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Current Status of the Pallid Sturgeon in the Middle Mississippi River

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Current Status of the Pallid Sturgeon (*Scaphirhynchus albus*) in the Middle Mississippi River: Habitat, Movement, and Demographics

Principle Investigators:

James E. Garvey, Edward J. Heist, and Ronald C. Brooks
Fisheries & Illinois Aquaculture Center &
Department of Zoology
Southern Illinois University, Carbondale 62901-6511

David P. Herzog and Robert A. Hrabik
Open River and Wetlands Field Station
Missouri Department of Conservation
Jackson, Missouri 63755

K. Jack Killgore, Jan Hoover, and Catherine Murphy
Engineer Research and Development Center
US Army Corps of Engineers
Vicksburg, MS 39180

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Synthesis

- This report summarizes the status of the pallid sturgeon (*Scaphirhynchusalbus*) in the Middle Mississippi River (MMR; River Miles, RM 0-200) during fall 2002 through spring 2005. The most likely threat to population recovery is reduced reproductive capacity (i) through limited rearing and nursery habitat and (ii) through loss of reproductively mature (primarily ovigerous female) adults. Most of the research conducted during this time has been published in the peer-reviewed scientific literature. All chapters have been reviewed by peer scientists, with corresponding responses included herein (Chapter 12).
- Pallid sturgeon as identified with morphomeristic indexes were rare relative to their congener, shovelnose or hackleback sturgeon (*S. platorynchus*), with ratios of pallid sturgeon in the samples declining with increasing latitude from the lower Mississippi River below Baton Rouge, LA (1:6) to the MMR (1:82) (Killgore et al. 2007a, Chapter 2). This does not reflect total abundance, just the relative numbers of both species in samples.
- 139 pallid sturgeon were sampled with a combination of gears including trot lines, gill nets and trawls (about 0.002 fish/hour); fork length averaged across seasons and gear types was 763 mm. Conventional randomized sampling stratified across habitats would require substantive effort to have sufficient statistical power to detect differences among gears and seasons (Phelps et al. in revision, Chapter 1). Pallid sturgeon are indeed very rare relative to shovelnose sturgeon in the MMR.
- A combined sampling and telemetry effort (*N*= 87 fish tracked) demonstrated that pallid and shovelnose sturgeon use different habitats when non-reproductive, with

pallid adults selecting wing dike areas with sandy substrate (Chi square analysis, $p < 0.0001$); acoustic Doppler profile surveys demonstrated that the ecotone between contrasting flow velocities (average bottom velocity = 0.9 m/s), likely facilitated by bendways created by complexes of island point bars and side channels (and mimicked by wing dikes), appears to be an important component of non-reproductive habitat selection by adults (Koch et al. submitted, Chapter 3). Use of the main channel increased significantly with declining discharge and water level during summer.

- Following a spring rise in water level and temperature, pallid sturgeon moved great distances to apparent upstream (16.9 km/d) or downstream (73.4 km/d) spawning locations; the Chain of Rocks (COR) of the MMR below Low Water Dam 27 (RM 189) was a frequent destination (Chapter 3).
- During May when spawning likely occurs, sonically tagged pallid sturgeon were located < 500 m from known gravel bars in the MMR ($p < 0.05$; Koch et al. submitted; Chapter 3).
- Recaptures of externally tagged pallid sturgeon and telemetry of internally ultrasonically tagged individuals demonstrated movement out of the MMR into the Missouri River and into the lower Mississippi River below the confluence of the Ohio River (Chapter 3).
- Hatchery-produced fish have recruited to the pallid sturgeon population, with at least 6% of adults sampled after 2004 being recognizable hatchery fish. More individuals were likely of hatchery origin because checking for tags was inconsistent among years. The length-weight relationship of hatchery pallids was similar to wild individuals (ANCOVA, $p > 0.05$). However, insufficient numbers of known hatchery

fish were tracked with telemetry to determine whether wild and hatchery individuals behave similarly (e.g., spring movement, habitat use).

- Using a morphomeristic character index (Wills et al. 2001), putative hybrids between shovelnose and pallid sturgeon appeared to be rare among adults (< 1% of total sturgeon catch; N ≈100; Murphy et al. 2007a, Chapter 4); however, we typically only used a character index to confirm suspected pallids. Hybrid characters in putative shovelnose were most likely underestimated.
- Annual mortality rate of pallid sturgeon based on catch-curve analysis was high (31-37%, depending on gear type, $p < 0.05$) for a sturgeon species and similar to independently derived estimates for commercially fished shovelnose sturgeon (Colombo et al. 2007a, Killgore et al. 2007b; Chapters 7-8).
- In this Executive Summary, we combine data from the various published chapters with unpublished data to demonstrate that adult (probably > 6 years) pallid population density based on mark-recapture techniques and estimates of mortality in the MMR likely was less than 4,900 and perhaps as low as 1,600 individuals.
- Yield-per-recruit harvest modeling for shovelnose sturgeon in the MMR suggested that overfishing, likely combined with limited habitat, was reducing both biomass and offspring production (Colombo et al. 2007a, Chapter 7). Given that pallid sturgeon have a similar mortality rate and mature later, then more severe demographic responses to harvest likely occur for this species (Tripp et al. 2009, Chapter 11).
- Genetic markers (nuclear DNA microsatellites) distinguished among pallid, shovelnose, and putative hybrid sturgeon ($p < 0.05$; Schrey et al. 2007a, Chapter 5).

Genetic and morphological identification was largely concordant; “hybrids” were genetically more similar to shovelnose, indicating they were backcrosses.

- Pallid sturgeon exhibited significant differences in DNA microsatellite allele frequencies among reaches across their range indicating historical restrictions to gene flow (Schrey et al. 2007b, Chapter 6). Thus, stocking programs should employ local broodstock where available to prevent outbreeding depression (i.e., introducing potentially “non-adaptive” genetic traits into locally specialized populations).
- Production of annual cohorts in shovelnose sturgeon declined with increasing harvest in the MMR. Although not yet derived, a relationship between adult stock and the production of offspring likely exists. Assuming a similar response to harvest of pallid sturgeon, then incidental or intentional harvest will greatly curtail pallid reproductive success (Tripp et al. 2009, Chapter 11).
- Morphological anomalies are relative common (9%) in adult pallid sturgeon, typically caused by anthropogenic sources (Murphy et al. 2007b, Chapter 9).
- Diets revealed that piscivory is prevalent in pallid sturgeon and thus fish are likely an important energy source (Hoover et al. 2007, Chapter 10).
- Habitat for adult pallid sturgeon foraging and residence (i.e., holding station in flow) in the MMR appears to be adequate and related primarily to wing dike areas, although all habitats with the exception of the inside of tributary mouths have been occupied. We hypothesize that some wing dikes (some were used preferentially over others) mimic natural depositional areas adjacent to the main channel (e.g., upstream island tips within the main channel). If adult pallid sturgeon densities increase, wing dikes creating preferred habitat will likely become limited and habitat restoration that

creates needed main-channel conditions (i.e.,island areas that provide an ecotone between flow with deposition, causing an accumulation of insects and small insectivorous fish) likely will facilitate foraging, growth, and ultimately reproductive condition.

- The availability and quality of reproductive habitat for spawning and production of offspring in the MMR is currently the greatest gap in our knowledge (Figure 2) and likely the key for developing a fruitful conservation plan for recovery (see DeLonay et al. 2007, Wildhaber et al. 2007 for similar issues in the Missouri River basin). The future of the pallid population in the MMR depends on high survival of adults through maturity combined with high survival of eggs, embryos, and larvae at several likely spawning and nursery areas within the MMR, which include the COR (but consider the caveat that the lowhead dam at this area may be a barrier during low flow), near tributary confluences in the main channel, and perhaps side channels.
- Pallid sturgeon capture data are available on the web in a GIS format (http://fishdata.siu.edu/move.htm).

Justification and Approach.

Distributed throughout the Mississippi and Missouri River basins, pallid sturgeon have always been considered a rarity (Bailey and Cross 1954). Nearly two decades ago, concerns about declining abundance and failing reproduction throughout the range prompted the federal government to list this species under the Endangered Species Act (Federal Register 1990). One reason cited for the decline has been habitat alteration by the US Army Corps Engineers (ACE), which occurs to enhance navigation and control flooding (US Fish and Wildlife Service 2000, USFWS). To mitigate environmental effects of navigation maintenance activities in the MMR, the St. Louis District of the ACE sought to assess the status of the regional pallid sturgeon population and determine its habitat needs. This study was a response to the issuance of the USFWS's Final Biological Opinion for Operation and Maintenance of the 9-Foot Navigation Channel on the Upper Mississippi River in 2000 (US Fish and Wildlife Service 2000). The primary goal was to identify habitat needs of pallid sturgeon in the context of their life history. This research also sought to assess the status of the species relative to expectations from other reaches and historical accounts.

The 200-mile long MMR is a geologically unique, transitional zone between the lower Mississippi River and the Missouri River (Figure 1). It is relatively narrow compared to reaches below the Ohio River confluence; channel depth for navigation is maintained by channel training structures such as wing dikes plus revetments and by an active program of dredging. Confinement and simplification of the main channel likely reduce habitat features such as instream islands and side channels, although there is some suggestion that pre-settlement physical characteristics (e.g., channel width) of the MMR are somewhat similar to present conditions (US Army Corps of Engineers 2005). Water quality in the last century was very poor in the MMR, largely due to the marked influence of the developing urban, St. Louis area (Kittrell 1958). More than likely many aspects of water quality in the MMR have improved in recent decades (but see Koch et al. 2006 for some contemporary concerns).

During fall 2002 through spring 2005, we sought to quantify potential habitat characteristics necessary for facilitating growth and survival of pallid sturgeon (primarily adults) in the MMR. We also determined whether habitat needs changed seasonally by documenting movement patterns. In particular, nothing was known about dispersal of adults, particularly relative to reproduction. Other sturgeon populations contain individuals that migrate long distances to specific spawning areas (Bramblett and White 2001) and we presumed the same for pallid sturgeon in the MMR. We used sampling and telemetry to overlay the spatial distribution of individuals on a precise habitat template of the MMR and then quantify selection for habitat features. We also used telemetry to quantify movement of adults in a preliminary attempt to determine seasonal movement and identify spawning areas. When possible, fish were uniquely tagged at capture to estimate population density.

At the inception of this project, no baseline demographic information existed for pallid sturgeon in the MMR. A baseline was needed to establish current conditions and evaluate population responses to management. We determined basic demographic features of the population including size and age structure, mortality, and abundance. Hybridization between the pallid sturgeon and its more abundant congener is suspected (Wills et al. 2001; Schrey et al. 2007a; this report). If this is true, degradation of the population may occur through introgression – alleles unique to the shovelnose population will enter the pallid population as hybrid individuals backcross with the parental stock. Thus, to determine whether pallids are genetically distinct and whether hybridization does occur, we used DNA microsatellite markers and screened individuals across a range of morphomerisitic characteristics.

Since the study began, the Caspian Sea and Volga River sturgeon fisheries were recognized as collapsed (Pala 2005). Importation of caviar into the US was restricted, increasing demand for domestically produced caviar. We quantified commercial harvest of shovelnose sturgeon relative to their abundance in the MMR. Given that pallid sturgeon are difficult to distinguish physically without using complex indexes and reach large sizes, harvest of this species likely occurs unintentionally (Bettoli et al. 2009); illegal harvest also continues to occur, despite the best efforts of conservation law enforcement. Therefore, we considered pallid sturgeon population dynamics in the context of potential harvest. Because harvest is preferential for sexually mature, “black-egg” females, sturgeon populations should be particularly sensitive.

Although we have approached this research from the perspective of identifying habitat needs for adults and generating baseline information about the species, we ultimately need to organize our research in the context of the entire life history (Figure 2; Wildhaber et al. 2007). Schedules of maturation in pallid sturgeon are not well known, but it is likely that males probably do not mature until age 5-7 (or older) and females at age 10 or greater (Figure 2; Tripp et al. 2009). Females may spawn as infrequently as every 3-10 years. In many fishes, reproductive potential is unlimited in the adult populations because of high inherent fecundity and frequent spawning (Garvey et al. 2009). However, given infrequent spawning and small population size, it is likely that variation in spawning success translates to variation in cohort production in pallid sturgeon (Figure 2). Reponses of shovelnose sturgeon to harvest and contribution to cohort strength should shed light on potential responses of pallid sturgeon to declining adult abundance in its population. If habitat is limited for adult spawning or the survival of eggs and larvae, then the population will be in jeopardy (Figure 2).

Goals.

Given the justification outlined above, we pursued the following goals for pallid sturgeon in the MMR (Figure 2):

- Quantify gear effectiveness for assessing available adult non-reproductive habitat (Chapters 1, 2, 3)
- Determine preference for adult habitat (Chapter 3)
- Assess seasonal movement of adults in the context of reproduction (Chapter 3)
- Estimate population growth, size and age structure, mortality rate, and energy sources (Chapters 2,4,7,8,9,10)
- Develop genetic tools for identifying hybridization and separation between species (Chapters 5,6)
- Assess the impact of other human-induced factors such as harvest and pollution (Chapter 7,9,11)
- Generate strategies for mitigating human effects (e.g., identify habitat characteristics to be emulated in the MMR; reduce harvest of sensitive individuals) and develop techniques to quantify benefits to the species.

Contributions.

During the course of this study, we lost two important participants in this research effort, Dr. Robert Sheehan and Mr. Dan Erickson. They played integral roles in the development and implementation of this research. Their good sense, insight, and friendship will be sorely missed. Many of the chapters describing results herein are manuscripts that are submitted, in press, or published in the peer-reviewed literature.

Resulting data have been presented at several regional and national meetings; two oral presentations won Best Paper awards. This research also has contributed to the training of four masters students (Jackson, Colombo, Koch, and Tripp), two PhD students (Schrey, Phelps), and one post-doctoral associate (Spier) at SIUC. A cast of thousands was involved in this research and many are listed as authors on the chapters contained in this report. Several members of the commercial fishing community were contracted to help sample pallid sturgeon. Funding was provided by the St. Louis District; Dr. Tom Keevin provided technical guidance. Funding also was provided by the Mississippi Valley Division for pallid sturgeon studies in the lower Mississippi River. Much of the genetics analysis was funded by the US Fish and Wildlife Service. Reviews were provided by the US Fish and Wildlife Service, Missouri Department of Conservation, Illinois Department of Natural Resources, and several anonymous scientists. We appreciate their comments, incorporating necessary changes in this section as well as the published and unpublished chapters. We address all specific comments in Chapter 12.

Major Results.

General.

During each season (fall, spring, summer, winter) of fall 2002 through late spring 2005, we sampled a total of 143 pallid sturgeon, of which four fish were recaptured (Table 1). Of those four recaptured fish, one fish at Chain of Rocks (COR; RM 189-190) was recaptured twice below the lowhead dam. During the course of the study, sampling effort was distributed across gillnets, trawling, and trotlining, with over 64,000 hours of fishing expended (0.002 pallids/hour; Table 1; see Chapter 1). In addition to capturing pallid sturgeon, 11,459 shovelnose sturgeon were sampled resulting in a ratio of pallid to shovelnose of 1:82 (0.2 shovelnose/hour; Table 1). Mean fork length $\underline{+}$ 1 standard deviation (mm FL) of all pallids sampled across all gear types was 763 $\underline{+}$ 101 (Figure 3). The relationship between FL and wet weight (kg) was Weight = 7.285E-10*Length$^{3.26}$ (R^2=0.89). From combined sampling by Missouri Department of Conservation and SIUC, we successfully aged 75 MMR pallids using pectoral fin ray sections, of which the same age was agreed upon by two independent readers. No asymptote to length was found; growth was linear from age 6 through age 15 (no older fish occurred; fork length in mm = 37.2 x age in years + 421; R^2=0.65; Figure 4). For pallid sturgeon collected using random stratified sampling across all gear types, we had insufficient statistical power to detect differences in abundance among seasons or habitats (Chapter 1, Phelps et al. in revision).

In a related effort, trotlining by ERDC personnel was conducted along the Mississippi River from the MMR RM 190 to lower Mississippi RM 100 (Chapter 2, Killgore et al. 2007a; Figure 5). In this analysis, the ratio of pallid to shovelnose declined from 1:6 at lower Mississippi RM 100-310 to the COR in the MMR (MMR RM 189) where the ratio was 1:77 (Table 2). Catch rates of both pallid and shovelnose were quite high at COR relative to other reaches (Table 2). The high vulnerability of shovelnose sturgeon to trotlines and concentration of sturgeons at COR relative to other reaches probably contributed to this distinctly lower ratio between the congeners at the northernmost sampling reach. Length of trotlined pallid sturgeon increased from 620 mm mean FL to 756 mm FL along this broad latitudinal gradient (Table 3; Chapter 2). This pattern is predicted by Bergmann’s Rule for many taxa (see Garvey and Marschall 2005).

Habitat.

It was hypothesized that habitat for pallid sturgeon in the MMR was related to the physical structure of the main channel. Sampling with multiple gear types revealed that pallid sturgeon were vulnerable to trotlining and 3-inch mesh gill nets, typically set adjacent to the open main channel, often near wing dikes and at times near island areas (see Chapter 1). Small sample sizes restricted our ability to assess these patterns statistically. Although impossible to standardize, drifting trammel nets also effectively sampled pallid sturgeon adults. Randomly setting gear across habitat types very rarely sampled pallid sturgeon. Only when gears were set in areas known to contain pallid sturgeon (i.e., “directed sampling”) were individuals captured. Statistical analysis did show that shovelnose sturgeon were more vulnerable to capture behind wing dike areas and, being typically smaller bodied and perhaps residing in different habitats, they were more frequently selected by 2-inch mesh gill nets and trawling (Chapter 1). However, shovelnose sturgeon probably are not a good surrogate for inferring seasonal habitat use of pallid sturgeon due to apparent differences in gear vulnerability (and low power of stratified sampling for pallid sturgeon, Chapter 1).

Because our research demonstrated that pallid sturgeon are too rare to effectively sample across habitats with a stratified random program of trawling, gillnets, and other gears (Chapter 1), we surgically implanted ultrasonic tags in 87 adult pallid sturgeon, and tracked 5,362 miles with boat-mounted hydrophones (Chapter 3). By 2005, a network of stationary, automatically logging hydrophones also was in place in the MMR (Table 4). The Cobb classification scheme (US Army Corps of Engineers 1999) was modified to include more resolution relative to wing dike habitats in the river. Confirming the results of the sampling survey, statistical analysis of preference demonstrated that the tagged pallid sturgeon occupied wing dike areas in far greater proportion than expected. Surveys of bottom flow velocities with Acoustic Doppler Current Profiling (ADCP) and substrate with qualitative benthic grabs demonstrated that pallid sturgeon used areas of contrasting flow (average of 0.9 m/s) with sandy bottoms. Island tips and inside tributary mouths were never used by tagged adult fish and unconsolidated, muddy bottoms were avoided.

Moving in a river is typically energetically expensive and is usually related to some important life history event such as reproduction. During each year, we found that pallid sturgeon individuals often remained relatively stationary for months only to move great distances upstream or downstream during spring (> 16 km/d or 10 miles/d for one individual; average 0.6 km/d or 0.4 miles/d). This movement was statistically associated with a combined spring rise in water temperature and water level (Chapter 3; Figure 6). The automated receiver network was essential for collecting this information.

The COR at RM 189-190 was a frequent destination of migrating fish (Figure 6), which is congruent with the high catch rates of sturgeon at this area (Chapter 2). We are unsure whether the lowhead dam at COR (Low Water Dam Number 27) was a barrier to movement of adult sturgeon or a reproductive and staging area given that large gravel and sand deposits are located below the dam. Supposedly, a barrier would cause an aggregation of fish as they attempted to pass. However, we have documented three pallid sturgeon moving across this dam and into the Missouri River during spring when river stage was about 16 feet (St. Louis Gage, Chapter 3). Thus, the role of the lowhead dam as a barrier during spring migration is questionable, although we do not know about effects at lower river stages. Other spring aggregations occurred in the MMR (Meramec River confluence, RM 158-163; Kaskaskia River confluence, RM 115-117; Grand Tower area, RM 79-81; Thebes area, RM 29-44) and may be destinations for staging and spawning.

These results demonstrate that a combination of physical sampling and telemetry provided complementary information about the habitat use and movement of pallid sturgeon in the MMR (also see DeLonay et al. 2007). The ability for wing dikes to concentrate flow and simultaneously provide refuge in shear zones of lower velocity next to swiftwater is an important component of adult life histories. These channel training structures probably provide a function similar to that historically provided by islands, side channels, and perhaps braided channels. Although we suspect that the simultaneous spring movements among fish and increased proximity to gravel bars are due to spawning, we have yet to link the movements to the production of eggs and larvae at the purported migratory destinations, although this has recently been accomplished in the Missouri River (Aaron Delonay, USGS, unpublished data).

Given that we documented multiple spring aggregations and assuming a relationship to spawning, it is quite likely that reproductive segregation occurs in the MMR. Clearly, morphological variation is marked throughout the Mississippi River basin (see Chapters 2 and 4) and these differences may be due to both environmental and genetic differences. Genetic differences were very small among shovelnose sturgeon from different river reaches (Schrey et al. in press). Allele frequency differences among reaches were greater in pallid sturgeon and were probably due to some reproductive isolation as a function of reproductive site fidelity among individuals (Chapter 6, Schrey et al. 2007b). Identifying spawning aggregations and determining whether this leads to genetic structure within the MMR and other reaches is paramount to developing conservation plans for this species, with the goal of preserving genetic diversity.

In shovelnose sturgeon, we have found strong variation among individuals in contamination by organochlorine pesticides (Koch et al. 2006). Contaminant loading in the brain–hypothalamic-pituitary complex is positively related to intersexuals in the MMR and it is likely that exposure occurs during early life before and during sexual determination and maturation (Koch et al. 2006). It is not unlikely that similar patterns occur in pallid sturgeon and early exposure is probably due to the contaminant loads in spawning sites selected by adults and nursery areas used by offspring. Identifying areas of adult fidelity for spawning and areas of juvenile settlement is important for assessing risk of contaminant exposure and degree of future reproductive problems in the population.

Demographics, Life History, and Density.

The late age at maturity, large and relatively sparse eggs, migratory spawning behavior, and special spawning needs (e.g., depositing demersal, adhesive eggs in a large river with a moving, unstable bed may reduce survival) of sturgeon make them particularly susceptible to loss of spawning habitat or interference with reproduction. To compensate for these conditions and successfully produce on average one successful generation during a lifetime, species with these life history characteristics must commit to long life spans with multiple spawning forays. The population's engine relies on high survival of adults, particularly mature females; any perturbation that prevents adults from reproducing including loss of spawning and nursery habitat, impedance of fish passage, or selective mortality of mature adults will place the population in jeopardy (Wildhaber et al. 2007).

Before we quantify the current status of the pallid sturgeon population, we need to determine what exactly a pallid sturgeon is. To address the debate about whether "pure" pallid sturgeon remain in the MMR, we assessed current morphomeristic indices (Chapter 4) and DNA microsatellite markers (Chapter 5) to evaluate the degree of hybridization with shovelnose sturgeon. Considerable variation exists in the performance of current character indices used by biologists in the field to identify pallid sturgeon (Chapter 4). Only with sophisticated ordination techniques might individuals be separated based on morphological and meristic characters (Chapter 4).

Genetic analyses (N= 157 fish) conducted independently of morphological identification confirmed that there are two genetic groups of *Scaphirhychus* in the MMR and that these groups were concordant with morphologically identified pallids and shovelnose (Chapter 5). Morphological intermediates varied in their genetic affinity to either pallid or shovelnose groups but many were more similar to shovelnose, indicating F1 hybrids were backcrossing to the numerically dominant shovelnose. Although a large random sample from both populations has not been screened for the degree of hybridization, less than 1% of the putative pallid sturgeon that we screened morphomeristically were identified as hybrids. However, it is important to note that only pallid sturgeon that were suspected to have intermediate characteristics were screened.

Because hybrids appear to be closer genetically and perhaps morphologically to shovelnose, a concerted effort where all *Scaphirhynchus* sturgeon are screened genetically needs to be done to quantify the true rate of hybridization among the two populations in the MMR.

Although behavior, habitat use, and trophic status of pallid sturgeon were all different than those of shovelnose, both species probably undergo similar demographic responses to perturbations associated with reproduction such as loss of spawning and rearing habitat and loss of adults due to harvest. Thus, demographic characteristics of the abundant shovelnose sturgeon such as mortality rate and recruitment variability might have some similarity to that of the rare pallid. We quantified annual mortality rates of shovelnose sturgeon from their age structure (via annuli on pectoral fin rays) and discovered that rates were quite high (up to 37%) relative to other, unharvested shovelnose populations which experience less than 10% annual mortality (Chapter 6). More alarming was the sharp, highly significant negative relationship between an index of annual year-class strength and the harvest of shovelnose (Figure 7). Given that harvest of shovelnose sturgeon is increasing in the upper Mississippi River system, this suggests that production of year-classes will be reduced concurrently. Recruitment appears to be declining through time. During the past 5 years of standardized sampling in the MMR, the age distribution of shovelnose sturgeon in the MMR has been shifting toward older individuals with fewer apparent recruits comprising the population (Figure 8; Tripp et al. 2009).

Given that we had sufficient information about mortality and vital rates in shovelnose sturgeon and it is legally harvested, we modeled responses of biomass and offspring production in the population to a range of fishing mortality rates and size-selective harvest limits for this species (Chapter 7; Colombo et al. 2007a). The model revealed that current rates of size-dependent harvest of shovelnose sturgeon in the MMR are not sustainable and that a substantive reduction in production was occurring. This further supported our conclusion that the mortality rates we quantified exceed those of a stable sturgeon population.

Given our limited sample size for pallid sturgeon, making population inferences was difficult. However, aging data from the combined sampling effort across three years demonstrated that pallid mortality rate (37% per year) was similar to that of shovelnose sturgeon (Chapter 7; Figure 9). A separate, independently derived annual mortality estimate solely from trotlining was similar (31% per year; Chapter 8). This was much higher than a mortality estimate by our group of 17% derived for trotlined pallids from the lower Mississippi River (Chapter 8), where harvest for all sturgeon is illegal but some poaching may be occurring. Although pallid individuals from the Missouri River have been found to live for 60 years, the oldest individual we captured in the MMR was 15 years (Figure 9) and growth had not yet decelerated (see previous section). We suggest that the similarity in mortality and truncated age structure with this species' commercially fished congener is not coincidental and likely related at least in part to harvest (see Bettoli et al. 2009). Population growth is typically quite sensitive to age at maturity. Given that pallid sturgeon likely mature later than shovelnose, then this species is likely more sensitive to size-dependent harvesting, which likely is occurring.

Our mark-recapture effort (unpublished data) for shovelnose sturgeon yielded sufficient individuals to generate a crude population estimate. This is likely for individuals > 6 years, because this is the age when they are typically fully recruited to our sampling gear. We were limited by the small sample of recaptures to a modified Schnabel multiple census effort (Ricker 1975). Because we extended the effort across multiple years of the study, we assumed that marked individuals had an annual mortality probability of 37% and applied an annual exponential decay to the sample size of marked individuals at large (Table 5). From this, we generated an estimate of 136,000 shovelnose adults (upper 95%: 160,000; lower 95%: 116,000). A separate approach using the catch relationship

$$C_t = \left(\frac{F_t}{Z}\right) N_t \left(1 - e^{-(F_t + M)}\right)$$

where C_t is current harvest in the fishery (in numbers), F_t is instantaneous fishing mortality, Z is total instantaneous mortality, and M is natural mortality can be used to estimate N_t, population size (in numbers). Our last robust catch estimate from the MMR was in 2001, which was about 36,250 individuals, assuming that the average shovelnose sturgeon in the creel was 0.8 kg (see Chapter 7 for harvest estimates). Assuming about 10% natural annual mortality and including 37% total mortality, our estimate of N from this catch equation for 2001 was 155,159 individuals, well within the confidence intervals around the mark-recapture estimate.

If we assume a ratio between congeners of 1:82, then the pallid population may only be comprised of 1,600 individuals in the MMR. Conversely, given the four recaptures of pallids out of 139 at large in the MMR, a crude Petersen estimate would be 4,900 individuals, although the error is very high and we cannot account for mortality of marked individuals at large in the population across years.

Clearly the pallid population is small in the MMR and it is no surprise that hatchery reared individuals, confirmed by coded wire tag to be fish released from Blind Pony Fish Hatchery, Missouri in 1994, began to recruit to our gear by 2004. One 1994 hatchery fish that we captured in 2004 was confirmed to be 10 years old from aging its sectioned pectoral fin ray. The total proportion of known hatchery-reared pallid in our samples was 9 of 139 fish (6%). However, if we restrict our analysis to fish that were routinely scanned for coded wire tags after Fall 2004 (the tags placed in some hatchery fish), then the proportion in our samples increased to 22% of pallids captured (also see Chapter 2). These pallids were aged and their ages compared to the population at large. Fork lengths at age were similar to that predicted for the entire population using the linear regression model provided earlier (all FL in mm; Age 6: predicted = 645, hatchery = 541; Age 7: predicted = 682, hatchery = 689; Age 8: predicted = 719, hatchery = 684; Age 12: predicted = 868, hatchery = 802; Age 14: predicted = 942, hatchery = 879). An Analysis of Covariance confirmed that there was no effect of origin (hatchery or wild) on length at age; however, given that only seven hatchery fish could be included in the analysis, our power was poor. Given the recent preponderance of hatchery-reared individuals in the population, it likely is the transition from adult spawning to production of offspring that is the bottleneck for population production in the MMR (Figure 2).

Summary and Conservation Implications.

We have not yet amassed sufficient data to generate a relationship between the abundance of adult spawners and the number of young produced and recruiting to the population (Figure 2). However, indirect evidence (i.e., from relationships between cohort strength and harvest) suggests that a strong one exists for shovelnose sturgeon and likely for its congener. These sorts of relationships typically arise in fish populations that are declining and that have limited access to reproductive habitat such as those of Pacific salmon and Atlantic cod (see Chapter 7, 11). If the pallid population is reaching low numbers- a difficult conclusion to make given its historical rarity relative to shovelnose and a lack of historical data- then concerns about hybridization and limited numbers of recruits come into sharp focus.

Assuming that our population estimate is remotely accurate, the number of females contributing eggs to the population during each year is likely quite limited. To illustrate, recall that female *Scaphirhynchus* sturgeon mature late – perhaps at age 10 or greater - and may only spawn once every 3-5 years (Colombo 2004, Tripp et al. in press; Chapter 7). If age-10 pallid sturgeon comprise perhaps 10% of the population and of that 50% are females, then only 5% of the individuals are sexually mature females. If only 33% of those mature females are ovigerous during any one year, then only about 2% of the population is contributing eggs during any given year. If the population is as small as 1,600 individuals, then only 32 females spawn each year. Obviously, egg harvest of a single female will negatively affect reproduction in the population. Although anecdotal, our ability to capture and sonically tag mature, black-egg females was limited (see Chapter 3). On one date in December 2004 at COR we tagged 11 fish including a black-egg female. It was the only fish that we were unable to relocate. Although this female may have rapidly moved out of the area, it also may have been harvested. Without adults to drive reproduction in the population, attempts to enhance and protect spawning habitat will be futile without supplemental stocking.

Clearly, pallid sturgeon did not evolve with wing dikes, although this is the habitat selected in the MMR. Habitat with complex, contrasting flow patterns and areas of sand deposition appears to be ideal, likely facilitating foraging. We suspect that the choice of wing dike habitats is associated with foraging and we have good evidence that pallid sturgeon are piscivorous (Chapter 10; Hoover et al. 2007), even early in life (Gerrity et al. 2006). Because we are speculating about the foraging benefits of wing dikes, better evidence of prey availability in these areas plus better resolution of habitat use and position are needed. But, given that adults grew linearly in length through the oldest age in our samples, it is unlikely that growth is limited by residing at these habitats. Further, water quality has been improving in the MMR since the last century, so this habitat characteristic may be recovering for pallid sturgeon. It is important to note that pallid sturgeon densities are likely low in the MMR relative to historical levels. If so, then as densities increase with successful natural recovery or hatchery-reared individuals recruit well to the population, habitat and associated energetic costs/benefits might become an important limiting factor for adults.

Following the installation of the stationary hydrophone array and our intensive tracking effort during late 2004 through spring 2005, we began to enhance our understanding of spring movement and its potential relationship to spawning. However, we failed to link these movements with reproduction. In our view, a central key to enhancing pallid sturgeon is getting adults to arrive unharmed (i.e., unmolested and unharvested by fishers and unaffected by navigation) at spawning areas and allowing them to spawn successfully. Black-egg female pallid sturgeon are very rare in the population (only four were identified during our tagging study). The conservation community needs to improve its ability to capture and then follow these individuals to purported spawning aggregations, similar to efforts occurring in the Missouri River.

We have collected larvae and small juveniles in our trawling (Chapter 1), of which some have been confirmed to be pure pallids (Schrey 2007; Heist and Boley, unpublished data). Fall spawning of shovelnose sturgeon and perhaps pallid sturgeon has been confirmed (Tripp et al. in press). However, aging these young sturgeon and thus determining their origin and linking this to adult activity at sites within the MMR is challenging. To identify important spawning and rearing areas, the origin and destination for young sturgeon as well as their growth and survival at these locations need to be quantified.

For any population, the ultimate measure of success is the successful transition of offspring to reproductive age, typically known as recruitment. This is currently the largest gap in our knowledge of the life history of pallid sturgeon (Figure 2). We know little about the species composition and degree of hybridization of young produced at sites described herein (Chapter 5). A preliminary screen of larval sturgeon from the lower Missouri River and the MMR suggests a high degree of hybridization, although one genetically pure pallid was found (Heist and Boley, unpublished data). Given that embryos and larvae are impossible to identify physically, biologists must rely on genetics for identification of larvae and assessment of spawning success.

As with adults, we recommend that larval and juvenile production be monitored regularly throughout the MMR using the appropriate gear types (Chapter 1). As mentioned earlier, a relationship between adult spawners and the production of young has not yet been established. If one exists, then we might be able to predict the reproductive potential of the population by quantifying adult abundance. However, how this reproductive potential is realized can only be determined by sampling young produced. Developing a standardized index of offspring abundance and following trajectories of growth and survival will likely be a sensitive indicator of population status, variable adult (i.e., black egg female) survival, and response to habitat enhancement.

Literature Cited.

Bailey, R.M. and F.B. Cross. 1954. River sturgeons of the American genus *Scaphirhynchus*: characters, distribution, and synonymy. Papers of the Michigan Academy of Sciences, Arts, and Letters 39:169-208.

Bettoli, P. W., M. Casto-Yerty, G. D. Scholten, and E. J. Heist. 2009. Bycatch of the endangered pallid sturgeon (*Scaphirhynchus albus*) in a commercial fishery for shovelnose sturgeon (*Scaphirhynchus platorynchus*). Journal of Applied Ichthyology 25(1):1-4.

Bramblett, R.G. and R.G. White. 2001. Habitat use and movements of pallid and shovelnose sturgeon in the Yellowstone and Missouri Rivers in Montana and North Dakota. Transactions of the American Fisheries Society 130:1006-1025.

Colombo, R. E. 2004. Reproductive demographics of the shovelnose sturgeon (*Scaphirhynchus platorynchus*). Masters thesis, Southern Illinois University.

Colombo, R.E., J.E. Garvey, N.D. Jackson, R. Brooks, D.P. Herzog, R.A. Hrabik, and T.W. Spier. 2007. Harvest of Mississippi River sturgeon drives abundance and reproductive success: a barbinger of collapse? Journal of Applied Ichthyology 23:444-451.

DeLonay, A.J., D.M., Papoulia, M.J. Wildhaber, G.E. Mestl, D.W. Everitt, amd K.A. Chojnacki. 2007. Movement, habitat use, and reproductive behavior of shovelnose sturgeon and pallid sturgeon in the Lower Missouri River. Pages 23-102, C.Korschgen, editor. Factors affecting the reproduction, recruitment, habitat, and population dynamics of pallid sturgeon and shovelnose sturgeon in the Missouri River. USGS Open-File Report 2007-1262.

Federal Register. 1990. Determination of the endangered status for the pallid sturgeon, final rule. Sept 6, 1990. 55(173): 36641-36647.

Garvey, J.E., and E.A. Marschall. 2003. Understanding latitudinal trends in fish body size through models of optimal seasonal energy allocation. Canadian Journal of Fisheries and Aquatic Sciences 60(8):938-948.

Garvey, J.E., R.A. Wright, and E.A. Marschall. 2009. Searching for threshold shifts in spawner recruit relationships. Canadian Journal of Fisheries and Aquatic Sciences 66:312-320.

Gerrity, P.C., C.S. Guy, and W.M Gardner. 2006. Juvenile pallid sturgeon are piscivorous: a call for conserving native cyprinids. Transactions of the American Fisheries Society 135:604-609.

Hoover, J.J., S.G. George, and K.J. Killgore. 2007. Diet of shovelnose sturgeon and pallid sturgeon in the free-flowing Mississippi River. Journal of Applied Ichthyology 23:494-499.

Killgore, K.J., J.J. Hoover, S.G. George, B.R. Lewis, C.E. Murphy, and W. E. Lancaster. 2007. Distribution, relative abundance and movements of pallid sturgeon in the free-flowing Mississippi River. Journal of Applied Ichthyology 23:476-483.

Killgore, K.J., J.J. Hoover, J.P. Kirk, S.G. George, B.R. Lewis, and C.E. Murphy. 2007. Age and growth of pallid sturgeon in the free-flowing Mississippi River. Journal of Applied Ichthyology 23:452-456.

Kittrell, F.W., 1958. Pollution of interstate waters of the Mississippi River in the St. Louis metropolitan area. Robert A. Taft Sanitary Engineering Center, Cincinatti, Ohio PB-216 902; Distributed by US Department of Commerce, National Technical Information Service.

Koch, B.T, J.E. Garvey, M.J. Lydy. 2006. Elevated organochlorines in the brain-hypothalamic-pituitary complex of intersexual shovelnose sturgeon. Environmental Toxicology and Chemistry 25:1689-1697.

Murphy, C.E., J.J. Hoover, S.G. George, and K.J. Killgore. 2007. Morphometric variation among river sturgeons (*Scaphirhynchus* spp.) of the Middle and Lower Mississippi River.

Murphy, C.E., J.J. Hoover, S.G. George, B.R. Lewis, and K.J. Killgore. 2007. Types and occurrence of morphological anomalies in *Scaphirhynchus* spp. of the Middle and Lower Mississippi River. Journal of Applied Ichthyology 23:354-358.

Pala, C. 2005. Ban on beluga sturgeon caviar points to sturgeon's worldwide decline. Science 310:37.

Phelps, Q.E., D.P. Herzog, R.C. Brooks, V.A. Barko, D.E. Ostendorf, J.W. Ridings, S.J. Tripp, J.E. Garvey, and R.A. Hrabik. In revision. Comparison of three common gear types to sample sturgeons in the Middle Mississippi River. North American Journal of Fisheries Management.

Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Bulletin of the Fisheries Research Board of Canada 175.

Schrey, A.W., and E.J. Heist. 2007. Stock structure of pallid sturgeon analyzed with microsatellite loci. Journal of Applied Ichthyology 23:297-303.

Schrey, A.W., B.L. Sloss, R.J. Sheehan, R.C. Heidinger, and E.J. Heist. 2007. Genetic discrimination of middle Mississippi River *Scaphirhynchus* sturgeon into pallid, shovelnose, and putative hybrids using multiple microsatellite loci. Conservation Genetics 8:683-693.

Schrey, A., R. Colombo, J. Garvey, and E. Heist. In press. Stock structure of shovelnose sturgeon analyzed with microsatellite DNA and morphological characters. Journal of Applied Ichthyology.

Tripp, S.J, R.E. Colombo, and J.E. Garvey. 2009. Declining recruitment and growth of shovelnose sturgeon in the Middle Mississippi River: implications for conservation. Transactions of the American Fisheries Society 138:416-422.

Tripp, S., Q. Phelps, R. Colombo, J. Garvey, B. Burr, D. Herzog, and R. Hrabik. In press. Maturation and reproduction of shovelnose sturgeon in the Middle Mississippi River. North American Journal of Fisheries Management.

US Army Corps of Engineers, St. Louis District. 2005. Geomorphology study of the Middle Mississippi River. Applied River Engineering Center Publication.

US Fish and Wildlife Service. 2000. Final biological opinion for the operation and maintenance of the 9-foot navigation channel of the Upper Mississippi River. Prepared by the US Fish and Wildlife Service Rock Island Field Office, Rock Island, Illinois; Marion, Illinois; Twin Cities Field Office, Bloomington, Minnesota, USA.

Wildhaber, M.L., DeLonay, A.J., Papoulias, D.M., Galat, D.L., Jacobson, R.B., Simpkins, D.G., Braaten, P.J., Korschgen, C.E., and Mac, M.J., 2007, A conceptual life-history model for pallid and shovelnose sturgeon: U.S. Geological Survey Circular 1315, 18 p.

Wills, P.S., R.J. Sheehan, B.L. Sloss, and R. Clevenstine. 2001. Differentiation of pallid sturgeon and shovelnose sturgeon using an index based on meristics and morphometrics. American Fisheries Society Symposium 28:249-258.

Table 1. Total sturgeon sampling effort in the Middle Mississippi River from May 2002 through Summer 2005 by Missouri Department of Conservation, Southern Illinois University-Carbondale, and Corps of Engineers Waterways Experiment Station.

Stats by Gear	**MDC**	**SIU**[1]	**CEWES**	**Total**
GILLNETS				
Sample Number	1,308	790	6	2,104
Hours Fished[1]	21,868	12,433	96	34,397
Number of Shovelnose	3,391	2,510	8	5,909
Number of Pallids	23	19	0	42
TRAWLS				
Sample Number	1,657	518	3	2,178
Hours Fished	124.7	50.7	0.5	175.9
Number of Shovelnose	957	130	3	1,090
Number of Pallids	3	0	0	3
TROTLINES				
Sample Number	829	223	359	1,411
Hours Fished	19,224	4,626	5,744	29,594
Number of Shovelnose	1,127	260	3,073	4,460
Number of Pallids	32	2	41	75
TOTAL ALL GEAR				
Sample Number	3,794	1,531	368	5,693
Hours Fished	41,217	17,110	5,841	64,167
Number of Shovelnose	5,475	2,900	3,084	11,459
Number of Pallids	58	21	41	120

[1] Gillnet effort does not include pallid sturgeon captured by commercial fishermen because hours fished could not be determined.

Table 2. (From Chapter 2) Statistical summary of abundance (catch-per-unit-effort) for pallid and shovelnose sturgeons captured in the Mississippi River using trotlines from 1997 to 1998, and 2000-2006. The lowermost reach of the Mississippi River (Mile 0-100) was not included because no sturgeon were collected (n=25). For analytical purposes, the Middle Mississippi River was divided into two reaches – below Chain of Rocks (CR) to the mouth of the Ohio River and at CR. Values for mean abundances with different letters along a row are significantly ($p<0.05$) different according to the Student-Newman-Keuls multiple range test.

Species and Statistic	Reach				
	100-310	310-680	680-985	MMR wo/CR	MMR CR
Number of trotlines	144	574	145	273	86
Pallid sturgeon					
Mean	0.31^{a}	0.15^{b}	0.18^{b}	0.12^{b}	0.29^{a}
Standard deviation	0.68	0.47	0.62	0.33	0.59
Coefficient of variation	223	306	346	284	203
Maximum collected per line	4	5	5	2	3
Total collected	44	88	26	32	25
Shovelnose sturgeon					
Mean	1.88^{a}	2.76^{b}	5.41^{c}	4.22^{c}	22.24^{d}
Standard deviation	3.39	3.84	8.39	5.45	12.41
Coefficient of variation	180	138	155	129	56
Maximum collected per line	20	28	50	32	43
Total collected	271	1593	784	1151	1913
pallid:shovelnose (totals)	1:6	1:18	1:30	1:36	1:77

Table 3. (From Chapter 2) Statistical summary of fork length (mm) for pallid and shovelnose sturgeons captured in the Mississippi River using trotlines from 1997 to 1998, and 2000-2006. The lowermost reach of the Mississippi River (Mile 0-100) was not included because no sturgeon were collected. For analytical purposes, the Middle Mississippi River was divided into two reaches – below Chain of Rocks (CR) to the mouth of the Ohio River and at CR. Values for mean length with different letters along a row are significantly ($p<0.05$) different according to the Student-Newman-Keuls multiple range test.

Species and Statistic	Reach				
	100-310	310-680	680-985	MMR wo/CR	MMR CR
Pallid sturgeon					
Number Collected	44	88	26	32	25
Mean	620^{a}	702^{b}	741^{b}	758^{b}	756^{b}
Standard deviation	110	111	65	87	96
Minimum	405	410	540	541	553
Maximum	789	965	854	889	995
Shovelnose sturgeon					
Number Collected	265	1547	775	1123	1887
Mean	539^{a}	587^{b}	599^{c}	621^{d}	578^{b}
Standard deviation	80	81	82	72	77
Minimum	328	265	285	289	273
Maximum	852	860	818	831	790

Table 4. List of VR2 (Vemco Lmtd.) stationary receivers in the MMR during spring 2005.

VR2	Buoy Type	ID	River Mile
3094c	can (#8)	MO River	3.4MO
3064c	can (#5)	COR above 1	194.4
3090c	can (#2)	COR above 2	194.2
3115c	can (#4)	COR below 1	187.7
3095	can (#12)	COR below 2	187.7
3066	nun (#3)	Mosenthein SC	185.3
4945	bottom	Meremac	161.5
3098	can (# none)	Osborn chute	144.5
4940	nun (new)	Osborn chute	144.5
3065	can (#11)	Establishment	130.3
3061	nun (#14)	Moro Island	119.9
4943	can (# new)	Moro Island	119.8
4944	bottom	Kaskaskia	118
3097	can (#4)	Rockwood Island	101
4941	can (# new)	Cottonwood	72
4939	nun (new)	Cottonwood	72
4942	Bottom	Big Muddy	76
3096	nun (#15)	Hamburg	62.5
3093	can (#7)	Thebes	44
3116	nun (new)	Thebes	44
3091	nun (#15)	Boston Bar	9.7
3092	nun (#9)	Cairo	0.5

Table 5. Multiple census mark-recapture data for shovelnose sturgeon captured in the Middle Mississippi River during 2002 through 2005. Adjusted marked individuals at large (Adjusted M column) were generated assuming a 37% annual mortality rate.

	Sum of caught C	Sum of tagged U	Sum of recap R	M	Adjusted M	C X M
Summer 02	95	29	0	0	0	0
Fall 02	468	312	4	29	26	12280
Winter 02	460	383	15	341	306	140784
Spring 03	1990	1725	31	724	623	1240726
Summer 03	212	176	0	2449	2125	450499
Fall 03	211	197	3	2625	2082	439307
Winter 03	286	275	7	2822	2062	589774
Spring 04	1013	966	17	3097	2115	2142229
Summer 04	678	325	3	4063	2788	1889970
Fall 04	847	813	3	4388	2816	2385463
Winter 04	404	352	9	5201	3284	1326731
Spring 05	2347	1933	52	5553	3290	7721576
Summer 05	264	31	0	7486	4726	1247650
					N	136021
					$N_{\text{lower 95\% CI}}$	115543
					$N_{\text{upper 95\% CI}}$	160131

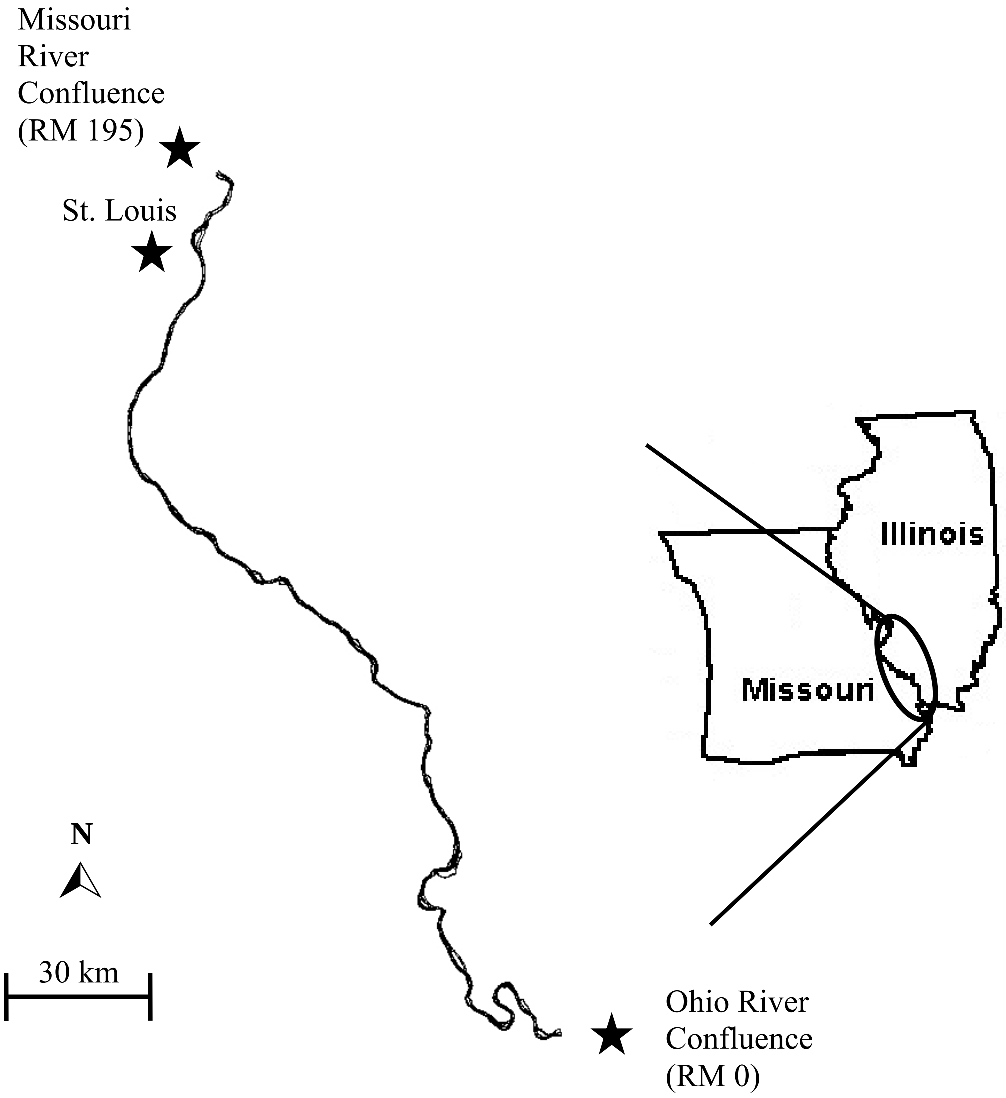
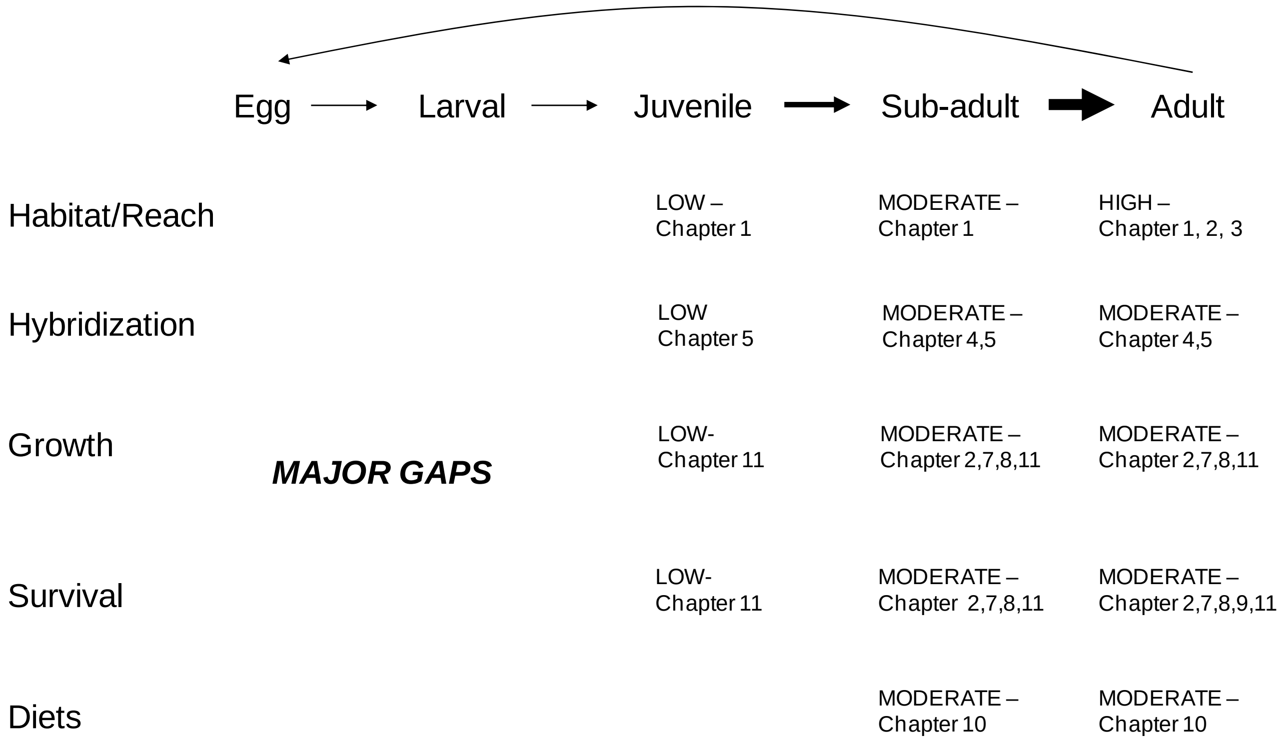


Figure 1. Middle Mississippi River (MMR) in which pallid sturgeon were studied during 2002 through 2005. Stars indicate location of river confluences, which coarsely bound the MMR. The MMR extends upstream to the Mel Price Lock and Dam.



	Egg	Larval	Juvenile	Sub-adult	Adult
Habitat/Reach			LOW – Chapter 1	MODERATE – Chapter 1	HIGH – Chapter 1, 2, 3
Hybridization			LOW Chapter 5	MODERATE – Chapter 4,5	MODERATE – Chapter 4,5
Growth	***MAJOR GAPS***		LOW- Chapter 11	MODERATE – Chapter 2,7,8,11	MODERATE – Chapter 2,7,8,11
Survival			LOW- Chapter 11	MODERATE – Chapter 2,7,8,11	MODERATE – Chapter 2,7,8,9,11
Diets				MODERATE – Chapter 10	MODERATE – Chapter 10

Figure 2. State of the current knowledge of important factors affecting pallid sturgeon in the Middle Mississippi River as a function of important life stages. Arrows depict transitions between life stages; arrow thickness corresponds to the extent of our knowledge about each transition. Chapters correspond to those in the report. See Wildhaber et al. 2007 for a more sophisticated conceptual model.

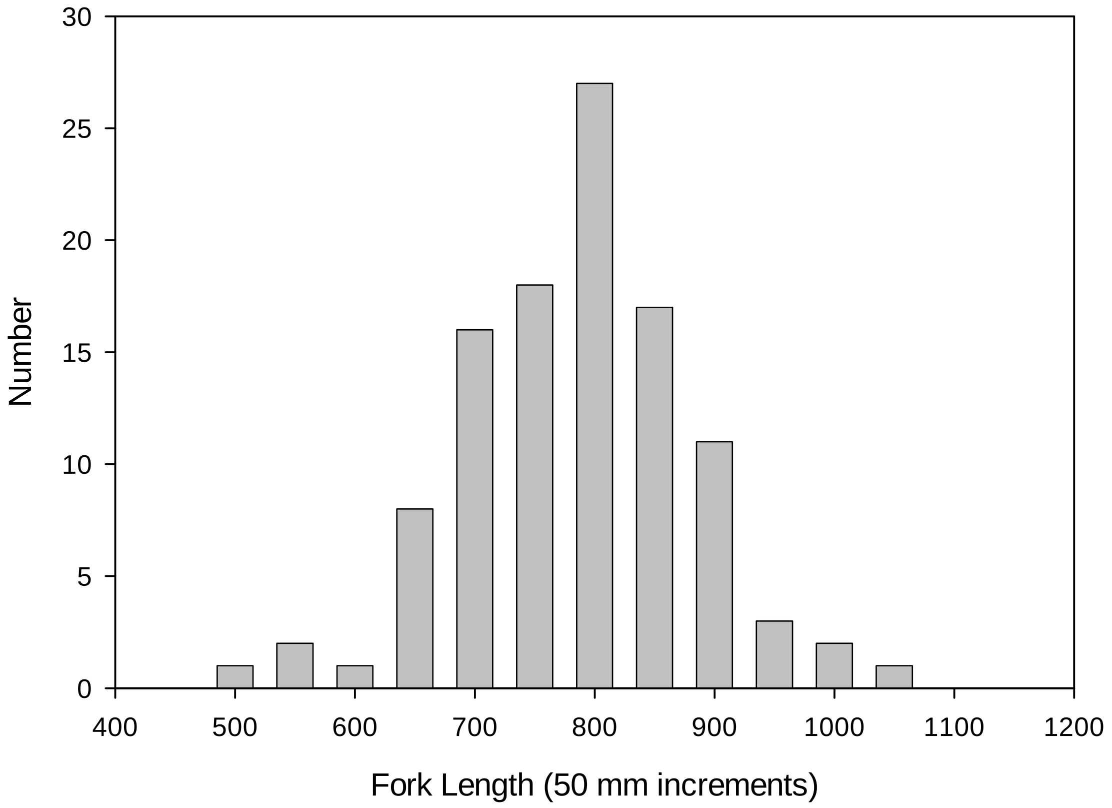


Figure 3. Length frequency distribution of pallid sturgeon in the MMR sampled with gill nets, trawls, and trotlines during 2002 through 2005. Fish greater than 650 mm FL were typically implanted with ultrasonic tags. Smaller pallid sturgeon also likely occurred in samples but were unidentified because of lack of reliable morphomeristic indexes.

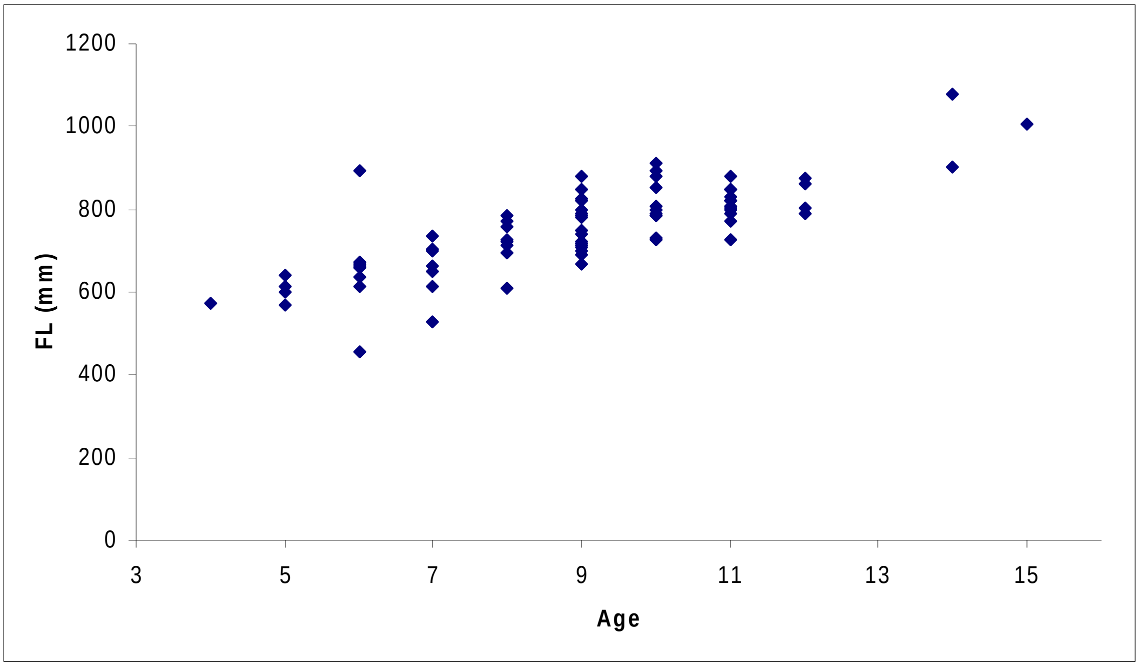


Figure 4. Fork length (FL) at age for 75 pallid sturgeon in the MMR sampled with gill nets, trawls, and trotlines during 2002 through 2005; these fish were aged independently by two SIUC biologists. The relationship was linear, suggesting that adult growth had not decelerated by the oldest age.

Figure 5. Sites of standardized trot-lining conducted to sample pallid and shovelnose sturgeon across a latitudinal gradient in the Mississippi River.

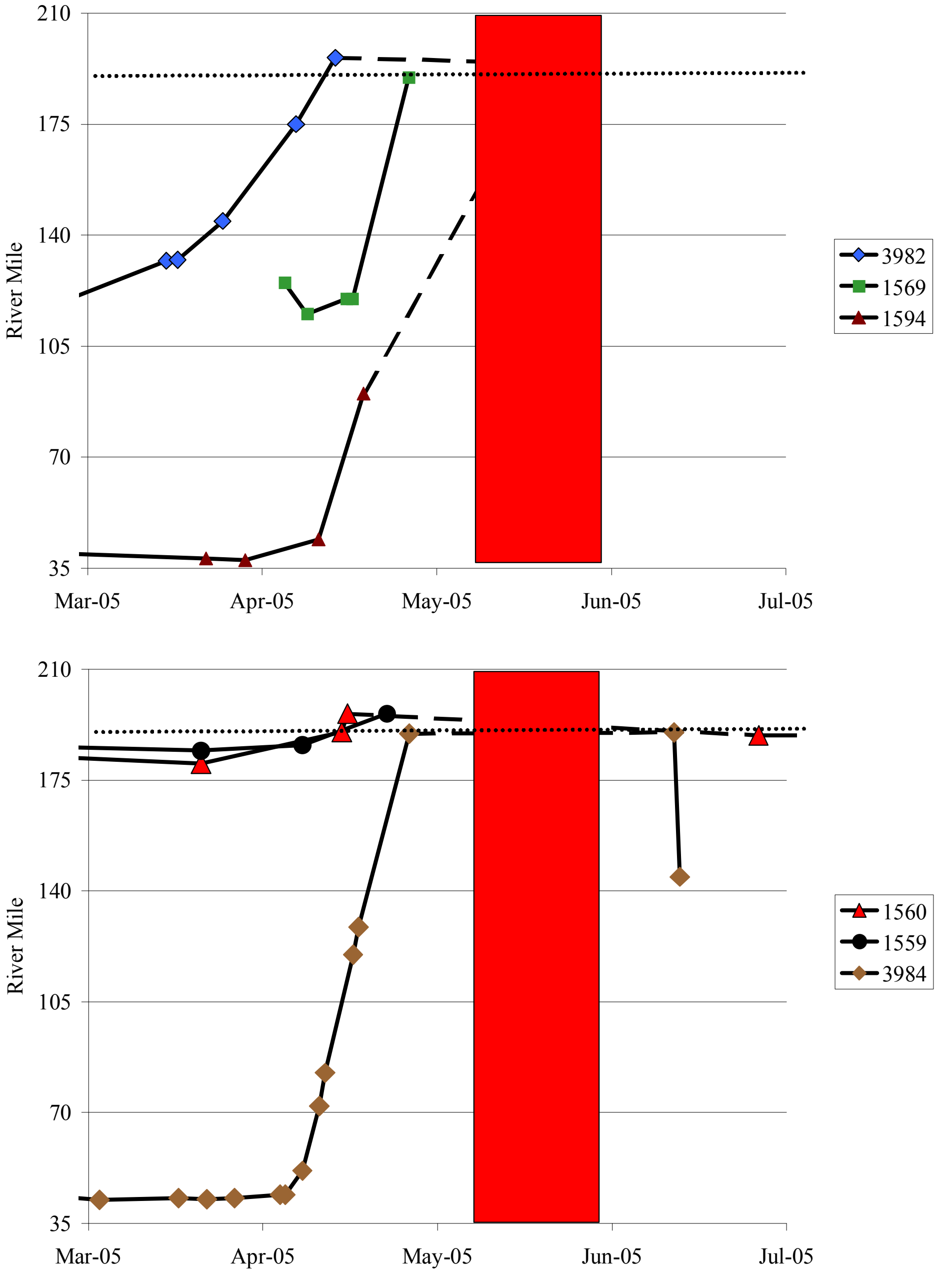


Figure 6. Movement of six adult pallid sturgeon in the MMR during spring 2005. The dashed line is the location of the Chain of Rocks. The highlighted area includes the dates when we hypothesize that temperatures and water levels were optimal for spawning. Each number is the individual tag identification for each fish.

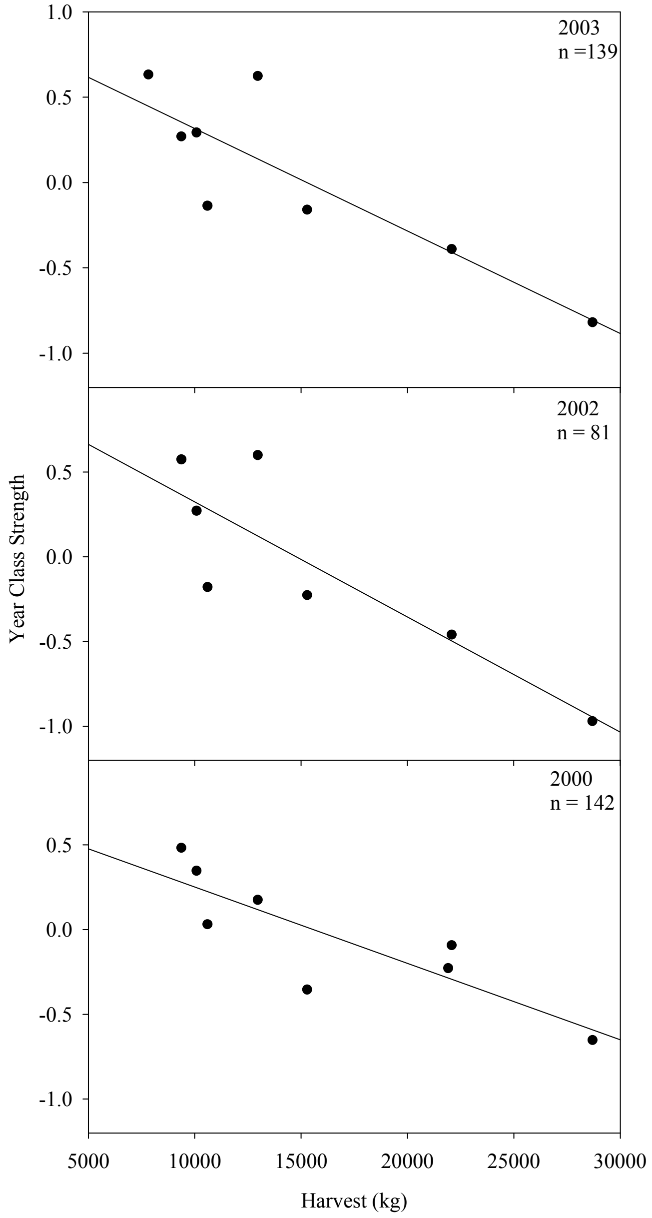


Figure 7. Relationship between Mississippi River harvest by Illinois and Missouri commercial fishers and year class strength as derived from residuals from catch-curves for shovelnose sturgeon sampled during 2003, 2002 and 2000. A value of 0 indicates no deviation from average abundance of an annual cohort. Positive and negative values indicate strong and weak cohorts in the population, respectively.

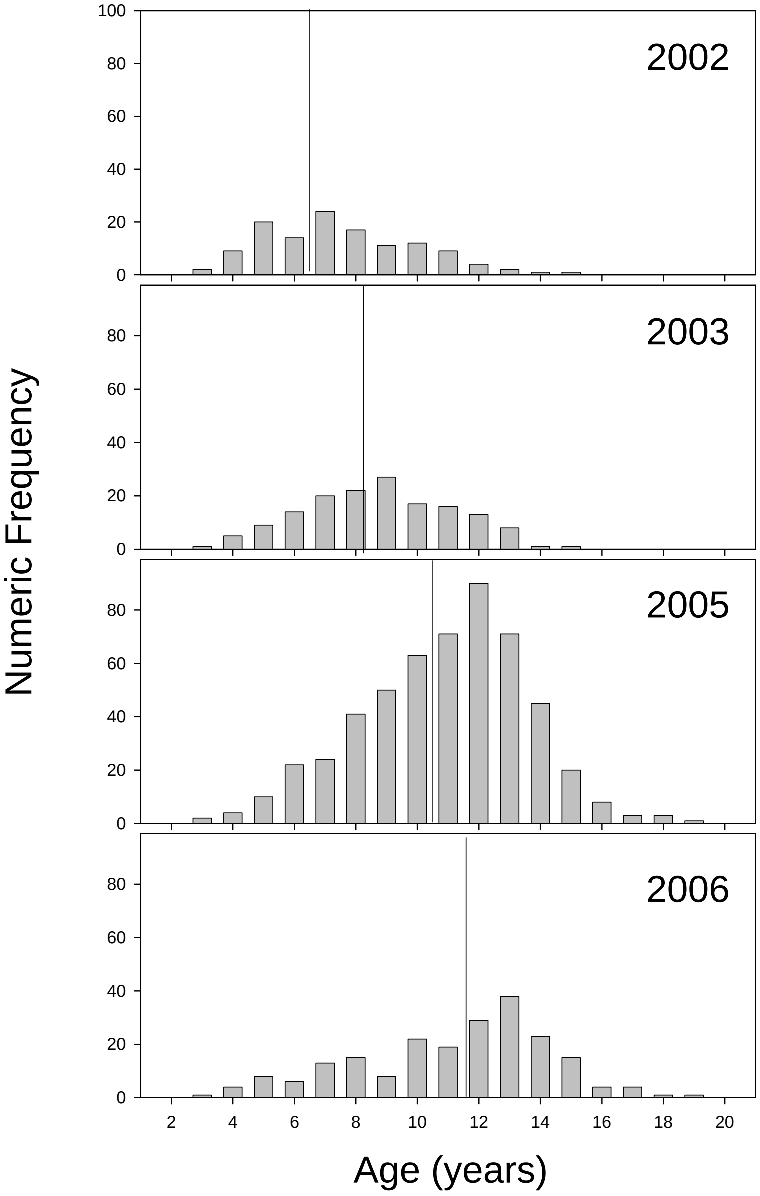


Figure 8. Change in age distribution of shovelnose sturgeon in the Middle Mississippi River during 2002 through 2006 (see Trippet al. 2009). Fish were captured with standardized gill net sets. Vertical lines represent median age within each year. Such shifts toward older individuals indicate declining production of young individuals.

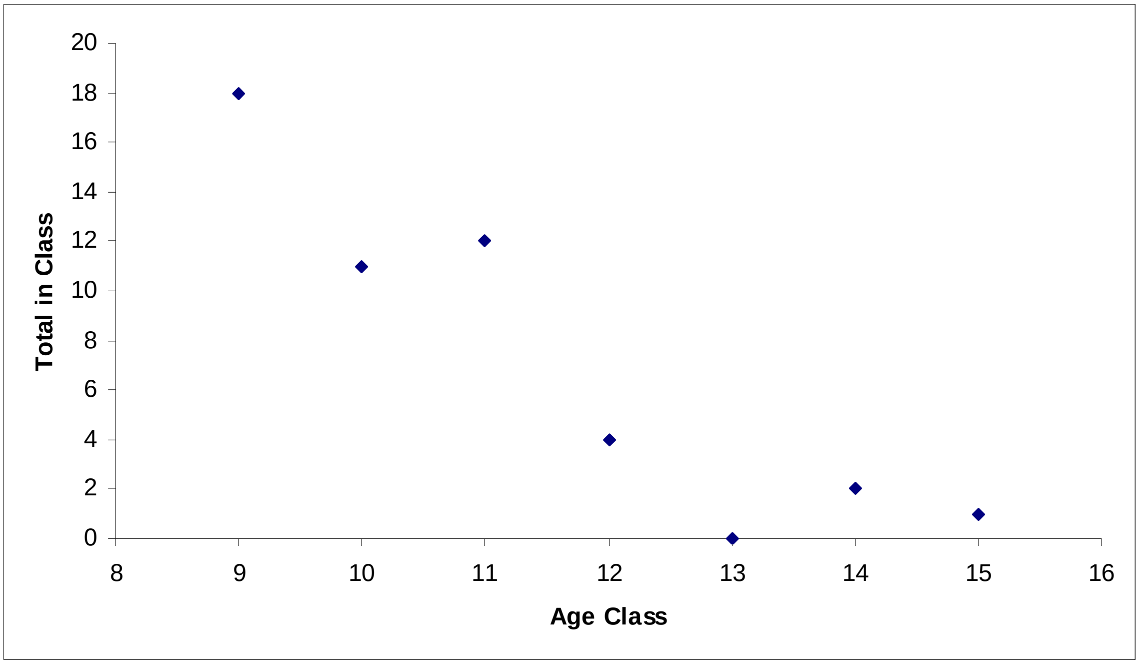


Figure 9. Declining age-dependent catch of pallid sturgeon sampled with gill nets during 2002 through 2005 in the Middle Mississippi River. A log-linear regression best explained this relationship (R^2=0.73).

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CHAPTER 1: SAMPLING AND SIZES

Comparison of three common gear types to sample sturgeons in the Middle Mississippi River

Quinton E. Phelps*[1], David P. Herzog[2], Ronald C. Brooks[1], Valerie A. Barko[3], David E. Ostendorf[2], Joseph W. Ridings[2], Sara J. Tripp[1], James E. Garvey[1], and Robert A. Hrabik[2]

[1]*Fisheries and Illinois Aquaculture Center,*
Department of Zoology,
Southern Illinois University,
Carbondale, Illinois, USA 62901

[2]*Open Rivers and Wetlands Field Station,*
Missouri Department of Conservation,
3815 East Jackson Boulevard,
Jackson, Missouri, USA 63755

[3]*John A. Logan College,*
700 Logan College Road,
Carterville, Illinois USA 62918

*Corresponding author email: qphelps@siu.edu

Abstract

We evaluated the efficacy of several gears commonly used to sample shovelnose sturgeon, *Scaphirhynchus platorynchus,* pallid sturgeon, *S. albus,* and lake sturgeon, *Acipenser fulvescens* in large rivers. We stratified habitats and randomly sampled sites with trawls, gill nets, and trotlines in the Middle Mississippi River from June 2003 through May 2005 (N = 3,476 samples). A total of 3,523 shovelnose sturgeon, 31 pallid sturgeon, and 13 lake sturgeon were captured. When sample sizes were adequate (based on power analysis), we used a mixed analysis of variance procedure to determine the relative impact of season and gear type on sturgeons catch-per-unit-effort. Kolmogorov-Smirnov non-parametric tests were used to determine whether length-frequency distributions for each species differed among gears. Overall, the power analyses indicated adequate sample sizes for comparing shovelnose sturgeon standardized catch-per-unit-effort (SCPUE) among seasons; however, too few pallid or lake sturgeon were collected to make statistical comparisons. Shovelnose sturgeon catch rates varied among gears and seasons; season and gear type interacted in the ANOVA model. Among gear types, 5.08-cm gill nets had the highest SCPUE for sampling shovelnose sturgeon, and catch rates were highest during spring. Shovelnose sturgeon length-frequency distributions depended on gear type. Sampling for shovelnose sturgeon can be achieved in large rivers using stratified random sampling with this combination of gear. However, pallid sturgeon and lake sturgeon may be too rare to sample using this approach.

Introduction

Sturgeon stocks throughout the world are declining because of habitat modification/degradation and overharvest (Birstein 1993). In the United States, exploited sturgeon stocks in large rivers have declined over the past decade as commercial fishing has increased, in part, to satisfy demand from the caviar market (Colombo et al. 2007). There are three sturgeon species (Family Acipenseridae) found in the Mississippi River (i.e. lake sturgeon, *Acipenser fulvescens*, pallid sturgeon, *Scaphirhynchus albus*, and shovelnose sturgeon, *S. platorynchus*); however, only shovelnose sturgeon can be legally harvested. Pallid sturgeon were federally listed as an endangered species in 1990, and lake sturgeon are protected by regulation and/or strict protocols in all of the Mississippi River basin states. Anthropogenic factors, such as harvest and habitat modification, can cause rapid declines in fish populations (Berkes and Gonec 1982; Dewees 1989; Hesse and Mestl 1993; Warren and Burr 1994; Martin 1995; Post et al. 2002; Piller et al. 2004). Sturgeon species are especially vulnerable to population declines due to their late age at maturation and subsequent slow population growth rates. For example, shovelnose sturgeon in the Middle Mississippi River, which extends between the Missouri and Ohio Rivers(MMR), become sexually mature at 5-7 years of age, and lake sturgeon do not reach sexual maturity until 20 years of age (Pflieger 1975; Keenlyne and Jenkins 1993). Male pallid sturgeon reach sexual maturity within 5-7 years, and females do not mature until 15-20 years of age (Keenlyne and Jenkins 1993). Accordingly, all Mississippi River basin states have restricted harvest regulations or have closed commercial harvest to all sturgeon species.

Harvest of shovelnose sturgeon is still allowed in the MMR. Recent efforts have been implemented by surrounding state conservation agencies to prevent overfishing through more stringent harvest regulations. However because restricted caviar importation into the United States has increased value of native US sturgeon roe (Gnam 1998), commercial fishing pressure will likely increase. Therefore, it is important to closely monitor the population status of sturgeon species in North American rivers, which requires using accurate collection methods. Methods used to sample fishes vary according to the targeted species and life stage, and often require using a multi-gear approach (Schwanke and Hubert 2004). Because field sampling is time consuming and expensive, many researchers seek sampling methods that yield robust information for their efforts (Arterburn and Berry 2002; Colvin 2002; Sammons et al. 2002; Benson et al. 2005).

Multiple gears have been used to collect benthic fishes in riverine environments (Herzog et al. 2005; Wanner et al. 2007). Several gears have been employed to capture sturgeons. For example, gill nets with varying mesh size have been used to capture lake sturgeon (Adams et al. 2006), shovelnose sturgeon (Colombo et al. 2007), and pallid sturgeon (Garvey et al. 2006). Herzog et al. (2005) used two trawl diameters to capture shovelnose sturgeon and pallid sturgeon in the MMR. Furthermore, Killgore et al. (2007) used trotlines baited with earthworms to capture pallid sturgeon. Efficiency of these gears may depend on seasonal locations or movements of the sturgeon species. Thus, our objective was to determine the most effective method of collecting sturgeons in the MMR. To facilitate our objective, we deployed three gear types (i.e., gill nets, trawls, and trotlines) simultaneously in the MMR over multiple seasons and years to evaluate catch rates and provide guidance to biologists sampling sturgeon species in large river systems.

Materials and Methods

The MMR is unimpounded and contains over 900 river training structures (e.g. wing dikes, pile dikes, closing structures; Unpubl. data, U.S Army Corps of Engineers, St. Louis District), which deflect flow toward the navigation channel and are typically submerged during spring river flows. There are 30 side channels within the MMR (U.S. Army Corps of Engineers 2003); however, few are connected to the main channel during low river stage, often because closing structures divert water away from them (Rasmussen 1979; Pitlo 1998; Barko and Herzog 2003).

The MMR study reach was from river kilometer (RKM) 309 near St. Louis, MO to RKM 0 at Cairo, IL (Figure 1). We used a stratified-random sampling design to obtain unbiased estimates of mean catch from June 2003 through May 2005 (see Gutreuter 1993; Gutreuter et al. 1995). Sampling was completed by dividing the MMR into 20 equal-length segments, each with several typical habitats, including channel border open (i.e. dikes absent), channel border dike (i.e. between wing dikes), main channel adjacent to the thalweg, behind wing dike, tributary mouth, downstream island tip, and side channel.. Each segment was assigned a number and then we randomly selected the sampling order of each segment. This was done four times each year by season: summer (June-August), fall (September-November), winter (December-February), and spring (March-May). We attempted to sample 366 sites randomly distributed across all 20 segments during each season Randomly selected alternate sites were sampled when primary sites were inaccessible or deemed unsafe for sampling.

Gear Descriptions

Trawls, gill nets, and trotlines were compared across the river segments. For trawling, two, bow-mounted benthic-type otter trawls were used. One was a 4.87-m wide, dual mesh, Missouri trawl with an interior 19.05-mm mesh bag and an exterior cover of 4.76-mm (Herzog et al. 2005). The cod end contained 3.18-mm mesh. The other trawl was 7.62-m wide containing a 19.05-mm mesh body and cod-end. Both trawls were weighted with chain on the footrope. Each otter board for the 4.87-m and 7.62-m trawls was 38.1-cm high, 76.2-cm long, and weighed 13.6-kg. Methods of deploying and retrieving trawls followed Herzog et al. (2005). Trawls were towed downstream for 3 minutes and two transects parallel to shore were completed at each sample site for each trawl type and habitat, with the exception of the channel border dike where one haul was completed at each site. At all habitats but the channel border dike, one haul occurred in shallow water (e.g., < 3 m in depth) near the shoreline and the second haul was in deep water (e.g., > 3 m in depth) away from the shoreline. At the channel border dike, one haul was completed through the downstream scour hole parallel to flow.

We compared two types of gill netsy. The gill nets were 5.08-cm and 7.62-cm bar mesh, each composed of a single panel 45.7-m long and 3.05-m deepwith 0.52-mm diameter monofilament nylon netting. Both gill nets had a 12.7-mm float line and 13.6-kg lead core line. Gill nets were deployed parallel to flow in locations of high water velocity (> 0.5 m/s) and as perpendicular as possible to the shoreline in lower water velocities (< 0.5 m/s). Nets were set for a period of 24-h when surface water temperature was below 12.7 ˚C and no longer than 3-h when surface temperature exceeded 12.7 ˚C per pallid sturgeon collection requirements (United States Fish and Wildlife Service 2005). Three-hour gill net sets were conducted randomly during the daylight hours. Two of the same type gill nets were set at each site with one near the shoreline and one away from the shoreline at all habitats when conditions allowed. Otherwise, one gill net was set downstream from the other. At the channel border dike habitat, one gill net was set on the downstream side mid-dike and the other set near the dike tip parallel to the flow.

A single type of trotline set was used. Trotlines were 60.96-m long with a 3.18-mm diameter solid braid main line. Drops were 22.9-cm long and attached to the main line every 3.05-m using a 1.17-mm nylon tarred twine containing 1/0 barrel swivels on both ends. A single 3/0 stainless steel Eagle claw O'Shaughnessy® j hook was attached to a swivel end of each dropper (20 hooks per line). Hooks were baited with bait shop purchased night crawlers, *Lumbricus terrestris*, covering the entire hook and shaft. Methods for fishing trotlines were similar to Morrow et al. (1998) and were further developed by W. Lancaster in the Lower Mississippi River, where the technique is known to be successful in capturing *Scaphirhynchus* spp. (J. Killgore pers. comm. U.S. Army Corps of Engineers). Trotlines were set parallel to flow in all habitats regardless of velocity. Trotlines were set for 24-hours in all seasons. Two trotlines were set at each site with one set near the shoreline and one away from the shoreline when conditions allowed. Otherwise, one trotline was set downstream of the other. At the channel border dike habitat, one trotline net was set mid-dike and the other set near the tip parallel to the flow.

Sturgeon Metrics

Sturgeons were identified to species based on morphometric analyses (Wills et al. 2002) and fork lengths (FL; to nearest mm) were recorded. Muscle tissue samples were taken for genetic identification (Schrey et al. 2007).

Statistical Analysis

Due to distinct differences in life histories of the three MMR-basin sturgeons (Page and Burr 1991) gear efficiencies were determined separately for each species. Standardized catch-per-unit-effort (SCPUE) was calculated for each gear (e.g., 3-h gill net set extrapolated to 24-h set, 24-h set for gill nets, 24-h trotline set, and each 3-minute transect for trawls). For comparing among gears, we assumed equal effort (in terms of personnel time) was expended to deploy and retrieve each gear type. Hence, in addition to standardizing effort within gear types, the effort to deploy and retrieve all gear types was considered standardized. We used power analyses to determine number of samples required to detect a difference in catch rates among gear types (i.e., achieve 0.8 power among gears for each species). Thus if the power analyses deemed sample sizes adequate, then we would ensure with 80% probability that we did not commit Type II error (i.e., failing to reject the null hypothesis when it was indeed false). With the high variability in catch rates, conventional ANOVA's (Analysis of Variance) were deemed inadequate for comparing gear efficiencies among seasons. Consequently, when sample size was sufficient we used the mixed model two-way ANOVA procedure in SAS Version 9.1 (SAS Institute, 2002 North Carolina) to compare sturgeon catch rates among gears and across seasons. Simple statistical comparisons for gear and season were made using the Least Square Means procedure.

When enough sturgeons were captured (N > 300; Vokoun et al. 2001), length-frequency distributions were compared using several two-sample Kolmogorov-Smirnov tests. For all statistical procedures, alpha was maintained at 0.05.

Results

We completed 3,476 units of standardized effort for all gears deployed in this study, which consisted of 1,664 trawl hauls, 1,159 gill net sets, and 653 trotline sets. We captured 3,523 shovelnose sturgeon, 31 pallid sturgeon, and 13 lake sturgeon.

Shovelnose Sturgeon

Based on the results of the power analysis, we acquired adequate sample sizes for comparing among gears and among seasons for shovelnose sturgeon. Specifically, to achieve 0.8 power, or detect differences in catch rates, a combined 365 units of effort for all gears or 73 units of effort per gear type were needed (Figure 2). During this study we acquired a sample size of 3,476, which is approximately 89% more than what was needed to achieve 0.8 power.

With adequate sample sizes, the results of the mixed model indicated interaction between season and gear type influenced shovelnose sturgeon catch rates ($F = 19.71$; df = 12, 3456; $P < 0.001$). Because the interaction was significant, we compared shovelnose catch rates among gear types by season. Catch rates from the 5.08-cm gill nets were higher (Mean SCPUE = 3.6) than trotlines (Mean SCPUE = 0.8; $P < 0.001$), and both gears had significantly higher catch rates than the remaining gear types (Mean SCPUE = 0.5 - 0.6; all comparisons $P < 0.001$). In each season, 5.08-cm gill nets collected shovelnose sturgeon at the highest rates (Figure 3). During winter, 5.08-cm gill net catch rate (Mean SCPUE = 2.2) was higher than rates of all other gear types (Mean SCPUE = 0.08-0.1; $P < 0.001$) except trotlines (Mean SCPUE = 0.7, $P = 0.1844$). During spring, 5.08-cm gill nets had a mean SCPUE of 6.6 shovelnose sturgeon per set which was significantly higher than all other gear types (Mean SCPUE = 0.5 - 1.6; $P < 0.001$). During summer, 5.08-cm gill nets and the 4.87-m trawl had a similar mean SCPUE of 1.2 shovelnose per set ($P = 0.051$); however, that rate was statistically different than that of the 7.62-m trawl (Mean SCPUE = 0.8; both comparisons $P < 0.01$). The remaining two gears (trotlines and 7.62-cm gill nets) during summer collected fewer shovelnose sturgeon per effort (Mean SCPUE = 0.1) than all other gears (all comparisons $P < 0.01$). Fall mean catch rates were higher for 5.08-cm gill nets (Mean SCPUE = 4.9) than all other gear types (Mean SCPUE = 0.1 - 0.3; all comparisons $P < 0.001$).Overall shovelnose sturgeon catch rates were highest in spring (all comparisons $P < 0.001$).

Shovelnose sturgeon lengths for all gear types ranged from 1 – 105 cm FL. Differences existed in length-frequency distributions among gear types (Kolmogorov-Smirnov Asymptotic test statistic; KSa range = 2.62-38.22; all comparisons $P < 0.001$; Figure 4). Differences were most striking when comparing both trawls versus the remaining gear types, predominantly due to the susceptibility of immature shovelnose sturgeon to trawls during summer. The majority (70.3 %) of shovelnose sturgeon collected with 4.87-m trawls were less than 15 cm (FL). The 7.62-m trawls collected more large shovelnose sturgeon than the 4.87-m trawls, but also collected smaller sturgeon at higher rates than the remaining gears. Trotlines and the two gill nets had similar size distributions; however, quantitative differences existed ($P < 0.001$). The 7.62-mm gill nets caught sturgeon that were slightly larger (mean FL = 631, median FL = 638 mm, range

FL = 374-1050 mm) than sturgeon collected with trotlines (mean FL = 605, median FL = 615 mm, range FL = 491-950 mm) or 5.08-cm gill nets (mean FL = 605, median FL = 614 mm, range FL = 390-819 mm, all comparisons P < 0.001, Figure 4).

Pallid Sturgeon

Because only 31 pallid sturgeon were collected during this study,, differences among seasons and gear types could not be identified. The power analysis for gear indicated that we would have had to complete 2,173 (10,865 units of effort equally distributed among gears) sampling efforts for each gear type employed to achieve 0.8 power, (Figure 2). Seasonal catch rates ranged from 0.02 in the spring to 0.01 in the remaining seasons. Pallid sturgeon were collected using trotlines (Mean SCPUE = 0.03), 5.08-cm gill nets (Mean SCPUE = 0.02), and 7.62-cm gill nets (Mean SCPUE = 0.1). Trotlines had the highest catch rates during winter (Mean SCPUE = 0.05) and fall (Mean SCPUE = 0.04); 7.62-cm gill nets collected more pallid sturgeon during the latter spring periods (Mean SCPUE = 0.05). Fork lengths ranged from 455 to 1090-mm with a mean FL of 753-mm and median FL of 790-mm for all gears combined.

Lake Sturgeon

Lake sturgeon were rare; we would have had to complete 2,383 (11,915 sampling efforts distributed equally across gears) for each gear to achieve 0.8 power (Figure 2). Lake sturgeon were captured during fall (n = 2), winter (n = 6), spring (n = 2), and summer (n = 3). The majority of lake sturgeon were captured using trotlines (n = 10); two were captured in 7.62-cm bar mesh gill nets, and one was captured using 5.08-cm bar mesh gill nets. Length ranged from 780-mm to 1210-mm FL.

Discussion

Capture rates for sturgeons in our studywere low and varied among species. Our gear power analysis calculations suggest that extreme effort and funds are needed to undertake a statistically valid large river sturgeon investigation. This was the first such effort conducted to collect sturgeons from a very large, open-river reach using a random, unbiased sampling design to compare gear efficiencies. Various gears have been used to capture shovelnose sturgeon, pallid sturgeon and lake sturgeon (Carlson and Pflieger 1981; Carlson et al. 1985; Morrow et al. 1998; Benson et al. 2005), but these studies were often conducted during one season or focused efforts near previously sampled locations thought to contain target species. The major issue with these aforementioned studies was multiple gears were not evaluated in an unbiased manner across seasons which may have overestimated density.

Shovelnose and pallid sturgeon size distributions among gears may have contributed to the different catch rates among gears. Shovelnose sturgeon are smaller bodied than the other two species and were likely more susceptible to smaller mesh gill nets; larger pallid sturgeon were more efficiently captured with larger meshes. Multiple mesh size gill nets were developed for sampling fish in shallow benthic habitats and are effective at capturing fishes with daily movements (Bronte and Johnson 1984; Hubert and O’Shea 1992). We speculate that these gill nets were effective in capturing both shovelnose and pallid sturgeon because these species are benthic and do not have restricted home ranges (Pflieger 1975). We were unable to capture lake sturgeon efficiently, which, as with pallid sturgeon, may be attributed to the presumed low relative abundance in the MMR.

We speculate that gill nets did not perform equally well across seasons because ofseasonal movement or activity. Gill nets were typically most effective in the spring and fall and least effective in the summer and winter. Moos (1978) reported that shovelnose sturgeon move up to 250 km and Schmulbach (1974) found movements as high as 534 km in the Missouri River. Bramblett and White (2001) reported pallid sturgeon movement over 200 km and noted the potential for longer range movements when large reaches of unobstructed river are available. Garvey et al. (2006) reported that tagged pallid sturgeon in the MMR often migrated long distances during late March through May (i.e., spawning migrations), and movements were related to water temperature and discharge. More recent telemetry data collected in the Upper Mississippi River have indicated that sturgeon movement may be related to increased water levels and discharge (R Brooks, Southern Illinois University-Carbondale unpublished data). Both (i.e., water levels and discharge) tend to be highest during spring and fall and lowest during the summer and winter months. Sturgeon movements would indeed coincide with higher spring catch rates.

Though it seems intuitive that the effectiveness of passive gear is correlated to fish movement, it may also be possible that catch rate differences were attributed to sampling protocol. One plausible explanation may be because of the mandated 3-h gill net sets when water temperature exceeded 12.7 ˚C (e.g., late spring – early summer). Gill nets captured sturgeons at higher rates during late spring/early summer when the spring spawning period peaked, and summer catch rates were possibly reduced by the mandated shortened soak period.

Another possible explanation for the reduced 3-h gill net catch rates could be that the nets were set only during daylight hours, potentially missing crepuscular and nocturnal movements.

Among all gear types compared in this study, we have clearly illustrated that gill nets produce the highest catch rates for shovelnose and pallid sturgeon, respectively, and that the fish are most readily collected during spring and fall. Thus, we suggest large river fishery managers should maximize shovelnose sturgeon catchability by employing 5.08-cm gill nets during spring and fall. Furthermore, if biologists have existing data, we suggest conducting power analyses on them to ensure adequate sample sizes are reached for future sampling events. Although we attempted to sample a suite of habitats that are indicative of the MMR, other habitats such as the thalweg and upstream island tip, may have affected catch rates. Random effort may be employed to determine areas where the fish tend to be more susceptible; this is especially true if little or nothing is known about the sturgeon behavior in the system that is under investigation. Directed and standardized effort should be employed after high use habitat areas are determined to maximize catch rates and assess trends through time.

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Literature cited

Adams, W. E. Jr., L. W. Kallemeyn, and D. W. Willis. 2006. Lake sturgeon population characteristics in Rainy Lake, Minnesota and Ontario. Journal of Applied Ichthyology 22:97-102.

Arterburn, J. E. and C. R. Berry, Jr. 2002. Effect of hook style, bait type and river location on trotline catches of flathead and channel catfish. North American Journal of Fisheries Management 22:573-578.

Barko V. A. and D. P. Herzog. 2003. Relationship among side channel, fish assemblages and environmental gradients in the unimpounded upper Mississippi River. Journal of Freshwater Ecology 18:377-382.

Benson, A. C., T. M. Sutton, R. F. Elliot, and T. G. Meronek. 2005. Evaluation of sampling techniques for age-0 lake sturgeon in a Lake Michagan tributary. North American Journal of Fisheries Management 25:1378-1385.

Berkes, F., and T. Gonec. 1982. A mathematical model on the exploitation of northern whitefish with gill nets. North American Journal of Fisheries Management 2:176-183.

Birstein, V. J. 1993. Sturgeons and paddlefishes: threatened fishes in need of conservation. Conservation Biology 7:773:787.

Bramblett, R. G. and R. G. White. 2001. Habitat use and movement of pallid and shovelnose sturgeon in the Yellowstone and Missouri Rivers in Montana and North Dakota. Transactions of the American Fiserheis Society 130:1006-1025.

Bronte, C. R. and D.W. Johnson. 1984. Occurrence of sport fish in a commercial net fishery in Kentucky. North American Journal of Fisheries Management 3: 239-242.

Carlson D. M. and W. L . Pflieger. 1981. Abundance and life history of the lake, pallid, and shovelnose sturgeons in Missouri. Final Report to the Missouri Department of Conservation, Endangered Spp. Project SE-1-6, Jefferson City, Missouri.

Carlson D. M., W. L. Pflieger, L. Trial, and P. S. Haverland. 1985. Distribution, biology, and hybridization of *Scaphirhynchus albus* and *S. platorynchus* in the Missouri and Mississippi Rivers. Environmental Biology of Fishes 14:51-59.

Colombo, R. E., J. E. Garvey, N. D. Jackson, D. P. Herzog, R. A. Hrabik, R. C. Brooks, B. T. Koch, T. W. Spier. 2007. Harvest of Mississippi River sturgeon drives abundance and reproductive success: a harbinger of collapse? Journal of Applied Ichthyology 23: 444-451.

Colvin, M. A. 2002. A comparison of gill netting and electrofishing as sampling techniques for white bass in Missouri's large reservoirs. North American Journal of Fisheries Management 22:690-702.

Dewees, C. M. 1989. Assessment of the implementation of individual transferable quotas in New Zealand's inshore fishery. North American Journal of Fisheries Management 9:131-139.

Garvey, J. E., E. J. Heist, R. C. Brooks, D. P. Herzog, R. A. Hrabik, and K. J. Killgore. 2006. Current status of the pallid sturgeon (*Scaphirhynchus albus*) in the Middle Mississippi River: habitat, movement and demographics. Final report to U.S. Army Corps of Engineers, St. Louis district.

Gnam, R. 1998. Implementation of 1997 CITES listing made effective April 1, 1998. Pages 192–214 in D. F. Williamson, G. W. Benz, and C. M. Hoover, editors. Proceedings of the symposium on the harvest, trade and conservation of North American paddle-fish and sturgeon. TRAFFIC North America/WorldWildlife Fund, Washington, DC.

Gutreuter, S. 1993. The need for spatially randomized sampling of fishes in the long term resource monitoring program. U.S. Fish and Wildlife Service, Environmental Management Technical Center, Technical Report 92-T001, Onalaska, Wisconsin.

Gutreuter, S., R. Burkhardt, and K. Lubinski. 1995 Long term resource monitoring program procedures: fish monitoring. National Biological Service, Environmental Technical Center, LTRMP Technical Report 95-P002-1, Onalaska, Wisconsin.

Herzog, D., V.A. Barko, J. S. Scheibe, R. A. Hrabik, and D. E. Ostendorf. 2005. Efficacy of a benthic trawl for sampling small-bodied fishes in large river systems. North American Journal of Fisheries Management 25: 594-603.

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

Hubert, W. A. and D. T. O’Shea. 1992. Use of spatial resources by fishes in Grayrocks Reservoir. Prairie Naturalist 23: 61-68.

Keenlyne, K. D. and L. G. Jenkins. 1993. Age at sexual maturity of the pallid sturgeon. Transactions of the American Fisheries Society 122: 393–396.

Killgore, K.J., J. J. Hoover, J. P. Kirk, S. G. George, B. R. Lewis and C. E. Murphy. 2007. Age and growth of pallid sturgeon in the Lower Mississippi River. Journal of Applied Ichthyology 23: 452–456.

Martin, C. 1995. The collapse of the northern cod stocks: whatever happened to 86/25? Fisheries 20: 6-8.

Moos, R. E. 1978. Movement and reproduction of shovelnose sturgeon *Scaphirynchus platorynchus*, in the Missouri River, South Dakota. Doctoroal dissertation. University of South Dakota, Vermillion.

