have restricted historical spawning migrations and fragmented paddlefish populations within the river. However, the optimal foraging conditions created by the upstream reservoirs sustain large populations of adult paddlefish which support substantial recreational fisheries. These recreational harvest fisheries are maintained through intensive stocking since the early 1980’s due to the inundation of all known spawning habitat by Truman Dam (Russell et al. 1980). The unimpounded river reach downstream of Bagnell Dam supports a smaller recreational paddlefish fishery and is not supplemented by direct stocking, relying on natural reproduction and immigration. Reproductive success in the lower Osage River may be strongly influenced by restricted access to upstream spawning habitat by Osage River Lock and Dam #1, hereafter referred to as L&D1. Located at rkm 20, this structure potentially restricts access to 112 rkm of upstream habitat in the Osage River.

Zigler et al. (2004) studied both upstream and downstream passage of paddlefish past lock and dams on the Mississippi River and found that mean hydraulic head (the difference in water elevation upstream and downstream of the structure) and water temperature were important variables determining successful passage. These authors concluded that mean dam head was directly proportional to water velocities and that greater hydraulic head resulted in greater velocities and decreased passage success. Water temperatures also were related to increased swimming activity and movement, including spawning migrations, which corresponded to increased fish passage. In contrast to the adjustable roller and tainter gate system on the Mississippi River navigation dams, the Osage River lock and dam has a fixed dam structure that creates a hydraulic head greater than 1 m except under high flow conditions (Figure 2). Hydraulic head at L&D1 is also affected by mainstem-tributary interactions due to the proximity to the Missouri River confluence (20 km downriver from L&D1). High Missouri River flows can increase river stage in the lower Osage River mouth extending upstream over 30 rkm (Del Lobb, personal communication). Increased river stage from the Missouri River can potentially influence fish passage by decreasing hydraulic head and reducing water velocities at L&D1. Lastly, L&D1 is no longer operated as a functioning lock and dam, so incidental fish passage during lock operation does not occur.

Paddlefish passage upstream of the Osage River lock and dam remains poorly understood, but can provide valuable insights into limitations on fish passage at low-head dam facilities. The objectives of our study were to 1) develop a model to relate environmental conditions (river discharge, water temperature, and photoperiod) to observed upstream migration of paddlefish past a low-head dam and 2) apply this model to historical and future river conditions to predict frequency of annual spring passage conditions. Our modeling approach will allow us to analyze historical passage conditions to determine the frequency of restricted passage conditions, and thereby provide evidence to evaluate the need for structural modification to facilitate fish passage. This model also will provide a useful forecasting tool for estimating the effects of discharge on paddlefish passage under varying flow and temperature conditions. Such an approach provides an invaluable tool for managing upstream discharge releases in regulated rivers or predicting passage effects from altered precipitation and discharges that are anticipated to occur with global climate change.

Study Site

We defined the lower Osage River as the 132 km stretch of free-flowing river beginning at the confluence with the Missouri River and extending upriver to Bagnell Dam (Figure 1). Average annual discharge at Bagnell Dam is 295 cms (Hauck and Nagel 2000). Both Truman and Bagnell Dams are operated primarily for hydroelectric generation and flood control, resulting in reduced flood peaks and daily peaking flows.

Osage River Lock and Dam #1 is located 20 rkm upstream of the Missouri River confluence. The structure is composed of a 12.8-m wide and 67-m long lock chamber joined to a low head dam approximately 3-m high and 256-m wide, spanning the entire river channel (Schulte 1992). Under typical river flows, the majority of river discharge is diverted through the lock chamber and only during periods of high discharge does water over-top the dam (Figure 2). This structure was built in the early 1900's to facilitate early steamboat travel on the river, but was decommissioned in 1951 due to insufficient use (Schulte 1992). After decommissioning, the U.S. Army Corps of Engineers sold L&D1 to a consortium of four private land owners that surround the structure. The Missouri Department of Conservation is currently negotiating a proposal to modify or remove L&D1 to increase fish passage, but this proposal is further complicated by the presence of five federally listed and seven state listed mussel species located just upstream of the structure (S. McMurray, Missouri Department of Conservation Mussel Specialist, personal communication).

Methods

Data Collection

Discharge, water temperature, and photoperiod were monitored to model effects of environmental variables on upstream paddlefish migration during the spring spawning period (March-June) in 2007-2009. Daily discharge data for the lower Osage River (OR) were obtained from U.S. Geological Survey (USGS) gauging station (06926000) downstream of Bagnell Dam (rkm 130). The gauging station downstream of Bagnell Dam, as opposed to downstream near St. Thomas (USGS gauging station 0696510), was selected because of the direct management implications to regulated discharge releases from Bagnell Dam. Flow data were also obtained from the closest upstream gauging station on the Missouri River (MR) that records discharge, which was near Boonville, MO (Missouri rkm 316) approximately 100 km above the mouth of the Osage river confluence. The Boonville gauging station provides a representative measure of discharge at the mouth of the Osage River as no large tributaries enter the Missouri River between Boonville and the confluence of the Osage River (Galat et al. 2005). Osage River temperature was recorded hourly at L&D1 using continuous recording dataloggers ([1]Onset Co., Pocasset, Ma, Model TBI32) placed upstream and downstream of the lock and dam site. Average daily river temperature was calculated from the hourly data. Fluctuations in average daily temperature can increase variability and dips in daily temperatures may not truly represent the thermal regime experienced by the fish. Consequently, we compared average daily temperature with cumulative temperature units (CTU) as a potentially more relative indicator of temperature effects on passage and used in many developmental studies (Braaten et al. 2008). CTU's were calculated as the sum of the average daily temperature beginning on 1 March, the earliest date that paddlefish were detected entering the Osage River, which more closely represented the temperature regime that paddlefish were experiencing prior to upstream migration. Hydraulic head was measured at the lock and dam site using two data logging pressure transducers ([1]Solinist, Georgetown, ON, Model 3001) placed upstream and downstream of the lock and dam site to better understand the hydraulic conditions affecting passage and compare our results with other passage studies. Greater hydraulic head differences at the lock and dam also increase turbulent flow and water velocity, which potentially results in greater difficulty for upstream passage.

Paddlefish sampling started in early March of each year when fish began entering the lower Osage River, but prior to significant upstream movement above L&D1. Paddlefish were captured using both monofilament gill nets (10.1, 12.7, and 15.24 bar mesh) and monofilament trammel nets (7.6 interior bar mesh, 30.5 exterior bar mesh). We selected these mesh sizes to target large adult paddlefish and minimize bycatch of other species (Paukert and Fisher 1999). Sampling was conducted 5-6 days per week until the majority of transmittered paddlefish began moving upstream. All sampling was conducted in the Osage River downstream of the lock and dam and upstream of the Missouri River to minimize the risk of capturing Missouri River migrants and maximize the number of paddlefish moving upstream in the Osage River.

Each paddlefish captured was measured for eye-to-fork length (EFL), weighed, and tagged with a uniquely numbered metal jaw tag for rapid visual identification of recaptures. Gravid adults of both sexes were targeted for transmitter implantation to more effectively monitor spawning migrations and maximize the number of upstream passages. Gonadal tissue was assessed macroscopically by making a 5-8 cm incision near the ventral midline just anterior to the pelvic girdle to identify sex and reproductive status. Categorization of sex and reproductive status was based on visual criteria created for lake sturgeon by Bruch et al. (2001). All gravid females and a subsample of reproductive males were selected for transmitter implantation. Individual fish movements were monitored by inserting a uniquely pulse-coded Combined Acoustic Radio Transmitter (CART) with a tag life of 565 days ([1]Lotek Inc., Newmarket, ON, Model CART16-3) inside the body cavity of selected individuals. An internal transmitter implant was chosen because of the longer retention, although the external antenna was trailed from a smaller posterior incision to increase radio transmittance and reception (Jepsen et al. 2002). To facilitate healing, surgical incisions were closed with an absorbable monofilament suture and sealed with a layer of surgical glue.

Telemetry

Three complimentary approaches (boat surveys, stationary receivers, and aerial surveys) were used to track paddlefish movements. This suite of methods allowed us to minimize the interval between locations and more accurately relate passage events to specific environmental conditions. Locations of paddlefish were obtained by boat surveys conducted 5-6 days per week between daylight hours from March through June. Paddlefish were located using a Lotek SRX400 receiver and unidirectional hydrophone.

Fish locations were obtained by maneuvering toward the transmitter signal until the maximum signal strength was obtained. Experimentation with fixed transmitter locations indicated that actual locations were within 10 m of estimated locations. GPS coordinates were recorded at each location using a Lowrance sonar unit with 12 Channel GPS WAAS receiver ([1]Lowrance, Tulsa, OK, Model LMS-480).

Helicopter surveys were used to supplement boat tracking once per week from March through April in 2007 and 2008. Flights were not conducted in 2009 due to budgetary restrictions. Aerial flights were conducted over the main channel from Bagnell Dam to the Missouri River. Signal strength of detected transmitters was used to determine approximate fish locations and GPS coordinates were recorded. Comparison of fish locations recorded by boat and helicopter made within 1 hour of each other revealed that helicopter locations were consistently within 100m of boat locations.

Stationary data-logging radio receivers were placed in the field to continuously record fish movements at two fixed locations: L&D1 (rkm 20) and near St. Thomas, MO (rkm 55) (Figure 1). Due to the large river width at L&D1, the stationary receiver could not effectively detect fish movement over the entire structure. Consequently, the receiver at L&D1 was positioned to detect passages occurring through the narrow lock chamber, which maintains upstream connectivity even under low flows. Paddlefish detected upstream of the lock and dam, but not detected by the stationary receiver, were assumed to have moved upstream over the low-head dam. Test transmitters used to evaluate the functionality of the receiver over variable flow conditions indicated that probability detection was high and fish were not moving through the lock undetected. A secondary stationary receiver was used to detect upstream movements of paddlefish and confirm upstream movements not detected by the receiver monitoring the lock. This secondary stationary site at rkm 55 was selected because the relatively narrow and shallow channel allowed effective detection of transmitters across the entire river width.

Statistical Analysis

The relationship between upstream passage and photoperiod, temperature, and discharge was modeled using logistic regression. Dates with one or more paddlefish detected moving upstream of the lock and dam were scored as a success, individual fish passages were not scored independently to avoid bias from pseudo-replication of passage days. Two non-passage dates were randomly selected for each successful passage date within the upstream migratory period (1 March – 31 May) of the same year. Two non-passage dates were chosen to increase sample size and more accurately represent non-passage dates because the random selection was likely to choose passage days where fish could have passed but did not, underrepresenting true non-passage dates. Our response variable (upstream passage success: yes or no) was then modeled against our environmental variables: Osage and Missouri River discharge, average daily temperature, cumulative temperature, and photoperiod. Due to the low samples sizes within individual study years, we pooled passage across all three study years.

We chose an information-theoretic model selection approach because reasonable *a priori* hypothesis could be developed from an understanding of paddlefish movement and the lock and dam flow dynamics. *A priori* we hypothesized that flow conditions would physically limit passage at L&D1 regardless of temperature or photoperiod. Consequently, a two-step model selection approach was used to reduce our candidate model set by initially selecting the best fit flow model from a subset of possible flow models, this best fit flow model was then included in subsequent temperature and photoperiod models. The best fit models were selected using Akaike's Information Criterion corrected for small sample sizes (AICc) (Burnham and Anderson 1998). The best models choices were selected within 2 AIC_c units of the best fit model (lowest ΔAIC_c) and model averaging was used if two or more models were selected. Small sample sizes prevented us from using an independent data set to validate our model. Consequently, we used a randomized bootstrap procedure to validate our best fit model (Verbyla and Litiatis 1989).

The overall best fit model for describing passage was applied to historical flow and temperature data to determine the potential frequency that L&D1 restricts upstream paddlefish movement during the spring spawning migration. The model was used to calculate the passage probability for each day during the upstream migratory period (1 March – 31 May) over the period of 1939-2009 from which there was reliable discharge and temperature data. Historical discharge data were obtained from the same USGS gauging stations used to develop the model (Bagnell Dam and Boonville). Historical river temperature was estimated using a linear relationship between stream temperature and the 30d running average of atmospheric temperature near Jefferson City, MO obtained from National Climatic Data Center (NCDC). Sufficient gaps in the daily atmospheric temperature record existed for the period 1965-1976, which resulted in these years being excluded from the analysis.

Results

Transmitters were placed in 86 paddlefish captured downstream of Lock and Dam #1 over all three study years (Table 1). Overall 36% of transmittered paddlefish were gravid females, 44% were reproductive males, and the reproductive condition of the remaining 20% could not be identified in the field and were most likely non-spawning individuals. To our knowledge, no transmitters malfunctioned prior to upstream movement and no mortalities were observed immediately following tagging.

Approximately one-half of the transmittered individuals in each year did not move upstream of L&D1, but instead exited the Osage River prior to optimal spawning temperatures reaching 16 ^{o}C. Out of 86 total paddlefish tagged downstream of L&D1, a total of 41 paddlefish moved upstream over all three study years. The suite of tracking methods used in this study resulted in identification of upstream passage events to within a 24 hour period or less for all individuals. However, only two upstream movements were detected by the stationary receiver monitoring lock passage at the lock and dam. The ability of the stationary receiver at the lock to detect test transmitters under a range of river flows, suggests the remaining 39 detections of paddlefish upstream of L&D1 are assumed to have occurred by paddlefish moving over the low-head dam rather than through the lock chamber.

Spring discharge peaks were similar in magnitude and duration compared to the previous 30 years of discharge data (Figure 3). Upstream passages over all three years occurred at various combinations of Osage and Missouri river discharges (Figure 4). Initial passages in 2007 occurred at high Missouri River discharges (>2,800 cms), but low Osage River discharges (<280 cms). Subsequent passages occurred at lower

Missouri River discharges (<2,800 cms), but higher Osage River discharges (>850 cms). All upstream passages occurred at combined river discharge greater than 2,975 cms (Figure 4). A broken-line regression was fitted to the hydraulic head data to represent the discharge (2,975 cms), at which hydraulic head in the lock chamber and over the dam were at a minimum of 1 m or less (Figure 5). At discharges below 2,975 cms hydraulic head increased rapidly and represents more challenging physical conditions for upstream passage.

In addition to the variation in discharge patterns between years, timing of high discharge events and corresponding upstream passages varied considerably among years (Figure 4). Passage events occurred over a ten day period from 27 April – 7 May in 2007. In contrast to the narrow passage window in 2007, passages over L&D1 in 2008 occurred over a 28 day period from 3-30 April. Passages in 2009 occurred during two discrete periods from 30 March – 2 April and 28 April – 15 May, but no passages were detected between 3-27 April during a period of low Missouri River discharge (Figure 4).

Upstream passages across all years occurred at temperatures between 8.0 - 16.8 ^{o}C with a mean of 12.5 ^{o}C (SD 3.0), except for one outlier in 2008 where a fish initially moved upstream in early March but subsequently moved back downstream. Similar to average daily temperature, CTU's ranged from 210 to 790 with a mean of 468 (SD 195). All but one passage occurred during high water events at temperatures exceeding 8.0 ^{o}C and CTU's exceeding 310 despite high water events occurring in early to mid-March in 2008 and 2009 when water temperatures were between 4 - 8^{o}C.

Passage events were pooled across all three years in the model analysis due to the relatively low number of upstream passage events in individual study years. The flow model including the interaction effect between Osage and Missouri river discharges had the strongest support (AIC_c = 96.615, w_i = 0.9219) and was used in the subsequent temperature and photoperiod models (Table 2). The quadratic temperature models had better support than linear models (ΔAIC_c>10), and the CTU model had much stronger support than the average daily temperature model (Table 2). None of the models including photoperiod increased the model fit above 2 ΔAIC units. Overall, the best fit model included the interaction effect between Osage and Missouri River discharges and the quadratic CTU function (AIC_c = 75.814, w_i = 0.9988) (Table 2). Results from the boot-strap procedure showed percent concordant pairs for the best fit model was 96%, indicating a high degree of model fit and accurate predictability.

Using the best fit model, passage probabilities curves for 5, 25, 50, 75, and 95% were plotted at the optimal passage temperature of 435 CTU (Figure 6). All but the 95% curve shows a negative interaction between Osage and Missouri river flows. Missouri River discharges less than 2,500 cms require Osage River discharges exceeding 850 cms for greater than 50% passage probability. In contrast, when Missouri River discharges exceed 2,800 cms, the Osage River discharge required for greater than 50% passage probability drops rapidly. Successful passage events were plotted at the optimal CTU of 435 in the figure for reference, showing that all but three passages occurred above the 50% passage probability curve.

The results of our retrospective model analysis showed that passage varies considerably by year. We summed the number of days that exceeded passage probabilities of 5, 25, 50, 75, and 95% during the spring migratory period from 1 March through 31 May (n=92) for the period of historical record (1939-2009) to illustrate the effect on paddlefish passage during the spring spawning migration (Figure 7). The missing years in the figure are due to an incomplete atmospheric temperature record and the inability to estimate stream temperature. Forty-two years (69%) had more than one passage day exceeding our estimated 50% passage probability. Passage may have been restricted in 19 years (31%) with no days exceeding 50% passage probability and an additional 10 years (17%) had 5 or fewer passage days exceeding 50% passage probability. Overall, nearly half (48%) of the years examined provided 5 or fewer days with greater than 50% modeled upstream passage probability.

Discussion

Our results showed that transmittered paddlefish were able to successfully pass upstream of the lock and dam in all three study years and that these study years were likely representative of most years (Figure 3). Despite successful passage, the timing and duration of upstream movement was highly variable and dependent upon high flow events occurring during an optimal temperature range of 10-20^{o}C. We did not observe any relationship between upstream movement and photoperiod, nor did any models including photoperiod significantly reduce our AIC values. Similarly, Paukert and Fisher (2001) did not observe any influence of photoperiod on upstream migration of paddlefish most likely due to the more direct influence of discharge and temperature. McCormick et al. (1998) differentiated photoperiod as a priming factor ultimately responsible for physiological readiness in Atlantic salmon, but not directly responsible for proximate behavioral cues. Although photoperiod likely synchronizes annual cycles such as gonadal development and physiological processes, more proximal cues such as temperature and flow may provide better predictors for triggering upstream movement and spawning due to their direct effects on embryo development and larval growth.

We observed upstream passages occurring over a wide range of Osage and Missouri River discharges. Combined discharges of the two rivers above 2,975 cms decreased the hydraulic head at the lock and dam to less than 1 m, likely facilitating upstream passage. These results are similar to Zigler et al. (2004) who found passage probability increased when hydraulic head was less than 1 m in Mississippi River locks and dams. However, many other studies (Purkett 1961; Paukert and Fisher 2001; Miller and Scarnecchia 2008) report that paddlefish move upstream in response to increases in river discharge. In contrast, we observed a significant number of upstream movements in 2008 and 2009 during periods of high, but stable discharge (Figure 4). Our data suggest that the hydraulic head conditions of the lock and dam are a necessity for upstream passage and may supersede or mask the role of discharge cues for migration.

Inclusion of the interaction term between the Osage and Missouri River flows in our model highlights the important connections between mainstem and tributary flows. Higher Missouri River flows decreased hydraulic potential and facilitated passage even under low Osage River discharges. However, as Missouri River flows decreased, Osage River flows became increasingly more important for minimizing hydraulic head and facilitating upstream passage (Figure 6). Inundation of tributary mouths caused by high flows in the mainstem increases stage height and reduces water velocities in tributary mouths, which may create favorable conditions for upstream migration. Similarly, Valdez et al. (2001) found that mainstem flow pulses inundated habitat in tributary mouths in the Colorado River, which was beneficial for native flannelmouth and endangered humpback chubs to rest and ascend tributaries during their spawning migration. Consequently, mainstem flows in addition to tributary flows may serve as a critical component of upstream migration for fishes that routinely use tributaries to spawn or to rest during upriver migrations in the mainstem.