Morrow, J. V., J. P. Kirk, K. J. Killgore, and S. G. George. 1998. Age, growth, and mortality of shovelnose sturgeon in the lower Mississippi River. North American Journal of Fisheries Management 18: 725-730.

Page, L. M. and B. M. Burr. 1991. A field guide to freshwater fishes of North America north of Mexico. The Peterson Field Guide Series, volume 42. Houghton Mifflin Company, Boston, MA.

Pflieger, W. L. 1975. The fishes of Missouri. Missouri Department of Conservation, Jefferson City, MO. 372 pp.

Piller, K. R., H. L. Bart, Jr, and J. A. Tipton. 2004. Decline of the frecklebelly madtom in the Pearl river based on contemporary and historical surveys. North American Journal of Fisheries Management 133:1004-1013.

Pitlo, J., Jr. 1998. Fish populations associated with wing and closing dams on the Upper Mississippi River. Iowa Department of Natural Resources Technical Bulletin 7.

Post, J. R., M. Sullivan, S. Cox, N. G. Lester, C. J. Walters, E. A. Parkinson, A. J. Paul, L. Jackson, and B. J. Shute. 2002. Canada's Recreational Fisheries: The Invisible Collapse? Fisheries 27(1):6-17.

Rasmussen, J. L. 1979. A compendium of fishery information on the upper Mississippi River, 2nd ed. Upper Mississippi River Conservation Committee.

SAS. 2002. Version 9.1.3. SAS Institute, Cary, NC.

Sammons, S. M., D. A. Isermann, and P. W. Bettoli. 2002. Variation in population characteristics and gear selection between black and white crappies in Tennessee Reservoirs: Potential Effects on Management Decisions. North American Journal of Fisheries Management 22:863-869.

Schmulbach, J. C. 1974. An ecological study of the Missouri River prior to channelization. University of South Dakota, Completion Report, Project B-024-S, Vermillion.

Schrey, A. W., B. L. Sloss, R. J. Sheehan, and E. J. Heist. 2007. Genetic discrimination of Middle Mississippi River *Scaphirhynchus* Sturgeon into pallid, shovelnose, and intermediate classes with multiple microsatellite loci. Conservation Genetics 8:683-693.

Schwanke, C. J. and W. A. Hubert. 2004. Evaluation of three gears for sampling spawning populations of rainbow trout in a large Alaskan River. 2004. North American Journal of Fisheries Management 24:1078-1082.

U. S. Army Corps of Engineers. Avoid and Minimize Report: 2003. U. S. Army Corps of Engineers, St. Louis Missouri.

U.S. Fish and Wildlife Service. 2005. Biological procedures and protocol for collecting, tagging, sampling, holding, culture, transporting, and data recording for researchers and managers handling pallid sturgeon. Pallid Sturgeon Recovery Team Leader, U.S. Fish and Wildlife Service, 2900 4th Ave North, Suite 301, Billings, Montana.

Vokoun, J. C., C. F. Rabeni, and J. S. Stanovick. 2001. Sample-size requirements for evaluating population size structure. North American Journal of Fisheries Management 21:660–665.

Wanner G. A., D. A. Shuman, M. L. Brown and D. W. Willis. 2007. An initial assessment of sampling procedures for juvenile pallid sturgeon in the Missouri River downstream of Fort Randall Dam, South Dakota and Nebraska. Journal of Applied Ichthyology. 23:529–538.

Warren, Jr., M. J., and B. M. Burr. 1994. Status of freshwater fishes of the United States: overview of an imperiled fauna. Fisheries 19: 6-18.

Wills, P. S., R. J. Sheehan, R. Heidinger, B. L. Sloss, and R. Clevenstine. 2002. Differentiation of pallid sturgeon and shovelnose sturgeon using an index based on meristics and morphometrics. American Fisheries Society Symposium 28:249–258.

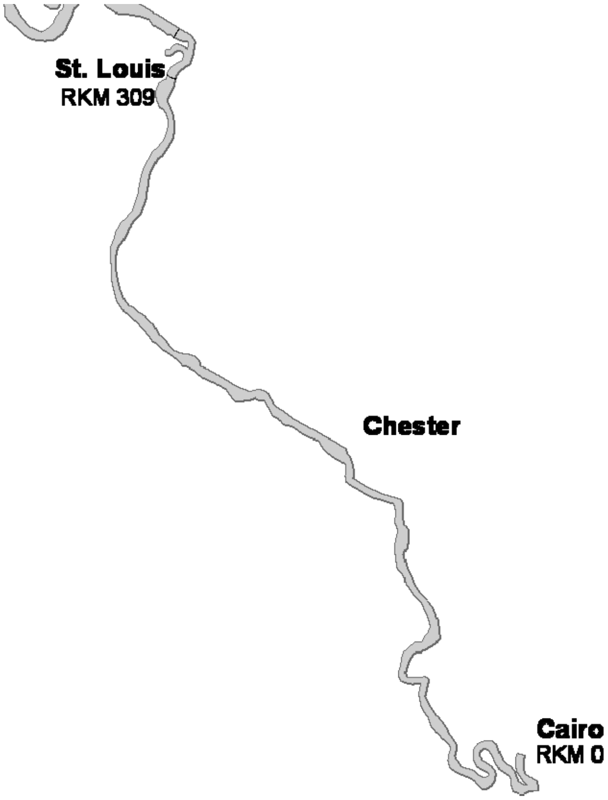
List of Figures

Figure 1. Map of the Middle Mississippi River.

Figure 2. Power analyses (based on analysis of variance procedure) demonstrating the influence of sample size per gear type to detect differences in standardized catch per unit effort among gears for each sturgeon species (shovelnose sturgeon, pallid sturgeon, and lake sturgeon). All data derived from sturgeons captured during all seasons from 2003-2005.

Figure 3. Mean shovelnose sturgeon catch per unit effort by season using gill nets, trawls, and trotlines from 2003-2005 in the Middle Mississippi River. Error bars denote standard error of the sample mean. Different letters represent significantly different means between gear types at $P < 0.05$.

Figure 4. Comparison of length frequency distributions of Middle Mississippi River shovelnose sturgeon collected during all seasons from 2003-2005. Kolmolgorov-Smirnov non-parametric procedures were to determine if differences occurred between gears. All length-frequency distributions were statistically different (all comparisons $P < 0.05$).



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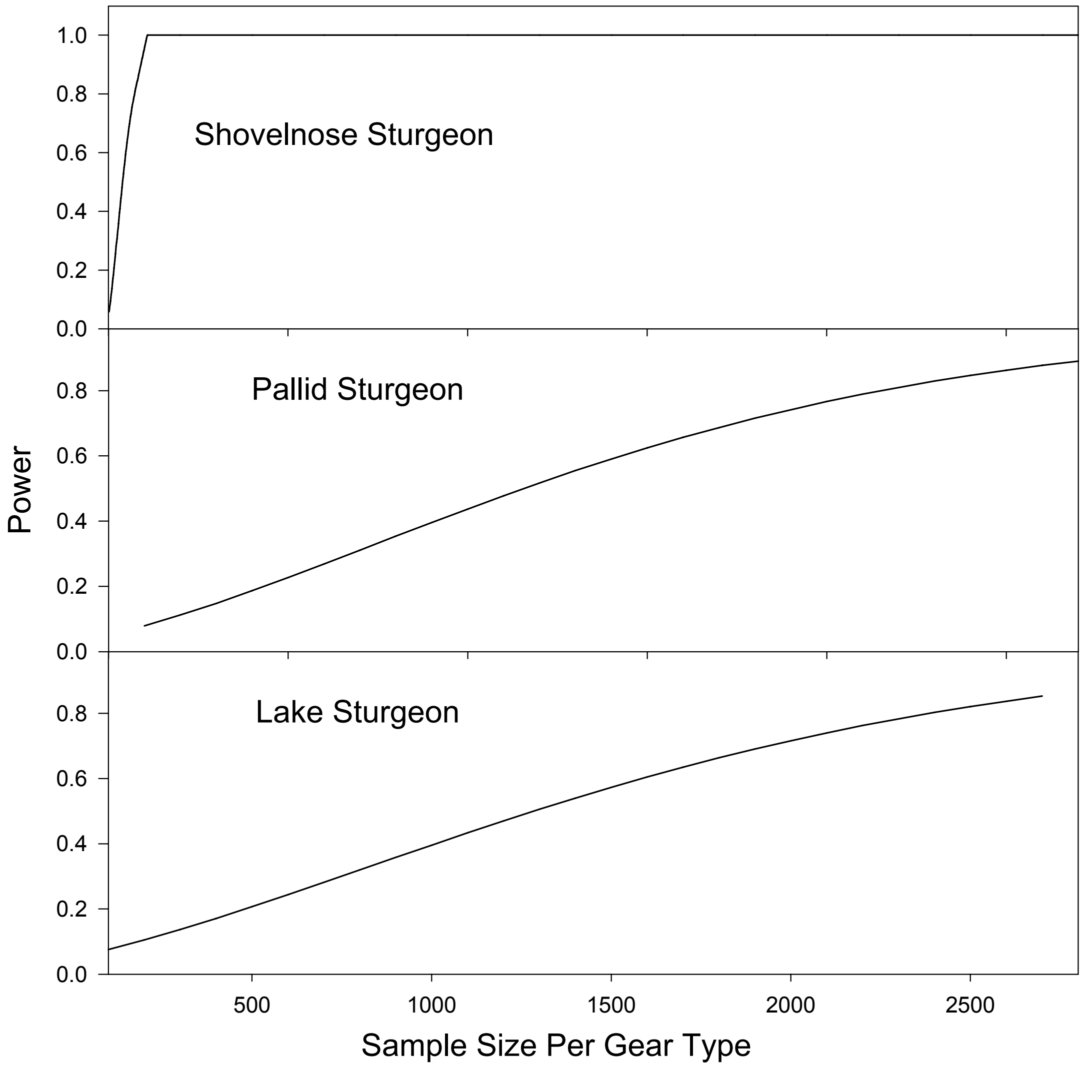
Shovelnose Sturgeon
Pallid Sturgeon
Lake Sturgeon
Power
Sample Size Per Gear Type
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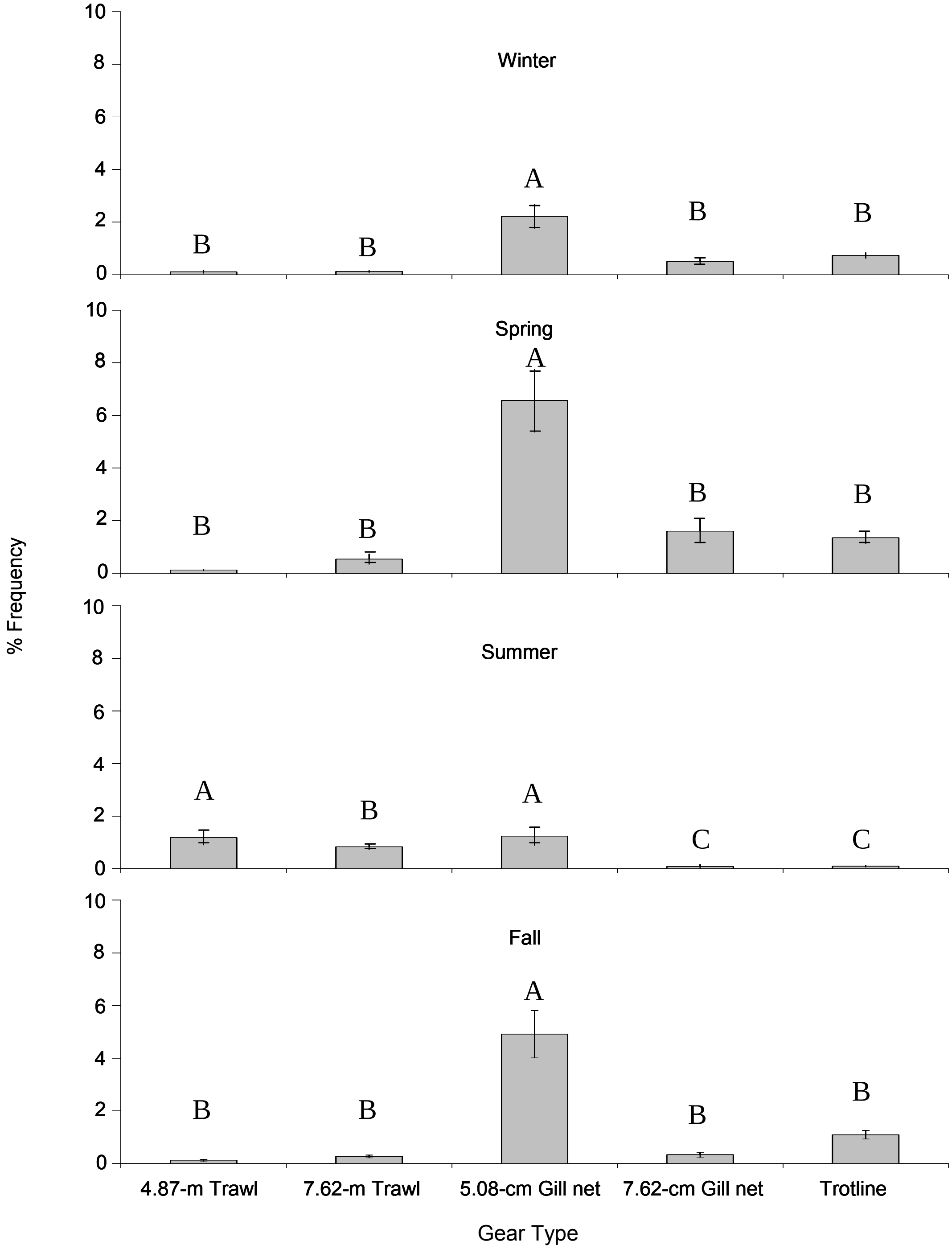
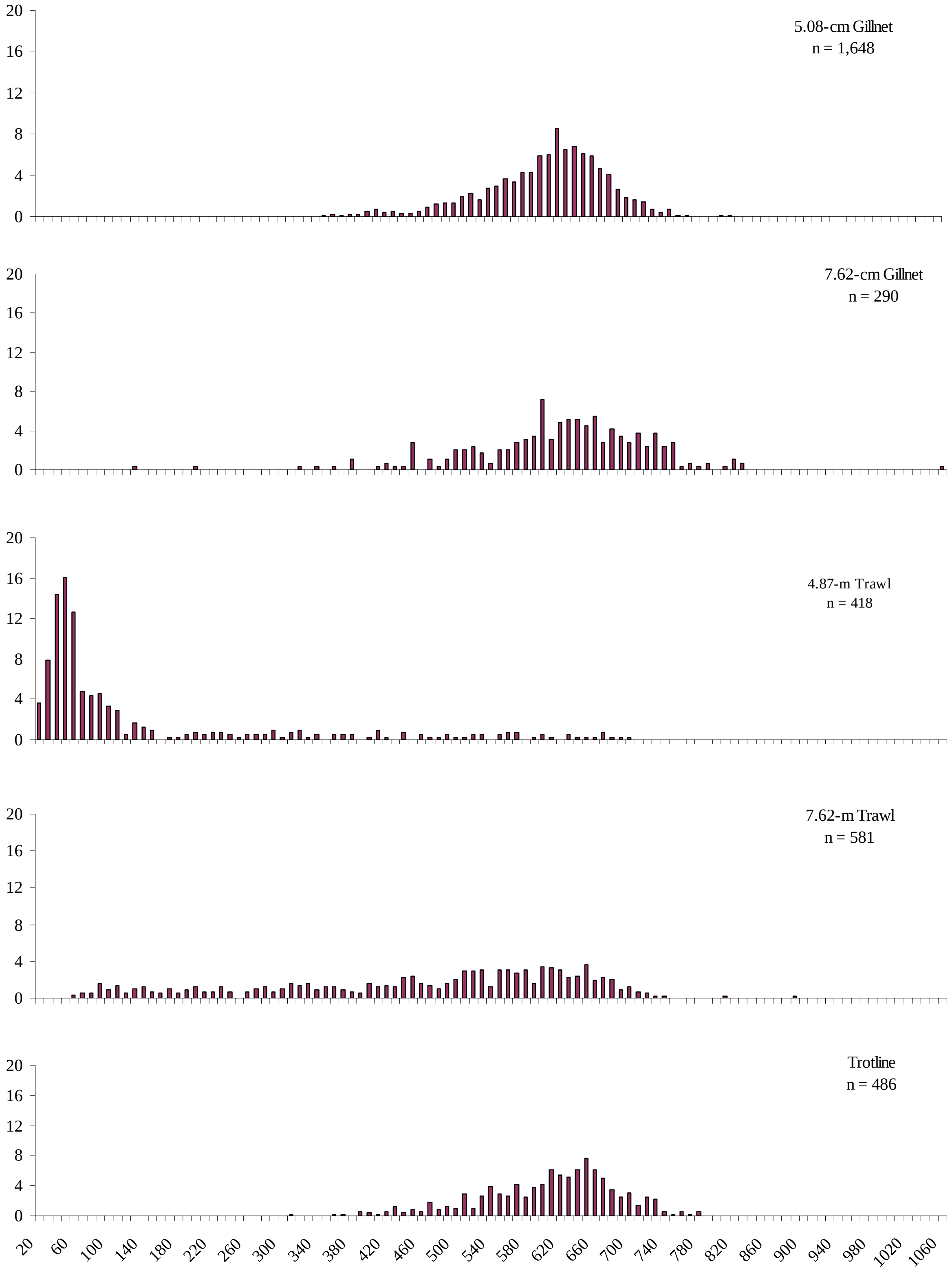
0.8
0.6
0.4
0.2
0.0
500
1000
1500
2000
2500

494
495
496

497




5.08-cm Gillnet
n = 1,648
7.62-cm Gillnet
n = 290
4.87-m Trawl
n = 418
7.62-m Trawl
n = 581
Trotline
n = 486
0
4
8
12
16
20
20
60
100
140
180
220
260
300
340
380
420
460
500
540
580
620
660
700
740
780
820
860
900
940
980
1020
1060

APPENDIX

Summary of Habitat Specific Catch Rates

Chapter 1, Phelps et al. in revision, focused on power to detect differences among gear and seasons with our extensive sampling effort for pallid sturgeon in the MMR during 2002-2005. Although we caught insufficient pallid sturgeon to detect differences among habitats at an acceptable level of power ($P < 0.10$), we briefly summarize the relative catch rates of pallid sturgeon across habitat types. See Chapter 1 for description of the methodology and habitat types.

In summary, pallid sturgeon were extremely rare in the catch relative to shovelnose sturgeon. Regardless of whether pallid sturgeon sampling site selection was directed or randomized, these fish were caught in all habitat types with the exception of inside of tributary mouths. This may simply be a function of lower relative sampling effort in these sites. Given low power, it is impossible to infer habitat preference from this effort.

Table 1. Total number of samples and number of sturgeon caught (in parentheses) during each year in the Middle Mississippi River, using a combination of gears including gill nets, trammel nets, trawling, and trot lines. See Chapter 1 for a full description. Directed sampling was implemented in areas of known high densities of sturgeon. Random sampling was stratified across habitats. n/a = no data available.

	Shovelnose Sturgeon (N=9,275)					Pallid Sturgeon (N=79)				
	Directed			Random		Directed			Random	
Habitat Type	**2002-2003**	**2003-2004**	**2004-2005**	**2003-2004**	**2004-2005**	**2002-2003**	**2003-2004**	**2004-2005**	**2003-2004**	**2004-2005**
Channel border w/dike	164 (474)	n/a	109 (299)	395 (294)	337 (306)	164 (6)	n/a	109 (1)	395 (3)	337 (2)
Open channel border	261 (242)	4 (8)	254 (754)	319 (264)	218 (197)	261 (1)	4 (2)	254 (5)	319 (2)	218 (1)
Island tip	321 (514)	n/a	141 (311)	470 (550)	368 (663)	321 (7)	n/a	141(5)	470 (5)	368 (8)
Main channel	16 (15)	n/a	8 (6)	173 (61)	136 (33)	16 (1)	n/a	8 (0)	173 (3)	136 (0)
Side channel	219 (334)	n/a	81 (335)	235 (109)	248 (493)	219 (3)	n/a	81 (3)	235 (1)	248 (2)
Trib. Mouth	87 (17)	n/a	n/a	48 (1)	7 (1)	87 (0)	n/a	n/a	48 (0)	7 (0)
Wing dike	257 (1417)	7 (117)	143 (906)	326 (344)	204 (240)	257 (5)	7 (2)	143 (7)	326 (2)	204 (2)

CHAPTER 2: SIZES AND RELATIVE ABUNDANCE

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Distribution, relative abundance and movements of pallid sturgeon in the free-flowing Mississippi River

By K. J. Killgore, J. J. Hoover, S. G. George, B. R. Lewis, C. E. Murphy and W. E. Lancaster

United States Army Engineer Research and Development Center, Environmental Laboratory, Vicksburg, MS, USA

Summary

A multiyear study of pallid sturgeon distribution and relative abundance was conducted in the lower and middle Mississippi river (LMR and MMR, respectively). The LMR and MMR comprise the free-flowing Mississippi River extending 1857 river kilometers (rkm) from its mouth at the Gulf of Mexico upstream to the mouth of the Missouri River. A total of 219 pallid sturgeon and 6018 shovelnose sturgeon was collected during the periods 1996–1997 and 2000–2006. Trotlines baited with worms were the primary collecting gear. The smallest pallid sturgeon captured on trotlines was 405 mm FL and the largest was 995 mm FL. Mean size of pallid sturgeon was statistically smaller in the Mississippi River below the Atchafalaya River near Baton Rouge, LA (621 mm FL). Mean abundance (catch per trotline night) of pallid sturgeon was highest at water temperatures around 10°C. There was a latitudinal trend in mean abundance of pallid and shovelnose sturgeon, but the pattern differed between species. Pallid sturgeon abundance was statistically ($P < 0.05$) higher (0.3 fish per trotline night) in the lower reach between the Atchafalaya River and New Orleans (rkm 154–507), and at the Chain of Rocks (COR), a low water dam near the mouth of the Missouri River. Pallid sturgeon abundance between these two locations was statistically the same (0.12–0.23). Shovelnose sturgeon abundance increased going upstream, but was disproportionally higher at the COR (22 fish per line compared with < 6 fish per line in other reaches). Overall, the ratio between pallid and shovelnose sturgeon varied from a high of 1 : 6 at the lower reach, and gradually decreased upstream to a low of 1 : 77 at the COR. Based on differences in sturgeon abundance, size and habitat characteristics, the free-flowing Mississippi River can be divided into two reaches in the MMR (i.e. COR is a separate location), and four reaches (i.e., including the Atchafalaya River) in the LMR where management goals may differ.

Introduction

The pallid sturgeon *Scaphiryhnchus albus* was federally listed as an endangered species in 1990 (Federal Register, 1990), and a recovery plan was approved in 1993 (Dryer and Sandvol, 1993). The apparent rarity of the pallid sturgeon is highlighted by the paucity of records in the early scientific literature. The original taxonomic description was based on nine specimens collected near the mouth of the Illinois River (Forbes and Richardson, 1905). Re-description of the species was based on 17 specimens from eight localities (Bailey and Cross, 1954). Records compiled for a 70-year-period totaled only 250 observations (Kallemeyn, 1983). Approximately 76% were from the Missouri River in Montana and the Dakotas, and most of those were from inter-reservoir reaches. Since then, a large number of pallid sturgeon have been documented in the Atchafalaya River (Constant et al., 1997).

Presently, pallid sturgeon are known to occur throughout the Missouri River, its tributaries (i.e. Yellowstone and Platte rivers), the un-impounded middle Mississippi River (MMR) between the mouths of the Missouri and Ohio rivers (MMR), the lower Mississippi River between the mouth of the Ohio River and mouth of the Mississippi River at Head-of-Passes (LMR), and the Atchafalaya River in southern Louisiana (Bailey and Cross, 1954; Carlander, 1969; Kallemeyn, 1983; Dryer and Sandvol, 1993; Etnier and Starnes, 1993; Constant et al., 1997; Tranah et al., 2001). The pallid sturgeon occurs sympatrically with the shovelnose sturgeon (*S. platorynchus*) in parts of the Mississippi–Missouri River Basin (Lee, 1980ab; Everett et al., 2003). The shovelnose sturgeon, however, occurs over a wider geographic range than the pallid sturgeon, inhabiting the impounded upper Mississippi River, Ohio River and tributaries, and formerly inhabiting the Rio Grande Basin from which the pallid sturgeon has not occurred (Lee, 2003).

Prior to this study, the distribution and abundance of pallid sturgeon in the LMR was poorly documented and subject to speculation. Only 28 records of pallid sturgeon were cited in the recovery plan published in 1993, and the only confirmed population occurred in the Atchafalaya River at Old River Control Structure (Dryer and Sandvol, 1993). Sampling a large, turbulent river for a species that prefers main channel environments has likely hampered efforts to document population status.

We began to collect shovelnose sturgeon in the LMR between 1996 and 1997 as part of a morphomeristic study of this species; pallid sturgeon were collected incidentally (Murphy et al., 2007). A formal study of pallid sturgeon in the LMR began in 2000 and we continued to sample various locations through spring 2006. A similar effort was completed in the MMR from 2001 to 2004 as part of an interagency (Missouri Department of Conservation, Southern Illinois University, Corps of Engineers St. Louis District) study. This study was a response to the issuance of the U. S. Fish and Wildlife Service, 2000 Biological Opinion for the operation and maintenance of the 9-foot navigation channel on the Upper Mississippi River (U. S. Fish and Wildlife Service, 2000). Therefore, the information provided herein was based on collections made in the Mississippi River between 1996 and 2006, but the majority of sampling occurred in the 2000s.

We describe geographic distribution, relative abundance (i.e. catch-per-unit-effort, CPUE), and variation in mean size of pallid and shovelnose sturgeon collected in the un-impounded Mississippi River from its mouth at the Gulf of Mexico to the mouth of the Missouri River. The results of this study provide a baseline to support and measure conservation efforts for pallid sturgeon in the free-flowing Mississippi River.

Study area

The free-flowing portion of the Mississippi River extends 1847 river kilometers (rkm) from its mouth upstream to the mouth of the Missouri River. The geographic extent of our sampling allowed us to separate sturgeon abundance into discrete reaches with similar geomorphic attributes. Saucier (1991) indicated that the former junction of the Red River (now the Atchafalaya River) is where the alluvial valley of the Mississippi River ends and the delta plain begins. From the Atchafalaya River down to New Orleans, the river has steep, sloping banks, few sandbars and no major dike fields. Below New Orleans, dominant substrate shifts from mostly sand to sand/mud mix and salt water intrusion during low flows is typical. Therefore, the lowermost section of the LMR was divided into two discrete reaches for analytical purposes: Head of Passes (rkm 0) to New Orleans (rkm 154) and New Orleans to the Atchafalaya River at the old river control structure (rkm 502).

Schumm et al. (1994) identified 24 reaches from the Atchafalaya River to the mouth of the Ohio River (rkm 1533). Identification of reaches by Schumm et al. (1994) was based on visual analysis of maps prepared by Fisk (1944), which represent the period before the major bendway cut-off program of the 1930s, and more current maps that reflected channel maintenance activities by the Corps of Engineers. Schumm et al. (1994) identified geological structures (faults and uplift) that influenced valley slope, recognized the influence of major tributaries, discussed lithologic (sediment) controls and considered different patterns in river morphology (width, sinuosity) in order to determine river reach boundaries.

One major conclusion of the study by Schumm et al. (1994) was that the Mississippi River between the Arkansas River and Red River was more active geomorphologically (i.e. higher slope with changing sinuosity patterns) than reaches between the Ohio and Arkansas rivers. In addition, the majority of anthropogenic cut-offs were made below the mouth of the Arkansas River. Therefore, the Mississippi River between the Atchafalaya and Ohio rivers was divided into two discrete reaches: Atchafalaya River, which includes the mouth of the Red River at the old river control structure, to the mouth of the Arkansas/White River (rkm 935) and the Arkansas/White River to the mouth of the Ohio River (Fig. 1). The 314-rkm section of the Mississippi River between the Ohio and Missouri rivers was also designated as a discrete reach, referred to as the MMR. Based on the 1998 navigation charts of the Mississippi River published by the Corps of Engineers, the MMR has numerous dike fields (5.78 dikes/rkm) compared with the LMR between the Ohio and Atchafalaya Rivers (2.52 dikes/rkm). Consequently, the MMR is swifter and narrower than the LMR. A unique feature of the MMR is the Chain of Rocks (COR) near St. Louis, Missouri, a naturally occurring low water dam, reinforced with concrete and rip-rap, which is the only obstruction (at low water) to upstream movement of sturgeon and other fish in the MMR and LMR. The above considerations resulted in the identification of five reaches based on primarily geomorphic features (Table 1).

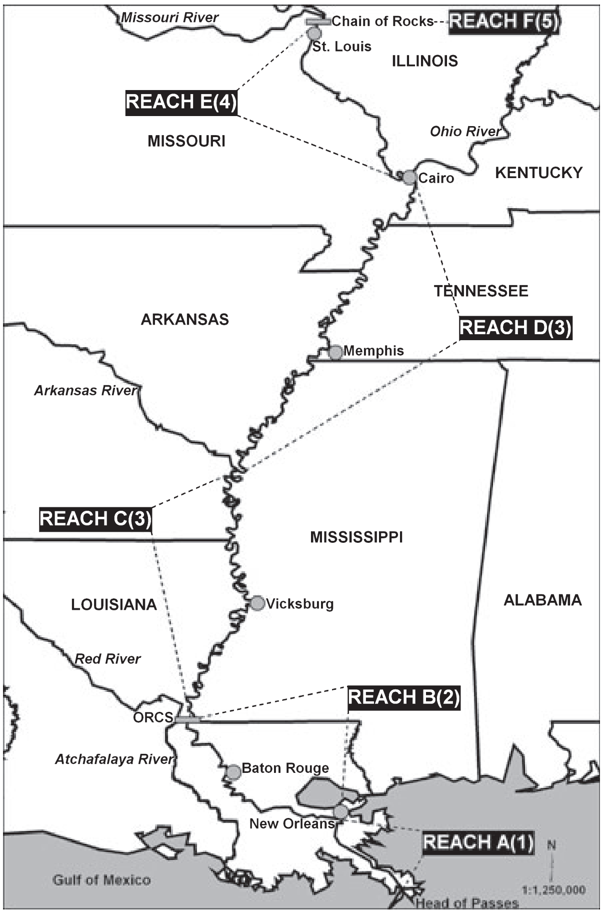

Fig. 1. Location of *a priori* (alpha) and *a posteriori* (numeric) study and management reaches, respectively, in the free-flowing Mississippi River. ORCS is the Old River Control Structure at the confluence of the Atchafalaya and Mississippi rivers

Materials and methods

Two approaches were used to select sampling sites. From 2000 to 2002, an intensive study of two major geomorphic habitats characteristic of the Mississippi River (bendway and straightway) was conducted. The representative bendway (Togo

Table 1
Designation and description of river reaches used in analysis

Designation	Reach description	River kilometer
A	Mouth of the MS River – New Orleans	0–153
B	New Orleans – Atchafalaya	154–502
C	Atchafalaya – Mouth of the Arkansas	503–935
D	Arkansas – Mouth of the Ohio	936–1533
E	Mouth of the Ohio – Mouth of the Missouri	1534–1847[1]
F	Chain of Rocks	1839.5

[1] Navigation charts reset rkm in the Mississippi River to 0.0 at the mouth of the Ohio River.

Bendway, rkm 665–669) and straightway (Baleshed/Stack Island, rkm 777–782) were selected *a priori* and samples were collected repeatedly during all seasons. However, low catches of pallid sturgeon and interest in other reaches of the lower Mississippi River prompted us to expand the geographic scope and target sites that maximize probability of pallid sturgeon capture. Therefore, all sites were subjectively chosen between 2003 and 2006 to increase sample size of pallid sturgeon and evaluate geographic distribution of this migratory species.

Each sampling location was identified as either a straightway (including crossing) or bendway (e.g. point bar). Some bendways had well-developed side channels associated with islands and were designated as such. Three sampling gear types were used to capture fish: trotlines, gill nets and otter trawls. Replicate numbers of each gear type and consistent deployment techniques were used during each sampling event to facilitate statistical analysis of temporal and spatial trends.

Trotlines (61 m long, 60 dropper lines spaced every 0.9 m tied to 2/0 hooks) were baited with worms (Canadian night crawlers), fished overnight along the bottom and retrieved the following morning. Up to eight trotlines were deployed per night at each site, each fishing approximately 16 h. Trotlines were reefed into a ‘jump box’ typically used by commercial fishermen. A buoy and anchor were deployed at the upstream position of the line and the box was slowly rotated as the boat drifted downstream, thus allowing the line to be deployed within minutes without tangling. Small weights attached to the line every 7.6 m maintained bottom position. Trotlines could be placed in either slack or swiftwater habitats. Experimental mesh gill nets (27.4 m by 1.8 m, six mesh panels ranging from 23 to 76 cm) were set concurrently with trotlines in slackwater areas such as dike pools or near shore locations; two nets were usually tied together but data were kept separate. At least two gill nets were set at each site in the late afternoon and retrieved the following morning, usually over a 16-h period. A 4.9-m Missouri benthic trawl, based on the design by Hertzog et al. (2005), was used to sample smaller benthic fishes. The distance traveled, average speed and depth range were recorded during each trawling event.

All fish captured were identified to species, enumerated and total length (also fork length for sturgeon) was measured. Additional morphometric measurements and meristic counts were taken on pallid sturgeon to verify species designation *a posteriori* as described by Murphy et al. (2007). Prior to release, shovelnose and pallid sturgeon were externally tagged with t-anchor bar spaghetti tags. A toll-free phone number along with the tag number were inscribed on each tag. In addition, all pallid sturgeon specimens were scanned for the presence of a Passive Integrated Transponder (PIT) tag, and if no tag was detected, a non-encrypted PIT tag was inserted at the base of the dorsal fin. Beginning in the autumn of 2004, all sturgeon were scanned for coded wire tags to determine if individuals were of hatchery origin.

The abundance of pallid and shovelnose sturgeon, expressed as catch-per-unit-effort (CPUE) with effort being a trotline set overnight, and the pallid to shovelnose ratio (total numbers collected), were enumerated for the five pre-designated reaches. CPUE was transformed as the log 10 + 1 because the Shapiro-Wilk statistic in SAS (SAS Institute, 2000) indicated non-normalized data; results are reported using non-transformed values, however. The Student–Newman–Keuls multiple range test was used to identify classification variables that were significantly different from each other.

Results

From 1996 to 1997 and 2000 to 2006, we sampled 73 different sites in the LMR and 29 sites in the MMR. Many of these sites were sampled repeatedly, resulting in a total number of sampling nights of 188 and 63 for the LMR and MMR, respectively. A total of 219 pallid sturgeon and 6018 shovelnose sturgeon was caught in the Mississippi River. Out of this total, 162 (72%) and 57 (26%) pallid sturgeon were caught in the LMR and MMR, respectively. For shovelnose sturgeon, 2943 (49%) and 3075 (51%) individuals were caught in the LMR and MMR, respectively. Trotlines were the primary gear used to catch pallid sturgeon. We fished 1247 trotlines for approximately 16 h each during the study catching 215 pallid sturgeon. A total of 245 gill nets set approximately 16 h each captured three pallid sturgeon, and 345 trawls captured one adult pallid sturgeon. Due to the low capture rate of gill nets and trawls, all subsequent analyses were conducted using only trotlines.

Catch rate of pallid and shovelnose sturgeon was higher at lower temperatures, peaking at 10°C and slowly declining to almost zero when water temperatures exceeded 20°C (Fig. 2). Trotlines captured 21 species overall (Table 2). Notable species collected during the study included lake sturgeon (*Acipenser fluvescens*), sicklefin chub (*Macrhybopsis meeki*), and stonecat (*Noturus flavus*). Thirty lake sturgeon ranging in size from 663 to 1275 mm fork length (FL) were collected only in the MMR. From October 2004 thru May 2005, all sturgeon captured in the MMR were consistently scanned for coded wire tags (CWT) indicating hatchery origin. During this time, CWT’s were detected in three of the 11 (i.e. 27%) lake sturgeon scanned. One sicklefin chub, a species with a reduced distribution (Everett et al., 2004), was caught on a trotline. Stonecats were collected at numerous locations between rkm 576, which is a new downstream range extension (Ross, 2001), and Melvin Price Lock and Dam immediately above the Missouri River. In the LMR, blue catfish (*Ictalurus furcatus*) comprised 50.0% of all individuals collected, whereas shovelnose comprised 36.6%. All other species comprised 5% or less of the total individuals collected; pallid sturgeon comprised 2.2%. In the MMR, shovelnose sturgeon comprised 60.4% of the total number of individuals collected, whereas blue catfish comprised 25.6%. Channel catfish (*Ictalurus punctatus*) comprised 8.6%, while all other species were < 1.5%; pallid sturgeon comprised 1.1% of the total catch.

We documented 12 recaptures of pallid sturgeon, five of which were recaptured below the mouth of the Ohio River. Of these five, only one individual was originally tagged by us. It was

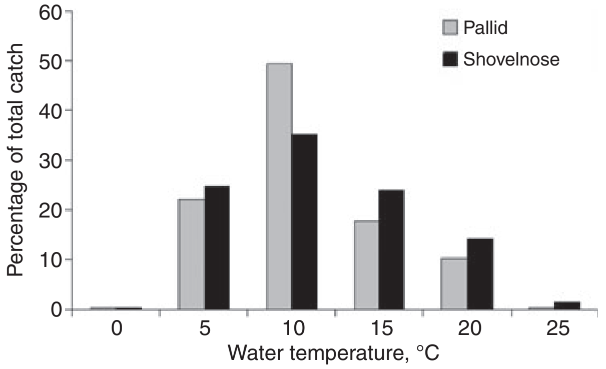

Fig. 2. Percent of total catch of pallid and shovelnose sturgeon in the middle and lower Mississippi River combined during 1996–1997, and 2000–2006 as a function of water temperature

Table 2
Species and total number of fish caught by trotlines (n = 1247) in the lower and middle Mississippi River between 1996–1997, and 2000–2006. Species are arranged in decreasing order of abundance

Common name	Genus–species	Number collected
Shovelnose sturgeon	*Scaphirhynchus platorynchus*	5712
Blue catfish	*Ictalurus furcatus*	4915
Channel catfish	*Ictalurus punctatus*	818
Freshwater drum	*Aplodinotus grunniens*	240
Pallid sturgeon	*Scaphiryhnchus albus*	215
Flathead catfish	*Pylodictis olivaris*	180
Smallmouth buffalo	*Ictiobus bubalus*	77
American eel	*Anguilla rostrata*	58
Silver chub	*Macrhybopsis storeriana*	31
Lake sturgeon	*Acipenser fulvescens*	30
Black buffalo	*Ictiobus niger*	13
Common carp	*Cyprinus carpio*	11
Stonecat	*Noturus flavus*	8
Paddlefish	*Polyodon spathula*	2
Gizzard shad	*Dorosoma cepedianum*	1
Sicklefin chub	*Macrhybopsis meeki*	1
Silver carp	*Hypophthalmichthys molitrix*	1
Quillback	*Carpiodes cyprinus*	1
Shorthead redhorse	*Moxostoma macrolepidotum*	1
Sauger	*Stizostedion canadense*	1
Walleye	*Stizostedion vitreum*	1

tagged on April 9, 2002, at rkm 1274 near Osceola, AR, with a length of 694 mm FL. A commercial fisherman recaptured this individual on May 20, 2002, in the Obion River near Bogota, TN, approximately 48 km above the confluence with the Mississippi River. Therefore, it traveled upstream approximately 92 km from the initial capture location. No reliable lengths or weights were taken before the fish was released.

Another pallid sturgeon (of the five mentioned above) was recaptured 4 years after its release into the Mississippi River by the Blind Pony Fish Hatchery, MO, on October 15, 1997, at rkm 1430 near New Madrid, Missouri (Killgore et al., 2002). The fish was approximately 300 mm FL at the time of release. We captured the fish on February 14, 2002, near Greenville, Mississippi, 582 km downstream of the original release site in the MMR (Reach E). It was 557-mm FL, which indicates that it grew 4.9 mm per month. Three pallid sturgeon were recaptured that were originally tagged by the Missouri Department of Conservation and released in the MMR. These fish ranged in size from 501 to 559 mm FL and were caught in the LMR between rkm 848 and 1374. All three pallid sturgeon were released in 1997. Two were stocked in the Mississippi River (rkm 1488 and 1708) and recaptured in 2002 (rkm 848) and 2003 (rkm 1048), respectively. One was stocked into the Missouri River at rkm 46 and recaptured in the Mississippi River in 2002 (rkm 1048).

Hatchery fish were also detected in the MMR. From October 2004 thru May 2005, all pallid sturgeon captured in the MMR were consistently scanned for coded wire tags (CWT) indicating hatchery origin. CWT were detected in seven of 15 pallid sturgeon (47%) caught during this period. Mean length of these seven individuals was 737 mm FL ranging from 541 to 913 mm FL.

Targeted sampling resulted in significantly more sturgeon per unit effort than non-targeted sampling of representative sites over time. Targeted sampling began in 2002 when trotlines were set specifically to catch sturgeon without regard to available habitat. Mean catch (±SD) of pallid and shovelnose sturgeon during non-targeted sampling at representative sites (i.e. Togo Bendway and Baleshed/Stack Island) was 0.03 ± 0.18 and 1.42 ± 3.40, respectively. During targeted sampling within the same study reach where representative sites were located (Reach C, Fig. 1), mean abundance of pallid and shovelnose sturgeon was considerably higher (0.22 ± 0.56 and 3.53 ± 3.87, respectively). These values were significantly different among sampling approaches for pallid ($F_{0.05,573} = 24.73$, $P < 0.001$) and shovelnose ($F_{0.05,574} = 89.01$, $P < 0.001$) sturgeon.

There were significant differences in mean abundance for pallid and shovelnose sturgeon among reaches, but the pattern differed between species (Table 3). Pallid sturgeon abundance was highest in Reaches B (between New Orleans and the Atchafalya River) and COR. For shovelnose sturgeon, abundance was significantly different among all reaches. Shovelnose sturgeon abundance increased going upstream, but was disproportionally higher at the COR (22 fish per line compared with <6 fish per line in other reaches). In addition, pallid sturgeon abundance was more variable (coefficient of variation ranged from 203% to 346%) than shovelnose (56 to 180%). The maximum number of sturgeon caught on one line was five for pallid and 50 for shovelnose sturgeon. Overall, the ratio between pallid and shovelnose sturgeon varied from a high of 1 : 6 in Reach B, and gradually decreased upstream to a low of 1 : 77 at the COR.

Mean fork length of pallid sturgeon was significantly ($P < 0.05$) lower in Reach B (Table 4). There was also a trend of increasing length in an upstream direction although not significant. The smallest pallid sturgeon captured on a trotline was 405 mm FL in Reach B and minimum size increased in an upstream direction. The largest pallid sturgeon caught was 995 mm FL in Reach F. Shovelnose sturgeon exhibited a similar trend of increased length in an upstream direction (Table 4). Mean length of shovelnose sturgeon was statistically ($P < 0.05$) the same in two reaches (Reaches C and COR). However, all other reaches were significantly different from each other. The smallest shovelnose sturgeon captured on a trotline was 273 mm FL at the COR; the largest was 860 mm FL in Reach C.

Discussion

Pallid sturgeon were widely distributed in the free-flowing Mississippi River with disparate centers of abundance suggesting that reach-specific management considerations may be warranted. They were most abundant at the extremes of their range: lower reach between the Atchafalaya River and New Orleans and immediately below the Chain of Rocks dam near the mouth of the Missouri River. Abundance was similar between these two extremes. Conversely, shovelnose sturgeon exhibited a definite latitudinal trend of increasing abundance from the lower reach upstream to the COR. No sturgeon were collected below New Orleans (Reach A), possibly due to lower sampling effort, avoidance of salt water and low habitat variability (e.g. lack of point bars, mud-dominated substrate). The most downstream location where pallid sturgeon were collected during our study was at rkm 233.3 in Reach B.

The ratio of pallid to shovelnose sturgeon relative abundance has been reported to range from 1 : 5 (Etnier and Starnes, 1993) to 1 : 400 (Kallemeyn, 1983; Carlson et al., 1985) at various locations. Although these ratios are anecdotal (Etnier and Starnes, 1993) or based on limited effort and data (Kallemeyn, 1983; Carlson et al., 1985), they provide the only historical information against which to compare our results. Pallid : shovelnose ratios may also prove useful in developing

Table 3
Statistical summary of abundance (catch-per-unit-effort) for pallid and shovelnose sturgeon captured in the Mississippi River using trotlines from 1996 to 1997, and 2000–2006

	Reach (rkm)				
	B	C	D	E	F
Species and statistic	New Orleans–Atchafalaya River (154–502)	Atchafalaya River–Mouth of Arkansas River (503–935)	Mouth of Arkansas River–Mouth of Ohio River (936–1533)	MMR wo/COR (1534–1847)	COR (1839.5)
Number of trotlines	144	574	145	273	86
Pallid sturgeon					
Mean	0.31^{a}	0.23^{b}	0.18^{b}	0.12^{b}	0.29^{a}
Standard deviation	0.68	0.56	0.62	0.33	0.59
Coefficient of variation	223	254	346	284	203
Maximum collected per line	4	5	5	2	3
Total collected	44	81	26	32	25
Shovelnose sturgeon					
Mean	1.88^{a}	3.53^{b}	5.41^{c}	4.22^{c}	22.24^{d}
Standard deviation	3.39	3.87	8.39	5.45	12.41
Coefficient of variation	180	110	155	129	56
Maximum collected per line	20	23	50	32	43
Total collected	271	1301	784	1151	1913
Pallid : Shovelnose (totals)	1 : 6	1 : 16	1 : 30	1 : 36	1 : 77

Non-targeted samples were deleted for this analysis. The lowermost reach of the Mississippi River (Reach A, rkm 0–153) was not included because no sturgeon were collected (number of trotlines = 25). For analytical purposes, the Middle Mississippi River was divided into two reaches–between the mouths of the Missouri and Ohio rivers excluding Chain of Rocks (MMR wo/CR) and Chain of Rocks (COR) excluding the remainder of the MMR. Values for mean abundances with different letters along a row are significantly ($P < 0.05$) different according to the Student–Newman–Keuls multiple range test.

Table 4
Statistical summary of fork length (mm) for pallid and shovelnose sturgeon captured in the Mississippi River using trotlines from 1996 to 1997, and 2000–2006 excluding non-targeted sites

	Reach (rkm)				
	B	C	D	E	F
Species and statistic	New Orleans–Atchafalaya River (154–502)	Atchafalaya River–Mouth of Arkansas River (503–935)	Mouth of Arkansas River–Mouth of Ohio River (936–1533)	MMR wo/COR (1534–1847)	COR (1839.5)
Pallid sturgeon					
Number collected	44	81	26	32	25
Mean	620^{a}	709^{b}	741^{b}	758^{b}	756^{b}
Standard deviation	110	111	65	87	96
Minimum	405	410	540	541	553
Maximum	789	965	854	889	995
Shovelnose sturgeon					
Number collected	265	1259	775	1123	1887
Mean	539^{a}	587^{b}	599^{c}	621^{d}	578^{b}
Standard deviation	80	81	82	72	77
Minimum	328	283	285	289	273
Maximum	852	860	818	831	790

The lowermost reach of the Mississippi River (Reach A, rkm 0–153) was not included because no sturgeon were collected ($n = 25$). For analytical purposes, the Middle Mississippi River was divided into two reaches–between the mouths of the Missouri and Ohio rivers excluding Chain of Rocks (MMR wo/CR) and at the Chain of Rocks (COR) excluding the remainder of the MMR. Values for mean length with different letters along a row are significantly ($P < 0.05$) different according to the Student–Newman–Keuls multiple range test.

management plans for both species of sturgeon. For example, ratios can be used to determine risk of incidental take of pallid sturgeon during commercial harvest of shovelnose sturgeon.

Our study indicated that pallid : shovelnose sturgeon ratio ranged from 1 : 6 in Reach B to 1 : 77 at the COR, thus showing a latitudinal trend. Shovelnose sturgeon, as well as pallid sturgeon, congregate below the COR during low water when the dam is impassable. Sturgeon may also prefer this area for spawning or staging because of the presence of widespread gravel bars and proximity to the Missouri River. Regardless of the reasons, the immediate area below COR is characterized by a disproportionate number of shovelnose sturgeon.

Although it has been reported that pallid sturgeon attain sizes of 167 cm TL and 31 kg (Carlander, 1969; Lee, 1980a; Kallemeyn, 1983), smaller individuals less than 100 cm TL are more typical in the LMR and MMR. Reach-specific differences in average length for both shovelnose and pallid sturgeon do occur, however. Northern latitudes of the Mississippi River have a shorter growing season than southern latitudes (Eggleton et al., 2004). Both pallid and shovelnose sturgeon appear to grow faster at cooler water temperatures suggested by the fact that average size was lowest in the most southern reach, and average lengths steadily increased going north into cooler waters (Murphy et al., 2007). The exception was at the COR where the average length decreased compared with lower reaches.

Increased growth rates at higher latitudes are consistent with Bergmann's rule stating that the body size of animals should increase with increasing latitude (Lindsey, 1966). To cope with long winters in northern latitudes, energy is allocated to growth in size initially rather than growth in reproductive tissues, although Bergmann's rule does not necessarily apply to all fish species (Garvey and Marschall, 2003). An alternative hypothesis for smaller individuals in southern latitudes is that river sturgeon utilize lower reaches for feeding and growth and move upstream as adults for spawning. Pallid sturgeon are known to migrate upstream during the spawning season (Bramblett, 1996; Hurley et al., 2004), and based on our personal observations, the presumed spawning substrates of pallid sturgeon (i.e. gravel bars) are more common in northern latitudes.

Recapture data indicated new distributional records, downstream movement of hatchery fish, and recruitment of hatchery fish derived from brood stock in the Missouri River into the Mississippi River. The pallid sturgeon originally tagged near Osceola, AR and recaptured in the Obion River near Bogota, TN, represents the first documented case of a pallid sturgeon occurring in this tributary of the Mississippi River. The pallid sturgeon released from the Blind Pony Fish Hatchery, MO, near New Madrid, MO and recaptured near Greenville, MS, documents long distance downstream movement of hatchery fish (582 rkm), and a long-term retention rate (i.e. 5 years) of T-anchor spaghetti tags (Killgore et al., 2002). At least eight pallid sturgeon captured in the MMR were of hatchery origin. Pallid sturgeon have been stocked into the Missouri River since the late 1990s to augment the depleting numbers of this endangered species (Gerrity et al., 2006). Our recaptures in the MMR indicate that hatchery fish are being recruited into the population, and considering the length range, must be represented by multiple year classes.

Trotlines were an effective gear to catch sub-adult and adult pallid and shovelnose sturgeon. The smallest specimen captured on trotlines was 405 and 273 mm FL for pallid and shovelnose sturgeon, respectively. Other gears, such as trawling (Hertzog et al., 2005), will be necessary to sample for smaller, young-of-the-year sturgeon. Trotlines are a versatile technique, however, catching a wide range of sizes. Trotlines can sample a variety of riverbed forms where benthic fish distribution differs (Wildhaber et al., 2003). They can be deployed in the channel border and channel with deep water, fast current and steep sloping banks, habitats typically associated with pallid sturgeon (Bailey and Cross, 1954; Carlander, 1969; Kallemeyn, 1983; Carlson et al., 1985; Keenlyne et al., 1992, 1994a,b; Bramblett, 1996; Constant et al., 1997; Liebelt, 1996; Hurley et al., 2004). Their versatility allows for a sampling approach targeting preferred swiftwater habitats (e.g. dike tips, steep sloping banks, channel border) resulting in pallid sturgeon catches that are seven times more effective based on our comparison with non-targeted efforts. Non-targeted effort may be necessary to evaluate habitat preferences when the goal is to compare all available habitats, but catch will be substantially lower.

All trotlines were baited with worms to maintain consistency in sampling protocol so results can be compared range-wide. All of the worms used during the study were considered night crawlers, many going by the name 'Canadian' and 'fantail.' There are several advantages of using worms. They can be easily obtained and stored for long periods. Worms can be 'threaded' onto the hook, thus remaining intact during deployment and fishing. It generally took 15 min for one person to bait a 60-hook line and deployment of the trotline from the jump box took approximately 5 min once a sampling location was selected. Therefore, within a few hours, six to eight trotlines could be baited and deployed by a two-person crew. We usually used an additional boat to take habitat and location information on all trotlines deployed.

Worms also attract a variety of other fish species that comprise the large-bodied benthic community of channel and channel border habitats in the free-flowing Mississippi River. Of the 21 species collected, shovelnose sturgeon and catfishes were the most abundant. The dominance of shovelnose sturgeon in the middle reach and blue catfish in the lower reaches suggest competitive influences on distribution or differences in habitat preferences. Other species commonly caught, such as suckers and freshwater drum, were typical of channel habitats and many are permanent residents for much of their life history (Baker et al., 1991; Dettmers et al., 2001). We documented the presence of rare and sensitive species as well, including freshwater eel, stonecat and sicklefin chub. Large-bodied species associated with pallid sturgeon were primarily shovelnose sturgeon and catfishes. However, smaller-bodied fishes present in the benthic assemblage may be important forage for piscivorous pallid sturgeon, particularly the chubs (Gerrity et al., 2006).

Conservation of pallid sturgeon requires an understanding of its distribution and abundance in discrete reaches of the free-flowing Mississippi River. The recovery plan for pallid sturgeon groups the entire MMR and LMR into one recovery priority management area (RPMA). In 1993, when the recovery plan was published (Dryer and Sandvol, 1993), there were inadequate data to separate the free-flowing Mississippi River into more than one RPMA. However, our study indicates that discrete reaches of the LMR and MMR should be recognized in any management plan regardless if there are no changes to the designations of RPMA. Although pallid sturgeon may move freely between reaches, the relationships between mean relative abundance, average length of sturgeon and representative habitat characteristics suggest that there are five reaches of the free-flowing Mississippi River with unique properties:

Reach 1 (Study reach A)

The coastal or lowermost reach below New Orleans. The absence of sturgeon in the coastal reach is likely due to avoidance of salinity and marginal habitat including mud-dominated substrates and homogeneous channel characteristics.

Reach 2 (Study reach B)

The deltaic reach between New Orleans and the Atchafalaya River. In this reach, pallid sturgeon abundance is highest, average size is lowest and the pallid : shovelnose ratio is highest. Steep sloping banks, deep channels, reduced floodplain, reduced number of sandbars and few dikes characterize this reach (Baker et al., 1991). In addition, a large tributary population of pallid sturgeon occur in the Atchafalaya River (Constant et al., 1997).

Reach 3 (Study reaches C and D)

The reaches between the Atchafalaya River and the mouth of the Ohio River. Pallid sturgeon abundance and mean size is similar in these areas. This reach has extensive floodplains, wide channels, well-developed point bars and numerous secondary channels (Baker et al., 1991). Further subdivision of this relatively long reach may be warranted due to the presence of commercial fishing in the upper portion of the reach, and the influence of the Ohio River and MMR near the upstream terminus.

Reach 4 (Study reach E)

The middle reach between the mouths of the Ohio and Missouri rivers. Pallid sturgeon abundance begins to decline relative to the lower reaches, but mean size for both pallid and shovelnose sturgeon is highest. Floodplain area is reduced and channel is swifter than the lower reaches due to extensive dike fields. There is preliminary evidence that this reach may contain important spawning habitat for pallid sturgeon (D. Herzog, Missouri Department of Conservation, pers. comm.). It is also an area of intense commercial fishing for shovelnose sturgeon.

Reach 5

The Chain of Rocks, although a small reach compared with the others, is an area where pallid sturgeon abundance is comparable to the deltaic reach (Study Reach B) but with larger individuals. Shovelnose sturgeon abundance is disproportionally higher than any other reach, and the low water dam may result in a concentration of sturgeon during certain times of the year making them particularly vulnerable to commercial harvesting. Conservation plans must consider the unique conditions of the COR.

Our study clearly indicates that pallid sturgeon occur throughout the MMR and LMR, except possibly for the coastal reach, and they can be most efficiently captured during the colder months of the year with trotlines. Although pallid sturgeon were the 5th most abundant species captured, they are relatively rare compared with shovelnose sturgeon and catfish, representing < 1.5% of the total catch overall. A substantial effort was expended to capture the 219 pallid sturgeon during this study (e.g. almost 20 000 trotline hours were expended). The rarity of pallid sturgeon may be characteristic of this species, but continuing studies are necessary to monitor population attributes among the reaches, document reproductive success and evaluate the potential of incidental take during shovelnose sturgeon harvest in states that still allow commercial fishing.

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References

Bailey, R. M.; Cross, F. B., 1954: River sturgeons of the American genus *Scaphirhynchus*: characters, distribution, and synonymy. Pap. Mich. Acad. Sci. Arts Lett. **39,** 169–208.

Baker, J. A.; Killgore, K. J.; Kasul, R. L., 1991: Aquatic habitats and fish communities in the lower Mississippi River. Rev. Aquat. Sci. **3,** 313–356.

Bramblett, R. G., 1996: Habitats and movements of pallid and shovelnose sturgeon in the Yellowstone and Missouri rivers, Montana and North Dakota. PhD thesis. Montana State University, Bozeman, MT, 210 pp.

Carlander, K. D., 1969: Handbook of freshwater fishery biology, volume one. Iowa State University Press, Ames, Iowa, 752 pp.

Carlson, D. M.; Pflieger, W. L.; Trial, L.; Haverland, P. S., 1985: Distribution, biology, and hybridization of *Scaphirhynchus albus* and *S. platorynchus* in the Missouri and Mississippi rivers. Env. Biol. Fish. **14,** 51–59.

Constant, G. C.; Kelso, W. E.; Rutherford, D. A.; Bryan, C. F., 1997: Habitat, movement, and reproductive status of pallid sturgeon (*Scaphirhynchus albus*) in the Mississippi and Atchafalaya rivers. Report prepared for U.S Army Engineer New Orleans District, 78 pp.

Dettmers, J. M.; Gutreuter, S. W.; Soluk, D. H., 2001: Patterns in abundance of fishes in main channels of the upper Mississippi River system. Can. J. Fish. Aquat. Sci. **58,** 933–942.

Dryer, M. P.; Sandvol, A. J., 1993: Recovery plan for the pallid sturgeon (*Scaphirhynchus albus*). USFWS, Denver, CO, 55 pp.

Eggleton, M. A.; Miranda, L. E.; Kirk, J. P., 2004: Assessing the potential for fish predation to impact zebra mussels (*Dreissena polymorpha*): insight from bioenergetics models. Ecol. Fresh. Fish. **13,** 85–95.

Etnier, D. A.; Starnes, W. C., 1993: The fishes of Tennessee. University of Tennessee Press, Knoxville, TN, 681 pp.

Everett, S. R.; Scarnecchia, D. L.; Power, G. J.; Williams, C. J., 2003: Comparison of age and growth of shovelnose sturgeon in the Missouri and Yellowstone rivers. North Am. J. Fish. Manage. **23,** 230–240.

Everett, S. R.; Scarnecchia, D. L.; Ryckman, L. F., 2004: Distribution and habitat use of sturgeon chubs (*Macrhybopsis gelida*) and sicklefin chubs (*M. meeki*) in the Missouri and Yellowstone Rivers, North Dakota. Hydrobiologia **527,** 183–193.

Federal Register, 1990: Determination of endangered status for the pallid sturgeon; final rule. Sept. 6, 1990. **55,** 36641–36647.

Fisk, H. N., 1944: Geological investigation of the alluvial valley of the lower Mississippi River. Mississippi River Commission, Vicksburg, MS, 78 pp.

Forbes, S. A.; Richardson, R. E., 1905: On a new shovelnose sturgeon from the Mississippi River. Bull. Ill. State Lab. Nat. Hist. **7,** 37–44.

Garvey, J. E.; Marschall, E. A., 2003: Understanding latitudinal trends in fish body size through models of optimal seasonal energy allocation. Can. J. Fish. Aquat. Sci. **60,** 938–948

Gerrity, P. C.; Guy, C. S.; Gardner, W. M., 2006: Juvenile pallid sturgeon are piscivorous: a call for conserving native cyprinids. Trans. Am. Fish. Soc. **135,** 604–609.

Hertzog, D. P.; Barko, V. A.; Scheibe, J. S.; Hrabik, R. A.; Ostendorf, D. E., 2005: Efficacy of a benthic trawl for sampling small-bodied fishes in large river systems. North Am. J. Fish. Manage. **25,** 594–603.

Hurley, K. L.; Sheehan, R. J.; Heidinger, R. C.; Wills, P. S., 2004: Habitat use by Middle Mississippi River pallid sturgeon. Trans. Am. Fish. Soc. **133,** 1033–1041.

Kallemeyn, L., 1983: Status of the pallid sturgeon. Fisheries **8,** 3–9.

Keenlyne, K. D.; Grossman, E. M.; Jenkins, L. G., 1992: Fecundity of the pallid sturgeon. Trans. Am. Fish. Soc. **121,** 139–140.

Keenlyne, K. D.; Henry, C. J.; Tews, A. P.; Clancey, P., 1994a: Morphometric comparisons of upper Missouri River sturgeons. Trans. Am. Fish. Soc. **123,** 779–785.

Keenlyne, K. D.; Graham, L. K.; Reed, B. C., 1994b: Hybridization between the pallid and shovelnose sturgeons. Proc. S. D. Acad. Sci. **73,** 59–66.

Killgore, K. J.; Hoover, J. J.; Hrabik, R. A.; 2002: Pallid sturgeon captured four years after its release. Am. Curr. **28,** 30.

Lee, D. S., 1980a: *Scaphirhynchus albus* (Forbes and Richardson), Pallid sturgeon. p. 43. In: Atlas of North American freshwater fishes. D. S. Lee (Ed.). North Carolina State Museum of Natural History, Raleigh, NC, 854pp. .

Lee, D. S., 1980b: *Scaphirhynchus platorynchus* (Rafinesque), shovelnose sturgeon. p. 44. In: Atlas of North American freshwater fishes. D. S. Lee (Ed.). North Carolina State Museum of Natural History, Raleigh, NC, 854 pp.

Liebelt, J. E., 1996: Lower Missouri River and Yellowstone River Pallid sturgeon study, 1994–1995 Report. Western Area Power Administration Grant Report No. BAO-709, 57 pp.

Lindsey, C. C., 1966: Body sizes of poikilotherm vertebrates at different latitudes. Evolution **20,** 456–465.

Murphy, C. E.; Hoover, J. J.; George, S. G.; Killgore, K. J., 2007: Morphometric variation among river sturgeons (*Scaphirhynchus* spp.) of the middle and lower Mississippi River. J. Appl. Ichthyol. **23,** 313–323.

Ross, S. T., 2001: Inland fishes of Mississippi. University Press of Mississippi, Oxford, MS, 624 pp.

SAS Institute, 2000: SAS OnlineDoc, version 8. SAS Institute, Cary, NC.

Saucier, R. T., 1991: Geomorphology, stratigraphy, and chronology, lower Mississippi valley. In: Quaternary nonglacial geology: conterminous U. S., The geology of North America. R. B. Morrison (Ed.). Geological Society of America, Boulder, CO, pp. 550–563.

Schumm, S. A.; Rutherfurd, I. D.; Brooks, J., 1994: Pre-cutoff morphology of the lower Mississippi River. In: The variability of large alluvial rivers. S. A. Schumm and B. R. Winkley (Eds). American Society of Engineers Press, New York, pp. 13–44.

Tranah, G. J.; Kincaid, H. L.; Krueger, C. C.; Campton, D. E.; May, B., 2001: Reproductive isolation in sympatric populations of pallid and shovelnose sturgeon. N. Am. J. Fish. Manage. **21,** 367–373.

U. S. Fish and Wildlife Service, 2000: Biological opinion for the operation and maintenance of the 9-foot navigation channel on the Upper Mississippi River. Prepared by Marion Suboffice, Marion, IL; Twin Cities Field Office, Bloomington, Minnesota, USA.

Wildhaber, M. L.; Lamberson, P. J.; Galat, D. L., 2003: A comparison of measures of riverbed form for evaluating distributions of benthic fishes. N. Am. J. Fish. Manag. **25,** 543–557.

Author's address: K. Jack Killgore, United States Army Engineer Research and Development Center, Environmental Laboratory, 3909 Halls Ferry Road, EE-A, Vicksburg, MS 39180, USA.
E-mail: jack.killgore@erdc.usace.army.mil

CHAPTER 3: HABITAT AND MOVEMENT

Habitat Use and Movement of Naturally Reproducing Pallid Sturgeon in the Mississippi River

Brian Koch[1], Ronald C. Brooks[2], Amanda Oliver[3], David Herzog[4],
James E. Garvey[2,5,7], Robert Hrabik[4], Robert Colombo[2,5], Quinton Phelps[2,5],and Timothy Spier[6]

[1]Illinois Environmental Protection Agency, 1021 N. Grand Ave E. PO Box 19276. Springfield, IL 62794
[2]Fisheries and Illinois Aquaculture Center, Southern Illinois University, Carbondale, IL 62901
[3]St. Louis District, US Army Corps of Engineers, St. Louis, MO 63103
[4]Open Rivers and Wetlands Field Station, Missouri Department of Conservation, Jackson, MO 63755
[5]Department of Zoology and Center for Ecology, Southern Illinois University, Carbondale, IL 62901
[6]Department of Biology, Western Illinois University, Macomb, IL 61455
[7]Corresponding author: jgarvey@siu.edu

Abstract

Pallid sturgeon (*Scaphirhynchus albus*) is a US federally endangered species that maintains a naturally reproducing population in the Middle Mississippi River (MMR), which extends 322 km between the Missouri River and Ohio River confluences. We surgically implanted 88 pallid sturgeon (> 600 mm fork length) during 2002 through 2005 with ultrasonic transmitters and quantified their habitat use with boat-mounted hydrophones (8,629 km tracked). In addition, we quantified seasonal movement with stationary data-logging hydrophones. During all years and seasons, wing dike areas were used disproportionately relative to their abundance. During each spring, pallid sturgeon moved from wing dikes, closer to islands (~ 1 km), and within about 100 m of known gravel bars. Unique flow and substrate characteristics of wing dikes likely emulate missing habitat complexity (i.e., islands, sand bars, gravel). During spring, gravel bars appear to be used for reproduction.

Introduction

Sturgeons are economically important, largely due to demand for caviar. Because of their great fiscal value, they are overharvested and thereby one of the most imperiled fish in the world (Boreman 1997). In addition, loss of habitat and connectivity, particularly in rivers, also is contributing to the decline by reducing sustainability and preventing sturgeon from completing their life cycle (Pikitch et al. 2005; Colombo et al. 2007). For these species to recover, basic habitat requirements for all life stages within naturally occurring populations must be quantified (Bajer and Wildhaber 2007). Knowledge of habitat needs should allow restoration and conservation, and perhaps support sustainable harvest of some sturgeon species.

The pallid sturgeon (*Scaphirhynchus albus*) is a non-anadromous species in the rivers of the central US that historically occurred from the Gulf of Mexico in the Mississippi River through the Yellowstone River tributary of the Upper Missouri River. It was listed as federally endangered in 1990, largely because of loss of reproduction in the upper Missouri River. However, in the Mississippi River, natural reproduction is still occurring (Hrabik et al. 2007), although the magnitude of reproductive success and potential hybridization with the congener shovelnose sturgeon (*S. platorynchus*) are unknown.

The free-flowing Mississippi River provides all the habitat characteristics necessary to allow it to complete its life cycle (Killgore et al. 2007). Given the range-wide US federal mandate to recover the pallid sturgeon, quantifying the use of habitat areas in the river and movement among locations within this river should provide some insight into the baseline needs of the species throughout its range. Hurley et al. (2004) found that adult pallid sturgeon from a 50-km segment of the Mississippi River frequented island areas and wing dikes. We revisited this approach by expanding both the spatial and temporal resolution of our telemetry effort to better understand habitat needs and movement in the river. Specifically, we quantified habitat use across a large 306-km reach of the river and then linked this to the movement of pallid sturgeon, particularly during the spring spawning season.

Methods

Study Area.

Habitat use and movement were quantified in the entire Middle Mississippi River (MMR) which is free-flowing and extends from the confluence of the Ohio River at Cairo, Illinois (RKM 0) upriver to the confluence of the Missouri and Mississippi Rivers (RKM 322; Figure 1). This reach contains a unique feature in the Mississippi River at Chain of Rocks (COR) located below a lowhead dam (Lock and Dam 27; RKM 306). This area is turbulent with extensive rock substrates. The MMR has been altered significantly to control flooding and to facilitate navigation. Subsequently, the MMR has been separated from most of its floodplain via levees and the channel has been narrowed and deepened using control structures including several hundred, typically above-water wing dikes and continually submersed bendway wiers. The MMR still maintains a spring flood pulse, although the rise and drop in water levels are steeper than those that occurred in historical hydrographs (Sparks and Spink 1998).

Telemetry.

Telemetry data were collected during fall 2002 through fall 2005. However, techniques, technology, and approaches changed during this period. During 2002 through 2005, telemetry was conducted via boat-mounted, manual tracking. Most of the extensive manual tracking ceased by summer 2006. During 2004 through late 2005, fish locations were monitored by an array of stationary, data-logging hydrophones (see below) emplaced throughout the MMR. Thus, the spatial and temporal resolution of our tracking data changed through time and thus affected our choice of analyses.

Naturally occurring adult pallid sturgeon (> 600 mm fork length; N=88 total) were collected from throughout the MMR for telemetry using a combination of trawling, gillnets, and trotlines during fall 2002 through fall 2005. Sonic transmitters were surgically inserted in these fish following Sheehan et al. (2002). If possible, sex and maturational stage were determined during surgery by examining gonads (Colombo et al. 2007). Fish collected during 2002 through 2004 were implanted with ultrasonic Sonotronics transmitters (Sonotronics Company,Tucson, Arizona); thereafter, Vemco coded transmitters (Amirix Systems Incorporated, Halifax, Nova Scotia) were used. Battery life ranged from 177 d to 1,139 d, depending on transmitter size and power.

A Sonotronics receiver USR-91 and boat-mounted, directional hydrophone arrays (two or three hydrophones per array) were used to detect all transmitter ultrasonic pulses and to determine serial numbers of Sonotronics transmitters. Vemco VR60 or VR100 receivers and omnidirectional hydrophones were used to decode Vemco transmitters after fish were initially located with the Sonotronics array. Tracking was conducted by idling the boat moving downstream (approximately 9-11 km/h). After initial contact, each fish was located using triangulation with the directional hydrophone. Depth, surface water temperature, and substrate (i.e., gravel, sand, or silt) using soundings or benthic grabs were recorded at each location.

The number of fish implanted with transmitters varied among years, although transmitter life increased through time (number of tagged fish per year: 2002 = 4; 2003 = 19; 2004 = 44; 2005 = 21). During high discharge (i.e., spring), most tracking was conducted using a boat on each side of the river moving in tandem downstream. During each year, we attempted to track the entire 322-km reach bi-weekly and increase effort to sample the respective reaches weekly during spring pre-spawn, spawn and post-spawn periods. A more intensive, 24-h tracking effort was conducted on 27 April, 2005, in which we followed three pallid sturgeon hourly in the COR tailwater below the lowhead at Lock and Dam 27.

Because our research during 2002-2003 revealed that pallid sturgeon frequently move many kilometers during pre- and post-spawn periods, we deployed Vemco VR2 stationary, data-logging hydrophone receivers in the river during spring 2004 (Figure 1). Receivers were mounted on navigation buoys fitted with brackets and painted yellow for identification as research equipment. Additional VR2s were deployed in spring 2005, with several being placed in tandem to promote better coverage of the river and increase the likelihood of detecting study fish. VR2s were also deployed in several MMR tributaries and the confluence of the Missouri River to detect fish leaving the study area (Figure 1). On average, 20 operational VR2s were present in the MMR during 2004 through 2005.

Habitat.

During the manual tracking effort during 2002-2005, we used location data in two ways. We assessed how pallid sturgeon used major structural features by comparing location within areas that they occupied to the actual area (in m^2) of these features in the MMR. For some habitat features that comprised a small area of the river but might have important life history roles during spawning in spring (e.g., gravel bars), we also conducted an analysis of distance (m) to each structure during April through May of each year.

For our aerial analysis of habitat preference, all pallid sturgeon relocations were overlaid on a detailed MMR Geographic Information System (GIS) Digital Orthophoto Quadrangle (DOQ) map that was used to define several habitat features (Sheehan et al. 2002) and quantify their areas (m^2). Referred to as the Cobb classification (US Army Corps of Engineers 1999), the data set originally included habitats classified as main channel (MC), channel border open (CBO), wing dike (WD), between wing dike (BWD); channel border dikes (CBD), and island tips (IT) (Figure 2). The original Cobb classifications were based on a combination of depth contours and locations in reference to the thalweg and/or wing dikes. A shortcoming of this classification was the characterization of wing dike habitats, which were delineated by constructing polygons directly around the physical structure of each wing dike. Although it accurately depicted size and shape of each wing dike, unique habitats created by the structures including high velocity areas immediately upriver and scour areas immediately downriver were not included. To remedy this problem, we modified the original Cobb habitat features to better describe habitat availability in the MMR. Modifications were made using depth-contour data within the original data set as well as a detailed bathymetry map from the US Army Corps of Engineers. Three specific wing dike habitats (Figure 2) were created to account for the unique hydrodynamics produced: 1) areas upriver of wing dikes, including the wing dike tips (75 meter maximum upstream radius), were classified as wing dike tips upstream (WTU); 2) areas downriver of wing dikes associated with scouring were defined as wing dike scours (WDS); and 3) areas immediately downriver of WDS bordering the main channel were defined as wing dike scours downstream (WDSD). The wing dike structures (i.e., rip rap) included in the original Cobb classification were differentiated from the new habitats and retained as WD. All remaining habitats were left unchanged from the original Cobb DOQ (Sheehan et al. 2002.). Total area of each habitat type in the modified feature data set was calculated using Arc Toolbox and Hawth's Analysis Tools (Version 3.17; (Beyer 2004)) for ESRI ArcMap 9.2 (ESRI 2007).

For quantifying the distance of each fish to habitat features during spring spawning of 2002 through 2005, we gathered feature classes from the St. Louis District Army Corps of Engineers GIS database. Features used were dike centerlines (now treated as a linear feature rather than areas), island boundaries, and gravel bar boundaries. Dike centerlines were digitized from as-built design files, 0.305 m x 0.305 m 2006 DOQs, historical records, hydrographic surveys and field observations. Visible gravel substrates were digitized using a Trimble Beacon-on-a-Belt (BoB™) GPS receiver and GeoExplorer 3 system during two helicopter flights on September 16 and 30, 2002. Flights covered the entire MMR and were flown at about 30 m above the river surface. All habitat feature classes were converted to 10 x 10 m pixel rasters. We used Spatial Analyst (ArcGIS 9.2, ESRI® 2007) to calculate the straight line distance between each pixel's midpoint and the midpoint of the nearest habitat. These files were then masked using a water course dataset to remove data beyond the water line. To extract habitat features for each location, we used Hawths Analysis Tools (Beyer 2004) to create and populate a new data column for each habitat variable within the sturgeon location attribute table by entering the pixel value (distance) that intersected the sturgeon location.

Analysis.

Selection of habitat areas during 2002 through 2005 quantified by the modified Cobb index was tested using fish as the primary sampling unit with statistical inferences based on individual fish as replicates (Manley et al. 1993; Otis and White 1999; Rogers and White 2007). Log-likelihood ratio chi-square tests were used to determine whether study fish were selecting habitats differently. A second log-likelihood chi-square test was used to determine whether study fish selected for specific habitats (Manley et al. 1993; DeGrandchamp et al. 2008). The difference between the two chi-squares was used to determine whether, on average, pallid sturgeon were using habitats in proportion to their availability. Due to their small areas relative to the remaining habitat types, it was necessary to combine individual wing dike habitats (WTU, WD, WDS, WDSD) into one (WD) to statistically compare overall habitat selection by season. Seasons were defined by water temperature and annual period as follows: 0-10°C = winter; 10-20°C following winter = spring; > 20°C = summer; 10-20°C following summer = fall. The four individual wing dike habitats were then analyzed separately to provide further insight into habitat preferences. Specific habitat selectivity by season was compared and tested where selectivity index values (SI) greater than 1.0 indicated selectivity and values less than 1.0 indicated selection against that habitat (Manley et al. 1993). Bonferroni confidence intervals were constructed around each habitat type to ensure probability of all intervals containing their true parameter values was 1-alpha (Thomas and Taylor 1990). Overlap of confidence intervals among habitat types would be indicative of insignificance for selectivity. SAS Institute software was used in conjunction with internet accessible software (Littel et al. 1996; FishTel at www.wildlife.state.co.us/aquatic) for habitat selectivity and Bonferroni confidence intervals. Bonferroni multiple comparison tests were used to demonstrate significance within each of the independent variables ($\alpha = 0.10$).

For distance analyses of pallid sturgeon location data collected during spring 2002 through 2005, we used two-way factorial ANOVAs [factors: location (actual versus random) and month (March, April, May)] to test for differences in each habitat association during March, April and May with Tukey pairwise comparisons for the month effect within significant models (Zar 1999). Data were square root transformed when residuals were nonlinear and variances deviated significantly from normal. In the case of distance from gravel bars, the variance deviated from normality after transformation. We also analyzed these data using a Kruskal-Wallis test, with multiple comparisons for significant tests (Zar 1999). To determine whether distributions followed a random pattern, we generated random points in the MMR using Hawths Analysis Tools and calculated the habitat values associated with these points.

The number of random points that were generated equaled the number of telemetry locations with a value for each habitat feature.

We defined pallid sturgeon movement during 2002 through 2005 as minimum displacement in terms of kilometers per day, which is the difference in river kilometers between consecutive locations divided by the number of days between locations. Both manual and stationary logging data were combined to determine whether movement varied by season and year. Only one VR2-generated detection for each study fish per day per VR2 was used for analyses. A mixed model analysis of variance was employed (Rogers and Bergersen 1995; Rogers and Bergersen 1996; Rogers 1998; Rogers and White 2007). Distance was converted to log-transformed meters per day and was the dependent variable; season and year (fixed effects) were independent variables. Random effects were the interactions of fish by season and fish by year. Additional independent variables including water level, weekly changes in water level, and water discharge were tested for their influence on movement. Water level and discharge observations were obtained from a USGS gaging station at St. Louis, MO (RKM 290). Water level and discharge were categorized as low (0 - 2 m; 0 - 4,950 cms), medium (> 2 - 4 m.; > 4,950 - 8,100 cms), and high (> 4 m; >8,100 cms), respectively. To isolate significant effects, a multiple regression framework was used which coupled mixed model analysis of variance with a random coefficients model (Littell et al. 1996) using Akaikes's Information Criterion (AIC) model selection (Burnham and Anderson 1998).

Results

A total of 8,629 km of the MMR was manually tracked by boat during fall 2002 through summer 2005 with nearly half of the effort (4,019 km) conducted in 2005. Manual tracking resulted in 612 locations for 84 pallid sturgeon (95% detection rate); fish relocations by boat ranged from 1 to 27. Stationary receivers (VR2s) logged 29,074 detections from 35 individual fish. Consequently, VR2s accounted for 138 (29%) of all recorded locations after being on-line starting in 2004. The maximum number of detections per study fish increased to 63 when VR2 detections and manual locations were combined. We were able to determine the sex of 46 sturgeon, with 13 being female. Of these fish, only 1 female and 2 males were apparently ready to spawn by spring of the year of capture.

Pallid sturgeon were typically located with manual tracking at water depths of 6-12 m (60%), and were rarely located at depths < 3 m (14%; Table 1). Fish were most often located on sand (48%), sand/gravel (26%), or rock substrate (24%), while mud/silt substrate was less frequented (2%). They were located on sand substrate more during post-spawn periods (66%), with sand/gravel (19%) and rock substrate (11%) use decreasing. During spring, when water temperatures were within purported spawning temperatures (17.0 - 21°C), fish were most often located on sand (44%), sand/gravel (30%) or rock substrate (27%).

With the modified-Cobb, area-use analysis, pallid sturgeon were located at least once in seven of the 10 habitats (Figure 3); they were not located off island tips (IT), in tributary mouths (TM), or areas associated with main structures of wing dikes (WD). Selectivity analyses of habitat areas indicated that individual fish used Cobb-classified habitats differently ($X^2 = 537.2$; $p < 0.0001$) and selected for habitat types ($X^2 = 970.3$; $p < 0.0001$). Although WTU, WDS, and WDSD habitats constituted only 7.1% of available habitats, study fish were located in those areas 47% of the time across years (Figure 3). Fish selected the combined four wing dike habitats above their proportional availability (SI = 4.6). When analyzing only among the individual wing dike habitats, except for the aforementioned dike structure area (WD; no locations), there were no selectivity differences among WTU, WDS, and WDSD habitats ($X^2 = 56.5$; $p = 0.31$). Selectivity index values were less than 1.0 for all remaining habitats, and none of these habitats were selected for more than another. Pallid sturgeon were located in MC and CBO habitats 44% of the time, and these open river habitats became increasingly important during low-flow summer periods. During winter, study fish were most often located in WDS (26%), MC

(23%), and WDSD (18%) habitats. Use of WDT habitat (9%) was lowest during winter periods. Fish were rarely located in SC and BWD habitats, with the majority of locations occurring during spring.

Distances of fish to potentially important structures during spring often were closer than expected based on random expectations. Distance to wing dikes depended on location (ANOVA: $F_{1,465}$=28.7, p<0.001) and month (ANOVA: $F_{2,465}$=12.0, p<0.001), with a significant interaction (ANOVA: $F_{2,465}$=9.9, p<0.001) occurring between the two (Figure 4). Pairwise comparisons within month showed a difference between March and the other two months (Tukeys, p<0.05; Figure 4). Distance to wing dikes was closer (about 100m) than random in March (Figure 4). Because the distribution of wing dike means were non-normal and may have affected ANOVA results, we also conducted a Kruskal Wallis test that confirmed the monthly differences (p< 0.05; Figure 4). Distance to islands depended on location (ANOVA: $F_{1,465}$=42.8, p<0.001) and month (ANOVA: $F_{2,465}$=7.0, p< 0.01), with a significant interaction occurring between the two (ANOVA: $F_{2,465}$=10.0, p<0.001) (Figure 4). Multiple pairwise comparisons among actual locations among months showed that pallid sturgeon moved within about 1,000 m of islands by late spring (Tukeys, p<0.05; Figure 4), although these were not different than expected randomly. Patterns of movement to gravel bars appeared to be similar to those for islands (location: $F_{1,465}$=41.0, p<0.001; month: $F_{1,465}$=4.8, p<0.01; interaction: $F_{1,465}$=5.0, p<0.01; Figure 4), with significant differences occurring among all months (Tukeys, p<0.05; Figure 4). Pallid sturgeon were typically < 500 m from gravel bars by May and this was much closer than that of random expectation (Figure 4).

Across all years, total movement of pallid sturgeon ranged from none detected (n = 4 fish) to > 300 km. Eleven study fish moved more than 100 km. Movement extremes ranged from 16.9 km/d upriver to 73.4 km/d downriver (Table 2), and the largest range detected within the MMR by any individual sturgeon was 292 km. Seven fish left the MMR: five migrated upriver into the Missouri River during spring 2005; two migrated downriver to the lower Mississippi River during summer 2005. Season was unrelated to total distance moved (ANOVA, p = 0.17). However, incorporating direction into movement revealed movement patterns for all study fish combined. When daily movements were averaged, with upriver movements being positive and downriver movements negative, study fish moved most in the summer (-1.5 km/d) and spring (0.60 km/d), and least in the fall (0.07 km/d) and winter (-0.05 km/d) (ANOVA, p<0.05).

Based on AIC model selection criterion, movement was best predicted by a combination of water levels and temperatures which were positively related to movement with slopes of 0.09 (SE = 0.02) and 0.04 (SE = 0.02). On average, study fish moved upstream each year during April when water temperatures reached 12 - 14°C. Similarly, water level significance is underscored by its presence in the top four AIC models, as evident by examining movement patterns during pre-spawn periods in 2004 and 2005. Our intensive tracking in 2005 provided an intensive case history of behavior. Movement rates and patterns in 2005 varied among individuals but matched our general AIC analysis with environmental cues. During February through March 2005, movement was minimal (Figure 5). Movement increased water levels and temperatures rose during April. The greatest upriver movement occurred over a short period when temperatures rose from 14°C to 18°C in early April (Figure 5). Immediately following suspected spawning, fish moved downstream and then held station until late May (Figure 5). On 22 May through 25 May, fish moved downstream.

Our hourly tracking below the Chain of Rocks (COR) lowhead dam area on 27 April 2005 provided another revealing descriptive study. Two of the six fish moved very similarly. Although several hours apart, the two fish navigated an exact pathway along the Missouri side of the tailwater towards a shallow, cobbled flat below the lowhead dam. Neither fish was located after approaching within 100 m of the dam. Following their disappearance, one individual was not located again, and the other was relocated on 13 June at MMR RKM 305 (below COR lowhead dam) and again on 15 June at RKM 233. Three other study fish displayed similar behavior at COR during April, but following their disappearance from the tailwater, they were relocated upriver of the lowhead dam between 14 and 23 April by a stationary receiver deployed in the Missouri River (12 km upriver of COR dam). One of these fish was monitored returning by the stationary VR2 receiver in the Missouri River and was relocated several times on 27 May moving rapidly downriver toward Chester, Illinois (RKM 177).

Discussion

The MMR is a unique system because it contains a population of naturally reproducing pallid sturgeon by which the habitat needs for recovery may be quantified and perhaps extended to other reaches such as the highly channelized lower Missouri River. Habitat is not only defined by small-scale features that a fish uses during a single time, but also reach-wide characteristics such as habitat features that interact to allow spawning or act to facilitate movement among habitat locations. Our results show that at one spatial (area) and temporal (annual) scale, adult pallid sturgeon appear to be using structures (i.e., dikes) that provide unique flow characteristics that may facilitate growth or survival. By approaching the data at another spatial (distance to locations) and temporal (monthly) scale, we found that pallid sturgeon move from one habitat type to likely carry out spawning in another.

Habitat use.

During most of the year, MMR pallid sturgeon prefer wing dike habitats. With little historic habitat (e.g., in-channel islands, gravel and sand bars, shallow shoals) remaining in the channelized MMR, wing dike habitats are likely used by pallid sturgeon and other native fishes because of the increased habitat complexity they create (Barko et al. 2004). For example, as water approaches upstream of wing dikes (WTU), a transition is created from sandy-bottomed, slower moving waters to areas with predominately gravel or rock substrate and increased flow. As flow is directed from wing dikes and towards the main channel, scour holes are created (WDS), and substrate is remobilized and deposited behind wing dikes; often creating steeply sloped sand bars that likely harbor many prey items.

Additionally, these scouring areas behind wing dikes create large eddies which may hold drifting invertebrates and provide current breaks for small-bodied fishes. Downstream of WDS habitats, a seam is created between slow and fast water (WDSD), which likely transports and settles out prey items. In general, wing dikes deflecting water flow often create the largest scour holes and sand deposits which are habitat characteristics apparently sought by adult pallid sturgeon. This is supported by the depths that pallid sturgeon typically occur, as tracked fish were found 80% of the time in depths greater than 6 m, with 20% of these relocations occurring between depths of 12 and 18 m.

Telemetry-based habitat use of pallid sturgeon in the MMR has been quantified in other systems including the MMR (Hurley et al. 2004). Our habitat use results differed from Hurley et al. 2004 in one fundamental way – we did not find a strong affinity for island habitat while these investigators did. A drawback to past telemetry efforts on MMR pallid sturgeon (Hurley et al. 2004) was that the majority of study fish were captured by commercial fishers between RKM 177 - 225. The majority of tracking effort was therefore exerted in this isolated area, which has a suite of macrohabitats that does not reflect the entire MMR. Thus, the possibility for the investigators to overestimate use of islands and perhaps other habitat types was greater than in our effort. Pallid sturgeon in the current study were captured at various dates, locations, and habitats throughout the MMR from 2002 to 2005, thereby reducing the bias of capture site on relocation data. With enhanced telemetry equipment, an improved ability to classify and quantify habitat, and increasing the number of study fish and relocations through homogenous tracking effort, we were better able to quantify MMR pallid sturgeon habitat use.

Substrate is likely an important variable influencing the presence or absence of pallid sturgeon because it influences food availability and spawning habitat suitability. Throughout all seasons, study fish were most often located on sand substrate (48%) and least often on mud or silt substrates (2%). There was no seasonal shift in substrate type; although sand substrate was used more during summer (66%) than other seasons. This may be in response to seasonal changes in foraging opportunities.

Emerging invertebrates may be abundant in sand substrate during late spring and summer (Corkum et al. 2006), thereby requiring little energy expenditure by pallid sturgeon. Hoover et al. (2007) found that MMR pallid sturgeon diet depended on season, as invertebrates composed a much higher percentage of total food volume during spring (30.5%) compared to winter (4.4%).

When we focused our analysis on the distance to habitats during spring, we found a decline in the use of dikes and a strong association with gravel substrates during May spawning, which supports the assumption that this species spawns in shallow, rocky areas as do other sturgeon (McCabe and Tracy 1994). Although the pallids moved within 1 km of islands during spring as spawning approached, we are unsure of the reason for this pattern. Large island areas may be more abundant in proximity to gravel and are likely negatively correlated with dikes. Conversely, island secondary channels may allow rapid access to refuge if discharge increases rapidly during spring. This is supported by anecdotal evidence. Two tagged pallid females used side channels nearly continuously during the historically high flooding of spring 2008 (R. Brooks unpublished data).

Movement.

In congruence with the spring patterns of habitat use, pallid sturgeon moved most during spring and early summer, and least in fall and winter, similar to counterparts in the Yellowstone and upper Missouri Rivers (Bramblett and White 2001). Again, we presume that increased movement in the MMR during spring and early summer was associated with spawning, even for immature individuals. Several fish exhibited steady upriver migrations during spring followed by rapid downriver movements in early summer, similar to white sturgeon in the Sacramento River, California (Schaffter 1997) and shovelnose sturgeon in the upper Mississippi River (Hurley et al. 1987). Movement patterns differed among pallid sturgeon in the MMR. In some cases, extended movement occurred before and after the spawning period; in others, little or no movement was observed during the same periods. A few fish also moved downriver during pre-spawn periods rather than upriver. Additionally, migratory movements of several sturgeon may have been missed because they likely migrated into the Missouri River and were not relocated post-spawn. The high incidence of movement of both spawning condition and immature fish during the spawning period is not uncommon in many species and may be providing “practice runs” whereby individuals learn where successful spawning occurs (Robichaud and Rose 2004).

Our intensive sampling during spring 2005 improved resolution about pallid sturgeon movement during its spawning season. Sturgeon spawning behavior is typically characterized by pre-spawn, upriver migrations, a period of spawning activity, and then culminates with downriver, post-spawn migrations (Paragamian and Kruse 2002). Water temperature has been identified as an important variable to cue the onset of spawning behavior for sturgeon populations (Parsley et al. 1993, McCabe and Tracy 1994, Paragamian and Wakkinen 2002). Combining our movement data with reported spawning temperature ranges for pallid sturgeon, we postulate that the spring 2005 spawning period was May 10 - 27, when water temperatures ranged from approximately 17°C to 21°C. Though larval pallid sturgeon were not captured during spring 2005, our proposed spawning period matches well with a previous larval sample collected near Grand Tower, IL (RM 78) on 31 May 2000 (Hrabik et al. 2007) and the timing of other young sturgeon appearing in the MMR during 2006 and 2007 (Tripp 2007).

Water temperatures are not likely the only factors influencing MMR pallid sturgeon spawning behavior. Several authors (McCabe and Tracy 1994; Auer and Baker 2002; Paragamian and Wakkinen 2002) postulated that increased water levels and discharges prompt spawning events in sturgeon populations by exposing spawning substrate through the remobilization of sediment (Paragamian and Wakkinen 2002) or by assuring proper dispersal of future larvae. In fact, some populations spawn at highest daily flows (McCabe and Tracy 1994).

Direction.

Although our approach has improved our understanding of the basic behavior of pallid sturgeon in the MMR, the number of relocations for individual study fish varied and our information about spawning condition fish, particularly gravid females, was limited. The majority of females observed were not in spawning condition, while a higher proportion of males may have been reproductively viable. This was expected because female pallid sturgeon may spawn every 3 to 10 years, whereas males reproduce every 2 to 3 years (Keenlyne and Jenkins 1993). Limited tag life prohibited us from observing migratory behavior of individuals in consecutive years, and it is possible that MMR pallid sturgeon make annual spring migrations, regardless of reproductive condition. Missouri River pallid sturgeon have been found to make spring migrations to specific areas of the Yellowstone River in consecutive years (Bramblett and White, 2001); thus, pallid sturgeon may exhibit annual homing fidelity to previous spawning areas, similar to other sturgeon populations (Heise et al. 2004).

In summary, we have found that habitat needs and movement are linked and both must be facilitated to enhance the recovery of pallid sturgeon. Although wing dikes provide preferred habitat for adults, they certainly do not represent the habitat in which this species evolved. We must better understand the contribution of these habitats to foraging and growth from an energetics perspective to determine how more natural habitats might be built or conserved within the MMR. From the perspective of spawning, our data are beginning to suggest that accessible gravel habitat and perhaps, during some years, proximity to island areas are needed to facilitate adult success. However how these habitat types interact to enhance spawning still must be better understood before habitat improvements may be made in this highly altered system.

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Literature Cited

Auer, N. A.; Baker, E. A., 2002: Duration and drift of larval lake sturgeon in the Sturgeon River, Michigan. J. Appl. Ichthyol. **18,** 557–564.

Bajer, P. G.; Wildhaber, M. L. , 2007: Population viability analysis of Lower Missouri River shovelnose sturgeon with initial application to the pallid sturgeon. J. Appl. Ichthyol. **23,** 457-464.

Barko, V. A.; Herzog, D.P; Hrabik, R.A.; Scheibe, J.S., 2004: Relationship among fish assemblages and main-channel-border physical habitats in the unimpounded upper Mississippi River. Trans. Am. Fish. Soc. **133,** 371-384.

Beyer, H. L. 2004. Hawth's Analysis Tools for ArcGIS. Available at http://www.spatialecology.com/htools

Boreman, J., 1997: Sensitivity of North American sturgeons and paddlefish to fishing mortality. Env. Biol. Fish. **48,** 399-406.

Bramblett, R. G.; White, R.G., 2001: Habitat use and movements of pallid and shovelnose sturgeon in the Yellowstone and Missouri Rivers in Montana and North Dakota. Trans. Am. Fish. Soc. **130,** 1006-1025.

Burnham, K. P.; Anderson, D.R., 1998: Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York, USA.

Carlson, D. M.; Pflieger, W.L.; Trial, L.; Haverland, P.S., 1985: Distribution, biology and hybridization of *Scaphirhynchus albus* and *S. platorhynchus* in the Missouri and Mississippi rivers. Env. Biol. Fish. **14,** 51-59.

Colombo, R.E.; Garvey, J.E.; Wills, P.S., 2007: Gonadal development and sex-specific demographics of the shovelnose sturgeon in the Middle Mississippi River. J. Appl. Ichthyol. **23,** 420-427.

Corkum, L. D.; Ciborowski, J. J.H.; Dolan, D.M., 2006: Timing of *Hexagenia* (Ephemeridae: Ephemeroptera) mayfly swarms. Can. J. Zool. **84,** 1616-1622.

Degrandchamp, K. L.; Garvey, J.E.; Colombo, R.E., 2008: Movement and habitat selection by invasive Asian carps in a large river. Trans. Am. Fish. Soc. **137,** 45-56.

Gardner, W. M., 1995: Yellowstone River paddlefish spawning study. Progress Report on Project No. F-78-R-1. Montana Department of Fish, Wildlife, and Parks, Helena, Montana. 189 pp.

Garvey, J.E.; Heist, E. ; Brooks, R.C; Herzog, D.; Hrabik, R.; Killgore, K.J., 2006: Current Status of the Pallid Sturgeon (*Scaphirhynchus albus*) in the Middle Mississippi River: Habitat, Movement, and Demographics, Final Report. St. Louis District, US Army Corps of Engineers.

Heise, R. J.; Slack, W. T.; Ross, S. T.; Dugo, M. A., 2004: Spawning and associated movement patterns of Gulf Sturgeon in the Pascagoula River drainage, Mississippi. Trans. Am. Fish. Soc. **133,** 221-230.

Hildebrand, L.; McLeod, C.; McKenzie, S., 1999: Status and management of White Sturgeon in the Columbia River in British Columbia, Canada: an overview. J. Appl. Ichthyol. **15,** 164-172.

Hoover, J. J.; George, S.G.; Killgore, K. J., 2007: Diet of shovelnose sturgeon and pallid sturgeon in the free-flowing Mississippi River. J. Appl. Ichthyol. **23,** 494-499.

Hurley, S. T.; Hubert, W. A.; Nickum, J. G. 1987: Habitats and movements of shovelnose sturgeons in the upper Mississippi River. Trans. Am. Fish. Soc. **116,** 655–662.

Hrabik, R. A., Herzog, D. P., Ostendorf, D.E.; Petersen, M. D.; 2007: Larvae provide first evidence of successful reproduction by pallid sturgeon, *Scaphirhynchus albus*, in the Mississippi River. J. Appl. Ichthyol. **23,** 436-443.

Hurley, K. L.; Sheehan, R. J.; Heidinger, R. C.; Wills, P. S.; Clevenstine, B., 2004: Habitat use by middle Mississippi River Pallid Sturgeon. Trans. Am. Fish. Soc. **133,** 1033–1041.

Keenlyne, K.D., 1997: Life history and status of the shovelnose sturgeon, *Scaphirhynchus platorynchus*. Env. Biol. Fish. **48,** 291-298.

Keenlyne, K.D.; Jenkins, L. G., 1993. Age at sexual maturity of the pallid sturgeon. Trans. Am. Fish. Soc. **122,** 393-396.

Killgore, K. J.; Hoover, J. J.; George, S.G.; Lewis, B. R.; Murphy, C. E.; Lancaster, W.E., 2007: Distribution, relative abundance and movements of pallid sturgeon in the free-flowing Mississippi River. J. Appl. Ichthyol. **23,** 476-483.

Kynard, B.; Henyey, E.; Horgan, M., 2002: Ontogenetic behavior, migration, and social behavior of pallid sturgeon, *Scaphirhynchus albus*, and shovelnose sturgeon, *S. platorynchus*, with notes on the adaptive significance of body color. Env. Biol. Fish. **63,** 389-403.

Littell, R. C.; Milliken, G. A.; Stroup, W. W.; Wolfinger, R. D., 1996: SAS System for Mixed Models. SAS Institute, Inc., Cary, North Carolina.

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

McCabe, G. T., Jr.; Tracy, C. A., 1994: Spawning and early life history of white sturgeon, *Acipenser transmontanus*, in the lower Columbia River. Fish. Bull. **92,** 760-772.

Otis, D. L.; White, G. C., 1999: Autocorrelation of location estimates and the analysis of radio tracking data. J. Wildl. Manage. **63,** 1039-1044.

Paragamian, V. L.; Kruse, G.; Wakkinen, G., 2001: Spawning habitat of Kootenai River white sturgeon, post-Libby Dam. North Am. J. Fish. Manage. **21,** 22–33.

Paragamian, V. L.; Wakkinen, V. D., 2002: Temporal distribution of Kootenai River white sturgeon spawning events and the effect of flow and temperature. J. Appl. Ichthyol. **18,** 542–549.

Paragamian, V. L.; Wakkinen, V. D.; Kruse, G., 2002: Spawning locations and movements of Kootenai River white sturgeon. J. Appl. Ichthyol. **18,** 608–616.

Parsley, M. J.; Beckman, L. G.; McCabe, G. T., Jr., 1993: Spawning and rearing habitat use by white sturgeons in the Columbia River downstream from McNary Dam. Trans. Am. Fish. Soc. **122,** 217-227.

Pikitch, E. K.; Doukakis, P.; Lauck, L.; Chakrabarty, P.; Erickson, D. L., 2005: Status, trends and management of sturgeon and paddlefish fisheries. Fish Fish. **6,** 233-265.

Quist, M. C.; Tilma, J. S.; Burlingame, M. N.; Guy C. S., 1999: Overwinter habitat use of shovelnose sturgeon in the Kansas River. Trans. Am. Fish. Soc. **128,** 522–527.

Robichaud, D.; Rose, G.A., 2004: Migratory behaviour and range in Atlantic cod: inference from a century of tagging. Fish Fish. **5,** 185-214.

Rogers, K. B., 1998: Habitat use by largemouth bass and northern pike on the Rocky Mountain Arsenal, Colorado. Doctoral dissertation. Colorado State University, Fort Collins.

Rogers, K. B.; Bergersen, E.P. 1995: Effects of a fall drawdown on movement of adult northern pike and largemouth bass. North Am. J. Fish. Manage. **15,** 596-600.

Rogers, K. B.; White, G. C., 2007: Analysis of movement and habitat use from telemetry data. In: Analysis and interpretation of freshwater fisheries data. C. S. Guy; M. L. Brown (Ed.). American Fisheries Society, Bethesda, Maryland. pp. 625-674.

Rogers, K. B.; Bergersen, E. B., 1996: Application of geographic information systems in fisheries: habitat use by northern pike and largemouth bass. In: Multidimensional approaches to reservoir fisheries management. L. E. Miranda; D. R. DeVries (Ed.). American Fisheries Society Symposium 16, Bethesda, Maryland. pp. 315-323.

Schaffter, R.G., 1997: White sturgeon spawning migrations and location of spawning habitat in the Sacramento River, California. Calif. Fish Game **83,** 1-20.

Sheehan, R. J., R. C. Heidinger, P. S. Wills, M. N. Jackson, R. Colombo, and A. Miller. 2002. Middle Mississippi River Pallid Sturgeon habitat use project. Southern Illinois University at Carbondale. Year 6, Annual Progress Report. Carbondale, Illinois.

Sparks, R. E.; A. Spink, 1998: Disturbance, succession and ecosystem processes in rivers and estuaries: Effects of extreme hydrologic events. Regul. Rivers: Res. Manage. **14,** 155-159.

Sulak, K.J.; J. P Clugston, 1998: Early life history stages of Gulf sturgeon in the Suwannee River, Florida. Trans. Am. Fish. Soc. **127,** 758-771.

Thomas, D. L.; Taylor, E. J., 1990: Study designs and tests for comparing resource use and availability. J. Wildl. Manage. **54,** 322-330.

Tripp, S.J., 2007: Understanding how harvest influences the life history and demographics of shovelnose sturgeon in the Middle Mississippi River. MS Thesis, Southern Illinois University, Carbondale, IL.

Zar, J.H., 1999: Biostatistical analysis, Fourth Edition. Prentice Hall, New Jersey.

Table 1. Middle Mississippi River water depth ranges and number of pallid sturgeon contacts within each range. Pallids were located between Cairo, Illinois (river mile 0) and St. Louis, Missouri (river kilometer 322).

Depth (m)	Contacts	Percent	Cumulative frequency	Cumulative percent
0-3	67	14.05	67	14.05
3-6	25	5.24	92	19.29
6-9	129	27.04	221	46.33
9-12	157	32.91	378	79.25
12-15	66	13.84	444	93.08
15-18	27	5.66	471	98.74
>18	6	1.26	477	100

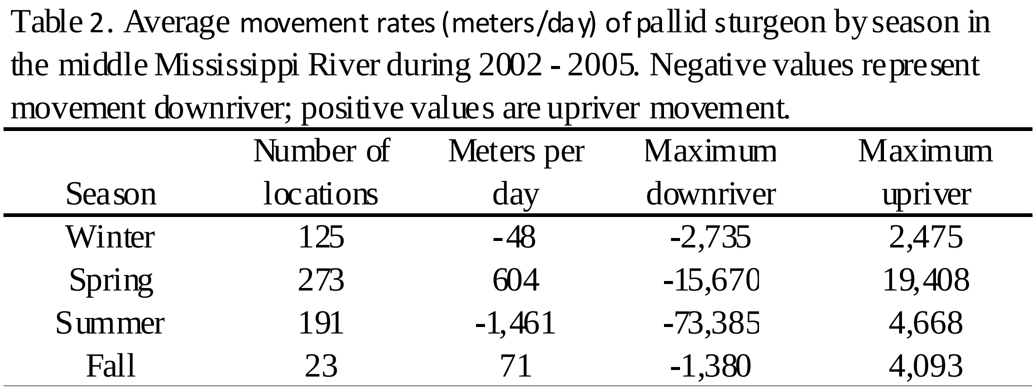

Table 2. Average movement rates (meters/day) of pallid sturgeon by season in the middle Mississippi River during 2002 - 2005. Negative values represent movement downriver; positive values are upriver movement.

Season	Number of locations	Meters per day	Maximum downriver	Maximum upriver
Winter	125	-48	-2,735	2,475
Spring	273	604	-15,670	19,408
Summer	191	-1,461	-73,385	4,668
Fall	23	71	-1,380	4,093

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Figure 1. The Middle Mississippi River study area from Cairo, Illinois (RKM 0) to the Missouri River located above the Chain of Rocks (COR) lowhead dam (RKM 306). Light circles on the river indicate areas where stationary receivers were deployed during 2004 and 2005.

Figure 2. Images of the Cobb classification for the middle Mississippi River before and after the addition of specific wing dike shape files. Acronyms represent the habitat types as follow: MC = Main channel; BWD = Between wing dike; CBD = Channel border dike; CDO = Channel border open; WD = Wing dike; WTU = Wing dike tip upstream; WDS = wing dike scour; WDSD = wing dike scour downstream. Island tip and tributary mouth habitat are not illustrated.

Figure 3. Percent of habitat available in the Middle Mississippi River versus the percent of that pallid sturgeon were located in those habitats during for each season during 2002 - 2005. Habitat availability represented with blue bars. Acronyms represent the following: BWD: between wing dikes (13.8%); CBO: channel border open (25.9%); MC: main channel (40.0%); SC: side channel (9.9%); WDSD: scour area below wing dike (2.1%); WDS: scour area at tip of wing dike (2.8%); WTU: wing tip up (2.2%); WD: wing dike structure (3.0%); TM: tributary mouth (0.1%); IT: island tip (0.3%).

Figure 4. Comparison of the mean (+ SE) depth (m) and distance (m) from various river features for Pallid Sturgeon telemetry locations collected from 2002 – 2006 and randomly generated locations. Letters associated with telemetry locations denote significant differences between the telemetry location habitat associations for months with different letters.

Figure 5. Average weekly movements of pallid sturgeon by year in the Middle Mississippi River during 2005 with river stage and water temperature.

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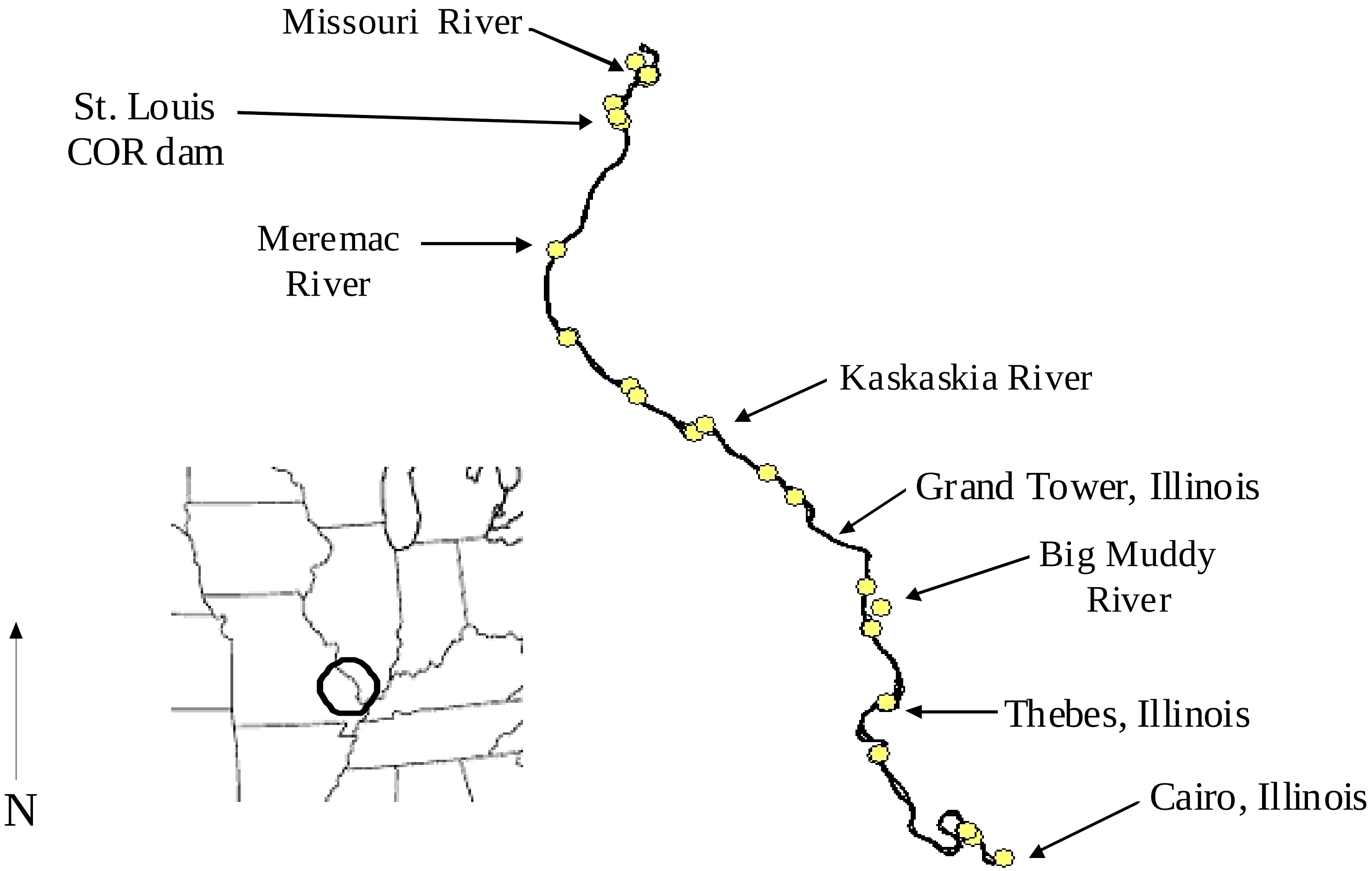

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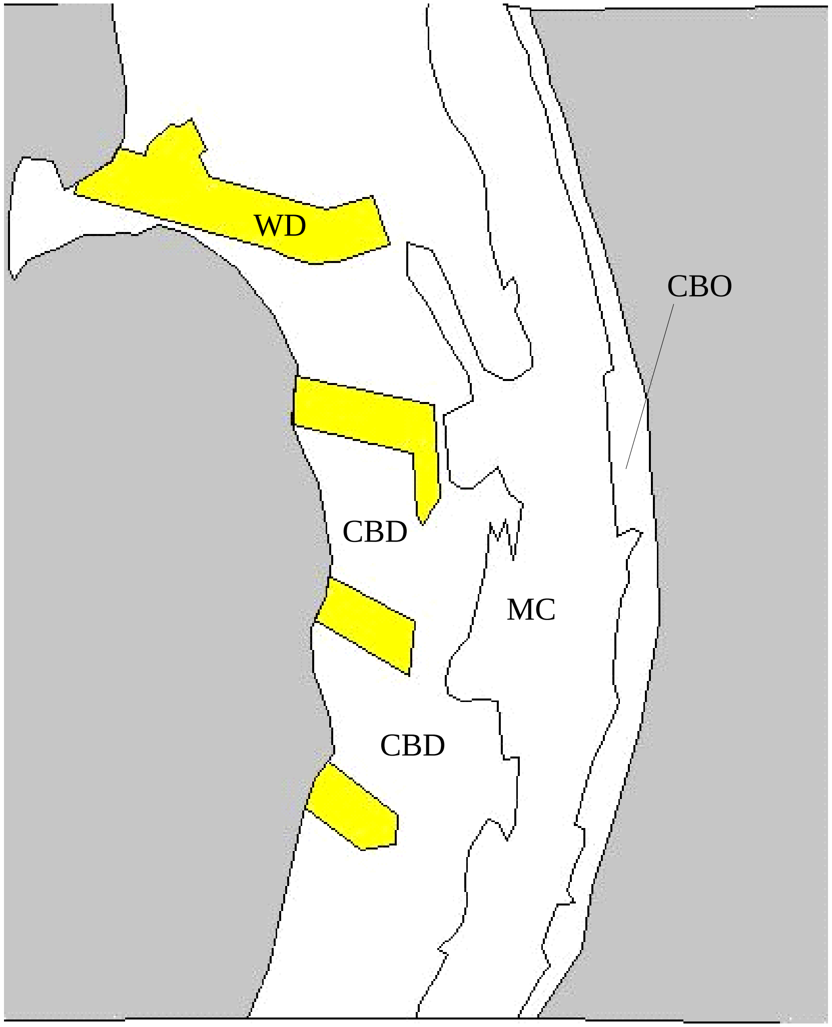
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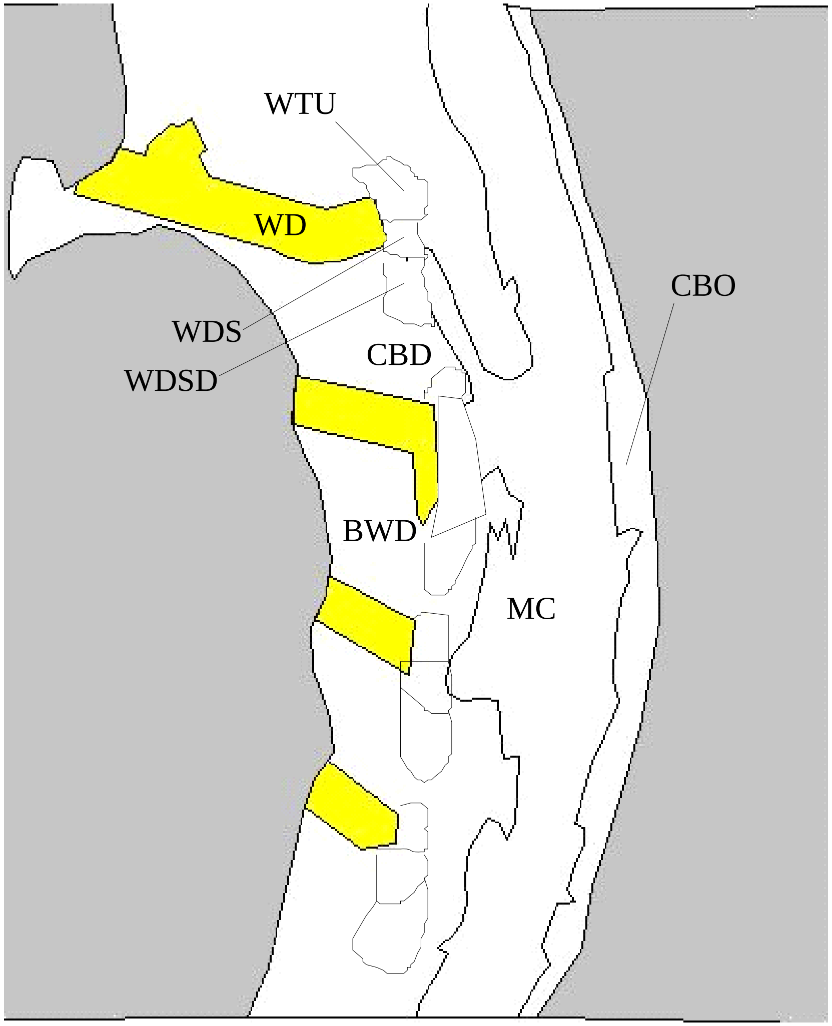
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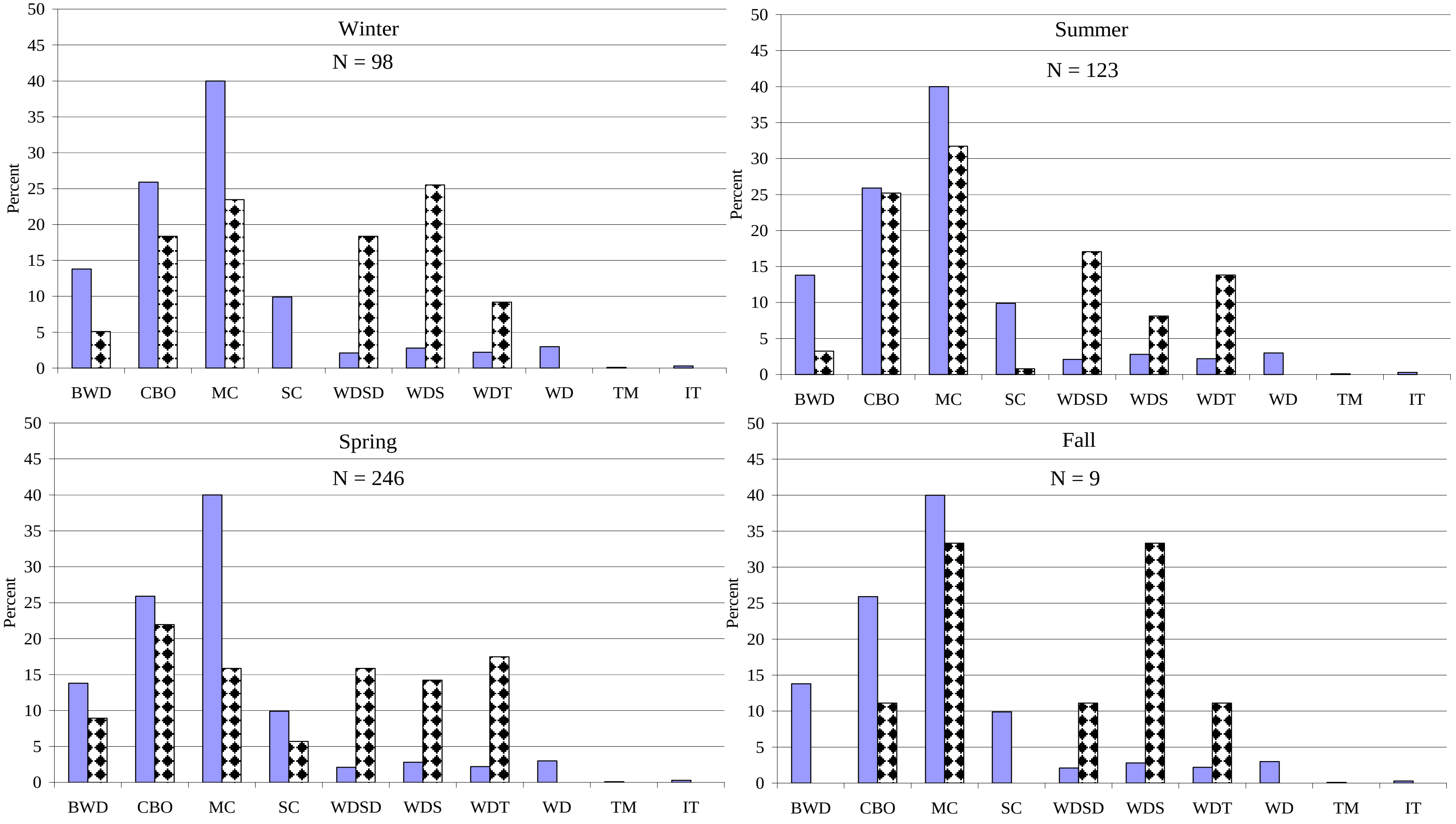
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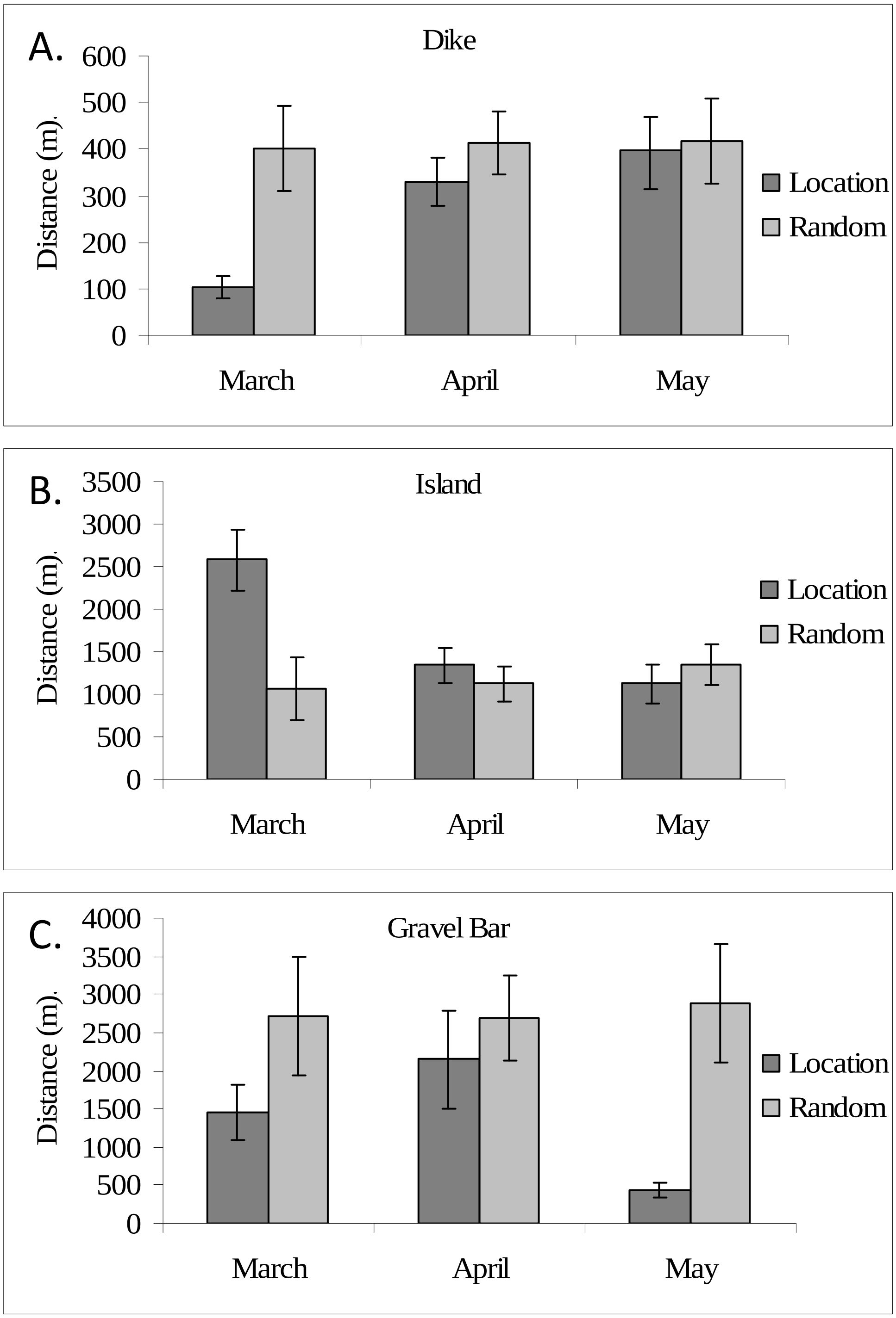
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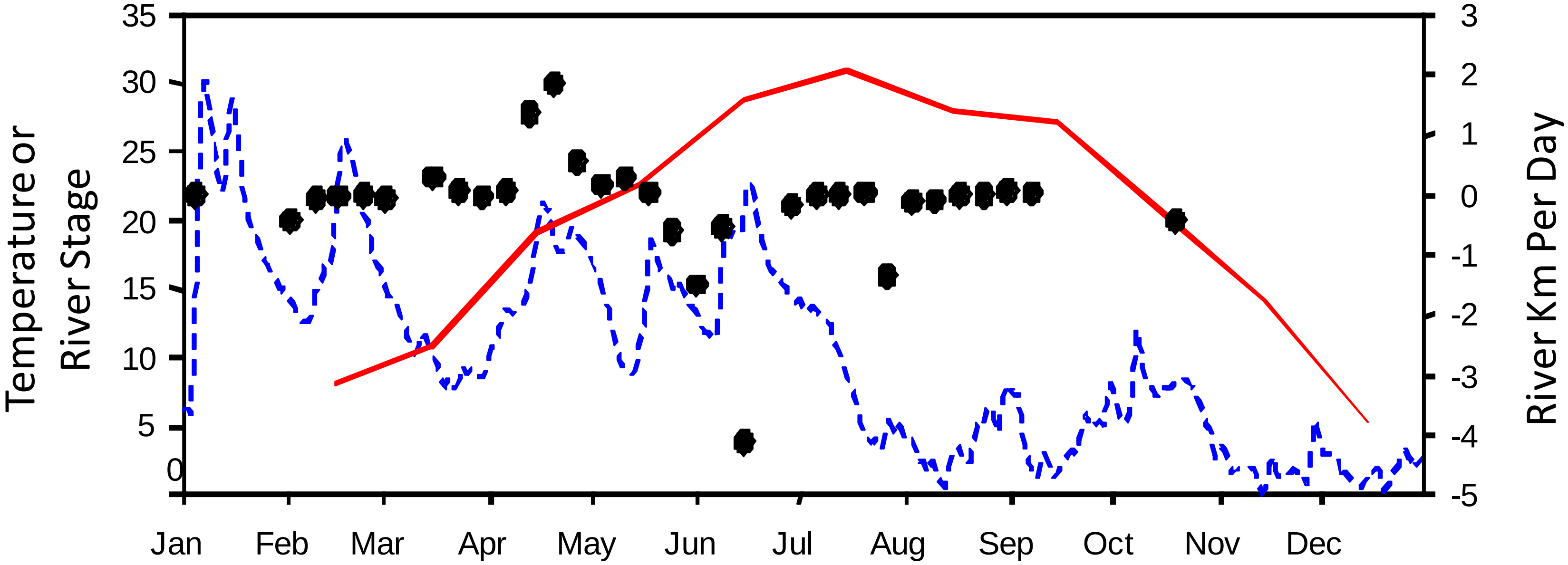
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Pallid Sturgeon Movement and Habitat Selection in the Middle Mississippi River
2003 - 2005

Brian Koch, Ronald Brooks, James Garvey, Dave Herzog, and Bob Hrabik

Introduction

The lack of biological information on middle Mississippi River (MMR) pallid sturgeon, both pre and post habitat modification, continues to limit our knowledge on the habitat requirements of this organism throughout its life cycle. The MMR has been extensively modified through the construction of levees and navigation aid structures, which has consequently reduced the diversity and abundance of historical habitats available to Pallid Sturgeon. The reduction of sinuous, free-flowing channels, as well as functional side channels, islands, and sandbars, may limit spawning and rearing habitat of MMR Pallid Sturgeon. Current habitat availability may differ from historic times, but is likely amenable for inhabitation by Pallid Sturgeon. Through telemetry, information on present-day habitat use and selection may be collected and utilized to facilitate the recovery and establishment of this species in the MMR.

Past telemetry observations by Southern Illinois University, Carbondale, Illinois (SIUC) have provided insight into the habitat preferences of MMR Pallid Sturgeon (Hurley et al, 2004). From 1995 to 2001, 29 Pallid Sturgeon were tagged and released in the MMR. Approximately 4,250 miles of tracking effort was exerted over this period, with the greater part of effort being expended between river miles 81 and 142. The effort resulted in 195 locations. The majority of fish were relocated in main channel habitat, followed by main channel border and between wing dike habitats. Analysis with Strauss's selectivity index, which takes into account the availability of each habitat type, found Pallid Sturgeon to display a positive selection for main channel borders, downriver island tips, between wing dikes, and wing dike tip habitats. A negative selection was found for the main channel, downriver wing dike, and upriver wing dike habitat.

Though previous observations have broadened our knowledge of Pallid Sturgeon habitat use in the MMR, there were several limitations of past research that were improved upon during this study. Specifically, the relatively low sample size and number of relocations limited the analyses of data, and without the aid of bathymetry charts and DOQ maps of the MMR, habitat availability data was derived from measurements taken at twenty randomly selected one-mile stretches. In addition, only 19 of 195 observations were recorded during spring; habitat use and movement throughout the spawning period continues to be poorly understood. By utilizing advances in telemetry equipment, improving the classification and quantification of available habitat, and acquiring a higher number of study fish and relocations for a robust analysis of data, our knowledge of Pallid Sturgeon habitat use in the MMR may be greatly enhanced through telemetry. Furthermore, by placing a concerted, equally distributed tracking effort throughout the spring and early summer, habitat use and movement throughout the spawning season may be characterized as well, which would greatly benefit recovery efforts.

Methods

Specifications and Techniques

From fall 2002 through spring 2005, a total of 87 Pallid Sturgeon were fitted with sonic tags by SIUC and, in 2005, Missouri Long-Term River Monitoring Station at Jackson, Missouri (LTRM) personnel (Table 1). Study fish were captured at various locations throughout the MMR by SIUC, LTRM, and Waterways Experiment Station (WES) personnel, as well as by commercial fishermen, which allowed for a thorough examination of movement and habitat use throughout the MMR. The transmitters (Table 2) were surgically inserted in the sturgeon following the same protocol as described by Sheehan et al. (2002). If possible, sex was determined during surgery using the classification of Colombo (2004). Fish collected from 2002 to 2004 were fitted with Sonotronics transmitters with a uniquely pulsed code at 40 kHz, and fish collected from 2004 to 2005 were fitted with Vemco brand coded transmitters to allow for the integration of permanently stationed receivers to aid in relocations.

Tracking was conducted by SIU from 2002 to 2005 with a Sonotronics USR-91 receiver with a dual hydrophone array. Fish were located by tracking downriver at an approximate speed of 9-11 km/h. After initial contact was made, triangulation techniques were used to pinpoint the fish location. Sonotronics transmitters were manually decoded by their unique stream of numeric pings, and Vemco transmitters were decoded with a Vemco VR60 receiver with directional and omni-directional hydrophones. Location coordinates, depth, and surface water temperature at each relocation were taken by GPS, and macrohabitat was observed and recorded as well (e.g., main channel, wing dike, etc.). Substrate at each relocation was determined by tactile sensation or sediment grab.

Due to specific sampling protocols from 2002 through 2004, and because telemetry was not a high priority during this period, tracking was not collected similarly in all three years. Most of the spring 2003 effort was directed at several pallids tagged in the Modoc, Illinois area with the intention of following the fish throughout the spawning season. In 2004, we attempted cover more of the upper reach of the MMR, but were only able to expend a limited number of days tracking. When possible, volunteers and researchers provided extra tracking effort sporadically throughout the study period until late winter 2004. Tracking effort was increased substantially in 2005 when SIUC and LTRM personnel made a concerted effort to prioritize telemetry data collection and equally survey the entire MMR. LTRM tracked middle Mississippi River miles (RM) 0-80 and all side channels in that reach; SIUC searched from RM 80 through RM 200. The goal was to sample the entire 200-mile reach at least bi-weekly, and when possible, the effort was increased to sample the respective reaches weekly.

Stationary Receivers

Tracking effort in the previous study and in 2003 revealed that Pallid Sturgeon typically move many miles during pre-spawn and spawning periods. As a result of their long-range movements, insufficient personnel were available for the time required to consistently locate transmittered pallids during the spring periods. During spring 2004, VEMCO (LTD) model VR2 stationary receivers were deployed in 11 areas of the river in an attempt to monitor Pallid Sturgeon movement (Table 3). The receivers were mounted in special brackets attached to navigation buoys (Appendix A-33). The buoys were deployed by the ACOE Pathfinder. Noise interference due to water velocity, bedload, and air bubbles in the Mississippi River limited the transmitters' detection ranges. Therefore, in spring 2005, additional VR2s were deployed; several in tandem to promote better coverage of the river and increase likelihood of detecting transmittered Pallids. Additionally, some VR2s were relocated to in an attempt to improve the detection coverage area (Table 3), three were deployed in tributaries of the MMR, and one was positioned approximately 4.8 km up the Missouri River.

Habitat classification

Relocations of Pallid Sturgeon were overlaid onto a detailed DOQ map of the MMR to assess habitat utilization and preference. Referred to as the Cobb classification (Army Corps, 1999 – U.S. Army Corps of Engineers, Rock Island District), this DOQ included habitats such as main channel, main channel border open, channel border dike, wing dike, side channel, and island tip downriver. However, according to field observations and bathymetry maps, wing dike habitats were underestimated by the Cobb classification, resulting in overestimates of main channel, channel border open, and channel border dike habitat. Furthermore, fish recorded in the field as occupying wing dike habitats were often classified under Cobb as inhabiting main channel, channel border open, or channel border dike habitats. To remedy this problem, the Cobb DOQ was modified to better describe habitat availability in the MMR. Modifications to the Cobb index were applied through the observation of depth-contour data within the DOQ, as well as through the ACOE bathymetry map and field observations. Three specific wing dike habitats were created (Figure 1). The area upriver of wing dikes, including the wing dike tips (maximum of 75 meter radius upriver from tip) was classified as WDU. Downriver areas of wing dikes associated with scouring was defined as WDS, and the area immediately downriver of these scours (bordering the main channel) was defined as WDSD. Areas of each habitat type were determined for the modified DOQ using Arc Toolbox and Hawth's Analysis Tools for GIS (Version 3.17). All remaining habitats were left unchanged from the original Cob DOQ.

Sinuosity

Channel sinuosity was characterized with the aid of Army Corps bathymetry maps (1999) and the Cobb DOQ. Based on the establishment of the thalweg, four separate macrohabitats were created and overlaid on the Cobb DOQ. Inside bends were characterized as the concave side of a river bend from the center of the thalweg to the shore, whereas outside bends were located from the center of the thalweg to the convex shore. Channel crossovers were characterized as the entire area where the thalweg crossed from one concave side of the river to the other concave side. Channel chutes were defined as the entire area where the thalweg was centered and lacked sinuosity of greater than one channel width. The total area of each macrohabitat was quantified to assess avoidance or selection by Pallid Sturgeon using methods previously described for habitat types.

Data Analysis

Sturgeon movement was described as minimal displacement in terms of miles per day, which is the difference of river miles between consecutive locations divided by the number of days between locations. Finer determination of movements was not warranted since periods between consecutive locations for a particular fish was rarely less than seven days.

In order to determine if movement varied by season and year, a mixed model analysis of variance was employed using SAS Institute software (Rogers 1998; Rogers and Bergersen 1995; Rogers and Bergersen 1996). Distance was converted to log-transformed meters per day and was the dependent variable in the model; season and year (fixed effects) were the independent variables. Random effects were the interactions of fish by season and fish by year. Seasons were defined by water temperature and annual period as follows: 0-10°C = winter; 10-20°C following winter = spring; over 20°C = summer; 10-20°C following summer = fall. Bonferroni multiple comparison tests were used to demonstrate significance within each of the independent variables ($\alpha = 0.10$).

Additional independent variables including water levels, weekly changes in water levels, and water discharges were tested for their potential to influence movement. Water level and discharge observations were obtained from USGS monitoring at St. Louis, MO (RM 180). To isolate significant effects, a multiple regression framework was used which coupled mixed model analysis of variance with a random coefficients model (Littell et al. 1996) using Akaikes's Information Criterion (AIC) model selection (Burnham and Anderson 1998). Inconsistent tracking effort prior to early spring 2005 is of limited use when attempting to fully describe movement patterns. We, therefore, ran statistical tests on all data combined and with 2005 data alone to ensure that differences in effort did not bias our results.

Habitat selection was determined by counting GPS locations of individual Pallid Sturgeon in specific habitat types previously described. ArcMap 9.1 was used to summarize the number of locations and the areas of each habitat type. Location coordinates were recorded in the field using global positioning systems (GPS) in the Universal Transverse Mercator system (UTM). Positions were projected using NAD1983 in Zone 16 North and overlaid on the previously described modified version of the Cobb index. The statistical tests were repeated to determine effects of river sinuosity on sturgeon positions.

Habitat selectivity was tested using fish as the primary sampling unit with statistical inferences based on individual fish as replicates (Manley et al. 1993; Otis and White 1999). Log-likelihood ratio chi-square tests were used to determine if fish were selecting habitats differently. A second log-likelihood chi-square test was run to determine if some of the sturgeon selected for specific habitats (Manley et al. 1993). Finally, the difference between the two chi-squares was used to describe whether, on average, the sturgeon were using the habitats in proportion to their availability. Specific habitat selectivity was compared and tested where values greater than 1.0 indicate selectivity and values less than 1.0 indicates selecting against that habitat (Manley et al. 1993). Bonferroni confidence intervals were constructed around each habitat type to ensure probability of all intervals containing their true parameter values is 1-alpha (Thomas and Taylor 1990). Overlap of confidence intervals among habitat types also would be indicative of insignificance for selectivity among those types. We used SAS Institute software in conjunction with internet accessible software (FishTel at www.wildlife.state.co.us/aquatic) for habitat selectivity and Bonferonni confidence intervals.

Results

Movement

Eighty-seven Pallid Sturgeon were surgically implanted with sonic transmitters from fall 2002 through spring 2005 (Table 1). A total of 5,362 miles were tracked during the 3-yr period; almost half of that effort (2,497 miles) was conducted in 2005. Without counting observations at release, there were 612 locations recorded for 84 sturgeon.

Three pallids were never located after transmitter implantation**,** and seven fish were known to leave the study area. Five fish left the study area by migrating upriver in the spring of 2005, and two additional fish migrated downriver in summer of 2005. The number of active transmitters ranged from six (late fall, 2002) to 49 (summer, 2004) and the number of relocations per transmitter ranged from 1 to 27 for manual effort throughout the study. Movements of individual pallids with one or more locations following release are illustrated in Appendix A. Stationary receivers (VR2s) recorded a total of 29,074 locations from 35 different sturgeon. Only one VR2-generated location per pallid per day was used for data analyses. Consequently, VR2s accounted for 138 (29%) of all recorded pallid locations from the time of their initial deployment in March 2004. The maximum number of detections per pallid increased to 63 when VR2 detections were included (Table 4).

Pallid Sturgeon generally exhibited a wide range of movement patterns; the extent of which was partially limited by the number of relocations for each fish, time between each location, and the life of the tags used. Movement of individual pallids ranged from none detected (n = 4 fish) to over 300 total km. Eleven pallids moved greater than 100 km during the life of their sonic transmitters. Daily movement extremes ranged from 16.9 km/d (#3984) upriver to 73.4 km/d downriver (#3984; Table 5). There were no statistically significant seasonal effects on distances moved (p=0.1702). However, incorporating direction into movement revealed patterns of movement for all pallids combined. When daily movements were averaged, with upriver movements being positive and downriver movements negative, pallids moved most in the summer (-1.5 km/d) and spring (0.60 km/d), and least in the fall (0.07 km/d) and winter (-0.05 km/d) (Table 6).

Based on the AIC model selection criterion, movement was best predicted by the combination of water levels and temperatures. The two variables were positively related to movement with respective slopes of 0.0941 (SE = 0.0248) and 0.0443 (SE = 0.0198). On average, pallids exhibited sustained periods of upriver movement during April of all three years when water temperatures were 13-14°C (Figures 2 - 4). The importance of water levels to movement is underscored by its presence in the top four AIC models, and the correlation between the two is evident when movements during prespawning periods in 2004 and 2005 are examined (Figures 3 and 4). During April 2003, water levels did not increase from approximately 5 feet above pool for two weeks following initial movements; however, following one week of little movement, pallid activity began to rise in concert with water levels (Figure 2). The levels eventually rose to over 20 feet, and increased movement was observed until water-level conditions made it impossible to track the fish.

Spring 2005

The research in spring 2005 prioritized telemetry in an effort to identify possible spawning locations, habitat use, and movement characteristics during prespawning, spawning, and post-spawning periods. Since effort prior to 2005 was limited and inconsistent, that data is of limited value when attempting to investigate the entire middle Mississippi River to determine movement trends influenced by annual periods or abiotic factors such as water temperatures and/or levels. Therefore, the remaining movement analyses will be reported from 2005 data only.

Pallid Sturgeon movement was limited during February and March 2005. In April, sudden increases in Pallid Sturgeon movement occurred as water levels and temperature increased. The greatest upriver movement occurred in mid-April when water temperatures rose from 14°C to 17.5°C (Figure 4). At that time, at least 10 of the 40 pallids with viable sonic transmitters were followed upriver to, or inhabited, the tailwater behind the Chain of Rocks (COR) lowhead dam (L&D 27) near St. Louis, Missouri. Six of the 10 pallids exhibited similar patterns of behavior in that all of them disappeared completely between 14 and 27 April (Table 7; Figures 5 and 6). Two of the six Pallids had been tracked on 27 April as part of 24-h, intensive tracking effort. Although several hours apart, the two pallids moved in nearly the same pathway along the Missouri side of the tailwater towards a shallow area below the lowhead dam (Figure 7). We were unable to locate either fish after they had approached within 100 m of the dam. Following their disappearance, one fish (#1569) was not relocated again; the other (#3984) was located on 13 June at RM 190.1, just below the COR lowhead dam. This pattern was repeated for three other Pallid Sturgeon; however, following their April disappearance from active tracking effort below the lowhead dam (Figures 5 and 6), these three fish (#3982, #1560, and #1559) were identified by a stationary receiver located in the Missouri River (approximately 4.8 km above the COR lowhead dam) between 14 and 23 April (Table 7). Movement of these fish over the lowhead coincided with increased water temperatures and discharges; likely indicating pre-spawn movement. Four of the six migrants were relocated in the middle Mississippi River 30 - 73 d after their disappearance when water temperatures were above optimal spawning conditions.

Pre-spawn movement was variable for many of the remaining Pallid Sturgeon tracked throughout spring 2005. Four Pallid Sturgeon were located near the COR lowhead throughout the pre-spawn and spawn periods (Figure 8). Only one of the Pallids (#1590) had migrated up to the tailwater; the other three pallids were found within 13 miles of the lowhead dam throughout spring. Pallids located in other areas of the river displayed various pre-spawning movements that ranged from very little movement to many miles in either direction (Appendix A).

Telemetered Pallid Sturgeon exhibited predictable movement patterns immediately following the perceived pre-spawn movements. Between 10 May and 18 May 2005, water temperatures ranged from 18.1°C to 20.7°C, and water levels rose from 9.0 to 18.5 ft. Despite increasing water levels, study fish movement was minimal during this period (Figure 4). However, significant downriver movement was observed in the following weeks signifying post-spawn movement. For instance, on 19 May, Pallid 1594 was found at RM 185 below COR and, on 23 May, it was relocated moving downriver on three separate occasions (RMs 160, 149, 145). Pallid 3982, which migrated over the COR lowhead in mid-April, was detected by a VR2 at RM 194 on 23 May and was relocated several times on 27 May moving rapidly downriver near Chester, Illinois (RM 110). Near RM 160 (Meremac River confluence), Pallids made short, downriver, pre-spawn movements, moved very little for a few weeks, and then made short post-spawn, upriver movements following the perceived spawning period (Figure 9). Timing of the post-spawn, upriver movements of these fish coincided with movements of other fish making downriver migrations. Pallid 1613 resided at RM 83 (above Grand Tower) for approximately three weeks in May, was lost from manual tracking after 25 May, and was later detected by a VR2 at RM 44 on 5 June. Water temperatures associated with the onset of these post-spawn movements fluctuated between 19.3 - 21.2°C. Because movement curtailed at 18°C, and a strong downriver movement occurred as temperatures reached upwards of 21°C, we postulate that Pallid Sturgeon spawning occurred between the two water temperatures during spring 2005. This temperature range persisted from May 10 to May 27.

When all of the data collected during 2005 are combined, it can be seen that particular areas are frequented by Pallid Sturgeon throughout the year (Figure 10). Areas where multiple fish were located during the spawning period include the tailwater at COR (RM 188-190), the Meremac confluence (RM 158-163), the Kaskaskia confluence (RM 115-117; Figure 11), near Grand Tower, IL (RM 79-81; Figure 12), and near Thebes, IL (RM 29-44). Areas where single pallids were located on multiple dates within the spawn period included RM 40, RM 101, RM 133-134, RM 164-165, and RM 170-171.

Habitat use

Throughout the year, Pallid Sturgeon were most often located on a sand substrate (48%) and least often on mud or silt substrates (2%; Table 8). During the period when the sturgeon were expected to have spawned (18 - 21°C), the pallids were most often located on sand substrate (44%). A mixture of sand and gravel substrate and rock substrates were used in similar proportions (26 - 30%) during winter and spring (Table 9). Pallids were most often located on sand during summer and fall (66%). Sixty percent of all locations were in 6 to 12 m of water, and pallids were rarely in water levels less than 3-m deep (2%; Table 10). According to our ADCP surveys, Pallids frequented habitats where water velocities averaged 90 cm/sec (Table 11). The fish appeared to be located in water similar velocity characteristics regardless of the habitat type in which they were located (Appendix B).

Pallids were found in seven of the 11 habitats described in our modified Cobb index. They were never located on island tips (ITU or ITD), the main structure of wing dikes, or tributary mouths. For the seven habitats they in which they were located, individual pallids were using the habitats differently ($X^2 = 537.18$; $p < 0.0001$), but they were selecting for habitat types ($X^2 = 970.31$; $p < 0.0001$; Table 12). When data for all the transmittered pallids is combined, the fish were selecting for specific habitat types ($\Delta X^2 = 433.13$; df = 4; $p < 0.01$), and they selected for habitats associated with wing dikes (SI = 4.589; $p = 0.10$; Table 13). The selectivity indices (SI) were less than 1.0 for the remaining habitats, and, based on the Bonferroni 95% confidence intervals for the remaining six habitats, no habitat was selected for more than another.

There was only one seasonal effect on habitat use; individual pallids did not use the habitats differently during summer periods ($X^2 = 56.5$; df = 52; $p = 0.3106$). As with all of the remaining data, they did select for the habitats used (Table 12) and specifically for wing dike habitats (Table 13).

Habitat selectivity was analyzed for data collected exclusively in 2005 since it is possible that the directed effort and limited range of data collection in the previous two years biased habitat selection ratios. However, the conclusions were the same (Table 14). As with the combined data, the fish selected for wing dike habitat (SI = 4.232; Table 15), and none of the remaining habitats had selection ratios which were significantly different from each other.

In order to determine if pallids were using the four habitats associated with wing dikes similarly, we analyzed data collected only in those habitats which included wing dike structures, scour areas, below the scour areas, and wing dike tips. The results indicated that no pallids were located on or very near the wing dike structures other than on the dike tips, and that there were no differences in selectivity among the three remaining habitat types within wing dikes ($X^2 = 56.5$; df = 52 ; $p = 0.3106$).

Although the selectivity index is informative, its efficiency to assess habitat use is diminished when habitat availabilities are drastically different; as with this study (0.1% - 40.0%; Figure 13). Therefore, we examined simple percentages of observations for habitat types in an attempt to further describe habitat use by Pallid Sturgeons in the MMR. Occurrence percentage charts are given for all years and seasons in Appendix C. Despite the fact that only 7.1% of the habitat available to the sturgeon was habitats created by wing dikes, the fish were found in those areas 47% of the time; which explains the habitat selectivity index results (Figure14). However, 44% of the Pallid locations were in main channel and channel border open habitats. The two habitats were especially important during summer; 57% of the locations occurred in open river habitats (Figure 15). During winter, the pallids were most often located in wing dike scour areas (26%) and the main channel (23%). Spring pallid locations were fairly evenly distributed among habitats associated with wing dikes and the open river. Pallids were located infrequently in side channels and between wing dikes. However, when side channels were used, it was most often during spring (6%).

Water discharge categories were used to determine their affect on habitat use. The Chi-square results were essentially the same for low (≤ 165,000 cfs) and medium (166,000 - 270,000 cfs) water discharges; individual pallids were using the habitats differently, they were selecting for habitat types, and they were selecting for specific habitat types (Table 16). During high water discharges (> 165,000 cfs), individual fish were not using habitats differently, nor were they selecting for the habitats used. However, collectively, the pallids were selecting habitats, and those habitats were associated with wing dikes (SI = 4.589; $p = 0.10$; Table 17).

Occurrence percentages were similar among the three discharges within habitat types. The pallids were most often located in wing dike habitats at all three discharges (44% - 51%). The largest shifts in habitat use appeared between main channel and channel border open habitats (Figure 16). At low discharge, 28% of the locations were in the main channel, and the pallid distributions shifted somewhat to channel border open areas as water increased.

Although water level and discharge data are necessarily correlated, there were differences in habitat association between the two variables. Unlike the two lower discharge categories ($p < 0.0001$), habitats were used differently by individual pallids at all water levels ($p < 0.0001$). The fish selected for the habitats used, and they selected for particular habitat types ($p < 0.0001$; Table 18). As with the previous results, pallids selected for wing dike habitats at all water levels (Table 19). Shifts in selectivity among the remaining habitats occurred, but there were no statistically significant differences in habitat selectivity among the remaining habitats.

Pallid Sturgeon were located in wing dike habitats at similar proportions at all water levels (13 - 21%). Among the wing dike habitats, the largest shift in use occurred immediately below the wing dike scour areas (WDSD) where 21% of the total locations occurred at low water levels versus 14% at the high water levels (Figure 17). Locations in the main channel versus channel border open areas were similar to those at the three water discharge categories; pallids used the main channel more at low water levels (36%), but at the higher water levels the fish were located more in the channel border open areas (26 - 27%).

Sinuosity was examined to determine if the pallids were selecting for a particular area of the river in regards to water flow characteristics. Included are inside bends (41.1%), crossover areas (24.1%), outside bends (19.3%), and straight reaches (14.2%). The tailwater area below Lock and Dam 27 could not be separated as a unique habitat type in the analyses since it represents only 1.0% of the total area in the middle Mississippi River.

When all seasons were combined, individual pallids were using areas differently ($X^2 = 455.5$; $p < 0.0001$), they were selecting for area types ($X^2 = 463.7$; $p < 0.0001$), but combined, the transmittered pallids were not selecting for specific areas ($\Delta X^2 = 8.2$; df=3; $p > 0.01$; Table 20). The insignificant ΔX^2 is apparent by examining SIs which range from 0.7 to 1.1 (Table 21). Results of seasonal effects were similar to the combined data except that, in spring, pallids selected for specific areas ($\Delta X^2 = 14.64$; df=3; $p < 0.01$; Table 20). However, the Bonferonni 95% confidence intervals indicated that the SIs were insignificant among the sinuosity types (Table 21). When we examine occurrence percentages, the results reflect those determined from the Chi-square and selectivity analyses. Inside bends were used most often; 41% of all locations with a range of 33% to 47% among seasons (Figure 18). Pallids used the tailwater area below Lock and Dam 27 in a greater proportion than its percent availability. This was especially true for fall and summer. However, the number of locations in those seasons were low, and effort was disproportionally skewed towards the tailwater.

Discussion

Previous SIUC telemetry efforts were prioritized towards Pallid Sturgeon habitat use, and the limited numbers of relocations provided little insight into movement throughout the MMR (Hurley et al. 2004, Sheehan and Heidinger 2002). Additionally, the majority of tracking effort was concentrated between Grand Tower and Rush Island, Illinois (RM 80-140); therefore, migratory movement out of this area was poorly understood, and the importance of upriver and downriver areas was unknown. Furthermore, with only 19 of 195 observations being recorded in the spring, habitat use and movement throughout the spawning season could not be quantified (Hurley et al. 2004). Research conducted under the current study provides improved estimates of habitat use, as well as valuable information on spring behavior and macrohabitat use, all of which may be useful to future research on MMR Pallid Sturgeon.

Because telemetry was not a priority from 2002-2004, data collected from this period was limited in scope compared to 2005. The number of relocations for individual study fish was variable depending on several factors, including transmitter life and pulse interval, release date and site, and tracking effort. Most importantly, study fish tagged prior to 2005 were not relocated as often due to limited effort, as well fewer numbers of stationary receivers. Season of capture was also important, as study fish tagged in the spring (April and May) often disappeared soon after release and provided little information. The most inclusive migratory data came from fish that were captured in lower portions of the MMR from late fall to early spring. While COR is often targeted for directed sampling of Pallid Sturgeon, individuals tagged from this area are more likely to leave the MMR and provide little information.

One drawback to our study was the lack of information collected on reproductively viable females (stage F4). Throughout the study a total of four black egg individuals were tagged, but three of these fish were tagged with Sonotronics transmitters (not VR2 compatible) prior to 2005, when telemetry effort was minimal. The only black egg female tagged in 2005 was released at COR in early December and was last detected by a VR2 at RM 185 in early January, just prior to a period when river levels approached flood stage. This fish was one of eleven Pallid Sturgeon tagged in a three day period at COR, and was the only individual not relocated by manual tracking in early spring. The majority of females observed in this study were not in spawning condition, while a higher proportion of males were identified as being reproductively viable. This is not surprising, as female Pallid Sturgeon are believed to spawn every three to ten years, and males every two to three years (Keenlyne and Jenkins 1993). Although it would be ideal for each study fish to be in spawning condition, we found Pallid Sturgeon in non-reproductive conditions to make spring migrations similar to those of reproductively viable individuals. Bramblett and White (2001) observed similar seasonal movement patterns of pallid and Shovelnose Sturgeon (*Scaphirhynchus platorynchus*) in consecutive years, thus riverine sturgeon may make migratory runs each year, regardless of reproductive condition.

Seasonal movement

Movement rates of MMR Pallid Sturgeon could not be quantified in previous studies due to limited relocations (Hurley et al. 2004, Sheehan and Heidinger 2002). By increasing the amount of tracking effort from 2002 to 2005, and expending this effort in a homogenous fashion throughout the MMR, patterns of Pallid Sturgeon movement emerged. When observing daily movement rates of MMR Pallid Sturgeon by season, study fish moved most in the summer and spring, and least in the fall and winter, respectively. These results are similar to movement rates of Pallid Sturgeon from the Yellowstone and upper Missouri River (Bramblett and White 2001), where movement was greatest in the spring and summer and lowest in the fall and winter, respectively.

Higher movement rates of MMR Pallid Sturgeon in the spring and summer were likely associated with spawning activities of fish observed in 2004 and 2005. Several study fish exhibited steady upriver migrations in the spring followed by a rapid downriver movement in early summer following the spawning period. Highest daily movement rates occurred during downriver, post-spawn movement (73.4 km/d) and upriver, pre-spawn movements (16.9 km/d), similar to other sturgeon species (Schaffter 1997). Although season had no statistically significant effect on movement rates, this likely was due to several factors. Individual fish were not located the same number of times or at equal periods between locations, and there were considerable differences of movement patterns among Pallid Sturgeon. In some cases, extended movements were exhibited by sturgeon before and after the spawning period; in others, little or no movement was observed during the same periods. Some fish also appeared to move downriver during pre-spawn periods rather than upriver. Additionally, the entire migratory movement of several study fish was not recorded, as minimal pre-spawn movement was observed for study fish that migrated into the Missouri River, and post-spawn movement of several fish was likely not observed because of transmitter expiration during these periods.

Movement cues

Movement of Pallid Sturgeon in response to environmental conditions has been previously unstudied. Movement of MMR Pallid Sturgeon was positively correlated with water levels and temperatures, but this movement was dependent of season. More specifically, it appears that water temperatures primarily drive movement during the spawning season, while water levels influence movement in other seasons (late summer to early spring). Upriver movement was observed in April of all three years when water temperatures reached 13-14°C. Water levels and temperatures increased concurrently in 2004 and 2005, therefore upriver movement was related to both variables. However, upriver movement was observed in 2003 as water temperatures rose and water levels remained stable for two weeks, suggesting that water temperature cued migration. By considering all three years of spring movement, it appears that MMR Pallid Sturgeon become increasingly active around 13°C, and movement peaks as temperatures reach 17°C.

Water temperatures were important to the onset of spring migrations, but water levels were influential as well. In each spring, the greatest upriver movement occurred as water levels and temperatures rose together. Similar behavior has been observed in Kootenai white sturgeon (*Acipenser transmontanus*), and predictive models later indicated that temperature was the most important factor influencing migration, followed by river stage, while discharge and degree days were less important (Paragamian and Kruse 2001). When looking at movement of Pallid Sturgeon outside of the spawning season, water levels were positively related to movement. Study fish typically moved upriver as water levels increased, and downriver as water levels decreased, though the rates and distances of movement was much less than that of spring migrations.

Spring 2005 observations

As previously mentioned, MMR Pallid Sturgeon exhibited pre-spawn movement as temperatures rose from 13°C to 17°C. In 2003 and 2004, pre-spawn behavior of study fish was observed, but nearly all fish were lost as water levels and temperature rose prior to spawning. Through the aid of VR2 relocations, and by placing a concerted, weekly to bi-weekly effort on tracking the MMR, movement was well documented throughout the entire 2005 spawning season.

Sturgeon spawning behavior is often characterized by pre-spawn, upriver migrations, a period of spawning activity, and then culminates with downriver, post-spawn migrations (Paragamian and Kruse 2002). In spring 2005, study fish exhibited the greatest upriver movement as water temperatures rose from 14°C to 17.5°C, and pre-spawn, upriver movement slowed as temperatures reached 18°C. Most study fish exhibited post-spawn movement following the period of 10 May to 18 May, when water temperatures ranged from 18.1°C to 20.7°C and water levels increased from 9.0 – 18.5 ft. Water temperatures during the proposed spawning period (10 - 27 May) were similar to conditions that Pallid Sturgeon embryos and larvae have been collected at in the Yellowstone River (Gardner 1995 cited by Kynard et. al 2002). Furthermore, the closely related Shovelnose Sturgeon, which the Pallid Sturgeon is known to hybridize with (Carlson et al. 1985), spawn within these temperatures as well (Keenlyne 1997).

Water temperature is reported to be an important variable to the onset of sturgeon spawning (Parsley et al. 1993, McCabe and Tracy 1994, Paragamian and Wakkinen 2002), though other variables may influence spawning behavior as well. For example, water level and discharge prompt spawning events in other sturgeon populations (McCabe and Tracy 1994, Auer and Baker 2002, Paragamian and Wakkinen 2002) likely by exposing spawning substrate through the remobilization of sediment (Paragamian and Wakkinen 2002) or by assuring proper dispersal of future larvae. In fact, some populations spawn at highest daily flows (McCabe and Tracy 1994). Water level and discharge rose considerably during our proposed spawning period, which may have created optimal spawning conditions. Additionally, lunar phase is known to influence spawning events of other sturgeon populations (Sulag and Clugston 1998, Auer and Baker 2002), as spawning typically coincides with the new moon phase. In four consecutive years, Suwannee River Gulf Sturgeon spawned every year four to seven days after the new moon, and spawning events lasted ten to eleven days (Sulag and Clugston 1998). Similar behavior may occur in MMR Pallid Sturgeon, as a new moon occurred on May 8 in spring 2005. If Pallid Sturgeon spawn in a similar fashion to Gulf Sturgeon, spawning would have likely occurred between May 12-26, which matches well with our movement data, as the earliest post-spawn activity occurred between May 19 and May 27. Pallid Sturgeon may spawn in response to lunar phase if water conditions are acceptable, therefore this should be monitored in future studies attempting to characterize spawning events.

Several Pallid Sturgeon made typical pre and post-spawn movements in 2005, and the rapid upriver and downriver movement of these fish was used to estimate spawning conditions. However, not all study fish behaved similarly, as some individuals made pre-spawn, downriver migrations in the early spring followed by post-spawn, upriver migrations in mid-late May. Although sturgeon populations typically migrate upriver to reach potential spawning grounds, similar patterns of downriver, pre-spawn movement have been observed in White Sturgeon populations as well (Hildebrand et al. 1999). Additionally, several fish showed little migratory movement throughout the spring and summer of 2005. For example, some fish (#3988, 4049, 4050) were sedentary and showed little pre or post-spawn movement, while another fish (3981) inhabited a specific area from early April to late July before moving downriver, apparently in response to extremely low water levels. Interestingly, all of the aforementioned fish were identified as males, and similar patterns of movement have been observed in other riverine sturgeon. Paragamian and Kruse (2001) found male White Sturgeon to arrive at spawning grounds earlier and stay much longer than females, although the residency was highly variable and ranged from seven days to several months. Similar to Paragamian and Kruse (2001), the migratory behavior of our male study fish was variable, where some individuals left soon after the believed spawning period, and others stayed much later. Few known females were tagged in our study, but the females with well-documented movement showed more rapid pre-spawn and post-spawn movement compared to males, and likely inhabited spawning areas for a much shorter period (Figure 19). Paragamian and Kruse (2001) found female White Sturgeon migrate to their spawning reach within the narrowest time frame and leave soon after spawning; therefore, female movement may provide a better indication of spawning periodicity than movement of males. Furthermore, initial spawning events of White Sturgeon have been linked to the arrival of telemetered females (Paragamian and Wakkinen 2002); thus, if tracking effort can be sustained to consistently locate females during probable spawning periods, female Pallid Sturgeon should be the focus of further telemetry studies in the MMR.

Important macrohabitats

Telemetry observations from 2003-2005 identified several important macrohabitats, although less emphasis should be placed on observations from 2003-2004. Pre-2005 data was likely biased because of directed effort and an inability to relocate fish after leaving specific areas. For example, several Pallid Sturgeon were captured, tagged and released, and subsequently relocated in the Modoc area between 2003 and 2004. The majority of these fish were captured in the spring, and most relocations were acquired in the days and weeks immediately following release. As water temperatures increased most of these fish left the Modoc area, and were not relocated due to limited effort in other areas. Thus, with the majority of relocations occurring immediately after release, and very few observations occurring after departure from this area, Modoc appeared to be of importance pre-2005. However, with a more homogenous distribution of Pallid Sturgeon capture sites and tracking effort in 2005, few Pallid Sturgeon were relocated in the Modoc area in 2005, and none inhabited this area for an extended period of time to suggest an importance for staging or spawning.

When looking at 2005 data alone, it appears there are five important macrohabitats utilized by MMR Pallid Sturgeon: the COR tailwater, the Meremac confluence, the Kaskaskia confluence, the Grand Tower area, and an extended area near Thebes (RM 29-44) (Figure 10). Although the majority of observations in 2005 occurred throughout the spring, study fish that remained in the MMR throughout the summer used these same areas as well. Therefore, there was no apparent shift in macrohabitat use following the spawning season when looking at all study fish. As previously mentioned, study fish were not found to congregate with one another, as observed in studies on other sturgeon species (Paragamian et al. 2001, Heise et al. 2004). However, this does not refute the potential importance of these areas to spawning, as non-telemetered Pallid Sturgeon may have congregated with study fish. Furthermore, by only tracking study fish on a weekly basis throughout the spawning period, activity at times of absence was unknown. In contrast, the previously mentioned studies had the luxury of tagging numerous study fish within a small area to study spawning activity, whereas our objective was to study the entire MMR, which prohibited us from focusing on specific areas and daily movement of study fish.

The area of primary interest for future research may be the COR tailwater region, as this area produced the highest proportion of Pallid Sturgeon captures, and several study fish were relocated here throughout the proposed spawning period (Figures 5, 6 and

8). This area is thought by many to be an important spawning and/or staging area for MMR sturgeon species, as commercial fishermen collect large amounts of shovelnose sturgeon caviar here each spring, and numerous pallid and lake sturgeon are captured as well. However, it has often been suggested that high numbers of sturgeon captures in this area are in response to a barrier effect of the lowhead to migrating sturgeon. Observed movement of three study fish in April 2005 suggests that Pallid Sturgeon are capable of navigating the lowhead at a minimum river stage of 16 feet (St. Louis gauge), yet it is unknown whether Pallid Sturgeon can cross at lower water levels, as observed migrations occurred at relatively normal conditions. It appears that navigation over the lowhead may be occurring on the Missouri side of this area, as gradient is less formidable there, and study fish known to cross this obstacle were located there prior to departure from COR (Figure 7). Although COR may be utilized for spawning by downriver populations of Pallid Sturgeon, as evident by the migration of study fish from the Thebes and Chester region, upriver populations may primarily use this area for feeding or staging in the winter and early spring. This is implied by the movement of eleven study fish captured and released at COR in early December 2004. Following release, all study fish moved downriver in late winter, prior to dispersing in a variable fashion during pre-spawn conditions. Two individuals migrated into the Missouri River, five individuals made pre-spawn, downriver migrations to the area near the Meremac confluence, while only three individuals migrated back to COR and resided there throughout the spawning period. The remaining study fish was the previously mentioned black egg female, which was not relocated after early January. The use of COR for staging or feeding is likely explained by the heterogeneous, free-flowing nature of this area, which scours the river bottom and creates a diversity of substrate ranging from sand to large cobble, which may hold greater assemblages of prey items compared to downriver areas. The COR region is utilized by Pallid Sturgeon throughout all seasons, and should be protected to preserve resident populations, as well as to facilitate spawning habitat for downriver populations.

As previously mentioned, five of eleven study fish released at COR in December 2004 made pre-spawn migrations to an extended area (RM 170–158) near the Meremac confluence in spring 2005. Three of these study fish, all of which were reproductively mature males, inhabited a smaller stretch of river throughout the spawning period prior to making upriver, post-spawn movements (Figure 9). This area (RM 158-160) is quite suitable for sturgeon spawning, as the majority of the Missouri shoreline lacks wing dikes and is composed of bedrock, riprap, cobble and/or gravel. However, study fish were rarely relocated in areas of rock substrate, and were typically found utilizing wing dike habitat on the Illinois side, which lacks hard substrate typically associated with sturgeon spawning. Nevertheless, as previously mentioned, study fish were only relocated once a week, and since study fish were in close proximity to rock substrate, the potential for spawning in this area exists. The substrate and flow, coupled with the occurrence of downriver, pre-spawn migrations to this area, suggests that this stretch may be utilized as spawning habitat by Pallid Sturgeon.

The area near the Kaskaskia confluence may be of importance as well, as this area has been inhabited by several Pallid Sturgeon for extended periods of time throughout all years, despite having few Pallid Sturgeon captured and released there. The majority of relocations have been observed immediately downriver of the confluence (RM 117), in the MCB and CBD area of the Illinois side. This inside bend consists of sand and fine pebbles in CBD areas, and shifts to sand and small gravel in deeper MCB areas. In spring 2005, gill nets and trotlines were set in this area near telemetered Pallid Sturgeon, but rapid flow and numerous snags in this area made sampling difficult, therefore no Pallid Sturgeon were captured. Two study fish inhabited this area throughout the spawning period in 2005 (Figure 11). Interestingly, both fish were males that arrived at this area well before the spawning period, typical of male sturgeon populations (Paragamian and Kruse 2001).

The Grand Tower area has long been considered a potential spawning site for Pallid Sturgeon because of the large gravel and cobble bar located upstream of Cottonwood Island (RM 79). Although, we did not find any of our fish utilizing this area using telemetry during the spawning period, we did capture and implant several individuals from the upstream portion of the bar including milting male Pallid Sturgeon. Fish were located in upstream areas associated with rock substrate. The large scour hole behind Tower Rock (RM 80) held multiple fish during the spawning period, where substrate consists primarily of bedrock. Other upstream and downstream areas may be important for Pallid Sturgeon spawning as well, as multiple fish utilized the cobble and gravel channel border areas near RM 83. Although the single components of the Grand Tower area appear to be utilized intermittently by Pallid Sturgeon, the complex of all habitats together are unique among areas within the MMR. Additionally, Cottonwood Island has been a prominent feature in the MMR for decades. Habitat diversity of the Grand Tower area is an important feature to Pallid Sturgeon, but an overriding question regarding habitat stability may improve this area's worth in the long term.

The area near Thebes (RM 29-44) has produced several Pallid Sturgeon captures, and has subsequently produced several relocations of study fish. This area differs from upstream areas because of increased sinuosity and a presence of several small islands and side channels. Habitat scale may be important to Pallid Sturgeon in this river reach. Several off-channel areas and side channels are dominant features within this reach. For example, Thebes gap (RM 43) may have historically been important habitat for Pallid Sturgeon. This area is a bottleneck in the river that contained riffle-like habitat mid-channel. It was only recently that large bedrock and gravel were removed from the main channel to improve navigation. Nevertheless, VR2s deployed on the inside bend of this area have often relocated study fish for several consecutive days, suggesting a preference for this area. Additionally, two side channels in this reach include diverse habitat features such as large gravel bars and islands including Santa Fe Chute (RM 35-39) and Bumgard Island (RM 29-30). Access to these gravel bars and islands is limited because of channel maintenance structures. However, recent structure modifications have improved access to Santa Fe Chute. During telemetry we tracked an individual to the exact location of the modified dike structure. Telemetry data may indicate intermittent use in meso-habitats associated with this river reach. However, our definition of habitat will need to include scale when describing a large range species such as the Pallid Sturgeon.

Habitat use

A drawback to past telemetry efforts on MMR Pallid Sturgeon was that the majority of study fish were captured by commercial fishermen between the Chester and Rush Island, IL region (RM 110-140). The majority of tracking effort was therefore exerted in this area, which makes up a small portion of the MMR and lacks diverse habitats found in upriver and downriver stretches. Furthermore, the relatively low sample size and number of relocations in previous studies limited analysis of data, and without the aid of bathymetry charts and DOQ maps of the MMR, habitat availability data was derived from measurements taken at twenty randomly selected one-mile stretches. Pallid Sturgeon observed in the current study were captured at various dates, locations, and habitats throughout the MMR from 2002 to 2005, thereby reducing the bias of capture site on relocation data. With enhanced telemetry equipment, an improved classification and quantification of available habitat, and by acquiring a higher number of study fish and relocations through homogenous tracking effort, habitat use by MMR Pallid Sturgeon has been well quantified in this study.

It is apparent that MMR Pallid Sturgeon are selecting for wing dike habitats, as only 7.1% of available habitat was created by wing dikes, yet fish were found in those locations 47% of the time. With little historic habitat remaining, wing dike habitats are likely selected for due to the increased habitat complexity they create. As flow is directed off wing dikes and towards the main channel, scour holes are created and substrate is remobilized and deposited behind wing dikes. Continual scouring erodes away at these deposits and uproots aquatic invertebrates, which are thereby preyed upon by small bodies fishes sought after by Pallid Sturgeon. Similarly, upriver wing dike and WDSD habitats are likely utilized because of the transition or seam between slow and fast water, which transports and settles out prey items that can be easily attained. In general, wing dikes deflecting high flow often create the largest scour holes and sand deposits, which are habitat characteristics sought after by Pallid Sturgeon. This is reflected by the depths that Pallid Sturgeon typically inhabit, as study fish were found 80% of the time in depths greater than 6 m, with 20% of these relocation occurring between depths of 12 and 18 m.

By comparing our results to Hurley et al. (2004), there are several similarities as well as differences amongst studies, most of which being explained by contrasting habitat delineations. Hurley et al. (2004) found MMR Pallid Sturgeon to select for wing dike tips and between wing dikes, although upriver and downriver wing dike habitats were not selected for, in contrast to the present study. This is explained by differences in habitat delineation among Hurley et al. (2004) and the present study, as their between wing dike habitat was larger and partially constituted areas we currently delineate as upriver and downriver wing dike habitats. Hurley et al. (2004) found Pallid Sturgeon to display a positive selection for main channel borders and downriver island tips, while we found contrasting results. Again, this is likely attributed to differences in habitat delineations, as the main channel border characterization of Hurley et al. (2004) is comparable to our WDSD and MCBO sites, and downriver island tips in Hurley et al. (2004) comprised a much larger area than the present study.

No study fish were relocated in ITU, ITD, or TM habitats as delineated by Cobb classification, although numerous Pallid Sturgeon were found downriver or adjacent to these habitats. Due to channelization, most islands and side channels have degraded in response to restricted flow and increased sedimentation. A great proportion of these areas are likely unfavorable or inaccessible to Pallid Sturgeon, yet were still included in habitat selectivity indices using the Cobb delineation. Therefore, non-selectivity for these areas should not negate the importance of these areas, as the side channels and islands that Pallid Sturgeon do inhabit are often less degraded, with unrestricted seasonal flow and favorable substrate. When considering the five important macrohabitats, as previously described, it is interesting that all these areas are associated with islands and/or tributaries. Inhabitation is likely related to the dynamic flow and substrate in these areas, which may offer an abundance of food as well as spawning habitat. Although VR2s in the Kaskaskia, Big Muddy and Meremac Rivers provided little evidence to suggest inhabitation within tributaries, relocations of Pallid Sturgeon within side channels near Thebes suggests that side channels may be of importance, especially in the spring.

Parameters that influenced habitat use were season, water level and discharge, although no dramatic shift in habitat use occurred, as wing dike habitats were selected year-round. The most significant shift in habitat use appeared between main channel and channel border open usage by season, as these open river habitats became especially important during summer (57% of relocations). The shift to open river habitat usage in the summer is likely related to decreased discharge and water levels during this period, as 28% of locations were in the main channel during low discharge periods. Study fish likely sought open river habitats at this time in search of greater depth and flow, as decreased water levels and discharge reduced the depth and flow of wing dikes habitats. As water discharges increased, Pallid Sturgeon distributions shifted from main channel areas to shallower channel border open areas, likely in search of optimal flow. Although few relocations occurred in side channel habitats, which therefore limited statistical analysis, inhabitation of these areas was seemingly dependent on season and water conditions. In contrast to main channel usage, side channels were used primarily in the spring at higher water levels, likely because of increased accessibility, as well as favorable flow and substrate present during these periods.

Sinuosity of the MMR was quantified in order to address the importance of inside bends, crossover areas, outside bends, and straight reaches, with the COR tailwater being removed from analysis due to its unique characteristics. The influence of channel sinuosity and morphology on pallid and shovelnose sturgeon habitat use has been examined in other studies. For example, Bramblett and White (2001) found Pallid Sturgeon to inhabit sinuous channels with numerous islands, while Quist et al. (1999) found shovelnose sturgeon to select for channel crossover regions of the Kansas River. Quist et al. (1999) also found shovelnose sturgeon to use inside bends in proportion to their abundance, while outside bends were avoided in winter temperature extremes. In contrast to these studies, we found MMR Pallid Sturgeon to use all habitats in proportion to their availability, and no shift in habitat use occurred in relation to season, water level or discharge. The lack of selectivity for specific sinuosity habitats may be a reflection of the preference for wing dike habitats by Pallid Sturgeon. Wing dikes are found in all sinuosity habitats; therefore the habitat created by wing dikes is available in all areas, regardless of sinuosity. Furthermore, wing dikes are likely used as current breaks in high flows and extreme temperatures, hence areas that would typically be avoided under extreme conditions, such as outside bends, may still be utilized.

Substrate is likely an important variable determining the presence of Pallid Sturgeon, as substrate predicates the availability of food items, as well as the suitability of spawning habitat. Throughout all seasons combined, Pallid Sturgeon were most often located on a sand substrate (48%) and least often on mud or silt substrates (2%). There was no apparent shift in substrate use in response to season, although sand substrate was used more so in the summer than other seasons. This may be in response to changes in foraging behavior, as invertebrates inhabiting sand substrate are easily obtained and require little energy expenditure by Pallid Sturgeon during summer temperature extremes. In spring 2005, substrate use during the proposed spawning period did not differ from other periods, with sand substrate being primarily utilized. However, study fish inhabiting the five important macrohabitats during spring 2005 were often adjacent to rock substrate, and were capable of reaching preferred habitat in a short period of time. For example, four study fish were located near the COR tailwater area during the proposed spawning period in spring 2005. Three of these individuals were located within one kilometer of one another, in deep, rapid water with sand and fine gravel substrate. However, these individuals were also adjacent to shallow areas with large cobble substrate on the Missouri side, where buffer pads were placed in attempt to collect sturgeon eggs. Due to weekly tracking effort, it is unknown if movement to this area occurred during times of absence, but its quite possible considering the close proximity of this habitat.

Although a primary assumption has been that Pallid Sturgeon spawn in shallow, rocky areas, results from this study do not necessarily support or refute this idea. The preference for sand substrate during the spawning period is odd considering that sturgeon possess adhesive eggs, yet the potential for spawning in these substrates may exist. Kootenai River white sturgeon have been found to spawn in deep water, with substrate being composed of sand and small pockets of fine gravel (Paragamian et al. 2001). This specific population is geographically isolated from other white sturgeon due to the Bonnington Falls in British Colombia, Canada. While other white sturgeon populations spawn over rock substrate (McCabe and Tracy 1994), Kootenai River white sturgeon spawn in deep, sandy areas in response to suitable flow. This is suggested by the avoidance of nearby upriver areas, where an abundance of cobble substrate is available, but flow is less than optimal (Paragamian et al. 2001). Poor recruitment in this population has been attributed to anthropogenic disturbances, which have reduced spring flows and impacted the natural hydrograph, thereby influencing spawning behavior (Paragamian et al. 2001).

The effects of anthropogenic disturbances such as channelization, pollution, and over-fishing on Pallid Sturgeon reproduction are unknown, as very little information exists for this species. Results from the present study have provided valuable information concerning spawning conditions, as well as areas that may be of importance during this period. By utilizing this information, a more concerted effort may be exerted to characterize Pallid Sturgeon spawning behavior in the MMR. Through daily tracking of reproductively viable Pallid Sturgeon, coupled with the deployment of egg mats throughout the spawning period, spawning behavior of MMR Pallid Sturgeon may be closely studied, in hopes of advancing recovery efforts.

Literature Cited

Auer, N. A., and E. A. Baker. 2002. Duration and drift of larval lake sturgeon in the Sturgeon River, Michigan. Journal of Applied Ichthyology 18:557–564.

Bramblett RG, White RG. 2001. Habitat use and movements of pallid and shovelnose sturgeon in the Yellowstone and Missouri Rivers in Montana and North Dakota. *Trans Am Fish Soc* 130:1006-1025.

Burnham, K. P., and D. R. Anderson. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York.

Carlson DM, Pflieger WL, Trial L, Haverland PS. 1985. Distribution, biology and hybridization of *Scaphirhynchus albus* and *S. platorhynchus* in the Missouri and Mississippi rivers. Environmental Biology of Fish 14:51-59.

Colombo RE. 2004. Reproductive demographics and early life history of the shovelnose sturgeon (*Scaphirhynchus platorynchus*). Southern Illinois University, Carbondale, IL, USA.

Gardner, W. M. 1995. Yellowstone River Paddlefish spawning study. Progress Report on Project No. F-78-R-1. Montanna Department of Fish, Wildlife, and Parks, Helena, Montanna. 189 pp.

Heise, R. J., W. T. Slack, S. T. Ross, and M. A. Dugo. 2004.Spawning and associated movement patterns of Gulf Sturgeon in the Pascagoula River drainage, Mississippi. Transactions of the American Fisheries Society 133:221-230.

Hildebrand, L., C. McLeod, and S. McKenzie. 1999. Status and management of White Sturgeon in the Columbia River in British Columbia, Canada: an overview. Journal of Applied Ichthyology 15(19919):164-172.

Hurley, K. L. R. J. Sheehan, R. C. Heidinger, P. S. Wills, B. Clevenstine. 2004. Habitat use by middle Mississippi River Pallid Sturgeon. Transactions of the American Fisheries Society 133:1033–1041, 2004

Keenlyne KD. 1997. Life history and status of the shovelnose sturgeon, *Scaphirhynchus platorynchus*. Environmental Biology of Fish 48:291-298.

Keenlyne KD, Jenkins LG. 1993. Age at sexual maturity of the pallid sturgeon. Transactions of the American Fisheries Society 122:393-396.

Kynard, B., E. Henyey, and M. Horgan. 2002. Ontogenetic behavior, migration, and social behavior of pallid sturgeon, *Scaphirhynchus albus,* and shovelnose sturgeon, *s. platorynchus,* with notes on the adaptive significance of body color. Environmental Biology of Fishes 63:389-403.

Littell, R. C., G. A. Milliken, W. W. Stroup, and R. D. Wolfinger. 1996. SAS System for Mixed Models. SAS Institute, Inc., Cary, North Carolina.

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

McCabe, G. T., Jr., and C. A. Tracy. 1994. Spawning and early life history of white sturgeon, Acipenser transmontanus, in the lower Columbia River. Fish. Bull., 92(4): 760-772.

Otis, D. L., and G. C. White. 1999. Autocorrelation of location estimates and the analysis of radio tracking data. Journal of Wildlife Management 63:1039-1044.

Paragamian, V. L., G. Kruse, and V. D. Wakkinen. 2001. Spawning habitat of Kootenai River white sturgeon, post-Libby Dam. North American Journal of Fisheries Management 21:22–33.

Paragamian, V. L., and V. D. Wakkinen. 2002. Temporal distribution of Kootenai River white sturgeon spawning events and the effect of flow and temperature. Journal of Applied Ichthyology 18:542–549.

Paragamian, V. L., V. D. Wakkinen, and G. Kruse. 2002. Spawning locations and movements of Kootenai River white sturgeon. Journal of Applied Ichthyology 18:608–616.

Parsley, M. J., L. G. Beckman, G. T. McCabe, Jr. 1993. Spawning and rearing habitat use by white sturgeons in the Columbia River downstream from McNary Dam. Transactions of the American Fisheries Society 122(2): 217-227.

Quist, M. C., J. S. Tilma, M. N. Burlingame, and C. S. Guy. 1999. Overwinter habitat use of shovelnose sturgeon in the Kansas River. Transactions of the American Fisheries Society 128:522–527.

Rogers, K. B. 1998. Habitat use by largemouth bass and northern pike on the Rocky Mountain Arsenal, Colorado. Doctoral dissertation. Colorado State University, Fort Collins.

Rogers, K. B., and E. P. Bergersen. 1995. Effects of a fall drawdown on movement of adult northern pike and largemouth bass. North American Journal of Fisheries Management 15:596-600.

Rogers, K. B., and E. B. Bergersen. 1996. Application of geographic information systems in fisheries: habitat use by northern pike and largemouth bass. Pages 315-323 in L. E. Miranda and D. R. DeVries, editors. Multidimensional approaches to reservoir fisheries management. American Fisheries Society Symposium 16, Bethesda, Maryland.

Schaffter, R.G. 1997. White sturgeon spawning migrations and location of spawning habitat in the Sacramento River, California. California Fish and Game 83(1): 1-20.

Sheehan et al. 2002. Sheehan, R. J., R. C. Heidinger, P. S. Wills, M. N. Jackson, R. Colombo, and A. Miller. Middle Mississippi River Pallid Sturgeon habitat use project. Southern Illinois University at Carbondale. Year 6, Annual Progress Report. Carbondale, Illinois.

Sulak, K.J & Clugston, J.P. 1998. Early life history stages of Gulf sturgeon in the Suwannee River, Florida. Transactions of the American Fisheries Society. 127(5): 758-771.

Thomas, D. L., and E. J. Taylor. 1990. Study designs and tests for comparing resource use and availability. Journal of Wildlife Management 54:322-330.

Table 1. Pallid Sturgeon collected and released in the middle Mississippi River after sonic transmitters were surgically inserted.

Capture Date	Capture RM	PIT	Tag #	Tag Model	Expiration Date	Sex	FL(mm)
11/12/2002	162	41423e7b14	222	CHP-87-L	5/15/2004	U	725
11/19/2002	188	4142430a66	336	CHP-87-L	5/22/2004	U	670
11/19/2002	188	4142555e7c	244	CHP-87-L	5/22/2004	U	760
11/21/2002	128	41420b7608	233	CHP-87-L	5/24/2004	U	729
3/7/2003	140	116162615a	345	CHP-87-L	9/7/2004	U	625
3/12/2003	124	4214470025	335	CHP-87-L	9/12/2004	U	651
3/12/2003	124	4214470025	334	CHP-87-L	9/12/2004	U	721
4/2/2003	7	114945496A	333	CHP-87-L	10/3/2004	F4	807
4/3/2003	0	115222290a	354	CHP-87-L	10/4/2004	F	870
4/3/2003	7	115233672a	235	CHP-87-L	10/4/2004	F4	889
4/4/2003	71	4214453a4d	444	CHP-87-L	10/5/2004	M	822
4/11/2003	198	116176670A	456	CHP-87-L	10/12/2004	M2	771
4/18/2003	71	7f7f181d3b	555	CHP-87-L	10/19/2004	M2	615
4/23/2003	188	115224352a	234	CHP-87-L	10/24/2004	U	781
5/23/2003	190	4142484453	6666	CHP-87-L	11/23/2004	U	711
5/23/2003	190	42152e7915	367	CHP-87-L	11/23/2004	U	875
11/18/2003	190	115231222a	1537	V16-5H-R04K	5/13/2004	M	776
12/3/2003	97	1f520f5c24	1539	V16-5H-R04K	5/28/2004	F3	850
12/4/2003	35	134749696a	1542	V16-5H-R04K	5/29/2004	F1	680
12/4/2003	35	134712763a	1541	V16-5H-R04K	5/29/2004	M2	799
12/4/2003	35	133644532a	1540	V16-5H-R04K	5/29/2004	M2	824
12/5/2003	62	114954733a	1546	V16-5H-R04K	5/30/2004	M	774
12/18/2003	124	7f7f220639	1545	V16-5H-R04K	6/12/2004	M	705
3/17/2004	121	115227126A	1543	V16-5H-R04K	9/10/2004	U	846
3/18/2004	116	115224532A	1554	V16-5H-R04K	9/11/2004	U	742
3/18/2004	116	115222591A	1552	V16-5H-R04K	9/11/2004	U	787
3/18/2004	30.5	133667513A	1548	V16-5H-R04K	9/11/2004	U	820
3/25/2004	39.2	114961296a	1555	V16-5H-R04K	9/18/2004	U	870
3/25/2004	121	4142330319	1556	V16-5H-R04K	9/18/2004	M2	1005
3/26/2004	124	7f7f093265	1538	V16-5H-R04K	9/19/2004	M	710
3/26/2004	78.8	134662311A	3925	V16-4H-R04K	10/17/2005	U	736
3/26/2004	78.8	133734244A	1553	V16-5H-R04K	9/19/2004	U	784
3/26/2004	37	114961591A	1550	V16-5H-R04K	9/19/2004	U	797
3/26/2004	37	115236251A	1551	V16-5H-R04K	9/19/2004	U	857
3/30/2004	189	4142191932	3911	V16-4H-R04K	10/21/2005	M	667
3/30/2004	189	7f7f181d46	1549	V16-5H-R04K	9/23/2004	M	700
3/30/2004	189	7f7f21333b	1544	V16-5H-R04K	9/23/2004	M	895
4/15/2004	119	114947331a	3924	V16-4H-R04K	11/6/2005	M	667
4/16/2004	118	115235192a	3333	CHP-87-L	10/18/2005	M	810

Table 1. Continued.

5/5/2004	190	224035096f	7777	CHP-87-L	11/6/2005	M	965
5/5/2004	190	202231632a	4444	CHP-87-L	11/6/2005	F4	1080
5/15/2004	189	115232217A	1566	V16-5H-R04K	11/8/2004	U	791
5/20/2004	189	114934533A	1563	V16-5H-R04K	11/13/2004	U	778
5/20/2004	189	114962565A	1568	V16-5H-R04K	11/13/2004	U	824
10/21/2004	117	4549406F14	3982	V16-5H-R04K	5/20/2005	F2	878
11/3/2004	67	133848473A	3986	V16-5H-R04K	6/2/2005	U	724
11/9/2004	30.3	133625645A	1561	V16-5H-R04K	5/5/2005	M2	800
11/10/2004	146.3	155AOC6050	1567	V16-5H-R04K	5/6/2005	M	695
11/10/2004	29.4	133622451A	1562	V16-5H-R04K	5/6/2005	U	809
11/18/2004	45.3	134539285A	3984	V16-5H-R04K	6/17/2005	F6	854
11/19/2004	51.5	133715477A	1557	V16-5H-R04K	5/15/2005	F	807
11/23/2004	35.3	133625214A	3983	V16-5H-R04K	6/22/2005	F3	881
12/1/2004	190	115235273A	3988	V16-5H-R04K	6/30/2005	M2	710
12/1/2004	190	115231734A	3981	V16-5H-R04K	6/30/2005	M1	784
12/1/2004	190	115235267A	1558	V16-5H-R04K	5/27/2005	M2	794
12/1/2004	190	114933531A	1560	V16-5H-R04K	5/27/2005	M2	845
12/1/2004	190	114969574A	1565	V16-5H-R04K	5/27/2005	M2	995
12/2/2004	190	115223166A	1575	V16-5H-R04K	5/28/2005	M2	718
12/2/2004	190	115224645A	1571	V16-5H-R04K	5/28/2005	F4	793
12/3/2004	190	115232453A	1574	V16-5H-R04K	5/29/2005	M2	664
12/3/2004	189	115235647A	3985	V16-5H-R04K	7/2/2005	M2	690
12/3/2004	190	115225196A	1572	V16-5H-R04K	5/29/2005	M2	765
12/3/2004	190	115229634A	1559	V16-5H-R04K	5/29/2005	F2	913
12/14/2004	31	133618654A	1595	V16-6H-R04K	1/27/2008	U	755
12/14/2004	31	134734186A	1597	V16-6H-R04K	1/27/2008	U	824
12/14/2004	31	134473685A	1594	V16-6H-R04K	1/27/2008	M2	831
12/15/2004	1.8	115236664A	1577	V16-4H-R04K	7/8/2006	MV	660
12/15/2004	1.2	115229792A	1573	V16-5H-R04K	6/10/2005	F2	802
2/8/2005	13.1	4557733F1C	1593	V16-6H-R04K	3/23/2008	M	725
3/16/2005	119.4	454B326BO4	1581	V16-4H-R04K	10/7/2006	M	612
3/16/2005	124	45685AOF25	4050	V16-5H-R04K	10/13/2005	M2	785
3/22/2005	120	45575A3B52	4049	V16-5H-R04K	10/19/2005	M2	715
3/24/2005	6.7	115224351A	4046	V16-5H-R04K	10/21/2005	U	684
3/24/2005	51	133716646A	1589	V16-6H-R04K	5/6/2008	M	791
3/29/2005	57	134961671A	1586	V16-6H-R04K	5/11/2008	U	911
3/31/2005	78.6	133536093A	1587	V16-6H-R04K	5/13/2008	U	862
4/4/2005	97	4328687710	1590	V16-6H-R04K	5/17/2008	U	802
4/4/2005	100	432857510E	1588	V16-6H-R04K	5/17/2008	U	819
4/5/2005	120	455AOB556B	1569	V16-5H-R04K	9/29/2005	M	895
4/12/2005	79	45580C3519	183	V16-5H-R256	10/19/2005	U	770

Table 1. Continued.

4/12/2005	83	4311590219	1584	V16-6H-R04K	5/25/2008	U	779
4/12/2005	79	4557693F40	1583	V16-6H-R04K	5/25/2008	U	880
4/13/2005	48.8	134553091A	1585	V16-6H-R04K	5/26/2008	U	831
4/13/2005	79	4549632161	180	V16-5H-R256	10/20/2005	U	846
4/16/2005	79	134661330A	184	V16-5H-R256	10/23/2005	U	904
4/26/2005	84	432A730C1A	1613	V16-5H-R04K	11/23/2005	U	790
4/29/2005	79.3	136124124A	1591	V16-6H-R04K	6/11/2008	U	867

Table 2. Specifications for transmitters inserted in Pallid Sturgeon released in the middle Mississippi River from 2002 to 2005.

Transmitter model	Frequency (kHz)	Length (mm)	Diameter (mm)	Weight (g)	Pulse interval (seconds)	Tag Life (days)
Sonotronics - CHP-87-L	40	90	18	11.5	continuous	550
Vemco - V16-5H-R04K	69	92	16	16	5 - 30	177
Vemco - V16-5H-R04K	69	92	16	16	10 - 35	211
Vemco - V16-5H-R256	69	92	16	16	10 - 35	190
Vemco - V16-6H-R04K	69	90	16	14	20 - 69	1139
Vemco - V16-4H-R04K	69	65	16	10	20 - 69	570

Table 3. Locations of VEMCO stationary receivers (VR2) in Mississippi river and tributaries from March 2004 through July 2005. In some cases, the receivers were moved from their original positions during February and March 2005.

ID	River mile	Number of locations[a]	Longitude	Latitude
		March 2004 - January 2005		
Missouri River	197.0		-90.16271135	38.82574017
COR Above	194.4		-90.12218795	38.79683224
COR Above	194.4		-90.12329956	38.79744312
COR Above	193.5		-90.13382000	38.78980000
COR Above	193.5		-90.13253625	38.78901972
Mosenthein Side Channel	184.2	10	-90.19306264	38.68461331
Meremac River (in Mississippi River)	160.4	3	-90.34630210	38.37978998
Establishment Island	130.0	1	-90.14155794	38.06489521
Moro Island	119.8	10	-89.97797244	37.96433534
Rockwood Island	106.0		-89.77768670	37.87211671
Cottonwood Island	78.5		-89.51496975	37.60994255
Cape Girardeau	57.0		-89.45027129	37.34071403
Thebes	44.0	11	-89.46952000	37.21785000
Boston Bar	9.2		-89.23526771	37.03828004
Boston Bar	8.6	3	-89.22794533	37.03230031
Boston Bar	8.4	4	-89.22251620	37.03051748
		March 2005 - August 2005		
Missouri River	197.0	3	-90.16271135	38.82574017
COR Above	194.4		-90.12961000	38.79540000
COR Above	194.2	1	-90.12452000	38.79488000
COR Below	187.7		-90.20904059	38.72548337
COR Below	187.7		-90.21377927	38.72585578
Mosenthein Side Channel	185.3	1	-90.20279000	38.69613000
Meremac River (0.5 mi)	161.5	1	38.39737000	-90.34467000
Osborn Chute	144.5	3	-90.30403539	38.17789487
Osborn Chute	144.5		-90.30783065	38.17545599
Establishment Island	130.3	1	-90.12254983	38.04581447
Moro Island	119.9	12	-89.97776000	37.96412000
Moro Island	119.8		-89.97073109	37.96146455
Kaskaskia River (0.25 mi)	118.0		-89.94299000	37.98049000
Rockwood Island	101.0	2	-89.70295829	37.81570566
Crawford Towhead	71.2	6	-89.50136834	37.51134524
Crawford Towhead	71.2		-89.49693041	37.51236473
Big Muddy River (0.5 mi)	76.0		-89.47231000	37.56188000
Thebes	44.0	53	-89.46908437	37.21974333
Thebes	44.0	12	-89.46517692	37.22008592
Boston Bar	9.7		-89.24200000	37.04407000
Boston Bar	9.7		-89.23692000	37.04546000
Cairo	0.5	1	-89.14011788	36.98250000

a/ Number of days individual Pallid Sturgeon with transmitters were identified by receiver.

Table 4. Number of active tags identified during each year of the middle Mississippi River Pallid Sturgeon tracking study. The range of the number of detections per tag are given with and without the use of stationary receivers.

	With VR2 detections			
Year	Number of Active Tags	Percent of total active tags	Minimum detections per fish	Maximum detections per fish
2002	6	5	1	2
2003	22	18.3	1	27
2004	49	40.8	1	16
2005	43	35.8	1	63
	Without VR2 detections			
2002	6	5.1	1	2
2003	22	18.6	1	27
2004	49	41.5	1	7
2005	41	34.7	1	16

Table 5. Movement rates (meters/day) for 25 Pallid Sturgeon that exhibited extreme ranges after they were inserted with sonic transmitters and released in the middle Mississippi River during 2002 - 2005. Negative values represent movement downriver; positive values are upriver movement.

Downriver movement				Upriver movement			
Sonic transmitter	Number of locations	Maximum recorded	Average	Sonic transmitter	Number of locations	Maximum recorded	Average
3984	16	-73,385	-222	3984	16	16,883	-222
1553	7	-62,763	-16,115	1569	4	11,226	2,057
3982	17	-32,964	-1,188	1589	8	9,971	1,482
184	10	-19,331	-1,611	1560	5	9,335	1,940
1594	6	-13,544	236	1594	6	9,275	236
1613	8	-5,777	-644	1553	7	6,438	-16,115
4049	19	-4,827	-297	3982	17	4,829	-1,188
183	4	-4,226	-2,135	1554	7	4,668	689
1569	4	-3,942	2,057	1590	4	4,547	2,155
1589	8	-3,821	1,482	1586	4	4,447	3,175
3911	4	-3,587	-500	4046	62	4,105	87
1562	17	-2,873	-256	1543	15	4,093	222
1591	2	-2,834	-1,745	3983	16	3,496	344
3986	13	-2,735	-303	1587	5	2,466	301
3981	13	-2,723	-245	184	10	2,254	-1,611
1565	10	-2,664	52	1565	10	2,185	52
1556	1	-2,528	-2,528	222	27	1,610	56
1584	5	-2,242	-474	334	21	1,610	46
1593	12	-1,930	-243	1549	3	1,610	519
1572	11	-1,862	-181	3911	4	1,610	-500
3983	16	-1,608	344	1548	1	1,457	1,457
1567	15	-1,380	-189	3985	13	1,342	215
1543	15	-1,276	222	3986	13	1,128	-303

Table 6. Average movement rates (meters/day) of Pallid Sturgeon by season in the middle Mississippi River during 2002 - 2005. Negative values represent movement downriver; positive values are upriver movement.

Season	Number of locations	Meters per day	Maximum downriver	Maximum upriver
Winter	125	-48	-2,735	2,475
Spring	273	604	-15,670	19,408
Summer	191	-1,461	-73,385	4,668
Fall	23	71	-1,380	4,093

Table 7. Locations (river mile) and dates of Pallid Sturgeon suspected to have migrated into the Missouri River from the Middle Mississippi River during spring 2005.