Upstream movement occurred above average daily temperatures of 8°C in our study (Figure 4). Similarly, many other studies have noted the importance of water temperatures exceeding 8-10°C for triggering upstream movements of paddlefish (Purkett 1961; Paukert and Fisher 2001; Miller and Scarnecchia 2008). However, our best fit passage model selected the model with CTUs over average daily temperature for predicting upstream passage. CTUs are widely recognized as a more accurate predictor of physiological processes, such as embryo and larval development than average daily temperatures (Smith and King 2005; Braaten et al. 2008). Our results also support the evidence that CTUs may be a more accurate predictor of behavioral triggers over daily temperatures or temperature thresholds (Zydlewski et al. 2005; Sykes et al. 2009).

The strong support of both flow and temperature in our best fit model highlights the importance of multiple cues for triggering upstream movement. The lack of passage events during the high water events in early March and late May, suggest that optimal temperatures are required in addition to high water to trigger upstream movement, as shown by the importance of the quadratic CTU function in our model. Additionally, the absence of passages during optimal temperatures at low flows highlights the necessity of adequate flows for upstream passage.

Low-head structures that intermittently allow passage may restrict passage to periods of high discharge independent of optimal temperatures for migration and reproduction. Although paddlefish may access upstream spawning habitat during high water conditions, these high flow conditions may not occur at optimal temperatures for migration, reproductive development, or spawning. In 2008, high water throughout much of the spring resulted in early and more prolonged passage events. In 2007 and 2009, passages were restricted to narrow time periods when temperatures were already at or near optimal spawning temperatures, possibly resulting in delayed upstream migration and access to upstream spawning habitat at sub-optimal temperatures. Regulated low flows that caused delayed spawning migrations in Pacific salmon are known to decrease reproductive success by decreasing adult condition and reducing egg survival due to sub-optimal temperature conditions (Bjornn and Reiser 1991). Additionally, many fish will reabsorb their gametes if they are delayed in reaching upstream spawning habitat (Shikhshabekov 1971). Similarly, Russell (1986) noted that female paddlefish will potentially reabsorb eggs if optimal spawning conditions (temperature, flow, and photoperiod) are not synchronized, which could be an indirect result of delayed migration.

The results of our retrospective model analysis extrapolate well beyond the three years of data collection in our study, but provide a generalized picture of how variable and frequent passage conditions might be over time. Paddlefish successfully moved upstream of the lock and dam in all three years of our study, yet our retrospective analysis indicates that these three study years may not represent conditions in all years (Figure 7). Restricted upstream access could greatly reduce reproduction and recruitment success as a consequence of the paddlefish's specific behavioral and physiological adaptations for spawning in upriver habitats (Jennings and Zigler 2009). Although we did not directly compare paddlefish recruitment success between passage and non-passage years, restricted passage at L&D1 reduces access to upstream spawning habitat. Additionally, limited access to upstream spawning habitat reduces available habitat for downstream larval drift, which has been shown to reduce reproductive success in sturgeon (Kynard et al. 2007).

Development of a passage model provides managers with a tool for estimating passage probability based on specific river flows and optimal migration temperatures. Current regulations require Bagnell Dam to generate a minimal spring flow of 25.5 cms or 40% of the seven day rolling average inflow (Ameren 2007), which may be insufficient to allow upstream passage if Missouri River flow is below 2,800 cms (Figure 6). Using the interactive flow model to forecast passage probability over various combinations of river discharges will enable managers to improve dynamic minimal spring flow requirements for Bagnell Dam to ensure upstream passage under various flow regimes. For example, if Missouri River discharge was at 2,500 cms (mean monthly discharge for April), Osage River discharge would need to exceed 870 (95% CI: 800-940) cms to ensure 50% passage probability or greater (Figure 5).

Additionally, this model will also allow managers to identify the range of conditions that restrict passage and focus on creating more effective structural modifications to low-head dams. In the Osage River, lock and dam #1 allows upstream passage at discharges exceeding combined river discharge of 2,975 cms. So structure modifications to facilitate passage should focus on the restrictive low flow conditions below 2,975 cms that increase hydraulic head above 1 m and reduce passage probability. The ability to model passage and determine frequency and timing of passage restriction can focus management and assist with structured decision making in dam removal projects.

Knowledge of how fishes move upstream of low-head lock and dams is critical to designing effective passage modifications. Only two paddlefish were detected passing upstream through the lock chamber. Similarly, other studies have found that very few fish use lock chambers to pass upstream (Coker 1929; Zigler et al. 2004). Zigler et al. (2004) showed that paddlefish were rarely located immediately downstream of the lock chamber, and hypothesized that attracting flows were greater downstream of the dam tail waters, resulting in few paddlefish entering the lock chamber. Many fish species are known to select narrow ranges of velocities when encountering barriers to upstream migration, and optimal flows are critical for attracting fish toward passage structures and ultimately affect passage success (Moser et al. 2000; Bunt 2001). Capeleti and Petrere (2006) observed reduced passage efficiency because fish were more attracted to flows coming from the impassable spillway rather than to a fish ladder designed to facilitated passage. This observation indicates that even in low–head dams, attracting flows can strongly affect passage efficiency. Successful modification of low-head dams for fish passage could incorporate knowledge of attracting flows and tendency of fish to avoid using lock chambers for upstream movement.

Although the impacts of large dams on fish populations are well studied, the effects of intermittent passage over low-head and navigational dams are potentially complex. These structures may allow upstream passage at high flows; however, low water years can prohibit upstream migrations and result in failed or reduced year classes. Additionally, discharges that allow passage maybe decoupled from optimal temperatures cues, causing delayed migration and reduced reproductive potential despite potential upstream access. Numerous dam removal projects across the U.S. are currently underway or in development. Modeling frequency and timing of passage restrictions should aid in the decision and design of these projects (Shuman 1995, Hart et al. 2002). Quantitative fish passage models, similar to ours, are effective in determining limitations to passage and providing information to design flows that allow passage or to modify structures that facilitate passage during low flows.

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Table 1. Total number, sex ratio (male:female), and size range (eye-to-fork length) of paddlefish implanted with transmitters. Number of upstream passages over Osage River Lock and Dam#1 is also noted for each study year.

Study Year	Total Number Implanted	Sex Ratio (M:F)	Size Range (EFL cm)	Number of Upstream Passages
2007	20	16:4	73-112	10
2008	34	21:13	64-105	15
2009	32	18:14	72-109	16

Table 2. *A priori* flow, temperature, and photoperiod models predicting upstream passage of paddlefish over Osage River Lock and Dam #1. Model parameters, (standard errors), corresponding AIC_c values and AIC weights (w_i) are shown for each model.

Model Step	Model Parameters	AIC_c	ΔAIC_c	w_i
Step 1 – Flow Model				
Interaction Effect River Discharge	0.531(0.239)ORQ + 0.252(0.107)MORQ + 0.008(0.001)ORQ*MORQ	102.915	0.000	0.9219
Missouri River Discharge	0.001(0.000)MORQ	109.344	6.429	0.0370
Additive River Discharge	0.001(0.001)ORQ + 0.001(0.000)MORQ	109.752	6.837	0.0302
Osage River Discharge	0.004(0.001)ORQ	113.036	10.121	0.0058
Null Model	Null	113.364	10.449	0.0050
Step 2 – Temperature & Photoperiod Models				
Best Flow Model + Quadratic Cumulative Temp Units	0.486(0.162)ORQ + 0.152(0.056)MORQ + 0.004(0.001)ORQ*MORQ + 0.028(0.01)CTU + 0.000(0.000)CTU^2	75.814	0.000	0.9988
Best Flow Model + Quadratic Average Daily Temp	0.383(0.128)ORQ + 0.120(0.044)MORQ + 0.003(0.001)ORQ*MORQ + 2.120(0.735)AveT + -0.920(0.029)$AveT^2$	89.381	13.567	0.0011
Best Flow Model + Photoperiod	0.228(0.083)ORQ + 0.070(0.028)MORQ + 0.002(0.001)ORQ*MORQ + 0.120(0.131)Photo	102.287	26.473	0.0000
Best Flow Model + Linear Average Daily Temperature	0.266(0.086)ORQ + 0.072(0.028)MORQ + 0.002(0.001)ORQ*MORQ + -0.200(0.079)T	99.896	24.082	0.0000
Best Flow Model + Linear Cumulative Temp Units	0.276(0.089)ORQ + 0.074(0.029)MORQ + 0.002(0.001)ORQ*MORQ + -0.003(0.001)CTU	96.935	21.121	0.0000

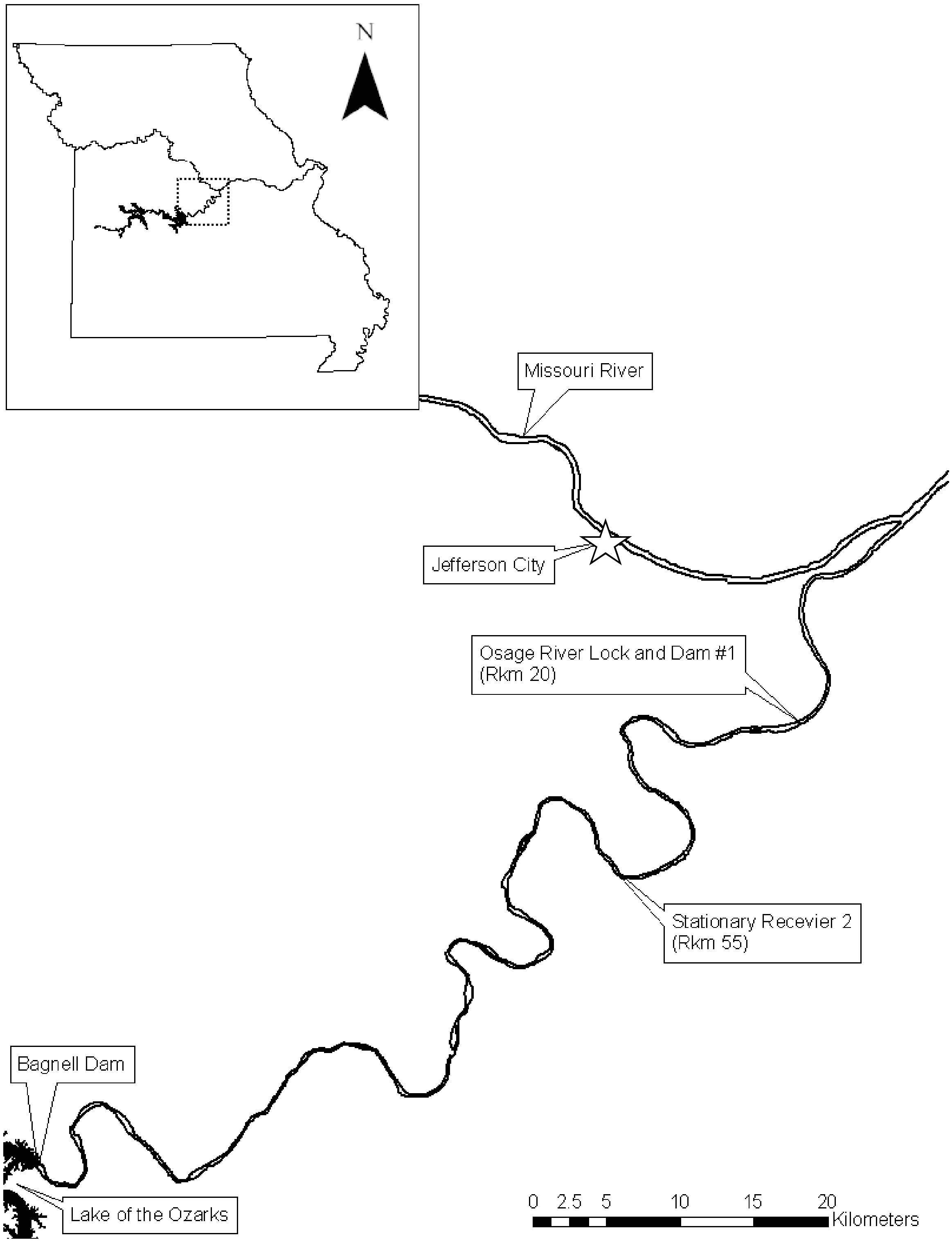


Figure 1. Map of the lower Osage River extending from the confluence with the Missouri River upstream to Bagnell Dam. Stationary telemetry receivers were placed at Osage River Lock and Dam #1 and a second upstream site (rkm 55). Inset shows location of the Osage River in relation to the State of Missouri.

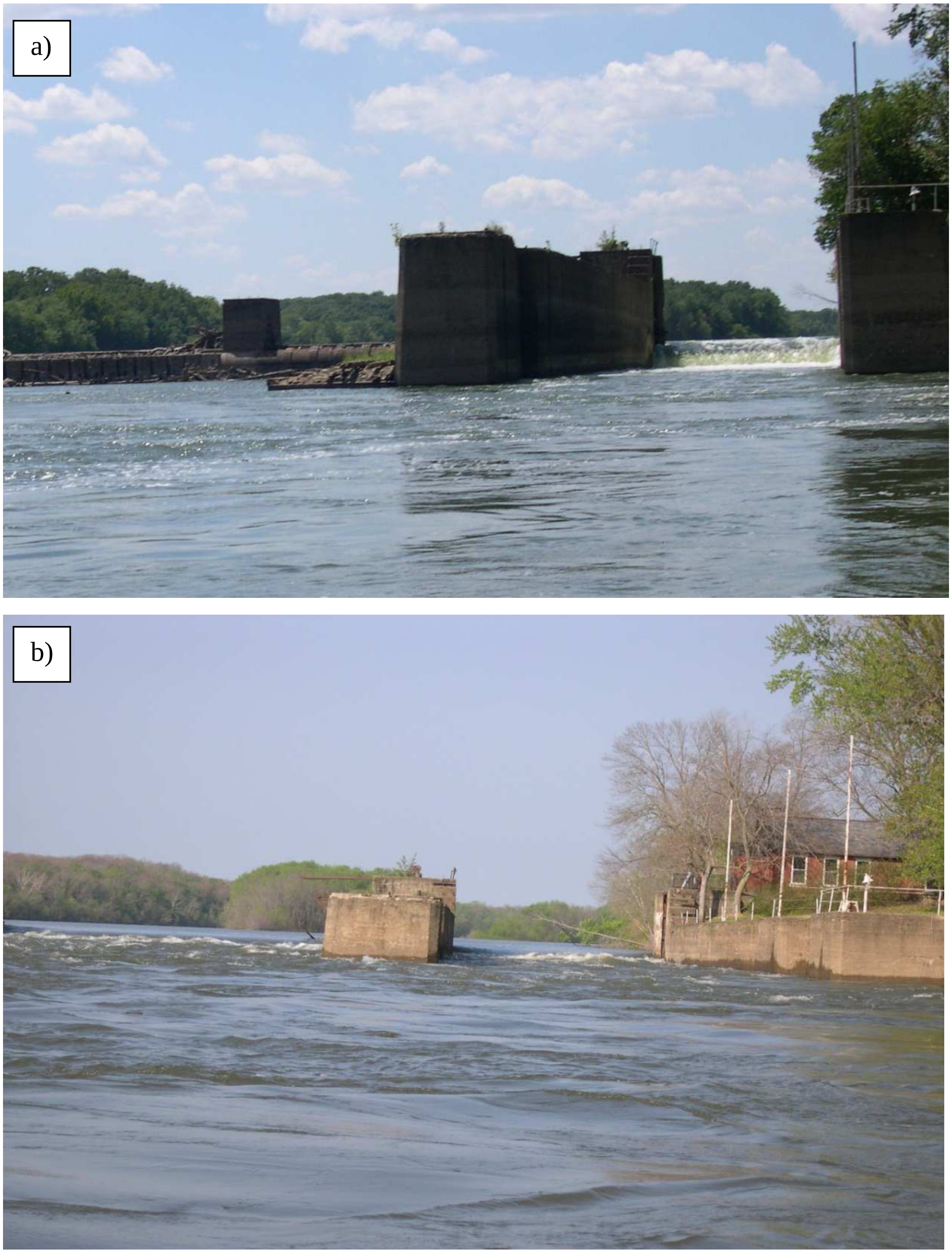


Figure 2. Upstream facing photo of Osage River Lock and Dam #1 comparing hydraulic conditions at a) low Osage River discharge (96 cms) and b) high Osage River discharge (849 cms).

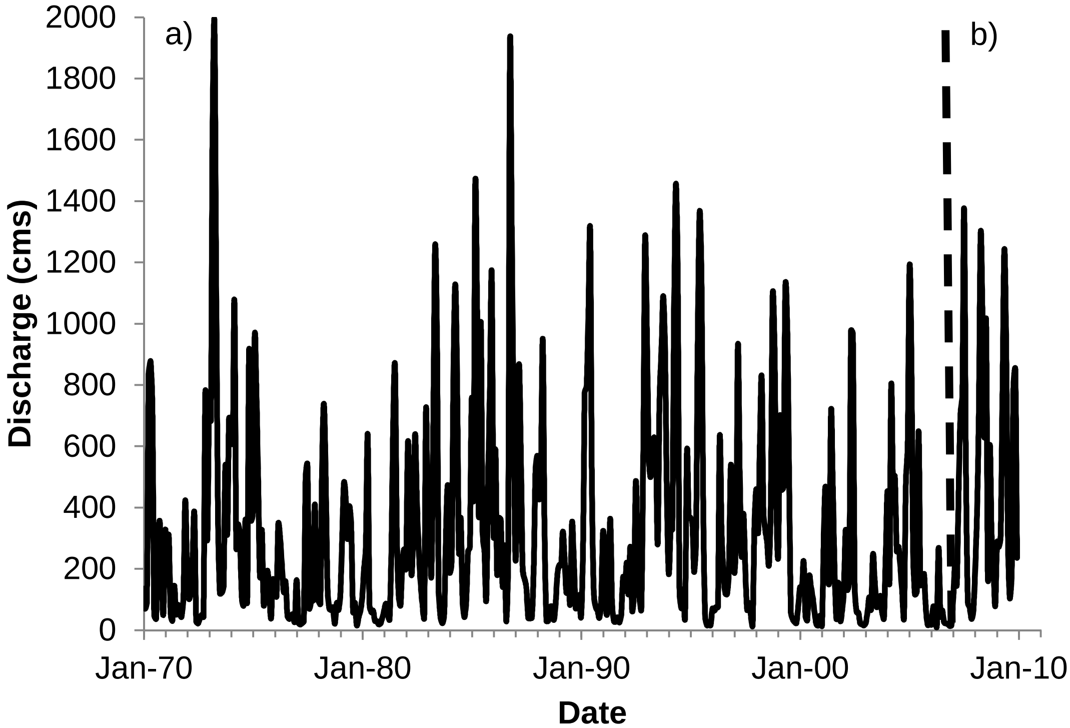


Figure 3. Mean monthly discharge of the Osage River comparing the magnitude and duration of spring floods during a) discharges over the period from 1970-2006 and b) the three year study period, 2007-2009.