Tag	Location Tagged	Date Tagged	Last pre-spawn location	Last pre-spawn location date	First post-spawn location	First post-spawn location date	Days Elapsed
3982	116	10/21/2004	196	14-Apr	194.2	23-May	39
3984	44	11/18/2004	189.6	27-Apr	190.1	13-Jun	47
1560	189	12/1/2004	196	16-Apr	189.1	28-Jun	73
1559	189	12/3/2004	196	23-Apr	--	--	--
1594	44	12/14/2005	90.1	19-Apr	185.0	19-May	30
1569	125	4/5/2005	189.7	27-Apr	--	--	--

Table 8. Middle Mississippi River substrate types associated with number of Pallid Sturgeon contacts within each type. Pallids were located between Cairo, Illinois (river mile 0) and St. Louis, Missouri (river mile 200).

Substrate	Contacts	Percent	Cumulative frequency	Cumulative percent
Mud/silt	8	1.86	8	1.86
Sand	206	47.91	214	49.7
Sand/gravel	113	26.28	327	76.05
Rock	103	23.95	430	100

Table 9. Middle Mississippi River substrate types associated with number of Pallid Sturgeon contacts within each type. Spring spawn period represents data collected when water temperatures were 18 - 21°C. Pallids were located between Cairo, Illinois (river mile 0) and St. Louis, Missouri (river mile 200).

	Winter (prespawn)		Spring (spawn)		Summer/fall (post-spawn)	
Substrate	Counts	Percent	Counts	Percent	Counts	Percent
Mud / silt	3	2.1			3	4.6
Sand	60	42.0	28	43.8	43	66.2
Sand/gravel	37	25.9	19	29.7	12	18.5
Rock	43	30.1	17	26.6	7	10.8

Table 10. Middle Mississippi River water depth ranges and number of Pallid Sturgeon contacts within each range. Pallids were located between Cairo, Illinois (river mile 0) and St. Louis, Missouri (river mile 200).

Depth (m)	Contacts	Percent	Cumulative frequency	Cumulative percent
0-3	67	14.05	67	14.05
3-6	25	5.24	92	19.29
6-9	129	27.04	221	46.33
9-12	157	32.91	378	79.25
12-15	66	13.84	444	93.08
15-18	27	5.66	471	98.74
>18	6	1.26	477	100

Table 11. Water flow means for areas where Pallid Sturgeon were located and an ADCP survey was performed.

		Surface Speed		Bottom Speed		Depth	
Area (m)	Number of fish	Mean	Std.	Mean	Std.	Mean	Std.
25	16	95	39	90	58	6	3
50	16	96	36	98	56	5	3

Table 12. Likelihood ratio chi-square results determining if Pallid Sturgeon located during 2002 - 2005 in the middle Mississippi River were using habitats in a similar way within seasons and when summarized for all seasons. Statistical significance was assumed at P<0.01.

Likelihood chi-square 1

Season	Temperature range	Observations	X^2	df	*P* -value	Conclusion: using habitat differently?
Winter	0-10°C	73	75.42	32	< 0.0001	Yes
Spring	10-20°C	189	290.38	112	< 0.0001	Yes
Summer	>20°C	76	56.5	52	0.3106	No
Fall	10-20°C	7	NA	NA	NA	NA
All seasons		476	537.18	268	< 0.0001	Yes

Likelihood chi-square 2

Season	Temperature range	Observations	X^2	df	*P* -value	Conclusion: selective for habitats used?
Winter	0-10°C	73	174.25	36	< 0.0001	Yes
Spring	10-20°C	189	497.62	116	< 0.0001	Yes
Summer	>20°C	76	143.22	56	< 0.0001	Yes
Fall	10-20°C	7	NA	NA	NA	NA
All seasons		476	970.31	272	< 0.0001	Yes

Comparison of likelihood chi-square 1 and 2

Season	Temperature range	Observations	X^2	df	Critical Value at *p* =0.01	Conclusion: selective for specific habitat types?
Winter	0-10°C	73	98.83	4	13.277	Yes
Spring	10-20°C	189	207.24	4	13.277	Yes
Summer	>20°C	76	86.72	4	13.277	Yes
Fall	10-20°C	7	NA	NA	NA	NA
All seasons		476	433.13	4	13.277	Yes

Table 13. Habitat selectivity for Pallid Sturgeon located in the middle Mississippi River using ultrasonic transmitters from fall 2002 through summer 2005. Habitats were determined using a modified version of Cobb's GIS index. Habitat types were only included in the selectivity tests when each type represented at least 5% of the total river area and when at least four locations were made in the habitat. Wing dam habitats were combined to allow them to be included in the selectivity statistics. Island and tributary mouth habitats are included in this table despite their insignificant areas and no locations. They were not used for selectivity tests. Fall habitat selectivity could not be performed because of insufficient data. Asterisks denote significant selectivity.

Habitat	Area (ha)	Percent habitat	Locations	Selectivity index	Lower Bonferroni 95% CI	Upper Bonferroni 95% CI
			Winter (0-10°C)			
Wing Dams	2,596.5	7.1	40	5.391*	2.163	8.619
Main Channel	10,240.8	40.0	15	0.512	0.051	0.974
Side Channel	2,536.1	9.9	0	0.000	0.000	0.000
Channel border dike	3,539.1	13.8	4	0.395	0.000	0.936
Channel border open	6,630.0	25.9	14	0.739	0.000	1.549
Tributary mouth	13.4	0.1	0	0.000	0.000	0.000
Islands	61.7	0.3	0	0.000	0.000	0.000
			Spring (10-20°C)			
Wing Dams	2,596.5	7.1	97	5.050*	3.405	6.694
Main Channel	10,240.8	40.0	30	0.396	0.106	0.686
Side Channel	2,536.1	9.9	14	0.746	0.000	1.594
Channel border dike	3,539.1	13.8	16	0.611	0.068	1.154
Channel border open	6,630.0	25.9	32	0.652	0.274	1.031
Tributary mouth	13.4	0.1	0	0.000	0.000	0.000
Islands	61.7	0.3	0	0.000	0.000	0.000
			Summer (>20°C)			
Wing Dams	2596.5	7.1	36	4.661*	3.146	6.175
Main Channel	10,240.8	40.0	22	0.722	0.398	1.046
Side Channel	2,536.1	9.9	0	0.000	0.000	0.000
Channel border dike	3,539.1	13.8	1	0.095	0.000	0.318
Channel border open	6,630.0	25.9	17	0.862	0.203	1.520
Tributary mouth	13.4	0.1	0	0.000	0.000	0.000
Islands	61.7	0.3	0	0.000	0.000	0.000
			All Seasons			
Wing Dams	2,596.5	7.1	222	4.589*	3.412	5.766
Main Channel	10,240.8	40.0	104	0.545	0.362	0.727
Side Channel	2,536.1	9.9	15	0.317	0.000	0.000
Channel border dike	3,539.1	13.8	31	0.470	0.159	0.781
Channel border open	6,630.0	25.9	104	0.842	0.564	1.120
Tributary mouth	13.4	0.1	0	0.000	0.000	0.691
Islands	61.7	0.3	0	0.000	0.000	0.000

Table 14. Likelihood ratio chi-square results determining if Pallid Sturgeon in the middle Mississippi River were using habitats in a similar way during 2005. Statistical significance was assumed at $P<0.01$.

	Observations	X^2	df	*P* -value	Conclusion:
Likelihood chi-square 1	279	299.23	152	< 0.0001	Using habitat differently
Likelihood chi-square 2	279	520.05	156	< 0.0001	Selective for habitats used
Difference	279	220.82	4	13.277	Selective for specific habitat types

Table 15. Habitat selectivity for Pallid Sturgeon located in the middle Mississippi River using ultrasonic transmitters during 2005. Habitats were determined using a modified version of Cobb's GIS index. Habitat types were only included in the selectivity tests when each type represented at least 5% of the total river area and when at least four locations were made in the habitat. Wing dam habitats were combined to allow them to be included in the selectivity statistics. Island and tributary mouth habitats are included in this table despite their insignificant areas and no locations. They were not used for selectivity tests. Asterisks denote significant selectivity.

Habitat	Area (ha)	Percent habitat	Locations	Selectivity index	Bonferroni 95% CI	Bonferroni 95% CI
Wing Dams	2,596.5	7.1	120	4.232*	3.106	5.358
Main Channel	10,240.8	40.0	54	0.483	0.289	0.677
Side Channel	2,536.1	9.9	15	0.541	0.000	1.167
Channel border dike	3,539.1	13.8	18	0.466	0.009	0.922
Channel border open	6,630.0	25.9	72	0.994	0.649	1.339
Tributary mouth	13.4	0.1	0	0.000	0.000	0.000
Islands	61.7	0.3	0	0.000	0.000	0.000

Table 16. Likelihood ratio chi-square results for water discharge comparisons to determine if Pallid Sturgeon in the middle Mississippi River were using habitats in a similar way within level ranges. Water discharges (cfs) were procured from USGS data at St. Louis. Statistical significance was assumed at P<0.01.

Likelihood chi-square 1

Water levels	Water discharge range (cfs)	Observations	X^2	df	*P* -value	Conclusion: using habitat differently?
Low	0-165,000	152	156.45	72	< 0.0001	Yes
Medium	166,000-270,000	76	150.86	76	< 0.0001	Yes
High	>270,000	45	97.89	124	0.9597	No

Likelihood chi-square 2

Water levels	Water level range (feet)	Observations	X^2	df	*P* -value	Conclusion: selective for habitats used?
Low	0-6	152	358.08	76	< 0.0001	Yes
Medium	6-13	76	275.05	80	< 0.0001	Yes
High	>13	45	143.34	128	0.1675	No

Comparison of likelihood chi-square 1 and 2

Water levels	Water level range (feet)	Observations	X^2	df	Critical Value at *p* =0.01	Conclusion: selective for specific habitat types?
Low	0-6	73	201.63	4	13.277	Yes
Medium	6-13	76	124.19	4	13.277	Yes
High	>13	45	45.45	4	13.277	Yes

Table 17. Habitat selectivity at three different water discharge levels for Pallid Sturgeon located in the middle Mississippi River using ultrasonic transmitters from fall 2002 through summer 2005. Water discharges were procured from USGS data at St. Louis, and level ranges are described as: Low levels = 0-165,000 cfs; Medium levels =166,000-270,000 cfs; High = 270,000+ cfs. Asterisks denote significant selectivity.

Habitat	Area (ha)	Percent habitat	Locations	Selectivity index	Lower Bonferroni 95% CI	Upper Bonferroni 95% CI
			Low discharge levels			
Wing Dams	2,596.5	7.1	89	5.761*	3.560	7.962
Main Channel	10,240.8	40.0	40	0.656	0.218	1.094
Side Channel	2,536.1	9.9	1	0.066	0.000	0.224
Channel border dike	3,539.1	13.8	6	0.258	0.000	0.710
Channel border open	6,630.0	25.9	16	0.406	0.047	0.764
Tributary mouth	13.4	0.1	0	0.000	0.000	0.000
Islands	61.7	0.3	0	0.000	0.000	0.000
			Medium discharge levels			
Wing Dams	2,596.5	7.1	58	4.259*	2.788	5.729
Main Channel	10,240.8	40.0	14	0.261	0.074	0.448
Side Channel	2,536.1	9.9	12	0.902	0.000	1.841
Channel border dike	3,539.1	13.8	12	0.646	0.000	1.315
Channel border open	6,630.0	25.9	38	1.092	0.656	1.529
Tributary mouth	13.4	0.1	0	0.000	0.000	0.000
Islands	61.7	0.3	0	0.000	0.000	0.000
			High discharge levels			
Wing Dams	2,596.5	7.1	20	4.373*	2.239	6.506
Main Channel	10,240.8	40.0	10	0.554	0.170	0.938
Side Channel	2,536.1	9.9	0	0.000	0.000	0.000
Channel border dike	3,539.1	13.8	2	0.321	0.000	0.853
Channel border open	6,630.0	25.9	13	1.113	0.404	1.822
Tributary mouth	13.4	0.1	0	0.000	0.000	0.000
Islands	61.7	0.3	0	0.000	0.000	0.000

Table 18. Likelihood ratio chi-square results for water level comparisons to determine if Pallid Sturgeon in the middle Mississippi River were using habitats in a similar way within level ranges. Water levels (feet) were procured from USGS data at St. Louis. Statistical significance was assumed at $P<0.01$.

Likelihood chi-square 1

Water levels	Water level range (feet)	Observations	X^2	df	*P* -value	Conclusion: using habitat differently?
Low	0-6	86	82.28	36	< 0.0001	Yes
Medium	6-13	140	183.95	96	< 0.0001	Yes
High	>13	75	109.73	60	< 0.0001	Yes

Likelihood chi-square 2

Water levels	Water level range (feet)	Observations	X^2	df	*P* -value	Conclusion: selective for habitats used?
Low	0-6	86	249.64	40	< 0.0001	Yes
Medium	6-13	140	332.58	100	< 0.0001	Yes
High	>13	75	179.94	64	< 0.0001	Yes

Comparison of likelihood chi-square 1 and 2

Water levels	Water level range (feet)	Observations	X^2	df	Critical Value at $p=0.01$	Conclusion: selective for specific habitat types?
Low	0-6	73	167.36	4	13.277	Yes
Medium	6-13	165	148.63	4	13.277	Yes
High	>13	60	70.21	4	13.277	Yes

Table 19. Habitat selectivity at three different water levels for Pallid Sturgeon located in the middle Mississippi River using ultrasonic transmitters from fall 2002 through summer 2005. Water levels (feet) were procured from USGS data at St. Louis, and level ranges are described as: Low levels = 0-6; Medium levels = 6-13; High = 13+. Asterisks denote significant selectivity.

Habitat	Area (ha)	Percent habitat	Locations	Selectivity index	Lower Bonferroni 95% CI	Upper Bonferroni 95% CI
			Low water levels			
Wing Dams	2,596.50	7.1	56	6.407*	3.606	9.207
Main Channel	10,240.8	40.0	23	0.667	0.088	1.246
Side Channel	2,536.1	9.9	0	0.000	0.000	0.000
Channel border dike	3,539.1	13.8	3	0.252	0.000	0.662
Channel border open	6,630.0	25.9	4	0.179	0.000	0.440
Tributary mouth	13.4	0.1	0	0.000	0.000	0.000
Islands	61.7	0.3	0	0.000	0.000	0.000
			Medium water levels			
Wing Dams	2,596.50	7.1	69	4.849*	3.373	6.325
Main Channel	10,240.8	40.0	20	0.356	0.096	0.617
Side Channel	2,536.1	9.9	6	0.432	0.000	1.175
Channel border dike	3,539.1	13.8	12	0.619	0.061	1.176
Channel border open	6,630.0	25.9	33	0.908	0.458	1.358
Tributary mouth	13.4	0.1	0	0.000	0.000	0.000
Islands	61.7	0.3	0	0.000	0.000	0.000
			High water levels			
Wing Dams	2,596.50	7.1	33	4.329*	2.250	6.049
Main Channel	10,240.8	40.0	8	0.266	0.062	0.470
Side Channel	2,536.1	9.9	7	0.940	0.000	1.941
Channel border dike	3,539.1	13.8	7	0.674	0.000	1.418
Channel border open	6,630.0	25.9	20	1.027	0.324	1.731
Tributary mouth	13.4	0.1	0	0.000	0.000	0.000
Islands	61.7	0.3	0	0.000	0.000	0.000

Table 20. Likelihood ratio chi-square results for sinuosity comparison to determine if Pallid Sturgeon in the middle Mississippi River were using habitats in a similar way within seasons and when summarize for all seasons. Statistical significance was assumed at P<0.01.

Likelihood chi-square 1

Season	Temperature range	Observations	X^2	df	*P* -value	Conclusion: using habitat differently?
Winter	0-10°C	73	124.89	24	< 0.0001	Yes
Spring	10-20°C	165	242.71	72	< 0.0001	Yes
Summer	>20°C	60	84.59	30	< 0.0001	Yes
Fall	10-20°C	7	NA	NA	NA	NA
All seasons		386	455.5	123	< 0.0001	Yes

Likelihood chi-square 2

Season	Temperature range	Observations	X^2	df	*P* -value	Conclusion: selective for habitats used?
Winter	0-10°C	73	132.47	27	< 0.0001	Yes
Spring	10-20°C	165	257.35	75	< 0.0001	Yes
Summer	>20°C	60	87.73	33	< 0.0001	Yes
Fall	10-20°C	7	NA	NA	NA	NA
All seasons		386	463.7	126	< 0.0001	Yes

Comparison of likelihood chi-square 1 and 2

Season	Temperature range	Observations	X^2	df	Critical Value at *p* =0.01	Conclusion: selective for specific habitat types?
Winter	0-10°C	73	7.58	3	11.345	No
Spring	10-20°C	165	14.64	3	11.345	Yes
Summer	>20°C	60	3.14	3	11.345	No
Fall	10-20°C	7	NA	NA	NA	NA
All seasons		386	8.2	3	11.345	No

Table 21. Sinuosity habitat selectivity for Pallid Sturgeon located in the middle Mississippi River using ultrasonic transmitters from fall 2002 through summer 2005. Habitats were determined using ArcMap 9.1. Asterisks denote significant selectivity.

Habitat	Area (ha)	Percent habitat	Locations	Selectivity index	Lower Bonferroni 95% CI	Upper Bonferroni 95% CI
			Winter (0-10°C)			
Inside bend	8,628.1	41.4	21	0.688	0.172	1.204
Crossover	5,026.2	24.1	17	0.956	0.000	2.037
Outside bend	4,019.9	19.3	22	1.547	0.000	3.392
Straight reach	2,960.3	14.2	13	1.241	0.000	3.080
			Spring (10-20°C)			
Inside bend	8,628.1	41.4	89	1.290	0.831	1.749
Crossover	5,026.2	24.1	35	0.871	0.269	1.473
Outside bend	4,019.9	19.3	30	0.933	0.115	1.751
Straight reach	2,960.3	14.2	11	0.465	0.000	1.098
			Summer (>20°C)			
Inside bend	8,628.1	41.4	26	1.036	0.595	1.478
Crossover	5,026.2	24.1	10	0.684	0.000	1.381
Outside bend	4,019.9	19.3	16	1.369	0.000	2.759
Straight reach	2,960.3	14.2	8	0.929	0.000	2.028
			All Seasons			
Inside bend	8,628.1	41.4	175	1.084	0.776	1.393
Crossover	5,026.2	24.1	98	1.042	0.609	1.476
Outside bend	4,019.9	19.3	76	1.011	0.269	1.752
Straight reach	2,960.3	14.2	37	0.668	0.119	1.217
			All Seasons with tailwater			
Tailwater	212.5	1.0	28	6.448*	0.763	12.132
Inside bend	8,628.1	41.4	179	1.013	0.710	1.315
Crossover	5,026.2	24.1	106	1.030	0.620	1.439
Outside bend	4,019.9	19.3	77	0.935	0.222	1.648
Straight reach	2,960.3	14.2	37	0.610	0.092	1.129

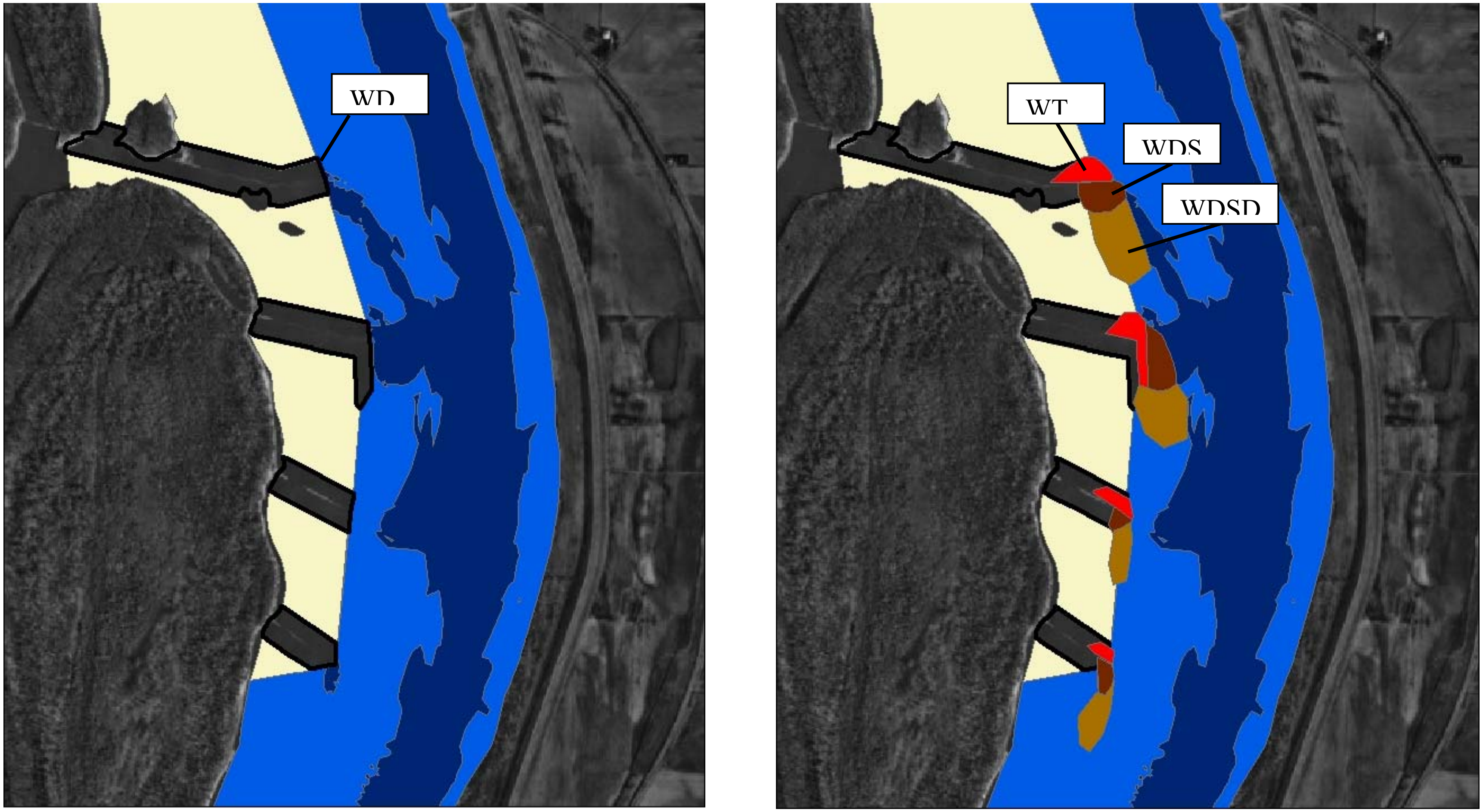


Figure 1. Images of the Cobb classification for the middle Mississippi River before and after the addition of specific wing dam shape files. Acronyms represent the habitat types as follow: WTU = Wing dam tip upstream; WDS = wing dam scour; WDSD = wing dam scour downstream.

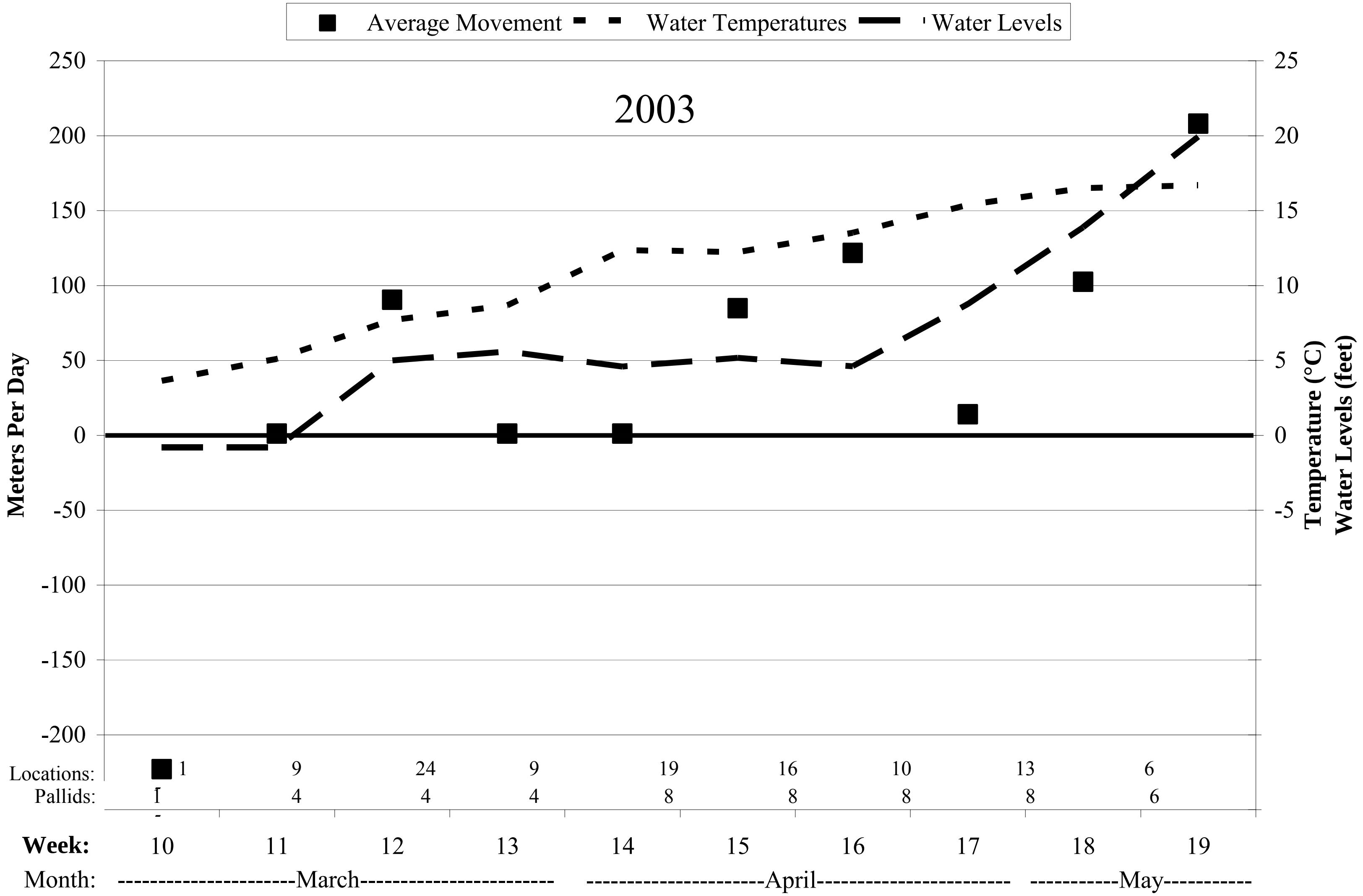


Figure 2. Average distances moved for Pallid Sturgeons implanted with sonic transmitters, released in the middle Mississippi River, and located during spring 2005. Locations and Pallids (bottom left of chart) represent the total number of locations made and number of individuals located in a given week. Negative meters per day indicates downriver movement; positive represents upriver movement.

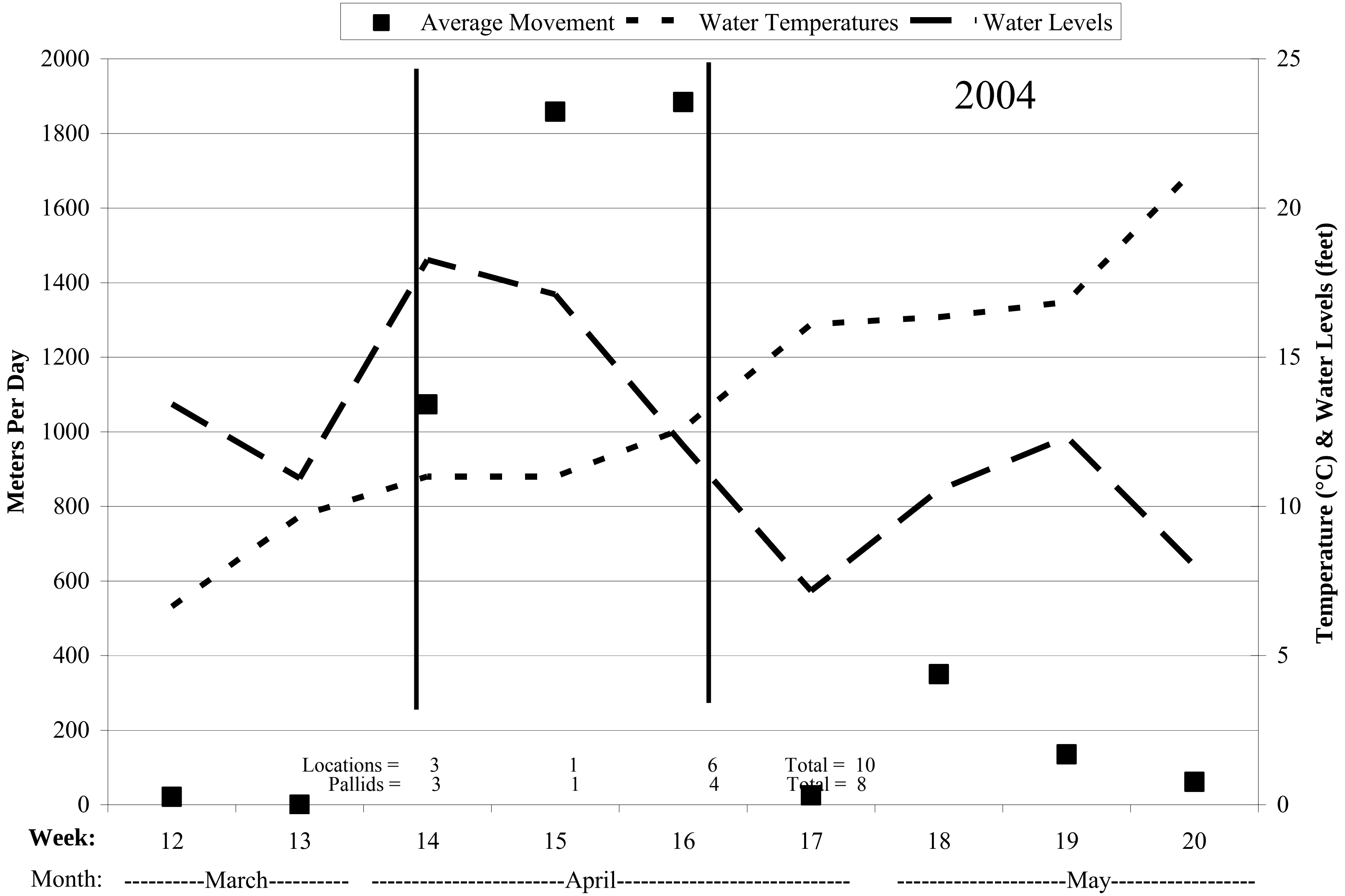


Figure 3. Average distances moved for Pallid Sturgeons implanted with sonic transmitters, released in the middle Mississippi River, and located during spring 2005. Locations and Pallids represent the total number of locations made and number of individuals located in a given week. Area between vertical bars represents postulated pre-spawn movement.

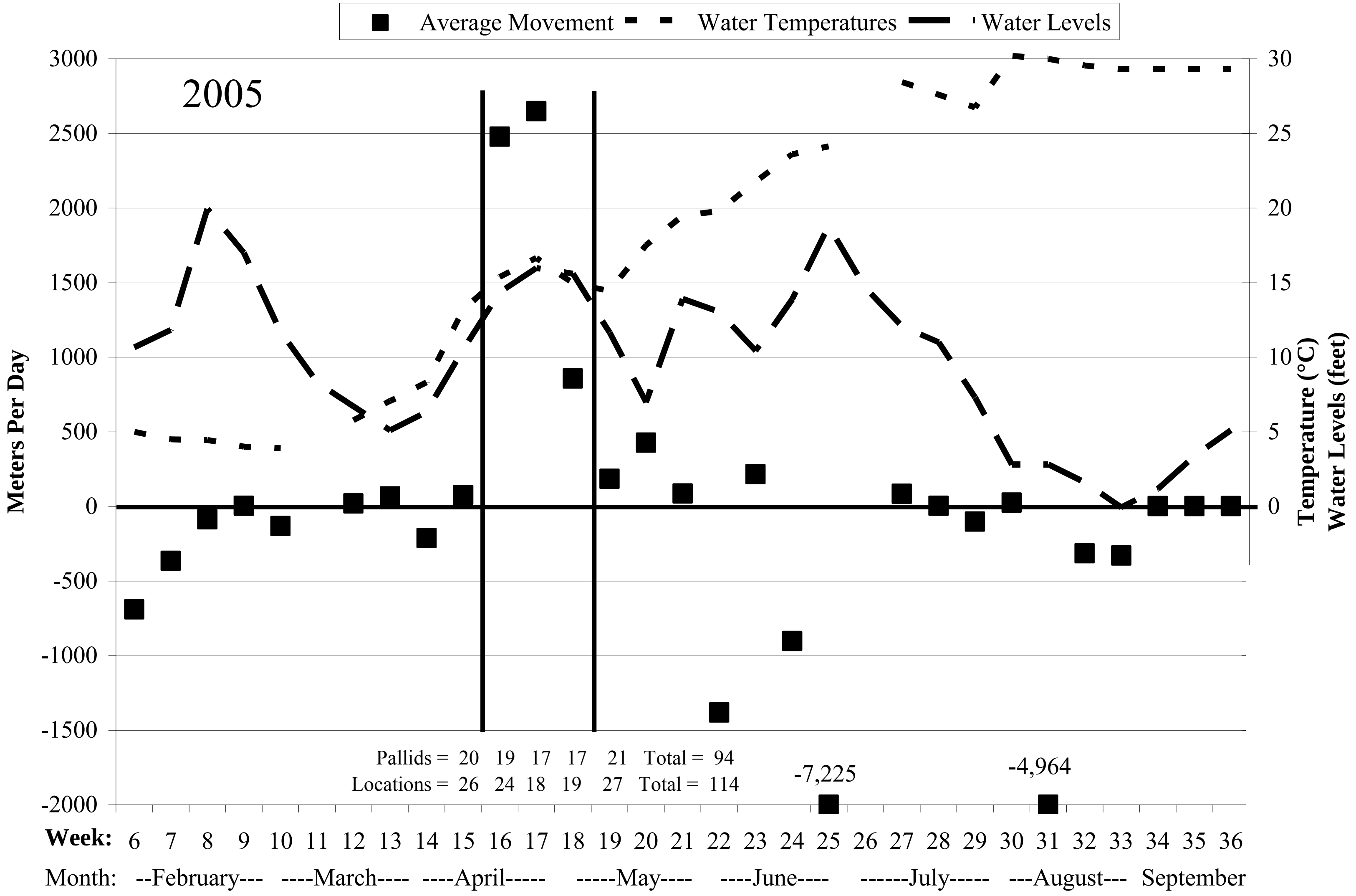


Figure 4. Average distances moved for Pallid Sturgeons implanted with sonic transmitters, released in the middle Mississippi River, and located during spring 2005. Locations and Pallids represent the total number of locations made and number of individuals located in a given week. Area between vertical bars represents postulated pre-spawn movement. Negative meters per day indicates downriver movement; positive represents upriver movement.

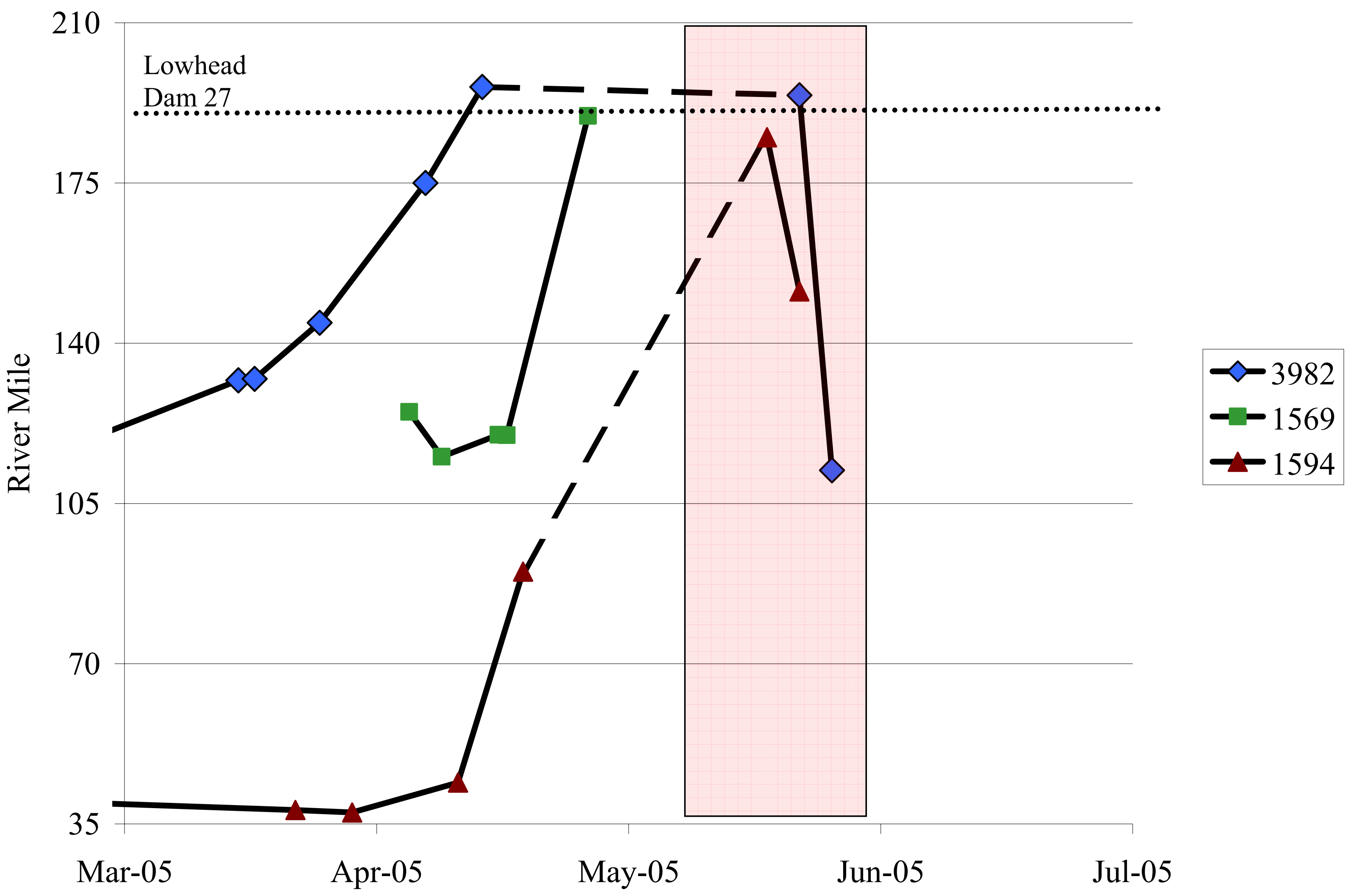


Figure 5. Observed movements of Pallid Sturgeon in spring 2005 in the middle Mississippi River below Lock and Dam 27 (Chain of Rocks, St. Louis, Missouri). Markers indicate individual relocations, red box denotes spawning period. The dotted line represents lowhead Dam 27. Dashed lines represent periods when the fish were suspected to have moved upriver beyond our tracking effort.

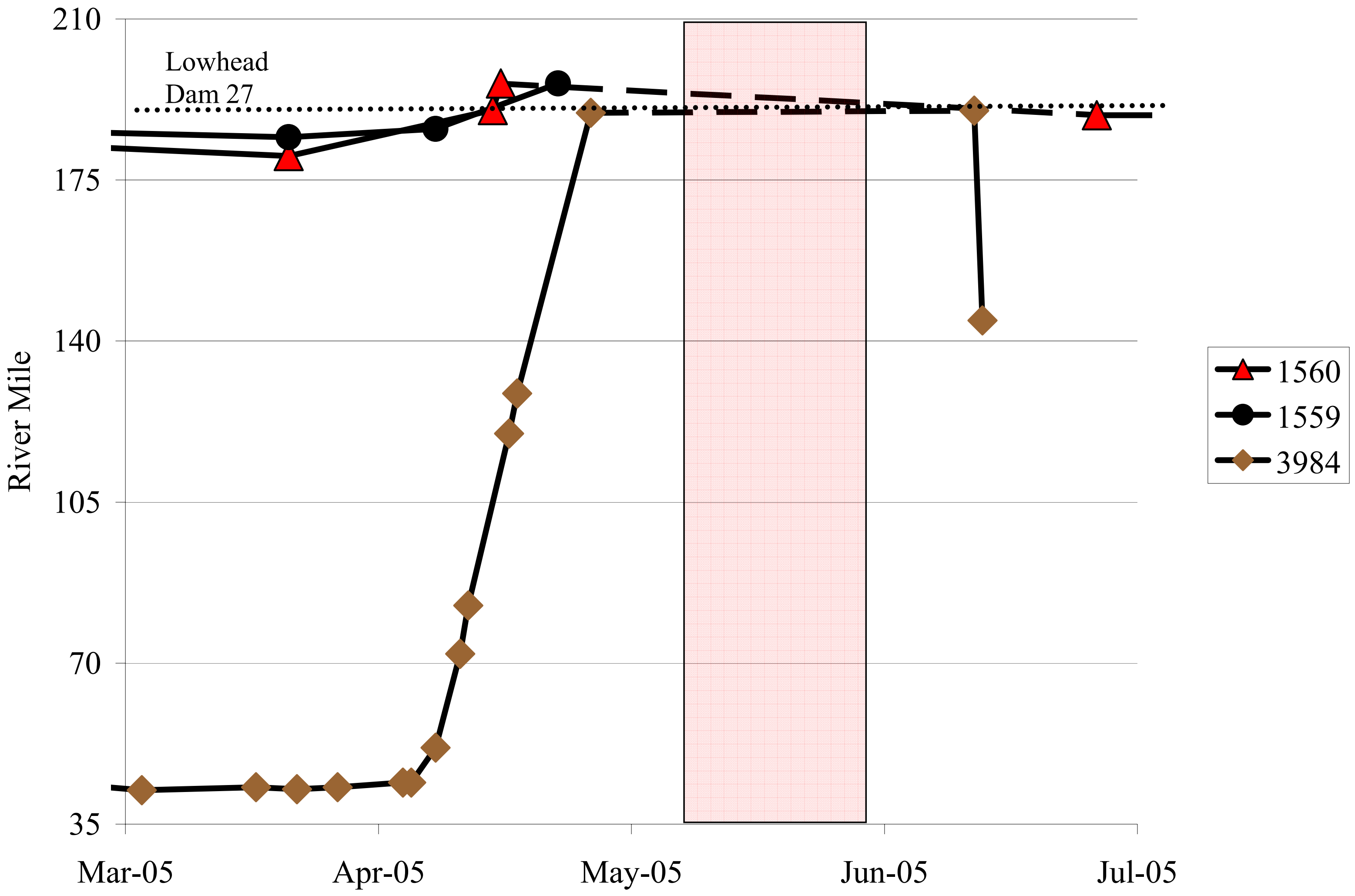


Figure 6. Observed movements of Pallid Sturgeon in spring 2005 in the middle Mississippi River below Lock and Dam 27 (Chain of Rocks, St. Louis, Missouri). Markers indicate individual relocations, red box denotes spawning period. The dotted line represents lowhead Dam 27. Dashed lines represent periods when the fish were suspected to have moved upriver beyond our tracking effort.

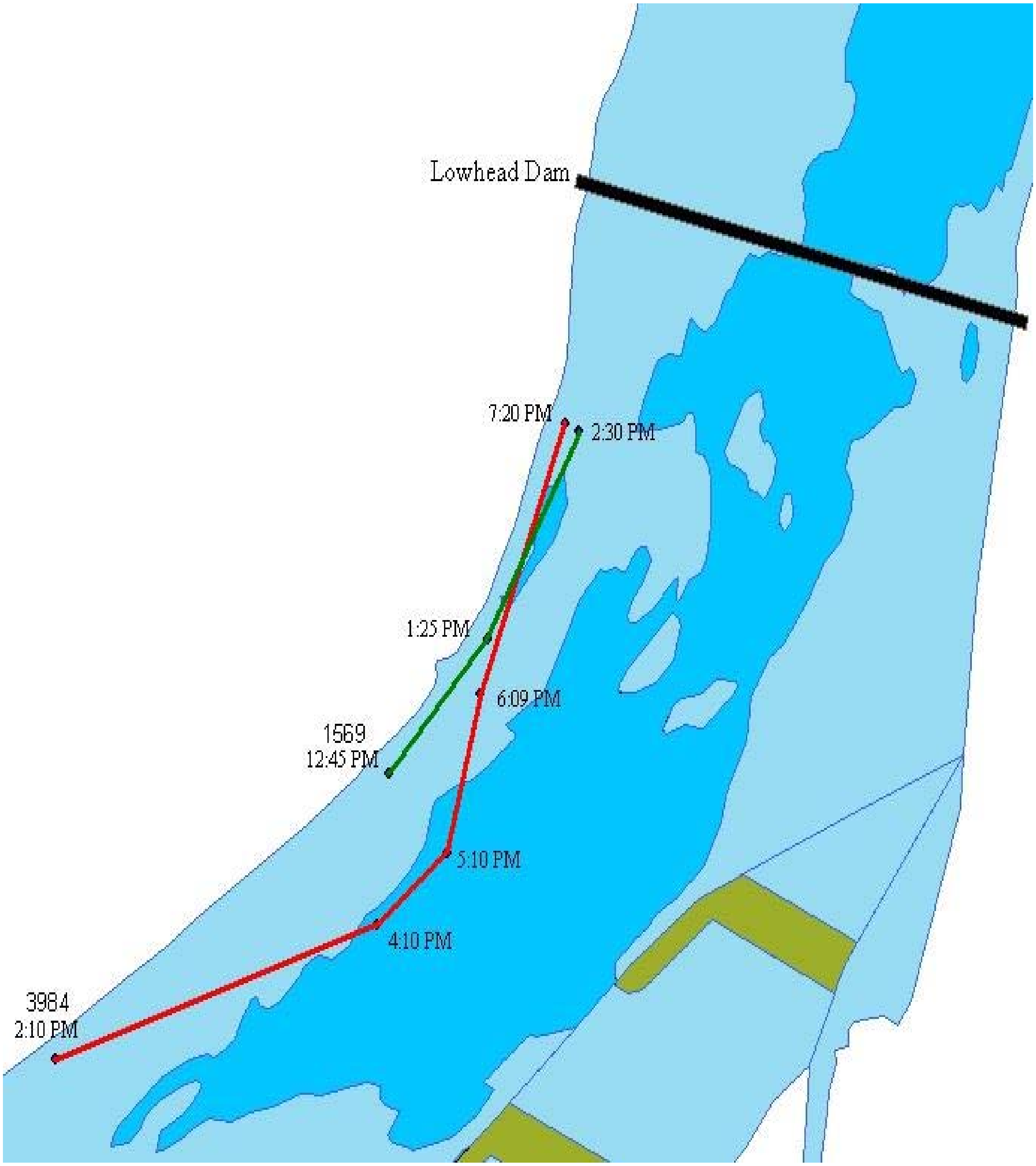


Figure 7. Locations of two Pallid Sturgeons implanted with sonic transmitters (3984 and 1569) during an hourly survey below Lock and Dam 27 in the middle Mississippi River (RM190).

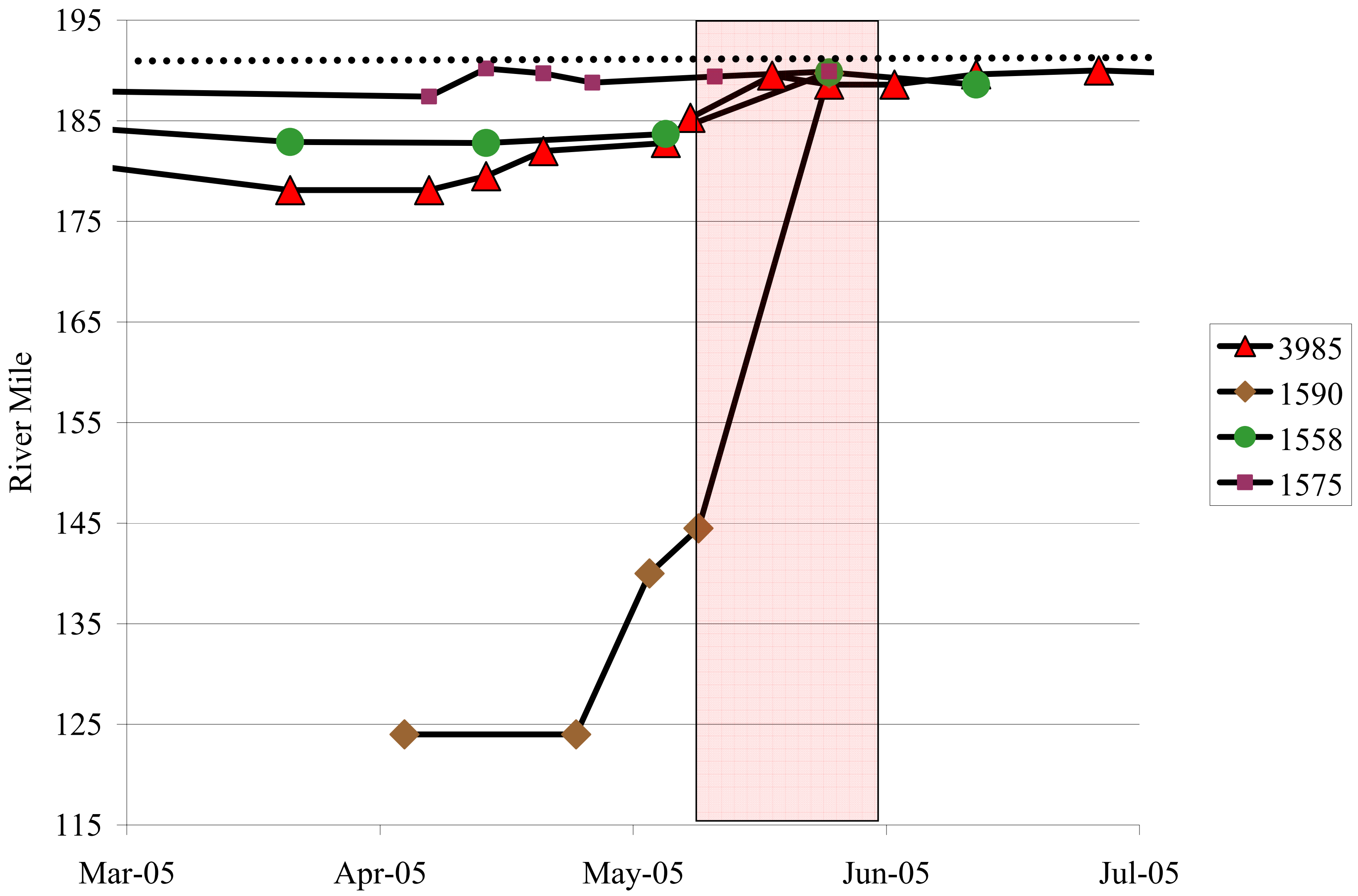


Figure 8. Observed movements of Pallid Sturgeon in spring 2005 in the middle Mississippi River below Lock and Dam 27 (Chain of Rocks, St. Louis, Missouri). Markers indicate individual relocations, red box denotes spawning period. The dotted line represents lowhead Dam 27.

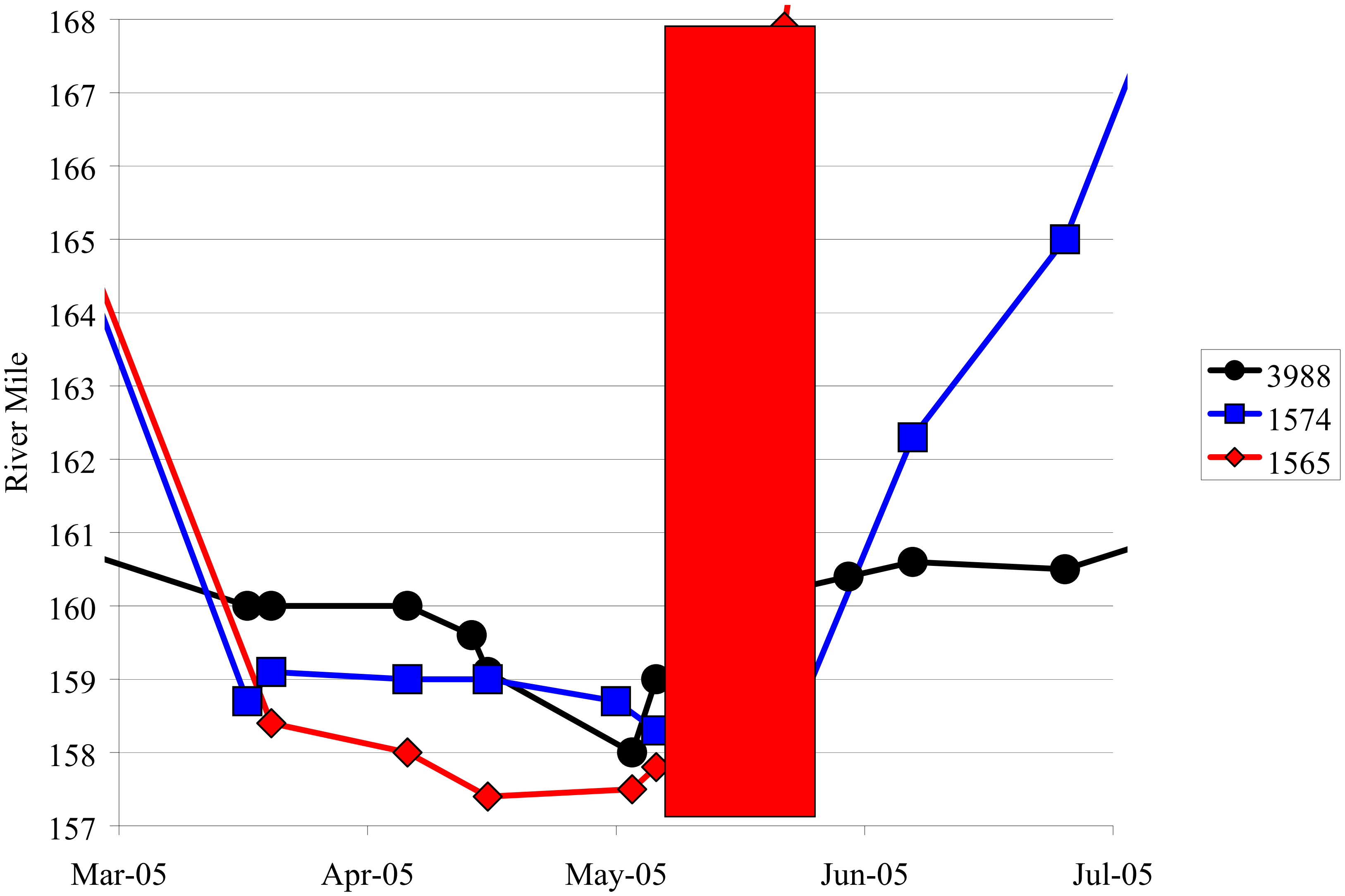


Figure 9. Observed movements of Pallid Sturgeon in spring 2005 below the Meremac River and middle Mississippi River confluence. Markers indicate individual relocations, red box denotes spawning period. The sturgeon were surgically implanted with sonic transmitters.

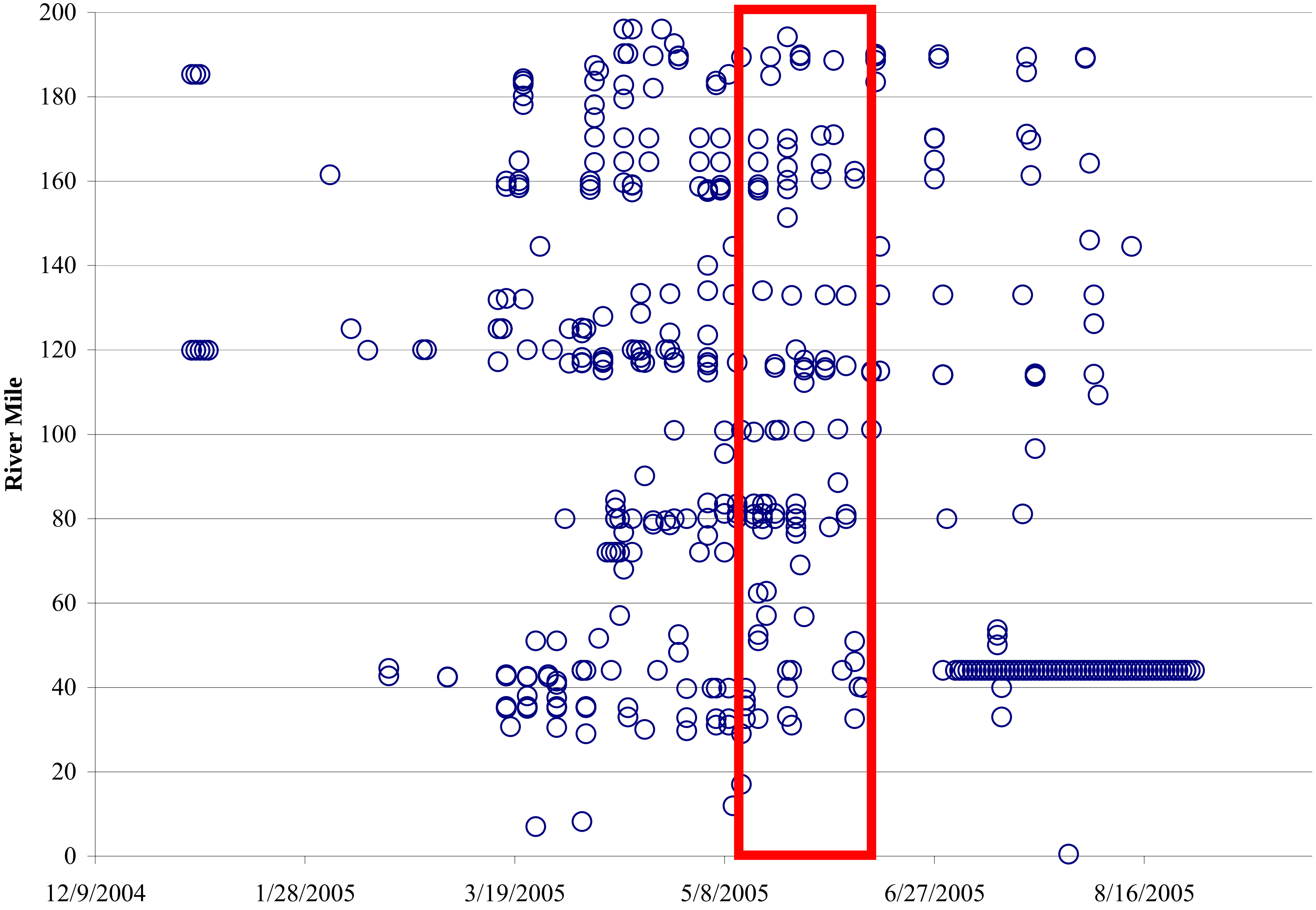


Figure 10. Locations of Pallid Sturgeon in the middle Mississippi River during spring 2005. Markers indicate individual relocations. The fish were located by manual tracking and with stationary receiver s located throughout the river.

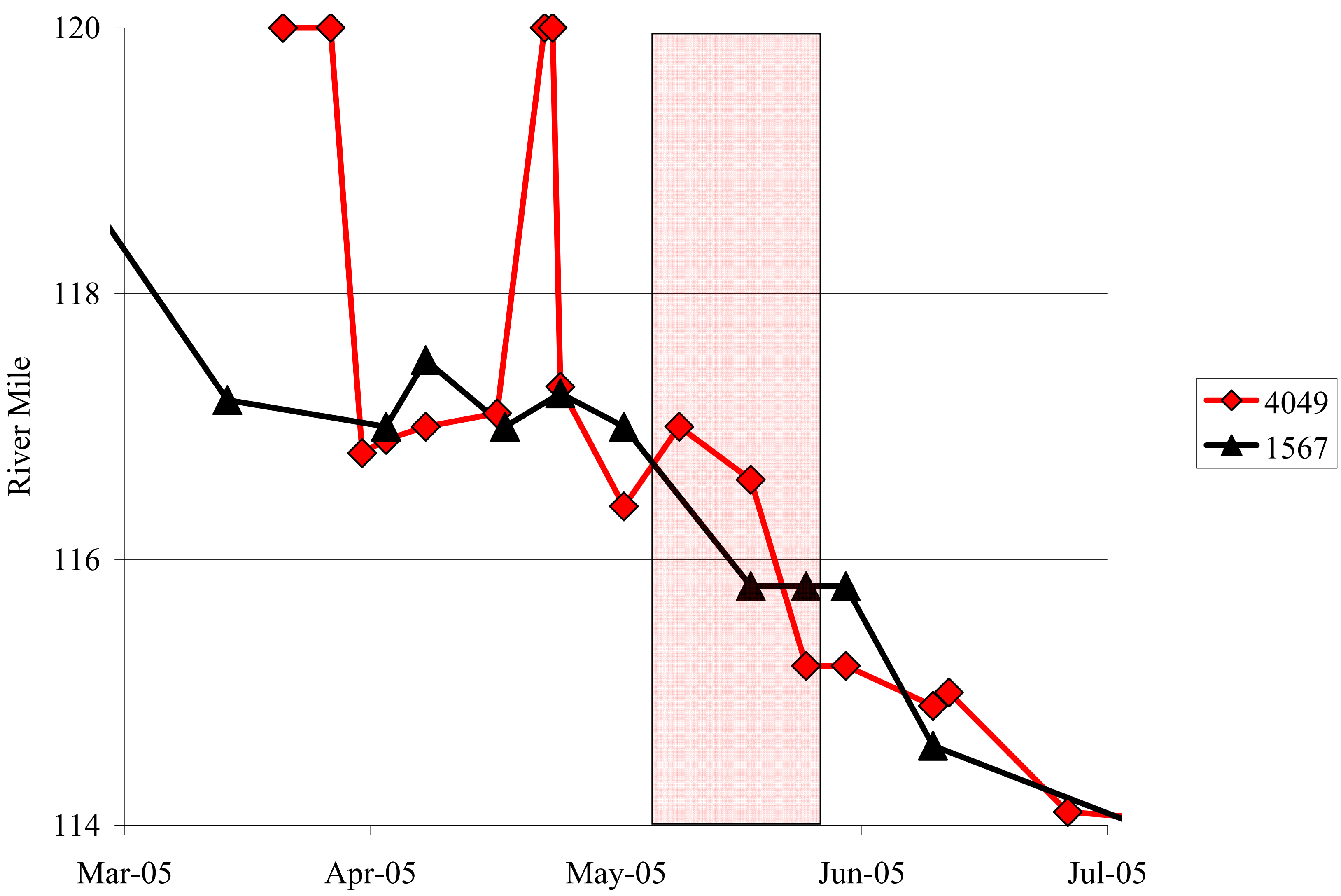


Figure 11. Observed movements of Pallid Sturgeon in spring 2005 below the Kasatkia River and middle Mississippi River confluence. Markers indicate individual relocations, red box denotes spawning period. The sturgeon were surgically implanted with sonic transmitters.

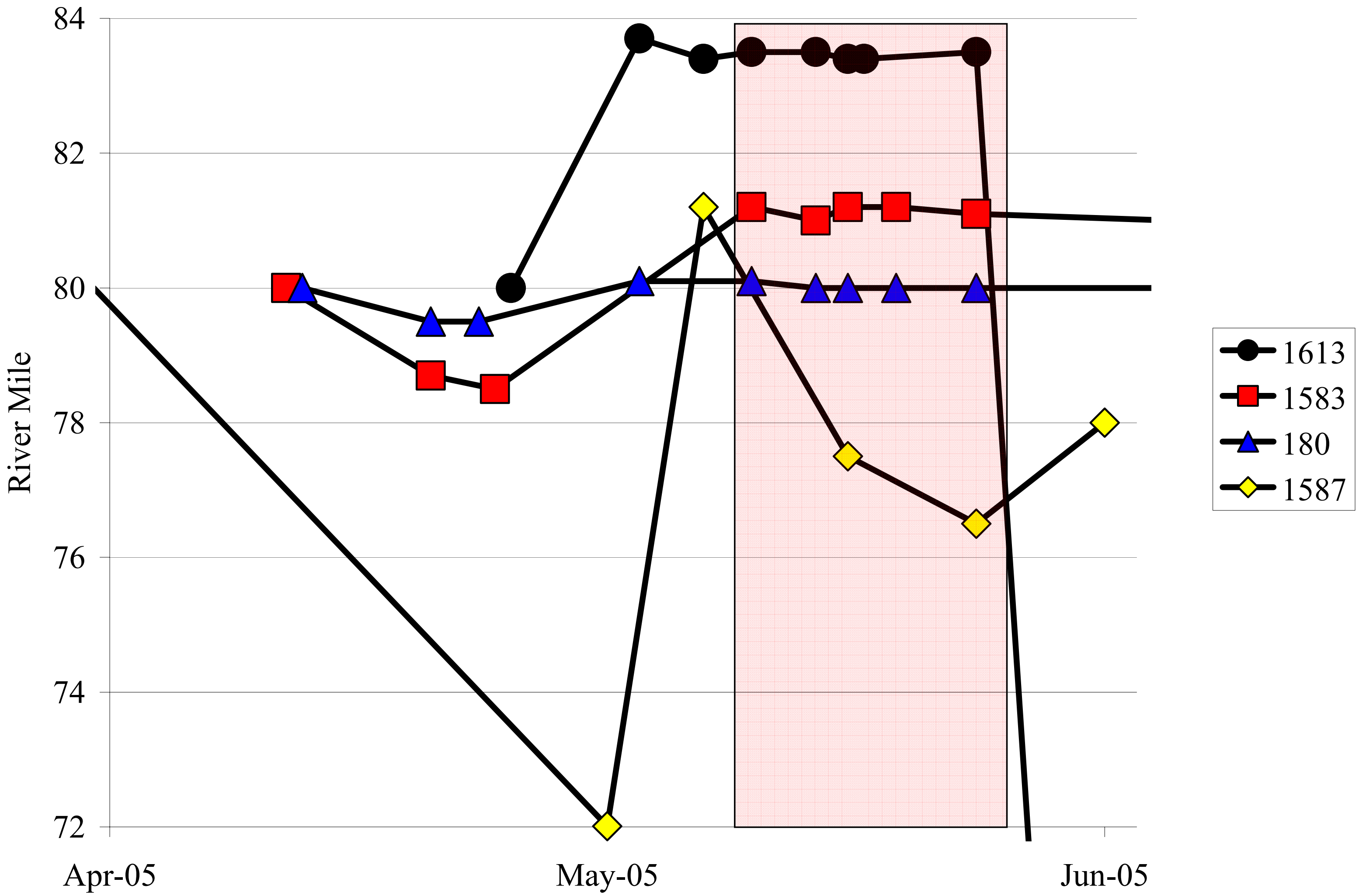


Figure 12. Observed movements of Pallid Sturgeon near Grand Tower, Missouri, in the middle Mississippi River during spring 2005. Markers indicate individual relocations.

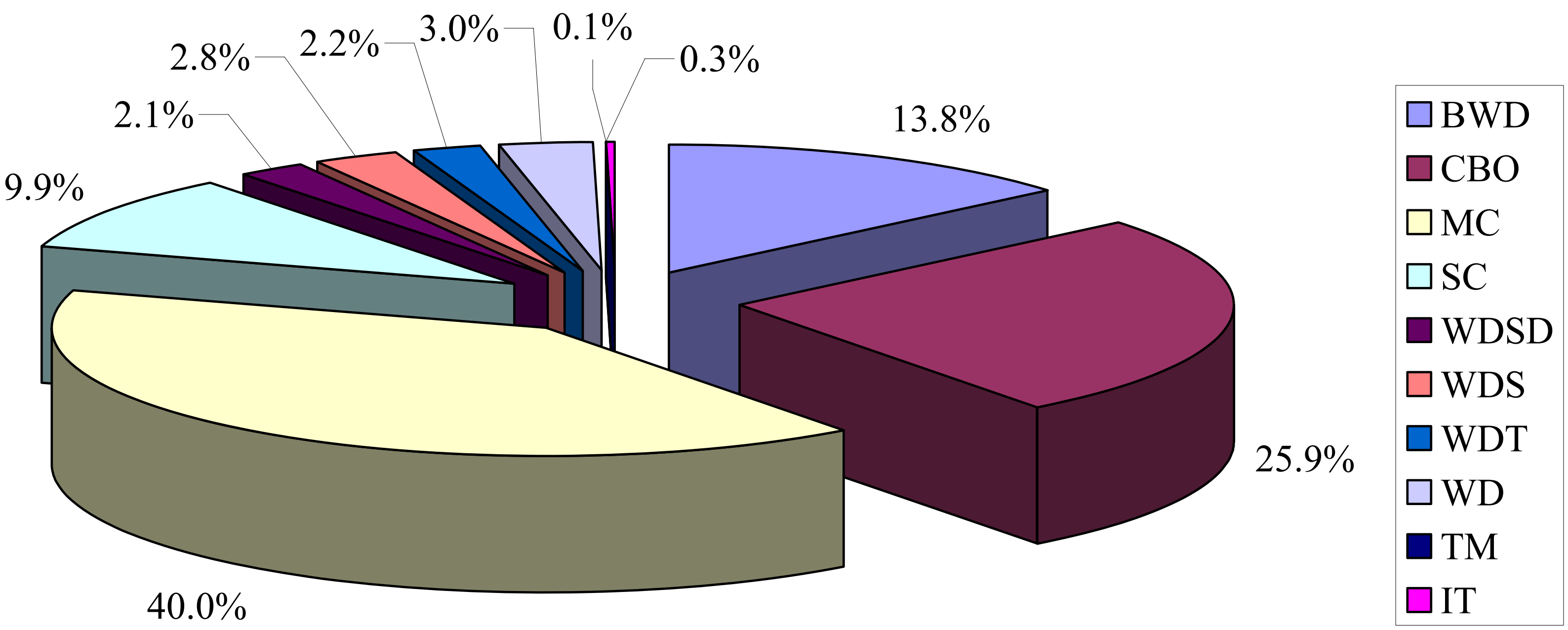


Figure 13. Habitat availability to fish in the middle Mississippi River. Acronyms represent the following: BWD: between wing dikes; CBO: channel border open (25.9%); MC: main channel (40.0%); SC: side channel (9.9%); WDSD: scour area below wing dam (2.1%); WDS: scour area at tip of wing dam (2.8%); WDT: wing dam tip (2.2%); WD: wing dam structure (3.0%); TM: tributary mouth (0.1%); IT: island tip (0.3%).

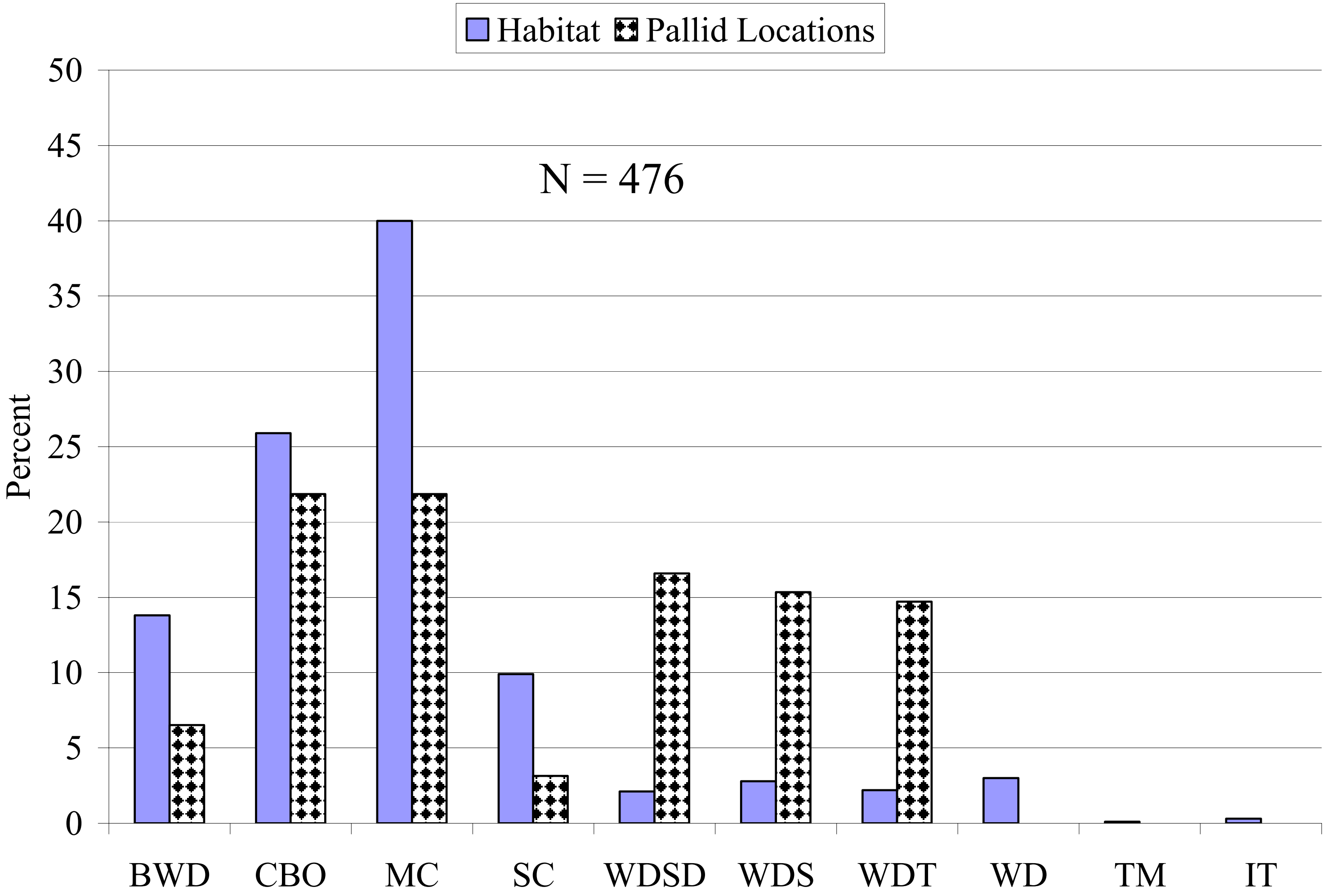


Figure 14. Percent of habitat available in the middle Mississippi River versus the percent of that Pallid Sturgeon were located in those habitats during 2002 - 2005. Habitat acronyms represent the following: BWD: between wing dikes; CBO: channel border open (25.9%); MC: main channel (40.0%); SC: side channel (9.9%); WDSD: scour area below wing dam (2.1%); WDS: scour area at tip of wing dam (2.8%); WDT: wing dam tip (2.2%); WD: wing dam structure (3.0%); TM: tributary mouth (0.1%); IT: island tip (0.3%).

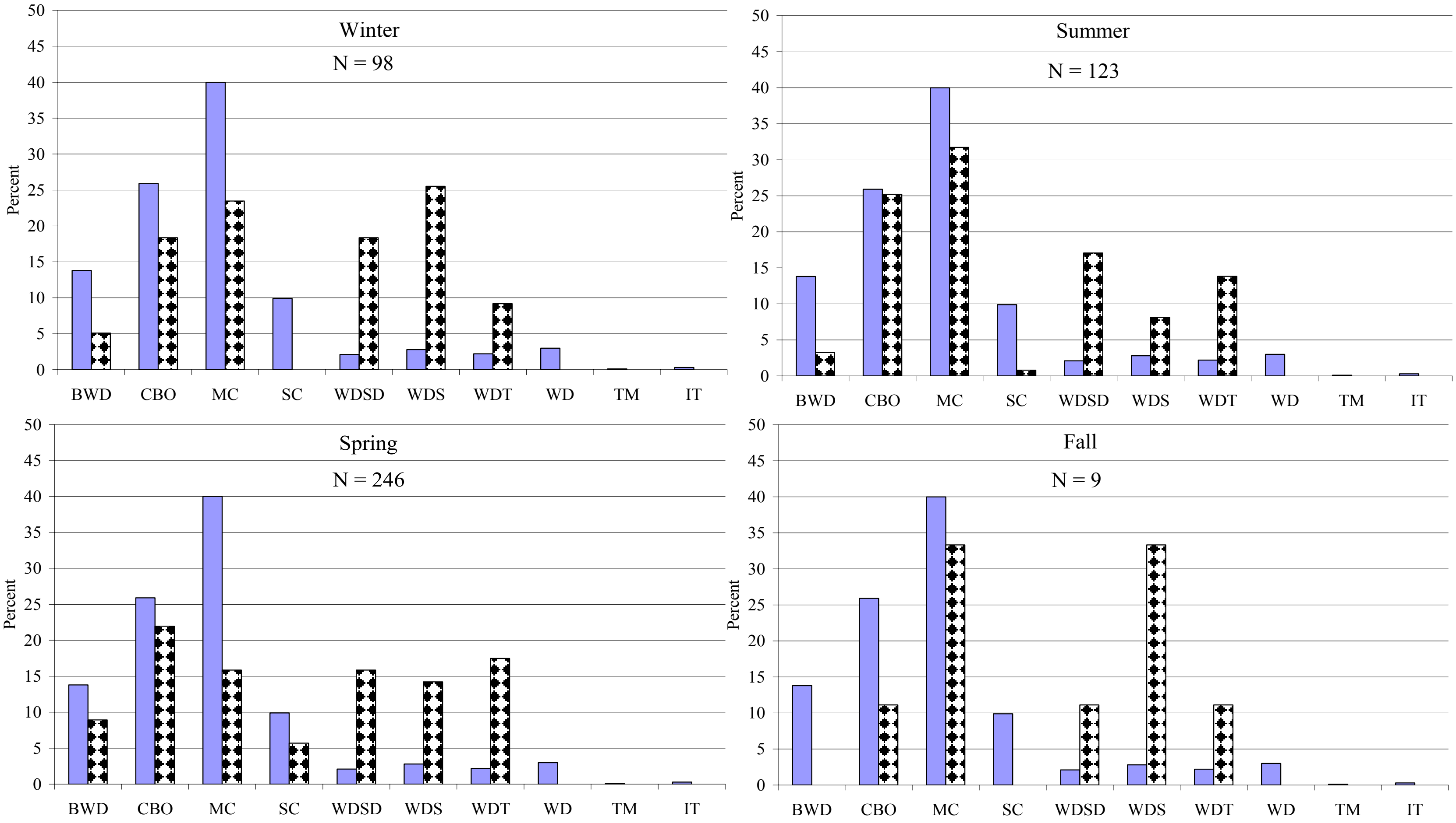


Figure 15. Percent of habitat available in the middle Mississippi River versus the percent of that Pallid Sturgeon were located in those habitats during for each season during 2002 - 2005. Habitat availability represented with blue bars. Acronyms represent the following: BWD: between wing dikes; CBO: channel border open (25.9%); MC: main channel (40.0%); SC: side channel (9.9%); WDSD: scour area below wing dam (2.1%); WDS: scour area at tip of wing dam (2.8%); WDT: wing dam tip (2.2%); WD: wing dam structure (3.0%); TM: tributary mouth (0.1%); IT: island tip (0.3%).

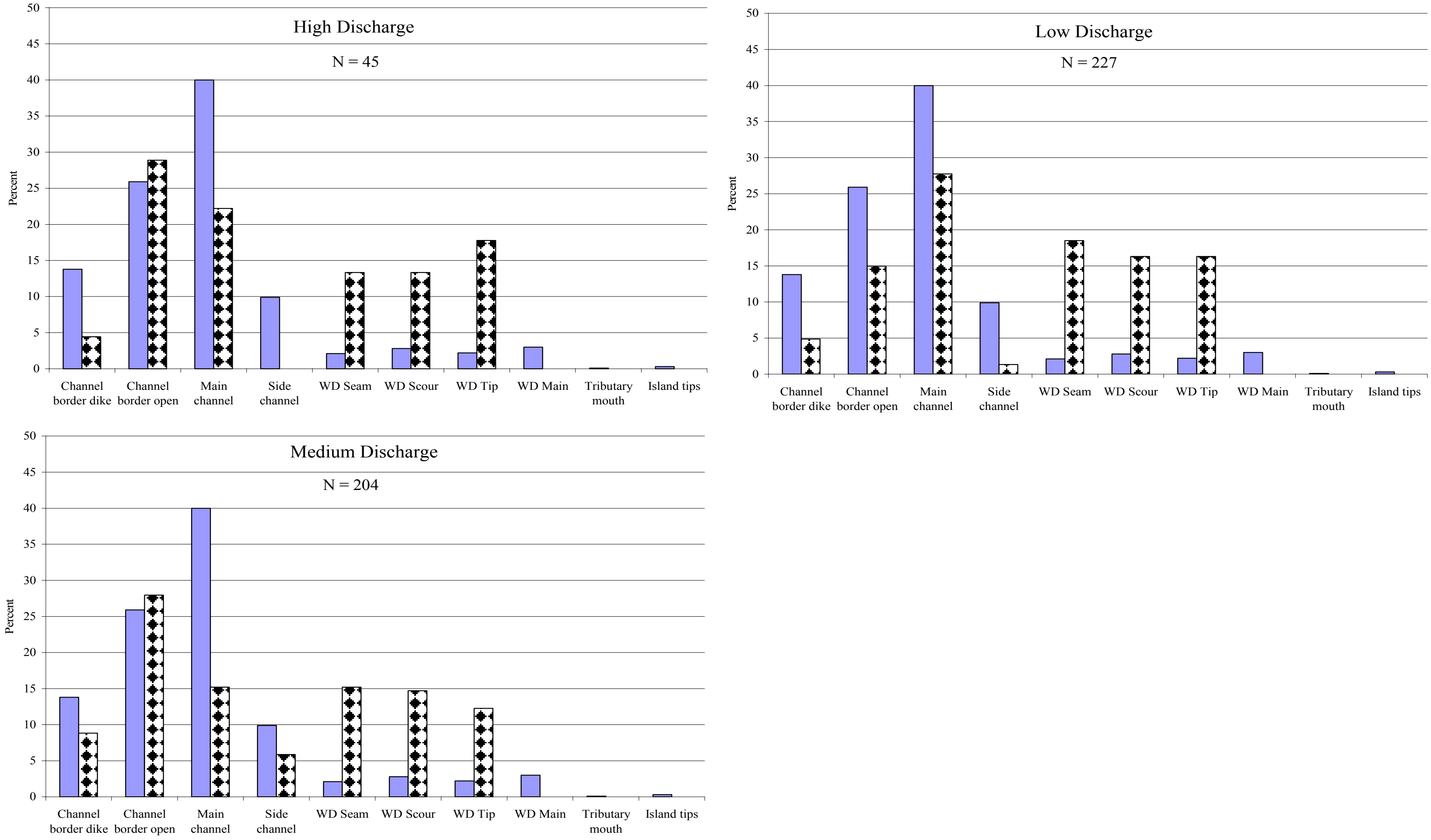


Figure 16. Percent of habitat available in the middle Mississippi River versus the percent of that Pallid Sturgeon were located in those habitats during for each water discharge level during 2002 - 2005. Habitat availability represented with blue bars. Acronyms represent the following: BWD: between wing dikes; CBO: channel border open (25.9%); MC: main channel (40.0%); SC: side channel (9.9%); WDSD: scour area below wing dam (2.1%); WDS: scour area at tip of wing dam (2.8%); WDT: wing dam tip (2.2%); WD: wing dam structure (3.0%); TM: tributary mouth (0.1%); IT: island tip (0.3%).

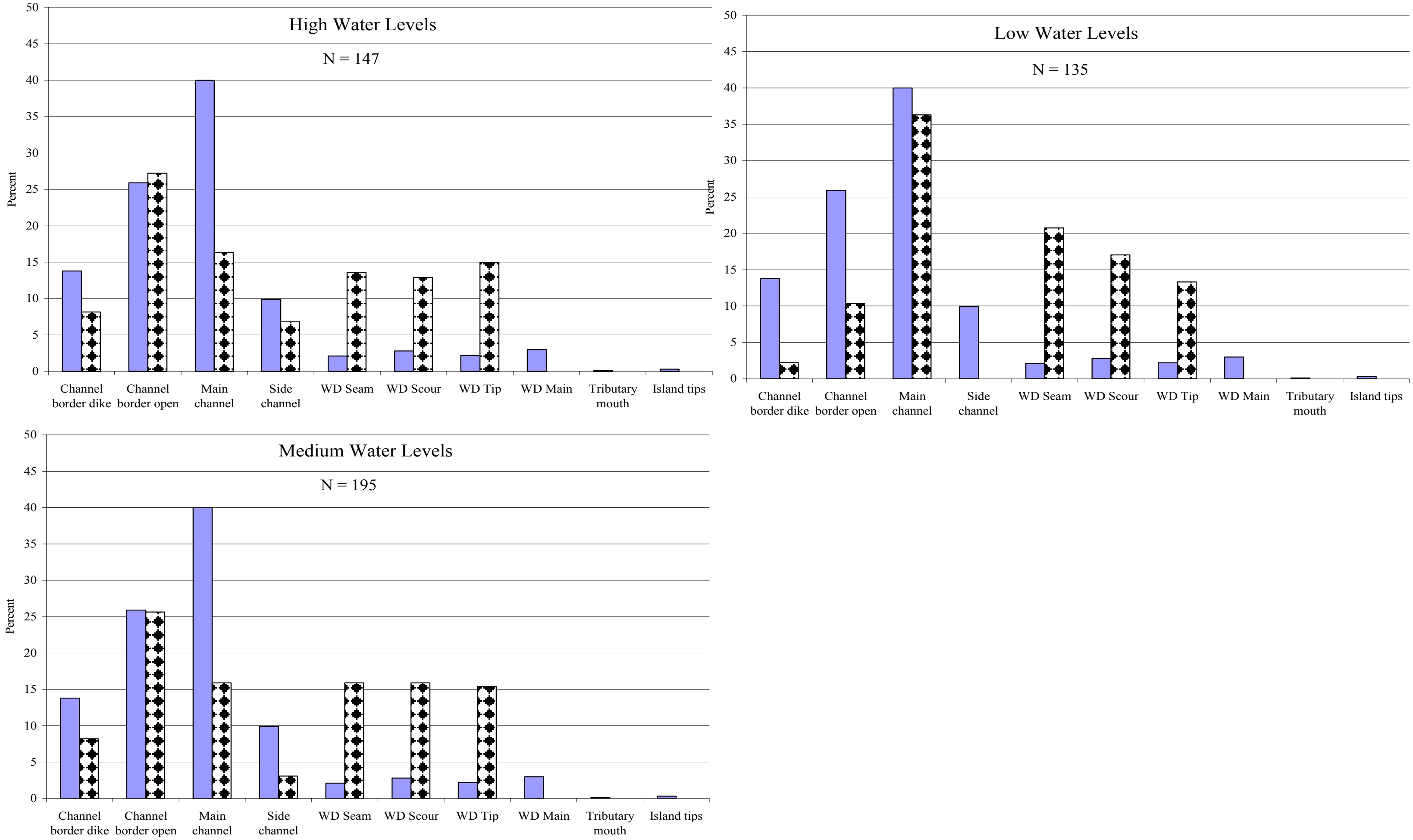


Figure 17. Percent of habitat available in the middle Mississippi River versus the percent of that Pallid Sturgeon were located in those habitats during for each range of water levels during 2002 - 2005. Habitat availability represented with blue bars. Acronyms represent the following: BWD: between wing dikes; CBO: channel border open (25.9%); MC: main channel (40.0%); SC: side channel (9.9%); WDSD: scour area below wing dam (2.1%); WDS: scour area at tip of wing dam (2.8%); WDT: wing dam tip (2.2%); WD: wing dam structure (3.0%); TM: tributary mouth (0.1%); IT: island tip (0.3%).

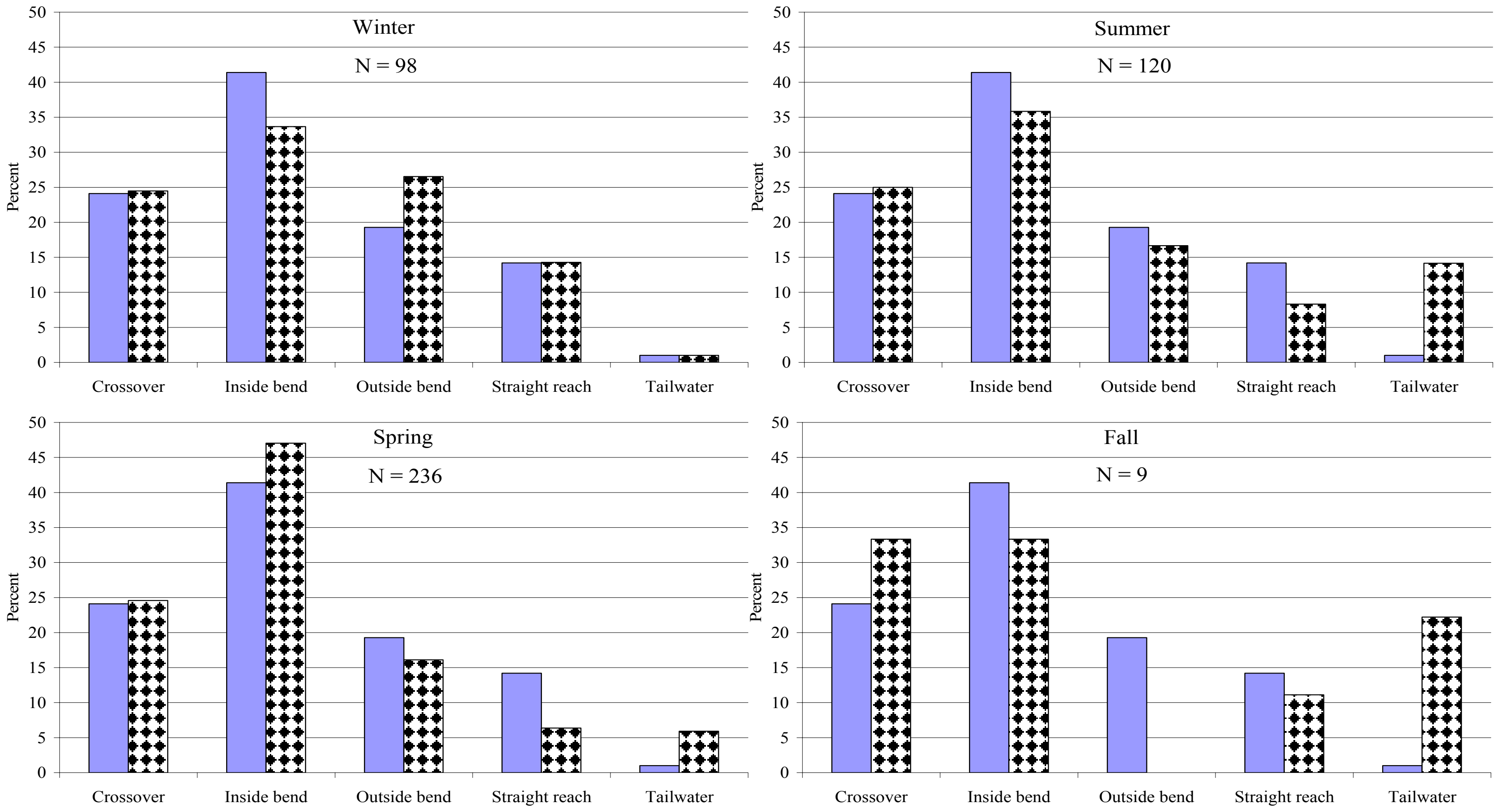


Figure 18. Percent of habitat available as defined by river sinuosity in the middle Mississippi River versus the percent of that Pallid Sturgeon were located in those habitats during for each range of water levels during 2002 - 2005. Habitat availability represented with blue bars.

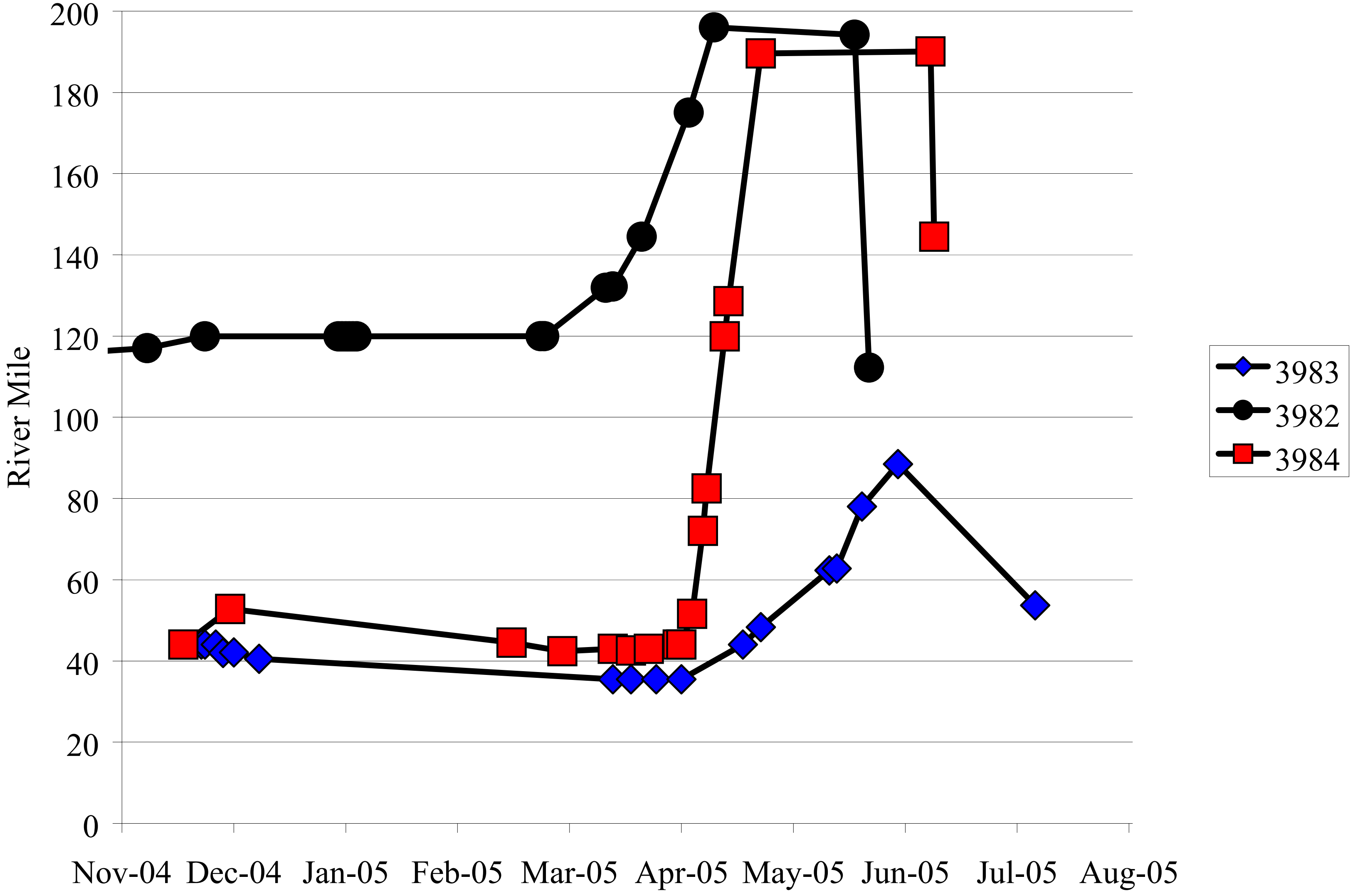
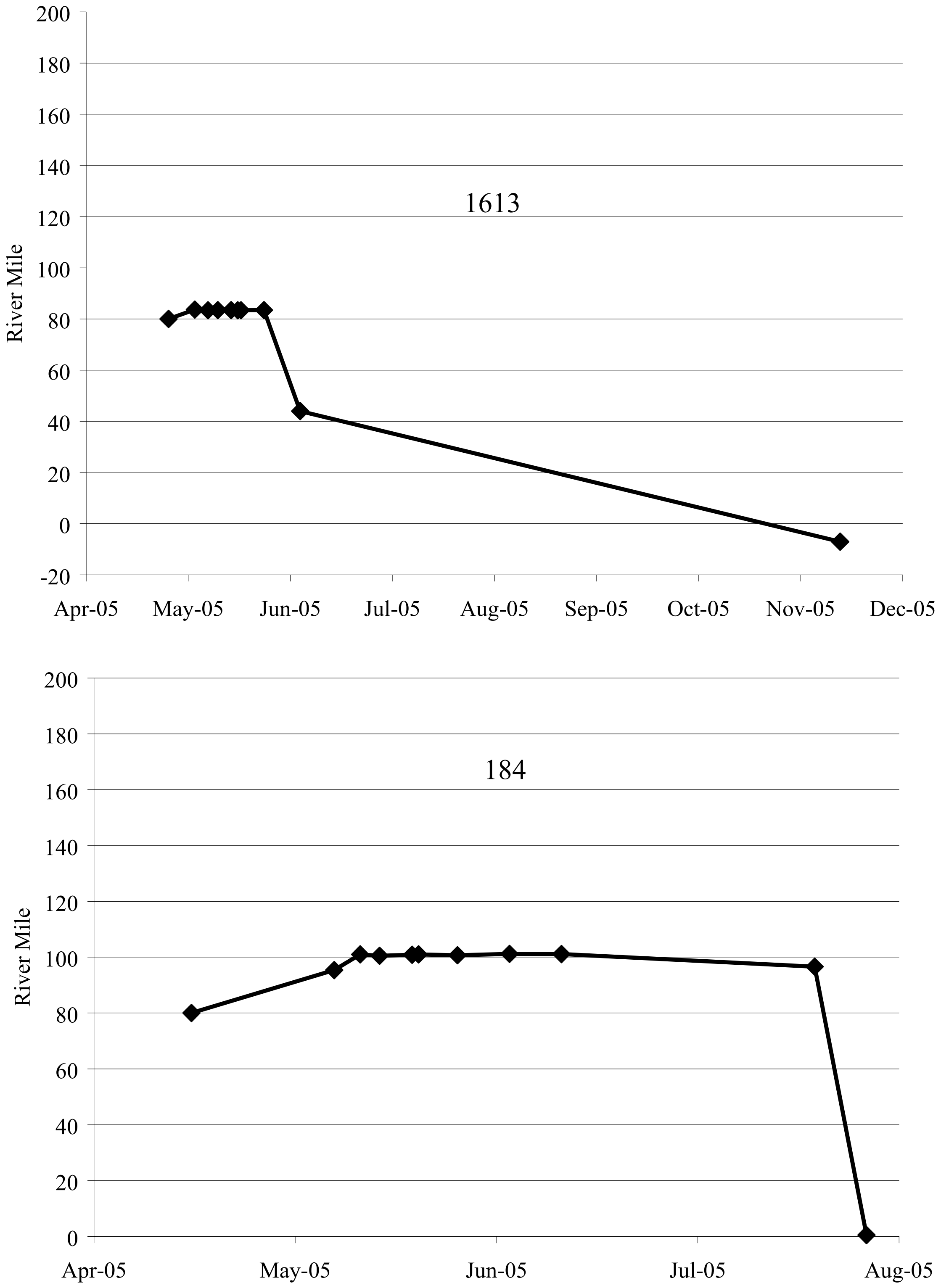


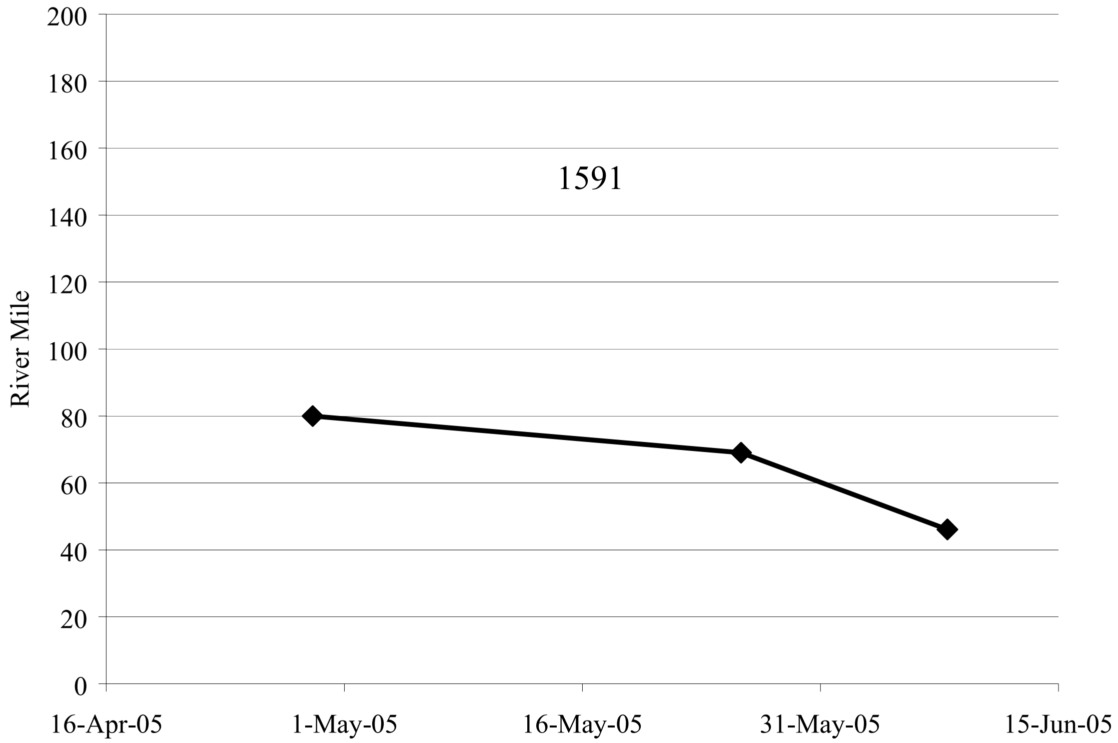
Figure 19. Observed migratory movement of female pallid sturgeon in the middle Mississippi River during spring 2005. Markers indicate individual relocations.