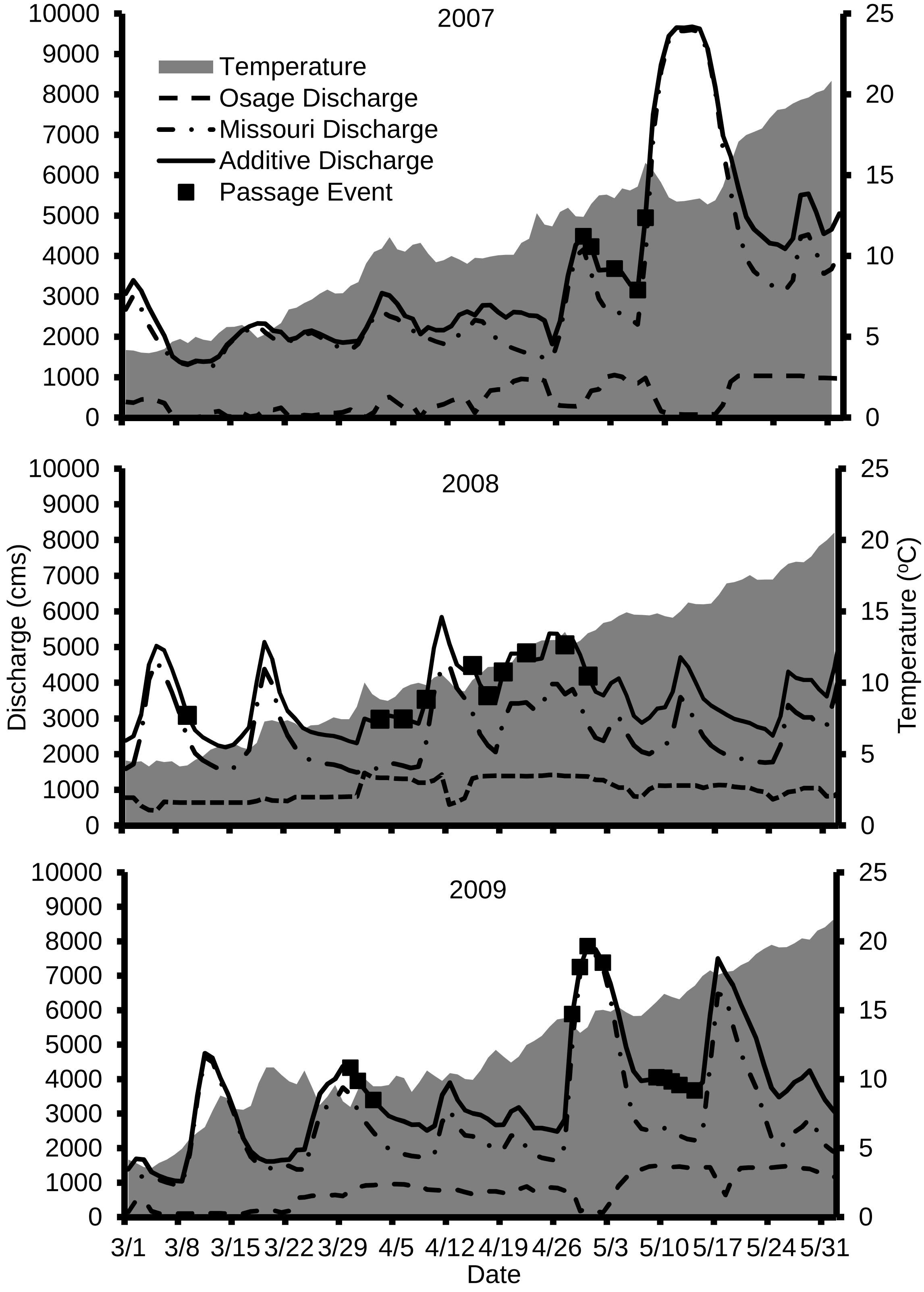


Figure 4. Timing of paddlefish passage upstream over Osage River Lock and Dam #1 in relation to temperature and river discharges for study years 2007-2009. No upstream passages occurred below a combined Osage and Missouri river discharge of 2,975 cms.

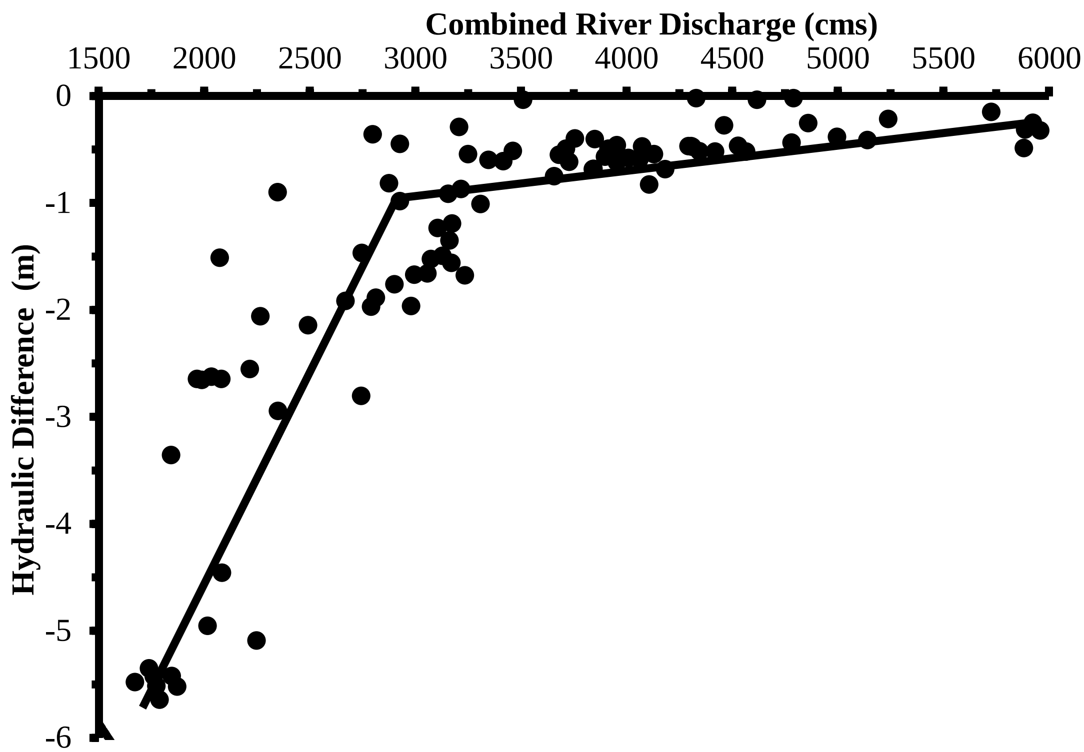
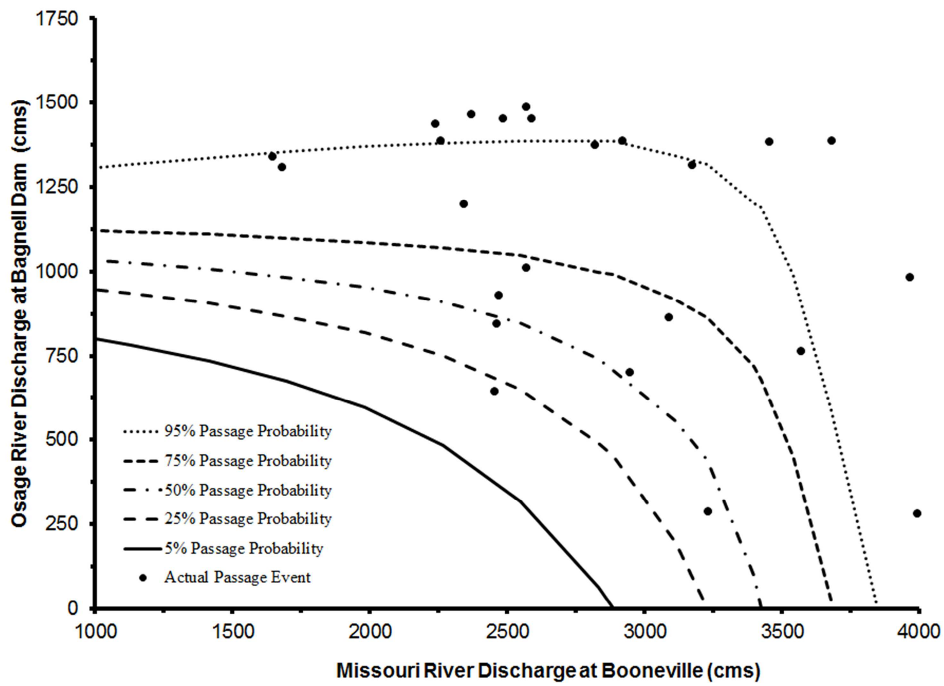


Figure 5. Hydraulic head (difference between upstream and downstream river stage) of Osage River Lock and Dam #1 at various combinations of Osage and Missouri river discharges recorded between March-October 2008. A broken-line regression was fit to the data using the lowest observed passage discharge of 2,750 cms for the break point ($p < 0.0001$, $R^2 = 0.8143$).



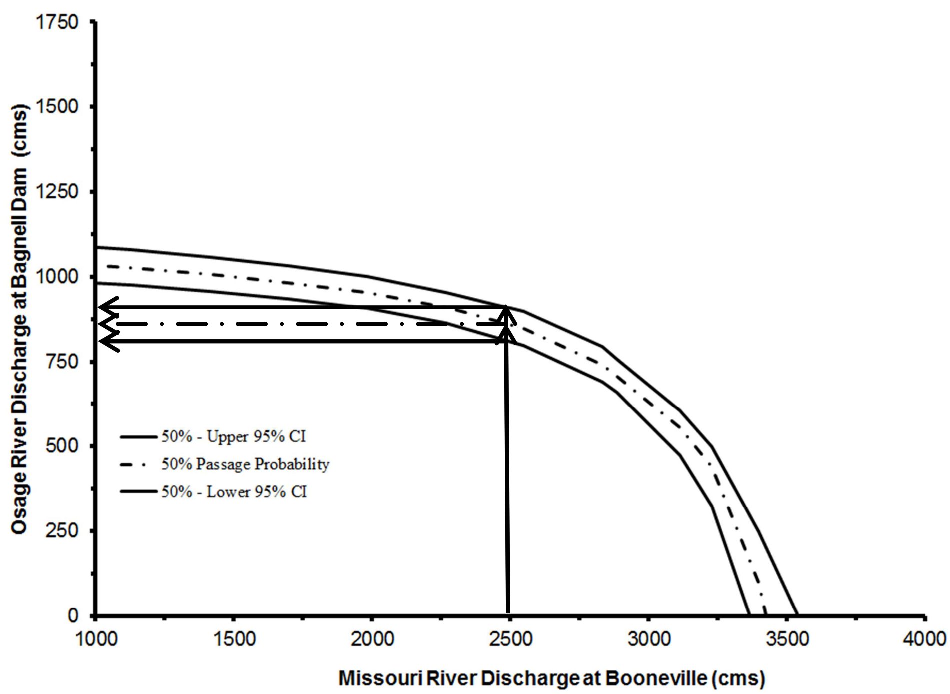


Figure 6. Probability curves predicting upstream passage of paddlefish over Osage River Lock and Dam #1 generated using passage model at an optimal temperature of 435 cumulative temperature units. Lower figure shows confidence interval for 50% passage probability and a hypothetical discharge combination for 50% passage probability.

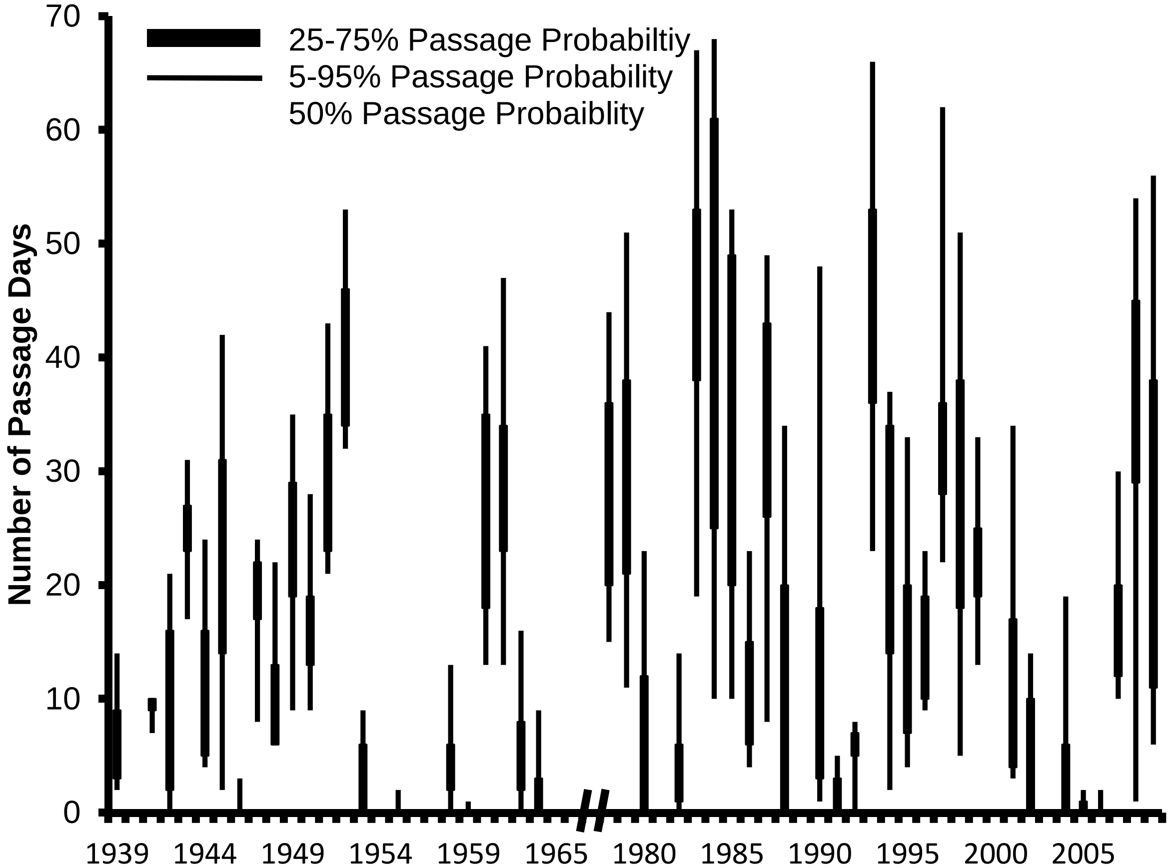


Figure 7. Number of passage days between 1 March and 31 May (n=92) corresponding to the estimated upstream paddlefish passage probability between 5-95% and 25-75%. The gap in x-axis corresponds to incomplete atmospheric temperature data for 1965-1976 and the inability to predict stream temperature.

Chapter IV

Effects of Regulated River Discharge on Paddlefish Spawning Movements and Spatial Use below a Hydroelectric Dam

Abstract

Alteration of river flows for hydroelectric generation, flood control, and reservoir management have the potential to disrupt fish behavior and habitat use downstream of dams. Paddlefish, a typical large-river migrant, often concentrate in dam tail waters during their spawning migration and are vulnerable to the effects caused by regulated river discharge. Our objectives were to 1) examine paddlefish movement patterns in response to regulated river discharge and temperature, and 2) determine the influence of regulated river discharge on residence time and spatial use downstream of a hydroelectric dam. Transmitters were surgically implanted into 86 paddlefish and locations were obtained daily from 1 March – 30 June, 2007-2009, resulting in a total of 1,936 individual paddlefish locations. Mean residence time below Bagnell Dam was 12.5 (SD = 6.8) days in 2007, 53.9 (SD = 15.6) days in 2008, and 36.6 (SD = 7.24) days in 2009. We observed three distinct discharge patterns associated with Bagnell Dam operation: 1) peaking, 2) flood mitigation and 3) flood release. Movement was generally restricted to less than 1 km/day during typical hydroelectric peaking operation, but increased to downstream movements of greater than 40 km during flood mitigation. Flood releases did not result in downstream movements greater than 2 km, but spatial use within core areas was lower during flood mitigation (3,592 ± 2,515 m^2) and flood release (7,716 ± 6,140 m^2) compared to peaking (11,739 ± 5,570 m^2). Model results supported our observations as linear discharge was the best predictor of movement distance and direction compared to temperature or temperature and discharge models (AIC = 454.59;

w_i = 0.9943). Although temperature plays an important role in synchronizing initial migration, temperature may be not be as strongly associated with daily movement, especially when fish are subjected to such large differences in discharge. Flood mitigation causing restricted flow releases and downstream displacement of fish, followed by subsequent rapid flood releases of stored water may not be sufficient to provide successful reproduction of paddlefish and other large-river migrants below large hydroelectric or flood storage dams.

Introduction

Alteration of natural flows is one of the most pervasive and damaging forms of disturbance to river environments caused by dams (Petts 1984; Stanford et al. 1996; Murchie et al. 2008). Flood control operations reduce the magnitude of peak flow events, and alter the timing and duration of summer and winter low-flow events by slowly releasing stored flood waters (Poff et al. 1997). Peaking operations raise discharge to meet periods of high electrical demand and reduce discharge during periods of low electrical demand, resulting in frequent and often rapid changes in discharge over a diel cycle. These changes to discharge affect habitat features such as water velocity and depth immediately downstream of the dam. These physical habitat changes may dramatically influence the spatial distribution of habitat use and community composition immediately downstream of a dam (Cushman 1985).

Paddlefish are a stereotypical large-river migrant, which have existed relatively unchanged for nearly 135 million years (Jennings and Zigler 2009). Paddlefish have evolved to make long-distance spawning migrations from deep, low-velocity overwintering habitat to upstream river reaches with fast velocities (0.5-1.5 m/s), adequate depth (> 3m), and coarse substrate required for successful reproduction (Russell 1986; Crance 1987). Upstream migrations are often rapid 20-40 km/day and are often associated with an increase in spring temperature and discharge (Russell 1986; Paukert and Fisher 2001; Firehammer and Scarnecchia 2006). Paddlefish hold in deep-water habitat immediately downstream of suitable spawning habitat until spawning is synchronized by a combination of temperature and flow (Purkett 1961; Pasch et al. 1980; Russell 1986; Papoulias et al. 2011). Residence time on the spawning grounds is variable but has been associated with the timing of successful environmental conditions for spawning (Donabauer et al. 2009). Paddlefish make rapid downstream migrations after spawning toward habitat more suitable for summer foraging (Russell 1986).

Large-scale declines in paddlefish populations over the last century have been attributed in part to habitat fragmentation and the restriction of spawning movements caused by dam construction (Gengerke 1986). Paddlefish in impounded rivers are restricted from extensive upstream spawning movements and typically concentrate in dam tailwaters during the spawning season (Pasch et al. 1980; Paukert and Fischer 2001; Stancill et al. 2002). Tailwaters downstream of large dams often have suitable depth, velocities, and substrate required for successful paddlefish spawning, but may have disrupted flow regimes that may interfere with spawning cues and behavior (Pasch et al. 1980). Regulated temperature and flow conditions of dam releases may alter spatial use of habitat and behavioral cues of paddlefish located in these tailwater regions and ultimately influence reproductive success.

Successful paddlefish spawning has been observed downstream of several hydroelectric dams (Pasch et al. 1980; Wallus 1986; Lein and DeVries 1998), yet most impounded rivers show poor reproduction and remain poorly studied (Jennings and Zigler 2000; Gerken and Paukert 2009). Restriction of spawning movements and disruption of spawning cues are considered the predominant threats limiting paddlefish reproduction in impounded rivers (Gerken and Paukert 2009). However, little attention has been given to understanding movement and spawning habitat use of paddlefish in relation to regulated discharge. Paukert and Fischer (2001) observed that spawning paddlefish did not move upstream in several Oklahoma Rivers during a year with extremely low flows and restricted dam releases. Firehammer and Scarnecchia (2006) observed a significant relationship between decreases in discharge and long downstream movements in the upper Missouri River below Fort Peck Dam. Additional studies on paddlefish reproductive success in response to peaking and flood control discharges are lacking.

The effects of regulated river discharge on paddlefish reproduction are still poorly understood, but have significant consequences for adequate protection and management of the species. Disruption of spawning movements and habitat use may be detrimental to paddlefish reproduction. The objectives of our study were to 1) document paddlefish movement patterns in response to regulated river discharge, and 2) determine the influence of regulated river discharge on residence time and spaital use of paddlefish downstream of Bagnell Dam. Optimizing regulated discharge to maximize human benefit and minimize environmental impact requires a more comprehensive understanding of the negative impacts to iconic riverine fishes that carry out critical life history processes (i.e. spawning) below hydroelectric impoundments.

Study Site

The Osage River, located in west-central Missouri, has two major impoundments that fragment paddlefish populations and alter the natural flow regime: Bagnell and Truman dams (Figure 1). The larger downstream dam, Bagnell Dam, is owned by Ameren UE and operated primarily for hydroelectric generation, with eight hydroelectric turbines capable of generating 171 kW at a maximum output of 1060 cms (Ameren 2007). Bagnell Dam was recently relicensed by the Federal Energy Regulatory Commission in 2007, which resulted in an agreement of increasing annual minimum flows from 12.7 to 25.5 cms or 40% of the previous seven day average of inflow. Ameren also has a memorandum of Agreement with the Army Corps of Engineers to alleviate downstream flooding in the Missouri River by reducing discharge below mandated levels of 25.5 cms. Ramping rates were also regulated in the new licensing agreement to reduce the rate of flood draw-downs to occur over a four day period. Lastly, Bagnell Dam is operated for maintenance of stable reservoir levels in Lake of the Ozarks between 210 and 213 m above sea level.

Migratory paddlefish have access to 132 km in the lower Osage River from the Missouri River upstream to Bagnell Dam (Figure 1). A decommissioned lock and dam is located 20 km upstream from the mouth, which restricts upstream movement to periods of high discharge and may delay initial upstream migration (Lallaman Chapter 3). Paddlefish spawning migrations begin in early to late March and paddlefish concentrate downstream of Bagnell Dam throughout the spawning season (April-May) (Lallaman Chapter 3, 5). A 6-week snag fishery for paddlefish is open from 15 March – 30 April.

Harvest is restricted within a no snagging zone extending 2 km downstream of the dam to the US 54 bridge.

Methods

Data Collection

Sampling for paddlefish began in early March of each year when they began entering and staging in the lower 20 km of the Osage River. Paddlefish were captured using both monofilament gill nets (10.1, 12.7, and 15.2 cm bar mesh) and monofilament trammel nets (7.6 cm interior bar mesh, 30.5 cm exterior bar mesh). We selected these mesh sizes to target large adult paddlefish and minimize bycatch of other species (Paukert and Fisher 1999). All sampling was conducted in the Osage River at least 2 km upstream of the Missouri River to minimize the risk of capturing Missouri River migrants resulting in the loss of fish moving out of the system.

Each paddlefish captured was measured for eye-to-fork length (EFL), weighed, and tagged with a uniquely numbered metal jaw tag for rapid visual identification of recaptures. Gravid adults of both sexes were targeted for transmitter implantation because our primary focus was spawning movement and habitat use. Previous studies indicate that paddlefish do not reach reproductive age prior to attaining 60 cm EFL (Reed et al. 1992), which is the minimal size threshold we used to identify mature individuals. Assessment of sex and reproductive status were further refined by macroscopically examining the gonadal tissue of all fish greater than 60 cm EFL. Gonads were visually examined by making a 5-8 cm abdominal incision near the ventral midline just anterior to the pelvic girdle. Categorization of sex and reproductive status was based on visual criteria created for lake sturgeon *Acipenser fulvescens* by Bruch et al. (2001).

All gravid females and a subsample of reproductive males were selected for transmitter implantation. Individual fish movements were monitored by inserting a uniquely pulse-coded Combined Acoustic Radio Transmitter (CART) with a tag life of 565 days ([1]Lotek Inc., Newmarket, ON, Model CART16-3) inside the body cavity of selected individuals. Surgical incisions to examine reproductive status were also used for internal transmitter implantation, although the external antenna was trailed from a smaller posterior puncture. Internal implantation allowed for maximal transmitter retention, whereas externally trailing the antenna increased radio signal transmittance and reception (Jepsen et al. 2002). Faster recovery and healing was encouraged by closing the surgical incisions with an absorbable monofilament suture and sealing with a layer of surgical glue.

Three complimentary approaches (boat surveys, stationary receivers, and aerial surveys) were used to track paddlefish movements. This suite of methods allowed us to minimize the interval between locations and more accurately relate movement patterns to specific changes in environmental conditions. Locations of paddlefish were obtained primarily by boat surveys conducted 5-6 days per week between day light hours from March through June. Prior to upstream migration over the lock and dam, the entire 20 km of the lower Osage River from Lock and Dam #1 to the Missouri River Confluence was tracked by boat. Once upstream migration began, the Osage River was blocked into roughly 40-rkm sections and tracking was conducted in a rotational pattern between sections. After all fish had migrated to below Bagnell Dam, tracking was concentrated to locate every individual within 12 rkm of the dam until downstream migration. Tracking switched back to rotating between the 40-rkm sections once fish began moving downstream.

Diel movement patterns were assessed to examine small-scale movement patterns and determine if significant differences existed between day and nighttime movement and spatial use. Three diel tracking studies were conducted on one randomly selected day in April and May, and June of each year. One randomly selected paddlefish was selected and located once every hour for 24 hours. If additional paddlefish were in close proximity, attempts were made to relocated these individuals as much as possible.

Paddlefish were located using a boat-mounted Lotek SRX400 receiver and unidirectional hydrophone ([1]Lotek, Newmarket, Ontario). Fish locations were obtained by maneuvering toward the transmitter signal until the maximum signal strength was obtained. Experimentation with fixed transmitter locations indicated that actual locations were within 10m of estimated locations. GPS coordinates, water depth, and surface temperature were recorded at each paddlefish's location using a Lowrance sonar unit with 12 Channel GPS WAAS receiver ([1]Lowrance, Tulsa, OK, Model LMS-480).

Helicopter surveys were used to supplement boat tracking once per week from March through April in 2007 and 2008. Flights were not conducted in 2009 due to budgetary restrictions. Aerial flights were conducted over the main channel from Bagnell Dam to the Missouri River. Signal strength of detected transmitters was used to determine approximate fish locations and GPS coordinates were recorded. Accuracy of paddlefish locations in the helicopter was assessed by determining the linear distance between helicopter and boat locations made within 1 hour of each other.

Stationary data-logging radio receivers were placed in the field to continuously record fish movements at two fixed locations: L&D1 (rkm 20) and near St. Thomas, MO (rkm 55) (Figure 1). The stationary receiver site at L&D1 was chosen to detect fish passage upstream of this structure in relation to environmental conditions (Lallaman Chapter 3). The large river width at L&D1 prevented the stationary receiver from effectively detecting fish movement over the entire structure. Consequently, the receiver at L&D1 was positioned to detect passages occurring through the narrow lock chamber, which maintains upstream connectivity even under low flows. This secondary stationary receiver site at rkm 55 was selected because the relatively narrow and shallow channel allowed effective detection of transmitters across the entire river width. The continuous data logging capacity of the stationary receivers allowed us to compare diel fish movements past a stationary point with diel movements recorded by boat.

Discharge and water temperature were monitored to identify potential relationships between environmental variables, paddlefish movement, and spatial use during the spring spawning period (March-June) in 2007-2009. Hourly discharge data downstream of Bagnell Dam were obtained from U.S. Geological Survey (USGS) gauging station (06926000) downstream of Bagnell Dam. Osage River temperature was recorded hourly at multiple sites (rkm's 2, 20, 55, 76, 110, and 130) along the lower Osage River using continuous recording data loggers ([1]Onset Co., Pocasset, Ma, Model TBI32). Diel movement was compared to hourly data, whereas large-scale movement was compared to average daily discharge and river temperature calculated from the hourly data of the nearest logger.

Movement Analysis

Paddlefish movement patterns were analyzed for directional relationships with both mean daily temperature and discharge. Latitude and longitude coordinates were imported into geographic information systems (GIS) software and overlaid on a digitized river map in ArcMap, ([1]Environmental Systems Research Institute, Redlands, California). River kilometers on the digitized map were designated to the nearest tenth of a kilometer and GIS software used to link each location to the nearest 0.1 km. Upstream and downstream movement distances were then calculated from changes in river kilometer between locations.

Absolute differences in environmental variables may not accurately reflect the magnitude of change over the range of all possible differences. For example, an increase in discharge from 100 to 200 cms has the same absolute difference as an increase from 900 to 1000 cms, but does not have the same relative change (50% vs. 10%, respectively). Estimation of discharge and temperature responses that more accurately reflected relative changes in overall magnitude were calculated using the log of the quotient as suggested by Firehammer and Scarnecchia (2006):

$$\Delta X = log_e(X_t/X_{t-d})$$

where X is discharge or temperature, t is the date of contact, and t-d is the time between last contact. Only detections within two consecutive days were used in the movement analysis, as long periods between detections and movement may have resulted in under-representing the true change in discharge or temperature over longer periods. Natural log transformation was used to normalize the data.

Relative distance and direction (upstream = positive movement) was then modeled against relative changes in linear discharge, quadratic discharge, linear temperature, quadratic temperature, and discharge and temperature interactions using linear regression. An information-theoretic model selection procedure was chosen because reasonable *a priori* hypothesis could be developed from an understanding of environmental variables on the direction (upstream or downstream) and distance of paddlefish movement. *A priori* we predicted that discharge and temperature would have linear or quadratic effects on movement either individually, additively, or interactively. The best fit models were selected using Akaike's Information Criterion (AIC) (Burnham and Anderson 1998). The best models choice was selected within 2 AIC units of the best fit model (lowest ΔAIC) and no model averaging was needed if the best-fit model was greater than 2 AIC units from the next best model. AIC model selection procedures only evaluate the candidate model set and may select the best model from a poor candidate model set. The accuracy of the best model selected by AIC was evaluated using a subset cross-validation (Boyce et al. 2002). Movement data from 2007 were used to develop the initial model and subsequently tested for concordance among predictive pairs using the 2008 and 2009 data.

Residence time was used to evaluate the duration of time spent downstream Bagnell Dam and evaluate the possible effect of regulated discharge on prolonging spawning behavior. Paddlefish frequently moved between several locations within a 10-km stretch downstream of the dam throughout the spawning period. Rapid downstream movement greater than 10 km without subsequent upstream movement was used as an indicator of post-spawning behavior. Residence time was calculated as the numbers of days between initial detection and the date of last detection within 10 km of Bagnell Dam.

Spatial Use Analysis

Changes in the spatial distribution of fish in relation to changes in discharge regime were tested using nearest-neighbor clustering and convex polygon technigques. Multiple core areas of intense spatial use were identified using a nearest-neighbor clustering technique suggested by Kenward et al. (2004) using Ranges V software. This approach allowed identification of intense areas of use by clustering nearest neighbor locations. Areal estimates for minimum convex polygons were calculated in ArcMap once clusters were identified. Only locations from boat surveys were used for spatial analysis, as helicopter and stationary receivers lacked accurate 2-D locations of paddlefish within the stream channel

Results

We observed a distinct difference in discharge patterns between the regulated Osage River compared to the neighboring and unregulated Gasconade River (Figure 2). Three distinct discharge patterns associated with Bagnell Dam operation were observed: 1) peaking: large oscillations in maximum and minimum daily discharge due to hydroelectric peaking; 2) flood mitigation: extreme decreases in discharge due to downstream flood mitigation, and; 3) flood release: high stable release of stored flood waters without peaking (Figure 3). Discharged peaked daily between 330 to 1050 cms during hydroelectric peaking and was the primary discharge pattern observed under non-flood conditions. During periods of flood mitigation, Bagnell Dam reduced discharge typically below 100 cms until downstream flooding had crested and was below flood stage. Flood release discharges were characterized by sustained discharges of 1000 to 1700 cms and were observed after flood periods as excess floodwaters were released downstream. Stable discharges of approximately 1000-1060 cms were observed when releases were solely through the powerhouse and stable discharges between 1060 and 1700 cms were observed during periods of additional spill gate releases.

Transmitters were placed in 86 paddlefish captured downstream of Lock and Dam #1 (Table 1). Overall, 36% of transmittered paddlefish were gravid females, 44% were reproductive males, and the reproductive condition of the remaining 20% could not be identified in the field and were most likely non-spawning individuals. Forty-six of the 86 transmittered individuals tagged near the river mouth did not move upstream to Bagnell Dam, but were harvested or exited the Osage River prior to upstream movement. Individuals that moved out of the Osage River prior to upstream migration were excluded from the movement or spatial use analysis. No mortalities were observed immediately following tagging or prior to upstream movement.

Movement Analysis

In total, 2,014 individual paddlefish locations were recorded for the 40 fish moving upstream in the Osage River over all three study years (Table 1). The suite of tracking methods used in this study resulted in 76% of consecutive relocations of individuals occurring within a 24 hour period and allowed for a smaller-scale analysis of movement and river condition. Boat locations represented the majority (92.2%) of all locations. Helicopter locations represented 3.8% of all locations and were typically within 100 m of boat locations made within 1 hour of each other (mean = 88.5 m, SD = 11.3 m). Eighty-one detections at stationary receivers (4%) provided additional data on movement rates and diel activity of paddlefish movement. Thirty-two (40%) of stationary receiver detections were recorded during day-light hours (Figure 4). Diel observations showed that average hourly movement rates were typically less than 1-km/hr (SD = 0.7 km/hr) and movement rates did not vary significantly between day-time or night-time hours ($t = 0.543$; $P = 0.2981$) (Figure 4).

Average upstream movement rates were rapid (mean = 22.3, SD = 13.2 km/day) and occurred during periods of high discharge. Paddlefish typically moved upstream and remained within 10 km of Bagnell Dam making minor movements (< 1 km) throughout the suspected spawning period. Large downstream movements greater than 10 km from Bagnell Dam were observed during periods of extreme low flow caused from mitigating downstream flooding (Figure 5). Model results for the AIC analysis selected the linear discharge model as the best fit to predict movement distance and direction (AIC = 454.59; $w_i = 0.9943$) (Table 2). No other models were within 10 ΔAIC units, suggesting that neither the temperature models or temperature and discharge models significantly improved model fit. Cross-validation procedures showed a 61% and 54% accurate classification using 2008 and 2009 validation data respectively, supporting the discharge model as the best candidate model.

Residence time varied considerably between all three years. Mean residence time was the shortest (mean = 12.5, SD = 6.8 days) in 2007 and all but three fish moved downstream within a 7 day period in mid-May. Residence time was the longest and most variable (mean = 53.9, SD = 15.6 days) in 2008 and intermediate (mean = 36.6, SD =

7.24) in 2009. Several males in each year remained upstream within 2 km of Bagnell Dam all summer, were relocated downstream of the dam the following spring, and migrated downstream after the second spring spawning season.

Spatial Use Analysis

Spatial use downstream of Bagnell Dam changed in relation to dam operation. The number of core areas did not change dramatically between peaking (n=5), flood mitigation (n=4), or flood release (n=6). However, mean core areas downstream of Bagnell Dam under flood mitigation (3,592 ± 2,515 m^2) and flood release (7,716 ± 6,140 m^2) were lower than during peaking (11,739 ± 5,570 m^2) (Figure 6). Paddlefish primarily occupied the low velocity area below the spill gates and several downstream areas during peaking flows. Periods of flood mitigation resulted in downstream movement and greater use of downstream areas. Periods of flood release shifted spatial use to more restricted areas downstream of the powerhouse and downstream areas.

Discussion

Regulated river discharge had observable differences in the timing, duration, and frequency of discharge in the Osage River, especially compared to a neighboring unregulated river, the Gasconade (Figure 2). The type of regulated discharge release (peaking, flood mitigation, or flood release) resulted in major differences in paddlefish spawning movement and spatial use downstream of Bagnell Dam. Our best fit model of paddlefish movement showed that linear mean daily discharge was the best predictor of paddlefish movement distances and direction (Table 2). Upstream movements were associated with increases in river discharge, whereas decreases in mean daily discharge, especially large decreases due to flood mitigation, were related to downstream movements of paddlefish. Downstream movement distance was proportional to the decrease in discharge, with larger discharge reductions (1,000 cms to < 25 cms) resulting in larger downstream movement of paddlefish (> 80 km) (Figure 4). Increased discharge following flood mitigation resulted in subsequent upstream movement, but repeated or prolonged displacement from upstream spawning areas could negatively affect reproduction (Young et al. 2011). The majority of past paddlefish movement studies have not observed significant downstream movements of paddlefish during the spring spawning migration (Southall and Hubert 1984; Moen et al. 1992; Paukert and Fischer 2001; Zigler et al. 2003). Firehammer and Scarnecchia (2006) observed similar movement responses to regulated river discharge in the upper Missouri River downstream of Fort Peck Dam. The authors hypothesized that frequent downstream movement would increase energy demands, decreasing fitness, and possibly result in decreased reproductive success of paddlefish.

Temperature was not included in the best-fit model, suggesting that temperature may not influence reach-scale movement and spatial use. The relatively small differences in temperature (6^{o}C to 18^{o}C) compared with the discharge changes associated with dam operation (<25 cms to >1,400 cms), may provide an explanation for the strong support of discharge over temperature. In contrast, temperature is often cited as an important migratory cue (Northcote 1984), and temperature was an important variable associated with initial upstream movement of paddlefish above the Osage River Lock and Dam (Lallaman Chapter 3). Papoulias et al. (2011) observed similar importance of temperature in shovelnose sturgeon *Scaphirynchus platorynchus* migration in the regulated Missouri River downstream of Gavins Point Dam, but observed much more variable spawning behavior in response to other environmental conditions, such as discharge. The contrasting importance of temperature in this study suggests that although temperature plays an important role in synchronizing initial migration, temperature may be not be as strongly associated with daily movement, especially when fish are subjected to such large differences in discharge.

Residence time was noticeably different among all three study years and may have subsequent implications for spawning success. Initiation of upstream migration did not occur at the same time each year as upstream passage over the lock and dam was dependent upon high discharge at optimal migratory temperatures (Lallaman Chapter 3). Downstream migration was also variable among years, although downstream movement was not physically restricted. The majority of paddlefish in 2007 moved downstream in May within a 7 day period and showed synchronous downstream movement indicative of post-spawning behavior observed in other species (Northcote 1984). A similar synchronous downstream movement pattern was observed in 2009, but occurring several weeks later in early June. Paddlefish movements in 2008 did not show any synchronization in downstream movement and they exhibited much higher residency times, suggesting that a synchronous spawning event may not have taken place possibly due to inadequate spawning cues. Donabauer et al. (2009) observed a significantly higher residency time of spawning catfish in a year with lower flows, but still observed mass downstream migration after an increase in flow and documented successful spawning. Displacement of paddlefish from upstream spawning habitat during flood mitigation, followed by immediate flood releases capable of mimicking natural flow cues to synchronizing spawning could result in failure of paddlefish to successfully capitalize on increased flows for spawning cues. Large rises (>500 cms) in spring discharge releases, that might simulate a natural spring rise, only occurred as a result of increased discharge during periods of flood release after a period of flood mitigation (Figure 3).