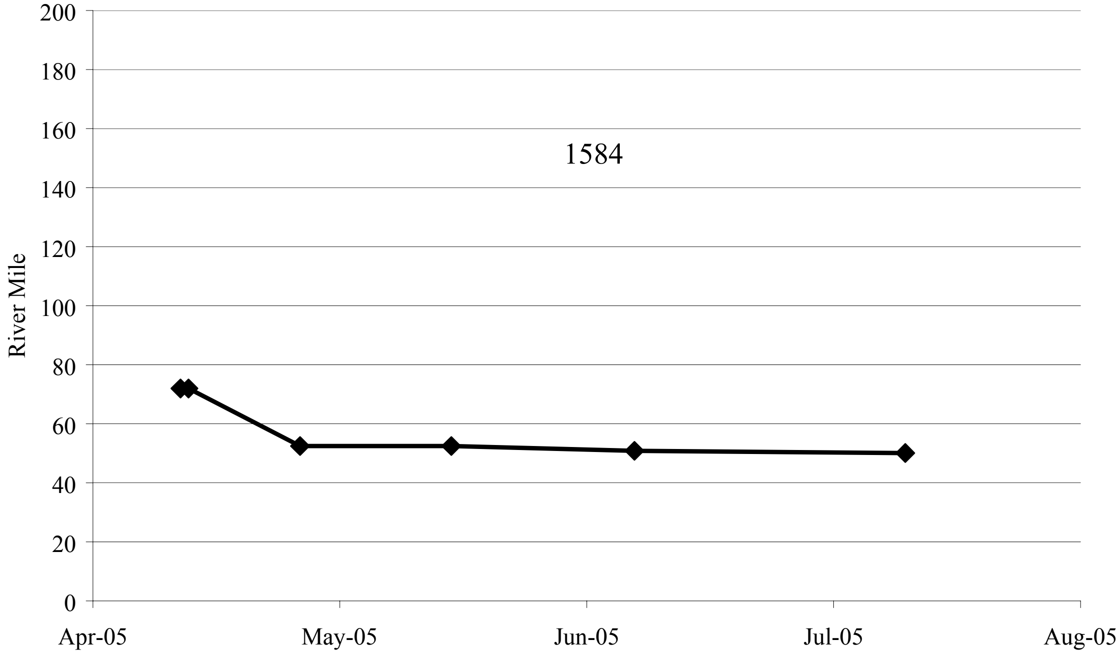
Appendix A

Movement of individual Pallid Sturgeon in the Middle Mississippi River 2003-2005. The fish were tracked by a combination of manual tracking effort and stationary receivers deployed on navigation buoys featured in this appendix.

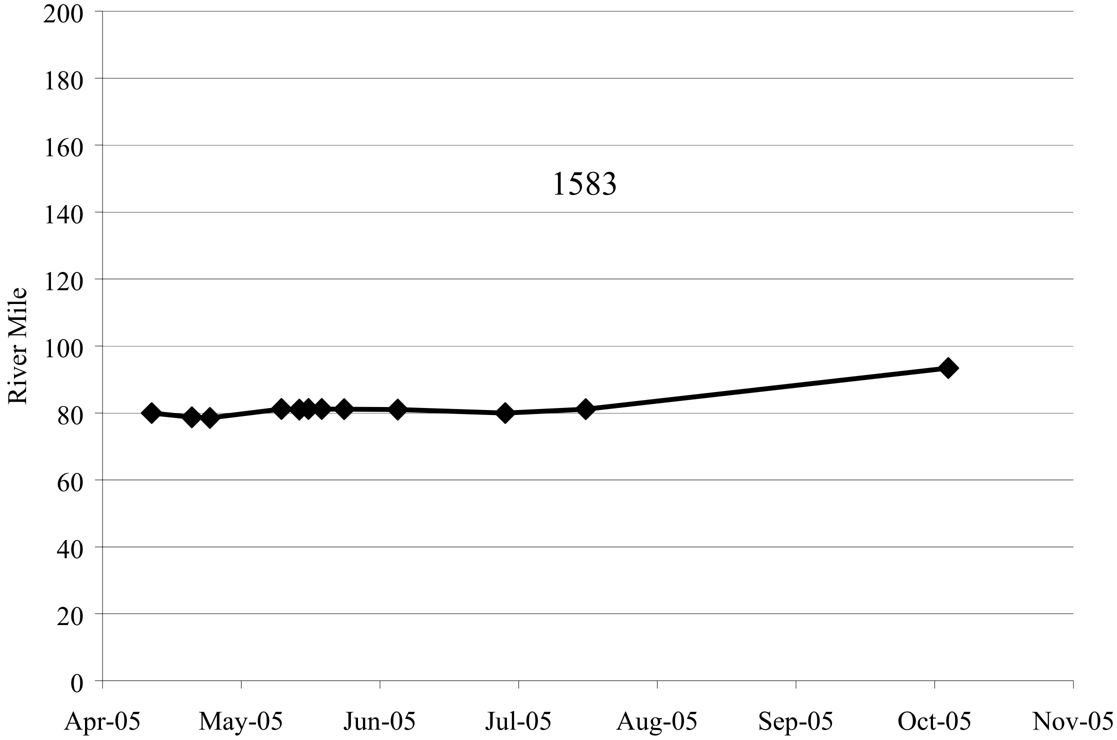


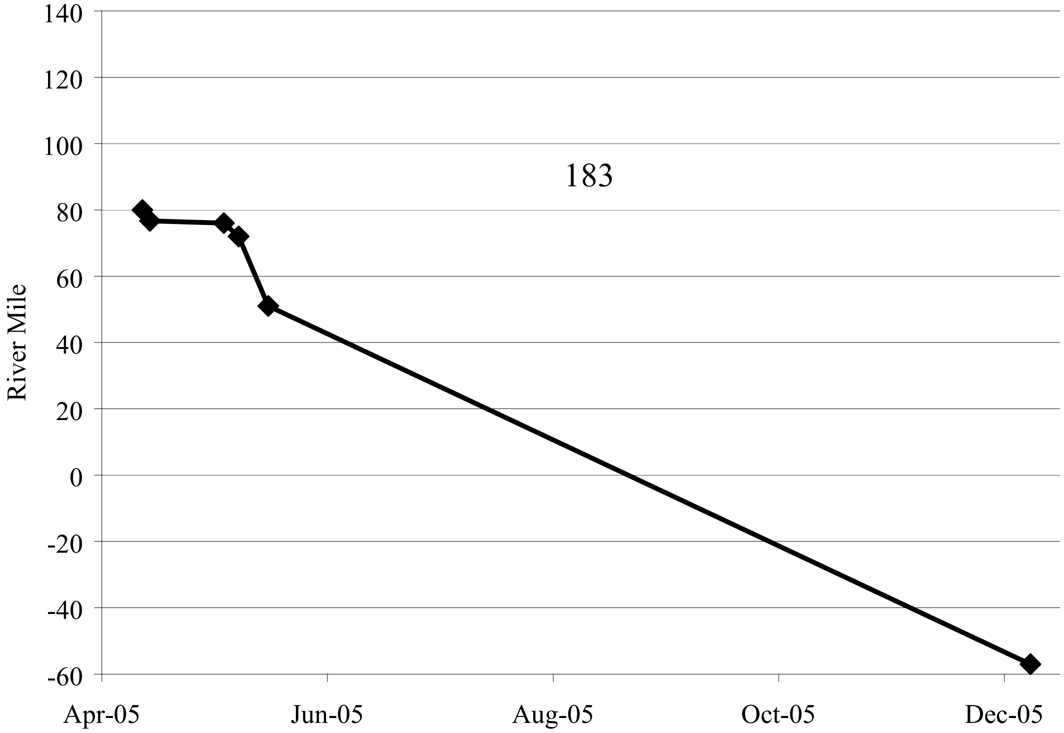
Appendix A-1. Observed movements of Pallid Sturgeon 1613 and 184 in the MMR from transmitter implantation until latest contact. Diamonds indicate individual relocations, dashed lines indicate times when pallid sturgeon left the study site.



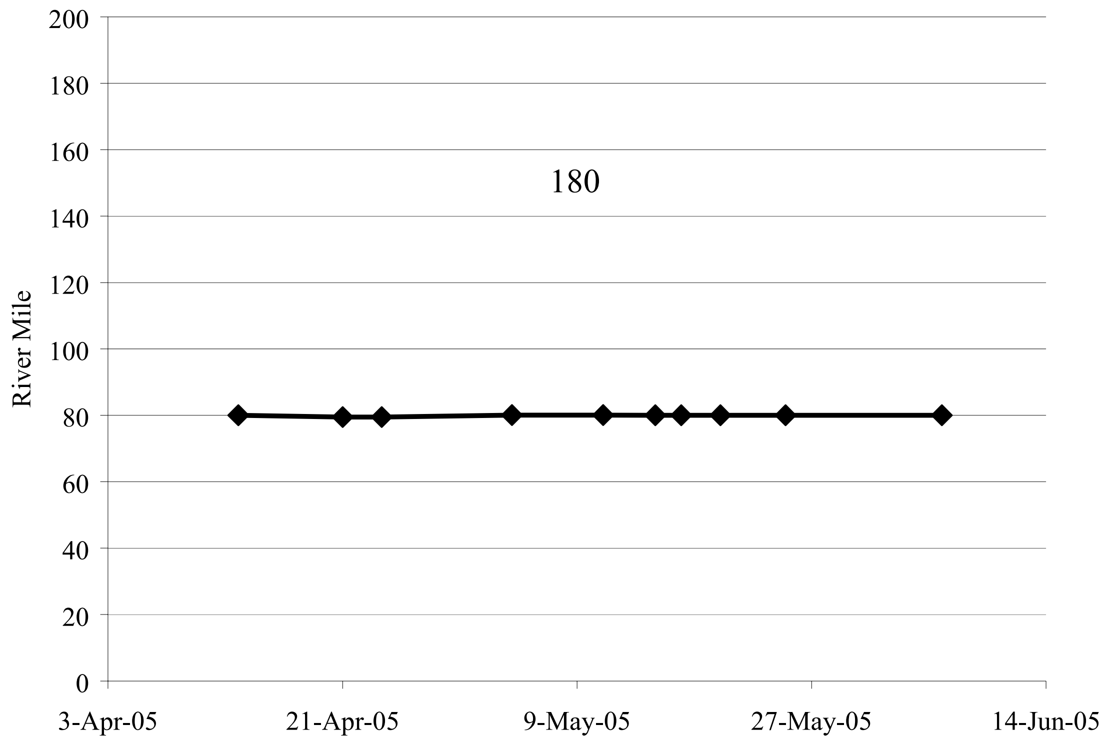


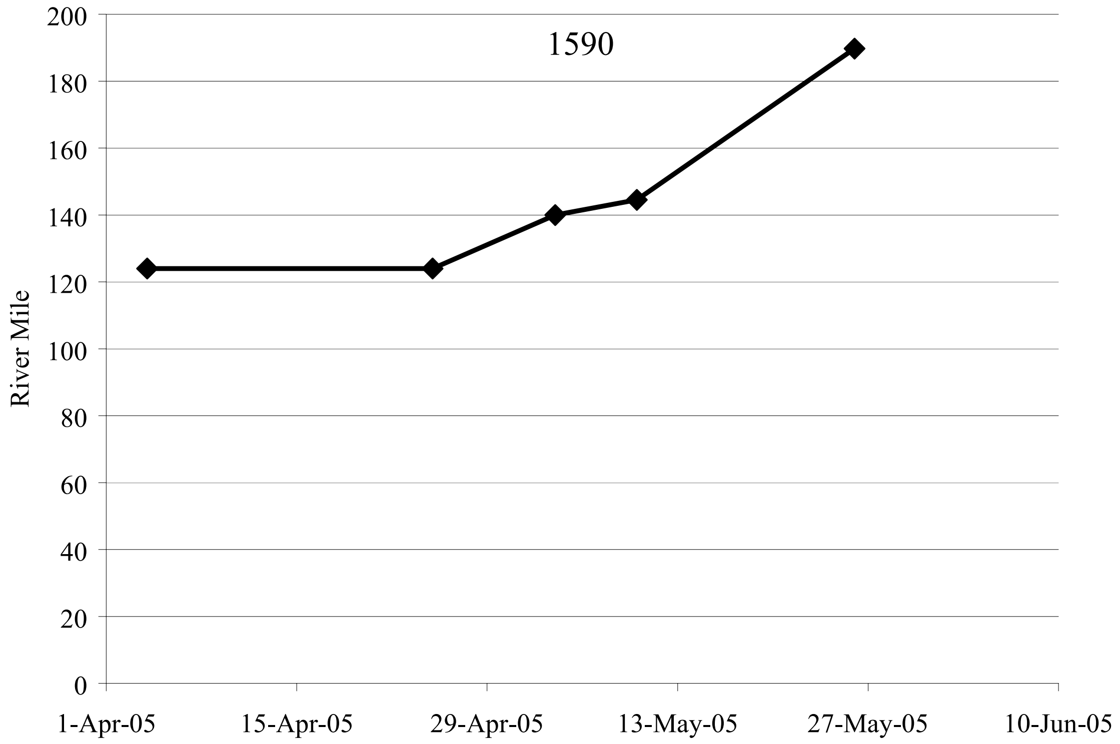
Appendix A-2. Observed movements of Pallid Sturgeon 1591 and 1584 in the MMR from transmitter implantation until latest contact. Diamonds indicate individual relocations, dashed lines indicate times when pallid sturgeon left the study site.



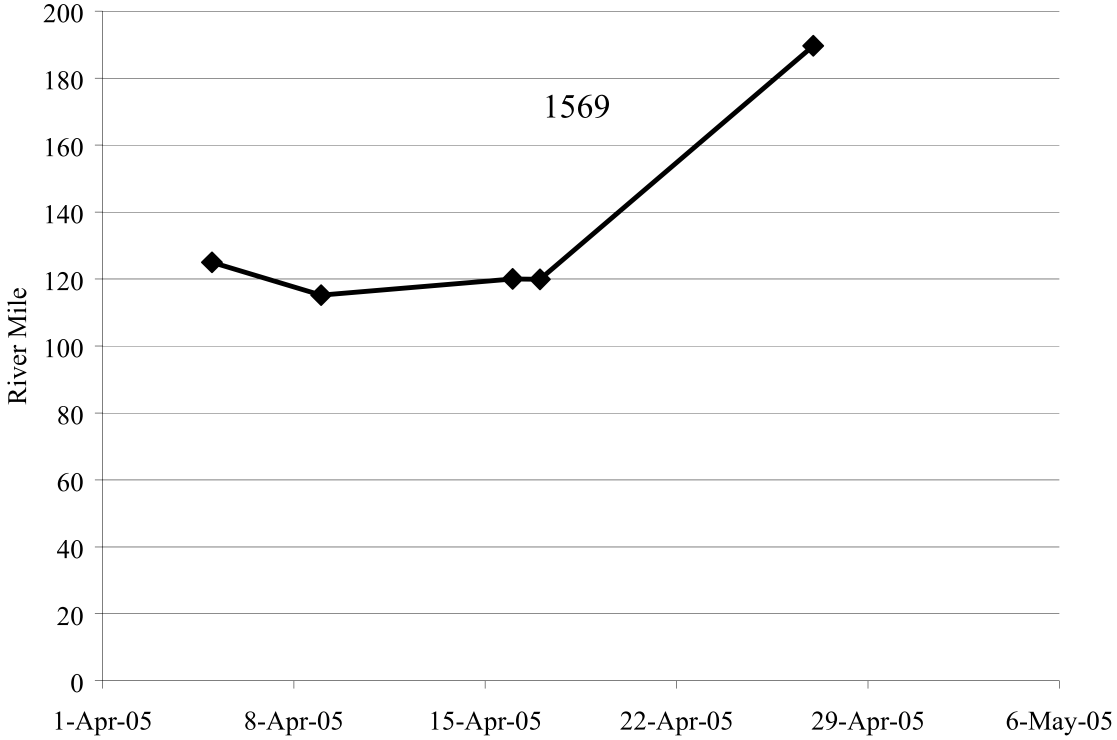


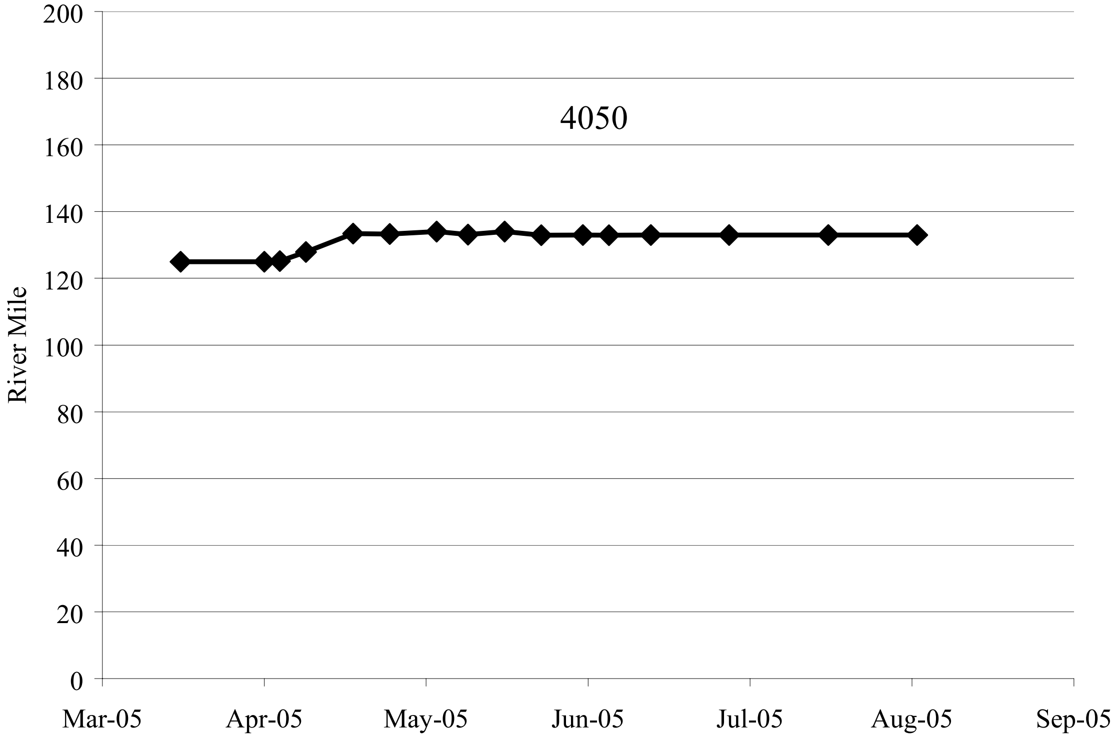
Appendix A-3. Observed movements of Pallid Sturgeon 1583 and 183 in the MMR from transmitter implantation until latest contact. Diamonds indicate individual relocations, dashed lines indicate times when pallid sturgeon left the study site.



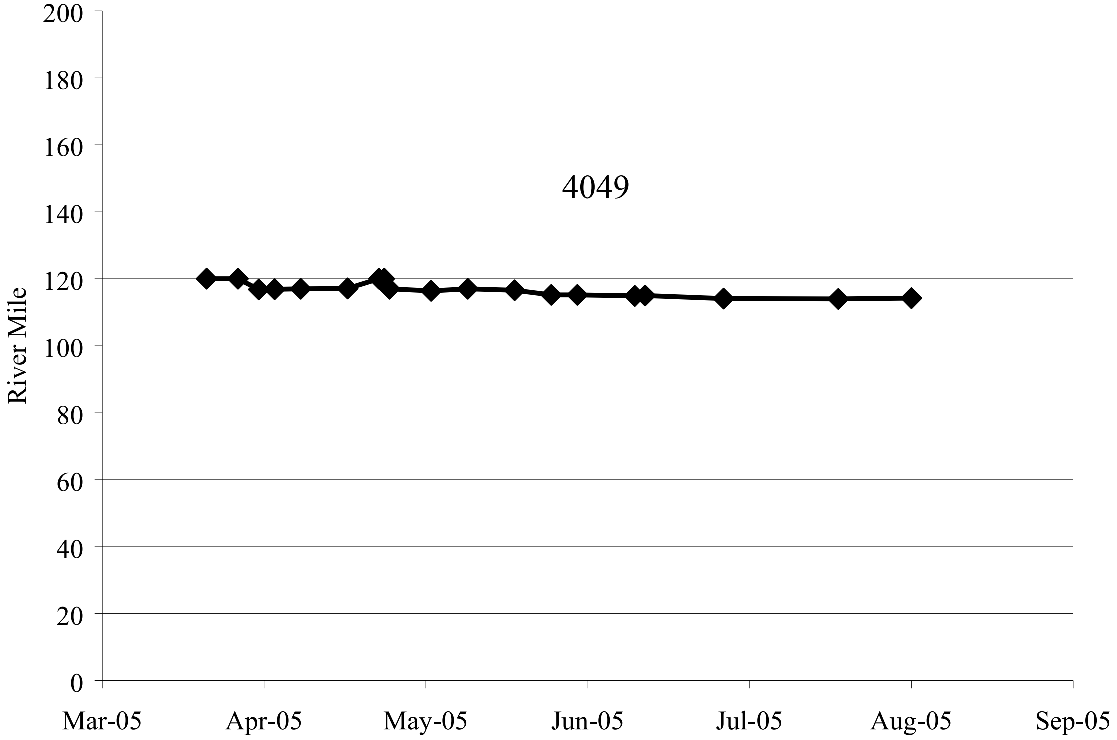


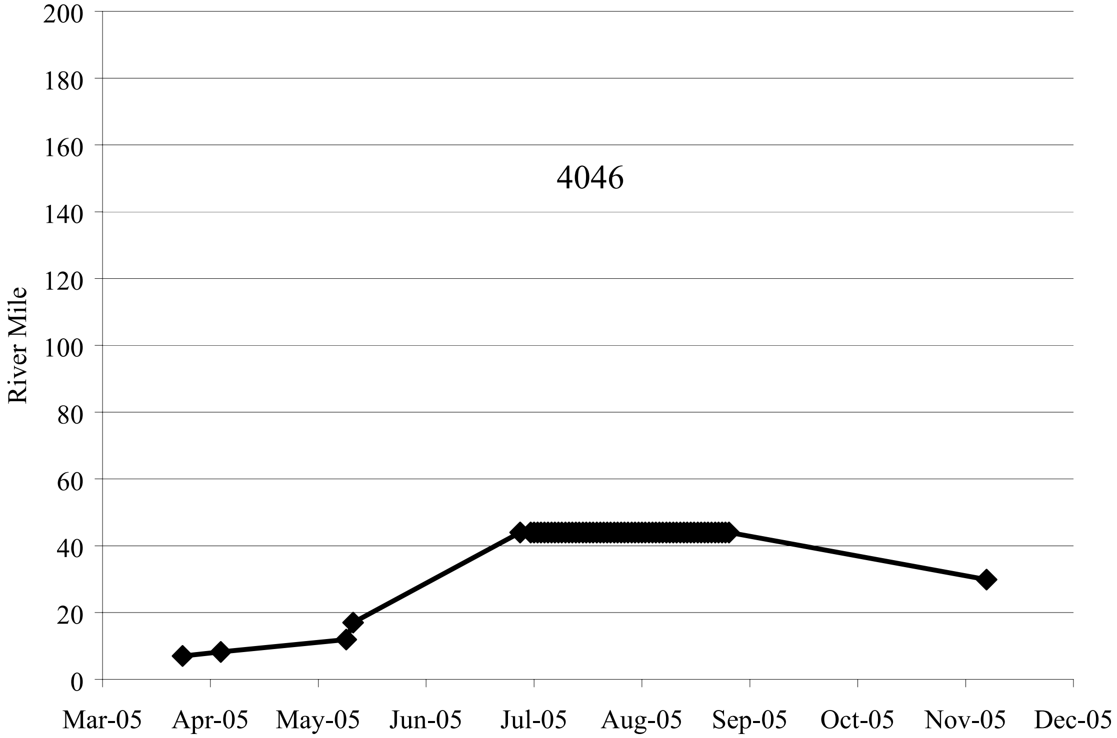
Appendix A-4. Observed movements of Pallid Sturgeon 180 and 1590 in the MMR from transmitter implantation until latest contact. Diamonds indicate individual relocations, dashed lines indicate times when pallid sturgeon left the study site.



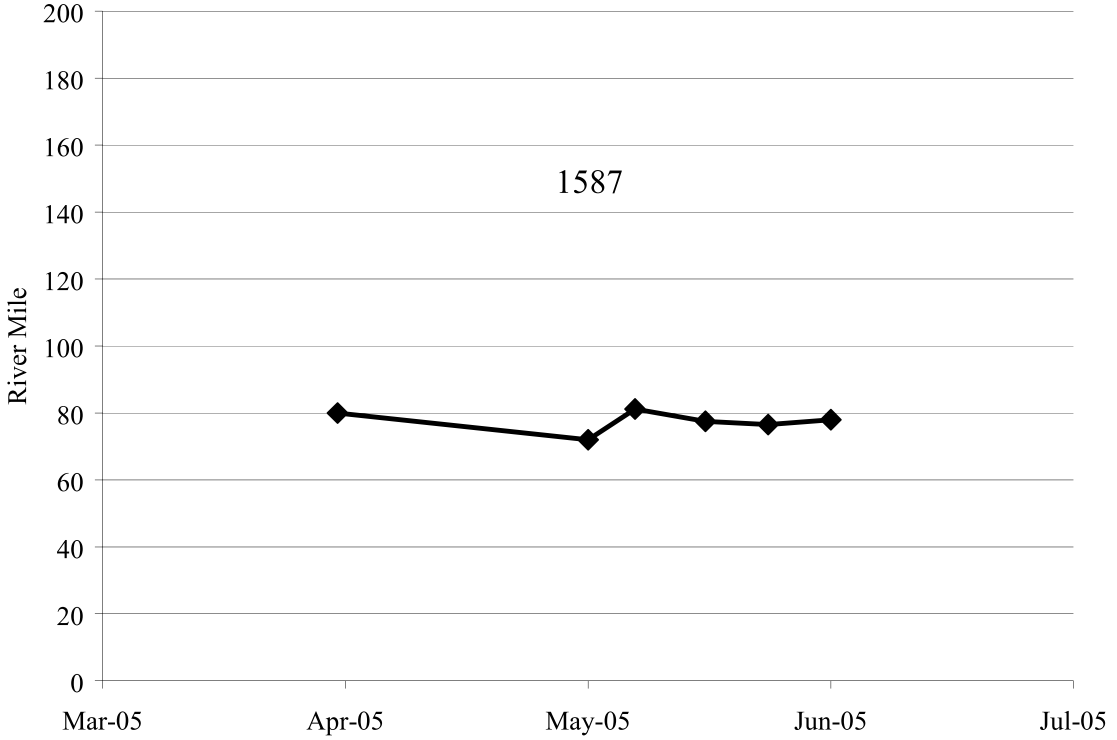


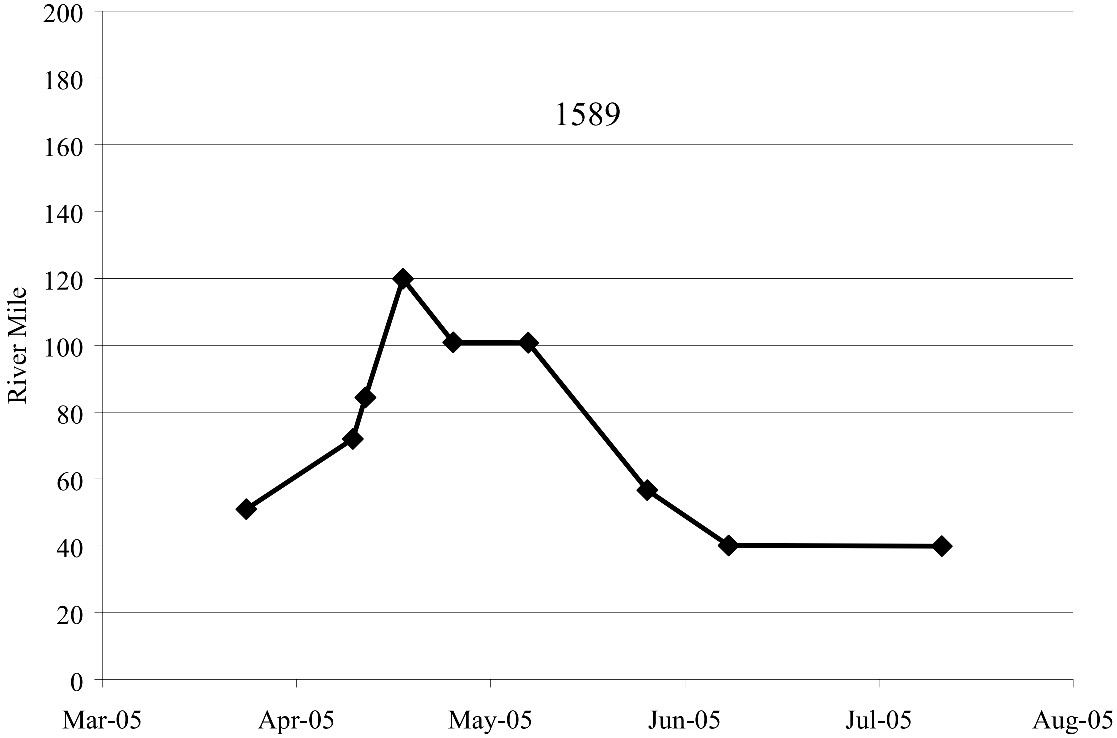
Appendix A-5. Observed movements of Pallid Sturgeon 1569 and 4050 in the MMR from transmitter implantation until latest contact. Diamonds indicate individual relocations, dashed lines indicate times when pallid sturgeon left the study site.



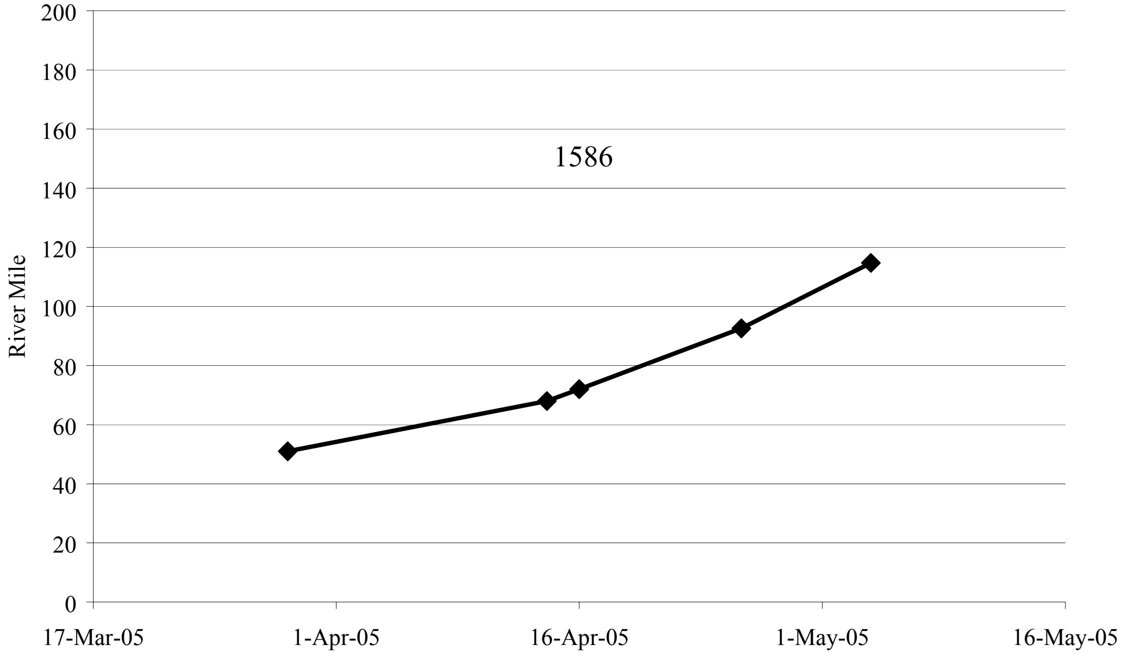


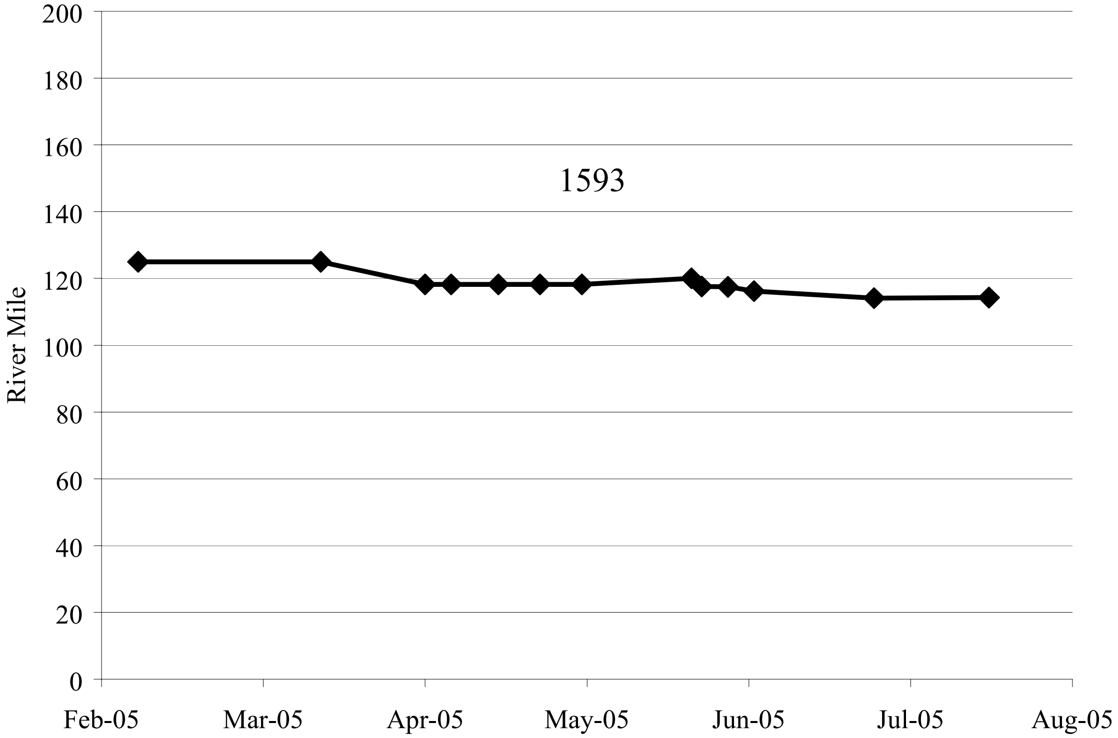
Appendix A-6. Observed movements of Pallid Sturgeon 4049 and 4046 in the MMR from transmitter implantation until latest contact. Diamonds indicate individual relocations, dashed lines indicate times when pallid sturgeon left the study site.



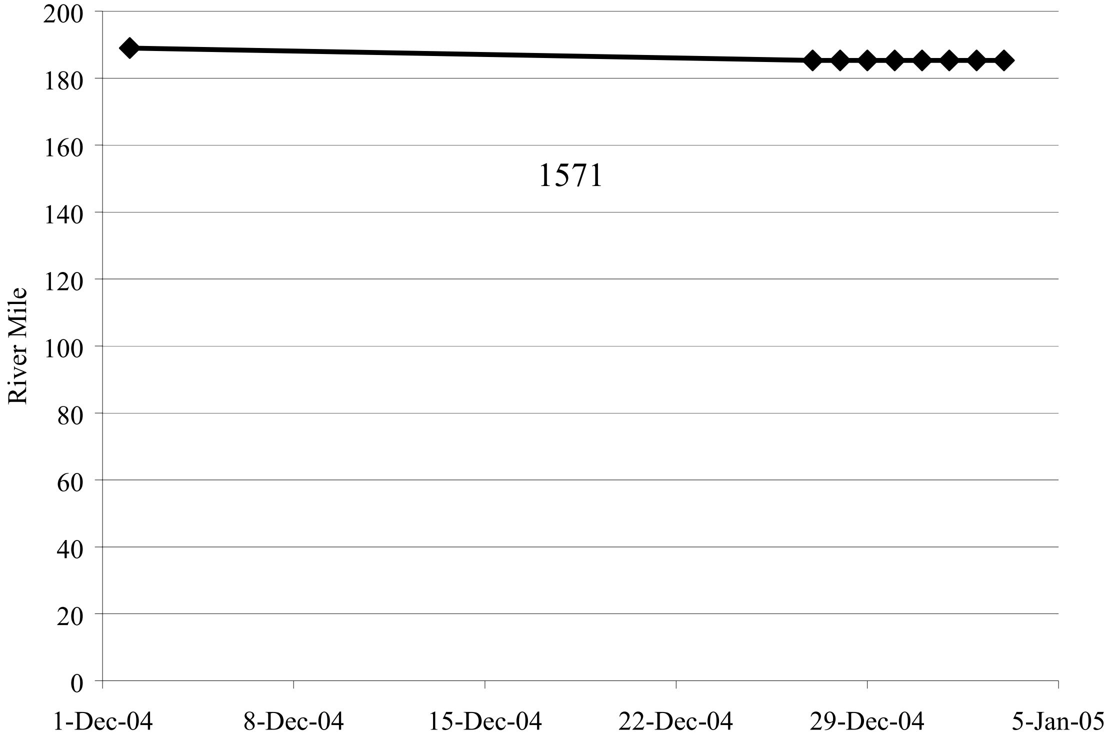


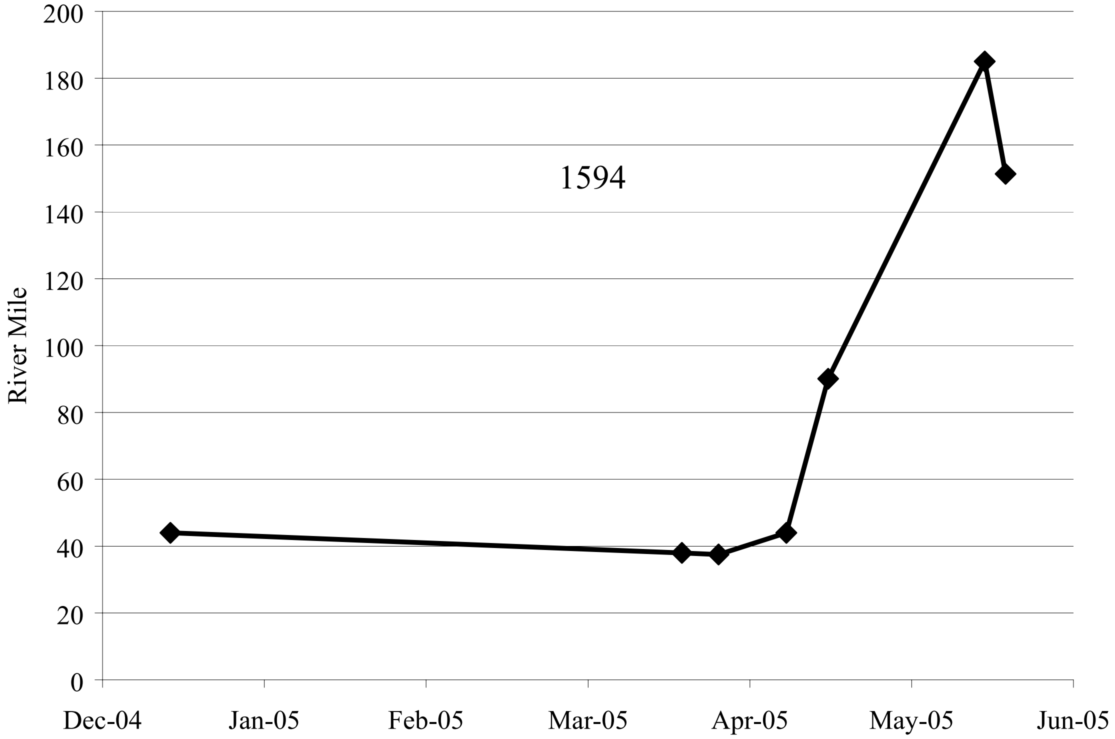
Appendix A-7. Observed movements of Pallid Sturgeon 1587 and 1589 in the MMR from transmitter implantation until latest contact. Diamonds indicate individual relocations, dashed lines indicate times when pallid sturgeon left the study site.



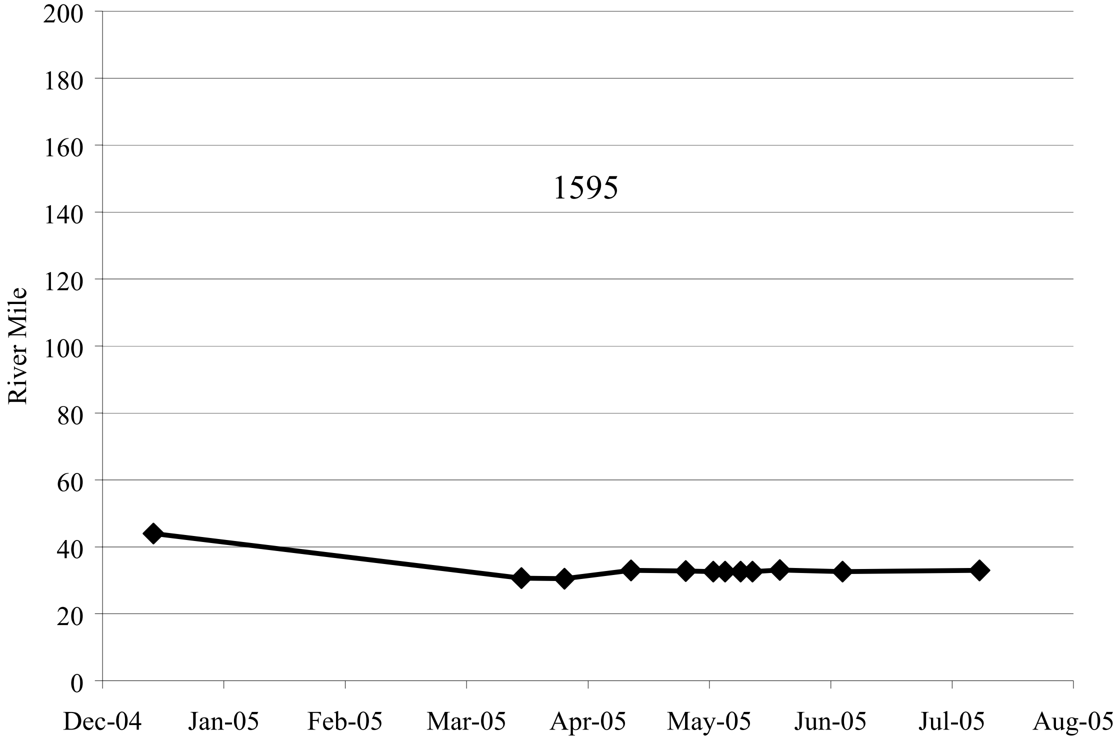


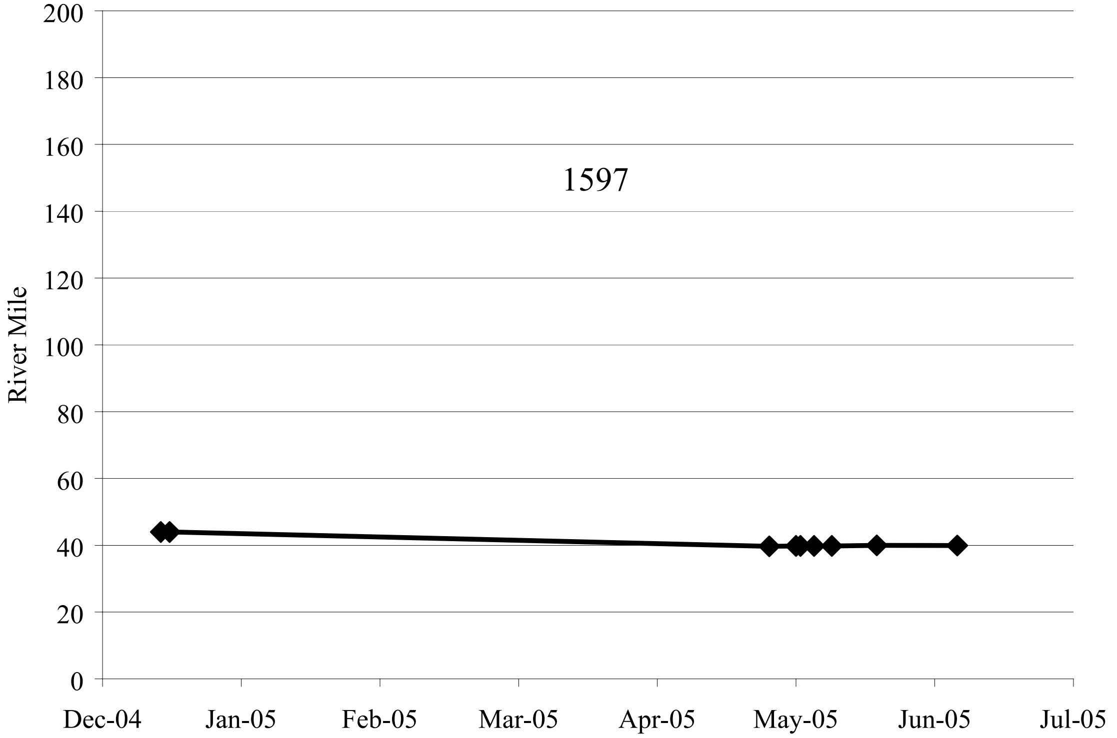
Appendix A-8. Observed movements of Pallid Sturgeon 1586 and 1593 in the MMR from transmitter implantation until latest contact. Diamonds indicate individual relocations, dashed lines indicate times when pallid sturgeon left the study site.



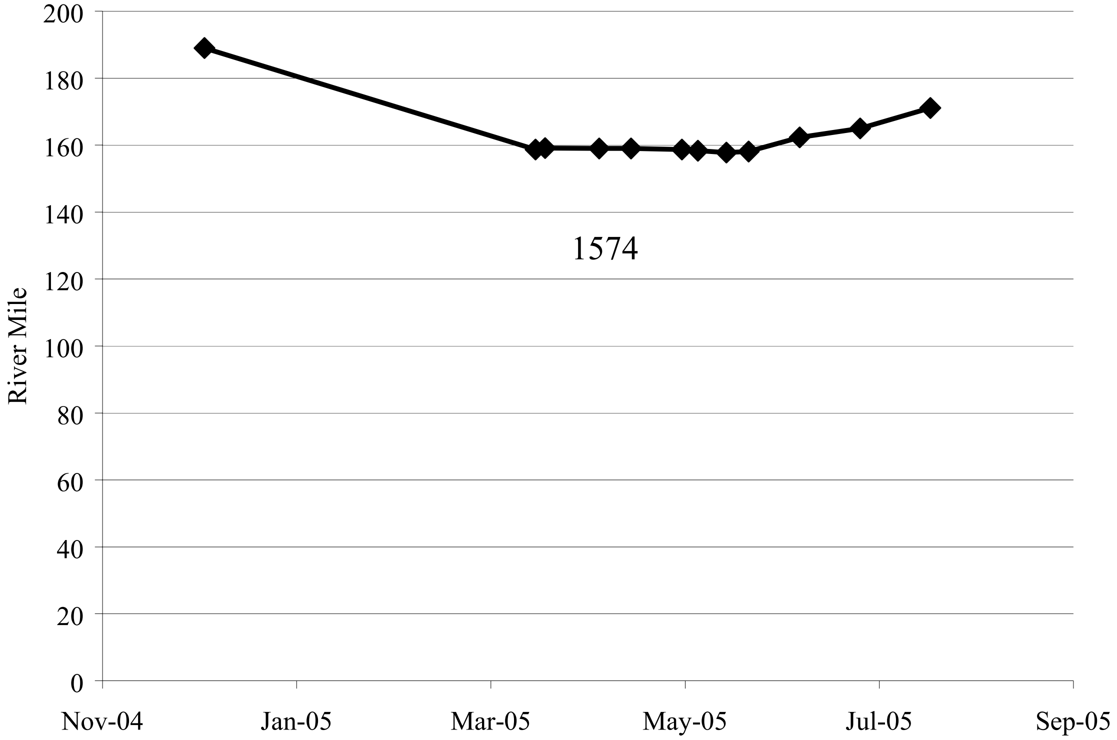


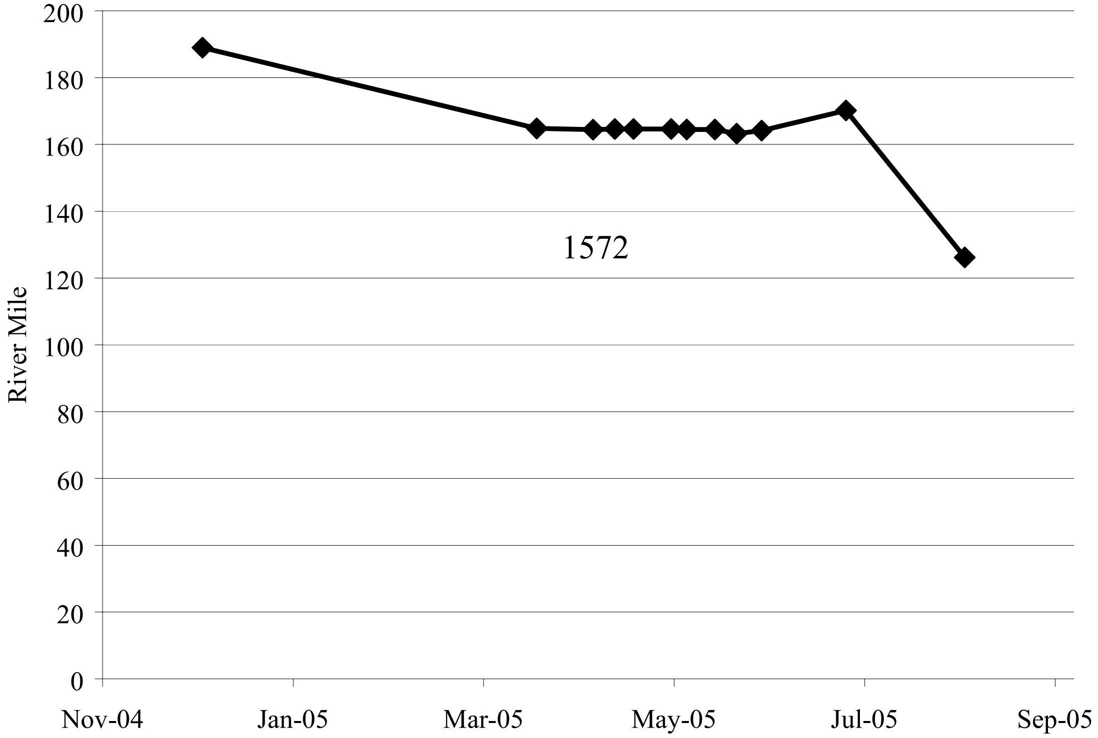
Appendix A-9. Observed movements of Pallid Sturgeon 1571 and 1594 in the MMR from transmitter implantation until latest contact. Diamonds indicate individual relocations, dashed lines indicate times when pallid sturgeon left the study site.



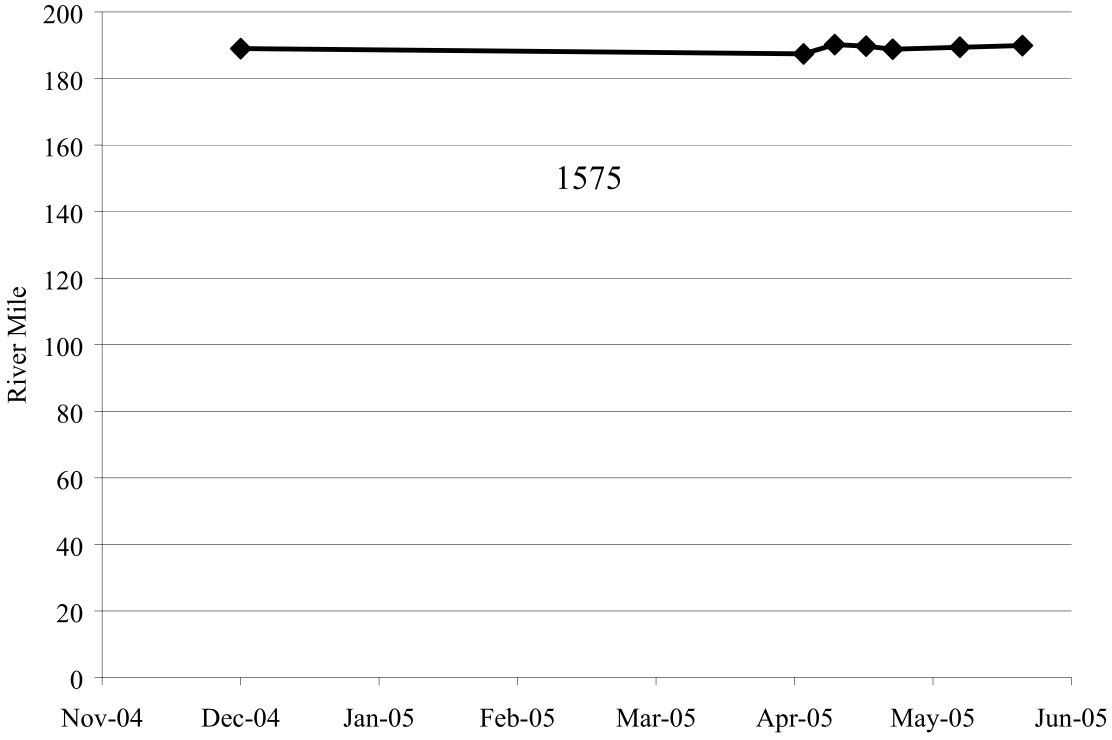


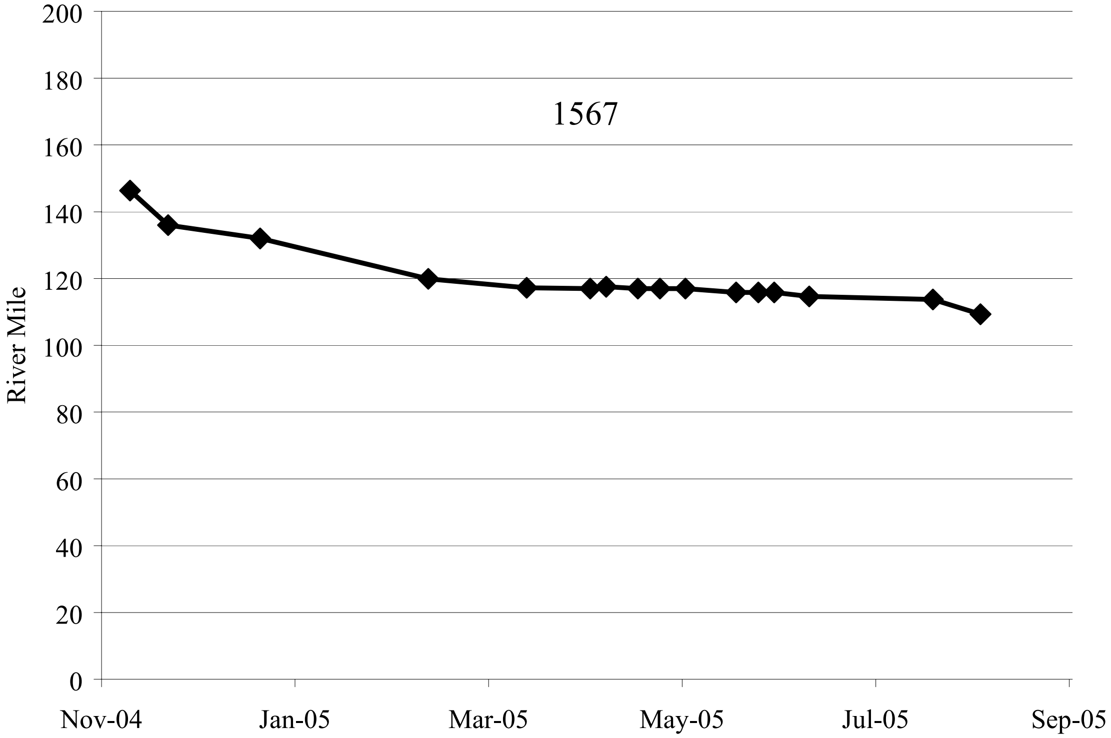
Appendix A-10. Observed movements of Pallid Sturgeon 1595 and 1597 in the MMR from transmitter implantation until latest contact. Diamonds indicate individual relocations, dashed lines indicate times when pallid sturgeon left the study site.



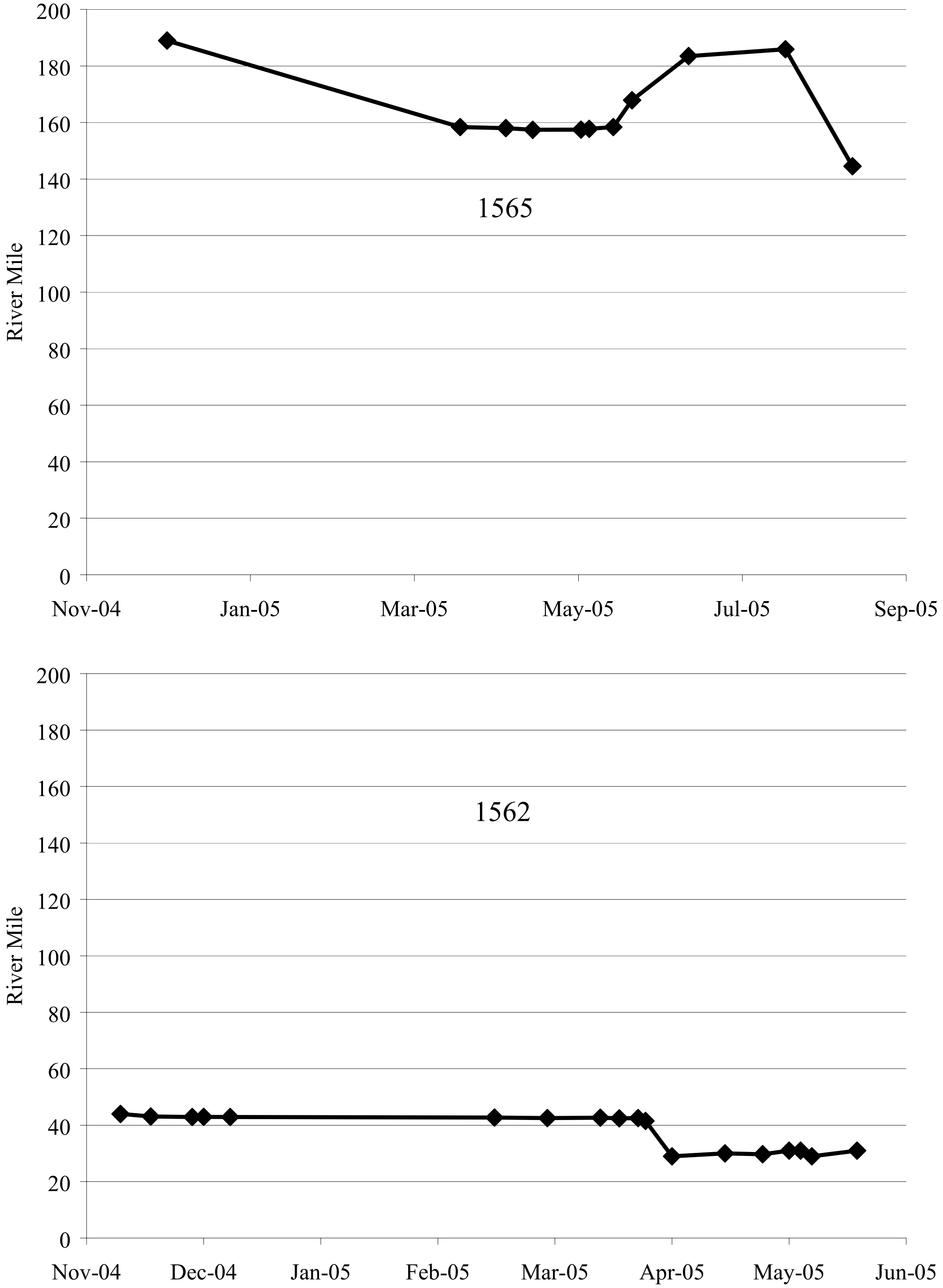


Appendix A-11. Observed movements of Pallid Sturgeon 1574 and 1572 in the MMR from transmitter implantation until latest contact. Diamonds indicate individual relocations, dashed lines indicate times when pallid sturgeon left the study site.

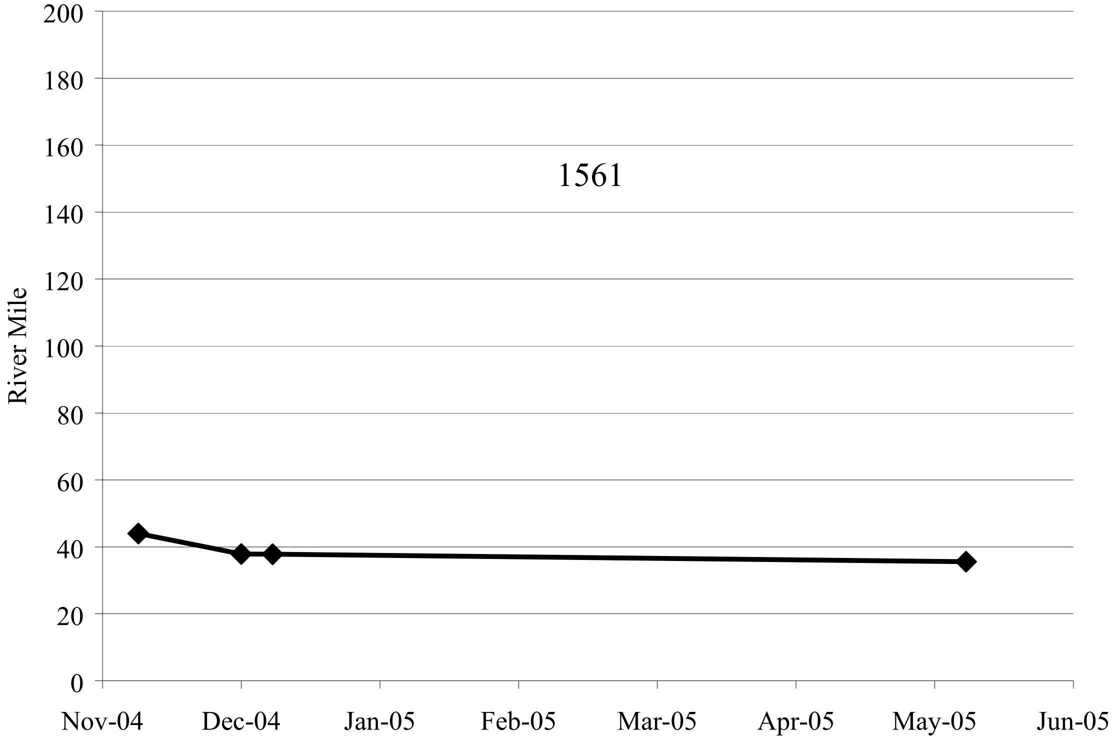


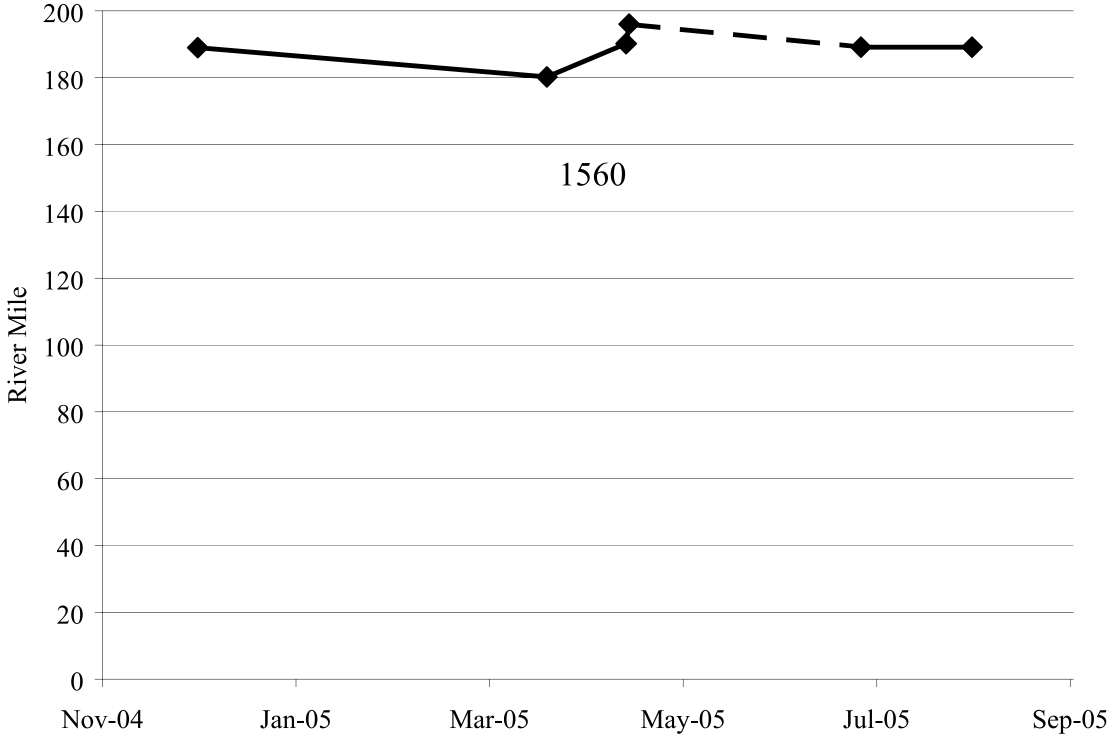


Appendix A-12. Observed movements of Pallid Sturgeon 1575 and 1567 in the MMR from transmitter implantation until latest contact. Diamonds indicate individual relocations, dashed lines indicate times when pallid sturgeon left the study site.

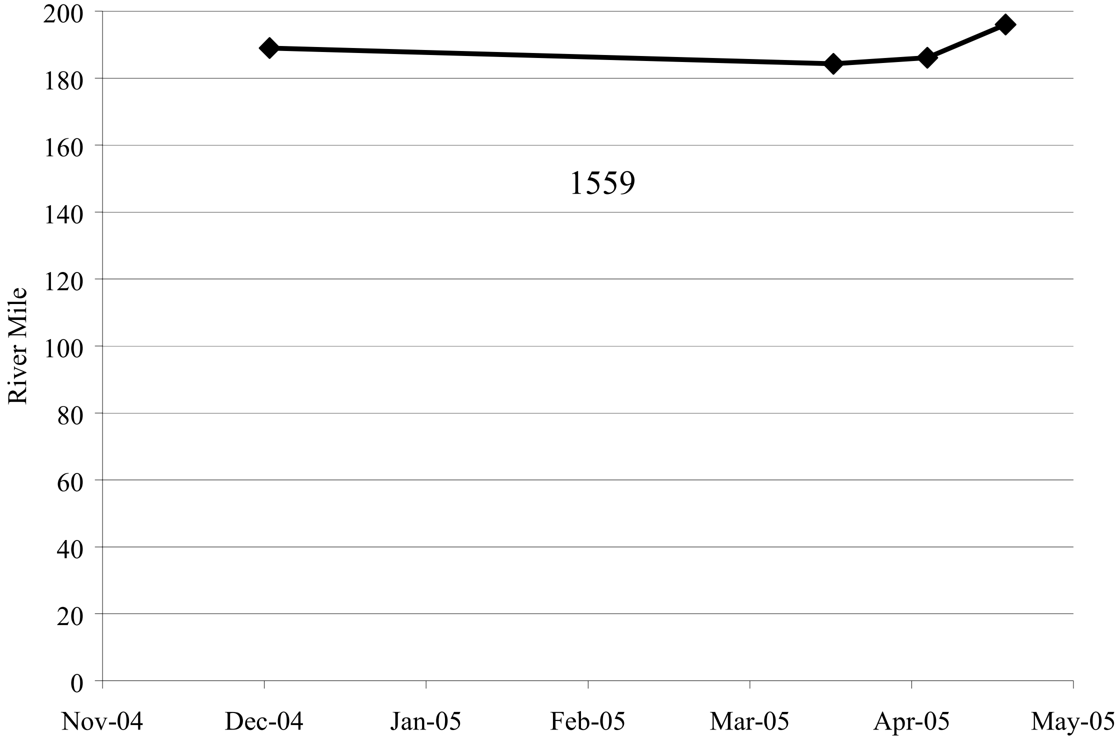


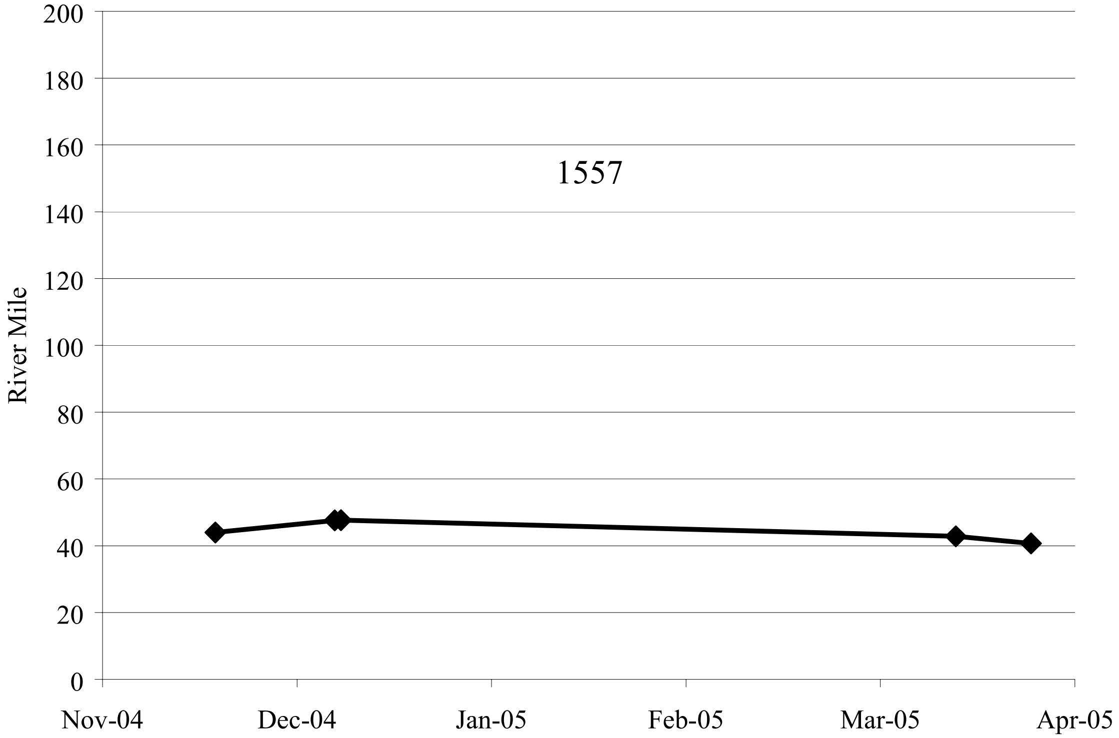
Appendix A-13. Observed movements of Pallid Sturgeon 1565 and 1562 in the MMR from transmitter implantation until latest contact. Diamonds indicate individual relocations, dashed lines indicate times when pallid sturgeon left the study site.



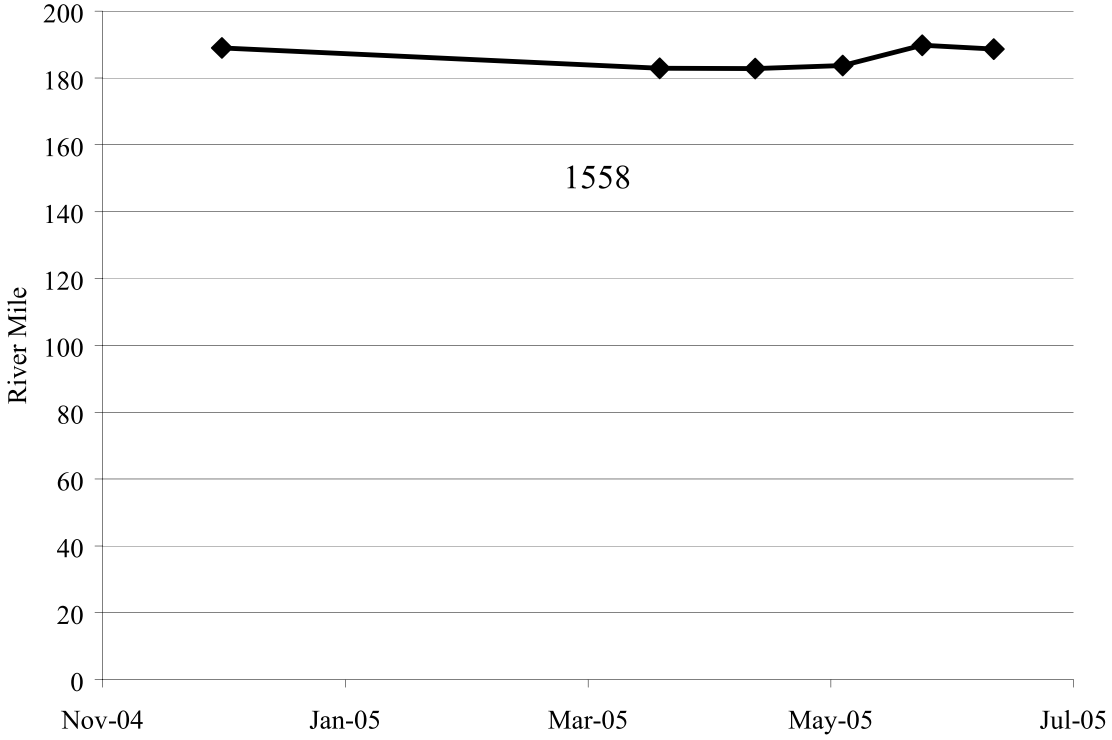


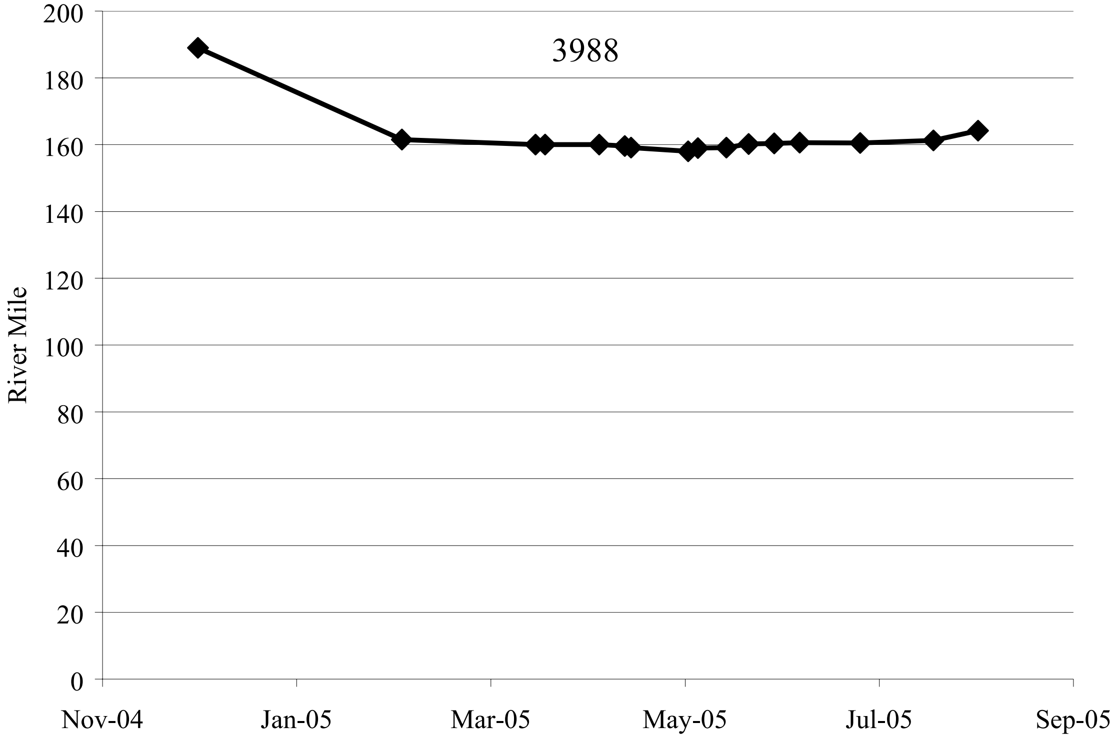
Appendix A-14. Observed movements of Pallid Sturgeon 1561 and 1560 in the MMR from transmitter implantation until latest contact. Diamonds indicate individual relocations, dashed lines indicate times when pallid sturgeon left the study site.



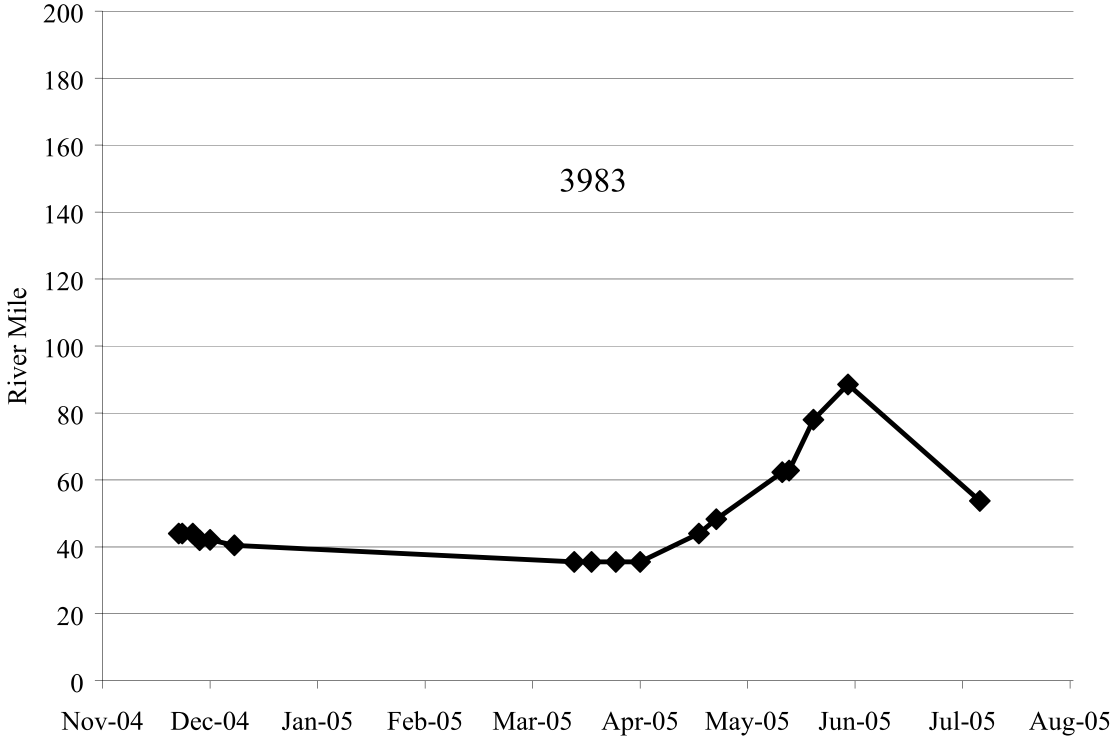


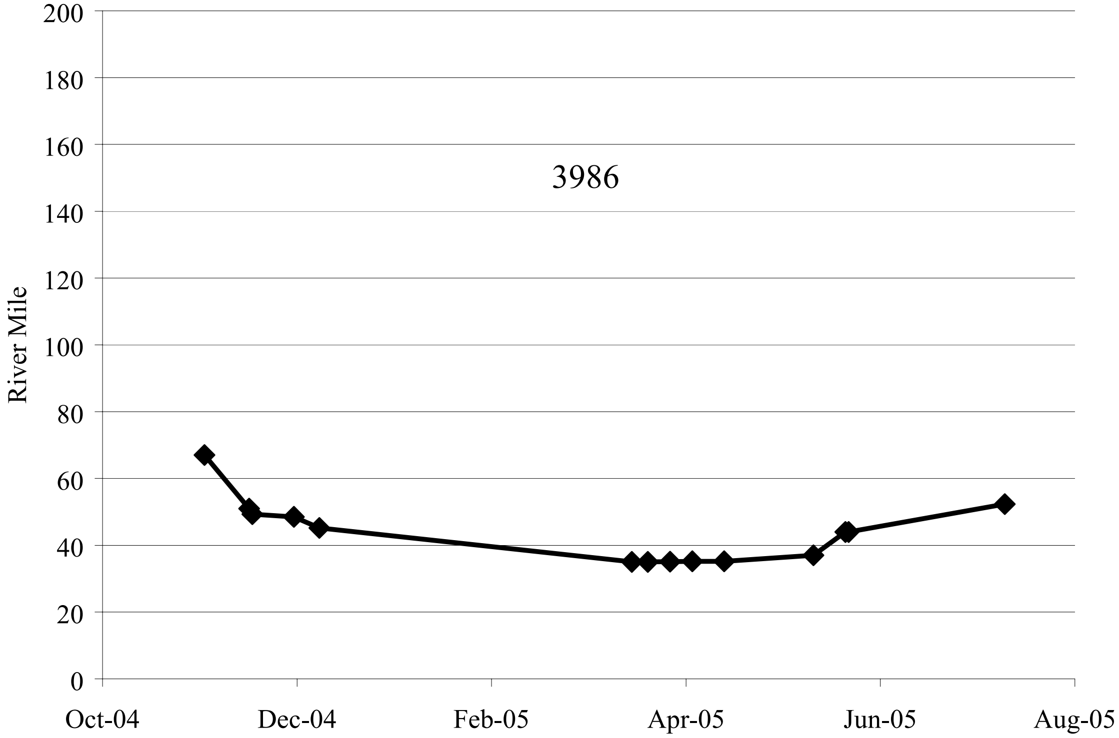
Appendix A-15. Observed movements of Pallid Sturgeon 1559 and 1557 in the MMR from transmitter implantation until latest contact. Diamonds indicate individual relocations, dashed lines indicate times when pallid sturgeon left the study site.



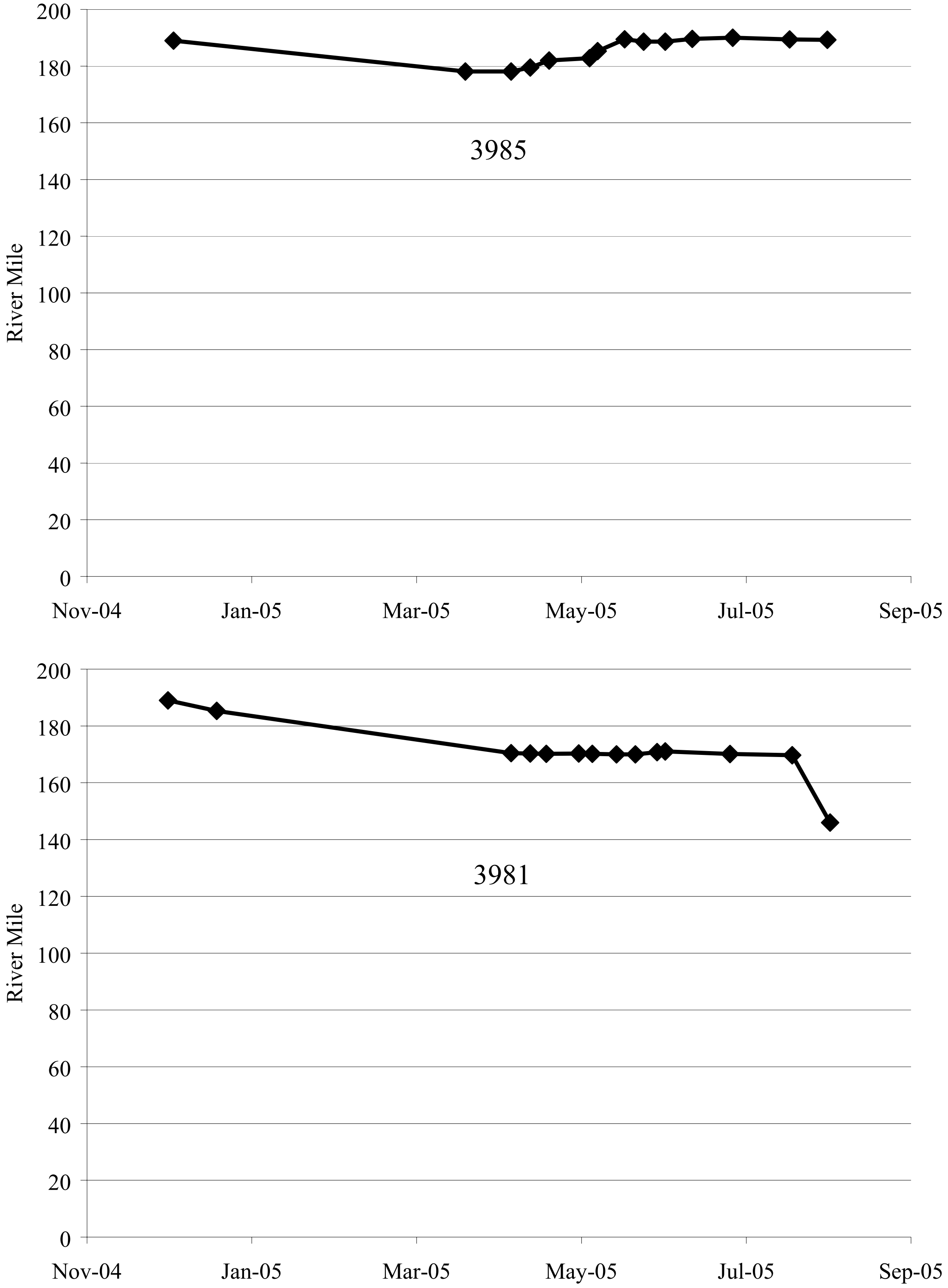


Appendix A-16. Observed movements of Pallid Sturgeon 1558 and 3988 in the MMR from transmitter implantation until latest contact. Diamonds indicate individual relocations, dashed lines indicate times when pallid sturgeon left the study site.

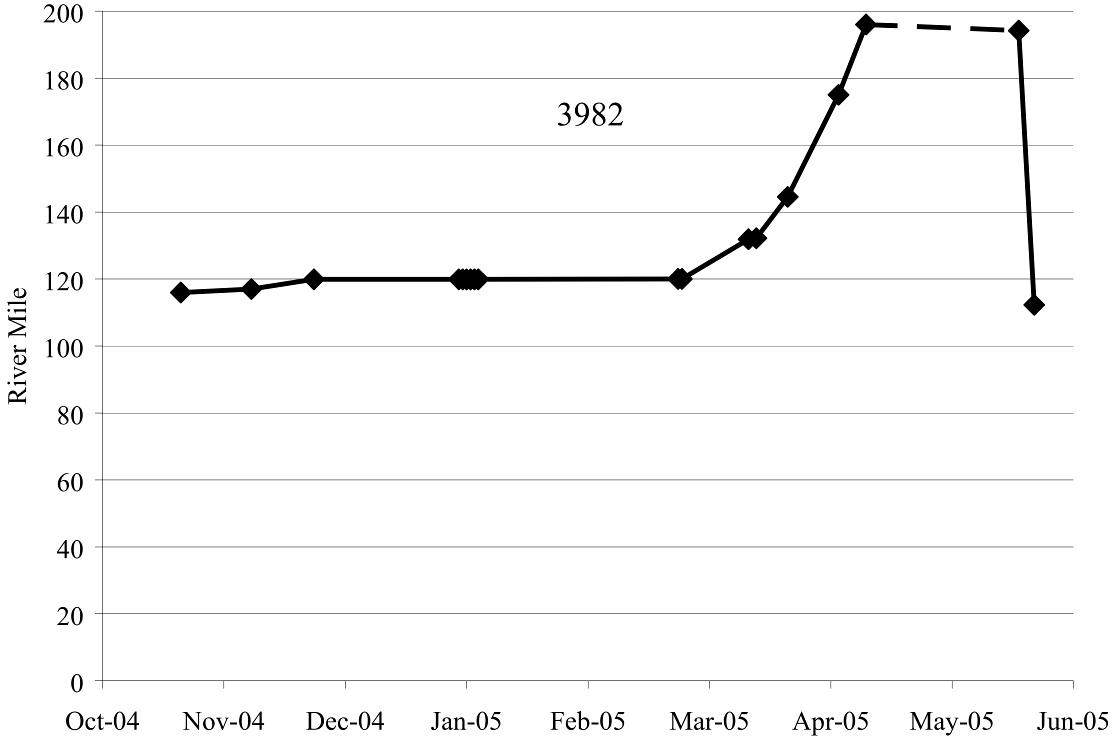


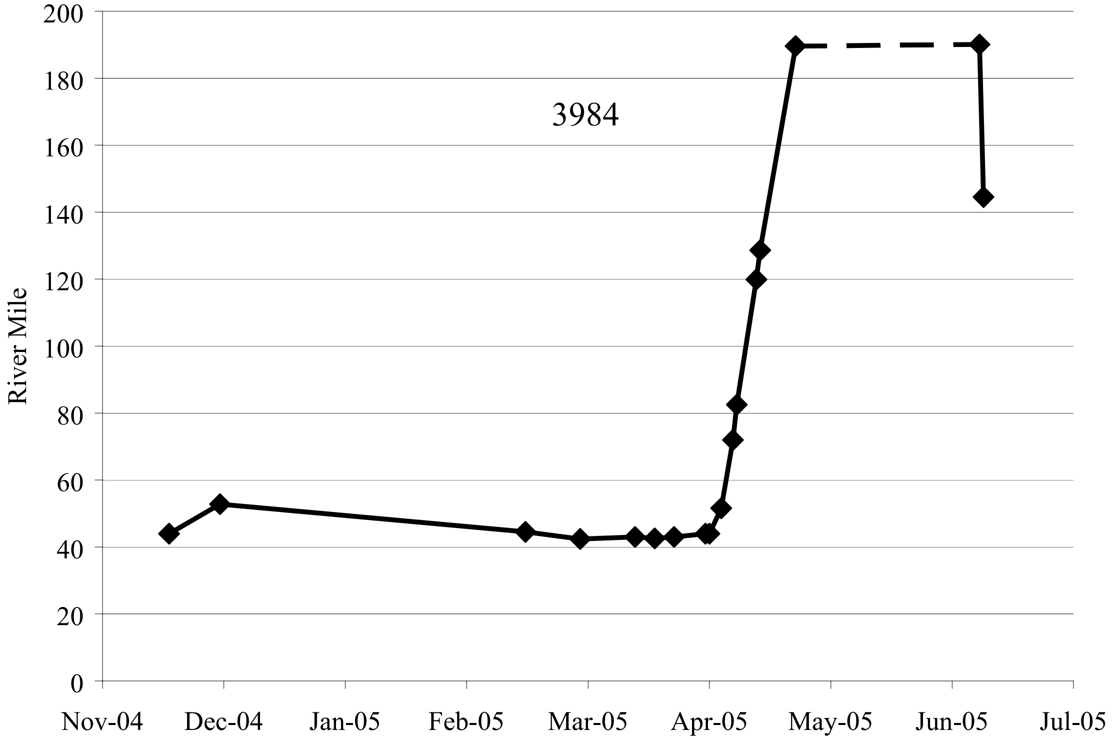


Appendix A-17. Observed movements of Pallid Sturgeon 3983 and 3986 in the MMR from transmitter implantation until latest contact. Diamonds indicate individual relocations, dashed lines indicate times when pallid sturgeon left the study site.

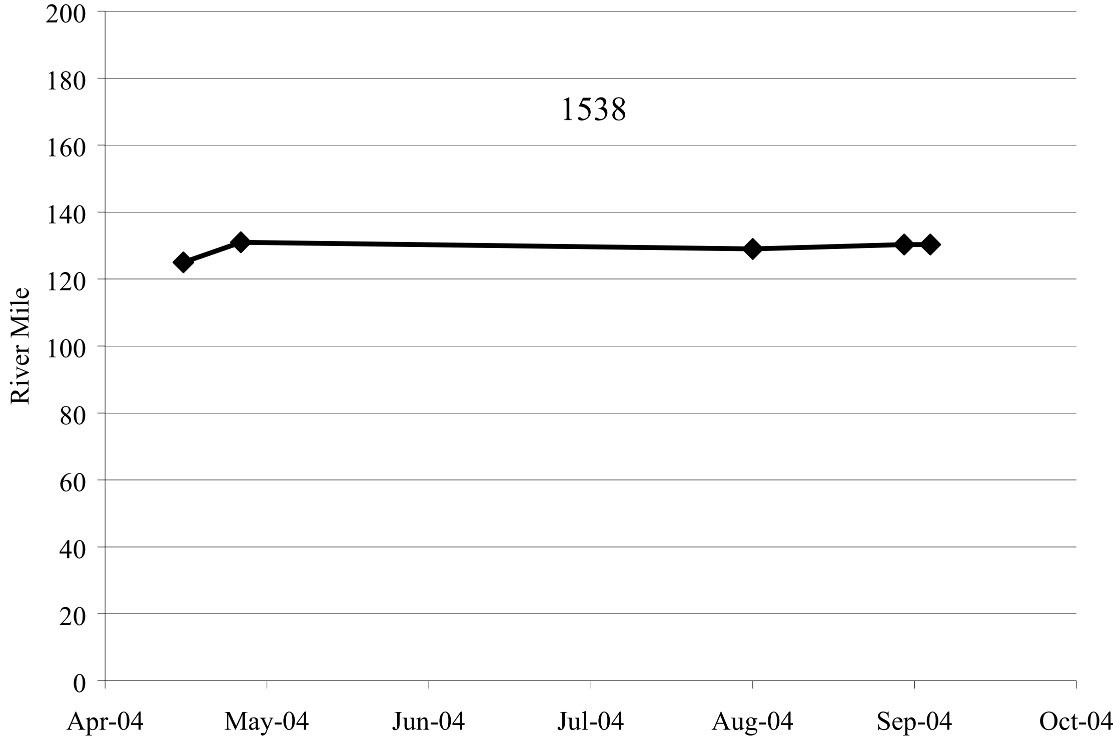


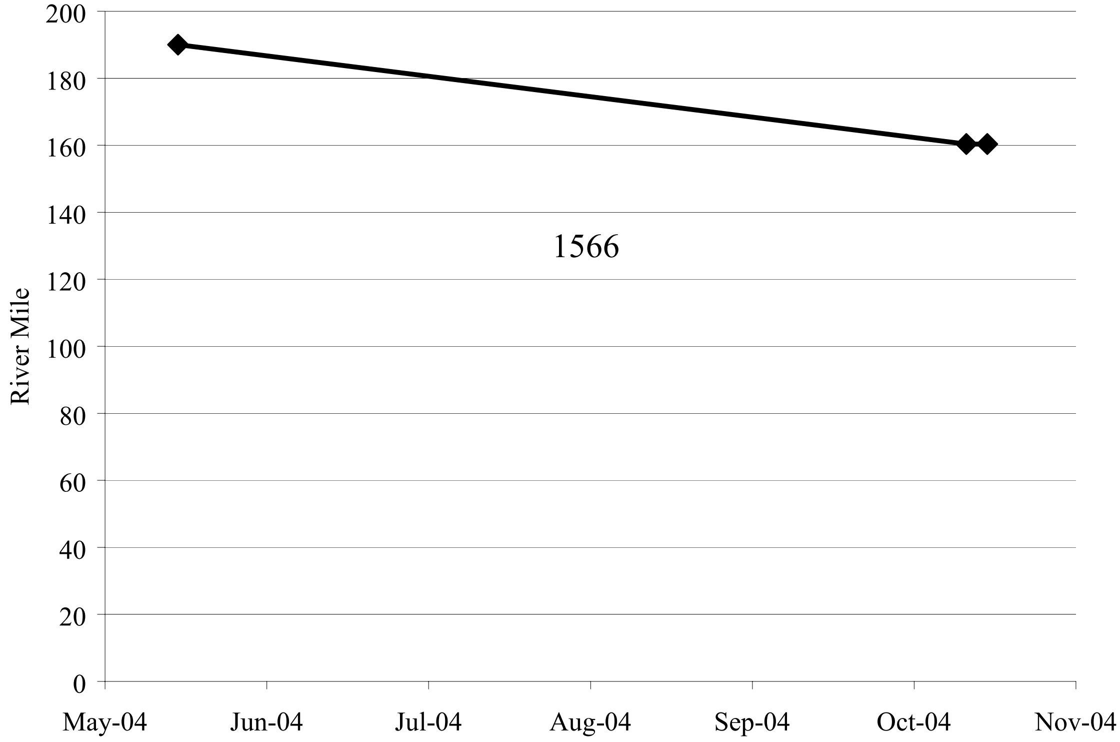
Appendix A-18. Observed movements of Pallid Sturgeon 3985 and 3981 in the MMR from transmitter implantation until latest contact. Diamonds indicate individual relocations, dashed lines indicate times when pallid sturgeon left the study site.