Diel observations of paddlefish were similar to previously published studies (Zigler et al. 1999). Migratory movements past the stationary receivers and diel observations did not show any significant differences between day and night and were typically made in direct response to changing discharge (Figure 4). Diel movements of paddlefish in response to peaking operations (<10 km/day) were not as pronounced as the larger downstream migrations (40 – 80 km/day) associated with flood mitigation (Figure 5). Young et al. (2011) recently reviewed the influences of hydroelectric discharge on stream fishes and found similar results throughout the literature with much larger flood flows having a greater effect on fish movement and spatial use, than smaller peaking flows. Large-magnitude changes in discharge caused by flood mitigation may be a greater influence on paddlefish movement in the Osage River than smaller-magnitude changes associated with peaking discharge.

Spatial use also showed significant changes in response to Bagnell Dam operation. Paddlefish occupied larger core areas, especially in the area immediately downstream of the spill gates, during typical peaking operation (Figure 6). Paddlefish use deep water habitat (Crance 1987; Zigler et al. 2003), which was reduced under flood control operation and likely resulted in paddlefish movement downstream in search of deeper habitat. During the largest drawdowns during flood mitigation, nearly all paddlefish occupied two deep-water holes (> 10-m depth), located at rkm 32 & rkm 113, created by gravel mining. The concentration of paddlefish in two artificial deep water areas suggests that natural deep water habitat downstream of Bagnell Dam may be scarce during extreme low water periods.

Downstream movement and spatial use in response to regulated discharge may have an additional indirect effect on harvest rates of paddlefish in exploited populations. Concentrated aggregations of paddlefish downstream of dams are often protected by restrictive or no harvest zones (Scholten 2009), as is the case downstream of Bagnell Dam. Flood mitigation concentrated paddlefish in several deep-water holes downstream from the dam, but outside of the protected no snagging zone (Figure 1). Timmons and Hughbanks (2000) suggest that area closures to protect paddlefish may be an effective and easily enforceable management strategy to protect paddlefish populations, yet displacement of paddlefish outside of protected areas below dams may increase harvest. Although no direct assessment of harvest was conducted in this study, increased vulnerability to harvest may be an additional consequence of paddlefish response to artificial low flows and require larger no harvest zones below dams.

The use of mean daily discharge does not necessarily capture the daily range in discharge or hourly rate of discharge change. Coefficients of variation in daily discharge can be a better predictor of organismal response to changes in discharge due to regulated flow release (Bunn and Arthington 2002). In this study, mean daily discharge was chosen as the simplest metric to analyze coarse scale differences in discharge releases compared to movement and spatial distribution. Future movement modeling should consider the use of multiple discharge metrics to better capture the effect of regulated discharge over different scales (Young et al. 2011).

Studies with controlled before-after measurements are difficult to obtain as the new construction of large hydroelectric dams has been greatly slowed in the United States and is occurring at a rapid pace in developing nations. Study of paddlefish in unregulated rivers is also problematic as most large rivers have already been impounded and few paddlefish populations are found in un-dammed or unregulated rivers (Russell 1986). This study provides a testable model of paddlefish response to changes in regulated discharge in the Osage River. Cooperation of large-dam operators to regulate flows based on model predictions and continued monitoring would provide additional strong evidence for modifying flows needed to enhance reproductive behavior and success of large-river fishes. Based on our results in the Osage River, regulated river discharges appear to affect paddlefish movement and spatial use downstream of dams, which likely influence reproductive success in regulated systems. Flood mitigation displaces species downstream likely as a result of reductions in deep water holding habitat and suitable spawning habitat during extreme low water events. Although flood control and hydroelectric generation provide positive societal benefits, the potential negative effects to spawning of migratory riverine fishes require a more comprehensive approach and better understanding of dam operation (peaking, flood mitigation, flood release) and the response of these fishes to specific discharge patterns.

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Table 1. Total number, sex ratio (male:female, M:F), and size range (eye-to-fork length, EFL) of paddlefish implanted with transmitters and the total number of locations observed in the lower Osage River between 2007-2009.

Study Year	Total Number Implanted	Sex Ratio (M:F)	Size Range (EFL cm)	Number of Locations
2007	20	16:4	73-112	547
2008	34	21:13	64-105	969
2009	32	18:14	72-109	497

Table 2. *A priori* flow and temperature models predicting movement of paddlefish in the lower Osage River. Model parameters (standard errors) and corresponding AIC values and AIC weights (w_i) are shown for each model.

Model	Model Parameters	AIC	ΔAIC	w_i
Linear Discharge	2.481(0.981)Q	454.59	0	0.9943
Linear Temp	0.432(0.673)T	465.82	11.23	0.0036
Quadratic Discharge	2.342(0.884)Q 5.753(1.642)Q^2	466.98	12.39	0.0020
Null Model	Null	499.82	45.23	0.0000
Quadratic Discharge*Temp	5.753(1.642)Q^2 0.186(.290)T^2 0.387(0.292)Q^2*T^2	498.32	43.73	0.0000
Quadratic Discharge + Temp	3.975(1.372)Q^2 0.173(0.312)T^2	487.55	32.96	0.0000
Linear Discharge + Temp	2.962(1.032)Q 0.592(0.479)T	486.72	32.13	0.0000
Quadratic Temp	0.513(0.565)T 0.323(0.467)T^2	477.13	22.54	0.0000

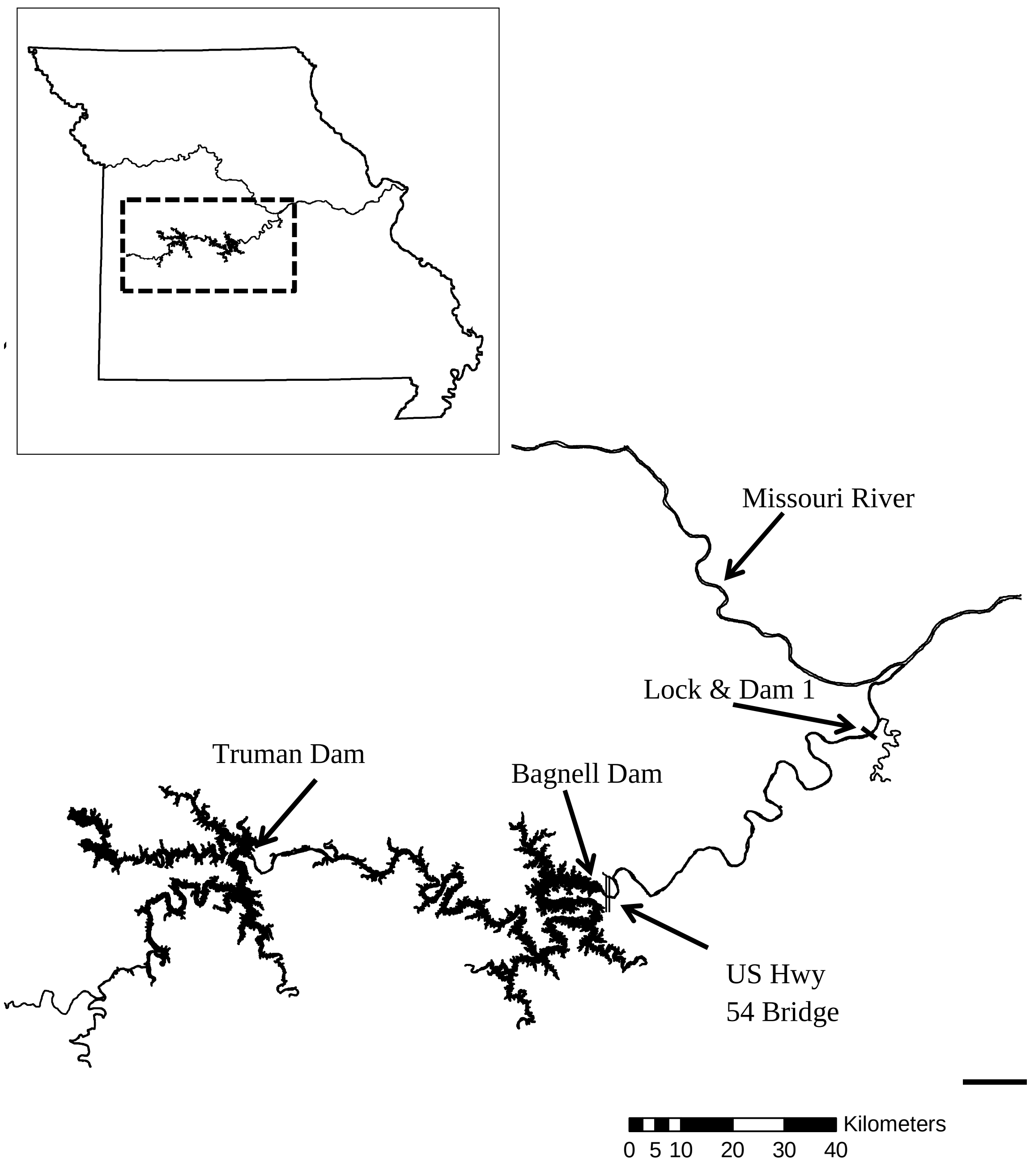

Figure 1. Map of the Osage River, showing the location of the two upstream dams.

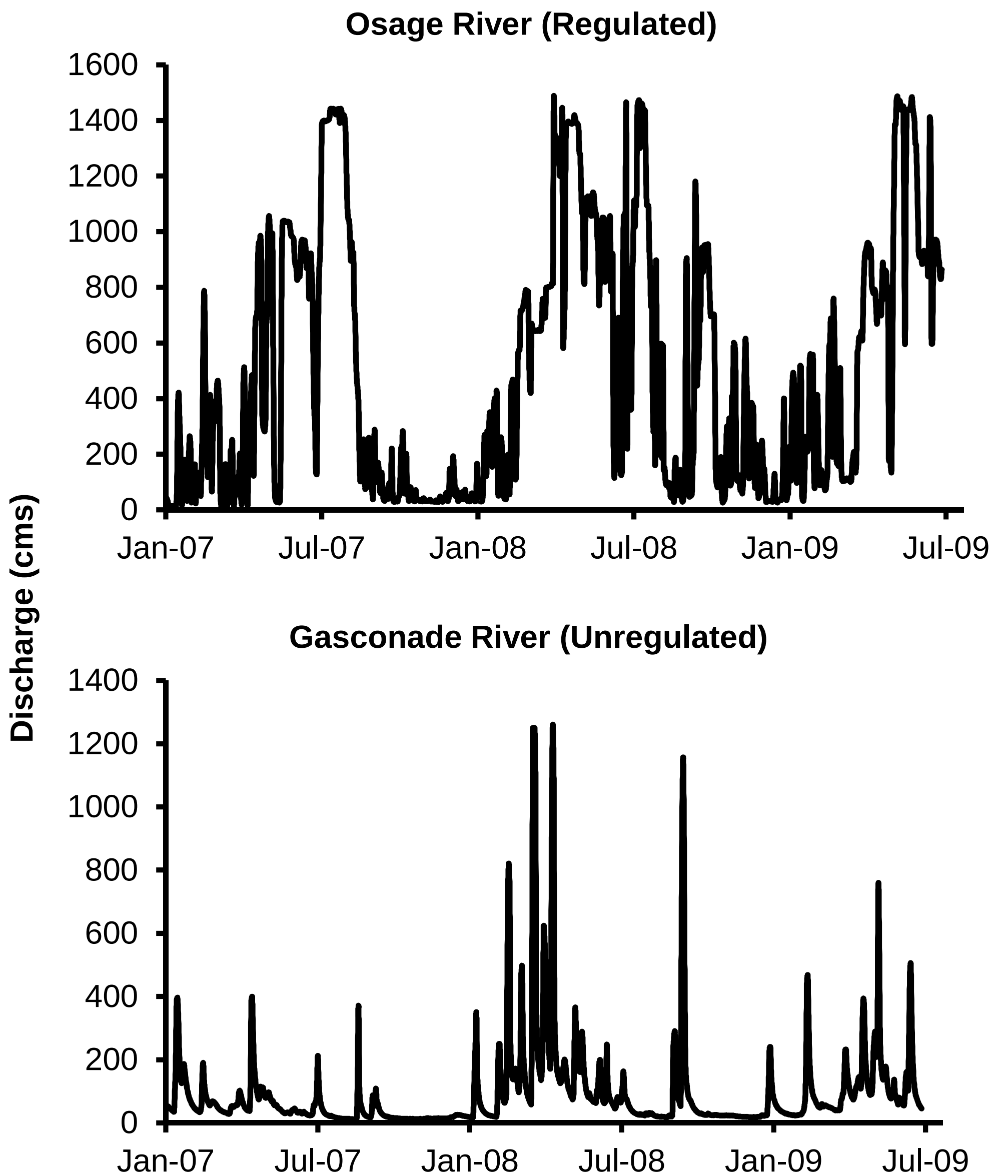

Figure 2. Comparison of mean daily discharge between the regulated Osage River at Bangell Dam and the neighboring, unregulated Gasconade River at Jerome, MO.

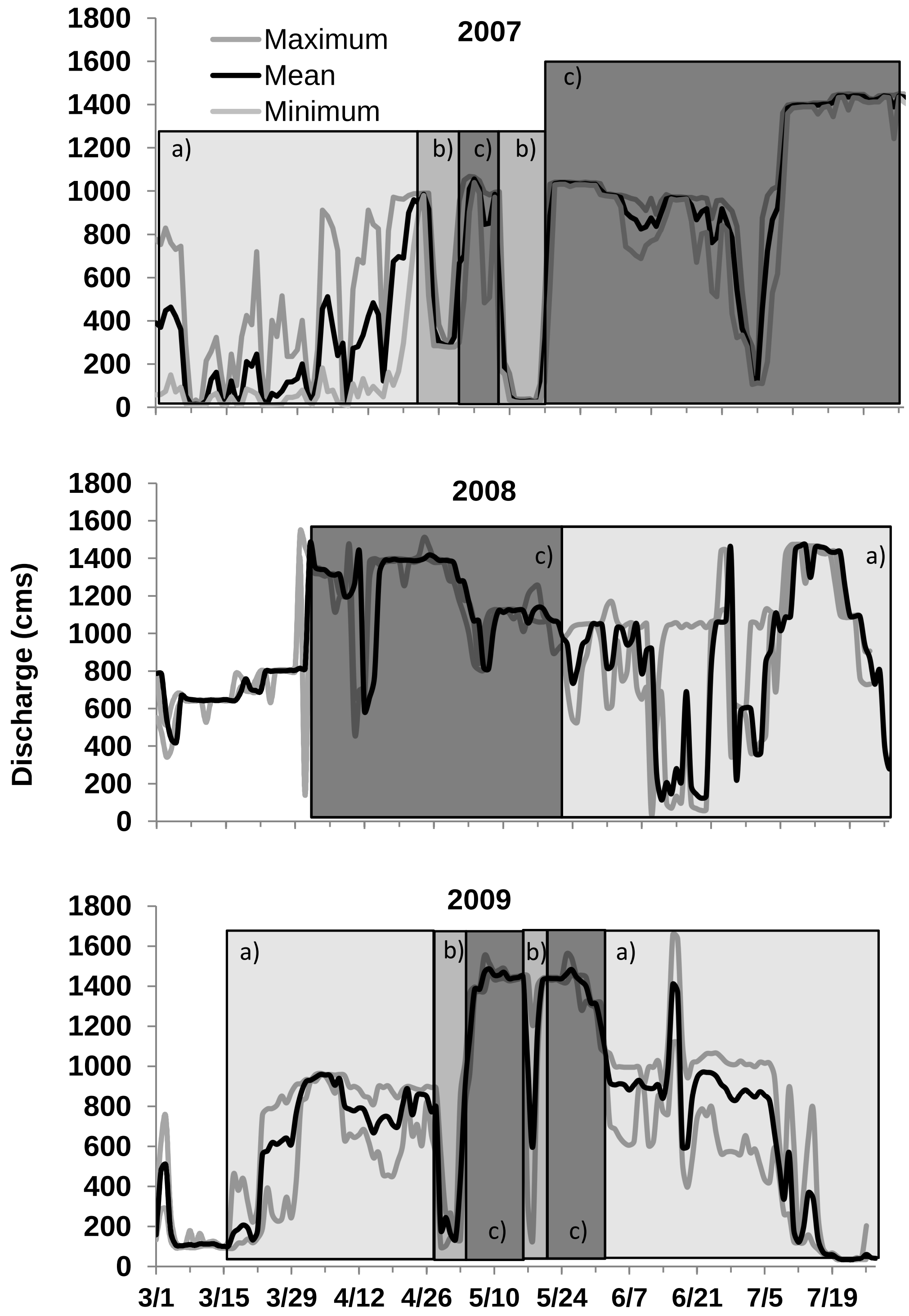

Figure 3. Maximum, minimum, and mean daily discharge data downstream of Bagnell Dam during the spring of 2007, 2008, & 2009. Three types of dam operation were observed: a) peaking: high variability of daily flow due to electrical releases, b) flood mitigation: reduction of nearly all water release to mitigate downstream flooding, and c) flood release: sustained high water releases of stored flood water.

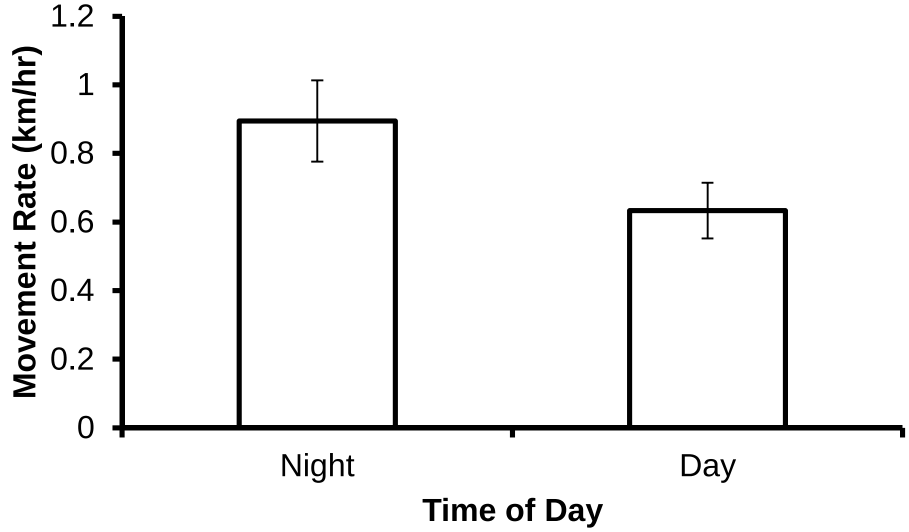

Figure 4. Comparison of mean hourly movement rates (+/- 1 standard error) of paddlefish tracked over a 24-hr cycle.

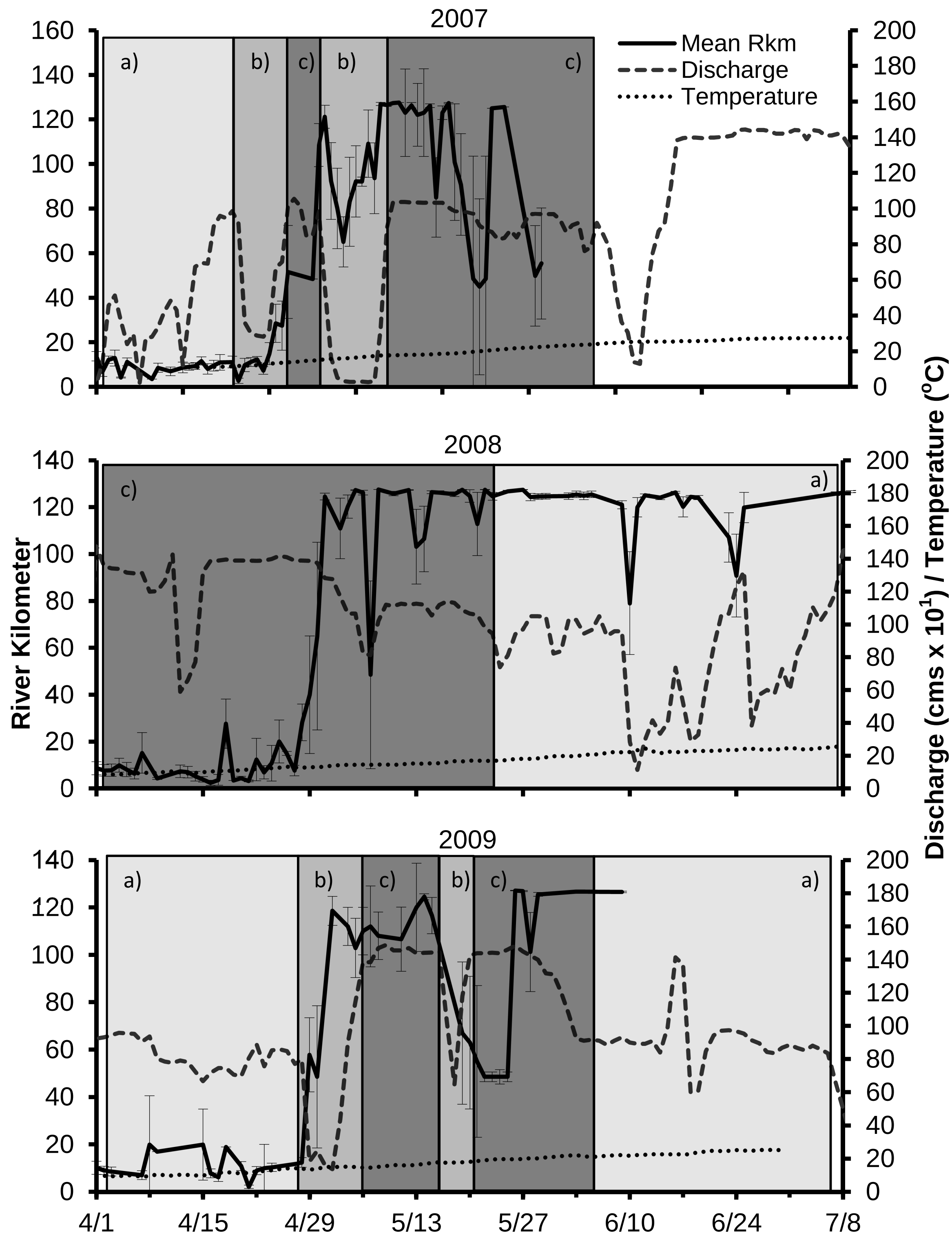

Figure 5. Mean river location of transmittered paddlefish and standard error (rkm) in relation to changes in mean daily discharge and mean daily temperature. Shaded areas represent the three different flow patterns observed: a) peaking, b) flood mitigation, and c) flood release.

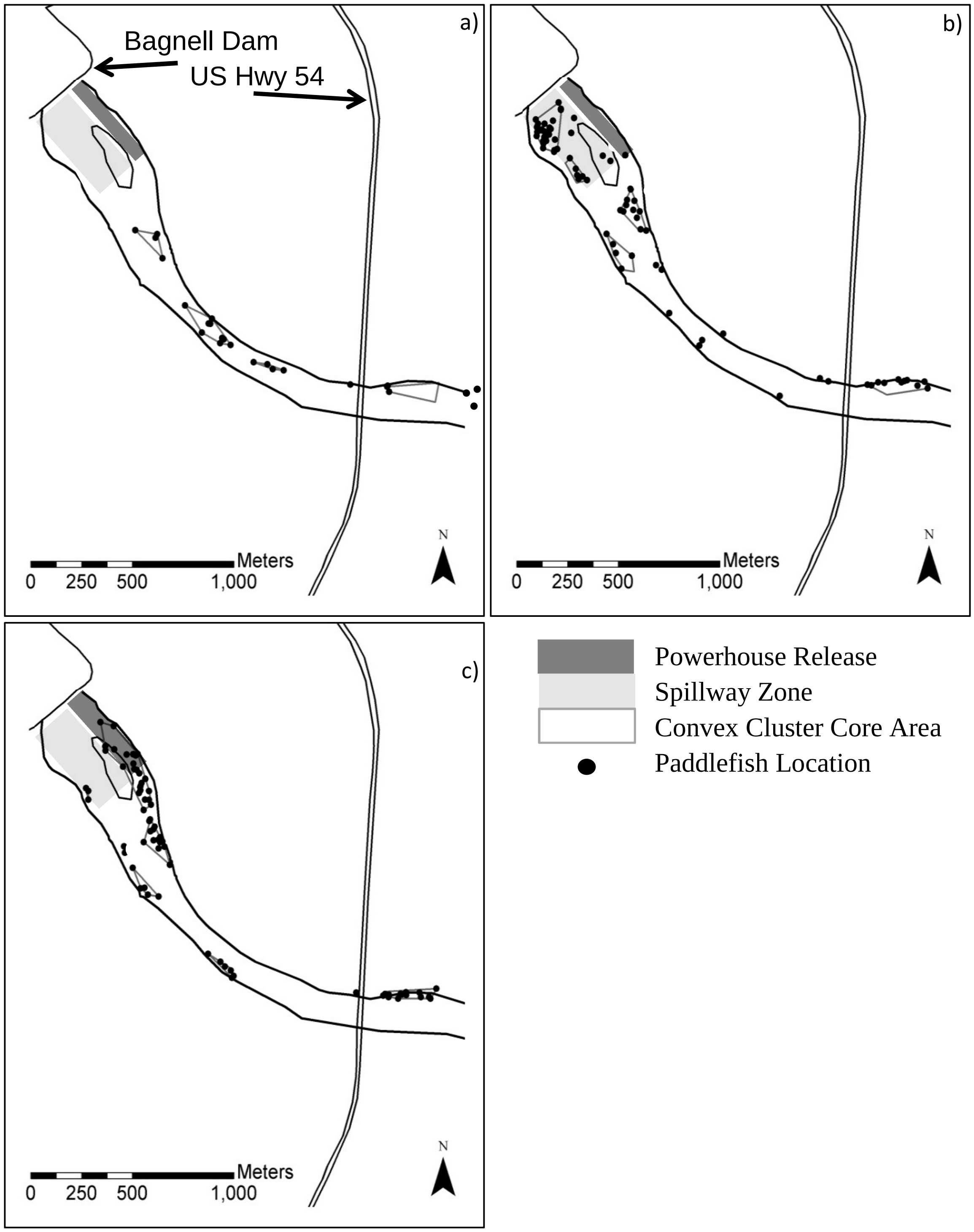

Figure 6. Changes in habitat use downstream of Bagnell Dam under three different discharge operations: a) flood mitigation (< 100 cms), b) peaking (300 cms to 1050 cms), and c) flood release from spill gates (>1050 cms). Minimum convex cluster polygons are outlined in grey.

Chapter V

Evidence of Limited Paddlefish Reproductive Success Downstream of a Hydroelectric Dam

Abstract

Alteration of the natural flow regime is believed to be a major disturbance to river ecosystems, especially to fish behavior and reproduction. Mitigating the alteration of natural flow regimes requires evidence of how these alterations influence the riverine ecosystem. Paddlefish are an archetypical large-river fish that have undergone significant population declines in response to increased dam construction and regulation of natural flow regimes. The spawning success of large-river fishes, like paddlefish, can be used as a measure of flow regime alteration. Paddlefish spawning in the lower Osage River is believed to occur immediately downstream of Bagnell Dam, a 45-m tall hydroelectric dam. Bagnell Dam is operated for multiple purposes, including hydroelectric generation, flood control, and maintenance of reservoir levels. This multipurpose operation results in a highly altered flow regime and provides an excellent opportunity to study the effects of flow alterations on the reproductive success of a large-river species. The objectives of this study were to 1) identify if paddlefish were successfully reproducing downstream of Bagnell Dam and 2) assess if altered flows from Bagnell Dam were correlated to paddlefish reproductive success and larval drift. Egg mats and larval drift nets were deployed in the springs of 2007, 2008, and 2009 to document spawning success and identify spawning locations. Additionally, attempts were made to capture female paddlefish after suspected spawning to document if there was significant egg loss and thereby provide further evidence of spawning. No eggs or spent females were captured

downstream of Bagnell Dam in any of the study years. Only one 28-d larva was captured in 2009, but likely migrated from above Bagnell Dam and did not conclusively provide evidence for spawning. The presence of gravid fish and suitable spawning habitat coupled with a lack of successful spawning evidence suggests that current dam operation may be limiting paddlefish reproductive success in the lower Osage River by failing to simulate a natural spring rise to trigger paddlefish spawning. Mitigation of hydroelectric dam release to benefit large river ecosystems requires a broader understanding of precisely how flow cues are disrupted by hydroelectric generation and flood control.

Introduction

The visible effects of large-scale habitat alteration cause by the transformation of free flowing river to large reservoir are well studied. However, the more subtle downstream effects caused by alteration of the natural flow regime have only recently gained more attention, especially in developing nations that are currently increasing the number of dam construction projects (Arthington et al. 2006; Zhang et al. 2011). Natural flow regimes vary with respect to the magnitude, frequency, duration, timing, and rate of change (Poff et al. 1997). However, most dams reduce this variability for beneficial human services such as flood protection, navigation, and maintenance of stable river and reservoir levels. River ecologists have argued that the protection of biodiversity and ecosystem function requires protecting the natural variability of the flow regime with regard to each of the above parameters (Arthington et al. 2006).

Many riverine species have optimally synchronized critical life history events to predictable seasonal changes in flow (Lytle and Poff 2004). The use of spring floods to cue spawning is seen as an adaptive trait in many riverine fish species. Increases in spring flow can condition spawning substrate by removing silt, aerate and prevent desiccation of eggs, and inundate floodplain habitat used for larval rearing (Bunn and Arthington 2002; Jacobson and Galat 2008). Disruption in magnitude, timing, and frequency of spring floods has been implicated in the reduction of reproductive success in numerous species (Bunn and Arthington 2002; Lytle and Poff 2004). Reduction in the magnitude of spring floods that may cue spawning, decoupling of the timing between flow events and temperature, and changes to the frequency of flow peaks, all have the potential to negatively affect reproduction of riverine fishes. Recent studies have begun to investigate manipulating or modeling flow regimes to increase fish reproduction, but still lack species specific information for large-river species like paddlefish (Alford and Walker 2011; Korman et al. 2011; Miller et al. 2011).

Paddlefish can serve as a model large-bodied, long-lived, and large-river migrant to evaluate the effect of altered spring flows on reproduction, as their spawning behavior is cued by a significant increase in flow occurring during a specific temperature window (Russell 1986). Paddlefish, like many large-bodied, big-river fishes, make long-distance spawning migrations in spring corresponding to increased water temperatures and flow (Russell 1986; Pflieger 1997; Paukert and Fisher 2001; Zigler et al. 2004). Actual paddlefish spawning events have been reported between 10 - 20^{o}C (Wallus 1986), although spawning between temperatures of 14-17^{o}C is more commonly observed (Purkett 1961; Pasch et al. 1980; Firehammer et al. 2006; O'Keefe et al. 2007). Once temperatures reach suitable spawning ranges, spawning events are typically associated with a moderate to large rise in river flow (Purkett 1961; O'Keefe et al. 2007). This increase in flow is believed to be a critical cue to stimulate spawning, and if suitable spawning cues are absent, female paddlefish may forgo spawning (Russell 1986). The ability to forgo spawning and reabsorb eggs is seen as an adaptive trait for a long-lived species, as conservation of energy resources may reduce the time required to develop eggs for the next spawning event, and increased success during the next spawning event may increase overall fitness (Rideout et al. 2005). However, repeated spawning failures due to a repeated lack of suitable flow cues would eventually result in severely reduced or zero fitness if successful spawning is never achieved.

After spawning, incubation of paddlefish eggs lasts 6–12 d depending on temperature (Yeager and Wallus 1982). High flows during the incubation period provide suitable aeration for developing eggs, prevent the dewatering of spawning sites, and desiccation of eggs. Purkett (1961) found paddlefish eggs stranded on a gravel bar after river levels dropped sharply in the upper Osage River. Similarly, sharp drops in river discharge have been associated with desiccation and reduced reproductive success of other river spawning species (Fraley and Decker-Hess 2006).

After hatching, paddlefish larvae swim up from the substrate into the water column and passively drift downstream in the current (Purkett 1961). Larval drift for many species occurs mainly at night, under low light conditions, as a possible mechanism to reduce predation. Wallus (1986) also observed that paddlefish larvae were more commonly collected at night. Downstream drift allows larvae to passively disperse downstream with the current from spawning sites into areas more favorable for rearing and growth: slower water velocity, shallow-water refuges from fish predation, and abundant food resources (Purkett 1961; Jennings and Zigler 2009). Flows are therefore thought to be critical for assuring that larvae drift into suitable rearing areas, such as floodplain or backwater habitats that provide abundant food resources and protection from predation (King et al. 2003).

Despite the potential negative consequences to reproduction, successful paddlefish spawning has been documented downstream of several hydroelectric dams (Pasch et al. 1980; Wallus 1986; Lein and DeVries 1998). However, estimates of reproductive success have not been evaluated for most paddlefish stocks and comparisons of reproductive success in regulated and unregulated rivers are lacking (Jennings and Zigler 2000). The critical components of the natural flow regime required for successful reproduction, such as timing and magnitude of spring floods, remain largely unknown. Without this knowledge, assessing the influences on reproductive success caused by differences in dam operation (i.e. peaking vs. run-of-the-river) and dam design (i.e. epilimnetic vs. hypolimnetic release) is difficult.

Optimization of ecological and societal benefits from regulated rivers will require additional knowledge of flow conditions that allow or favor successful reproduction for riverine fishes and preserve the ecological integrity of river communities. The lower Osage River provides an ideal location where paddlefish have access to suitable spawning habitat downstream of a mainstem dam, Bagnell Dam, which is currently operated for hydroelectric generation, flood control, and maintenance of stable reservoir levels for the upstream dam, Lake of the Ozarks (Lallaman, Chapter 4). The significantly altered flow regime in an area of suitable spawning habitat provides an excellent opportunity to examine the effects of modified flow on paddlefish reproductive success. The objectives of this study were to 1) identify if paddlefish were successfully reproducing downstream of Bagnell Dam and 2) assess if flows from Bagnell Dam were correlated to paddlefish spawning success and larval drift downstream of Bagnell Dam. Understanding the role of regulated flows in fish reproduction could provide managers with qualitative discharge criteria, such as minimum flows, maximums flows, and maximum rates of change required for successful fish reproduction in regulated river systems.

Study Site

Construction of Bagnell Dam in the early 1930's fragmented the Osage River into two distinct segments: the Upper and Lower Osage River. The reservoir created by Bagnell Dam, Lake of the Ozarks, provided optimal conditions for adult feeding and growth, while the free-flowing upper Osage River above the impoundment provided suitable access to spawning habitat and was the site of the first documented paddlefish spawning site (Purkett 1961). The construction of Truman Dam in the late 1970's inundated all known paddlefish spawning habitat in the upper Osage River and little evidence of natural reproduction has been observed since the completion of the upper dam (Russell 1986). As a result, the paddlefish fishery in Lake of the Ozarks and Truman Reservoir is currently maintained through intensive stocking efforts.

We defined the lower Osage River for the purposes of this study as the 132 km extending upriver from its confluence with the Missouri River to Bagnell Dam, the first major dam preventing upstream fish movement (Figure 1). A decommissioned low-head (< 5m) lock and dam, Osage River Lock and Dam #1, exists 20 rkm upstream of the Missouri River confluence; however, research has shown that this structure is potentially only a barrier to upstream migration during low flow years occurring on average once in every three years (Lallaman Chapter 3). Current habitat downstream of Bagnell Dam in the unimpounded lower Osage River is believed to be suitable for natural reproduction of paddlefish and similar lithopelagophilic species, like lake sturgeon *Acipenser fulvescens,* shovelnose sturgeon *Scaphirynchus platorynchus,* and blue sucker *Cycleptus elongatus*. Paddlefish are not directly stocked into the lower Osage River, although a small number of tagged fish from upstream reservoirs have been collected downstream of the dam. Concentrations of adult paddlefish aggregate downstream of Bagnell Dam in the spring and spawning is suspected to occur downstream of the dam.

The current operation of Bagnell Dam for hydroelectric generation, flood control, and stable reservoir levels results in severely altered spring flows, which may interfere with natural reproduction of paddlefish and other large lithopelagophilic spawners. Typical peaking hydroelectric generation results in flows alternating daily between a minimum of 25.5 cms and maximum hydroelectric output of1050 cms, corresponding to daily changes in river stage of 0.6-5.2 m. During periods of downstream flooding, Bagnell Dam reduces discharge releases under 25.5 cms for sustained periods to mitigate downstream high discharge in the Missouri River. Discharge of excess flood water upstream results in releases through the spillway and turbines in excess of 1050 cms typically sustained until the excess water is released. Natural discharge patterns of the unimpounded Gasconade River, a neighboring watershed, were used to contrast the regulated flow releases of the lower Osage River (Figure 2).

Methods

River Discharge and Temperature

Discharge and temperature data were recorded to assess possible associations with spawning events and larval drift. Mean daily discharge data for the lower Osage River were obtained from U.S. Geological Survey (USGS) gauging station downstream of Bagnell Dam (rkm 130). Osage River temperature was recorded hourly below Bagnell Dam using continuous recording data loggers (Onset Co., Pocasset, Ma, Model TBI32[1]). Average daily river temperature was calculated from hourly data.

Egg Sampling

Egg mats were deployed downstream of three suspected spawning sites in an attempt to verify spawning habitat (Figure 1). Suspected paddlefish spawning sites were identified by the presence and behavior of transmittered paddlefish in conjunction with documented paddlefish spawning habitat characteristics: depths greater than 3 m, velocities between 0.5-1.5 m/s, and substrate larger than 4 mm in diameter (Lallaman, Chap 3). Egg mats were constructed of a 0.5-m diameter floor buffing pad secured to a round rebar frame and secured in strings of 5 mats spaced approximately 5 m apart. Three strings of five egg mats were deployed in a 5 X 3 grid pattern equally spaced across the river width at depths greater than 5 m to avoid complications with stranding from drawdowns and peaking. Sampling began when transmittered paddlefish were detected near suspected spawning habitat and mats were checked approximately every other day or every three days until water temperatures exceeded known paddlefish spawning temperatures (20-22^{o}C). Depth and water temperature were recorded at all egg mat placement sites to quantify habitat characteristics at sampling sites. Water column velocities were initially measured at egg mat sites, but velocity measurements were discontinued due to lack of time and resources.

Attempts were made to recapture tagged female paddlefish at temperatures near or exceeding known spawning temperatures of 20^{o}C to assess visually if spawning occurred. A 2-4 cm surgical incision was made on abdomen just anterior to the pelvic girdle to examine the gonads macroscopically and to determine if a significant reduction in egg mass had occurred due to a spawning event. A blood sample was also collected and later analyzed to identify changes in plasma sex-steroid concentrations that may be associated with spawning (Lallaman, Chapter 2).

Larval Drift Sampling

Attempts to sample paddlefish larvae and determine reproductive success were accomplished using stationary drift nets. Larval drift nets were deployed downstream of the most downstream suspected spawning site (Figure 1). Two to six drift nets were set in vertically stacked pairs to sample both surface and benthic drift. Sampling for larval paddlefish began when water temperatures reached 15 ^{o}C and continued for two to six weeks to cover the period of potential larval drift (Purkett 1961; Wallus 1986). Sampling was conducted between two to four days per week. Larval drift paddlefish and related species, such as the lake sturgeon, occurs primarily at night (Wallus 1986; Smith and King 2005), so our sampling was concentrated during the nighttime hours of 6:00 pm to 4:00 am.