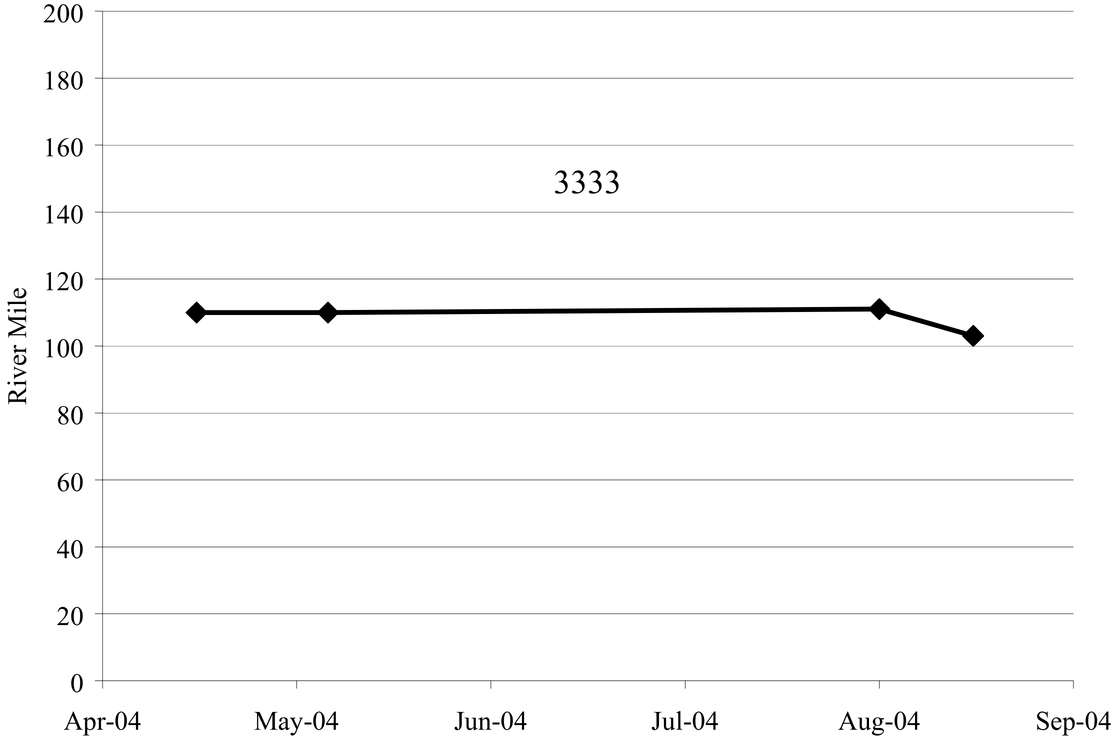


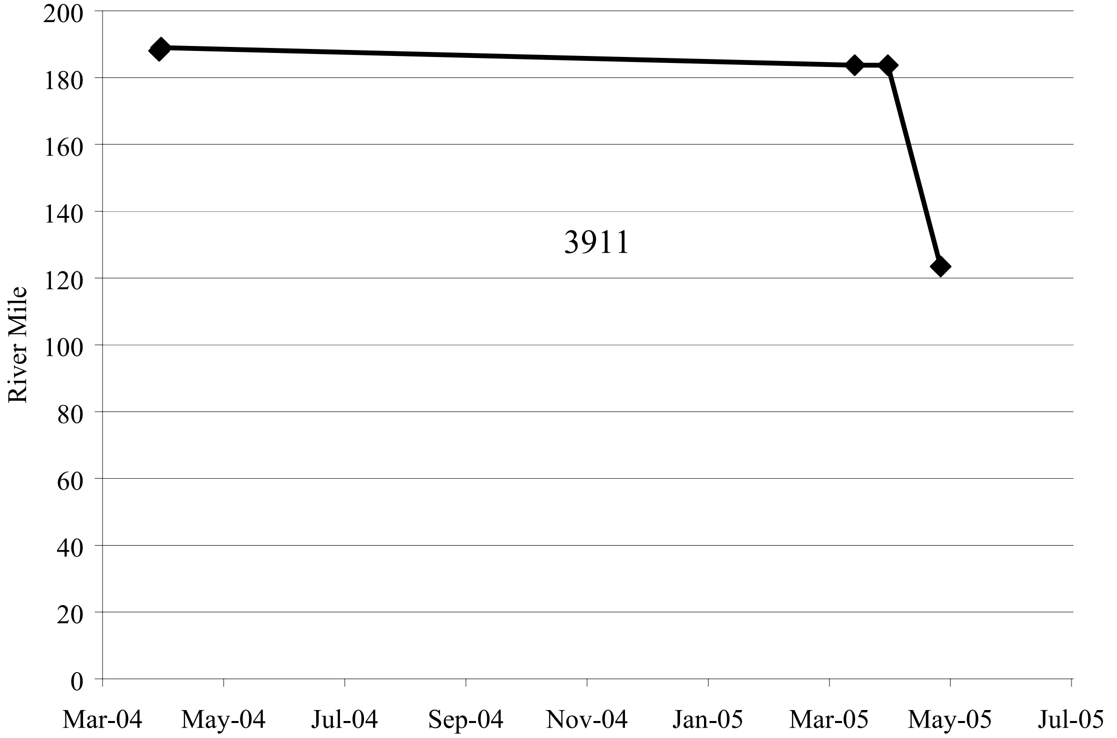
Appendix A-19. Observed movements of Pallid Sturgeon 3982 and 3984 in the MMR from transmitter implantation until latest contact. Diamonds indicate individual relocations, dashed lines indicate times when pallid sturgeon left the study site.



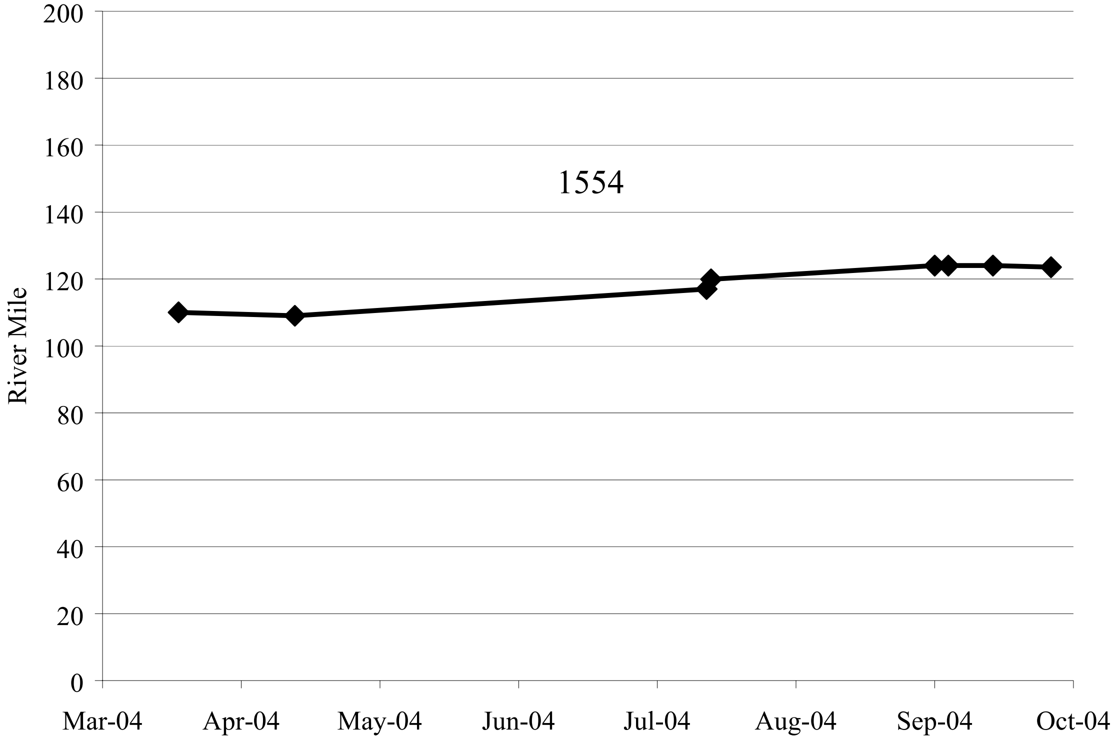


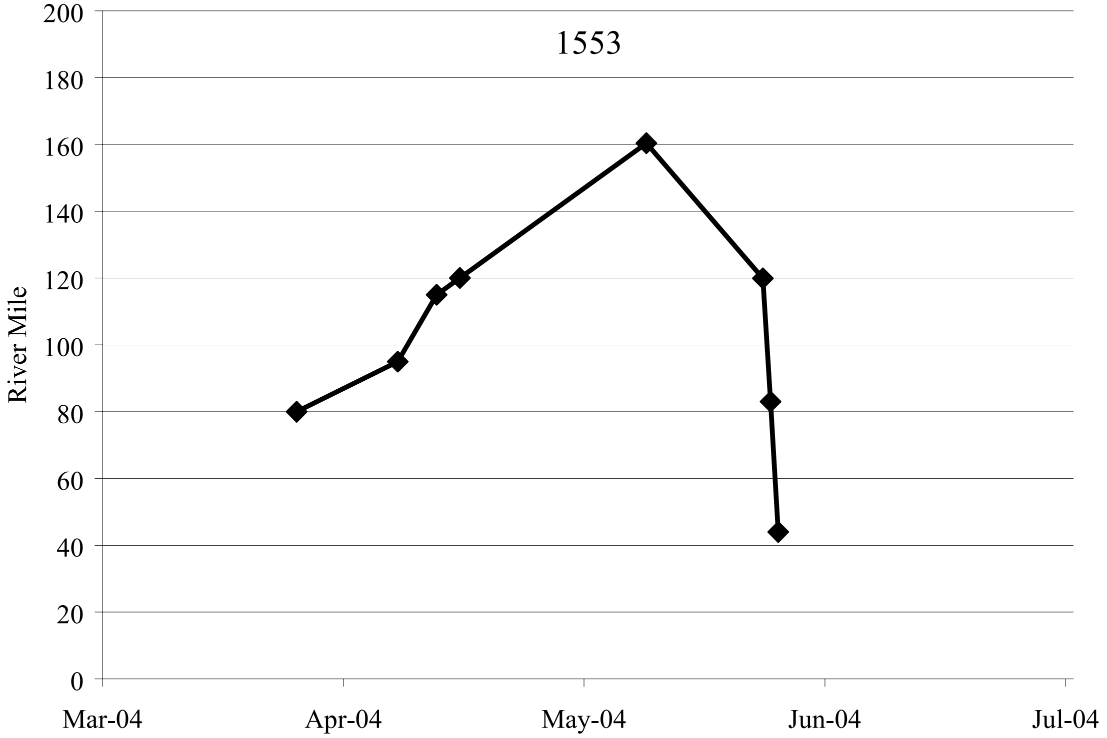
Appendix A-20. Observed movements of Pallid Sturgeon 1538 and 1566 in the MMR from transmitter implantation until latest contact. Diamonds indicate individual relocations, dashed lines indicate times when pallid sturgeon left the study site.



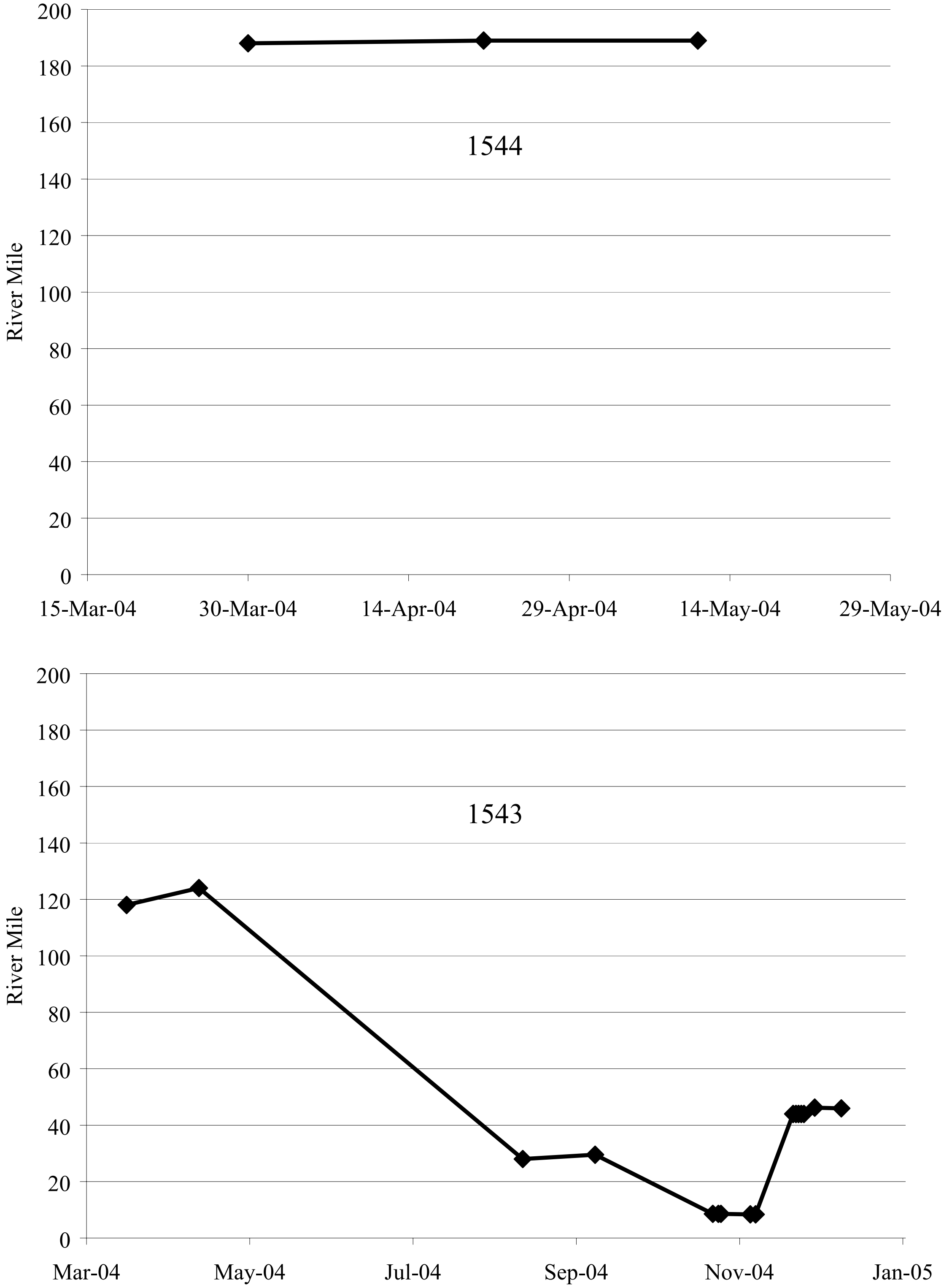


Appendix A-21. Observed movements of Pallid Sturgeon 3333 and 3911 in the MMR from transmitter implantation until latest contact. Diamonds indicate individual relocations, dashed lines indicate times when pallid sturgeon left the study site.

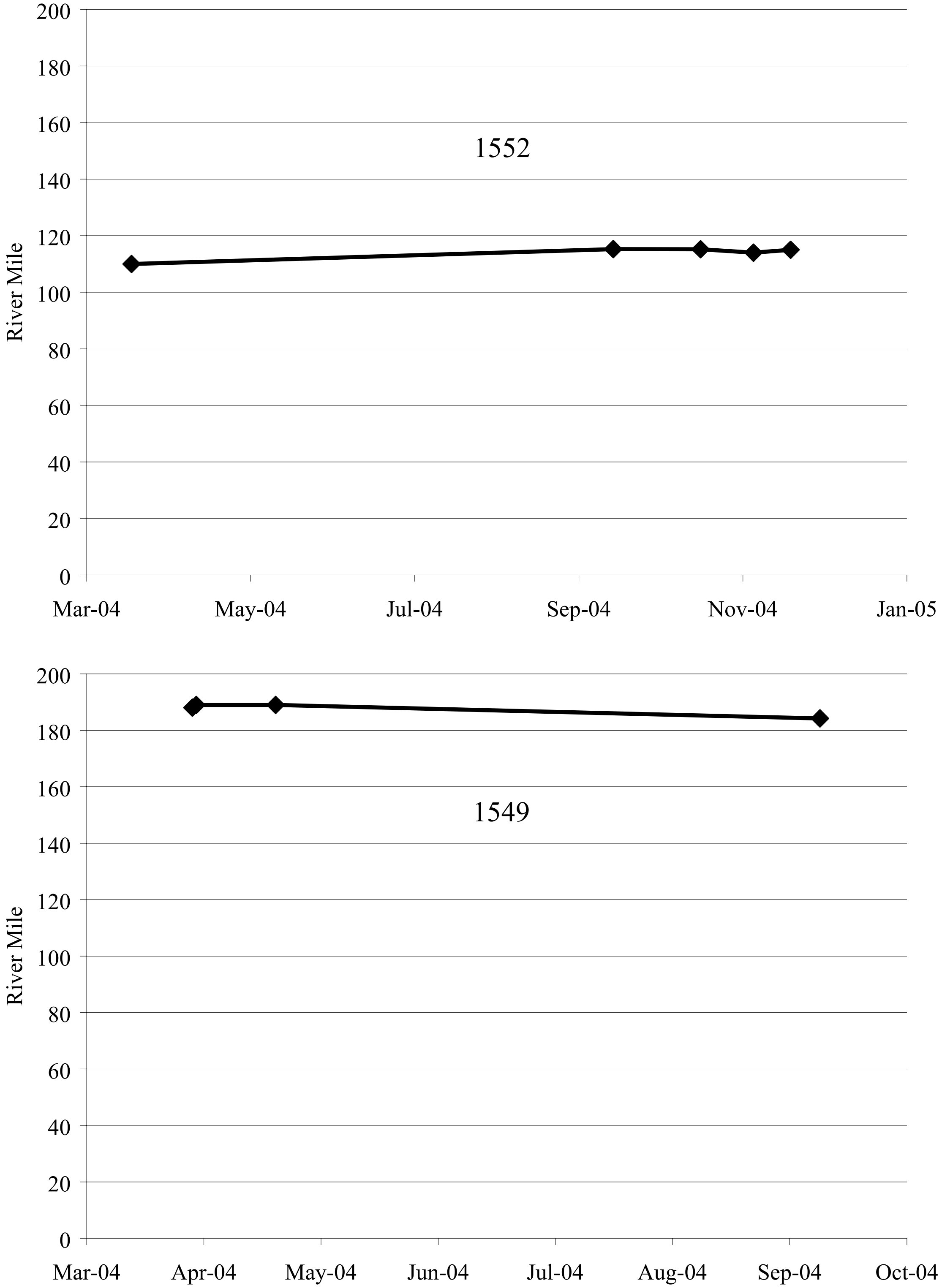




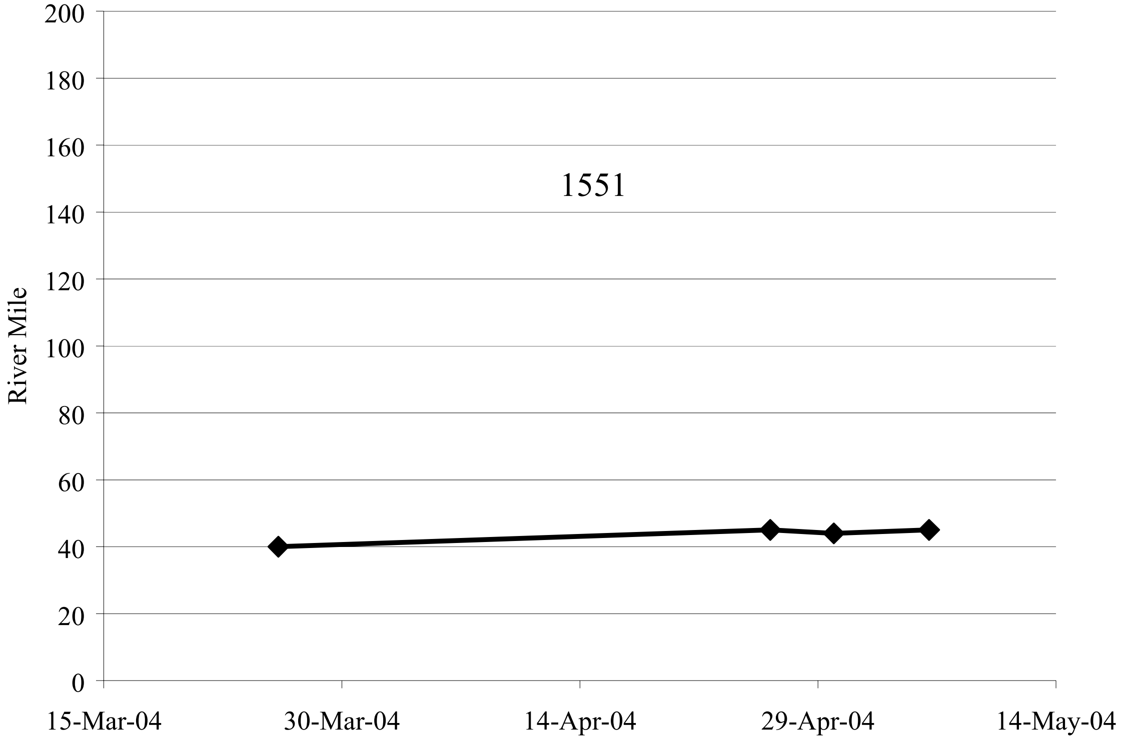
Appendix A-22. Observed movements of Pallid Sturgeon 1554 and 1553 in the MMR from transmitter implantation until latest contact. Diamonds indicate individual relocations, dashed lines indicate times when pallid sturgeon left the study site.

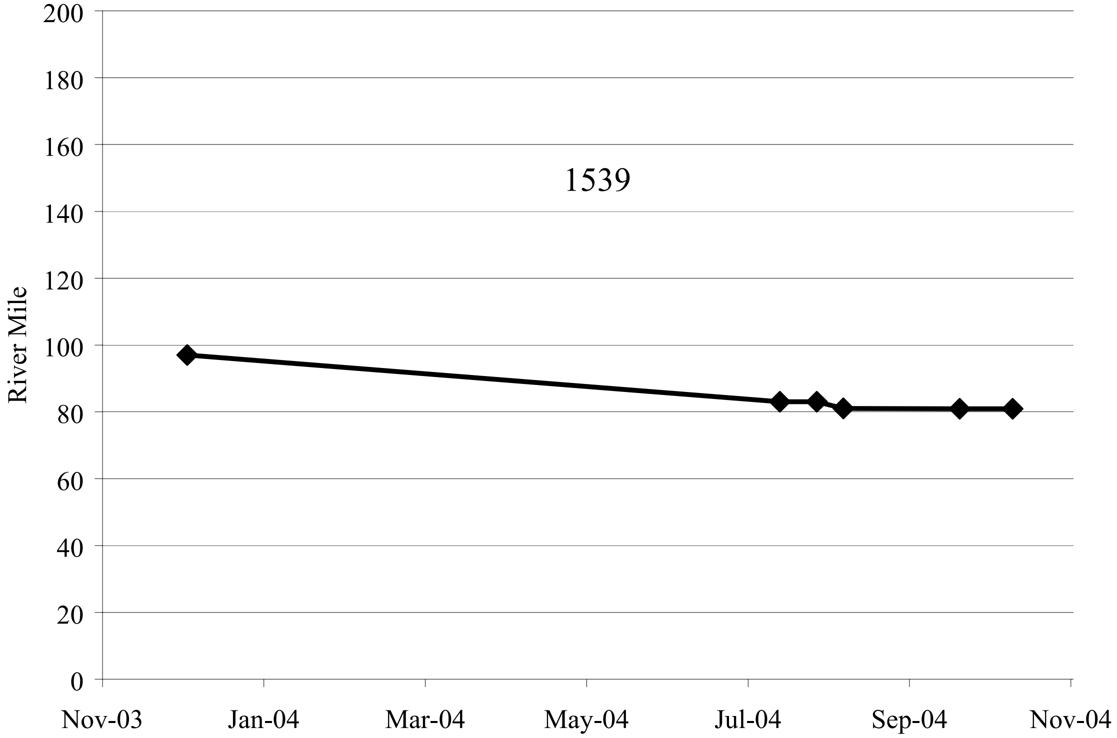


Appendix A-23. Observed movements of Pallid Sturgeon 1544 and 1543 in the MMR from transmitter implantation until latest contact. Diamonds indicate individual relocations, dashed lines indicate times when pallid sturgeon left the study site.

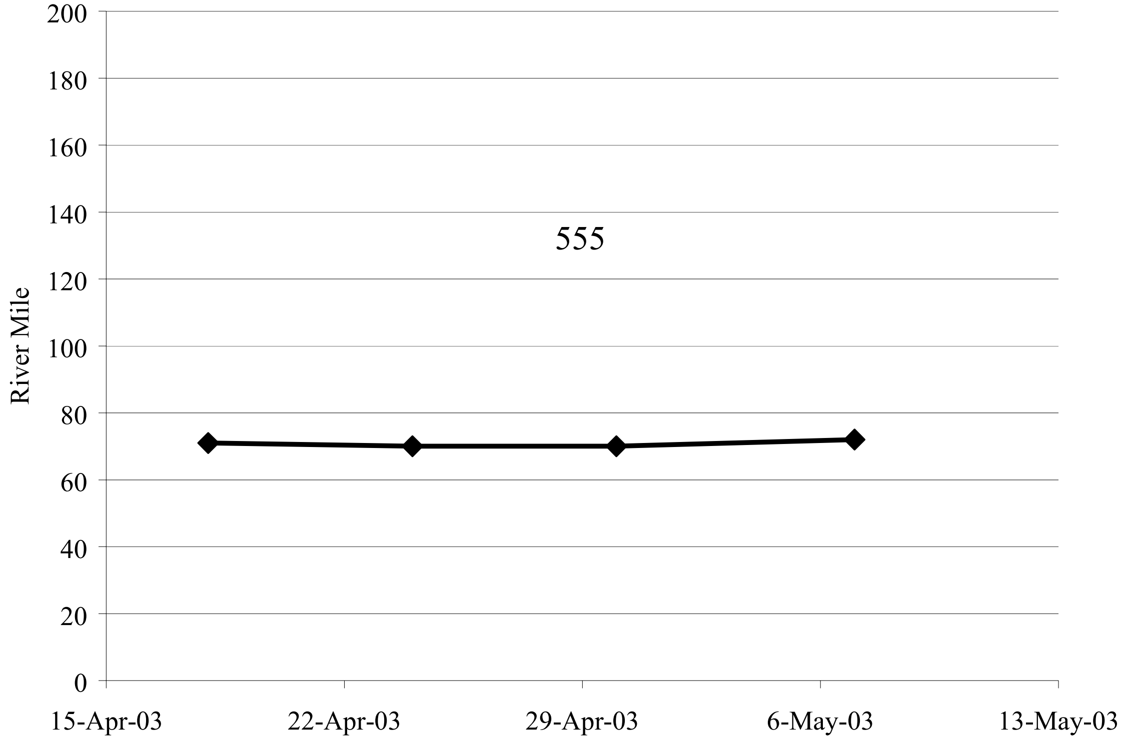


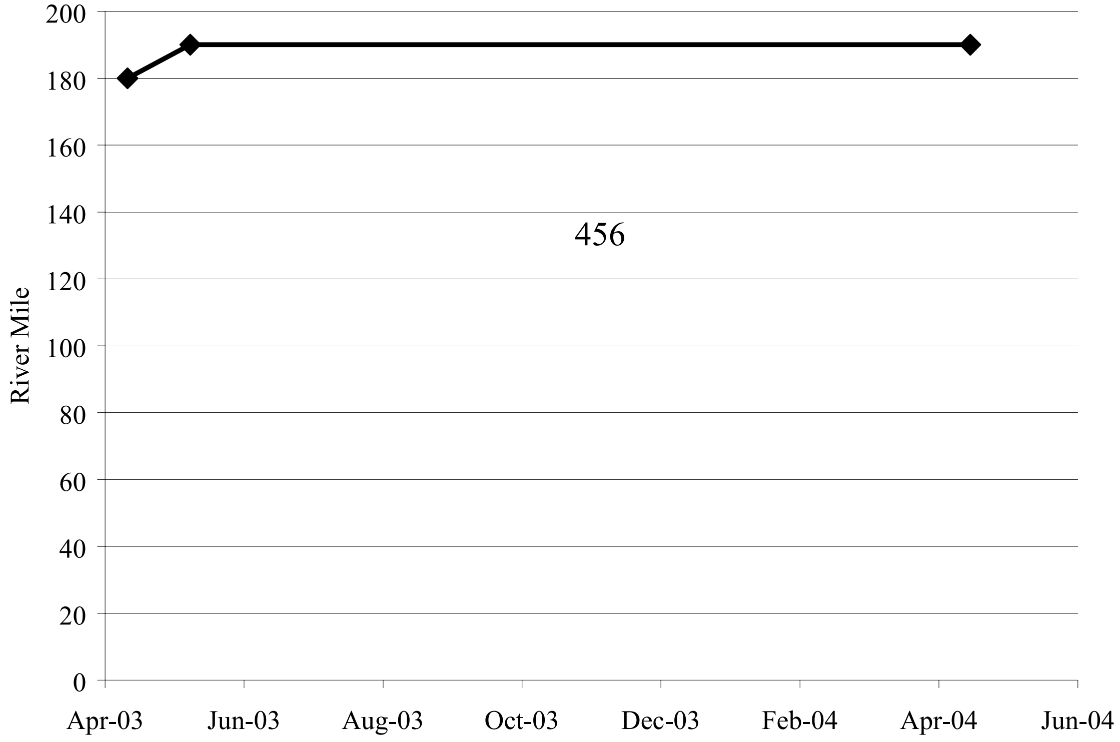
Appendix A-24. Observed movements of Pallid Sturgeon 1552 and 1549 in the MMR from transmitter implantation until latest contact. Diamonds indicate individual relocations, dashed lines indicate times when pallid sturgeon left the study site.



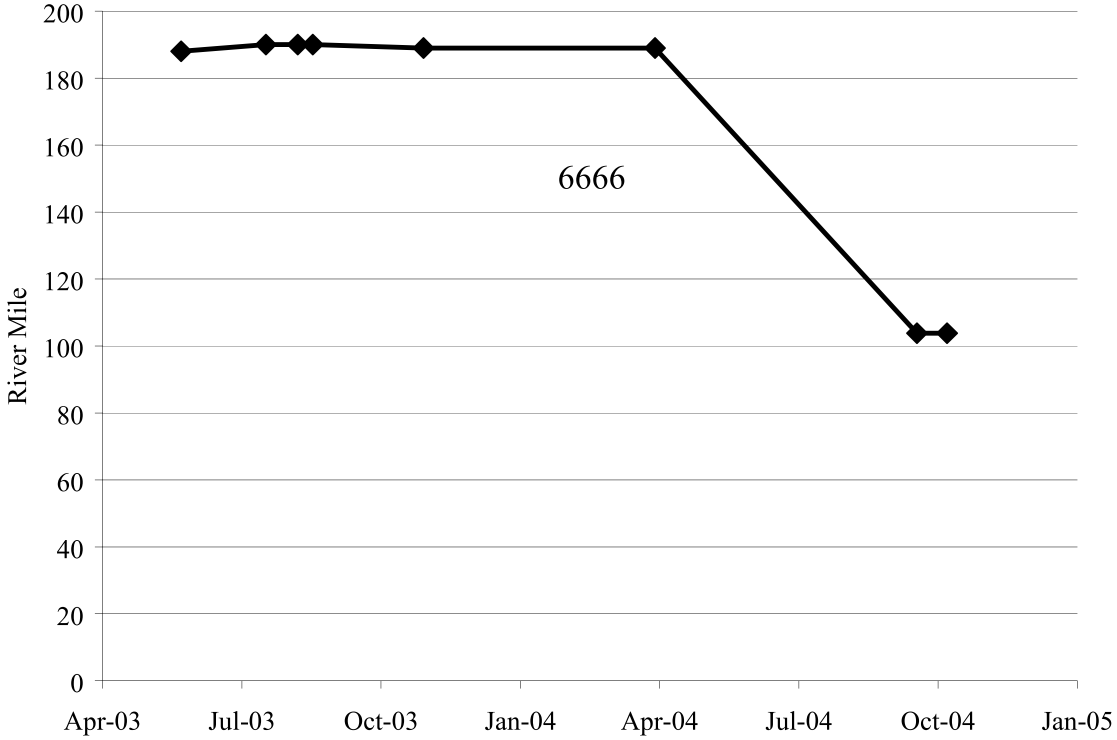


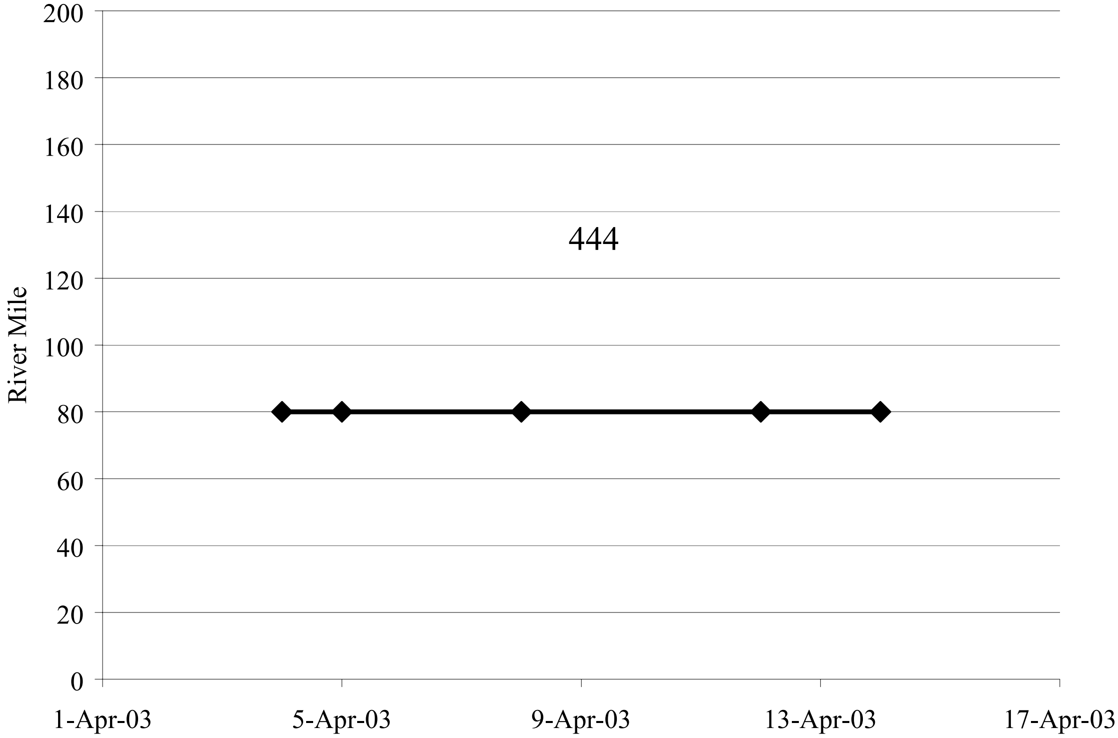
Appendix A-25. Observed movements of Pallid Sturgeon 1551 and 1539 in the MMR from transmitter implantation until latest contact. Diamonds indicate individual relocations, dashed lines indicate times when pallid sturgeon left the study site.



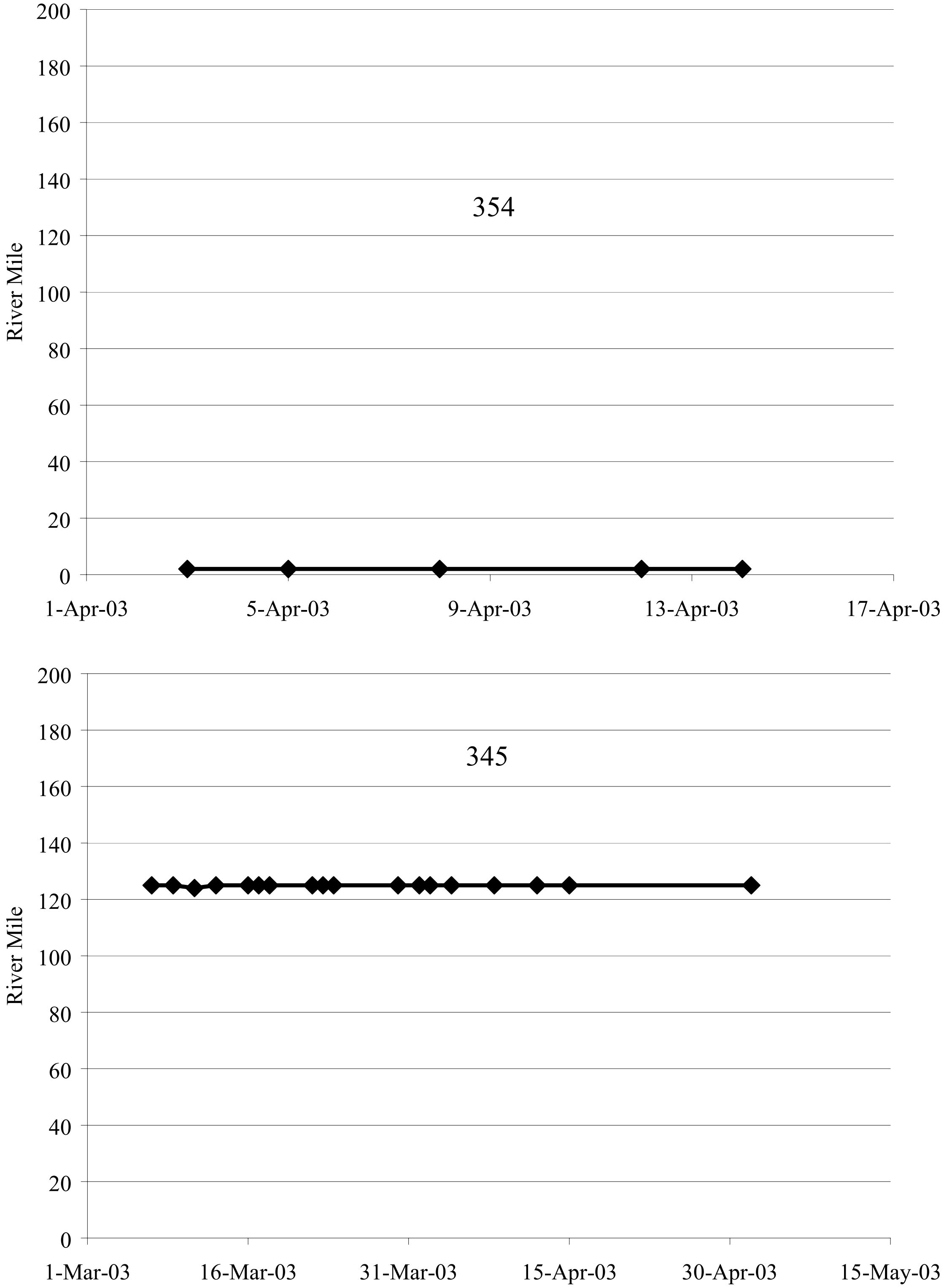


Appendix A-26. Observed movements of Pallid Sturgeon 555 and 456 in the MMR from transmitter implantation until latest contact. Diamonds indicate individual relocations, dashed lines indicate times when pallid sturgeon left the study site.

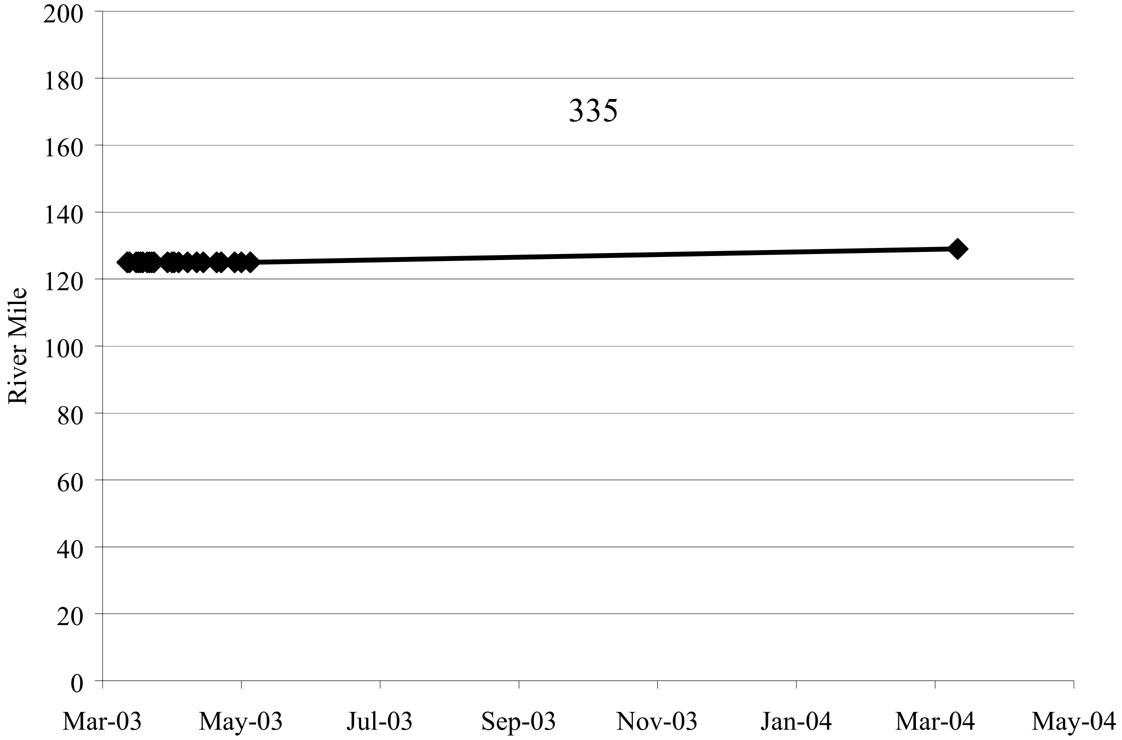


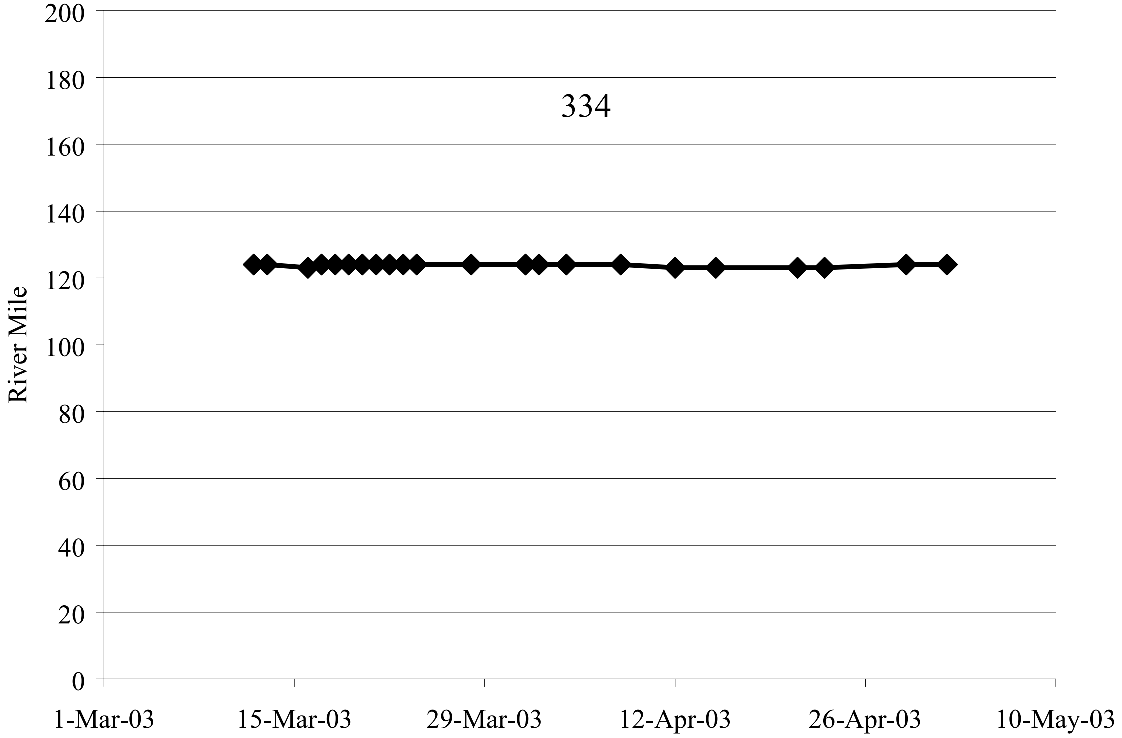


Appendix A-27. Observed movements of Pallid Sturgeon 6666 and 444 in the MMR from transmitter implantation until latest contact. Diamonds indicate individual relocations, dashed lines indicate times when pallid sturgeon left the study site.

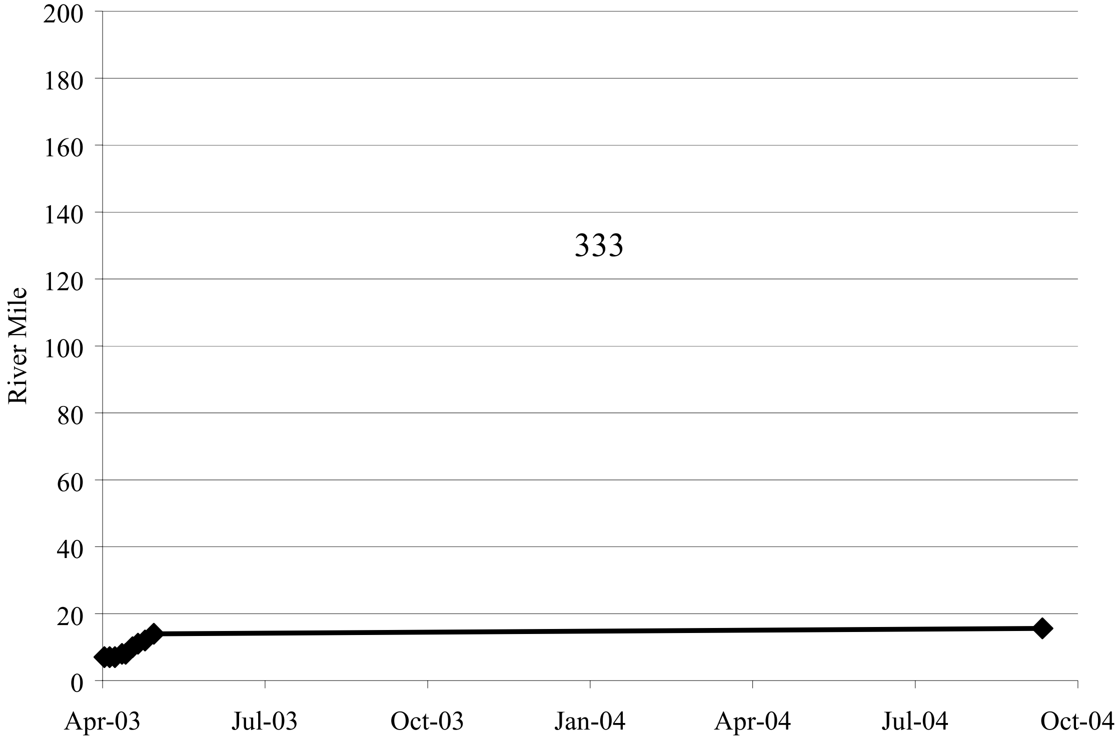


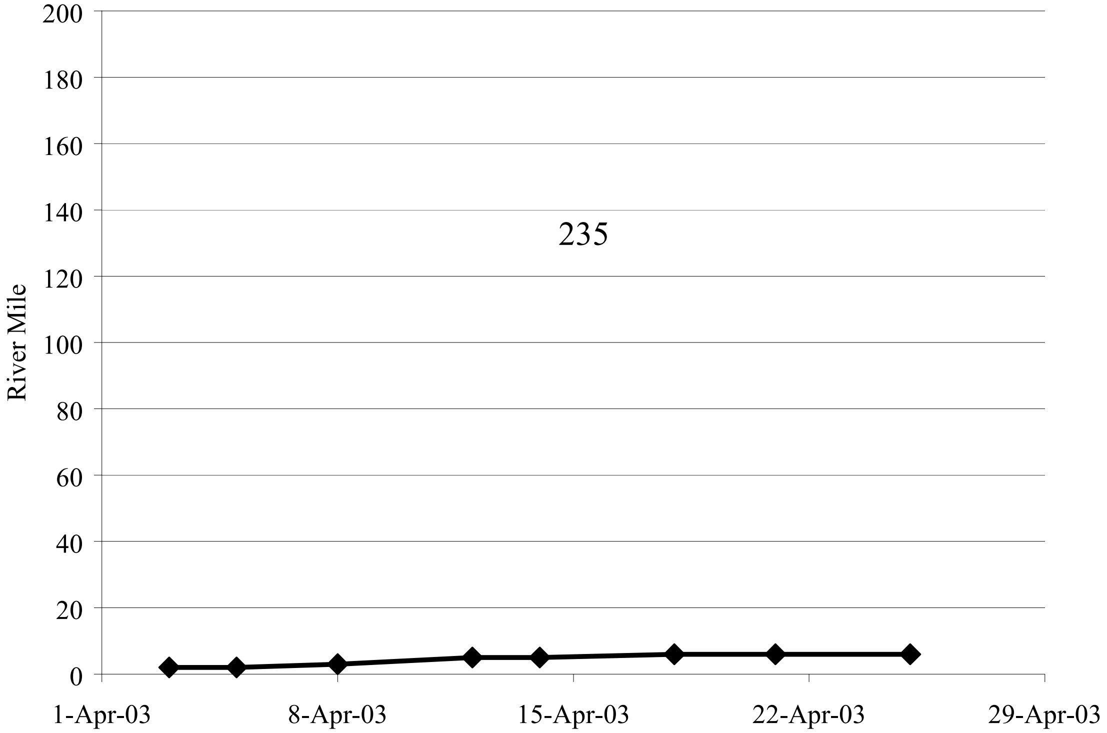
Appendix A-28. Observed movements of Pallid Sturgeon 354 and 345 in the MMR from transmitter implantation until latest contact. Diamonds indicate individual relocations, dashed lines indicate times when pallid sturgeon left the study site.



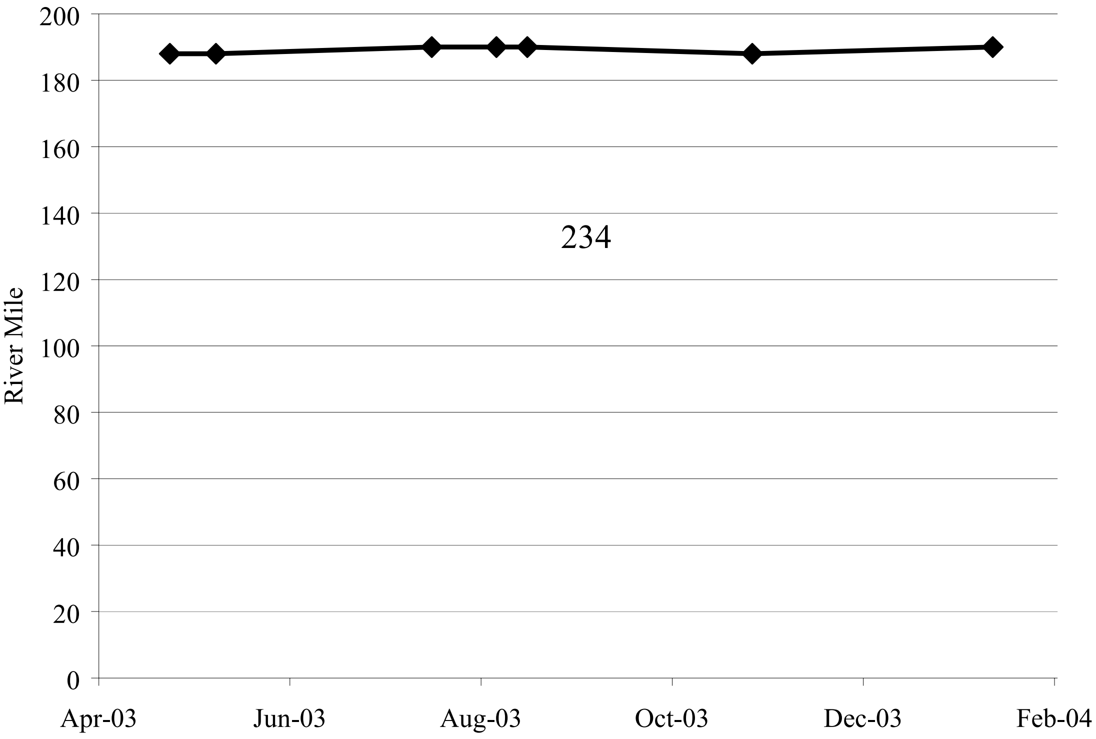


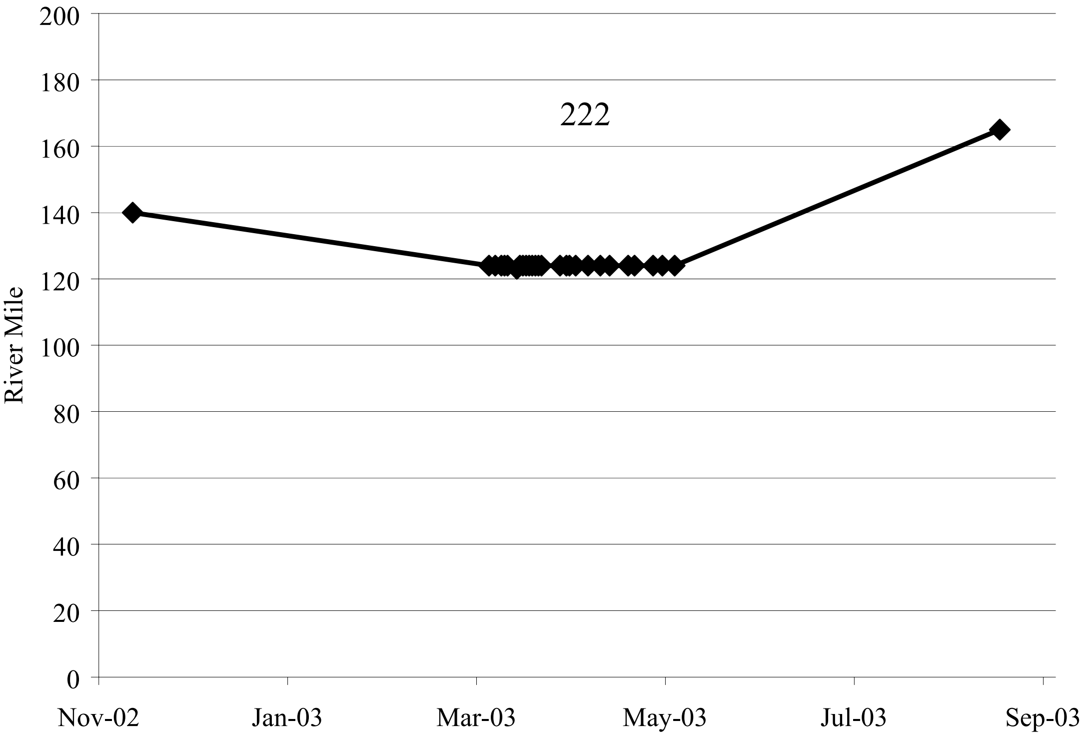
Appendix A-29. Observed movements of Pallid Sturgeon 335 and 334 in the MMR from transmitter implantation until latest contact. Diamonds indicate individual relocations, dashed lines indicate times when pallid sturgeon left the study site.



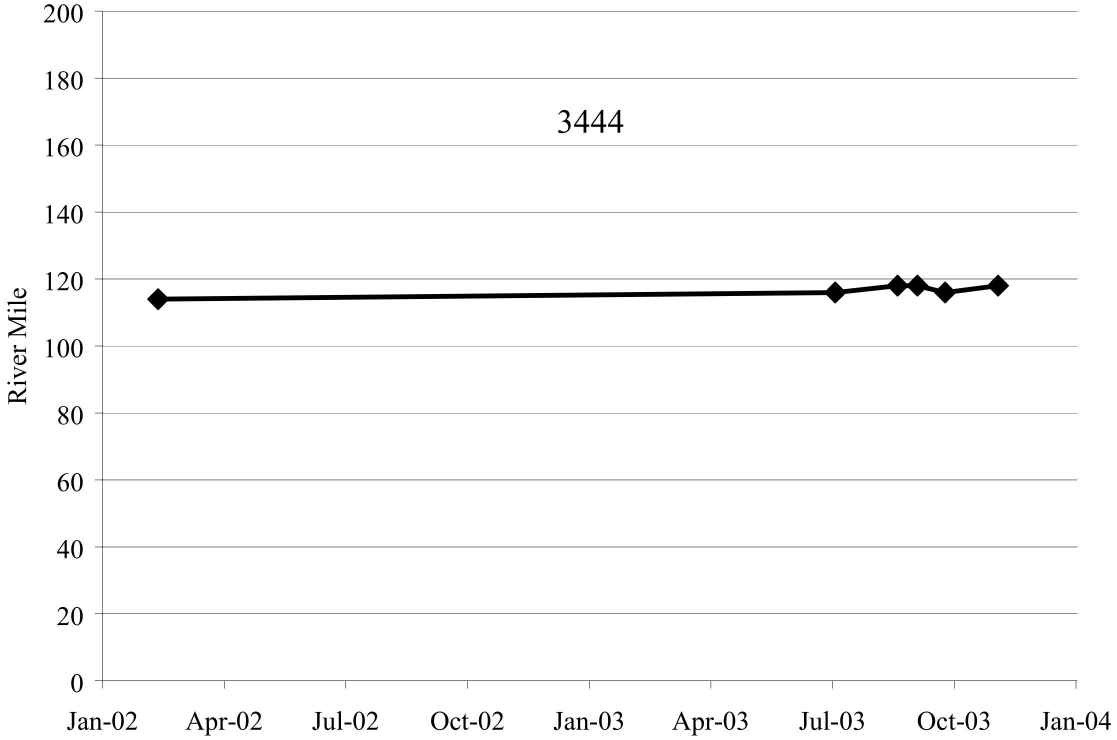


Appendix A-30. Observed movements of Pallid Sturgeon 333 and 235 in the MMR from transmitter implantation until latest contact. Diamonds indicate individual relocations, dashed lines indicate times when pallid sturgeon left the study site.





Appendix A-31. Observed movements of Pallid Sturgeon 234 and 222 in the MMR from transmitter implantation until latest contact. Diamonds indicate individual relocations, dashed lines indicate times when pallid sturgeon left the study site.

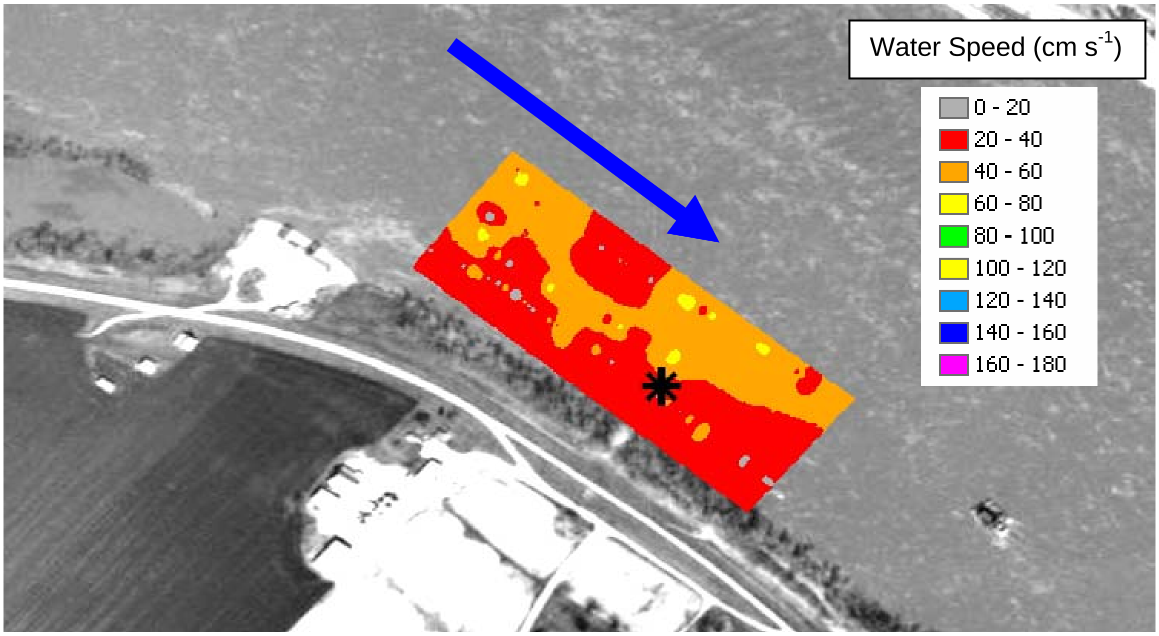


Appendix A-32. Observed movement of Pallid Sturgeon 3444 in the MMR from transmitter implantation until latest contact. Diamonds indicate individual relocations, dashed lines indicate times when pallid sturgeon left the study site.

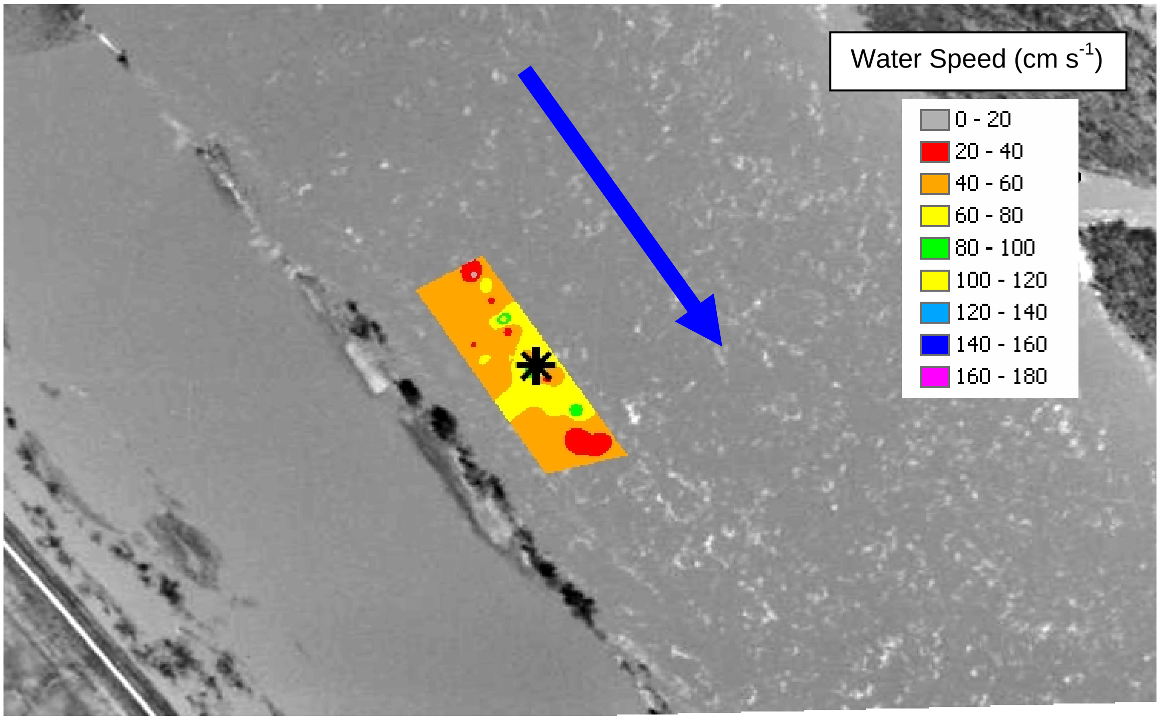
Appendix A-33. Navigation buoys modified, painted, and deployed to house VR2 (Vemco, LTD.) stationary reivers in the middle Mississippi River from spring 2003 through 2005.

Appendix B

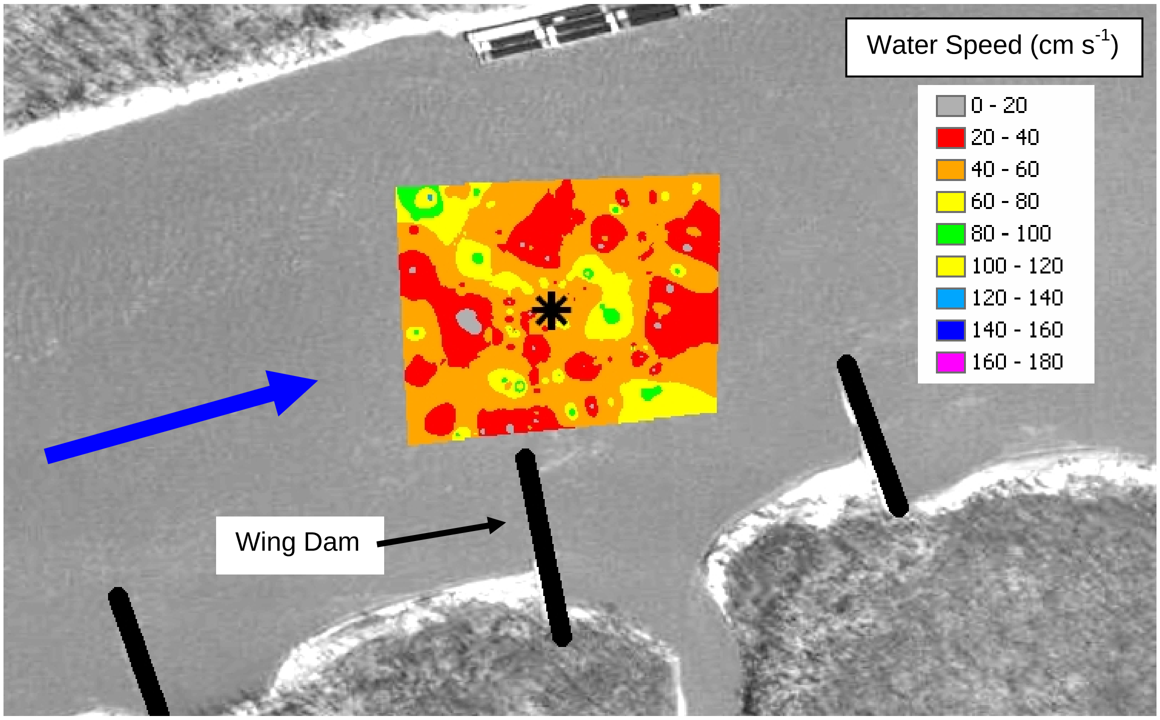
Acoustic Doppler Profiler (SonTek) images of various Pallid Sturgeon locations in the middle Mississippi River. Images represent river bottom water velocities. Aerial photos are USGS images (teraserver.com).Wing dam shapefile provided by U.S. Army Corps of Engineers, Rock Island District.



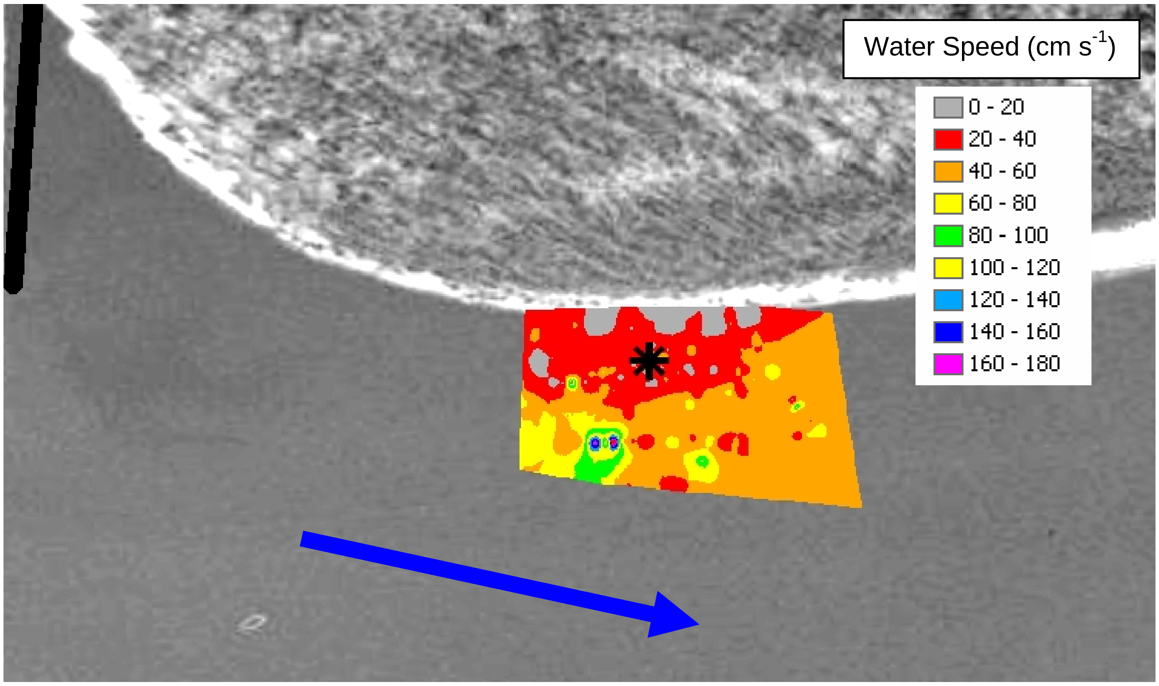
Appendix B-1. Bottom speed near a pallid sturgeon relocation in the Middle Mississippi River (sturgeon PS30, 4/14/04, river mile 109). Asterisk indicates location of the pallid sturgeon, while blue arrow indicates general direction of river flow.



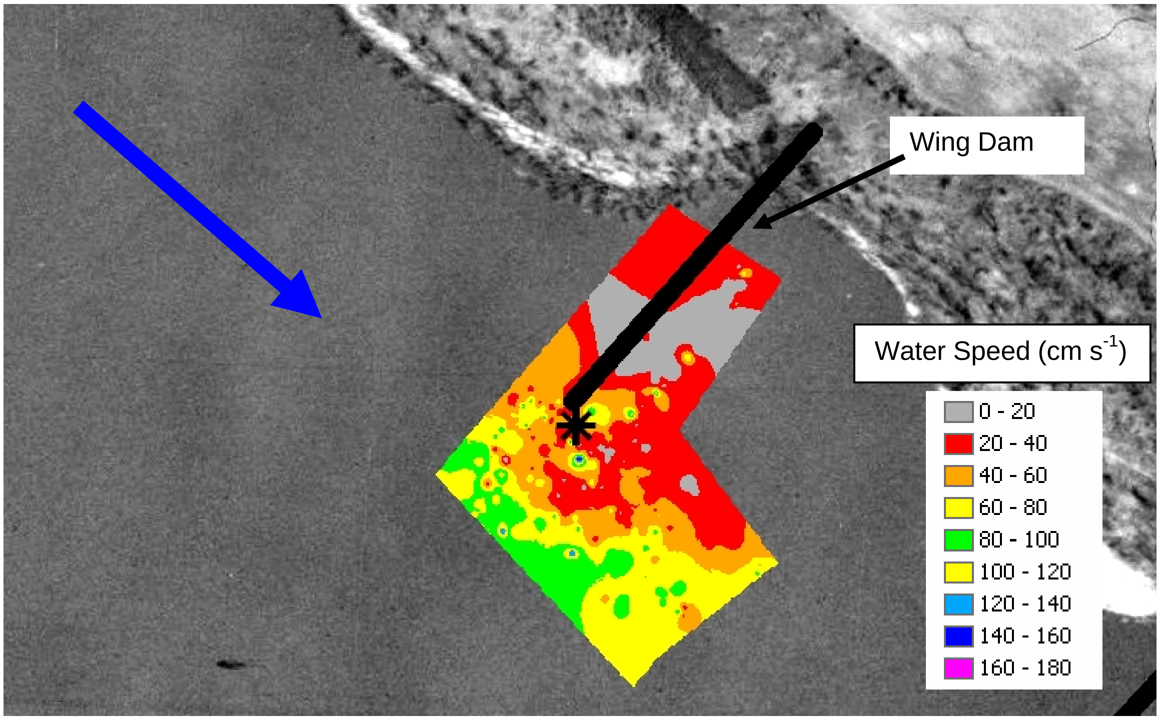
Appendix B-2. Bottom speed near a pallid sturgeon relocation in the Middle Mississippi River (sturgeon PS36, 4/14/04, river mile 114). Asterisk indicates location of the pallid sturgeon, while blue arrow indicates general direction of river flow.



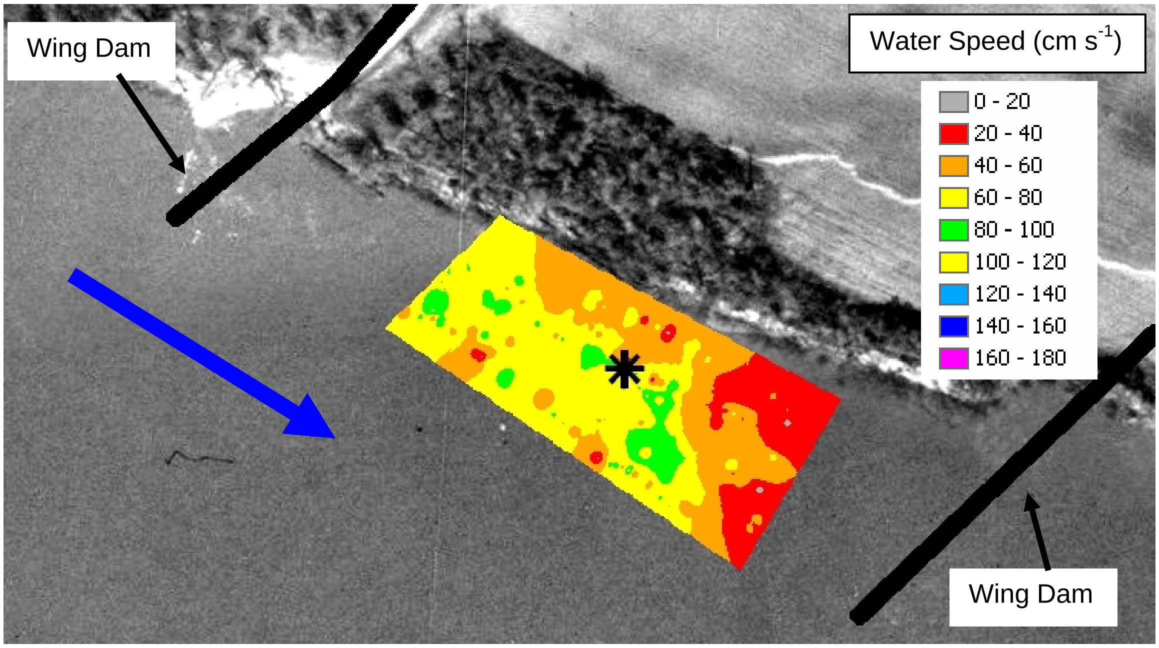
Appendix B-3. Bottom speed near a pallid sturgeon relocation in the Middle Mississippi River (sturgeon PS-2, 8/26/03, river mile 118). Asterisk indicates location of the pallid sturgeon, while blue arrow indicates general direction of river flow.



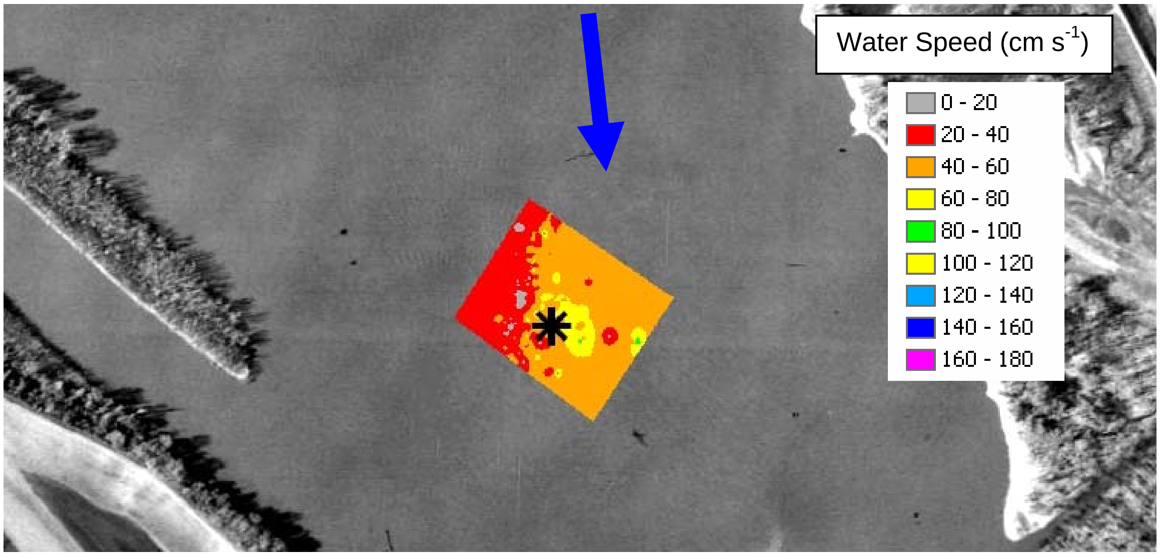
Appendix B-4. Bottom speed near a pallid sturgeon relocation in the Middle Mississippi River (sturgeon PS36, 4/16/04, river mile 120). Asterisk indicates location of the pallid sturgeon, while blue arrow indicates general direction of river flow.



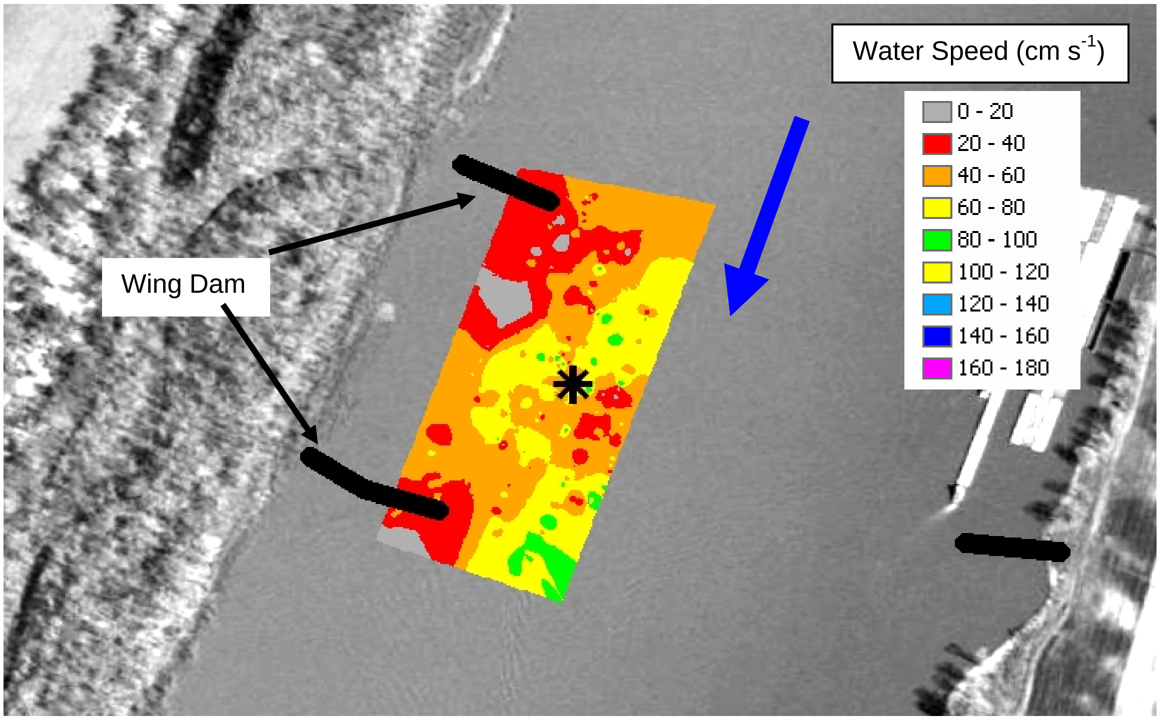
Appendix B-5. Bottom speed near a pallid sturgeon relocation in the Middle Mississippi River (sturgeon PS2, 3/13/03, river mile 124). Asterisk indicates location of the pallid sturgeon, while blue arrow indicates general direction of river flow.



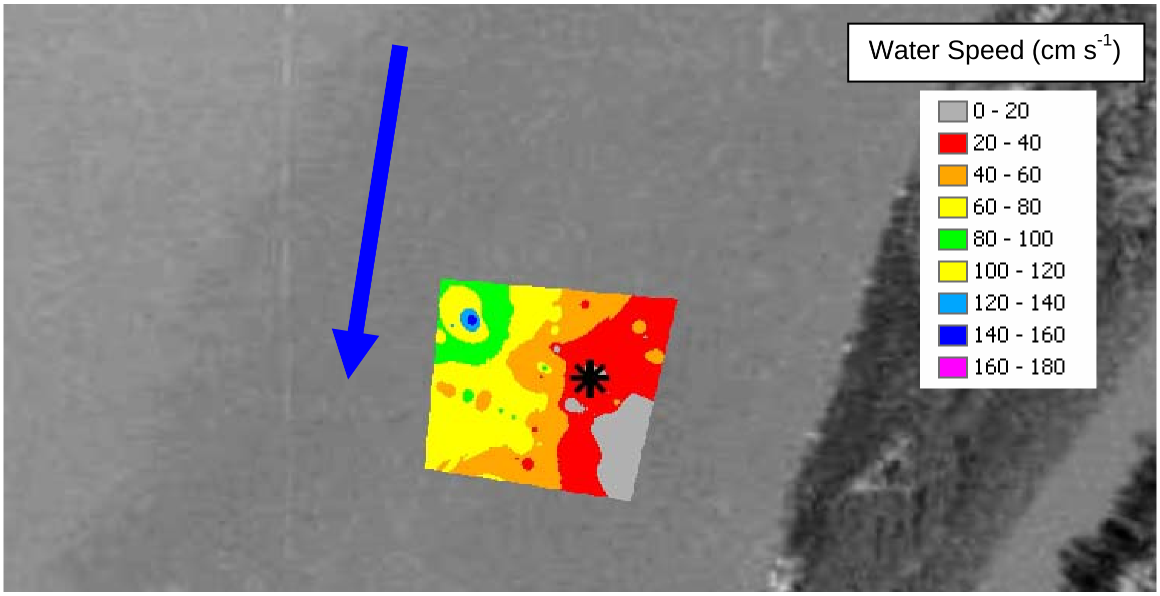
Appendix B-6. Bottom speed near a pallid sturgeon relocation in the Middle Mississippi River (sturgeon PS35, 4/16/04, river mile 125). Asterisk indicates location of the pallid sturgeon, while blue arrow indicates general direction of river flow.



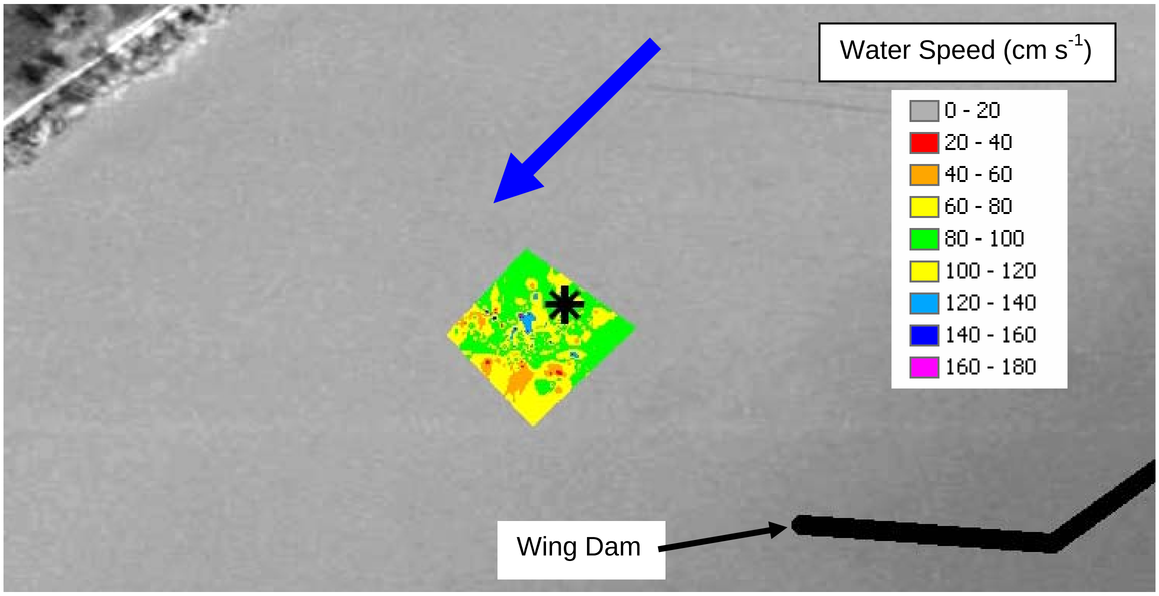
Appendix B-7. Bottom speed near a pallid sturgeon relocation in the Middle Mississippi River (sturgeon PS35, 4/27/04, river mile 130). Asterisk indicates location of the pallid sturgeon, while blue arrow indicates general direction of river flow. Note that the aerial photo was taken when water levels were much higher than they were when the sturgeon was relocated.



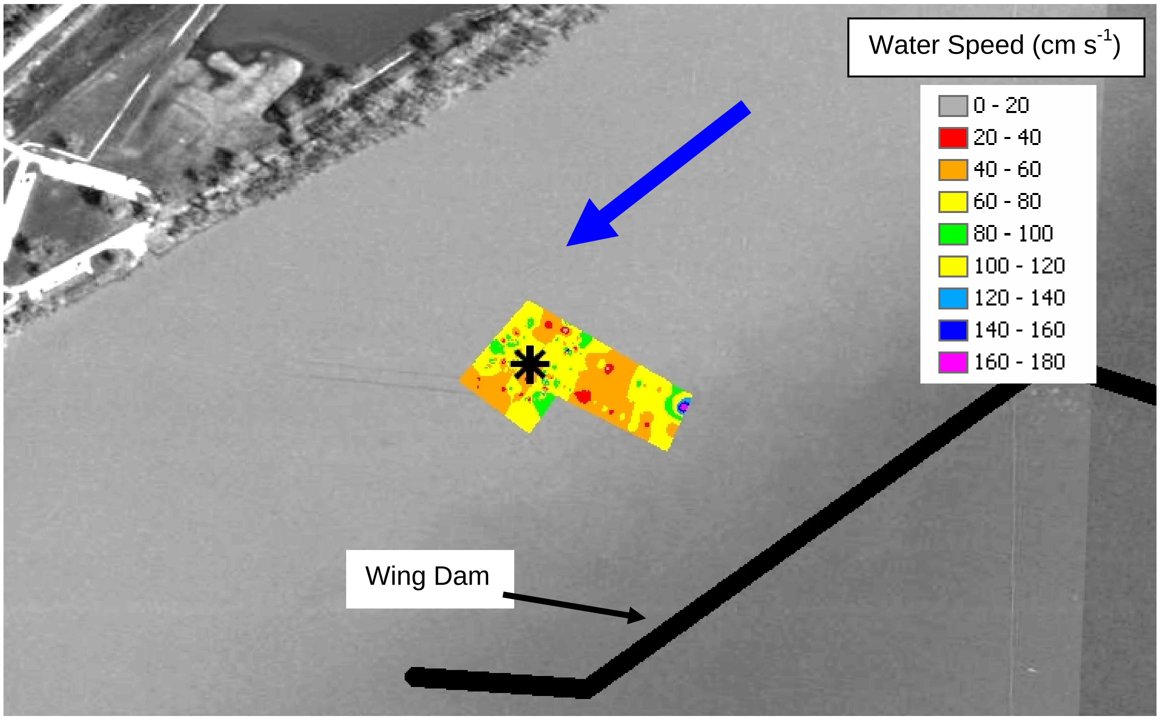
Appendix B-8. Bottom speed near a pallid sturgeon relocation in the Middle Mississippi River (sturgeon PS2, 8/19/03, river mile 165). Asterisk indicates location of the pallid sturgeon, while blue arrow indicates general direction of river flow.



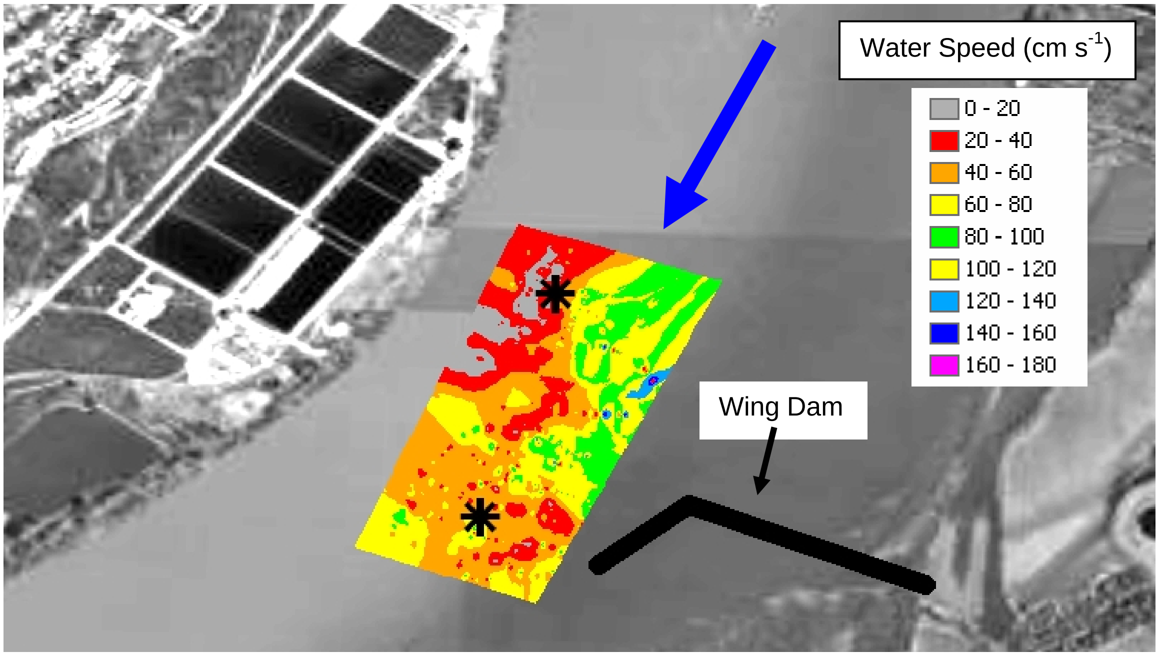
Appendix B-9. Bottom speed near a pallid sturgeon relocation in the Middle Mississippi River (sturgeon PS41, 4/21/04, river mile 187). Asterisk indicates location of the pallid sturgeon, while blue arrow indicates general direction of river flow.



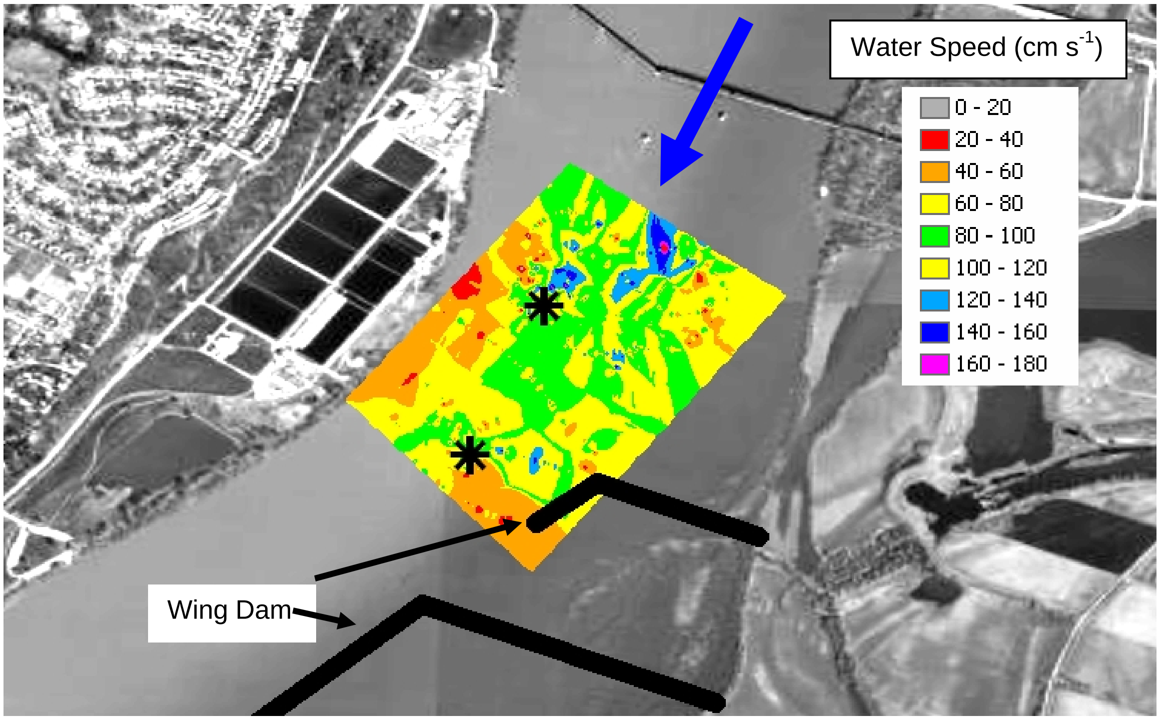
Appendix B-10. Bottom speed near a pallid sturgeon relocation in the Middle Mississippi River (sturgeon PS16, 10/30/03, river mile 189). Asterisk indicates location of the pallid sturgeon, while blue arrow indicates general direction of river flow.



Appendix B-11. Bottom speed near a pallid sturgeon relocation in the Middle Mississippi River (sturgeon PS18, 10/30/03, river mile 189). Asterisk indicates location of the pallid sturgeon, while blue arrow indicates general direction of river flow.



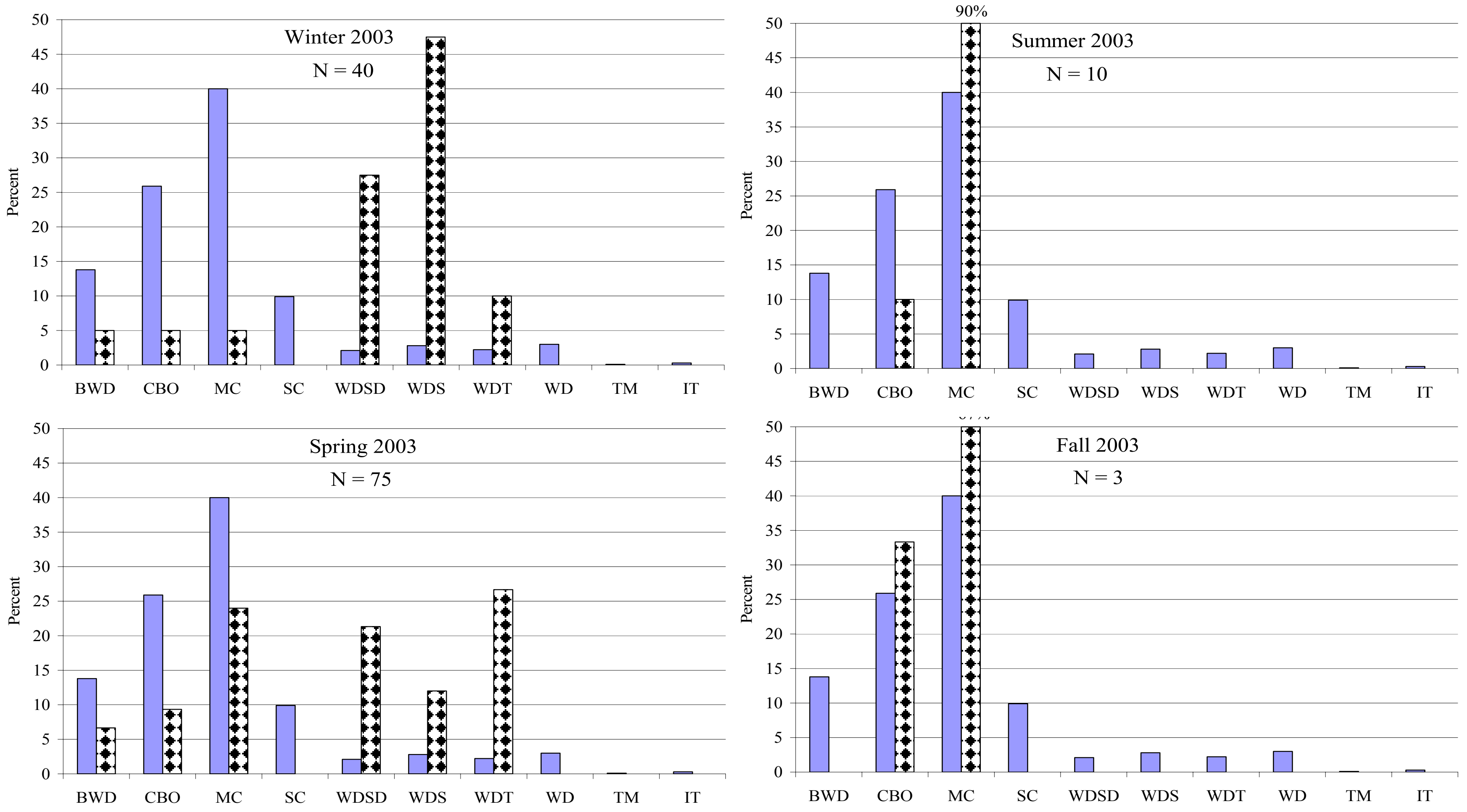
Appendix B-12. Bottom speed near a pallid sturgeon relocation in the Middle Mississippi River (sturgeon PS16 & PS18, 8/19/03, river mile 190). Asterisk indicates location of the pallid sturgeon, while blue arrow indicates general direction of river flow.