A General Oceanics flow meter (Model #2030)[1] placed at the mouth of each net was used to measure water velocity. An additional flow meter was attached the outside of a randomly selected net to measure the differences in water velocity caused by net resistance and determine sampling efficiency. Volume of water sampled was calculated as the product of velocity in front of the net and cross sectional area of the net. Cod ends were emptied approximately once per hour, and all larvae were sorted in the field. A random subsample of larvae were placed in labeled vials containing 80% ethanol for later laboratory identification. Age of larvae and time of spawning were determined from published developmental data (Ballard and Needham 1964) and compared to paddlefish of known age reared at Lost Valley State Fish Hatchery.

Data Analysis

Attempts to quantify drifting larvae were calculated from catch per unit effort (CPUE) was calculated as the number of larvae captured per m^3 of water sampled. Estimates of the total number of larva drifting were calculated using the formula:

$$P = (q \times N)/O \times K$$

Where P is the number of larvae passing the sample area, q is the flow volume in m^3/h, N is the number of larvae collected in one hour, O is the volume of water sampled in m^3/h, and K is a collection coefficient determined by comparing the difference in velocities in front of the net and beside the net.

Results

Mean daily discharges during the spring spawning period in 2007-2009 showed typical characteristics of a regulated river system. In all three years, periods of stable river flow were interspersed between periods of rapid changes in river flow, especially compared to unregulated Gasconade River (Figure 2). Downstream flooding in the Missouri River in 2007 and 2009 caused Bagnell Dam operators to decrease discharge rapidly from Bagnell Dam to alleviate downstream flooding, then immediately increase discharge to prior levels once the Missouri River had crested (Figure 3). No significant downstream flooding event occurred in 2008, however, several minor decreases and immediate increases in Bagnell Dam discharge did occur. No discharge event imitating a natural rise occurred downstream of Bagnell Dam during known spawning temperatures (10-20 ^{o}C) in any year of the study (Figure 2).

Egg mats were successfully deployed for 41 days between 5 May – 15 June, 2007. No fish eggs of any species were collected, although several clupeid larvae were captured on egg mats. Egg mats were not fished in 2008 or 2009 due to high river discharge and the inability to keep eggs mats securely anchored to the substrate.

Although no previously tagged females were recaptured, three gravid females were captured between 27 May – 18 June, 2008 and two gravid females were captured between 27 May – 1 June, 2009. These females were captured immediately downstream of Bagnell Dam. Water temperatures at the time of capture ranged between 18.7-22.9^{o}C, which is at the upper limit reported for paddlefish spawning. None of these females showed any evidence of egg loss or other visible indication of spawning readiness (i.e.

free flowing eggs, significant loss of body mass). Eggs in three of the females captured were very fragile and no longer dark in color, suggesting atresia and reabsorption.

Over all three study years, larval drift nets were fished for a total of 26 d, resulting in 402 net-hrs (Table 1). A total of 11,180 larval fish was captured, representing seven different families. Clupeidae (gizzard shad) and Moronidae (white bass) comprised 91% of the respective drift with Ictaluridae, Hiodontidae, Cottidae, and Centrarchidae occurring in very low numbers. Only one larval paddlefish was captured on 4 June, 2009 from a surface drift net. The estimated age for this individual based on size and development was approximately 28-30 d (G. Heidrich, Blind Pony Hatchery Manager, personal communication).

Discussion

The failure to collect paddlefish eggs, spent females, or a significant number of paddlefish larvae provide a strong weight of evidence to support the hypothesis that paddlefish reproduction downstream of Bagnell Dam is limited. Capture of paddlefish eggs or spent females would have provided direct evidence that temperature, flow, and habitat conditions were sufficient for successful spawning. Additionally, capture of larvae would have provided evidence of successful spawning, and habitat conditions sufficient for successful incubation and larval drift. The failure to collect eggs and the presence of female eggs undergoing atresia provide supportive evidence that paddlefish reproduction in the Osage River downstream of Bagnell Dam is a result of failed spawning activity and not egg or larval mortality.

Large rises in Osage River discharge during the spawning period of all three study years were preceded by sharp decreases in flow releases often exceeding 550 cms (Figure 3). Paddlefish often moved distances of 20 km or greater downstream from Bagnell Dam in response to these decreases in flow (Lallaman Chapter 4), which likely represents a significant and repeated disruption to normal spawning behavior in years with similar flow patterns (Figure 3). The absence of a natural rise in river discharge to synchronize and cue spawning activity and the displacement caused by rapid decreases in discharge releases are likely factors limiting successful paddlefish reproduction downstream of Bagnell Dam.

Although our failure to capture eggs could have been a result of sampling inefficiency, multiple studies have successfully collected paddlefish eggs using similar sampling techniques (Firehammer et al. 2006; O'Keefe et al. 2007; Miller et al. 2011). Firehammer et al. (2006) noted that sampling efficiency of egg mats was generally low but increased when fish were either highly concentrated (e.g., downstream of dams) or efforts were focused at known spawning locations. Despite observing a low number of reproductive females, the concentration of paddlefish at discrete locations downstream of Bagnell Dam should have increased our sampling success, if female paddlefish were successfully spawning in these areas.

Similar to egg mat efficiency, the failure to capture more than one paddlefish larva does not directly prove that reproduction was limited. However, estimates of spawning success in other systems have been inferred by collection of larval paddlefish using similar methods (Pasch et al. 1980; Wallus 1986; Hoxmeier and DeVries 1997). Under the assumption that successful reproduction was occurring downstream of Bagnell

Dam, the failure to collect more than one paddlefish larvae was unexpected. In contrast to egg mats which sample a small area, larval drift nets filter large volumes of water and have been successful at capturing paddlefish larvae in other systems (Wallus 1986). Additionally, collection of over 11,000 larvae representing seven different families indicates that our choice of gear was appropriate for sampling drifting larvae. Although rapid drops in river discharge could have resulted in desiccation and large egg mortality, gravel bars were visually searched during periods of low water and no evidence of spawning and subsequent egg desiccation was observed. The Missouri Department of Conservation conducted an additional 296 net-hrs of larval fish sampling in the lower Osage River between April and June, 2007 – 2009. This effort resulted in a similar capture of over 11,300 larvae from 11 families, but failed to capture any larval paddlefish (B. Landwer, Missouri Department of Conservation, personal communication). Collecting only one paddlefish larvae despite substantial effort by multiple researchers suggests that very few paddlefish larvae were present in the lower Osage River during our three years of study.

Despite indications of limited spawning success downstream of Bagnell Dam, three spent female paddlefish were captured in 2009 130 rkm downstream near the mouth of the Osage River on 7 May. Based on river temperatures, physiological condition, and behavior, these females most likely had recently spawned upstream of the Osage River, possibly in the Missouri River. Additional evidence of paddlefish reproduction in the Missouri River is has been observed from the collection of larval paddlefish by multiple studies (Tibbs and Galat 1997; Galat et al. 2004; Delonay et al. 2010)

Collection of larval paddlefish upstream near Blair, NE (Delonay et al. 2010) and spent females near the mouth of the Osage River in 2009 suggests that conditions for successful reproduction were present in the Missouri River, but not the lower Osage River. Although the magnitude in flow pulses varied markedly among sites in the Missouri River, flows associated with estimated spawning dates at both sites did not show the marked decreases compared with flow observed in the lower Osage River (Figure 4). Additional studies comparing the differences between reproductive success in the Osage and Missouri Rivers may highlight critical factors influencing reproductive success of paddlefish.

To our knowledge few studies have directly examined the effects of altered flows on spawning success of litopelagophilic spawners despite the prevailing assumption that alteration of natural flows by dams detrimentally affects paddlefish and sturgeon reproduction (Sparrowe 1986; Unkenholz 1986; Gerken and Paukert 2009). Multiple studies have observed positive relationships between river discharge or run-of-the-river flow conditions and larval CPUE (Wallus 1986; Auer 1996; Hoxmeier and DeVries 1997), but little direct evidence is reported about the magnitude of flow pulse needed to cue spawning or determine how increased frequency of daily and seasonal flow changes affects spawning behavior and success. Papoulias et al. (2011) found that photoperiod and temperature were able to explain overall geographic patterns in reproduction, but that synchronization of spawning was likely due to more proximate environmental variables such as flow cues. Young et al. (2011) recently conducted a review of hydropower flow releases and their effects on stream fishes. They conclude that the current knowledge gap is an understanding of the effect of magnitude, ramping rates, and timing of hydro flows on fish at various life stages. Our study provides strong evidence that sharp ramping of flows during the spring spawning period disrupts spring spawning in paddlefish and other similar lithopelagophilic large-river migrants attempting to spawn downstream of hydroelectric dams.

Large dams alter the natural flow regime to provide numerous societal benefits. The interaction between social and biological values associated with flow regulation are complex, ultimately requiring strong weight of evidence approaches to justify compromising societal benefit (i.e., reduced flood control efforts or hydroelectric generation) for increased biological benefit (i.e. increased reproductive success of fish). Identifying critical factors, such as magnitude, timing, frequency, and duration of spring floods that influence reproductive success downstream of hydroelectric dams is crucial for understanding reproduction requirements and successful management of large-river fishes.

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Table 1. Sampling dates and associated catch statistics for larval drift nets fished in the lower Osage River during the springs of 2007, 2008, and 2009.

Year	Sampling Dates	# Sample Days (net-hrs)	Total Larvae Captured	# Families Represented	# Paddlefish Larvae
2007	15 May - 25 June	12 (182)	5,596	7	0
2008	17, 25, 30 May 17, 24 June	5 (76)	2,102	5	0
2009	9 May - 10 June	9 (144)	3,482	6	1

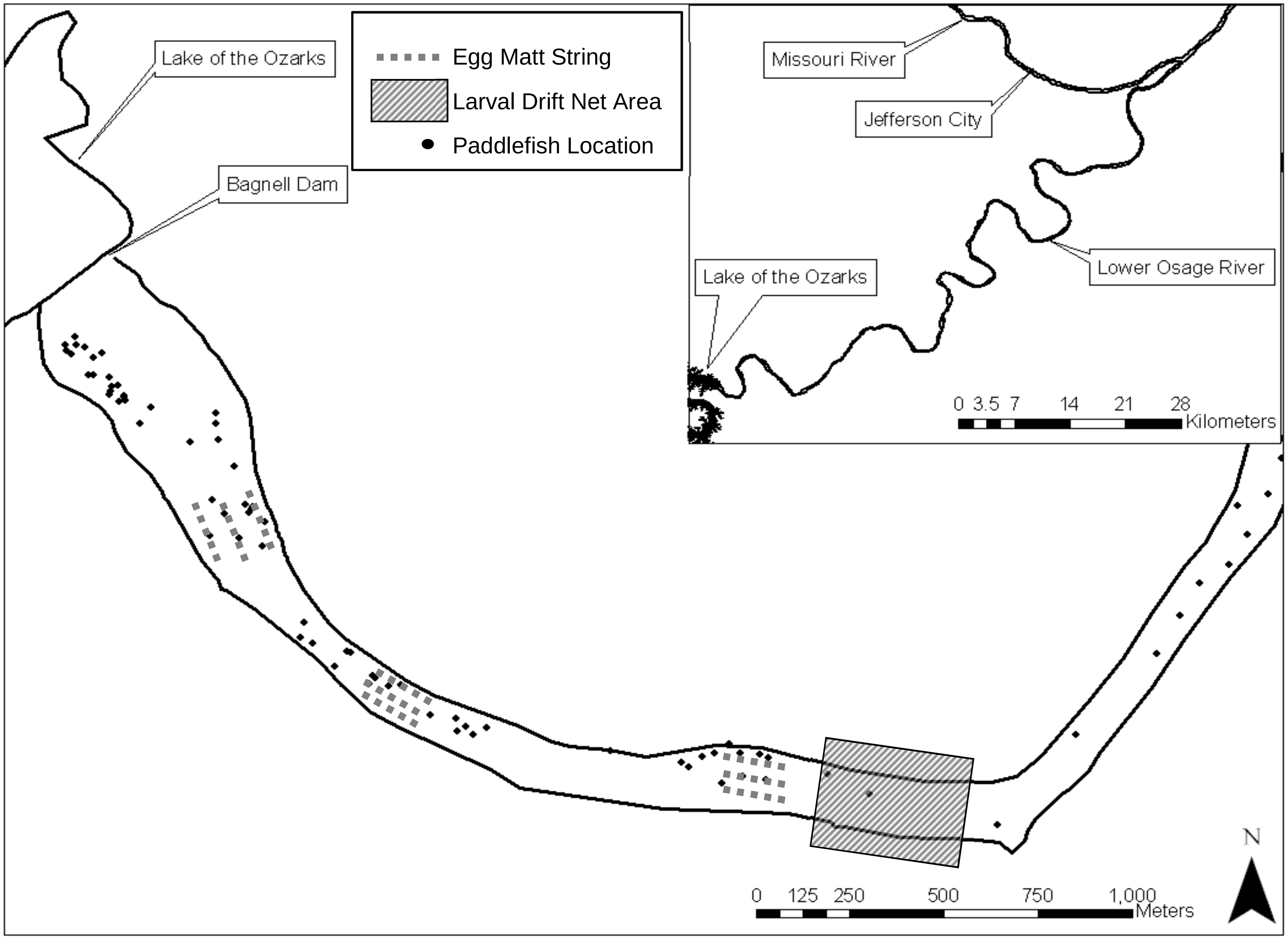

Figure 1. Map of the lower Osage River within enlarged study site area showing palcement of egg mats and larval drift nets in relation to paddlefish aggregations observed in 2007.

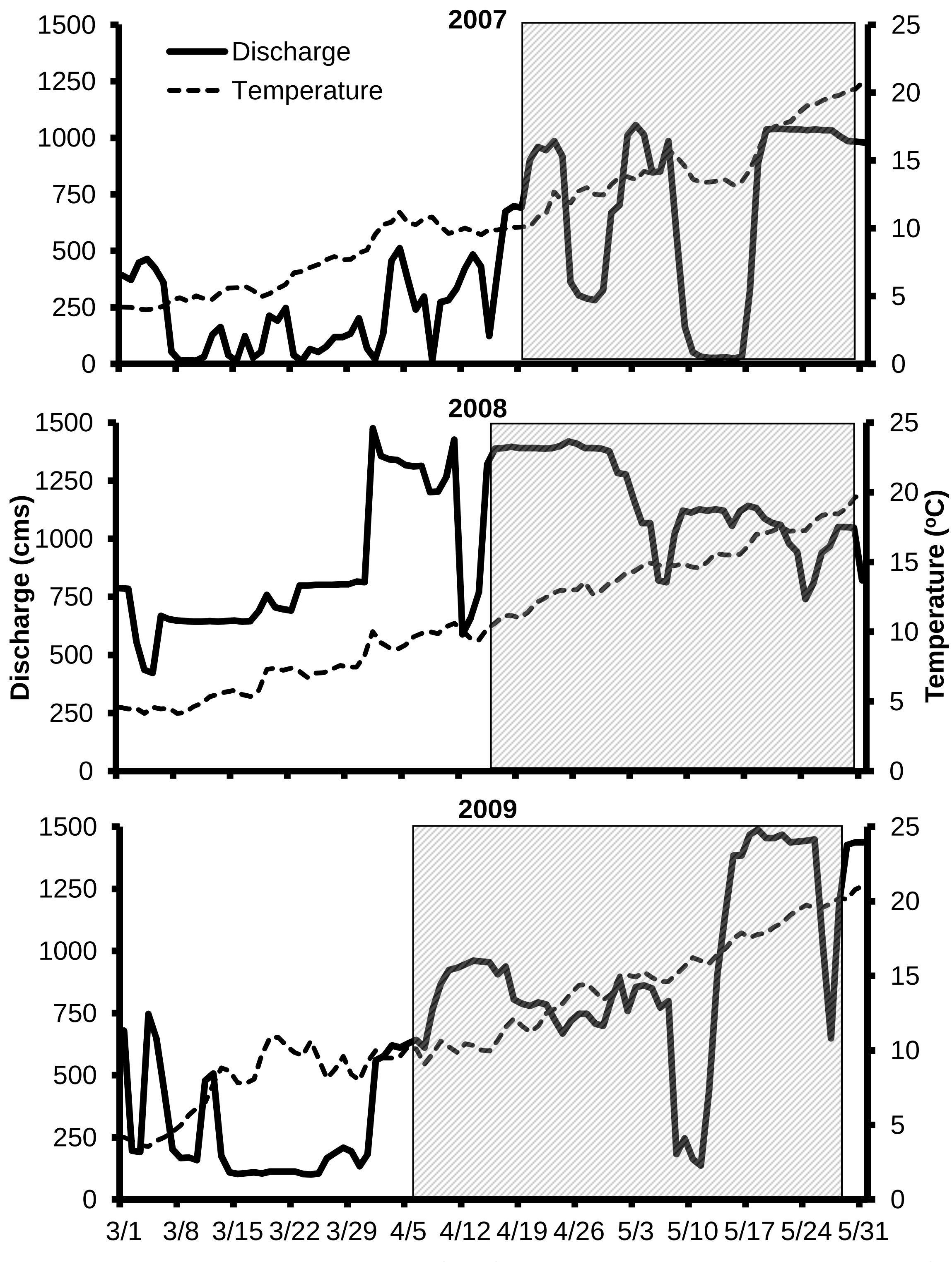

Figure 2. Discharge and temperature profiles for the lower Osage River in the spring of 2007, 2008, and 2009. Paddlefish spawning temperatures (10-20°C) are highlighted in each year.

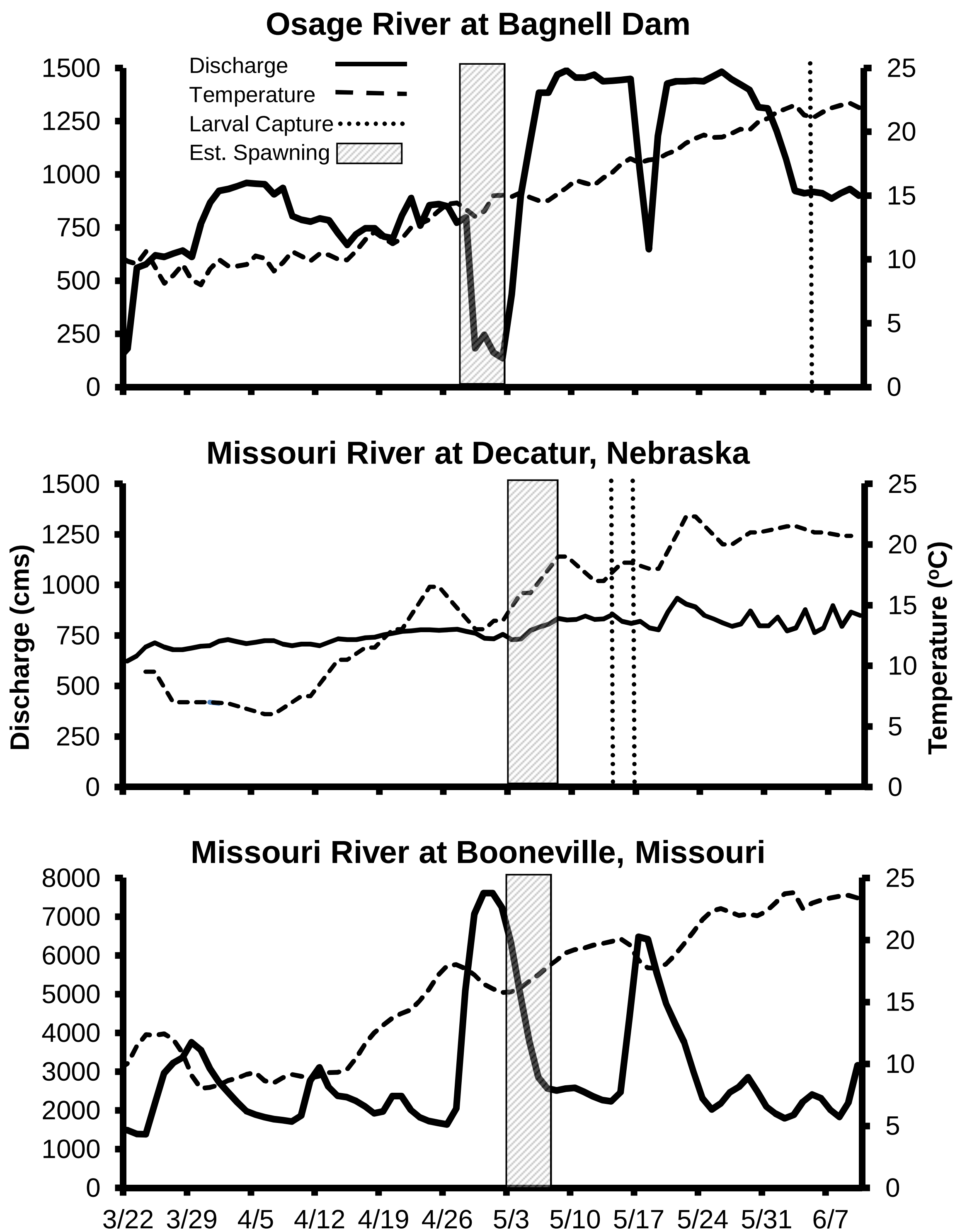

Figure 3. Comparison of Osage and Missouri River discharge and temperatures in the spring of 2009. Estimates of paddlefish spawning periods in the Osage River are back-calculated from capture of a 28-d old larvae, and estimates of spawning in the Missouri River and based on collection of newly hatched larvae (Decatur, NE) and collection of spent females (Boonville).

Chapter VI

Summary and Management Implications

Summary Conclusions

Comprehensive analysis of multiple factors that could limit North American paddlefish *Polyodon spathula* reproductive success in the lower Osage River identified potential bottlenecks to reproduction. Mature, reproductively ready adults had access to upstream spawning habitat downstream of Bagnell Dam, but little evidence of successful reproduction was observed. Based upon our initial concept diagram of known spawning requirements (Figure 1), our study provides credible support that altered river flows are the most probable cause of poor reproductive success. Altered flow regimes resulted in displacement of paddlefish downstream, shifts in habitat use downstream of the dam, and did not imitate a natural spring rise during optimal spawning temperatures. Maintenance of self-sustaining paddlefish populations will require more intensive management of minimum flows, maximum flow, and ramping rates during critical life history periods.

The scope of this study focused on paddlefish as an archetypical lithopelagophilic large-river migrant, yet the lower Osage River has over 80 species of native fish (Pflieger 1965). Lithopelagophilic and lithophilic spawners require very specific spawning conditions and represent over 15% of the fish species in the Mississippi River (Pflieger 1965), and also represent a guild that is highly susceptible to habitat disturbance caused by low-head dams (Helms et al. 2011). Lake sturgeon *Acipenser fulvescens*, for example, share nearly identical spawning requirements to paddlefish and are listed as an endangered species in throughout most of its range. Information gained from paddlefish in this study could be used to guide further investigation into community level effects on reproduction success of river fishes in altered rivers.

There are currently over 45,000 large (>15 m) dams worldwide and over 150 new dams being constructed each year, with the highest construction rate occurring in developing countries (Wu et al. 2003). The pervasive nature of this threat requires a more comprehensive understanding of alterations to magnitude, ramping rates, and timing of flow releases on critical life history stages, especially spawning, incubation, and larval rearing. Our study highlights the important interaction that large and low-head dams have on large-river migrants, and provides information on flow releases can be managed to facilitate upstream passage over low-head dams as well as increase reproductive success downstream of a hydroelectric dam.

Means Objective 1: Presence of Gravid Fish and Timing of Spawning

The use of non-invasive methods for sex determination, such as sex-steroid analysis, is becoming a more popular tool for evaluating both fish sex and reproductive status in hatcheries as well as wild populations (Davail-Cuisset et al. 2011; Hink et al. 2011; Papoulias et al. 2011). Physiological processes can provide greater detail on the timing of spawning events and influence of environmental conditions, such as temperature, discharge, and photoperiod, on reproductive success (Papoulias et al. 2011). In species with complex reproductive cycles, these tools are critical for accurate assessment of spawning population size and timing of physiological spawning readiness with environmental conditions.

Means Objective 2: Upstream Lock and Dam Passage

Retrospective analysis of Osage River Lock and Dam passage indicates that this structure acts as a semipermeable barrier, restricting upstream access during low flow years and acting as an additional limitation to reproductive success. The semipermeable nature of low-head dams may result in inconsistent upstream access and intermittent reproductive success for upstream migrants. Unfortunately, very few studies have focused on the effects of intermittent passage through lock and dams (Zigler et al 2004; Stuart et al 2007). Helms et al. (2011) quantified fish assemblages in 20 streams with low-head mill dams, and found that breached or decaying dams often disrupted fish communities as much as intact dams, supporting that partial passage over structures (i.e., through breaches or existing lock chambers) can still restrict community functions, such as movement and reproduction.

Dam removal has become a common restoration activity in the U.S., yet selection of removal projects is complicated by multiple factors, such as economical cost, societal benefit, and ecological impact (Poff and Hart 2002). Decisions on priority dam removal projects require predictive tools to assess ecological impact and benefit of removal (Kibler et al. 2011). The ability to model upstream passage restrictions provides managers with a quantitative tool for assessing impacts to migratory timing and access to upriver habitat, allowing for more comprehensive assessments of dam removal projects.

Means Objective 3: Use and Availability of Spawning Habitat

Riverine migrants typically concentrate downstream of dams without passage structures or with poorly designed structures. Spawning substrate for lithophilous spawners is typically available downstream of hydroelectric dams due to the high peak flows that scour and condition substrate (Harris and Hightower 2011; Young et al. 2011). McAdam (2011) found that the velocity and interstitial space of white sturgeon *Acipenser transmontanus* had significant effects on egg survival and larval drift, indicating that flows can be just as important for reproductive success as the presence of spawning substrate.

Movement and habitat use are also affected by dam operation and flow releases. Large changes in flow magnitude typically shift habitat use toward deeper slower velocity habitat and result in the downstream displacement of small fishes (Shirvell 1994; Pert and Erman 1994; Bell et al. 2001). Response of fish to daily peaking discharges is much more variable and is strongly dependent upon the organism and magnitude of flow change (Young et al. 2011). The majority of studies show similar results to our paddlefish data, that short-term changes to flow do not result in significant displacement downstream of adult fish (Gido et al. 2000; Heggenes et al. 2007). Habitat use information in response to changes in river flow are critical for informing flow models and predicting changes in habitat use in relation to proposed changes to managed flow releases.

Means Objective 4: Indicators of Successful Reproduction

Access to upstream spawning habitat in all three study years did not guarantee reproductive success downstream of Bagnell Dam. The capture of non-spawned female paddlefish with atretic eggs, the failure to successfully capture spawned eggs, and the capture of only one larval paddlefish suggest that reproduction is limited despite the presence of gravid fish and access to upstream habitat. Our evidence points to altered flows and rapid changes in discharge as the likely reason for failed reproductive success of paddlefish in the lower Osage River. Large fluctuations in hydroelectric output are often cited as a reason for disrupting fish behavior and reproduction, but few studies are able to directly show the mechanisms of disruption or provide recommendations on flow regulation (Young et al. 2011). Restoration of dam discharges to more natural, run-of-the-river conditions has resulted in significant increases in fish reproduction downstream of dams (Auer 1996). Dams that are not operated using a run-of-the-river regime, like Bagnell Dam, should experiment with more natural flow releases during critical reproductive periods (i.e., higher minimums, slower ramping, imitated spring rises) to optimize conditions for favorable reproduction (Young et al. 2011).

Management Implications

The Missouri Department of Conservation is currently undergoing negotiation to modify Osage River Lock and Dam #1 to facilitate upstream fish passage. Our results indicate reproductively ready paddlefish use the river for spawning migrations and that other large-river migrants such as blue sucker, lake sturgeon, shovelnose sturgeon, and pallid sturgeon potentially use this river for spawning as well. Osage River Lock and Dam #1 is likely a barrier to upstream movement except during large spring floods exceeding a combined Osage and Missouri river discharge of 2,800 cms. Paddlefish, as a large bodied species, are capable of generating large amounts of thrust (Drucker and Lauder 2000) and are likely capable of moving upstream under fast velocities that smaller bodies species may not be able to navigate. Conditions that facilitated upstream passage of paddlefish should be considered minimum requirements that potentially still exclude the upstream passage of smaller bodied species. Modification of Osage River Lock and

Dam #1 to incorporate a passage structure will need to consider requirements of a broad range of species to maximize upstream passage opportunities for a diversity of native species.

Modeling paddlefish passage upstream of Osage River Lock and Dam #1 provides managers with a predictive tool for estimating passage probability based on river temperature and interactive mainstem and tributary discharge. Retrospective analysis showed that passage was restricted as frequently as 33% of 58 years analyzed, and likely reduces spawning success by restricting access to upstream spawning habitat. Timing of passage events was different in all three study years and controlled by the occurrence of high-water events. Management of upstream passage may also address timing to ensure that fish can access upstream habitat prior to optimal spawning temperatures being reached. This model allows managers to set more dynamic minimum flow requirements from Bagnell Dam during critical migratory periods to maximize passage success under variable discharge conditions.

Although passage is a critical issue in the lower Osage River, access through a low-head dam to upstream habitat did not guarantee reproductive success of paddlefish. Current operation of Bagnell Dam for hydroelectric operation, flood control, and maintenance of stable reservoir levels severely alters the natural flow regime of the Osage River and interferes with spawning behavior of river fishes. Bagnell Dam has recently been relicensed until 2056 by the Federal Energy Regulatory Committee (FERC), so changes to current operation will require cooperative efforts with AmerenUE. However, structured decision making regarding operations of hydroelectric facilities should include detailed flow modeling and predict organismal response to proposed operation of these facilities. The rapid ramping and large drawdowns in the lower Osage River that resulted in significant displacement of spawning individuals, as well as overall reproductive failure should be addressed in future relicensing of hydroelectric facilities.

In addition to evidence of poor reproduction, population characteristics and supplemental data analysis also displayed evidence for overharvest of paddlefish in the lower Osage River. Late maturity and infrequent spawning of paddlefish result in a high degree of vulnerability to overharvest (Scholten and Bettoli 2005). The large proportion of juveniles and scarcity of mature females observed with hormone analysis is similar to age and sex structures of heavily exploited paddlefish populations (Lein and DeVries 1998; Timmons and Hughbanks 2002). Current harvest regulations on the lower Osage River are a two fish per day bag limit with a minimum eye-to-fork length limit of 61cm, which are the most liberal recreational paddlefish harvest regulations in the country (Bettoli et al. 2009). We anecdotally observed an approximate 20% harvest mortality of transmittered paddlefish during the recreational snagging season in each study year. The highest known sustainable recreational harvest rate of paddlefish is 15-17% for the Neosho/Grand Lake sport fishery in Oklahoma, which maintains high levels of natural reproduction (Combs 1982; Quinn 2009). Limited reproduction observed in three consecutive years may compromise the ability of this population to sustain the high harvest rates of other populations, without immigration from other populations. An estimate of 20% is likely an underestimate of true mortality of the adult population as many transmittered paddlefish exited the system prior to closure of the season and thus were not fully vulnerable to harvest. Harvest mortality in low waters years also may be greater as fish concentrate downstream of Osage River Lock and Dam #1 and may be susceptible to intense harvest. Severe low flows that resulted in displacement from the no-snagging zone downstream of dam and concentration in a limited number of deep water habitats may also increase vulnerability to harvest.

The maintenance of the recreational fishery in the lower Osage River may be reliant on immigration from other sources. Very little information exists on the spawning site fidelity of paddlefish (Russell 1986; Paukert and Fisher 2001). Nearly half of all paddlefish transmittered in the lower Osage River moved out of the river prior to spawning temperatures and presumably spawned in another tributary or the mainstem Missouri River. If paddlefish have relatively low spawning site fidelity, many of the fish present in the lower Osage River may represent fish spawned in other systems. Additionally, paddlefish that were marked with coded wire tags and stocked in the upper reservoirs have been captured in the lower Osage River, which represents another possible source of immigration.

No commercial harvest is allowed in the Osage or Missouri rivers. However, nine transmitter returns from commercial fisherman in Tennessee, Arkansas, and Louisiana suggest that Osage River migrants are making long distance post-spawning migrations and become vulnerable to commercial exploitation in the Mississippi, Ohio, and Tennessee rivers. Nine harvested fish from 92 transmittered paddlefish is a relatively small percentage (9.8%), however, small samples sizes and underreporting of harvested fish could contribute to a greater mortality rate than observed. Pracheil (2010) analyzed long distance migratory patterns of paddlefish and found long-distance migratory rates were as high as 10-20% of the population, suggesting that a large proportion of the lower Osage River population may be vulnerable to commercial harvest. Commercial harvesters often target large adult females for roe and can rapidly overexploit a population (Scholten 2009; Quinn 2009). Recreational and commercial exploitation rates of this population remain largely unknown, further study should focus on quantifying mortality rates of this population to ensure that overexploitation is not occurring.

Paddlefish, as well as other migratory, large-bodied riverine species, remain vulnerable to habitat alteration and overexploitation. Management of regulated river systems to maximize ecological benefit for spawning and larval rearing of fish requires a more comprehensive understanding of how current ramping and fluctuation between minimum and maximum discharges affects fish reproductive physiology, habitat use, synchronization of spawning, and survival of eggs and larvae. Peaking and restriction of flows during floods represent two common hydroelectric practices that could be manipulated to maintain societal benefit while minimizing ecological consequences caused by rapid transition of flows between two extremes. Providing a comprehensive research strategy that analyzes reproductive physiology, behavior, habitat use, and success can highlight reproductive bottlenecks as well as focus management efforts on critical discharge requirements for upstream low-head passage and synchronization of spawning downstream of hydroelectric dams.

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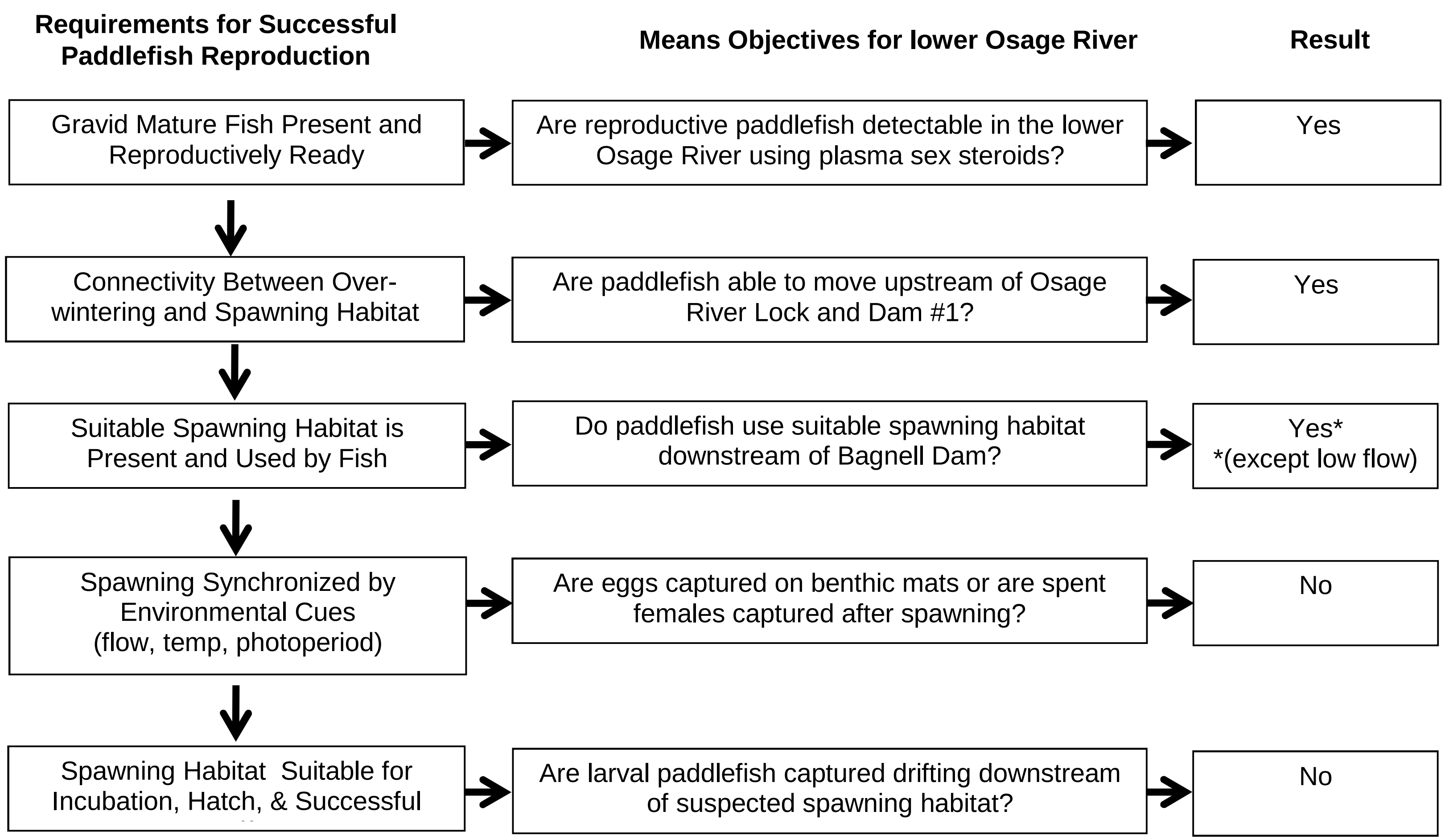

Figure 1. Conceptual diagram of paddlefish spawning requirements, means objectives, and simplified results. Gravid adult paddlefish were able to access upstream spawning habitat, but very little evidence for successful reproduction was observed, suggesting that altered flows are most likely responsible for limited reproduction.

VITA

Joshua Lallaman was born in Waukegan, IL to parents Roger and Barbara. Joshua attended Our Lady of Humility School and St Joseph's High School. Both of these Catholic schools provided him a strong foundation and appreciation of learning. Joshua also grew up hunting and fishing with his family and gained an appreciation for enjoyment of natural resources and their conservation.

The appreciation of outdoor conservation led to Joshua attending the University of Wisconsin – Stevens Point to obtain a B.S. in Fisheries. As an undergraduate, Joshua became involved in the student sub-unit of the American Fisheries Society, gaining an appreciation for professional service and student-led research.

After graduating from UW-SP, Joshua attended Central Michigan University for an M.S. in Biology. His Master's Thesis was titled: Stock Assessment and Summer Movement Patterns of Lake Sturgeon (Acipenser fulvescens) in the Manistee River, MI. Working with an ancient species of fish, like the lake sturgeon, instilled a sense of wonder about all primitive species.

Joshua then spent several years in the Upper Peninsula of Michigan, first at Michigan Technological University, then at Lake Superior State University. Both institutions reaffirmed Joshua's passion for teaching at the college level and led to application at the University of Missouri. Joshua is currently an assistant professor of Biology at Saint Mary's University of Minnesota.