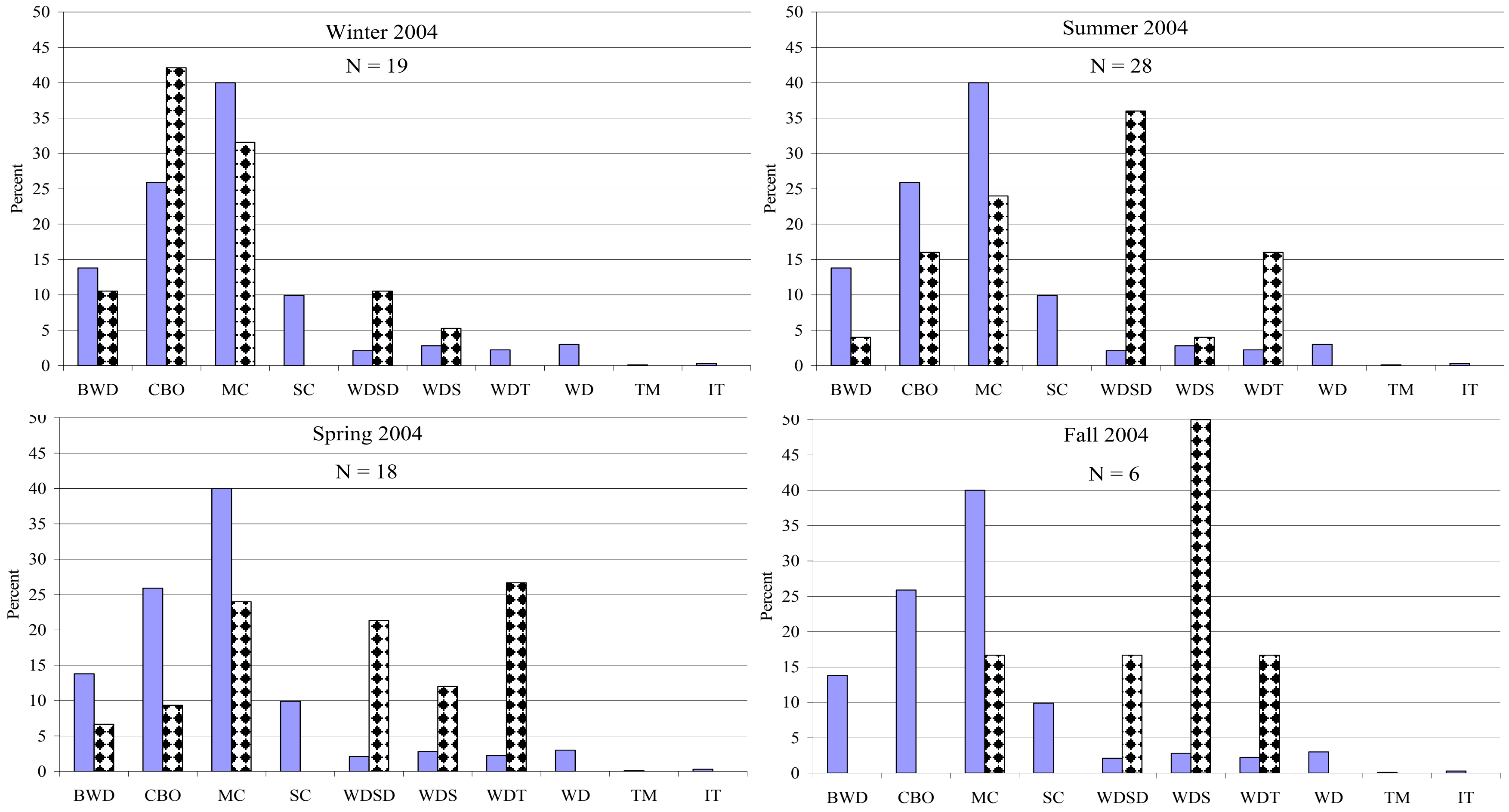
Appendix B-13. Bottom speed near a pallid sturgeon relocation in the Middle Mississippi River (sturgeon PS14 & PS40, 4/21/04, river mile 190). Asterisk indicates location of the pallid sturgeon, while blue arrow indicates general direction of river flow.

Appendix C

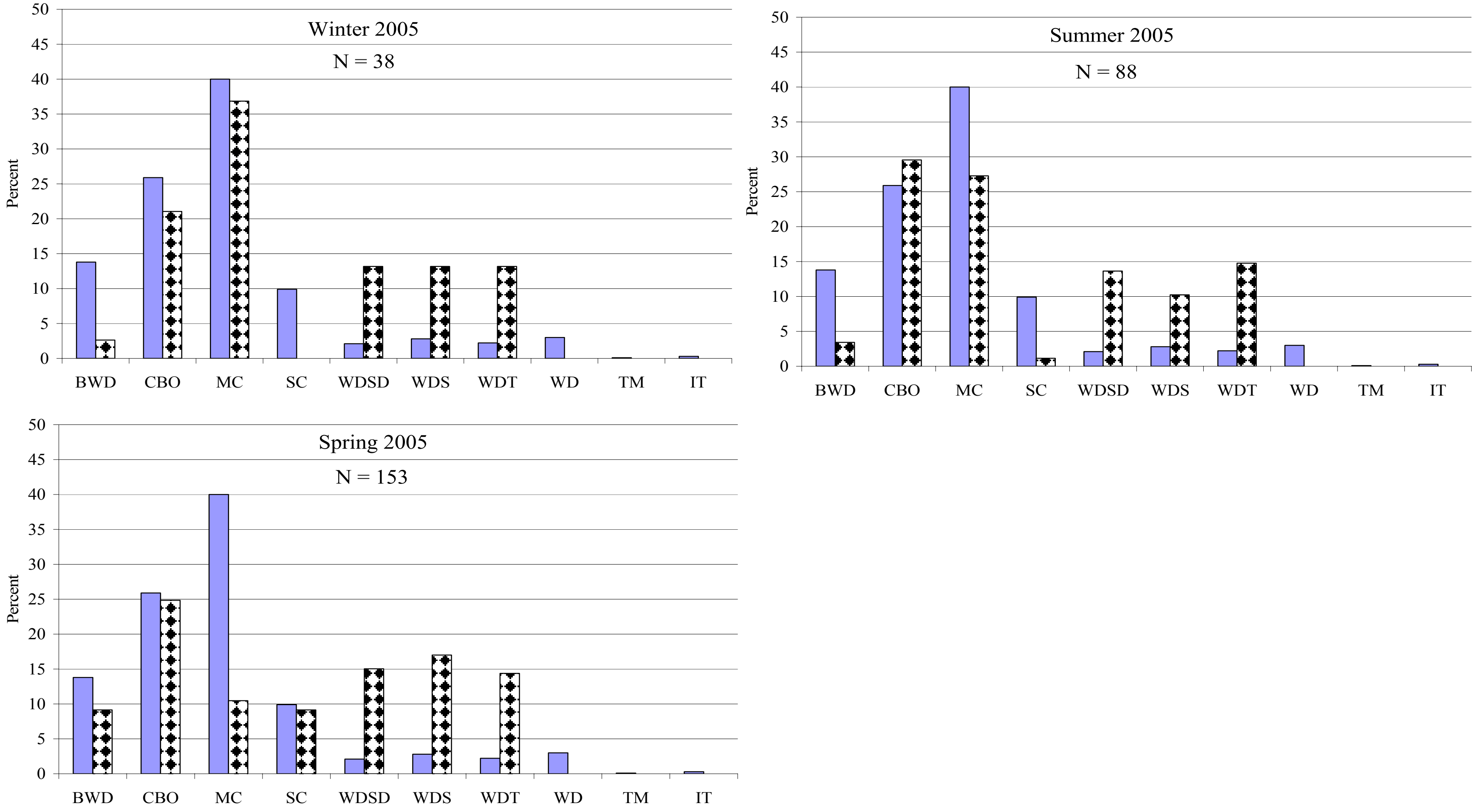
Percent occurrence of Pallid Sturgeon in several habitat types found in the middle Mississippi River. The Pallids were surgically implanted with ultrasonic transmitters and tracked from during 2003 through 2005. Two types of habitats are described: 1) habitats are from modified Cobb index as follows: BWD = between wing dikes; CBO = channel border open; MC = main channel; SC = side channel; WDSD = wing dam scour down; WDS = wing dam scour; WDT = wing dam tip; TM = tributary mouth; IT = island tip; and 2) based on river sinuosity.



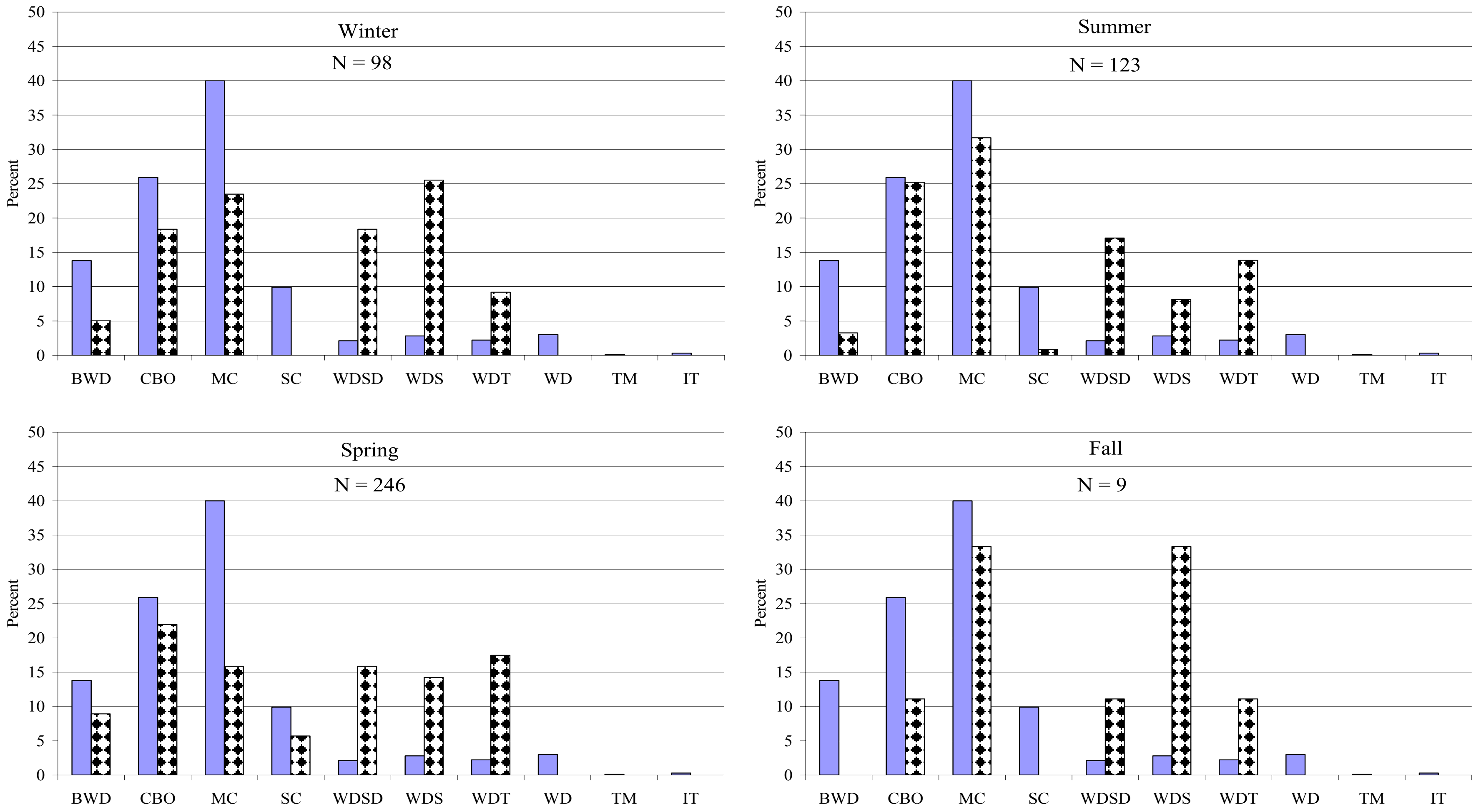
Appendix C-1. Percent habitat availability (solid bars) and seasonal use of transmittered Pallid Sturgeon in the middle Mississippi River during 2003. Habitat acronyms are from modified Cobb index as follows: BWD = between wing dikes; CBO = channel border open; MC = main channel; SC = side channel; WDSD = wing dam scour down; WDS = wing dam scour; WDT = wing dam tip; TM = tributary mouth; IT = island tip.



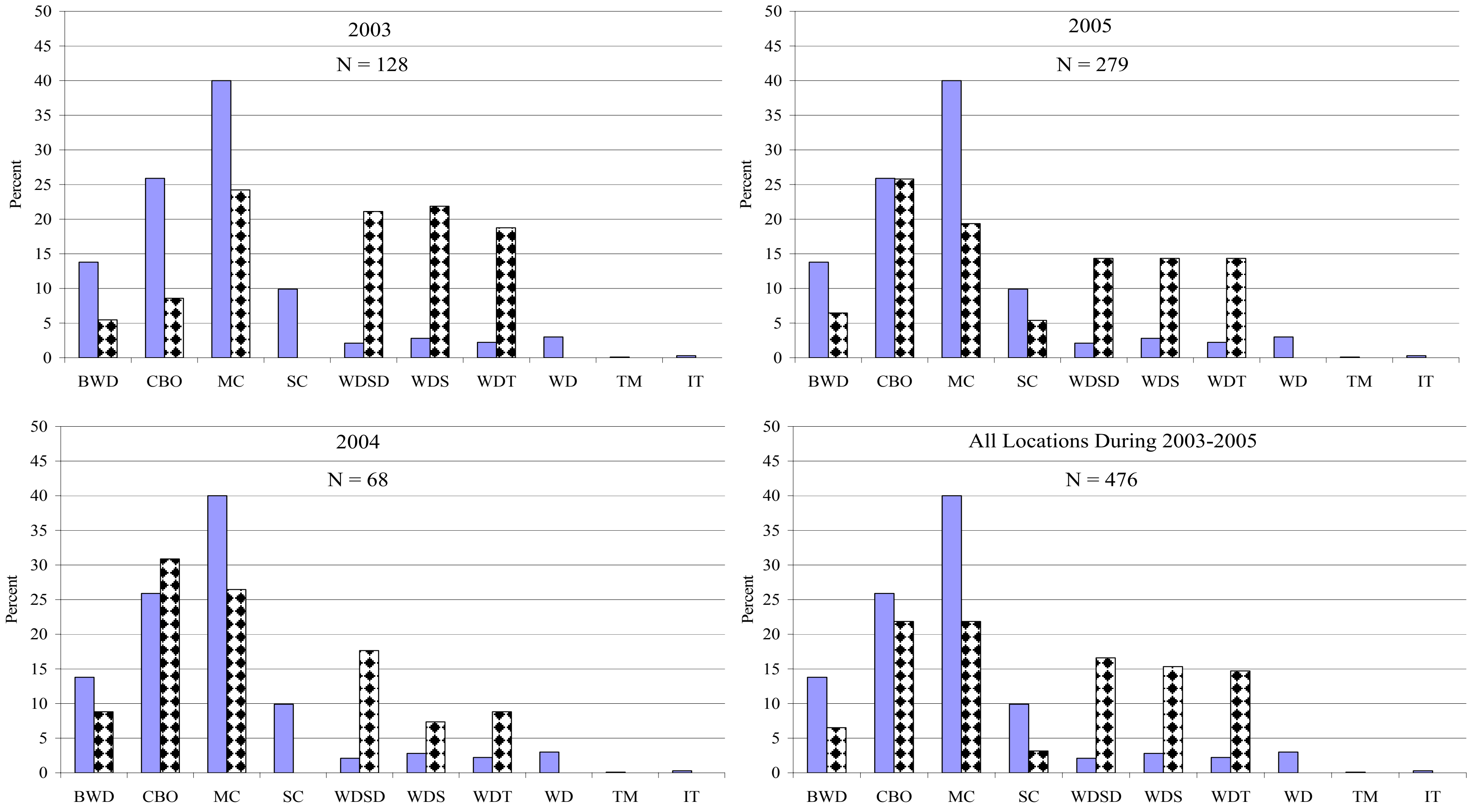
Appendix C-2. Percent habitat availability and seasonal use of transmittered Pallid Sturgeon in the middle Mississippi River during 2004. Habitat acronyms are from modified Cobb index as follows: BWD = between wing dikes; CBO = channel border open; MC = main channel; SC = side channel; WDSD = wing dam scour down; WDS = wing dam scour; WDT = wing dam tip; TM = tributary mouth; IT = island tip.



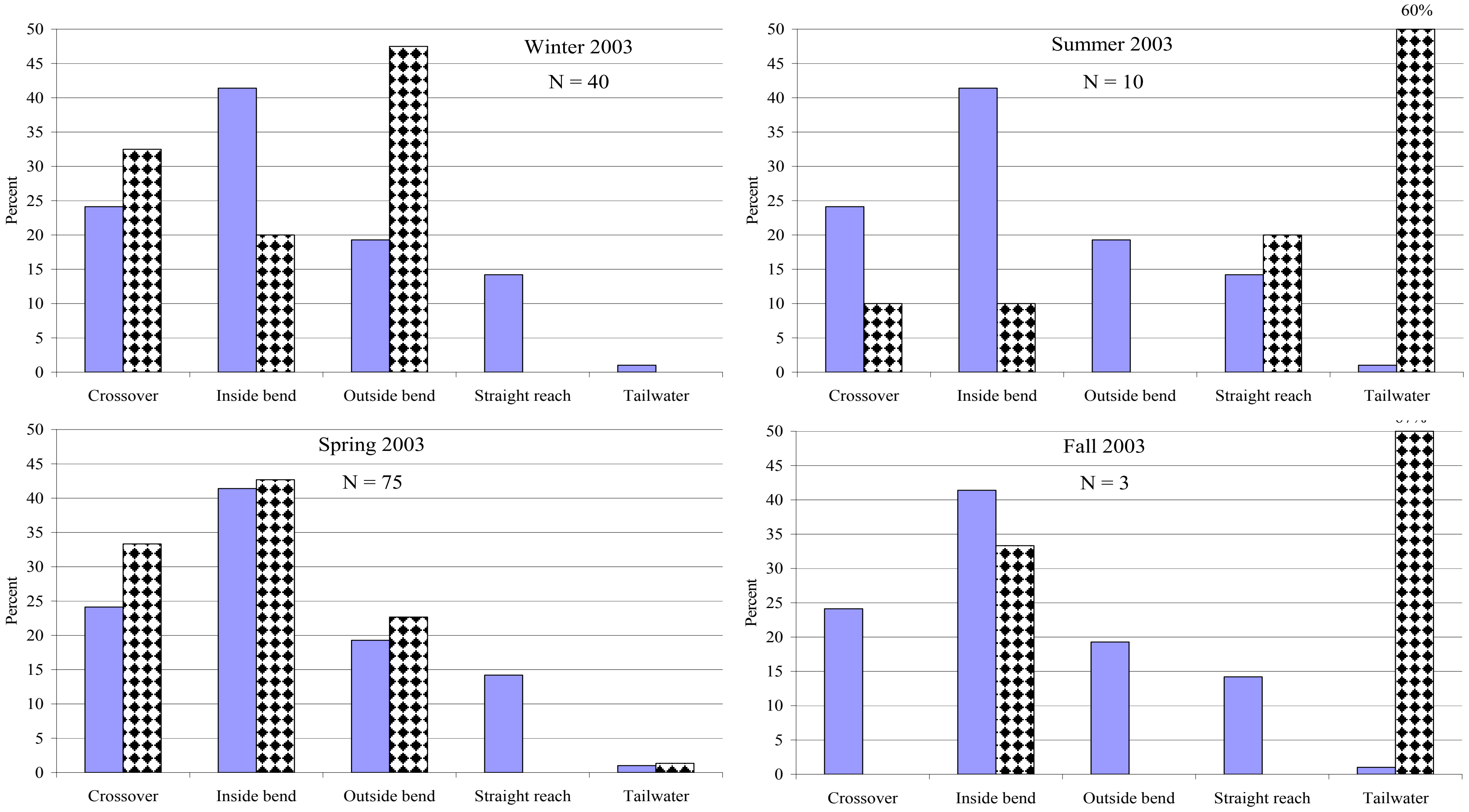
Appendix C-3. Percent habitat availability and seasonal use of transmittered Pallid Sturgeon in the middle Mississippi River during 2005. Habitat acronyms are from modified Cobb index as follows: BWD = between wing dikes; CBO = channel border open; MC = main channel; SC = side channel; WDSD = wing dam scour down; WDS = wing dam scour; WDT = wing dam tip; TM = tributary mouth; IT = island tip.



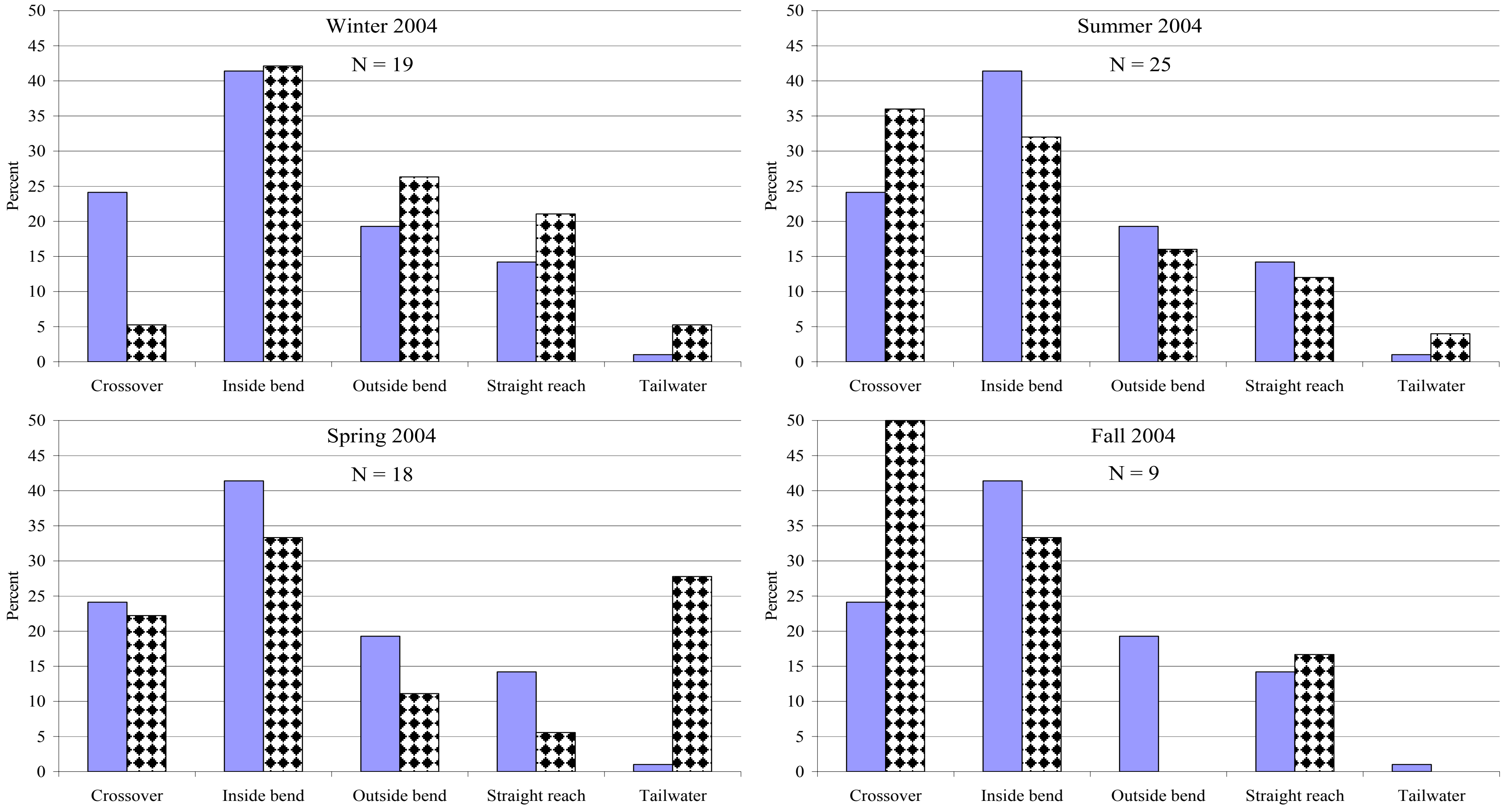
Appendix C-4. Percent habitat availability and seasonal use of transmittered Pallid Sturgeon in the middle Mississippi River during 2003 through 2005. Habitat acronyms are from modified Cobb index as follows: BWD = between wing dikes; CBO = channel border open; MC = main channel; SC = side channel; WDSD = wing dam scour down; WDS = wing dam scour; WDT = wing dam tip; TM = tributary mouth; IT = island tip.



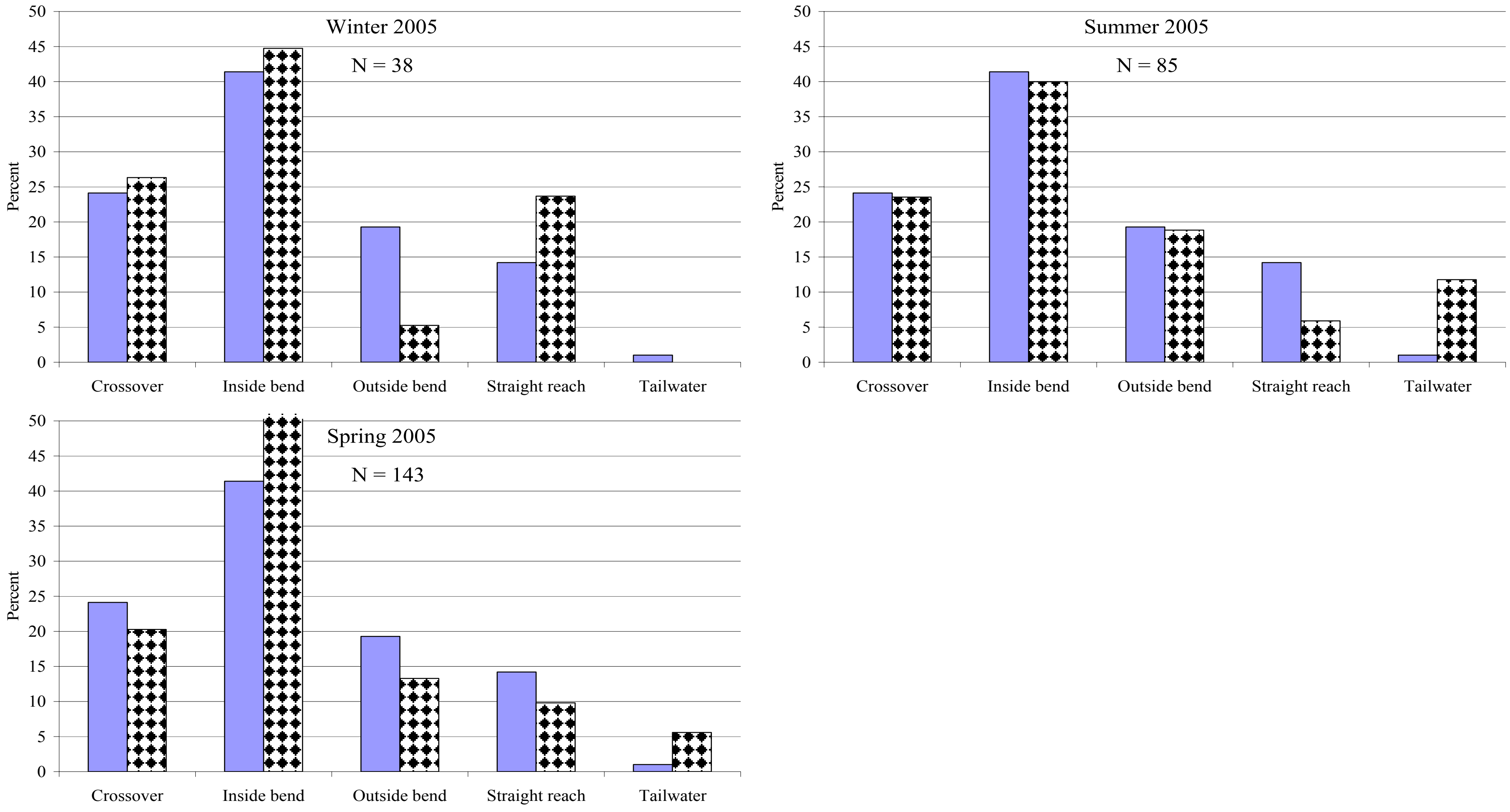
Appendix C-5. Percent habitat availability and annual use of transmittered Pallid Sturgeon in the middle Mississippi River. Habitat acronyms are from modified Cobb index as follows: BWD = between wing dikes; CBO = channel border open; MC = main channel; SC = side channel; WDSD = wing dam scour down; WDS = wing dam scour; WDT = wing dam tip; TM = tributary mouth; IT = island tip.



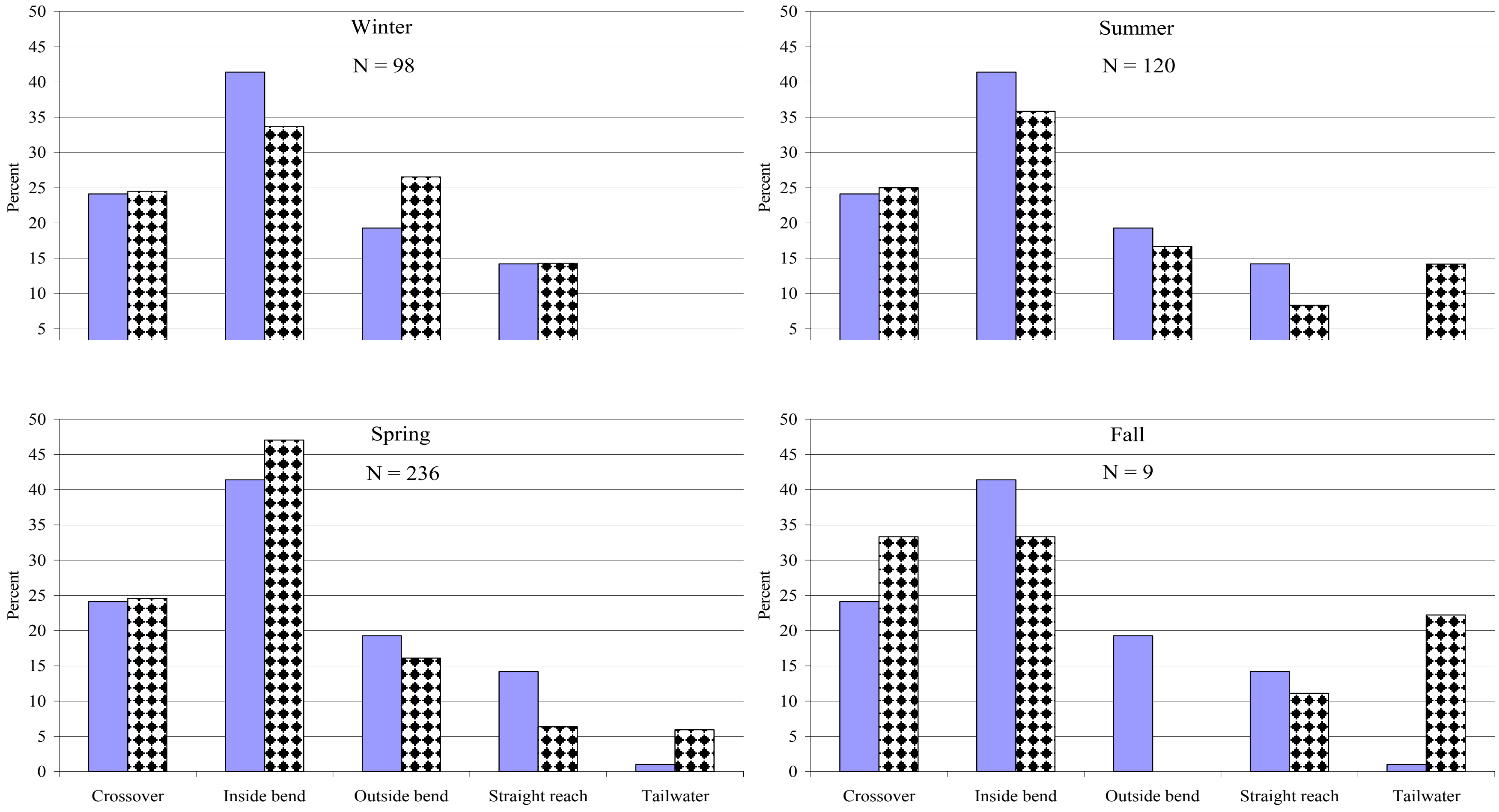
Appendix C-6. Percent habitat availability based on sinuosity, and seasonal use of transmittered Pallid Sturgeon during 2003 in the middle Mississippi River.



Appendix C-7. Percent habitat availability based on sinuosity, and seasonal use of transmittered Pallid Sturgeon during 2004 in the middle Mississippi River.

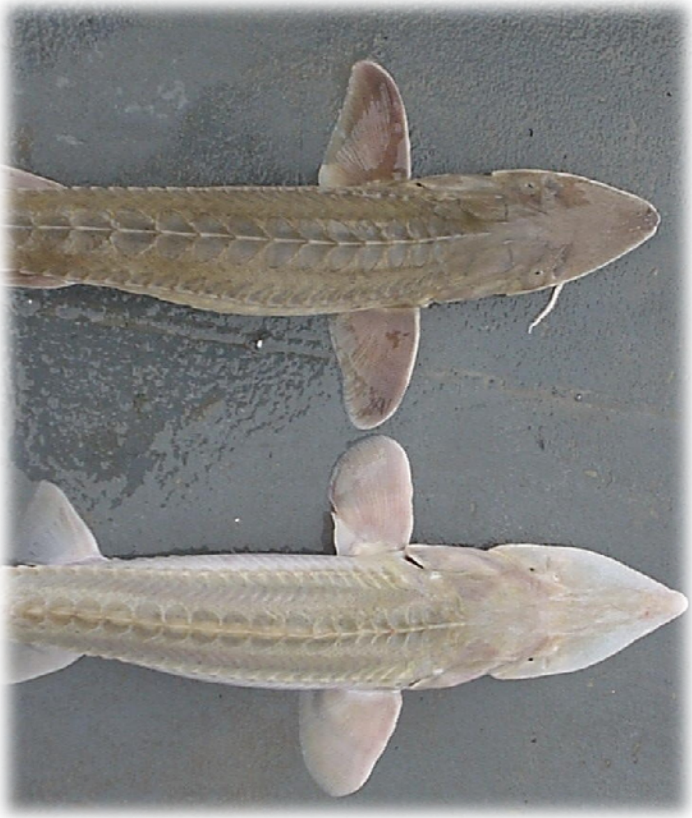


Appendix C-8. Percent habitat availability based on sinuosity, and seasonal use of transmittered Pallid Sturgeon during 2005 in the middle Mississippi River.



Appendix C-9. Percent habitat availability based on sinuosity, and seasonal use of transmittered Pallid Sturgeon during 2003 - 2005 in the middle Mississippi River.

CHAPTER 4: MORPHOMERISTICS



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Morphometric variation among river sturgeons (*Scaphirhynchus* spp.) of the Middle and Lower Mississippi River

By C. E. Murphy, J. J. Hoover, S. G. George and K. J. Killgore

United States Army Corps of Engineers, Engineer Research and Development Center, Vicksburg, MS, USA

Summary

Pallid sturgeon (*Scaphirhynchus albus*) captured in the Middle and Lower Mississippi River (i.e. below St. Louis, MO, USA) are morphologically very similar to shovelnose sturgeon (*Scaphirhynchus platorynchus*). Available empirical data are limited to a few studies based on low sample sizes from disjointed populations. Geneticists are currently searching for markers that will differentiate the two species, but the need for unequivocal species-specific field characters remains. Continuation of commercial fishing for shovelnose sturgeon in some states necessitates an immediate means for accurate field identifications. Previous studies of lower basin river sturgeon classified individuals with simple morphometric character indices and interpreted intermediacy as interspecific hybridization. In this study, morphometric variation among *Scaphirhynchus* specimens from the Middle and Lower Mississippi River is examined for evidence of hybridization. Data are compared for large (>250-mm standard length) hatchery-reared and wild pallid specimens and wild shovelnose specimens. Specimens are compared using two morphometric character indices, two morphometric/meristic character indices and principal components analysis. Results indicate substantial morphological variation among pallid sturgeon below the mouth of the Missouri River. The amount of variation appears to decrease downstream in the Mississippi River. Sheared principal components analysis of morphometric data shows complete separation of shovelnose and pallid sturgeon specimens, whereas character indices indicate overlap. Both character indices and sheared principal components analysis demonstrate that pallid sturgeon in the Lower Mississippi River are morphologically more similar to shovelnose sturgeon than are pallids from the Upper Missouri River. This similarity, explained in previous studies as hybridization, may be the result of latitudinal morphometric variation and length-at-age differences between populations of the upper and lower extremes of the range.

Introduction

The pallid sturgeon (*Scaphirhynchus albus*) was distinguished from the shovelnose sturgeon (*Scaphirhynchus platorynchus*) in 1905 by 'its uniformly light color, relatively long head, very small eye, sharp and elongate snout, naked breast and belly, relatively small and numerous dermal scutes, numerous ribs and few-pointed gill rakers' (Forbes and Richardson, 1905). These morphometric, meristic and qualitative characters have been evaluated, revised and described repeatedly over the past 50 years (Bailey and Cross, 1954; Carlson and Pflieger, 1981; Keenlyne et al., 1994b; Snyder, 2002; Wills et al., 2002; Kuhajda et al., 2007) resulting in several descriptive indices, region-specific conservation of pallid sturgeons (U.S. Fish and Wildlife Service, 2006), and a need for more precise genetic discrimination. The listing of the pallid sturgeon as a federally endangered species in 1990 (U.S. Fish and Wildlife Service, 1990), the issuance of the U.S. Fish and Wildlife Service's Biological Opinion on the Upper Mississippi River – Illinois Waterway Navigation Project in 2004 (U.S. Fish and Wildlife Service, 2004), and the need for baseline life-history data for *Scaphirhynchus* spp. in the main stem Mississippi River (U.S. Fish and Wildlife Service, 2006) have propelled the question of species discrimination to the forefront of pallid sturgeon recovery in the Middle (mouth of Missouri River to mouth of Ohio River) and Lower (mouth of Ohio River to Gulf of Mexico) Mississippi River (MMR and LMR, respectively). Recently suggested phenomena that have confounded *Scaphirhynchus* species discrimination include interspecific hybridization (Carlson and Pflieger, 1981; Phelps and Allendorf, 1983; Carlson et al., 1985; Keenlyne et al., 1994a,b; Simons et al., 2001; Snyder, 2002; Wills et al., 2002; Tranah et al., 2004), geographic patterns in genetic and morphometric variation (Campton et al., 2000; Tranah et al., 2001; Everett et al., 2003; this study) and regionally unique microsatellite alleles (Rob Wood, pers. comm.).

While some recent progress has been made in genetic determination of species and lineage in sturgeons using microsatellite loci (McQuown et al., 2000; Heist and Schrey, 2004; Tranah et al., 2004), the endangered status of the pallid sturgeon necessitates a reliable and accurate method for field-identification of wild specimens. As long as commercial fisheries for shovelnose sturgeon remain open and discrimination of *Scaphirhynchus* species is ambiguous, the incidental take of pallid sturgeon remains a plausible hazard to recovery of the species. Accurate estimation of population size and status is critical for effective conservation, but misidentification coupled with the low capture rate of rare, endangered specimens could reduce that accuracy. Proper identification of specimens is also essential for correctly identifying patterns of habitat use/preference and life history traits.

Morphometric identification of sturgeon can be confounded by the effect of allometric growth (Mayden and Kuhajda, 1996; Bemis et al., 1997; Campton et al., 2000; Kuhajda et al., 2007), resulting in the misidentification of many younger or smaller pallid sturgeon specimens as shovelnose sturgeon. Allometry in sturgeon development also underscores the importance of size range of specimens used for morphometric evaluation (Mayden and Kuhajda, 1996; Bemis et al., 1997; Kuhajda et al., 2007). Combinations of certain morphometric characters have been suggested that facilitate identification of

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several larval stages of *Scaphirhynchus* specimens between 10 and 139 mm total length (Snyder, 2002), but the specimens used to derive those characters were the progeny of brood stock from one geographic region. Mean lengths-at-age of shovelnose sturgeon have been shown to vary greatly with geographic location (Everett et al., 2003), and allometric growth in *Scaphirhynchus* spp. has demonstrated that shovelnose and pallid sturgeon are often difficult to distinguish until a certain body size is attained (Bailey and Cross, 1954; Snyder, 2002; Kuhajda et al., 2007). In the case of the pallid sturgeon, therefore, geographic range may also be a possible influence on morphology, with changes reflected in relative distance from headwaters due to developmental responses to water temperature (Ruban and Sokolov, 1986; Keenlyne et al., 1994b; Campton et al., 2000) or due to underlying genetic differences (Campton et al., 2000; Tranah et al., 2001).

Reports of *Scaphirhynchus* specimens morphologically intermediate between pallid and shovelnose sturgeon (e.g. Carlson and Pflieger, 1981) initiated many morphometric and genetic investigations into interspecific hybridization (Phelps and Allendorf, 1983; Carlson et al., 1985; Keenlyne et al., 1994a,b; Morizot, 1994; Campton et al., 2000; Simons et al., 2001; Tranah et al., 2001; Wills et al., 2002; Tranah et al., 2004; Kuhajda et al., 2007). Most of these studies examined specimens from the Missouri and Middle Mississippi rivers, a few included specimens from the Atchafalaya River in Louisiana, but none examined specimens from the Lower Mississippi River proper – the largest area of sympatry between species. A variety of anthropogenic factors affecting the rate of natural hybridization have been proposed for Acipenseriformes including stocking of hatchery-reared hybrids, selective overfishing of one species (Bemis et al., 1997), and large-scale alterations to big-river habitats (Carlson et al., 1985; Bemis et al., 1997; U.S. Fish and Wildlife Service, 2006). Habitat modifications are presumed to have promoted hybridization by interfering with the reproductive isolating mechanisms between sympatric populations of pallid and shovelnose sturgeon (U.S. Fish and Wildlife Service, 1993, 2006; Quist et al., 2004).

Pallid sturgeon have been collected throughout the Missouri River and in the Mississippi River at and downstream of the mouth of the Illinois River at Grafton, IL, USA (Forbes and Richardson, 1905). The Lower Mississippi River extends unimpeded from the Gulf of Mexico to the mouth of the Ohio River at Cairo, IL, a distance of 1534 km. The river remains unimpeded throughout the 323 km Middle Mississippi River, which extends from the mouth of the Ohio River upstream to and just above the mouth of the Missouri River. From there, the Missouri River continues upstream unimpeded 1308 km to Gavins Point Dam. The flow and continuity of the upper Missouri River is interrupted by a series of large impoundments beginning at Gavins Point Dam, the Upper Mississippi River by a series of locks and dams. Pallid sturgeon are also found in the Atchafalaya River, a major distributary of the Lower Mississippi River regulated by the Old River Control Complex (ORCC) in Concordia Parish, LA, USA. The influence of these structures on movement and isolation of pallid sturgeon is not clearly understood, but the collection of morphologically intermediate, apparently hybrid sturgeon from these reaches is well-documented (Carlson and Pflieger, 1981; Phelps and Allendorf, 1983; Carlson et al., 1985; Keenlyne et al., 1994a,b; Morizot, 1994; Campton et al., 2000; Tranah et al., 2001; Wills et al., 2002; Tranah et al., 2004). Three of the studies (Campton et al., 2000; Tranah et al., 2001, 2004) refer to the Atchafalaya River as synonymous with the Lower Mississippi River and/or the extreme southern range of the pallid sturgeon. The Atchafalaya River differs from the Lower Mississippi River with respect to channel size (Saucier, 1998), discharge and water quality (Keown et al., 1986). While the ORCC (rkm 502.1) does allow for water exchange between the two rivers, fish would need to pass from the Atchafalaya to the Mississippi via the lock or against the flow via one of the control structures. Pallid specimens captured at this highly disturbed complex through the manipulation of flow regimes may not represent the general population of the unimpeded Lower Mississippi River. Pallid sturgeon have been collected historically as far south as Orleans Parish, LA (near New Orleans) (Bailey and Cross, 1954), and recently in St John the Baptist Parish, LA (rkm 233.3) (Killgore et al., 2007), making that the southernmost extreme of the pallid sturgeon's known range.

Central to our research on the conservation biology of river sturgeons are issues of taxonomic accuracy and the likelihood of interspecific hybridization. This paper uses two identification techniques, character indices and ordination, to describe variation among *S. albus*, *S. platorynchus* and morphologically intermediate specimens captured in the Middle and Lower Mississippi River from 1997 to 2006. It addresses five specific questions critical to the identification of river sturgeons and potential hybrids: (i) can a character index adequately discriminate between sympatric species, (ii) do morphometric-only character indices provide discrimination between species comparable to more conservative, morphometric/meristic indices, (iii) what is the level of agreement among different character indices, (iv) do multivariate analyses adequately discriminate between sympatric species, (v) do multivariate analyses adequately discriminate between species throughout their range of sympatry?

Materials and methods

Specimens examined

In 1996 and 1997, a series of *Scaphirhynchus* specimens was collected from the Mississippi River near Rosedale, MS (rkm 950) and preserved for detailed morphometric and meristic analyses. Data on 10 meristic and 58 morphometric characters were recorded from these specimens (prior to fixation) following Bailey and Cross (1954); Williams and Clemmer (1991), and Mayden and Kuhajda (1996) (Table 1). Analyses of data collected in the laboratory (e.g. fin ray counts) revealed that the series included *S. platorynchus* [n = 18, standard length (SL) 527–779 mm) and *S. albus* (n = 21, SL 563–795 mm), as well as intermediate specimens for which species could not be assigned (n = 2, SL 591–640 mm) (see Results). For the purposes of this study, these vouchered specimens compose Dataset 1, which was used to verify the identification of specimens that were measured and released during subsequent years.

In addition to the series of wild specimens, hatchery-reared *S. albus* specimens were also obtained from Gavins Point National Fish Hatchery (SD, USA), of which four were large enough to be included in this study (SL 276–542 mm). Parental stocks for hatchery specimens were collected from the confluence of the Yellowstone and Missouri rivers. The same suite of morphometric and meristic data was recorded for the hatchery specimens. These specimens were used in the initial analyses of Dataset 1 to examine differences in the upper and

Table 1
Morphometric and meristic data from vouchered specimens in Dataset 1. Proportional measurements given as 1000s of standard length. Coefficient of variation given as a percent

	Scaphirhynchus platorynchus (n = 18)				*Scaphirhynchus albus* (n = 21)				*Intermediate* (n = 2)			
	Min	Max	*x*	CV	Min	Max	*x*	CV	Min	Max	*x*	CV
Standard length (SL)	527	779	586.8	10.5	563	795	697.9	9.1	591	640	615.5	5.6
Proportional measurements (*as 1000s of SL*)												
Snout to dorsal fin origin	700	740	717	2	699	753	729	2	712	738	725	2
Posterior dorsal fin base to last keeled lateral plate	194	238	219	5	183	229	200	6	192	193	193	0
Snout to anal fin origin	735	792	758	2	732	811	772	3	672	770	721	10
Posterior anal fin base to last keeled lateral plate	182	229	207	6	167	215	185	7	169	181	175	5
Snout to pelvic fin origin	576	625	598	3	565	643	609	3	536	603	570	8
Posterior pelvic fin base to last keeled lateral plate	344	390	371	3	322	370	354	3	360	363	361	0
Snout to pectoral fin origin	235	279	259	5	253	311	282	5	234	272	253	11
Posterior pectoral fin base to last keeled lateral plate	674	722	696	2	634	689	668	2	623	675	649	6
Body width at shoulder girdle	104	117	109	4	108	133	118	5	101	118	110	11
Maximum body depth[2]	98	142	113	9	100	142	119	9	106	110	108	3
Least caudal peduncle depth	12	17	14	7	13	16	14	7	14	14	14	0
Caudal peduncle width (at plane of least depth)	20	26	23	7	20	27	24	8	20	29	24	27
Head width at operculum	80	94	89	4	90	111	98	5	83	99	91	12
Head width at parietal crest	78	88	85	3	82	99	90	5	78	92	85	11
Head width at suborbital spines	116	129	122	3	112	132	121	5	117	127	122	6
Interorbital width	69	84	76	5	75	92	82	6	71	86	78	13
Width between inferior nostrils	67	77	72	4	67	83	76	6	68	80	74	12
Maximum head width[2]	117	129	124	3	115	135	124	5	117	135	126	10
Head length[3]	242	286	266	5	260	324	295	6	247	295	271	12
Snout to parietal crest spine base	185	225	205	5	198	246	228	6	196	220	208	8
Rostrum length (snout to subopercular spine)[3]	173	207	195	5	187	219	207	4	183	207	195	9
Head depth just anterior to parietal crest[1]	66	78	71	5	66	86	76	7	65	79	72	14
Mouth width[1,3]	61	84	74	8	72	97	84	9	64	83	73	18
Mouth vertical gape	31	51	40	14	32	63	46	17	36	47	41	19
Mouth horizontal gape	48	70	62	10	58	92	74	14	55	63	59	9
Inner barbel base to anterior edge of mouth[1,3]	54	75	66	8	46	74	60	14	65	74	70	9
Maximum inner barbel length[1,3]	45	69	55	11	41	69	53	16	52	62	57	12
Maximum outer barbel length[3]	58	106	74	15	82	171	110	21	81	96	89	13
Snout to anterior base of outer barbel[1,3]	86	122	107	9	110	141	126	7	105	117	111	8
Snout to anterior base of inner barbel[3]	76	110	99	9	96	124	113	7	95	104	99	6
Orbit diameter[1,3]	10	14	12	9	7	11	9	13	9	10	9	9
Eye to inferior nostril	10	14	12	11	10	15	13	10	13	14	13	2
Eye to operculum origin	79	99	87	6	93	121	105	7	83	96	89	10
Superior nostril diameter	10	14	11	12	10	14	12	9	10	11	11	11
Inferior nostril diameter	17	26	23	11	20	27	23	8	19	24	22	15
Snout to center of pupil	129	166	153	6	148	186	168	6	147	163	155	7
Snout width at 20% distance from eyes to snout tip	114	127	121	3	109	132	121	6	114	133	124	11
Snout depth at 20% distance from eyes to snout tip	16	44	36	17	28	42	36	11	38	38	38	0
Snout width at 40% distance from eyes to snout tip	103	115	109	4	97	119	109	6	103	127	115	15
Snout depth at 40% distance from eyes to snout tip	24	32	27	8	16	31	26	14	25	26	25	3
Snout width at 60% distance from eyes to snout tip	82	100	92	5	79	104	91	7	91	112	102	15
Snout depth at 60% distance from eyes to snout tip	17	26	21	9	10	23	19	18	18	22	20	16
Snout width at 80% distance from eyes to snout tip	53	78	69	10	56	83	68	10	75	89	82	12
Snout depth at 80% distance from eyes to snout tip	14	19	16	8	6	20	14	22	14	17	15	15
Snout width at 90% distance from eyes to snout tip	25	52	44	15	35	54	44	13	44	61	53	22
Snout depth at 90% distance from eyes to snout tip	11	14	12	7	7	12	11	12	11	13	12	10
Dorsal fin base[1]	62	76	68	6	69	93	78	7	69	69	69	1
Dorsal fin height	68	90	80	7	71	95	84	7	76	90	83	12
Pectoral fin length	101	132	114	6	112	151	126	7	110	126	118	9
Anal fin base	33	42	39	6	40	76	49	16	43	44	44	3
Anal fin height	77	99	86	7	78	110	93	9	78	94	86	13
Pelvic fin base	35	48	42	9	40	53	48	7	43	48	46	7
Pelvic fin length	69	96	81	9	43	98	84	14	71	85	78	13
Caudal fin length, upper lobe (excluding filament)	101	292	204	28	105	265	172	24	206	237	222	10
Caudal fin length, lower lobe	95	120	103	8	93	120	107	7	89	110	99	14
Height of tenth lateral plate[3]	37	50	42	7	27	40	35	10	33	41	37	15
Lateral-ventrolateral inter-space (at tenth lateral plate)	12	30	22	27	25	46	35	15	24	26	25	8
Meristic counts (*whole counts*)												
Dorsal plates[2]	15	18	16	5	13	17	16	6	16	19	18	12
Lateral plates[1]	40	46	43	5	42	50	45	5	43	48	46	8
Lateral plates anterior to dorsal fin origin[1]	23	27	26	4	23	29	27	7	26	29	28	8
Post-anal plates	4	6	5	13	4	6	5	12	4	5	5	16
Ventro-lateral plates	11	14	12	6	11	14	13	6	12	13	13	6
Anal to caudal plates[1]	7	10	8	8	7	9	8	7	8	9	9	8
Dorsal fin ray count[1]	28	36	33	6	34	41	38	5	34	37	36	6

Table 1
(Continued)

	Scaphirhynchus platorynchus (n = 18)				*Scaphirhynchus albus* (n = 21)				*Intermediate* (n = 2)			
	Min	Max	*x*	CV	Min	Max	*x*	CV	Min	Max	*x*	CV
Pectoral fin ray count	43	49	46	4	43	50	46	5	47	48	48	1
Anal fin ray count[1]	19	21	20	4	23	26	24	4	22	23	23	3
Pelvic fin ray count	23	28	27	5	27	33	29	5	29	29	29	0

[1] Exact character suggested by Kuhajda et al. (2007); used in Dataset 2.
[2] Analogous to character suggested by Kuhajda et al. (2007); used in Dataset 2.
[3] Used in Dataset 3.

lower basin populations and to demonstrate the confounding effects their inclusion had on those analyses.

A subset of nine morphometric and six meristic characters similar to those suggested by Kuhajda et al. (2007) as useful in separating *S. platorynchus* from *S. albus* were employed to validate the identifications of the 41 vouchered specimens. When the exact character from Kuhajda et al. (2007) was not available, an analogous character from Dataset 1 was substituted (Table 1); if no analogous character was available, none was substituted. The reduced morphometric and meristic character set, Dataset 2 for the purposes of this study, included the following: SL, head depth just anterior to parietal crest, dorsal fin base, maximum body depth, orbit diameter, inner barbel base to anterior edge of mouth, snout to anterior base of outer barbel, maximum inner barbel length, maximum head width, mouth width, dorsal plate count, lateral plate count, lateral plates anterior to dorsal fin origin, anal to caudal plates, dorsal fin ray count and anal fin ray count.

A reduced set of 11 morphometric characters was recorded in the field for live wild-caught *Scaphirhynchus* specimens that were released (Table 2). Wild *Scaphirhynchus* specimens (n = 117, SL 382–900 mm) were captured throughout the Middle (Upper rkm 322–0) and Lower (Lower rkm 1534–250) Mississippi River from 2002 to 2006 primarily using trotlines (Killgore et al., 2007). Presumed pallid sturgeon and morphologically intermediate specimens were measured, weighed, examined for anomalies and external tags, photographed, and scanned for Passive Integrated Transponder (PIT) tags. Large body measurements were taken to the nearest millimeter using a measuring board and small morphometric measurements were taken to the nearest 0.01 mm using digital calipers. Fish were kept in an aerated live-well containing river water during processing. Morphometric characters recorded for these specimens included SL, head length, rostrum length, mouth width, inner barbel base to anterior edge of mouth, maximum inner and outer barbel lengths, snout tip to anterior bases of inner and outer barbels, orbit diameter, and height of tenth lateral plate. Fin ray counts were not recorded for these specimens due to the difficulty of obtaining accurate counts on live specimens in the field. Data from these specimens were incorporated with corresponding variables in Dataset 1 to create Dataset 3 (Tables 1 and 2).

Table 2
Morphometric data from reduced suite of morphometric characters used in analysis of field-identified LMR and MMR specimens in Dataset 3. Proportional measurements given as 1000s of SL. Coefficient of variation given as a percent

	'*Scaphirhynchus albus*' (n = 117)			
	Min	Max	*x*	CV
Standard length (SL)	382	900	674	14.9
Proportional measurements (as 1000s of SL)				
Head length	257	325	293	5
Rostrum length (snout to subopercular spine)	173	225	203	5
Orbit diameter	6	11	8	13
Maximum outer barbel length	72	146	101	14
Maximum inner barbel length	31	74	50	18
Snout to anterior base of inner barbel	100	144	120	8
Snout to anterior base of outer barbel	103	159	133	8
Inner barbel base to anterior edge of mouth	42	66	53	8
Mouth width	76	105	88	7
Height of tenth lateral plate	26	46	34	11

Analytical techniques

All analyses were performed using SAS (Version 9.1, SAS Institute, NC, USA). All characters were standardized or regressed with SL following the methods of Kuhajda et al. (2007). Two morphometric (mCI) and two morphometric/meristic (CI) character indices were employed to examine variation within the specimens in Dataset 1. Indices used different characters (Table 3) but all had five variables in common: head length, inner barbel base to anterior edge of mouth, inner barbel length, outer barbel length, and snout to base of outer barbel (Carlson and Pflieger, 1981; Keenlyne et al., 1994b; Wills et al., 2002).

We used the CI of Wills et al. (2002) to classify *a priori* 41 specimens from Dataset 1 into five categories: shovelnose (n = 11); shovelnose or hybrid (n = 7); hybrid (n = 2); pallid or hybrid (n = 6); and pallid (n = 15). Principal components analysis (PCA) of data from these specimens later revealed complete overlap occurred for shovelnose with shovelnose or hybrid and for pallid with pallid or hybrid, so that the specimens were collapsed into three taxonomic categories: shovelnose (n = 18); hybrid (n = 2); and pallid (n = 21) to simplify other analyses (except in the case of agreement among the indices).

To evaluate the ability of a morphometric index to discriminate among species, we calculated the Keenlyne et al. (1994b) mCI values for specimens in Dataset 1 with and without hatchery specimens and compared the results with those of specimens of known identity from Kuhajda et al. (2007). Similarly, we used the CI from Carlson and Pflieger (1981) to examine separation of species in Dataset 1 with and without hatchery specimens using both morphometric and meristic characters.

To further investigate the influence of meristic characters (e.g. dorsal and anal fin ray counts) on index accuracy and to

Table 3
Morphometric and/or meristic characters used by four character indices

	Carlson and Pflieger, 1981 CI	Keenlyne et al., 1994b mCI	Wills et al., 2002 CI	Wills et al., 2002 mCI
Head length	•	•	•	•
Inner barbel base to anterior edge of mouth	•	•	•	•
Inner barbel length	•	•	•	•
Outer barbel length	•	•	•	•
Snout to anterior base of outer barbel	•	•	•	•
Mouth width	•	•		
Rostrum length (snout to subopercular spine)	•			
Orbit diameter	•			
Height of tenth lateral plate	•			
Dorsal fin ray count	•		•	
Anal fin ray count	•		•	
Pectoral fin ray count	•			
Pelvic fin ray count	•			

determine the effects of using different characters, we examined agreement between the Wills et al. (2002) indices and among all four indices using the kappa statistic (Fleiss, 1981). Kappa is the proportion of agreement among raters (i.e. character indices) after chance agreement has been removed and ranges from 0 (chance agreement) to 1 (perfect agreement). Kendall's coefficient of concordance is a measure of the association among raters and ranges from 0 (complete disagreement) to 1 (complete agreement). The species value limits for the two Wills et al. (2002) indices were assigned by the authors and resulted in the five categories defined above. To compare the four indices, the three hybrid categories from Wills et al. (2002) were combined into one to capture all overlap between species. For the Carlson and Pflieger (1981) and Keenlyne et al. (1994b) indices, index value limits for each species were set based on overlap within the bimodal distributions of the data (i.e. hybrids were assumed wherever overlap occurred). This resulted in three categories used to compare the four indices: pallid, hybrid and shovelnose. Hatchery specimens were excluded from these analyses to improve separation of the data.

Principal components analysis was used to evaluate morphometric variation among specimens and to identify variables contributing substantially to that variation. Allometric growth in sturgeon, however, can create a size effect that influences the results of morphometric analyses including PCA. Statistical routines are available to 'shear' the size factor during multivariate analyses of morphometric data (Bookstein et al., 1985), revealing the true shape components. Using this technique, we examined the data from 58 morphometric characters in Dataset 1 for high-loading characters occurring in lower basin *Scaphirhynchus* specimens. Sheared PCA has been employed to analyze river sturgeons of known taxonomic identity (e.g. hatchery-reared pallid, shovelnose and hybrid sturgeon) and resulted in accurate and reliable specimen identification from multivariate analyses of 12 morphometric and six meristic characters (Kuhajda et al., 2007). Following these methods closely, we performed sheared PCA on morphometric data and regular PCA on meristic data from Dataset 2 to evaluate their effectiveness in distinguishing between sympatric shovelnose and pallid sturgeon from the lower basin. A separate sheared PCA was performed on morphometric data from Dataset 3 to evaluate variation in pallid sturgeon throughout the Mississippi River and to verify the accuracy of our field identifications (D. L. Swofford, SAS Program for computing sheared PCA, unpubl., 1984, privately distributed).

Results

A comparison of the frequency distribution of specimens in Dataset 1 with those of Kuhajda et al. (2007) along the Keenlyne et al. (1994b) morphometric character index showed broader index ranges for shovelnose and pallid specimens, indicating greater variation in the lower basin specimens (Fig. 1). When the upper basin hatchery-reared pallid specimens were included, the index values for the shovelnose almost completely overlapped with those of the pallids (Fig. 1a). The distribution for Dataset 1 without hatchery specimens appeared unimodal at 280, and the separation of the two species did not improve appreciably (Fig. 1b). With values of 160 and 380, respectively, the two intermediate specimens from Dataset 1 defined the outer limits of the area of overlap between the two species (Fig. 1b). Large upper basin hatchery-reared shovelnose specimens examined by Kuhajda et al. (2007) stood alone with a mode of 100, while the modes for hybrids and pallids completely overlapped at 340 (Fig. 1c).

Identical comparisons using the Carlson and Pflieger (1981) index exhibited similar patterns with improved species separation (Fig. 2). The frequency distribution of Dataset 1 appeared nearly bimodal with the hatchery-reared pallid specimens included, but the data overlapped completely between the modes of 360 and 540, for shovelnose and pallid, respectively (Fig. 2a). The exclusion of the hatchery pallids greatly improved the separation of Dataset 1 with only slight overlap, but the distribution of the data was not clearly bimodal (Fig. 2b). Similar to the Keenlyne et al. (1994b) index results for data from Kuhajda et al. (2007), the Carlson and Pflieger (1981) index completely separated shovelnose sturgeon, but could not effectively distinguish between hybrids and pallids (Fig. 2c). The two intermediate specimens from Dataset 1 fell near the range of overlap at 400 and 500, respectively. The index ranges for the specimens in Dataset 1 were much broader than those from Kuhajda et al. (2007), again indicating greater within-species variability.

Agreement among the character indices with regard to species designations for Dataset 1 was evaluated using frequency distribution, kappa (κ), and Kendall's coefficient of concordance (W) (Fig. 3). Frequencies between the Wills et al. (2002) indices differed for each of the five species categories (pallid, pallid or hybrid, hybrid, shovelnose or hybrid, and shovelnose) (Fig. 3a). Agreement between the two indices was low ($\kappa \leq 0.5$) for each of the individual categories and significant only for the 'pallid' and 'pallid or hybrid'

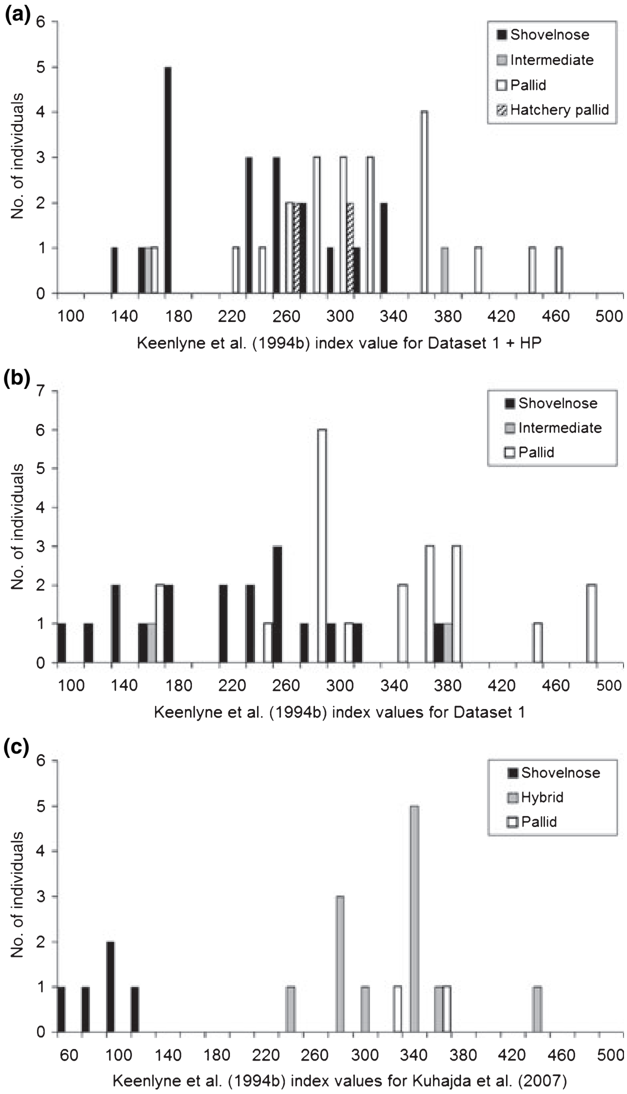

Fig. 1. Keenlyne et al. (1994b) morphometric character index values for (a) lower basin specimens from Dataset 1 plus hatchery-reared upper basin pallid specimens (HP); (b) lower basin specimens from Dataset 1 only; (c) hatchery-reared upper basin specimens of known origin, Kuhajda et al. (2007). Shovelnose-type specimens in black, intermediates/hybrids in gray, vouchered pallid-type specimens in white, and hatchery-reared pallids in dotted pattern. All specimens in large (>250 mm SL) size class

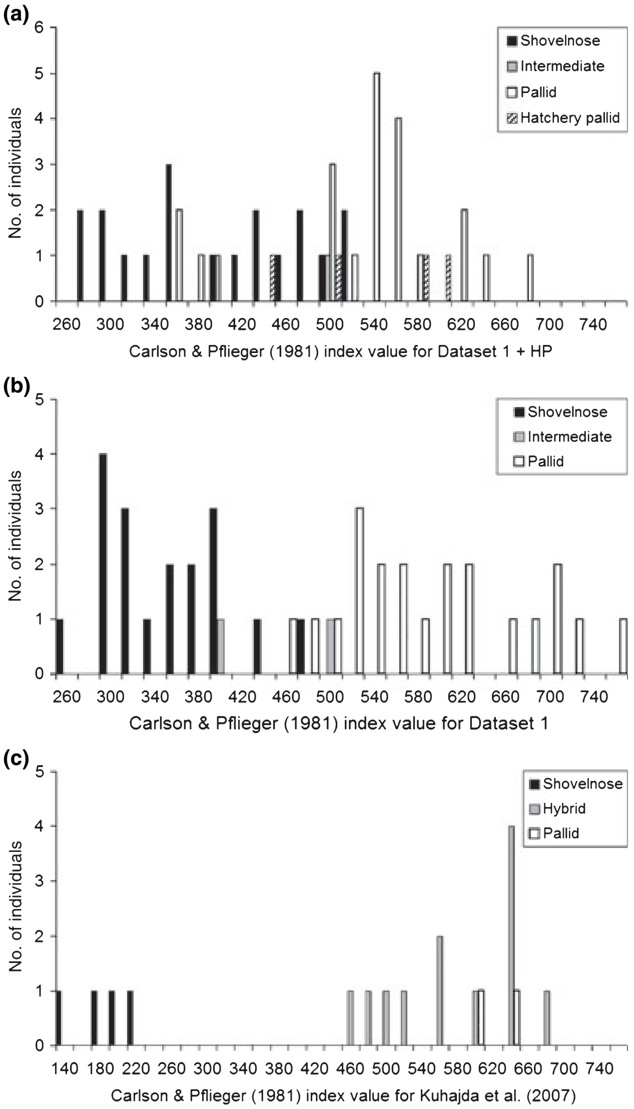

Fig. 2. Carlson and Pflieger (1981) morphometric/meristic character index values for (a) lower basin specimens from Dataset 1 plus hatchery-reared upper basin pallid specimens (HP); (b) lower basin specimens from Dataset 1 only; (c) hatchery-reared upper basin specimens of known origin, Kuhajda et al. (2007). Shovelnose-type specimens in black, intermediates in gray, vouchered pallid-type specimens in white, and hatchery-reared pallids in dotted pattern. All specimens in large (>250 mm SL) size class

categories ($P < 0.05$). Kendall's W, however, was high (0.91) and significant ($P < 0.0001$), indicating a strong association expected for these two indices developed with similar methods. The mCI assigned 73% of individuals to a hybrid category versus 37% hybrids with the CI, demonstrating that the inclusion of dorsal and anal fin ray counts greatly reduces ambiguity in species assignment of pallid and shovelnose sturgeon by these character indices.

Comparison of species assignment by all four indices demonstrated that the two mCI's assigned the majority of specimens to a hybrid category while the CI's designated fewer hybrids (Fig. 3b). Agreement among the indices was low for all species categories ($\kappa \leq 0.3$), and negative for the 'hybrid' category ($\kappa = -0.07$), which signified agreement weaker than would be expected by chance. Association among the four indices was moderate ($W = 0.62$) and significant ($P < 0.0001$), suggesting that the choice of characters and methods of development can influence the reliability of character indices.

Character loadings from the sheared PCA of 58 morphometric characters from Dataset 1 revealed that snout dimensions (particularly depths), barbel lengths and lateral-ventrolateral interspace were measured by sheared PC2 (Table 4). Sheared PC3 measured many of the same characters, but also quantified upper caudal fin length and body depths (Table 4). Kuhajda et al. (2007) used 51 morphometric characters in their study of upper basin specimens, several of which were not included in Dataset 1. The difference in characters may account for some of the disparity in results between the two studies, but dissimilarities in within-species shape between upper and lower basin specimens are also likely.

A plot of sheared PC II (morphometric data) and PC I (meristic data) from the analysis of Dataset 2 revealed distinct, albeit contiguous, groups for specimens scored as pallids and

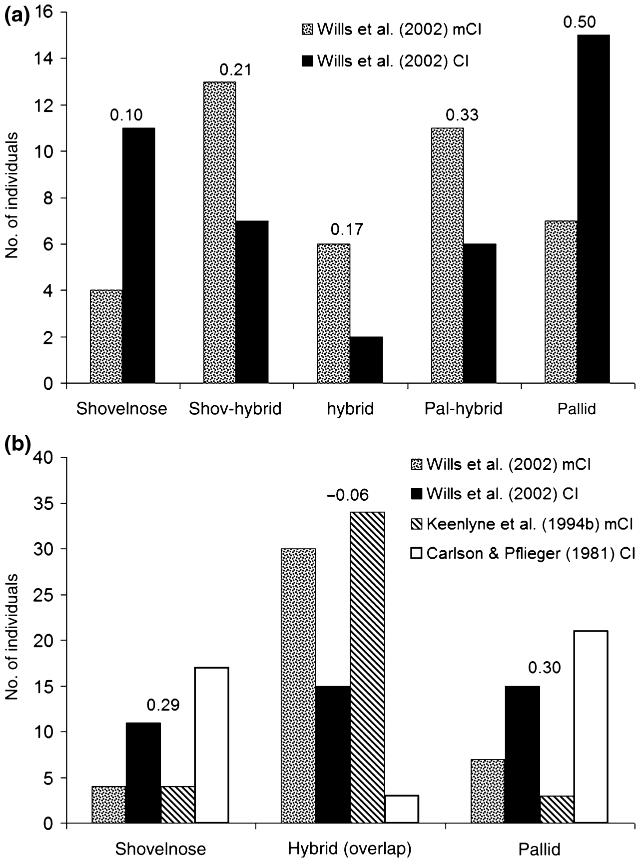

Fig. 3. Number of individuals from Dataset 1 assigned to (a) five species categories by morphometric and morphometric/meristic character indices from Wills et al. (2002) and (b) three categories by all four character indices. Agreement given as kappa value for each category

shovelnose by the Wills et al. (2002) CI (Fig. 4). No distinction could be made between 'pure' pallid specimens and those scoring in the 'pallid or hybrid' overlap category. Likewise, shovelnose and 'shovelnose or hybrid' specimens overlapped almost completely across both axes. Separation of the two species was complete even with upper basin hatchery-reared pallid specimens included, but the lower basin pallids also formed a cluster nearly distinct from the upper basin pallids (Fig. 4a). The distribution of morphometric data along the sheared PC2 axis clearly demonstrated that lower basin pallids are more similar to shovelnose specimens and slightly different from the upper basin specimens. When the hatchery specimens were removed from the analysis, separation of the groups improved mainly along the meristic PC1 axis (Fig. 4b). The two 'hybrid' specimens fell predictably between the two species groups.

Sheared PC 2 and 3 for the reduced morphometric character set of Dataset 2 were most strongly associated with inner barbel length and eye size, respectively (Table 5). Other high-loading ($|$ loading $|$ >0.3) characters for sheared PC2 were inner barbel base to anterior edge of mouth, orbit diameter, maximum body depth, snout to anterior base of outer barbel, and dorsal fin base. Inner barbel base to anterior edge of mouth was also a high-loading character for sheared PC3. Principal component 1 for meristic data from Dataset 2 was most strongly associated with fin rays and lateral plate counts, while PC2 tracked all four plate counts (Table 5).

Sheared PCA of Dataset 3 (reduced set of morphometric measurements from Dataset 1 plus data from LMR and MMR tag/release specimens) revealed that all field-identified specimens in question did cluster with verified pallid specimens across sheared PC2 and sheared PC3 (Fig. 5). All field-identified specimens from the MMR and LMR, as well as the upper basin hatchery-reared pallid specimens, were distinct from the shovelnose cluster along sheared PC2 (Fig. 5a). The highest degree of within-species variation occurred along sheared PC3, and the range for pallid specimens (Δ 0.38) along this axis was almost double that of shovelnose specimens (Δ 0.2). The upper basin hatchery-reared pallid specimens fell almost entirely within the cluster of MMR pallid specimens and partially within the LMR pallid cluster for this analysis of 11 morphometric characters. Removal of the upper basin specimens had no appreciable effect on the distribution of points (Fig. 5b).

Sheared principal components for Dataset 3 were associated with similar characters to the high-loading characters from Dataset 2 (Table 6). The highest-loading characters on sheared PC2 were inner barbel length and orbit diameter as in Dataset 2. Sheared PC3 tracked barbel lengths strongly, with the highest loading on outer barbel length. Other high-loading characters were snout to anterior base of inner and outer barbels, inner barbel base to anterior edge of mouth, and height of tenth lateral plate.

Separation of the two species occurred mainly along sheared PC2, whereas within-species variation was revealed along sheared PC3 (Fig. 5). Analysis of sheared PC values for LMR and MMR pallid specimens with river kilometer revealed increased variance downstream to upstream (Fig. 6). Mean sheared PC2 values were low (−0.05) downstream, increased (i.e. became more similar to shovelnose morphology) near the middle range (rkm 801–1200) and then decreased (−0.07) farther upstream (rkm 1601–2000) (Fig. 6a). Mean values for sheared PC3 exhibited a contrasting pattern, but also indicated differences in specimens below rkm 800 (Fig. 6b).

Discussion

Our data indicated that: (i) a morphometric character index should not be used exclusively to classify specimens as hybrids, (ii) morphometric/meristic indices provide better discrimination than exclusively morphometric measures, (iii) different morphometric indices can classify (or misclassify) specimens differently, (iv) multivariate analyses allow discrimination among sympatric populations of different species; (v) multivariate analyses provide better discrimination among species across the range than do character indices, but not necessarily among populations of the same species.

The sheared PCA revealed that field-identified specimens collected in the LMR and MMR for this study clustered with both hatchery-reared pallid specimens from the upper basin and voucher specimens that were verified using identification methods developed with upper basin sturgeon. Our study specimens were also distinct from all shovelnose specimens. Morphometric-only character indices assigned the majority of our study specimens to categories inclusive of putative hybrids, yet the pallid-hybrid specimens clustered with the pallid groups and the shovelnose-hybrid specimens overlapped almost completely with the shovelnose specimens in the sheared PCA. Only two specimens, classified as 'hybrid', appeared ambiguous across the analyses.

Table 4
Character loadings from sheared principal components analysis of 58 morphometric characters from Dataset 1 (excluding hatchery-reared upper basin pallid specimens). High-loading (| > 0.1 |) characters highlighted in bold

	Size	Sheared PC2	Sheared PC3
Standard length	0.11289	−0.00432	−0.02175
Snout to dorsal fin origin	0.13353	0.01130	−0.02037
Posterior dorsal fin base to last keeled lateral plate	0.07728	0.03490	−0.06571
Snout to anal fin origin	0.13927	0.02011	−0.03449
Posterior anal fin base to last keeled lateral plate	0.06775	0.04942	−0.09638
Snout to pelvic fin origin	0.14343	0.02630	−0.02770
Posterior pelvic fin base to last keeled lateral plate	0.09317	0.01034	−0.04358
Snout to pectoral fin origin	0.13841	−0.03763	0.03499
Posterior pectoral fin base to last keeled lateral plate	0.12627	0.06902	−0.06635
Body width at shoulder girdle	0.13330	−0.00568	−0.04297
Maximum body depth[2]	0.13229	−0.06206	**-0.16724**
Least caudal peduncle depth	0.11758	0.02745	**-0.12998**
Caudal peduncle width (at plane of least depth)	0.17490	0.05563	−0.06434
Head width at operculum	0.15408	0.00837	−0.04716
Head width at parietal crest	0.14992	0.02439	−0.02680
Head width at suborbital spines	0.11080	0.03484	−0.01115
Interorbital width	0.15443	0.00588	0.01638
Width between inferior nostrils	0.13894	0.00916	0.02383
Maximum head width[2]	0.10632	0.03752	0.01291
Head length[3]	0.14964	−0.03191	0.05366
Snout to parietal crest spine base	0.15734	−0.02219	0.04545
Rostrum length (snout to subopercular spine)[3]	0.13048	−0.02033	0.04551
Head depth just anterior to parietal crest[1]	0.13688	−0.01309	−0.04859
Mouth width[1,3]	0.15053	−0.02465	0.06393
Mouth vertical gape	0.22821	0.05691	0.03314
Mouth horizontal gape	0.17128	−0.04970	−0.00958
Inner barbel base to anterior edge of mouth[1,3]	0.10317	**0.21549**	0.05990
Maximum inner barbel length[1,3]	0.16885	**0.16303**	**0.12542**
Maximum outer barbel length[3]	0.24156	**-0.18350**	**0.17520**
Snout to anterior base of outer barbel[1,3]	0.14543	−0.09781	0.08245
Snout to anterior base of inner barbel[3]	0.14575	−0.07067	0.07444
Orbit diameter[1,3]	0.05599	0.08524	0.00243
Eye to inferior nostril	0.12655	−0.04473	0.04760
Eye to operculum origin	0.16214	−0.05100	0.05383
Superior nostril diameter	0.11387	−0.06992	0.01469
Inferior nostril diameter	0.14414	−0.07677	−0.04758
Snout to center of pupil	0.14434	−0.04501	0.05405
Snout width at 20% distance from eyes to snout tip	0.10715	0.03974	0.02107
Snout depth at 20% distance from eyes to snout tip	0.10018	**0.10478**	**0.21458**
Snout width at 40% distance from eyes to snout tip	0.10548	0.03412	0.03033
Snout depth at 40% distance from eyes to snout tip	0.07861	**0.22941**	**-0.20712**
Snout width at 60% distance from eyes to snout tip	0.09935	0.04519	0.01243
Snout depth at 60% distance from eyes to snout tip	0.07830	**0.39110**	0.09480
Snout width at 80% distance from eyes to snout tip	0.07174	0.05793	−0.03960
Snout depth at 80% distance from eyes to snout tip	0.05353	**0.43793**	**-0.10696**
Snout width at 90% distance from eyes to snout tip	0.07885	**0.11533**	**-0.10416**
Snout depth at 90% distance from eyes to snout tip	0.11731	**0.27123**	**-0.10327**
Dorsal fin base[1]	0.12810	−0.07364	−0.00905
Dorsal fin height	0.11345	0.00426	0.05302
Pectoral fin length	0.12216	−0.04227	0.03920
Anal fin base	0.14569	−0.01995	0.07691
Anal fin height	0.12423	0.00922	0.01356
Pelvic fin base	0.12791	−0.02686	0.03289
Pelvic fin length	0.14353	−0.00592	0.04376
Caudal fin length, upper lobe (excluding filament)	0.02723	−0.04283	**0.78183**
Caudal fin length, lower lobe	0.11308	−0.01910	0.02636
Height of tenth lateral plate[3]	0.09209	0.08139	−0.03751
Lateral-ventrolateral inter-space (at tenth lateral plate)	0.18148	**-0.53800**	**-0.26941**

[1] Exact character suggested by Kuhajda et al. (2007); used in Dataset 2.
[2] Analogous to character suggested by Kuhajda et al. (2007); used in Dataset 2.
[3] Used in Dataset 3.

Species assignments varied among the indices with poor agreement even though a similar suite of characters was employed by each index. This phenomenon seems to suggest that the characters used in an index should be carefully rated for their ability to discriminate between the two species and that characters that discriminate poorly should be considered for exclusion. While it is true that some morphometric characters vary between species and some do not, the exclusion of a character requires *a priori* knowledge of its effectiveness as a key and disregards its contribution to the shape of the organism. Beyond being obscured by allometry, the basic weakness of the character index is the inability to describe the overall shape differences between groups of organisms. The use of sheared PCA on a large suite of characters gives a closer comparison of overall shape and is, therefore, a superior method of morphometric analysis.

No previous morphometric studies on pallid and shovelnose sturgeon have examined specimens collected throughout the

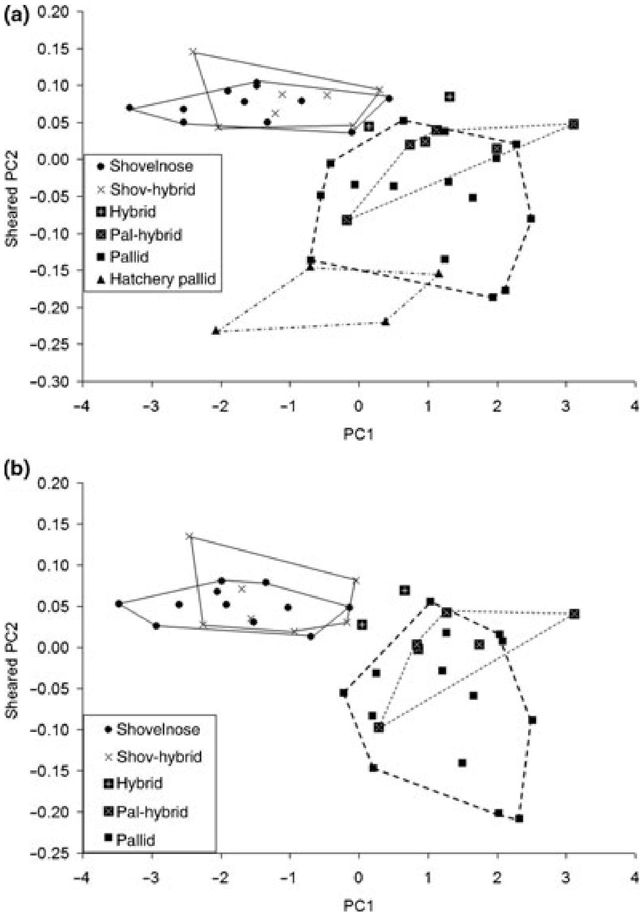

Fig. 4. Plot of sheared principal component 2 (morphometric data) and principal component 1 (meristic data) from analysis of Dataset 2 (a) with hatchery-reared upper basin pallid specimens and (b) lower basin specimens only. Shovelnose-type specimens grouped with solid lines, pallid-type specimens with dashed lines. Two 'hybrid' specimens not grouped

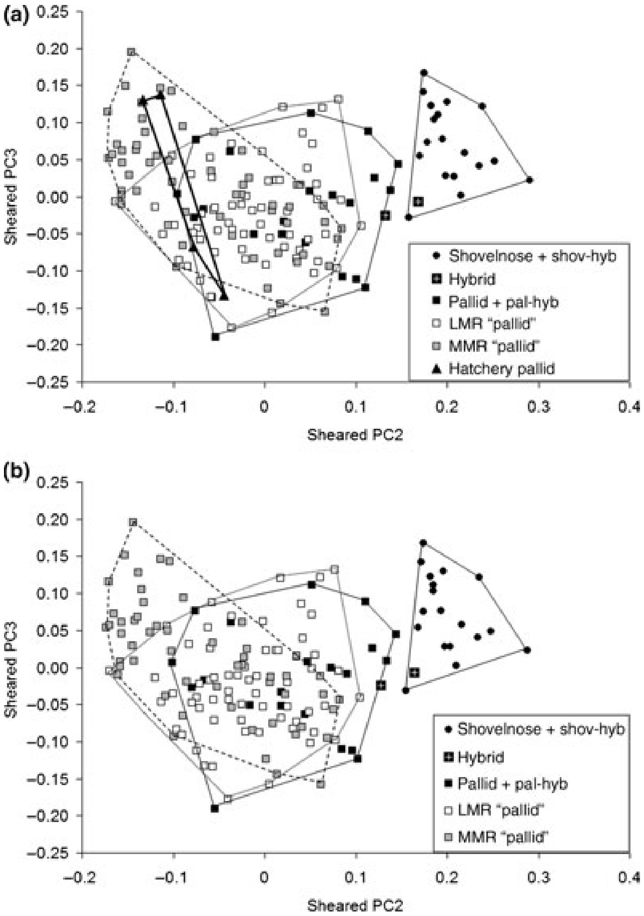

Fig. 5. Plot of sheared principal components 2 and 3 from analysis of Dataset 3 (Dataset 1 specimens plus field-identified LMR and MMR specimens). Vouchered specimens from Dataset 1 grouped with solid lines, hatchery specimens with heavy solid line, LMR specimens with dotted line, and MMR specimens with dashed line. Two 'hybrid' specimens not grouped

Lower Mississippi River, yet some have suggested that LMR sturgeon populations contain an abundance of hybrids (Campton et al., 2000, Allendorf et al., 2001; Tranah et al., 2004). While interspecific hybridization is one possible explanation for morphological intermediacy, it cannot be proven through phenotypic investigation. Genotypic analysis is a more reliable test of hybridization, but suffers from the same circular argument: the definition of species standards. Although hybridization, natural or otherwise, may occur between pallid and shovelnose sturgeon, morphometric and

Table 5
Character loadings from sheared principal components analysis (PCA) of morphometric data and regular PCA of meristic data from Dataset 2. High-loading (| >0.3 |) characters highlighted in bold

	Size	Sheared PC2	Sheared PC3
Standard length	0.26951	−0.07938	0.10657
Head depth just anterior to parietal crest[1]	0.33668	−0.12499	0.01701
Dorsal fin base[1]	0.33392	−0.23702	−0.01844
Maximum body depth[2]	0.31755	**−0.32778**	0.12290
Orbit diameter[1]	0.13961	0.28914	**0.91269**
Inner barbel base to anterior edge of mouth[1]	0.20250	**0.38365**	−0.29458
Snout to anterior base of outer barbel[1]	0.37710	−0.24037	−0.05492
Maximum inner barbel length[1]	0.43914	**0.66707**	−0.18623
Maximum head width[2]	0.25267	−0.00408	0.02446
Mouth width[1]	0.37720	−0.19221	−0.10162
	PC1	PC2	PC3
Dorsal plates[2]	0.05908	**0.515038**	**0.658205**
Lateral plates[1]	**0.45632**	**0.318798**	0.072155
Lateral plates anterior to dorsal fin origin[1]	**0.38237**	**0.427868**	0.043713
Anal to caudal plates[1]	0.22764	**0.422836**	**-0.710809**
Dorsal fin ray count[1]	**0.46273**	−0.234082	0.081063
Anal fin ray count[1]	**0.48782**	−0.245251	0.217814

[1] Exact character suggested by Kuhajda et al. (2007).
[2] Analogous to character suggested by Kuhajda et al. (2007).

Table 6
Character loadings from sheared principal components analysis of 10 morphometric characters from Dataset 3. High-loading (| > 0.3|) characters highlighted in bold

	Size	Sheared PC2	Sheared PC3
Standard length	0.27075	−0.00677	0.15306
Head length	0.29798	−0.15600	0.11706
Rostrum length (snout to subopercular spine)	0.27549	−0.11516	0.17262
Orbit diameter	0.18858	**0.42689**	**0.34917**
Maximum outer barbel length	0.40335	−0.16694	**−0.60366**
Maximum inner barbel length	0.34175	**0.46267**	**−0.48363**
Snout to anterior base of inner barbel	0.31247	**−0.33627**	0.21143
Snout to anterior base of outer barbel	0.31814	**−0.36351**	0.16450
Inner barbel base to anterior edge of mouth	0.26443	**0.37047**	0.04733
Mouth width	0.32094	−0.18513	−0.04290
Height of tenth lateral plate	0.27420	**0.33172**	**0.37179**

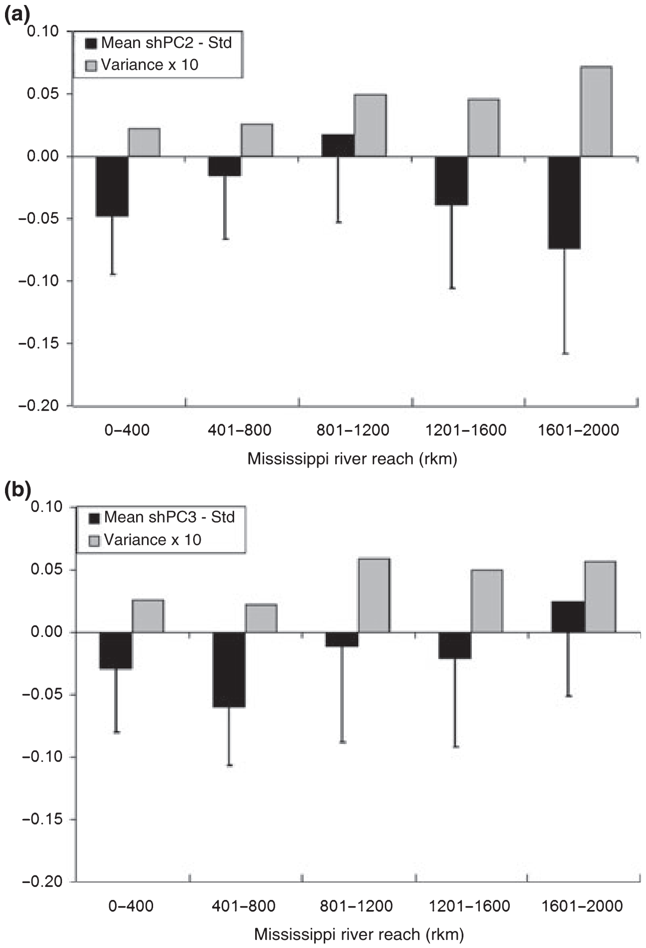

Fig. 6. Mean sheared Principal component values (see Fig. 5) minus one SD (black) and corresponding variance ×10 (gray) with river kilometer for field-identified LMR and MMR specimens; sheared PC2 (a) and sheared PC3 (b)

genetic standards must be clearly defined for the two species before species assignment, and particularly hybrid classification, using either method can be trusted.

Phenotypic, specifically morphometric, analysis is useful, however, for demonstrating the degree of intraspecific variation within a population. The broad latitudinal distribution of our specimens allowed for a comparison of variance by location downstream of the mouth of the Missouri River, which revealed a gradient with the highest variance occurring in the Middle Mississippi River (above rkm 1600) (Fig. 6). Greater morphological variation is expected for populations with high rates of hybridization and areas of contact between distinct populations. It has been suggested that pallid sturgeon in the northern and southern extremes of the range should be managed as genetically distinct populations (Campton et al., 2000; Tranah et al., 2001). If these populations are indeed distinct, the Middle Mississippi River, as the area of contact between the Missouri River and Lower Mississippi River populations, would be expected to comprise a more diverse pallid sturgeon population than the extremes of the range.

Keenlyne et al. (1994b) found that head length decreased in pallid sturgeon upstream to downstream whereas it increased in shovelnose sturgeon. They also cited a study of Siberian sturgeon, *Acipenser baeri*, in which morphometric characteristics, including head proportions and barbel lengths, were affected if water temperatures differed during the primary growth period of the young fish (Ruban and Sokolov, 1986). Our data demonstrated that pallid sturgeon in the Lower Mississippi River tended to be morphologically more similar than hatchery-reared pallids from the upper Missouri River to shovelnose sturgeon (Figs 4 and 5). If water temperature (minimum, maximum, or range) does indeed influence sturgeon morphology, especially head morphology, then comparison of *Scaphirhynchus* specimens from distant latitudes may be complicated by reasons other than hybridization.

Mean lengths-at-age for different shovelnose sturgeon populations in the Missouri and Mississippi rivers have been shown to vary greatly, possibly due to hydrographic and/or temperature differences (Everett et al., 2003). Length-at-age data for shovelnose sturgeon collected in the LMR below Rosedale, Mississippi (Morrow et al., 1998) fell slightly below upper Mississippi River (Iowa) shovelnose specimens (Everett et al., 2003) after age 5. Preliminary comparison of mean length-at-age data for our LMR pallid specimens (unpublished data) with the same upper Mississippi River (Iowa) shovelnose specimens showed near-perfect overlap. This suggests that pallid sturgeon in the lower basin may grow at the same rate as shovelnose sturgeon in the more northern latitudes. Together, allometric growth in species-specific morphometric characters, temperature-dependent early morphological development and regionally comparable growth rates for pallids and shovelnose could explain both the intraspecific variability and the interspecific similarity between pallid and shovelnose sturgeon throughout the middle and lower basin. It should be noted that growth rate data could be affected by the size-selectivity of gear used in the lower basin and/or inadequate recruitment in the upper basin. A study designed specifically to document differences in regional growth rates for both species is needed to provide a better understanding of potential relationships.

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References

Allendorf, F. W.; Leary, R. F.; Spruell, P.; Wenburg, J. K., 2001: The problems with hybrids: setting conservation guidelines. Trends Ecol. Evolut. **16,** 613–622.

Bailey, R. M.; Cross, F. B., 1954: River sturgeons of the American genus *Scaphirhynchus*: characters, distribution and synonymy. Michigan Acad. Sci. Arts Lett **39,** 169–208.

Bemis, W. E.; Findeis, E. K.; Grande, L., 1997: An overview of Acipenseriformes. Env. Biol. Fish **48,** 25–71.

Bookstein, F. L.; Chernoff, B.; Elder, R. L.; Humphries, J. M. Jr.; Smith, G. R.; Strauss, R. E., 1985: Morphometrics in evolutionary biology. Spec. Publ. 15. Acad. Nat. Sci., Philadelphia, PA, USA, 277 pp.

Campton, D. E.; Bass, A. L.; Chapman, F. A.; Bowen, B. W., 2000: Genetic distinction of pallid, shovelnose and Alabama sturgeon: emerging species and the US Endangered Species Act. Conserv. Genet. **1,** 17–32.

Carlson, D. M.; Pflieger, W. L., 1981: Abundance and life history of the lake, pallid and shovelnose sturgeons in Missouri. Final report, Endangered Species Project SE-1–6. Missouri Dept. of Conserv., Jefferson City, USA, 59 pp.

Carlson, D. M.; Pflieger, W. L.; Trial, L.; Haverland, P. S., 1985: Distribution, biology and hybridization of *Scaphirhynchus albus* and *S. platorynchus* in the Missouri and Mississippi Rivers. In: Sturgeon Symposium. S. Doroshov (Ed.). Env. Biol. Fish. **14,** 51–59.

Everett, S. R.; Scarnecchia, D. L.; Power, G. J.; Williams, C. J., 2003: Comparison of age and growth of shovelnose sturgeon in the Missouri and Yellowstone rivers. North Amer. J. Fish. Manage. **23,** 230–240.

Fleiss, J. L., 1981: Statistical methods for rates and proportions, 2nd edn. John Wiley & Sons Inc., New York, USA, 321 pp.

Forbes, S. A.; Richardson, R. E., 1905: On a shovelnose sturgeon from the Mississippi River. Bull. Illinois State Lab. Nat. Hist. **7,** 37–44.

Heist, E. J.; Schrey, A., 2004: Microsatellite tools for genetic identification of *Scaphirhynchus*. Fisheries Research Laboratory, Agreement # 3018126061: Interim Report, August 2003 – July 2004, Carbondale, IL, USA, 48 pp.

Keenlyne, K. D.; Graham, L. K.; Reed, B. C., 1994a: Hybridization between the pallid and shovelnose sturgeon. Proc. South Dakota Acad. of Sci. **73,** 59–66.

Keenlyne, K. D.; Henry, C. J.; Tews, A.; Clancey, P., 1994b: Morphometric comparisons of upper Missouri River sturgeons. Trans. Amer. Fish. Soc. **123,** 779–785.

Keown, M. P.; Dardeau, E. A. Jr.; Causey, E. M., 1986: Historic trends in the sediment flow regime of the Mississippi River. Water Resour. Res. **22,** 1555–1564.

Killgore, K. J.; Hoover, J. J.; George, S. G.; Murphy, C. E.; Lewis, B. R., 2007: Relative abundance and distribution of pallid sturgeon in the free-flowing Mississippi River. J. Appl. Ichthyol **23,** 476–483.

Kuhajda, B. R.; Mayden, R. L.; Wood, R. M., 2007: Morphological comparisons of hatchery-reared specimens of *Scaphirhynchus albus*, *S. platorynchus*, and *S. albus* × *S. platorynchus* hybrids (Acipenseriformes: Acipenseridae). J. Appl. Ichthyol. **23,** 324–347.

Mayden, R. L.; Kuhajda, B. R., 1996: Systematics, taxonomy, and conservation status of the Alabama sturgeon, *Scaphirhynchus suttkusi* Williams and Clemmer (Actinopterygii, Acipenseridae). Copeia **1996,** 241–273.

McQuown, E. C.; Sloss, B. L.; Sheehan, R. J.; Rodzen, J.; Tranah, G. J.; May, B., 2000: Microsatellite analysis of genetic variation in sturgeon: new primer sequences for *Scaphirhynchus* and *Acipenser*. Trans. Amer. Fish. Soc. **129,** 1380–1388.

Morizot, D. C., 1994: Genetic studies of *Scaphirhynchus* spp.. Report to the U.S. Army Corps of Engineers, Omaha District; U.S. Fish and Wildlife Service, Bismarck, North Dakota; U.S. Army Corps of Engineers, Mobile District. Genetic Analysis, Inc., Smithville, TX, USA, 41 pp.

Morrow, J. V.; Kirk, J. P.; Killgore, K. J.; George, S. G., 1998: Age, growth and mortality of shovelnose sturgeon in the Lower Mississippi River. North Amer. J. Fish. Manage. **18,** 725–730.

Phelps, S. R.; Allendorf, F. W., 1983: Genetic identity of pallid and shovelnose sturgeon (*Scaphirhynchus albus* and *S. platorynchus*). Copeia **1983,** 696–700.

Quist, M. C.; Boelter, A. M.; Lovato, J. M.; Korfanta, N. M.; Bergman, H. L.; Latka, D. C.; Korschgen, C.; Galat, D. L.; Krentz, S.; Oetker, M.; Olson, M.; Scott, C. M.; Berkley, J., 2004: Research and assessment needs for pallid sturgeon recovery in the Missouri River. Final report to the U.S. Geological Survey, U.S. Army Corps of Engineers, U.S. Fish and Wildlife Service, and U.S. Environmental Protection Agency. William D. Ruckelshaus Institute of Environmental and Natural Resources, University of Wyoming, Laramie, USA, 82 pp.

Ruban, G. L.; Sokolov, L. J., 1986: Morphological variability of Siberian sturgeon, *Acipenser baeri*, in the Lena River in relation with its culture in warm waters. J. Ichthyol. **26,** 88–93.

Saucier, M. H., ed., 1998: Water resources development in Louisiana. Prepared by U.S. Army Corps of Engineers, New Orleans District. New Orleans, LA, USA, 184 pp.

Simons, A. M.; Wood, R. M.; Heath, L. S.; Kuhajda, B. R.; Mayden, R. L., 2001: Phylogenetics of *Scaphirhynchus* based on mitochondrial DNA sequences. Trans. Amer. Fish. Soc. **130,** 359–366.

Snyder, D. E., 2002: Pallid and shovelnose sturgeon larvae – morphological description and identification. J. Appl. Ichthyol. **18,** 240–265.

Tranah, G. J.; Kincaid, H. L.; Krueger, C. C.; Campton, D. E.; May, B., 2001: Reproductive isolation in sympatric populations of pallid and shovelnose sturgeon. North Amer. J. Fish. Manage. **21,** 367–373.

Tranah, G. J.; Campton, D. E.; May, B., 2004: Genetic evidence for hybridization of pallid and shovelnose sturgeon. J. Hered. **95,** 474–480.

U.S. Fish and Wildlife Service, 1990: Determination of endangered status for the pallid sturgeon; final rule. Federal Register **55,** 36641–36647**.**

U.S. Fish and Wildlife Service, 2004: Final biological opinion for the Upper Mississippi River-Illinois Waterway System Navigation Feasibility Study. Prepared by U.S. Fish and Wildlife Service Rock Island Field Office, Rock Island, Illinois; Marion Suboffice, Marion, Illinois; Twin Cities Field Office, Bloomington, MN, USA.

U.S. Fish and Wildlife Service, 1993: Pallid sturgeon recovery plan. U.S. Fish and Wildlife Service, Bismarck, ND, USA.

U.S. Fish and Wildlife Service, 2006: Pallid sturgeon (*Scaphirhynchus albus*) range-wide stocking and augmentation plan. Prepared by the Pallid Sturgeon Recovery Team for Region 6, U.S. Fish and Wildlife Service, Denver, CO, USA.

Williams, J. D.; Clemmer, G. H., 1991: *Scaphirhynchus suttkusi*, a new sturgeon (Pisces: Acipenseridae) from the Mobile Basin of Alabama and Mississippi. Bull. Alabama Mus. Nat. Hist. **10,** 17–31.

Wills, P. S.; Sheehan, R. J.; Heidinger, R.; Sloss, B. L., 2002: Differentiation of pallid and shovelnose sturgeon using an index based on meristics and morphometrics. Amer. Fish. Soc. Symp. **28,** 249–258.

Author's address: Catherine E. Murphy, United States Army Corps of Engineers, Engineer Research and Development Center, 3909 Halls Ferry Road, EE-A, Vicksburg, MS 39180, USA.
E-mail: cmurphy@jayacorp.com

CHAPTER 5: GENETIC DISCRIMINATION

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ORIGINAL PAPER

Genetic discrimination of middle Mississippi River *Scaphirhynchus* sturgeon into pallid, shovelnose, and putative hybrids with multiple microsatellite loci

A. W. Schrey · B. L. Sloss · R. J. Sheehan ·
R. C. Heidinger · E. J. Heist

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Abstract The pallid sturgeon (*Scaphirhynchus albus*), which is protected under the US endangered species act, and shovelnose sturgeon (*S. platorhynchus*), which is legally harvested in some locations, are sympatric throughout the range of pallid sturgeon. There is considerable morphological overlap between the species making discrimination problematic. The inability to reliably differentiate between species across all life stages has hampered pallid sturgeon recovery efforts. Furthermore, the two species are believed to hybridize. This study used allele frequency data at multiple microsatellite loci to perform Bayesian and likelihood-based assignment testing and morphological measures and meristics to discriminate pallid, shovelnose, and putative hybrid sturgeons from the middle Mississippi River. Bayesian model-based clustering of the genetic data indicated that two natural genetic units occur in the region. These units correspond to morphologically identified pallid and shovelnose sturgeon. Some individuals were morphologically intermediate and many of these failed to strongly assign genetically as either pallid or shovelnose sturgeon, suggesting they may be hybrids. These data indicate that pallid sturgeon and shovelnose sturgeon are genetically distinct in the middle Mississippi River ($F_{ST} = 0.036$, $P < 0.0001$) and suggest that hybridization between pallid sturgeon and shovelnose sturgeon has occurred in this region with genetic distance estimates indicating the greatest distance is between pallid and shovelnose sturgeon, while hybrid sturgeon are intermediate but closer to shovelnose. This study demonstrates that assignment testing with multiple microsatellite markers can be successful at discriminating pallid sturgeon and shovelnose sturgeon, providing a valuable resource for pallid sturgeon recovery and conservation.

Keywords *Scaphirhynchus* · Microsatellite · Assignment testing · Endangered species · Species identification

Introduction

The pallid sturgeon (*Scaphirhynchus albus*, hereafter abbreviated PS) and shovelnose sturgeon (*S. platorhynchus*, hereafter abbreviated SS) are native to the Mississippi River drainage and are sympatric throughout the range of PS (Forbes and Richardson 1905; Bailey and Cross 1954). PS are protected in the US under the Endangered Species Act (Dryer and Sandoval 1993), while SS are legally harvested in several US states including some bordering the middle Mississippi River (MMR; Keenlyne 1997). What may be described as a morphological continuum exists between the two species making it difficult to reliably identify some specimens (Kuhajda and Mayden 2001; Wills et al. 2002). It is not currently known to what extent the morphological continuum is due to high variability within species or to hybridization between species. PS

A. W. Schrey (✉) · R. J. Sheehan · R. C. Heidinger ·
E. J. Heist
Fisheries and Illinois Aquaculture Center and Department of Zoology, Southern Illinois University Carbondale, Life Science II Room 173, 1125 Lincoln Drive, Carbondale, IL 62901-6511, USA
e-mail: aschrey@siu.edu

B. L. Sloss
US Geological Survey, Wisconsin Cooperative Fisheries Research Unit, College of Natural Resources, University of Wisconsin-Stevens Point, Stevens Point, WI 54481, USA

do have a distinctly greater maximum adult size of 1.7 m compared to 0.8 m for SS (Birstein 1993). However, in the middle Mississippi River both PS and SS adults are of similar size, and we are unaware of any *Scaphirhynchus* specimens greater than 1.2 m in length from the Mississippi River. Early life history stages of both species are morphologically more similar than are adults.

A recent study using nine microsatellite loci developed in sturgeon of the genus *Acipenser* found that morphologically intermediate *Scaphirhynchus* from the Atchafalaya River (a distributary of the Mississippi) tend to have intermediate genotypes (Tranah et al. 2004). These intermediate individuals have been taken as evidence for hybridization in the Mississippi River. Hybridization is a potential threat to the endangered PS (Allendorf et al. 2001; Rhymer and Simberloff 1996) because the discrete gene pool of the rare PS may be eroded by introgression from the more common SS causing extinction through hybridization. The lack of a reliable differentiation method, effective across regions and life stages, has hampered PS recovery efforts. PS recovery currently relies on stocking of offspring from wild-caught PS broodstock. Any inadvertent selection of hybrids or backcrosses as broodfish with subsequent release of large numbers of backcross offspring may further diminish the integrity of PS. Several morphological and meristic-based identification indices have been created in an attempt to discriminate between the species and their hybrids. However, none of these indices work adequately in all areas or for young sturgeon (Kuhajda and Mayden 2001).

Previous genetic studies using allozyme loci (Phelps and Allendorf 1983), restriction digests of nuclear amplicons (Genetic Analysis 1994 as cited in Wirgin et al. 1997), and DNA sequences (Bischof and Szalanski 2000; Straughan et al. 2002) fail to discriminate PS and SS species. The lack of discrimination is likely due to low levels of genetic variation (allozymes) and an absence of diagnostic differences (mtDNA) between species observed at the markers screened. Significant frequency differences in mitochondrial DNA haplotypes (Campton et al. 2000) and allele frequencies at five heterologous microsatellite markers (Tranah et al. 2001) were reported between PS and SS from the upper Missouri and Atchafalaya Rivers. However, neither genetic marker has detected diagnostic genetic differences among species. Also, it is not known if the absence of diagnostic differences is due to incomplete lineage sorting of ancestral polymorphisms or is due to secondary contact via introgressive hybridization (Campton et al. 2000). Tranah et al. (2004) suggest that multiple microsatellite loci are potentially better suited discriminating PS and SS than other methods. In their study, nine loci, some developed in the genus *Acipenser* could potentially be used to identify 90% of the individuals screened to species.

To date, no genetic study has investigated PS, SS, and putative hybrid sturgeon from the MMR, a region where the presence of hybridization has been suggested (Carlson et al. 1985). This study defines the MMR as the Mississippi River south from its confluence with the Missouri River (River Mile 195) near Saint Louis, Missouri, to the confluence of the Mississippi and Ohio Rivers at Cairo, Illinois (River Mile 0). Additionally, no study has attempted to delineate the two species using genetic assignment testing methods (first developed by Paetkau et al. 1995 and reviewed by Manel et al. 2005 and Hansen et al. 2001) that may discriminate species in the absence of diagnostic genetic differences. It is also possible for assignment testing methods to identify hybrid individuals (Vaha and Primmer 2006). Our objectives were to determine the number of distinct genetic groups within *Scaphirhynchus*, to ascertain if potential hybrid individuals were present in the samples collected, and to estimate the level of genetic differentiation among the identified groups. These objectives were addressed using genetic assignment testing methods with a large panel of microsatellite markers developed in *Scaphirhynchus*. We then compared results from genetic assignment to morphological identification based on a morphological character index (Wills et al. 2002) developed for MMR *Scaphirhynchus*.

Methods

Scaphirhynchus tissue samples ($n = 157$) were collected from the MMR. Putative PS and hybrid surgeon were sampled from multiple locations between the Missouri–Mississippi River confluence south to Cairo, Illinois (RM 195 to RM 0). Putative SS were sampled near Chester, Illinois (RM 110). Individual specimens were preliminarily characterized as PS, SS, and possible hybrid (Table 1) by collectors using the character index (CI) of Wills et al. (2002). The CI is a regression character index that uses five morphometric relationships (outer barbel length/inner barbel length, head length/inner barbel length, head length/mouth to inner barbel base distance, rostrum length/inner barbel length, and rostrum length/mouth to inner barbel distance) and two meristics (dorsal and anal fin ray counts) to discriminate PS and SS. The CI scores typical PS with negative (< –1.48 to –0.46) index values, SS with positive (0.52 to > 1.33) index values, and hybrid sturgeon as intermediate (–0.08 < CI < 0.36).

Table 1 Total number of *Scaphirhynchus* specimens screened from the middle Mississippi River reported by the initial morphological character index (CI) identification and the Bayesian genetic assignment test (Q-value) identification

Species	CI	Q-value	Combined
Pallid Sturgeon	44	30	29
Intermediate/Hybrid	19	43	55
Overlap Pallid/Hybrid	3	–	–
Hybrid	8	–	–
Overlap Shovelnose/Hybrid	8	–	–
Shovelnose Sturgeon	94	84	73
Total	157	157	157

Intermediates were defined as those individuals not belonging to either pallid or shovelnose sturgeon for each method. The final species designation was made by syntheses of both morphological and genetic methods

Wills et al. (2002) defined a region of overlap between PS and hybrid (–0.45 to –0.09) and SS and hybrid (0.37–0.51). Sturgeon that fall between the PS/hybrid, and hybrid/SS categories are assigned as PS/hybrid overlap and SS/hybrid overlap respectively.

Genomic DNA was extracted using the DNeasy Tissue Kit[1] (Qiagen, Valencia, CA) and stored at –20°C. Sixteen disomic microsatellite markers developed in *Scaphirhynchus* by McQuown et al. (2000) were optimized for this study (Table 2). Microsatellite loci were initially screened with radiolabeled techniques to determine which markers could be reliably scored. Polymerase chain reaction (PCR) was conducted at a final volume of 10 μl, containing 1 × PCR Buffer (50 mM KCl, 10 mM Tris HCl pH 9.0, and 1% Triton × 100®), 2 mM $MgCl_2$, 200 μM each dNTP, 0.1 unit *Taq* DNA polymerase, 0.14 μM each primer, and 1–20 ng template DNA. Prior to PCR the forward primer was end-labeled with $\gamma\ ^{32}$P adenosine triphosphate using T4 polynucleotide kinase. The PCR thermal profile included a 95°C initial denaturation of 4 m followed by 35 cycles of 95°C for 30 s, 56°C for 30 s, and 70°C for 30 s. PCR products were separated using 42 cm denaturing polyacrylamide gel electrophoresis for 3 h at 1600 V. Bands were visualized by autoradiography.

Once markers were determined to be polymorphic and amplify reliably, all individuals were screened in multiplex reactions on an ABI 377 (PE Applied Biosystems, Foster City, CA) with fragment analysis software. PCR conditions were identical to those used for the radioactive labeled PCR except, for each locus, fluorescent labeled forward primers (6-FAM, NED, or HEX; PE Applied Biosystems) and unlabeled reverse primers were combined in a primer cocktail (9 μM each primer). Final primer concentration in PCR was 0.15 μM. Thermal profiles for multiplex reactions were: 94°C 2 m, 5 cycles of 94°C 30 s, 54°C 30 s, 70°C 30 s, and 35 cycles of, 95°C 30 s, 56°C 30 s, and 70°C 30 s. PCR products were diluted (1:1) in loading buffer (deionized formamide, blue dextran EDTA, and The Gel Company MRK-400 size standard; The Gel Company, San Francisco, CA), loaded on a 5% Long Ranger (Cambrex Bio Science, East Rutherford, NJ) 36 cm gel, and run at 2500 scans/h for 2.5 h. Gel images were analyzed with Genescan v 3.1.2 (PE Applied Biosystems). Alleles were binned to raw size with Genotyper v 2.5 (PE Applied Biosystems). Alleles defined by Genotyper were scatter-plotted by size to define final bin boundaries and recoded to the inferred number of repeats corresponding to the defined size.

To identify the number of distinct groups and determine individual membership in the defined groups, a Bayesian model-based clustering of the genetic data was performed using STRUCTURE v 2.1 (Pritchard et al. 2000; Falush et al. 2003). To avoid overestimating the number of groups, the ΔK method of Evanno et al. (2005) was used to calculate the second order rate of change in the natural log probability of observing the data given the number of groups. Once the most likely number of groups was identified, another run was performed to identify individual membership in the identified groups. For all runs, the admixture model allowing correlated allele frequencies was used. Q-values were calculated with 0.95 posterior confidence regions (CR) describing the posterior probability of an individual's genotype belonging to each identified group. Analyses were conducted using 30,000 burn-in steps and 1,000,000 post burn-in steps.

The genetic assignment results were compared to the morphological discrimination by scatter-plotting Q-value (y-axis) against CI value (x-axis) for all individuals. This shows the level of concordance between methods and identifies potential hybrids. After comparing the results from both methods we set criteria to define PS and SS (see results), with individuals not meeting the defined criteria treated as intermediate and potential hybrids. The criteria were set to remove any potential hybrids and backcrosses from the baseline data, perhaps at the risk of eliminating some pure PS and SS from the baselines. We then used the baseline data to examine the assignment probabilities of potential hybrids.

GENECLASS v 2.1 (Piry et al. 2004) was used to jackknife the baseline PS and SS samples to reduce bias in self assignment. GENECLASS was also used to test the intermediate/hybrid individuals. The defined PS

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[1] The use of trade and product names throughout text does not imply endorsement by the United States Government.

Table 2 Summary statistics for the microsatellite loci screened in pallid, hybrid, and shovelnose sturgeons

Locus	θ	Pallid Sturgeon				Intermediate/Hybrid Sturgeon				Shovelnose Sturgeon			
		N	R	H_e	H_o	n	R	H_e	H_o	n	R	H_e	H_o
Spl-012	0.034*	29	4.93	0.583	0.345	47	7.08	0.675	0.532	71	6.86	0.732	0.676
Spl-015	0.027*	28	6.00	0.632	0.500	47	9.07	0.793	0.787	71	10.67	0.820	0.761
Spl-018	0.087*	29	5.86	0.485	0.517	47	7.52	0.711	0.638	72	5.50	0.622	0.597
Spl-019	0.011	29	5.00	0.733	0.724	47	6.32	0.767	0.787	72	7.16	0.797	0.819
Spl-030	0.053*	29	3.86	0.347	0.310	47	9.65	0.705	0.745	72	9.30	0.738	0.708
Spl-035	0.040*	29	10.65	0.803	0.793	47	15.92	0.900	0.894	72	16.26	0.918	0.889
Spl-036	0.033*	29	8.86	0.778	0.793	47	12.94	0.868	0.851	72	14.94	0.887	0.764
Spl-040	0.000	27	12.00	0.858	0.741	47	13.75	0.883	0.872	66	14.42	0.892	0.848
Spl-053	0.021*	29	5.00	0.699	0.828	47	10.44	0.794	0.809	72	8.80	0.779	0.819
Spl-056	0.072*	29	8.86	0.796	0.897	47	14.22	0.915	0.915	72	14.85	0.857	0.889
Spl-060	0.029*	29	6.86	0.776	0.897	47	6.72	0.680	0.681	72	5.21	0.575	0.556
Spl-101	0.017	29	5.93	0.751	0.690	47	7.50	0.810	0.830	71	7.97	0.820	0.915
Spl-106	0.014*	29	7.86	0.763	0.759	47	10.33	0.819	0.723	72	9.25	0.819	0.750
Spl-119	0.076*	29	5.93	0.704	0.828	47	9.44	0.814	0.766	72	9.50	0.807	0.667
Spl-158	0.027*	29	7.00	0.801	0.966	47	9.14	0.862	0.936	72	9.83	0.861	0.889
Spl-173	0.031*	29	4.93	0.680	0.759	47	6.99	0.774	0.787	72	7.85	0.851	0.806
Total	0.036*			0.699	0.709			0.798	0.785			0.798	0.772

Estimates of θ among pallid, hybrid, and shovelnose sturgeons are provided for each locus and combined over all loci with an asterisk denoting statistical significance. The number of individuals screened per locus (n), allelic richness (R), expected heterozygosity (H_e), and observed heterozygosity (H_o) are provided for each locus. No locus in any group was significantly out of Hardy–Weinberg equilibrium, and no loci pair in any group showed significant linkage disequilibrium

and SS individuals were treated as baseline samples from which allele frequencies were drawn for assignment testing, and we tested the assignment probabilities of the intermediate/hybrid individuals to each of these groups. We used the "assign or exclude individuals" option with the assignment criteria set at 0.05. The Rannala and Mountain (1997) assignment algorithm was used with probability of assignment calculated following the methods outlined in Paetkau et al. (2004) with 10,000 individuals generated for comparison.

GDA version 1d16c (Lewis and Zaykin 2001) was used to calculate the sample size, number of observed alleles, and observed and expected heterozygosities for each locus within each sample. FSTAT v 2.9.3 (Goudet 2001, an update of Goudet 1995) was used to calculate allelic richness and estimates of F_{ST} on the defined PS, SS, and intermediate/hybrid sturgeon. Allelic richness was estimated based on the lowest observed sample in a group. Weir and Cockerham's (1984) θ estimator of F_{ST} was calculated for each locus and combined across all loci among groups. A 95% confidence interval for θ was calculated by bootstrapping over loci and an exact G-test (Goudet et al. 1996) of genetic differentiation was performed assuming Hardy–Weinberg equilibrium (HWE) within groups. Tests for conformation to HWE and linkage equilibrium (LE) were also performed for each locus (or locus pair) in each sample. All tests used alpha = 0.05 with Bonferroni correction for multiple tests when appropriate (Rice 1989). The shared allele distance (DAS, Chakraborty and Jin 1993) was estimated among PS, SS, and hybrid sturgeon using the software package Populations version 1.2.28 (Langella 2002).

Results

Morphological analysis of all *Scaphirhynchus* specimens with the CI (Fig. 1, Table 1) identified 44 putative PS, 94 putative SS, 3 PS/hybrid overlap, 8 SS/hybrid overlap, and 8 hybrids, using categories defined by Wills et al. (2002). The majority (87.9%) of individuals were placed into either the PS or SS categories, with few individuals (12.1%) scoring as hybrid or hybrid overlap on the CI scale.

Bayesian assignment testing with Structure found evidence for two natural groups of *Scaphirhynchus* in the MMR. When alternately testing the data for the presence of one to four groups, the estimated probability of the data given the number of groups was maximized at two groups. The results showed a unimodal distribution with a sharp increase in probability from one to two groups, followed by increasing variability and lower probabilities with increasing number of groups and the *ad hoc* probability of two groups was near one (Falush et al. 2003; Pritchard et al. 2000). Assuming two groups were present also maximized the second order rate of change function, ΔK (Evanno et al. 2005). Thus the data support the presence of two genetically distinct groups of *Scaphirhynchus* in the MMR.

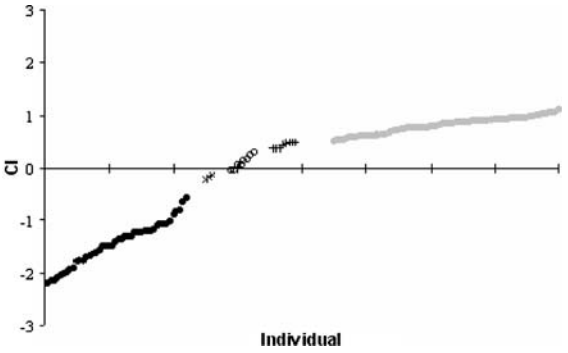

Fig. 1 Character index (CI) values for all *Scaphirhynchus* specimen ($n = 157$). Each point represents an individual and is coded by CI category (pallid = black circle, pallid/hybrid overlap = X, hybrid = open circle, shovelnose/hybrid overlap = +, and shovelnose = gray circle). Individuals classified as hybrid or in either hybrid overlap category were initially defined as intermediate

When we postulated the presence of two groups and allowed each individual's genotype to be comprised of elements from both groups, most individuals strongly assigned to one of the two groups (Fig. 2). We designated Q-values indicating 100% assignment to the group dominated by morphological PS as Q = 1 while those entirely assigned to the group dominated by morphological SS as Q = 0. A 95% CR is provided for each Q-value (Fig. 2). Individuals were categorized (Table 1) as PS or SS by Q-value, provided their 95% CR did not include 0.50. Individuals whose 95% CR included 0.50 were identified as intermediates.

Synthesizing the morphological (CI) and molecular (Q-value) discrimination results (Fig. 3) finds general agreement between techniques. Individuals were clustered into two major groups, which corresponded to PS (Quadrant II) and SS (Quadrant IV). Several individuals were intermediate, falling near the intersection of the axes, and a small number of individuals ($n = 4$) showed disagreement between morphological and molecular discrimination. These individuals all had more PS-like morphology and SS-like genotypes. Examining the graph and consulting both morphology and molecular tests allowed boundaries to be defined to identify the more confidently discriminated PS and SS. The intention was to create baseline groups of PS and SS while minimizing the potential of including hybrid individuals in either baseline. Final discrimination was made by combining both methods (Table 1), with PS ($n = 29$) defined by a CI less than –0.45 and a Q-value with a lower 95% CR bound greater than 0.50. SS ($n = 73$) were defined by a CI greater than 0.51 and a Q-value with an upper 95% CR bound less than 0.50. All individuals that did not meet both criteria were categorized as intermediate/hybrid ($n = 55$). Jackknifing the baseline PS and SS groups with GeneClass assigned all individuals back into the expected group with a score greater than 94%.

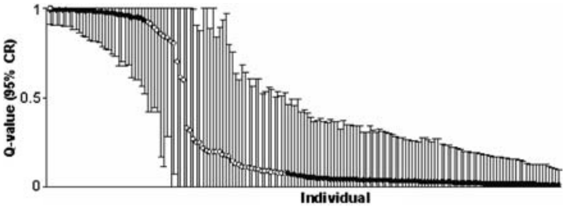

Fig. 2 Bayesian assignment testing results for *Scaphirhynchus* specimen indicating individual membership in each of the two identified groups are presented as Q-values, which indicate the proportion of each individual's genotype that was generated in the two identified natural groups. Each individual's Q-value is represented by a point with 95% credible regions. Values nearer one (1) indicate assignment to the group dominated by pallid sturgeon and values nearer zero (0) indicate assignment to the group dominated by shovelnose sturgeon. Q-values with 95% credible regions not including 0.50 are indicated by closed circles, while open circles indicate Q-value 95% credible regions including 0.50

Testing the intermediate/hybrid samples (i.e. those with 95% CR including Q = 0.5) with GeneClass (Fig. 4) identified 8 individuals with a probability greater than 0.90 of belonging to the SS group. These individuals, which are identified by open boxes on Fig. 3, had morphologies spanning the CI range

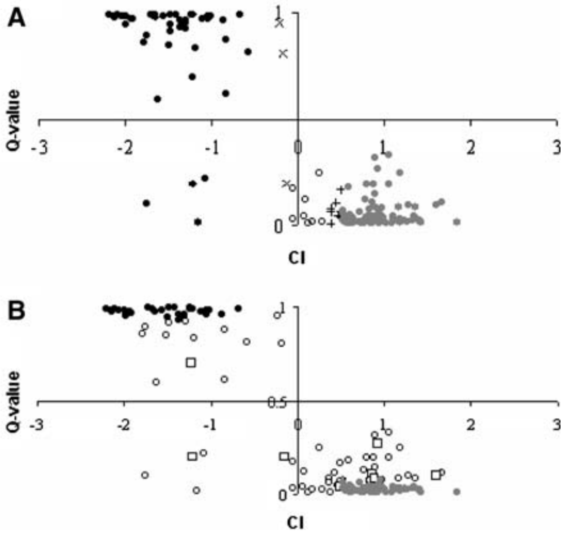

Fig. 3 Synthesis of molecular (Q-value) and morphological (CI) identification of *Scaphirhynchus* specimen. CI values are plotted on the x-axis and Q-values are plotted on the y-axis. Each point represents an individual. In A, the points are coded by CI category (pallid = black circle, pallid/hybrid overlap = X, hybrid = open circle, shovelnose/hybrid overlap = +, and shovelnose = gray circle). In B, the points are coded by final species designation (pallid = black, intermediate = open, and shovelnose = gray) and the eight intermediates that assigned to shovelnose are indicated as an open box

(5 were more SS-like, 1 was intermediate, and 2 were more PS-like). Due to the questionable identification of these 8 fish, which were morphologically and genetically unremarkable except for their inconsistent assignment using Structure and GeneClass, they were excluded from further analyses. The remaining 47 individuals in the hybrid/overlap categories did not assign to either baseline group with a probability greater than 0.90, indicating that their genotypes may have been comprised of elements from both PS and SS. These individuals were retained in the intermediate/hybrid category (hereafter abbreviated IS). The three defined groups, PS, SS, and IS, were used in subsequent analysis.

The microsatellite markers used were highly variable and sufficiently powerful to detect differences in allele frequencies between putative PS and SS (Table 2). Multiple alleles were observed at all markers, with allele richness based on a population size of 27 ranging from 3.86 to 16.26 and expected heterozygosity over all loci ranged from 0.699 to 0.798. Comparing PS to SS (Table 2) shows PS tend to exhibit fewer alleles per locus (lower allele richness at 14 of 16 loci) and lower expected heterozygosity (15 of 16 loci and averaged over loci). No locus in either PS or SS was identified as being significantly out of HWE, and no locus pair in any group was identified as being significantly out of LE. Interestingly, no significant departures from HWE or LE were observed in the intermediate group as well. Low frequency private alleles (Appendix) were observed at all loci except Spl-18 and Spl-53 when comparisons were made between putative PS and SS. PS had private alleles at 2 loci, all occurring as singletons, while SS had private alleles at 13 loci with 19 occurring as singletons and the most frequent observed in 3 of 71 SS. There were 7 private alleles among the 48 intermediates with 5 occurring as singletons, one present in two copies, and one present in five copies.

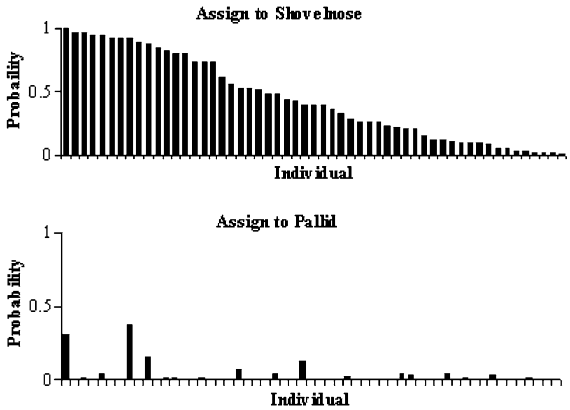

Fig. 4 The results of an assignment test are provided. The test compared intermediate individuals to individuals defined as shovelnose (Assign to Shovelnose) and pallid (Assign to Pallid) sturgeon. The assignment probability to shovelnose and pallid sturgeon for each individual is presented, with individuals plotted in the same order in each graph. Eight individuals assigned to shovelnose sturgeon with probabilities greater than 0.90. All other individuals were assigned to either group with a probability less than 0.90 and were classified as hybrids

Allele frequencies were significantly different between PS, IS, and SS ($F_{ST} = 0.036$, $P = 0.001$, Table 2), with a 95% confidence interval of 0.024–0.047. Individual locus estimates of F_{ST} ranged from <0.001 to 0.087 and 13 of the 16 loci exhibited statistically significant genic heterogeneity after Bonferroni correction. Pairwise estimates of F_{ST} among PS, IS, and SS were also statistically significant (Table 3) with the highest F_{ST} value observed between PS and SS ($F_{ST} = 0.074$) and the smallest value occurring between SS and IS ($F_{ST} = 0.011$). Estimating genetic distance among PS, IS, and SS (Table 3) with the DAS showed the greatest distance occurred between PS and SS. The IS were intermediate, yet nearer to SS than PS.

Discussion

Analysis of genotypes from 16 microsatellite loci developed in *Scaphirhynchus* resolved two distinct genetic groups of *Scaphirhynchus* in the MMR with most specimens strongly assigning to one of the two groups. Both Structure (Prichard et al. 2000) and ΔK (Evanno et al. 2005) identified two groups as most likely. These groups were largely concordant with morphologically identified PS and SS, with 29 of 44 (66%) genetically identified PS also morphologically PS and 73 of 94 (78%) genetically identified SS also morphologically SS.

Table 3 Pairwise estimates of θ calculated over all loci among pallid, hybrid, and shovelnose sturgeons are provided below the diagonal

	Pallid Sturgeon	Hybrid Sturgeon	Shovelnose Sturgeon
Pallid Sturgeon	***	0.119	0.253
Hybrid Sturgeon	0.035	***	0.036
Shovelnose Sturgeon	0.074	0.011	***

All θ values were significant ($P < 0.05$). Estimates of the shared allele genetic distance among pallid, hybrid, and shovelnose sturgeons are provided above the diagonal. The greatest observed distance is between pallid and shovelnose sturgeon, with hybrids being intermediate, yet closer to shovelnose sturgeon

Genetically assigned PS and SS exhibited a broad range of CI values (Fig. 3). These results suggest that while the morphological continuum between species may be partly due to hybridization there is also an appreciable amount of variation within each species. There were a relatively large number of morphological intermediates with CI scores between 1 and –1 (especially between 0 and 1) and a smaller number of genetic intermediates. Morphological intermediate tended to be genetically more similar to SS than PS (Fig. 3). Kuhajda and Mayden (2001) found that juvenile hatchery-reared PS × SS scored more similar to SS than PS on the Wills et al. (2002) index. Thus, perhaps some of the SS-like genetic intermediates may be F1 hybrids. We would also expect that if hybrids are fertile the most likely backcross would be between hybrids and the numerically superior SS. Based on the presence of two genetically and morphologically differentiated groups with a number of genetic and morphological intermediates, we believe that distinct PS and SS gene pools remain with some hybrid and perhaps backcross individuals in the MMR.

The number of PS, IS, and SS detected in our study (29, 55, 73) should not be interpreted as representative of the relative abundances of each morph in the MMR. We requested a sample of 100 SS from our collectors and could have acquired many more. We also requested all ‘‘intermediate’’ sturgeons our collectors could acquire and had to rely on tissue samples from specimens collected prior to the beginning of our study to sample sufficient numbers of PS. Southern Illinois University researcher Jim Garvey (personal communication in 2006), who heads a field research program that has been extensively sampling sturgeon from the MMR using a variety of gear and who provided most of the specimens used in this study, reports that the relative frequencies of the morphs in the MMR is more on the order of SS >> IS > PS. Carlson et al. (1985) categorized the 4355 sturgeon they collected from the Mississippi River as 4332 SS, 11 PS, and 12 hybrids. The apparently greater abundance of IS relative to PS in the MMR further indicates the dire state of PS stocks and that hybridization is an imminent threat to the survival and recovery of PS.

The current consensus among the PS recovery team is that spawning of wild-caught PS with subsequent release of offspring back into the wild is a critical component of PS recovery. This practice could exacerbate genetic threats to PS if hybrid or backcross *Scaphirhynchus* are used for broodstock. Birstein (1993) reported a maximum adult size of 1.7 m for PS compared to 0.8 m for SS. While very large PS occur in the upper Missouri River and thus any very large specimen of *Scaphirhynchus* can be assumed to be PS, we are unaware of PS longer than 1.2 m from the Mississippi River where both PS and SS have similar adult sizes. In our study, specimens from the three classes were similar in length with PS ranging from 653 to 982 mm, SS between 398 and 873 mm, and IS between 432 and 1190 mm. Thus, size can not be used as an indicator of species identity in the MMR. It is currently a controversial issue among sturgeon biologists whether the large PS in the upper Missouri represent a phenotype that does not occur in the southern part of the range or conversely whether the variation in adult size is entirely due to differences in age structure or growth among regions.

The level of concordance between genetic assignment and the CI shows that synthesis of molecular and morphological data provides additional measures for ensuring the purity of broodstock. Both methods identified two clusters in the data, and these clusters were highly concordant in identifying PS. Assignment testing identified 30 PS, 29 of which were CI PS and 1 was in the PS/hybrid overlap. Of 44 CI identified PS, 29 were genetic PS, 14 were IS, and 1 was SS. Thus, to reduce the likelihood of using hybrid or backcross *Scaphirhynchus* as PS broodstock, both molecular and morphological screening should be employed. While this might reduce the number of potential broodstock available for propagation and deviates from the principle of selecting broodstock as an unbiased sample of the spawning population (Miller and Kapuscinski 2003), we believe that the threat hybridization poses to PS recovery would be greatly exacerbated by stocking large numbers of hatchery-reared hybrid or backcross sturgeon.

Comparisons among defined PS, SS, and intermediate/hybrid sturgeon from the MMR found private alleles occurring among PS and SS. The majority of these private alleles were found within SS. Additionally, PS had fewer alleles and lower heterozygosity per locus. These results suggest that perhaps SS have a larger long term effective population size, which is consistent with current and historical abundance ratios. While a sample of F1 hybrids would be expected to exhibit excess heterozygosity relative to HWE, we did not find significant deviations within the intermediate group. This could be explained by the relatively similar allele frequencies in parent species, the likelihood that some of these intermediates may be introgressed, and the high amount of genetic variation relative to the number of individuals scored resulting in low power for the test of deviation from HWE. Additionally, as noted in the results section, the conservative screening process we used to ensure that no hybrids were retained in the PS group may have classified some pure PS or SS into the intermediate group. Thus, the excess heterozygosity expected in hybrids may have been offset by the excess homozygosity from mis-assigned pure PS or SS. Significant genetic differentiation was observed among groups. The highest pairwise F_{ST} and the greatest genetic distance was between PS and SS groups, with both tests finding the intermediate/hybrid sturgeon more closely related to SS. Taken together, the morphology and genetic data seem to suggest that introgressive hybridization has occurred between PS and SS, with hybrids more likely backcrossing with SS, as would be expected given the numerical superiority of SS.

This study demonstrates the successful use of assignment testing with microsatellite data to discriminate PS, SS, and putative hybrid sturgeon. Two genetically distinguishable groups within *Scaphirhynchus* in the MMR were observed. These two groups largely correspond to species differences inferred from morphological and meristic characters. The results are compatible with previous genetic studies of PS and SS, which detected significant haplotype and allele frequency differences between the two species in the Missouri and Atchafalaya Rivers using mitochondrial DNA control region sequences (Campton et al. 2000) and heterologous microsatellite markers (Tranah et al. 2001). Additionally, this study finds genetic and morphological intermediate individuals in the MMR suggesting evidence of hybridization similar to the evidence of hybridization found in the Atchafalaya River by Tranah et al. (2004).

The results from this study, in conjunction with additional work being conducted throughout the PS range, will be used to construct a baseline data set to characterize allele frequencies of PS and SS. Assignment testing with these baseline samples should provide valuable information for several recovery and conservation issues. These methods are expected result in a forensic tool, which is capable of identifying PS, SS, and hybrid sturgeon throughout the PS range. Being able to accurately discriminate species should facilitate multiple aspects of PS recovery including forensic identification of sturgeon for law enforcement purposes, estimating stock structure within PS to guide stocking plans, identifying larval and juvenile sturgeons to identify spawning habitat and monitor the effects of changes in flow regime, and to screen potential broodstock for PS propagation. It may also be possible to investigate hybridization among species using a combination of genetic and morphological criteria to determine the relative abundance of hybrid individuals and the potential threat they pose to PS recovery.

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Appendix

Appendix Allele frequencies for each of the sixteen microsatellite loci screened in putative pallid (PS), shovelnose (SS), and intermediate sturgeon (IS)

	Pallid	Shovelnose	Intermediate
Locus: 12			
N	29	71	48
P: 8	0	0.007	0.01
P: 9	0	0	0.01
P: 11	0.034	0.049	0.052
P: 12	0.552	0.282	0.479
p: 13	0.345	0.401	0.281
p: 14	0.052	0.042	0.063
p: 15	0	0.042	0.042
p: 16	0.017	0.162	0.063
p: 17	0	0.014	0
Locus: 15			
N	28	71	48
p: 10	0.036	0.106	0.063
p: 14	0.125	0.225	0.271
p: 15	0.571	0.317	0.344
p: 16	0.036	0.12	0.094
p: 18	0	0.007	0
p: 19	0	0.014	0.031
p: 20	0	0.035	0.021
p: 21	0.054	0.077	0.115
p: 22	0.179	0.028	0.031
p: 23	0	0.007	0.01
p: 24	0	0.021	0
p: 27	0	0.021	0
p: 29	0	0.007	0
p: 31	0	0	0.021
p: 33	0	0.014	0
Locus: 18			
N	29	72	48
p: 9	0	0	0.01
p: 10	0	0	0.01
p: 12	0.017	0	0.01
p: 13	0.086	0.021	0.042
p: 14	0.103	0.042	0.094
p: 15	0.707	0.417	0.479
p: 16	0.069	0.451	0.198
p: 17	0.017	0.028	0.135
p: 18	0	0.042	0.021

Appendix continued

	Pallid	Shovelnose	Intermediate
Locus: 19			
N	29	72	48
p: 18	0	0.014	0.01
p: 20	0.103	0.042	0.021
p: 21	0.172	0.25	0.177
p: 22	0.155	0.201	0.25
p: 23	0.448	0.25	0.344
p: 24	0.121	0.201	0.156
p: 25	0	0.028	0.042
p: 27	0	0.007	0
p: 31	0	0.007	0
Locus: 30			
N	29	72	48
p: 8	0	0.007	0
p: 10	0	0.007	0
p: 11	0	0.007	0
p: 12	0	0.007	0
p: 15	0	0	0.052
p: 16	0	0.007	0.01
p: 17	0.017	0.049	0.052
p: 18	0.793	0.458	0.531
p: 19	0.172	0.035	0.083
p: 20	0	0.181	0.063
p: 21	0	0.069	0.052
p: 22	0.017	0.118	0.094
p: 23	0	0.042	0.042
p: 24	0	0	0.01
p: 25	0	0.014	0.01
Locus: 35			
N	29	72	48
p: 8	0	0.007	0.021
p: 9	0	0.097	0.031
p: 10	0.052	0.021	0.083
p: 11	0.017	0.097	0.125
p: 12	0	0.111	0.094
p: 13	0.224	0.174	0.24
p: 14	0.207	0.021	0.052
p: 15	0.017	0.042	0.052
p: 16	0	0.049	0.063
p: 17	0.034	0.097	0.063
p: 18	0.017	0.021	0.01
p: 19	0	0.056	0.042
p: 20	0.328	0.028	0.042
p: 21	0.017	0.028	0.01
p: 22	0.069	0.007	0.021
p: 23	0.017	0.014	0.01
p: 24	0	0.076	0.021
p: 25	0	0.007	0.01
p: 26	0	0.007	0
p: 27	0	0.035	0
p: 29	0	0.007	0.01
Locus: 36			
N	29	72	48
p: 12	0	0.007	0
p: 14	0	0.007	0.01
p: 17	0	0	0.01
p: 18	0	0.021	0.01
p: 19	0	0.014	0
p: 20	0	0.014	0
p: 21	0.017	0.028	0.031
p: 22	0.121	0.028	0.073
p: 23	0.069	0.056	0.094
p: 24	0.172	0.139	0.167
p: 25	0.414	0.139	0.229
p: 26	0.034	0.201	0.188
p: 27	0	0.167	0.031
p: 28	0	0.063	0.021
p: 29	0	0.035	0.021
p: 30	0	0.007	0.021
p: 31	0.017	0.014	0.031
p: 32	0	0.021	0.01
p: 33	0.103	0.021	0.042
p: 34	0.052	0.007	0.01
p: 35	0	0.007	0
p: 36	0	0.007	0
Locus: 40			
N	27	66	48
p: 11	0	0	0.01
p: 12	0	0.008	0
p: 14	0	0.015	0.021
p: 15	0.019	0.015	0.052
p: 16	0.056	0.015	0.01
p: 17	0	0.045	0.042
p: 18	0.019	0.023	0.042
p: 19	0.019	0.045	0.01
p: 20	0.074	0.038	0.042
p: 21	0.241	0.152	0.146
p: 22	0.13	0.159	0.229
p: 23	0.222	0.189	0.135
p: 24	0.148	0.136	0.146
p: 25	0.019	0.045	0.021
p: 26	0.019	0.03	0.052
p: 27	0.037	0.023	0.031
p: 28	0	0.03	0
p: 29	0	0.03	0.01
Locus: 53			
N	29	72	48
p: 9	0	0.014	0.01
p: 10	0	0.014	0.021
p: 11	0.121	0.222	0.219
p: 12	0.034	0.111	0.052
p: 13	0.345	0.375	0.344
p: 14	0	0.021	0.01
p: 15	0	0.028	0.042
p: 16	0	0.014	0.01
p: 17	0.414	0.139	0.208
p: 18	0	0.056	0.021
p: 19	0.086	0.007	0.042
p: 20	0	0	0.01
p: 24	0	0	0.01
Locus: 56			
N	29	72	48
p: 16	0	0.014	0.01
p: 18	0	0.042	0.042
p: 19	0.017	0.049	0.052
p: 20	0	0.16	0.125
p: 21	0	0.319	0.104
p: 22	0	0.069	0.021
p: 23	0	0.028	0.01
p: 24	0.034	0.049	0.063
p: 25	0.017	0.021	0.042
p: 26	0.052	0.049	0.042

Appendix continued

	Pallid	Shovelnose	Intermediate
p: 27	0.034	0.028	0.021
p: 28	0.069	0.042	0.083
p: 29	0.293	0.014	0.115
p: 30	0.293	0.049	0.125
p: 31	0.19	0.035	0.135
p: 32	0	0.021	0.01
p: 33	0	0.007	0
p: 34	0	0.007	0
Locus: 60			
N	29	72	48
p: 21	0.138	0.007	0.01
p: 23	0	0.028	0.021
p: 24	0	0.021	0.021
p: 25	0.259	0.375	0.333
p: 26	0.328	0.535	0.448
p: 27	0.207	0.028	0.125
p: 28	0.034	0.007	0.031
p: 29	0	0	0.01
p: 30	0.017	0	0
p: 33	0.017	0	0
Locus: 101			
N	29	71	48
p: 8	0.017	0.056	0.083
p: 9	0.121	0.12	0.083
p: 10	0.103	0.246	0.292
p: 11	0.121	0.134	0.167
p: 12	0.414	0.282	0.24
p: 13	0.224	0.07	0.094
p: 14	0	0.07	0.031
p: 15	0	0.014	0.01
p: 16	0	0.007	0
Locus: 106			
N	29	72	48
p: 5	0	0.007	0.01
p: 6	0	0	0.01
p: 7	0.017	0	0.01
p: 9	0.017	0.007	0.021
p: 10	0.103	0.014	0.073
p: 11	0	0.118	0.063
p: 12	0.207	0.306	0.26
p: 13	0.19	0.139	0.115
p: 14	0.397	0.201	0.292
p: 15	0.034	0.132	0.073
p: 16	0	0.021	0
p: 17	0.034	0.021	0.042
p: 18	0	0.021	0.021
p: 19	0	0.014	0.01
Locus: 119			
N	29	72	48
p: 7	0.448	0.042	0.146
p: 8	0	0.014	0.01
p: 10	0	0.021	0.021
p: 11	0	0.035	0.01
p: 12	0.259	0.188	0.042
p: 13	0	0.313	0.115
p: 14	0.19	0.229	0.292
p: 15	0.034	0.09	0.26
p: 16	0.017	0.035	0.031
p: 17	0.052	0.021	0.063
p: 18	0	0	0.01
p: 19	0	0.014	0
Locus: 158			
N	29	72	48
p: 13	0	0.063	0.01
p: 14	0	0	0.01
p: 15	0.19	0.125	0.125
p: 16	0.086	0.104	0.083
p: 17	0.034	0.056	0.063
p: 18	0.052	0.222	0.156
p: 19	0.345	0.049	0.094
p: 20	0.19	0.215	0.25
p: 21	0.103	0.111	0.135
p: 22	0	0.035	0.063
p: 23	0	0.007	0.01
p: 25	0	0.014	0
Locus: 173			
N	29	72	48
p: 6	0.207	0.083	0.104
p: 7	0.121	0.097	0.073
p: 8	0	0.118	0.073
p: 9	0.5	0.243	0.406
p: 10	0	0.167	0.135
p: 11	0.155	0.167	0.135
p: 12	0	0.097	0.073
p: 14	0	0.028	0
p: 16	0.017	0	0

Alleles are identified by the inferred number of microsatellite repeats and the total number of alleles scored (*N*) is provided

References

Allendorf FW, Leary RF, Spruell P, Wenburg JK (2001) The problems with hybrids: setting conservation guidelines. TREE 16:613–622

Bailey RM, Cross FB (1954) River sturgeons of the American genus *Scaphirhynchus*: characters, distribution, and synonymy. Pap Mich Acad Sci Arts & Lett 36:169–208, 54

Birstein VJ (1993) Sturgeons and paddlefishes: threatened fishes in need of conservation. Conserv Biol 7:773–787

Bischof R, Szalanski AL (2000) Mitochondrial-DNA variation in pallid and shovelnose sturgeons, *Scaphirhynchus* (Pisces: Acipenseridae). Trans Nebr Acad Sci 26:19–21

Campton DE, Bass AL, Chapman FA, Bowen BW (2000) Genetic distinction of pallid, shovelnose, and Alabama sturgeon: emerging species and the US Endangered Species Act. Conserv Genet 1:17–32

Chakraborty R, Jin L (1993) A unified approach to study hypervariable polymorphisms: statistical considerations of determining relatedness and population distances. In: Chakraborty R, Epplen JT (eds) DNA fingerprinting: state of the science. AJ Jefferys Birkhauser, Verlag

Carlson DM, Pflieger WL, Trial L, Haverland PS (1985) Distribution, biology and hybridization of *Scaphirhynchus albus* and *S. platorhynchus* in the Missouri and Mississippi Rivers. Environ Biol Fish 14:51–59

Dryer MP, Sandoval AJ (1993) Recovery plan for the pallid sturgeon (*Scaphirhynchus albus*). US Fish and Wildlife Service, Denver, 55 pp

Evanno G, Regnaut S, Goudet J (2005) Detecting the number of clusters of individuals using the software structure: a simulation study. Mol Ecol 14:2611–2620

Forbes SA, Richardson RE (1905) On a new shovelnose sturgeon from the Mississippi River. Bull Illinois State Lab Nat Hist 7:37–44

Falush D, Stephens M, Pritchard JK (2003) Inference of population structure using multilocus genotype data: linked loci and correlated allele frequencies. Genetics 164:1567–1587

Goudet J (2001) FSTAT, a program to estimate and test gene diversities and fixation indices (version 2.9.3). Available from http://www.unil.ch/izea/softwares/ fstat.html. Updated from Goudet (1995). Cited Feb 2002

Goudet J (1995) FSTAT (vers. 1.2): a computer program to calculate F-statistics. J Hered 86:485–486

Goudet J, Raymond M, Demeeus T, Rousset F (1996) Testing differentiation in diploid populations. Genetics 144:1933–1940

Hansen MM, Kenchington E, Nielsen EE (2001) Assigning individual fish to populations using microsatellite DNA markers. Fish Fish 2:93–121

Keenlyne KD (1997) Life history and status of the shovelnose sturgeon, *Scaphirhynchus platorhynchus*. Environ Biol Fish 48:291–298

Kuhajda BR, Mayden RL (2001) Morphological comparisons of hatchery-reared specimens of *Scaphirhynchus albus*, *S. platorhynchus*, and *S. albus* × *S. platorhynchus* hybrids. Final Report US Fish and Wildlife Service Bismarck, North Dakota, 119 pp

Langella O (2002) Populations 1.2.28 (available at http://www.cnrs-gif.fr/pge/bioinfo/populations/index.php?lang = en#ancre-bibliographie. Cited 5 Dec 2002

Lewis PO, Zaykin D (2001) Genetic data analysis: computer program for the analysis of allelic data. Version 1.0 (d16c). Free program distributed by the authors over the internet from http://lewis.eeb.uconn.edu/lewishome/ software.html. Cited 2001

Manel S, Gaggiotti OE, Waples RS (2005) Assignment methods: matching biological questions with appropriate techniques. TREE 20:136–142

Miller LM, Kapuscinski AR (2003) Genetic guidelines for hatchery supplementation programs. In: Hallerman EM (ed) Population genetics: principles and applications for fisheries scientists. American Fisheries Society, Bethesda, MD

McQuown EC, Sloss BL, Sheehan RJ, Rodzen J, Tranah GJ, May B (2000) Microsatellite analysis of genetic variation in sturgeon: new primer sequences for *Scaphirhynchus* and *Acipenser*. Trans Am Fish Soc 129:1380–1388

Paetkau D, Slade R, Burden M, Estoup A (2004) Genetic assignment methods for direct, real-time estimation of migration rate: a simulation-based exploration of accuracy and power. Mol Ecol 13:55–65

Paetkau D, Calvert W, Stirling I, Strobeck C (1995) Microsatellite analysis of population structure in Canadian polar bears. Mol Ecol 4:347–354

Phelps SR, Allendorf FW (1983) Genetic identity of pallid and shovelnose sturgeon (*Scaphirhynchus albus* and *S. platorhynchus*). Copeia 1983:696–700

Piry S, Alapetite A, Cornuet J-M, Paetkau D, Baudouin L, Estoup A (2004) GeneClass2. A software for genetic assignment and first-generation migrant detection. J Hered 95:536–539

Pritchard JK, Stephens M, Donnelly P (2000) Inference of population structure using multilocus genotype data. Genetics 155:945–959

Rannala B, Mountain J (1997) Detecting immigration using multilocus genotypes. Proc Natl Acad Sci USA 94: 9197–9201

Rice WR(1989) Analyzing tables of statistical tests. Evolution 43:223–225

Rhymer JM, Simberloff D (1996) Extinction by hybridization and introgression. Annu Rev Ecol Syst 27:83–109

Straughan DJ, Burnham-Curtis ME, Fain SR (2002) Experimental search for forensically useful markers in the genus *Scaphirhynchus*. J App Ichthyol 18: 621–628

Tranah G, Campton DE, May B (2004) Genetic evidence for hybridization of pallid and shovelnose sturgeon. J Hered 95:474–480

Tranah GJ, Kincaid HL, Krueger CC, Campton DE, May B (2001) Reproductive isolation in sympatric populations of pallid and shovelnose sturgeon. N Am J Fish Manage 21:367–373

Vaha JP, Primmer CR (2006) Efficiency of model-based Bayesian methods for detecting hybrid individuals under different hybridization scenarios and with different numbers of loci. Mol Ecol 15:63–72

Weir BS, Cockerham CS (1984) Estimating F-statistics for the analysis of population structure. Evolution 38:1258–1370

Wills PS, Sheehan RJ, Heidinger R, Sloss BL, Clevenstine R (2002) Differentiation of pallid sturgeon and shovelnose sturgeon using an index based on meristics and morphometrics. Am Fish Soc Symp 28:249–258

Wirgin II, Stabile JE, Waldman JR (1997) Molecular analysis in the conservation of sturgeons and paddlefish. Environ Biol Fish 48:385–398

CHAPTER 6: STOCK STRUCTURE

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Stock structure of pallid sturgeon analyzed with microsatellite loci

By A. W. Schrey and E. J. Heist

Fisheries and Illinois Aquaculture Center and Department of Zoology, Southern Illinois University Carbondale, Carbondale, IL, USA

Summary

Recovery efforts for the endangered pallid sturgeon (*Scaphirhynchus albus*) include supplementation of wild stocks with hatchery reared progeny. Identifying the extent of genetic stock structure, which has previously been detected in samples from the range extremes, will help to determine whether stock transfers might be harmful. DNA microsatellite genotypes were screened in pallid sturgeon from the upper Missouri River, lower Missouri River, middle Mississippi River and Atchafalaya River and analyzed using a combination of Bayesian model-based and more traditional F-statistic based methods to characterize genetic differentiation. *Scaphirhynchus* specimens were collected by researchers active in the recovery effort and genotypes were screened at 16 microsatellite loci. Because there is considerable genetic and morphological overlap between pallid sturgeon, shovelnose sturgeon, and their hybrids, a combination of morphological and genetic techniques were used to eliminate shovelnose and possible hybrids from the sample. Genetic differentiation was detected among samples (overall $\theta = 0.050$, $P = 0.001$). Pairwise θ, genetic distances, and Bayesian assignment testing reveal that pallid sturgeon from the upper Missouri River are the most distinct group with pairwise comparisons of pallid sturgeon among all the remaining samples exhibiting lower θ values, higher genetic distances, and self assignment scores. Our results indicate that using local broodstock, when available, should be used for pallid sturgeon propagation. If local broodstock are not available, geographically proximate individuals would limit genetic differences between native and stocked individuals.

Introduction

The endangered pallid sturgeon (*Scaphirhynchus albus*) occurs in the Missouri and Yellowstone rivers, and the Mississippi River south of its confluence with the Missouri River (Kallemeyn, 1983; Dryer and Sandoval, 1993). The much more common shovelnose sturgeon (*S. platorhynchus*) occurs throughout the range of the pallid sturgeon (Keenlyne, 1997). The morphological similarity of species and the presence of morphological intermediates makes identification difficult for some specimens. The presence of morphological intermediates (Carlson et al., 1985) coupled with the finding that these morphological intermediates tend to be genetically intermediate (Tranah et al., 2004) indicates hybridization between pallid and shovelnose sturgeon.

Propagation of pallid sturgeon in locations where adult population sizes are small and there is a perceived absence of natural recruitment is a major focus of recovery efforts. A series of dams constructed between 1933 and 1963 prevents natural movement of pallid sturgeon in the Missouri River. Past stocking resulted in considerable transfer of stocks, including movement of offspring from broodstock collected above Fort Peck Dam, the uppermost dam on the Missouri River, to below Gavin's Point Dam, the lowermost dam on the Missouri, a transfer of over 800 river km. The pallid sturgeon recovery plan (Dryer and Sandoval, 1993) calls for integrating genetic data into recovery efforts. If sufficient genetic differentiation exists among pallid sturgeon populations, stock transfers may result in outbreeding depression (Templeton, 1986).

Pallid sturgeon genetic stock structure has been observed in samples taken from the species' range extremes. Campton et al. (2000) investigated mitochondrial DNA (mtDNA) control region sequence variation within pallid and shovelnose sturgeon and found that genetic distances between fish identified morphologically as pallid sturgeon from the upper Missouri River ($n = 19$) and the Atchafalaya River ($n = 10$) were nearly as great as those between pallid and shovelnose sturgeon from the same locations. Pallid sturgeon from the upper Missouri and Atchafalaya rivers did not share mtDNA haplotypes. Tranah et al. (2001) used five DNA microsatellite markers to study pallid and shovelnose sturgeon from the upper Missouri River and the Atchafalaya River. Later, Tranah et al. (2004) scored additional loci in most of the same individuals. Tranah et al. (2001) found significant allele frequency differences among all pairwise comparisons between pallid and shovelnose sturgeons. Notably, upper Missouri pallid sturgeon from two locations, upstream of Fort Peck Dam ($n = 9$) and downstream of Fort Peck Dam ($n = 11$), were found to be significantly different from Atchafalaya River ($n = 10$) pallid sturgeon. Tranah et al. (2004) likewise found the upper Missouri to be well differentiated from the Atchafalaya.

Previous genetic research indicated significant genetic heterogeneity among pallid sturgeon from the extremes of their geographic range. However, to date no published study has examined genetic diversity in pallid sturgeon across the more than 4000 river kilometers between the locations studied by Campton et al. (2000) and Tranah et al. (2001, 2004). Knowledge of the genetic characteristics of pallid sturgeon from the lower Missouri and middle Mississippi are necessary to guide stocking practices. Past stockings have mostly employed broodstock from either the upper Missouri or Atchafalaya, and pallid sturgeon from both of these regions have been stocked into the central portion of the range (Krentz et al., 2005). It is not known whether wild pallid sturgeon from the middle of the range are more similar to those at either extreme

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or whether they are genetically intermediate, in which case extra effort may be warranted to obtain local broodstock to replenish these regions. This project investigates stock structure across the range of the pallid sturgeon using sixteen microsatellite loci and specimens from the upper Missouri, lower Missouri, middle Mississippi and Atchafalaya rivers. A combination of Bayesian model-based methods, F-statistics, and genetic distances are used to determine the extent and pattern of genetic differentiation.

Materials and methods

Tissue samples taken from the pectoral fin were collected from specimens of*Scaphirhynchus*, including pallid, shovelnose, and morphologically intermediate specimens, by several researchers active in the pallid sturgeon recovery effort (Table 1, Fig. 1). Collectors were instructed to collect samples from all sturgeon with pallid or hybrid-like morphology and a limited number (30–100) of the more common shovelnose-like forms. The morphological character index (mCI) of Wills et al. (2002) was used to generate a putative morphological species identification for all specimens for which the necessary measurements were available. The mCI uses five morphometric ratios: outer barbel length to inner barbel length, head length to inner barbel length, head length to mouth-to-inner barbel base distance, rostrum length to inner barbel length, and rostrum length to mouth to inner barbel distance in order to separate pallid and shovelnose sturgeon on a regression character index. Wills et al. (2002) defined mCI categories for pallid sturgeon (index value −1.34 to −0.71), shovelnose sturgeon (index value 0.84 to 0.97), and an overlapping region including pallid, shovelnose, and putative hybrid sturgeon (index value −0.70 to 0.83).

Genotypes were determined for 477 specimens at 16 disomic microsatellite loci previously developed by McQuown et al. (2000). All genotyping was performed on an ABI 377 with fragment analysis software (Applied Biosystems). PCR (10 μL reaction volume) was conducted with 1–15 ng template DNA, 1 × PCR buffer (50 mM KCl, 10 mM Tris-HCl pH 9.0, and 0.1% Triton® ×100), 200 μM of each dNTP, 2 mM $MgCl_2$, 0.1 unit *Taq* DNA polymerase, and 0.15 μM each primer. For each locus, fluorescent labeled forward primers (6-FAM, NED, or HEX; Applied Biosystems) and unlabeled reverse primers were mixed in a cocktail (9 μM each primer). Thermal profiles for reactions were: 94°C 2 min, 5 cycles of 94°C 30 s, 54°C 30 s, 70°C 30 s, and 35 cycles of 95°C for 30 s, 56°C 30 s, and 70°C for 30 s. PCR products were diluted (1 : 1) in loading buffer (deionized formamide, blue dextran EDTA, and Rox-400 size standard; The Gel Company), loaded on a 5% Long Ranger (Cambrex) 36 cm gel, and run at 2500 scans per hour for 2.5 h. Resultant gel images were analyzed with GENESCAN v 3.1.2 (Applied Biosystems). Alleles were initially scored to raw size in base pairs with GENOTYPER v 2.5 (Applied Biosystems). To ensure uniform scoring, alleles identified by GENOTYPER were scatter-plotted by size and bin-boundaries were visually defined. Once bin boundaries were defined, alleles were recoded to the inferred number of repeats corresponding to the identified fragment size.

The first objective was to identify which of the genotyped specimens were pallid sturgeon using a combination of genetic assignment testing (Paetkau et al., 1995) and phenotypic data. Genotypes of all *Scaphirhynchus* specimen including suspected shovelnose and hybrid sturgeons were analyzed with Structure v 2.1 (Pritchard et al., 2000; Falush et al., 2003). Structure uses the multilocus genotypes of each individual without regard to *a priori* identification to estimate the number of genetic groups present in the data. No reference is made to geographic location of the sample or species identification, allowing estimates of both the number of genetic groups present and the strength of individual membership in each group. Initial runs of Structure indicated that the most likely number of natural groups showing genetic differentiation in the combined *Scaphirhynchus* data was two, with groups largely concordant

Table 1
Sample sizes of *Scaphirhynchus* specimens from four broadly defined geographic locations and number of pallid sturgeon (*Scaphirhynchus albus*), defined by Q-values greater than 0.70 and mCI scores less than −0.70, for each geographic sample

Sample	Location	*Scaphirhynchus* screened	Pallid sturgeon retained
Upper Missouri	Missouri River Above Ft. Peck Dam	89	49
Lower Missouri	Missouri River Mile 220–0	109	12
Middle Mississippi	Mississippi River Mile 200–0	174	43
Atchafalaya	Atchafalaya River Old River Control Channel	105	27

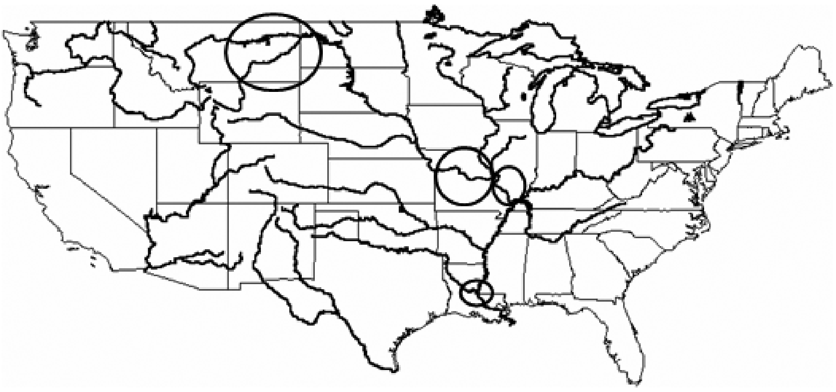

Fig. 1. Map indicating general sample locations of *Scaphirhynchus* specimens. Geographic locations identified by open circles from north to south: upper Missouri, lower Missouri, middle Mississippi, and Atchafalaya rivers

with morphological identification. A second Structure analysis was performed stipulating that the data included two genetic groups. The likelihood that an individual belongs to a particular group is reported as a Q-value, which describes the proportion of an individual's genotype that belongs to a particular cluster (i.e. Q-value 0.70 indicates 70% of an individual's genotype has a higher likelihood of belonging to that cluster). A model allowing alleles in an individual's genotype to come from both groups, in effect allowing for potential hybridization between groups (admixture model), and correlated allele frequencies, was run at a setting of 30 000 burn-in steps and 1 000 000 post burn-in steps.

Shovelnose and hybrid sturgeon were removed from the data to avoid confounding the estimates of genetic heterogeneity within pallid sturgeon with among-species comparisons. Fish were retained as pallid sturgeon if they had a Q-value greater than 0.7 for assignment to the cluster dominated by morphologically-identified pallid sturgeon. For fish with morphological data available, those with an mCI less than −0.7 were also retained. A Q-value greater than 0.70 indicates that more than 70% of the individual's genome is estimated to have come from the pallid sturgeon cluster based on the admixture model, which allows some individual's genomes to have been derived from multiple clusters. The mCI criteria chosen (mCI < -0.7) eliminates all individuals that were placed in the category indicating overlap between pallid sturgeon and hybrid sturgeon morphology, as defined by Wills et al. (2002). Thus, the criteria minimize the potential of including hybrids but possibly eliminate some pallid sturgeon.

Once hybrid and shovelnose sturgeon were removed from the sample, the number of alleles and the observed and expected heterozygosities were calculated for each locus using GDA version 1d16c (Lewis and Zaykin, 2001). Each locus in each sample was tested for Hardy–Weinberg Equilibrium (HWE) by comparing the observed estimate of F_{IS} to values calculated after permutating alleles among individuals within samples using FSTAT v 2.9.3 (Goudet, 1995). A total of 1280 permutations were performed for each locus within each geographic sample and the test was performed for both an excess of heterozygotes and an excess of homozygotes. FSTAT was also used to test for linkage disequilibrium between all pairs of loci by comparing G-statistics calculated from the sample data with 9600 randomly generated G-values based on sample allele frequencies. All significance tests were Bonferroni corrected for multiple comparisons when appropriate (Rice, 1989).

The most likely number of natural groups in the pallid sturgeon data (K) was estimated using Structure by comparing the likelihoods of $K = 1$ through 6. We tested for a larger number of groups than the number of geographic samples in the data because the number of genetic groups could be greater than the number of sampling localities, (e.g. geographic samples could contain mixtures of discrete spawning stocks). Again the admixture model with correlated allele frequencies was used with a setting of 30 000 burn-in steps and 1 000 000 post burn-in steps. Once the number of genetically differentiated groups was estimated the proportion (Q-value) of an individual's genotype that was more likely to have originated in each cluster was determined. Individuals were then sorted by geographic location to determine how the genetic groups related to geographic location.

To estimate genetic differentiation among geographic samples, Weir and Cockerham's (1984) θ, an unbiased estimator of F_{ST}, which can be thought of as the weighted variance in allele frequency among samples, was calculated over all four geographic samples and among all pairs of geographic samples for each locus and combined over all loci using FSTAT. A 95% confidence interval for the combined loci θ estimate was determined by bootstrapping across loci. Corresponding significance tests of genetic heterogeneity were calculated by permutation of alleles among samples for each test and performing the log-likelihood G-test of Goudet et al. (1996).

The shared allele distance (DAS; Chakraborty and Jin, 1993) was calculated among all pairs of geographic samples using Populations version 1.2.28 (Langella, 2002). Genetic distance measures based on the stepwise mutation model are perceived by some as being more appropriate for microsatellites than are F-statistics based on the infinite alleles model, especially among isolated populations (Paetkau et al., 1997). The shared allele distance uses the average proportion of shared alleles between populations, adjusting for within population variation, to estimate genetic distance among populations. Populations that have a higher proportion of shared alleles are taken as being more similar genetically than those that share a smaller proportion of alleles. Also, a Mantel test was performed with Poptools version 2.6.2 (Hood, 2004) to investigate the relationship between genetic differentiation and geographic distance. Geographic distance was estimated in river kilometers between geographic samples and genetic differentiation was calculated as $\theta/(1-\theta)$. Statistical significance was estimated by performing 10 000 iterations.

Results

Screening 477 *Scaphirhynchus* specimens (Table 1) at 16 microsatellite loci and comparing assignment testing and morphological index results discriminated individuals into two major clusters (Fig. 2). Of the fish that had mCI values less than −0.70 (i.e. were morphologically identified as pallid sturgeon), 86.6% possessed Q-values greater than 0.7 for the cluster dominated by pallid sturgeon. Thus, morphological and genetic identification were in close agreement between morphological and genetic identification.

The microsatellite loci were highly variable (Table 2) within the identified pallid sturgeon. The observed numbers of alleles ranged from 7 to 19 and allelic richness (based on the smallest sample size) ranged from 2.784 to 8.540. The average Hardy–Weinberg expected heterozygosity was 0.691, with values ranging from 0.224 to 0.843. No locus in any sample deviated

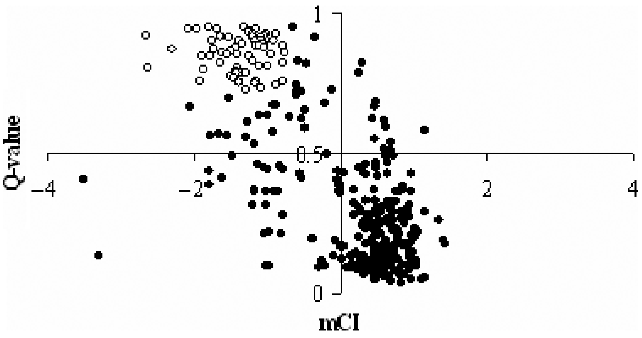

Fig. 2. Scatter-plot of genetic assignment testing (Q-value) on *y*-axis against morphological index (mCI scores) on *x*-axis for *Scaphirhynchus* specimens. Points in quadrant II: individuals having morphologies and genotypes consistent with pallid sturgeon (*S. albus*); quadrant IV: individuals consistent with shovelnose sturgeon (*S. platorynchus*). Open circles = individuals defined as pallid sturgeon (Q-value > 0.70 mCI < −0.70)

Table 2
Summary statistics indicating sample size (N), number of alleles (#A), allelic richness (R), and expected (He) and observed (Ho) heterozygosity for 16 microsatellite loci screened in pallid sturgeon (*Scaphirhynchus albus*). Estimates of θ for each locus and combined over loci is provided. Significance tests of genetic heterogeneity (P) reported for each θ estimate. The 95% confidence interval of the overall θ was (0.028, 0.080)

Locus	N	#A	R	He	Ho	θ	P
Spl-012	131	7	2.784	0.224	0.237	0.185	0.001
Spl-015	131	9	5.336	0.655	0.641	0.031	0.001
Spl-018	130	7	4.405	0.573	0.554	0.063	0.001
Spl-019	131	7	4.879	0.764	0.748	0.049	0.001
Spl-030	126	11	4.677	0.468	0.444	0.032	0.001
Spl-035	126	19	8.540	0.843	0.833	0.011	0.001
Spl-036	126	16	7.701	0.804	0.786	0.038	0.001
Spl-040	127	14	7.576	0.828	0.850	0.003	0.001
Spl-053	128	15	5.691	0.740	0.766	0.032	0.001
Spl-056	130	18	7.408	0.815	0.838	0.019	0.001
Spl-060	129	8	4.618	0.699	0.729	0.010	0.001
Spl-101	130	7	5.393	0.749	0.615	0.217	0.001
Spl-106	130	10	6.336	0.718	0.662	0.077	0.001
Spl-119	129	9	5.218	0.769	0.791	0.044	0.001
Spl-158	128	9	6.734	0.829	0.867	0.039	0.001
Spl-173	128	7	4.213	0.576	0.625	0.027	0.001
Total	131	–	–	0.691	0.687	0.050	0.001

significantly from HWE expectations. One pair of loci, Spl-60 and Spl-173, in the middle Mississippi River sample showed a significant deviation from linkage disequilibrium ($P < 0.0001$).

Bayesian model-based assignment testing using only genotype data without reference to the geographic origin of each specimen identified the most likely number of genetic clusters among pallid sturgeon as three (Fig. 3). In the upper Missouri sample 93.9% of pallid sturgeon had Q-values greater than 0.7 for cluster 1, while few fish outside the upper Missouri sample strongly assigned to cluster 1 (Fig. 4). Fish from the lower Missouri, middle Mississippi, and Atchafalaya were more strongly assigned to clusters 2 and 3, and a larger proportion of the fish from the middle Mississippi assigned to cluster 3 than did fish from the lower Missouri or Atchafalaya (Fig. 3).

The overall θ (combined overall loci and geographic samples) was 0.050 (Table 2) with a 95% confidence interval of (0.028–0.080) and was significant ($P = 0.001$). Values of θ across all samples for each locus (Table 2) ranged from 0.003 to 0.217. Pairwise θ estimates (Table 3) ranged from 0.0059 to 0.0679, with the highest values in comparisons involving the upper Missouri sample. Genetic heterogeneity between the lower Missouri and middle Mississippi and between the lower Missouri and Atchafalaya was not statistically significant. Significant genetic heterogeneity was observed among all other comparisons.

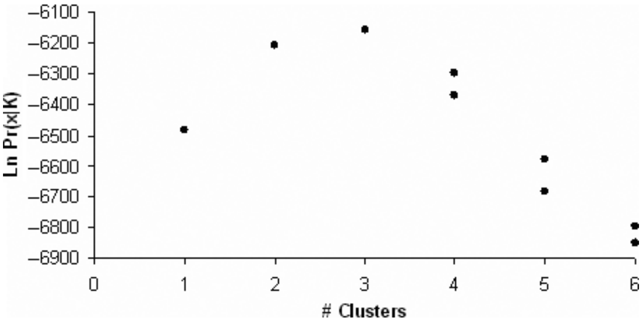

Fig. 3. Pallid sturgeon (*S. albus*) from four geographic samples: estimated natural log probability of observed genetic data (y-axis) given a specified number of clusters (x-axis) calculated by Structure for analysis

The shared allele distance (Table 3) among the upper Missouri and all other geographic samples was larger (range 0.1026–0.1489) than those between the other geographic samples (range 0.0145–0.0748). A Mantel test (Fig. 5) showed a strong correlation between genetic differentiation and geographic distance ($P = 0.038$).

Discussion

Significant genetic differentiation was detected within the range of the pallid sturgeon. The upper Missouri pallid sturgeon are most distinct, with lower Missouri, middle Mississippi, and Atchafalaya River individuals being more closely related to each other than to individuals from the upper Missouri. Similar conclusions could be drawn from analyses performed at an individual level, which did not use geographic sampling location *a priori*. Bayesian model-based assignment of pallid sturgeon identified three genetic clusters within the four geographic locations sampled. These three clusters could be characterized as one distinct upper Missouri group and two less distinct lower basin groups. Failure of the Bayesian analysis to better resolve the lower Missouri, Middle Mississippi, and Atchafalaya samples into distinct groups is indic-

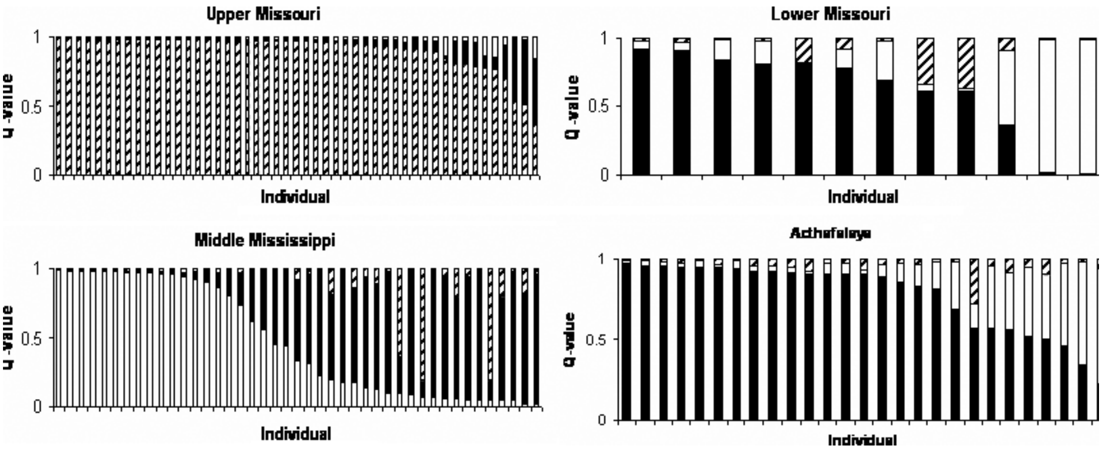

Fig. 4. Bayesian assignment testing results for pallid sturgeon assigned to three clusters. Each bar represents an individual pallid sturgeon (*Scaphirhynchus albus*). The fraction of the individual's genotype attributed to each of the clusters (Q-value) indicated by shading pattern (Cluster 1 = black hatch, Cluster 2 = black, and Cluster 3 = white)

Table 3
Pairwise estimates of θ calculated between all geographic sample pairs (below the diagonal), and the shared allele distance (DAS) among all geographic samples (above the diagonal)

	Upper Missouri	Lower Missouri	Middle Mississippi	Atchafalaya
Upper Missouri	–	0.1026	0.1405	0.1489
Lower Missouri	0.0546*	–	0.0145	0.0429
Middle Mississippi	0.0656*	0.0059	–	0.0748
Atchafalaya	0.0679*	0.0152	0.0257*	–

*Indicates significant test of genetic heterogeneity (θ).

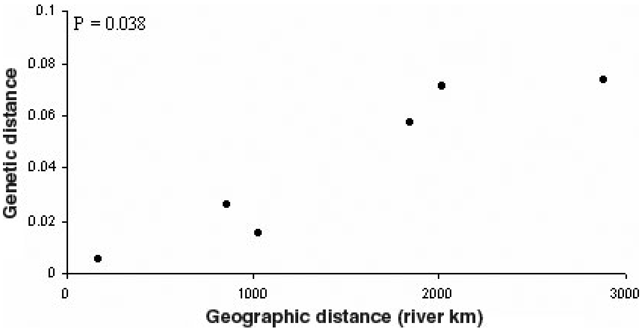

Fig. 5. Mantel test results comparing genetic distance, estimated as $\theta/(1\text{-}\theta)$, on y-axis; geographic distance, in river km, on x-axis. Correlation test between genetic and geographic distance was significant (P = 0.038)

ative of greater levels of gene flow among these locations. Because there are no barriers to movement among these regions, some of the fish included in specific geographic samples could have been migrants. Ideally, pallid sturgeon would have been sampled as either spawning adults or recently spawned juveniles, but the scarcity of pallid sturgeon makes this impossible. If pallid sturgeon exhibit natal philopatry for spawning locations, significant genetic structure may be apparent even if there is considerable mixing of groups between spawning events.

F_{ST} estimates indicated significant genetic differentiation among geographic regions. Pairwise F_{ST} comparisons including the upper Missouri sample had the highest observed F_{ST} values and were all significant. Estimates among the other samples had a lower magnitude and those including the lower Missouri sample, which contained the smallest number of pallid sturgeon, were not significant. DAS values were also greatest between the upper Missouri and all other areas. While dams prevent natural gene flow between the upper and lower Missouri, genetic divergence between regions might reflect historical limits to gene flow rather than genetic drift between recently isolated populations. Pallid sturgeon mature slowly and are very long-lived (Kallemeyn, 1983) and the fish from the upper Missouri sample are very large and are decades old. Thus, too few pallid sturgeon generations have occurred since the construction of the dams to result in significant genetic drift based solely on the dams acting as migration barriers. A Mantel test found a statistically significant correlation between geographic and genetic distance, thus geographic distance might serve as a surrogate for genetic distance when selecting broodstock.

The microsatellite data and analysis agree with and augment the studies of Campton et al. (2000) and Tranah et al. (2001), which found significant genetic differentiation between the extremes of the pallid sturgeon range. This study demonstrates that pallid sturgeon at the middle of the range are genetically intermediate, although more similar to those in the southern (Atchafalaya River) than northern extreme of the range. Less genetic differentiation was observed within samples from the lower Missouri, middle Mississippi, and Atchafalaya rivers compared to those found between the upper Missouri and all other samples.

Assigning individuals to species using microsatellite data and comparison to those derived from a suite of morphological characters indicate these identification methods are largely concordant. Similar to the findings of Tranah et al. (2004), morphological intermediates tended to be genetically intermediate, and a small percentage of individuals had disconcordant genetic and morphological assignments. The presence of genetic and morphological intermediates and individuals with disconcordant results could be explained by hybridization between pallid and shovelnose as suggested for similar results by Tranah et al. (2004). Nevertheless, since Structure analysis detects the presence of two well-defined clusters in all geographic samples and these clusters are concordant with morphology, it appears that genetically pure pallid sturgeon are extant and are represented in Fig. 2 by the individuals with Q-values near 1 and negative mCI values. Because shovelnose are far more numerous than pallid sturgeon, we would expect most backcross individuals to be hybrid × shovelnose crosses that would not genetically assign to the pallid cluster. It should be reiterated that we intentionally collected as many pallid and 'intermediate' fish as we could, thus the distribution of species in Fig. 2 is skewed toward pallid and intermediate morphologies. We were also cautious not to include potential hybrid sturgeon in our estimates of pallid sturgeon stock structure, and several of the fish we excluded may be pure pallid sturgeon. Growth of pallid sturgeon is allometric, with smaller individuals more similar to shovelnose morphologies. This might explain why some fish exhibited intermediate morphologies but strong genetic assignments to pallid sturgeon, i.e. they were small fish not yet exhibiting typical 'pallid' morphology.

The criteria used to identify pallid sturgeon for this study might be modified for other applications depending on the risks associated with failing to identify hybrid sturgeon. We believe the criteria are adequate to investigate stock structure by minimizing the potential of including hybrids while maintaining a sufficient number of pallid sturgeon for analysis. However, when selecting individuals for broodstock, more stringent assignment tests would be appropriate to avoid exacerbating the threats posed to pallid sturgeon recovery by hybridization. Using the individuals identified to species in this study as known baseline samples and assigning potential broodstock with WHICHRUN (Banks and Eichert, 2000) or GENECLASS (Piry et al., 2004) in concert with morphological criteria, would be more efficient for broodstock selection. With these assignment tests the stringency can be set to minimize the potential of including hybrids as broodstock.

These data provide information that can facilitate propagation efforts. Results indicate that pallid sturgeon stocks are genetically structured; thus using local broodstock would be preferable to stock transfers among regions. The range of the pallid sturgeon occupies more that 18° of latitude stretching from the foothills of the Rocky Mountains in Montana to the gulf coast of Louisiana. There are great differences in physical (thermal and flow regimes) and biological (species assemblages) attributes across this range and thus it might be expected that differences in selection pressures coupled with limited gene flow have resulted in adaptive evolution among stocks. Differences in the frequencies of presumably neutral markers such as microsatellites can not prove that adaptive differences among stocks are present but do indicate a lack of gene flow, a condition which is favorable to the evolution of adaptive differences. Further studies examining temperature and flow-related differences in survival and growth, such as those that have been performed in salmonids (Taylor, 1991) and centrarchids (Phillipp and Claussen, 1995), would be useful. Also, examination of markers that are more prone to the effects of selection, such as amplified fragment length polymorphisms (AFLP) and single nucleotide polymorphisms (SNPs) linked to functional genes may indicate a stronger signal and could perhaps identify candidate loci associated with adaptation (Rogers and Bernatchez, 2005). We note that due to the very low abundance of mature pallid sturgeon, collecting local broodstock may not be possible in some locations and demographic issues may outweigh concerns about outbreeding. However, the significant relationship between genetic and geographic distances indicate if local broodstock are not available that using geographically proximate individuals would be preferable. Additionally, we recommend that local allele frequencies should be used and the data collected can be used as pallid and shovelnose sturgeon baseline samples for genetic assignment testing of broodstock to minimize the potential of including hybrids.

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References

Banks M. A.; Eichert, W., 2000: Whichrun (version 3.2): a computer program for population assignment of individuals based on multilocus genotype data. J. Hered. **91,** 87–89.

Campton, D. E.; Bass, A. L.; Chapman, F. A.; Bowen, B. W., 2000: Genetic distinction of pallid, shovelnose and Alabama sturgeon: emerging species and the US Endangered Species Act. Con. Genet. **1,** 17–32.

Carlson, D. M.; Pflieger, W. L.; Trial, L.; Haverland, P. S., 1985: Distribution, biology and hybridization of *Scaphirhynchus albus* and *S. platorynchus* in the Missouri and Mississippi rivers. Environ. Biol. Fishes **14,** 51–59.

Chakraborty, R.; Jin, L., 1993: A unified approach to study hypervariable polymorphisms: statistical considerations of determining relatedness and population distances. In: DNA fingerprinting: state of the science. R. Chakraborty, J. T. Epplen, A.J. Jefferys (Eds). Birkhauser, Boston, MA, pp. 153–176.

Dryer, M. P.; Sandoval, A. J., 1993: Recovery plan for the pallid sturgeon (*Scaphirhynchus albus*). U.S. Fish and Wildlife Service, Denver, 55 p.

Falush, D.; Stephens, M.; Pritchard, J. K., 2003: Inference of population structure using multilocus genotype data: linked loci and correlated allele frequencies. Genetics. **164,** 1567–1587.

Goudet, J., 1995: FSTAT (version 1.2): a computer program to calculate F-statistics. J. Hered. **86,** 485–486.

Goudet, J.; Raymond, M.; Demeeus, T.; Rousset, F., 1996: Testing differentiation in diploid populations. Genetics. **144,** 1933–1940.

Hood, G. M., 2004: Poptools, Version 2.6.2. Available at, http://www.cse.csiro.au/poptools

Kallemeyn, L., 1983: Status of the pallid sturgeon. Fisheries **8,** 3–9.

Keenlyne, K. D., 1997: Life history and status of the shovelnose sturgeon, *Scaphirhynchus platorynchus*. Environ. Biol. Fishes **48,** 291–298.

Krentz, S.; Holm, R.; Bollig, H.; Dean, J.; Rhodes, M.; Hendrix, D.; Heidrich, G.; Krise, B., 2005: Pallid sturgeon spawning and stocking summary report. http://www.fws.gov/filedownloads/ftp_region6_upload/George%20Jordan/Pallid%20Sturgeon/Pallid%20Sturgeon%20Stocking%20Summary%201992–2004/pallid%20spawning%20and%20stocking%20summary%200512.pdf.

Langella, O., 2002: Populations 1.2.28. (available at http://www.cnrs-gif.fr/pge/bioinfo/populations/index.php?lang = en#ancre-bibliographie).

Lewis, P. O.; Zaykin, D., 2001: Genetic data analysis: Computer program for the analysis of allelic data. Version 1.0 (d16c). Free program distributed by the authors over the internet from http://lewis.eeb.uconn.edu/lewishome/software.html

McQuown, E. C.; Sloss, B. L.; Sheehan, R. J.; Rodzen, J.; Tranah, G. J.; May, B., 2000: Microsatellite analysis of genetic variation in sturgeon: new primer sequences for *Scaphirhynchus* and *Acipenser*. Trans. Am. Fish. Soc. **129,** 1380–1388.

Paetkau, D.; Calvert, W.; Stirling, I.; Strobeck, C., 1995: Microsatellite analysis of population structure in Canadian polar bears. Mol. Ecol. **4,** 347–354.

Paetkau, D.; Waits, L.P.; Clarkson, P. L.; Craighead, L.; Strobeck, C., 1997: An empirical evaluation of genetic distance statistics using microsatellite data from bear (Ursidae) populations. Genetics. **147,** 1943–1957.

Phillipp, D. P.; Claussen, J. E., 1995: Fitness and performance differences between two stocks of largemouth bass from different river drainages within Illinois. Uses and effects of cultured fishes in aquatic ecosystems. Am. Fish. Soc. Symp. **15,** 236–243.

Piry, S.; Alapetite, A.; Cornuet, J.-M.; Paetkau, D.; Baudouin, L.; Estoup, A., 2004: GeneClass2. A software for genetic assignment and first-generation migrant detection. J. Hered. **95,** 536–539.

Pritchard, J. K.; Stephens, M.; Donnelly, P., 2000: Inference of population structure using multilocus genotype data. Genetics. **155,** 945–959.

Rice, W. R., 1989: Analyzing tables of statistical tests. Evolution **43,** 223–225.

Rogers, S. M.; Bernatchez, L., 2005: Integrating QTL mapping and genome scans towards the characterization of candidate loci under parallel selection in the lake whitefish (*Coregonus clupeaformis*). Mol. Ecol. **14,** 351–361.

Taylor, E.B., 1991: A review of local adaptation in salmonidae with particular reference to Pacific and Atlantic salmon. Aquaculture **98,** 185–207.

Templeton, A., 1986: Coadaptation and outbreeding depression. In: Conservation biology: the science of scarcity and diversity. M. E. Soule (Ed.). Sinauer Associates Inc., Sunderland, MA, pp. 105–116.

Tranah, G. J.; Kincaid, H. L.; Krueger, C. C.; Campton, D. E.; May, B., 2001: Reproductive isolation in sympatric populations of pallid and shovelnose sturgeon. N. Am. J. Fish. Manegem. **21,** 367–373.

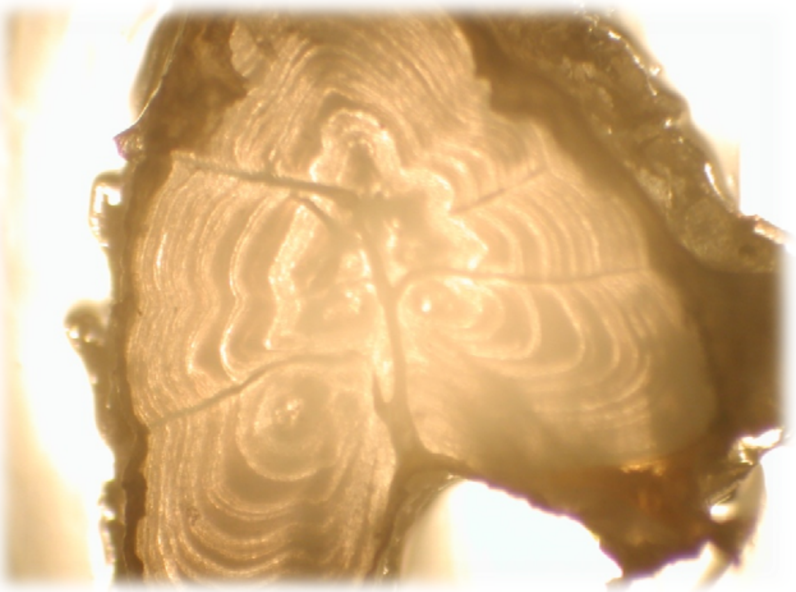
Tranah, G.; Campton D. E.; May, B., 2004: Genetic evidence for hybridization of pallid and shovelnose sturgeon. J. Hered. **95,** 474–480.

Weir, B. S.; Cockerham, C. S., 1984: Estimating F-statistics for the analysis of population structure. Evolution **38,** 1258–1370.

Wills, P. S.; Sheehan, R. J.; Heidinger, R.; Sloss, B. L.; Clevenstine, R., 2002: Differentiation of pallid sturgeon and shovelnose sturgeon using an index based on meristics and morphometrics. Am. Fish. Soc. Symp. **28,** 249–258.

Author's address: Edward J. Heist, Fisheries and Illinois Aquaculture Center and Department of Zoology, Southern Illinois University Carbondale, 1125 Lincoln Drive, Mailcode 6511, Carbondale, IL 62901, USA.
E-mail: edheist@siu.edu

CHAPTER 7: MORTALITY AND POPULATION DYNAMICS



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Harvest of Mississippi River sturgeon drives abundance and reproductive success: a harbinger of collapse?

By R. E. Colombo[1], J. E. Garvey[1], N. D. Jackson[1], R. Brooks[1], D. P. Herzog[2], R. A. Hrabik[2] and T. W. Spier[3]

[1]*Department of Zoology, Fisheries and Illinois Aquaculture Center, Southern Illinois University, Carbondale, IL, USA;* [2]*Missouri Department of Conservation, Resource Science Division, Open Rivers and Wetlands Field Station, Jackson, MO, USA;* [3]*Department of Biological Sciences, Western Illinois University, Macomb, IL, USA*

Summary

Within harvested populations, relationships between harvest intensity and reproductive responses are typically unclear, rendering regulatory decisions difficult. Harvest of the commercially important shovelnose sturgeon (*Scaphirhynchus platorynchus*) is increasing in the upper Mississippi River; standardized seasonal sampling revealed that adult abundance is declining. Relative density of annual cohorts varied negatively with historical harvest intensity ($r^2 = 0.84$), suggesting that removal of mature adults is reducing the contribution of cohorts to population density. The results of simulation modeling suggest that this currently unregulated fishery is experiencing both growth and recruitment overfishing. Further, the current proposed multi-state minimum length regulation was insufficient to maintain a sustainable stock. Only a more conservative minimum length limit (685 mm) produced yields that were sustainable at the current level of mortality and provided room for the fishery to grow. The annual mortality rate of the sympatric, federally endangered pallid sturgeon (*S. albus*) was similar to that of the shovelnose sturgeon population, raising concerns that harvest-induced mortality is affecting this congener's vital rates.

Introduction

The majority of fisheries worldwide are fully exploited, overharvested, or recovering (Botsford et al., 1997). Although harvest typically is implicated as the reason for the decline of exploited fish populations, habitat degradation either through fishing activities (Vitousek et al., 1997) or natural environmental change (Houde, 1987) may also contribute. Harvested populations likely collapse due to the removal of reproductively viable adults. This causes a reduction in reproductive ability and thus sustainability (Beverton and Holt, 1957; Ricker, 1975; Quinn and Deriso, 1999). Fish are often highly fecund and improved reproductive success may compensate for declining densities. Thus, distinct relationships between adult abundance and reproductive success are often weak or non-existent in populations until populations become very small (Koslow et al., 1987; Koslow, 1992). For species with specific spawning requirements, either access to or the availability of reproductive areas may interact with reductions in mature adults to hasten population declines (Birnstein, 1993). Although these concepts are widely accepted in fisheries ecology, robust field patterns are typically absent because of unclear patterns or high variation in assessment data (Myers, 2001).

Populations of sturgeon are threatened across the globe due to a combination of unregulated harvest and habitat loss (Williams et al., 1987; Birnstein, 1993; Boreman, 1997; Pikitch et al., 2005). The recent ban of importation of beluga sturgeon (*Huso huso*) eggs (caviar) into the United States by the US Department of the Interior (Pala, 2005) is testament to current concerns about declines. The commercial fishery for shovelnose sturgeon (*Scaphirhynchus platorynchus*), still allowed by several states in the Mississippi and Missouri river drainages of the US, may bear increased burden as market pressure for domestic roe increases (Keenlyne, 1997; Quist et al., 2002; Secor et al., 2002). Recreational harvest also occurs but is comparatively minor and likely not driven by market forces. Although still considered abundant in the center of its range, shovelnose sturgeon has declined or been extirpated in many drainages at the peripheries (Keenlyne, 1997). Of particular concern is that its larger and more fecund congener, the US federally endangered pallid sturgeon (*S. albus*), occurs sympatrically with this species throughout much of its range. Although illegal to harvest, the species is often difficult to distinguish visually from the shovelnose sturgeon and is likely harvested incidentally or is negatively affected by handling when captured as bycatch; poaching also occurs (Herzog, 2002; Secor et al., 2002).

Understanding how commercial harvest affects populations is essential for effective management of sustainable stocks and requires knowledge of the population age structure. To estimate the age structure of a population, an accurate measure of age is needed. For sturgeon the only currently acceptable ageing method uses the pectoral fin ray. This method has been validated in the lake sturgeon (Rossiter et al., 1995) and white sturgeon (Brennan and Cailliet, 1989). For the shovelnose sturgeon, this method has been shown to be the most precise (Jackson, 2004) and annulus formation has been validated (Whiteman et al., 2004). Once the age structure of a population is determined the mortality and growth rate can be determined.

A simple regression of the log-transformed frequency of each age group plotted against age (i.e. catch curve) provides an estimate of instantaneous mortality (Z) (Ricker, 1975). If harvest is at a level that cannot be compensated for by a reduction in the natural mortality of the population, mortality will increase. Further, the residuals in the catch curve may provide an estimate of year-class strength (Maceina, 1997; Sammons et al., 2002).

Because sturgeon are long-lived (> 20 years), reproduce late (age 5 or older), and are harvested primarily for eggs

(Keenlyne, 1997; Herzog, 2002; Pikitch et al., 2005), they are sensitive to the impact of harvest (Fabrizio and Richards, 1996) and the limited reproductive habitat on population dynamics, providing a model system for quantifying harvest effects on populations. One approach used to determine the influence of commercial exploitation is simulation modeling. Models such as the Beverton-Holt yield-per-recruit model have been effective at estimating the theoretic yield of populations as a function of alternative management strategies (Maceina et al., 1998; Quist et al., 2002). To assess the potential for harvest to remove adults before they have met their reproductive potential, the spawning potential ratio (SPR) can be calculated (Goodyear, 1993; Slipke et al., 2002). The SPR estimates the potential proportion of eggs a recruit will produce in an exploited population compared to that of an unexploited one. In an unexploited population the proportion is equal to one, and declines toward zero with increased fishing mortality. For many marine fisheries a SPR of 30% is considered the critical value below which the population reaches recruitment overfishing (Goodyear, 1993).

We present suggestive evidence of harvest-induced reproductive dynamics and potential population decline of one of the last commercially-viable sturgeon species, raising concerns about the impact of increasing domestic harvest. Further, using simulation modeling, we assessed how current and proposed management strategies may affect the population yield and reproductive potential of the MMR shovelnose sturgeon population.

Methods

Commercial harvest

We reviewed the historical data for shovelnose sturgeon flesh harvested in the upper Mississippi River (above confluence of the Ohio River) compiled by the states of Missouri and Illinois. We used these data because these states border the river reach in which our sampling occurred, although harvest also occurs in other states. To determine whether shovelnose sturgeon harvest was related to Russian caviar harvest, yield of Russian sturgeon was estimated from Pikitch et al. (2005).

Adult density

To provide an index of adult shovelnose sturgeon density in the unimpounded portion of the upper Mississippi River between Cairo, Illinois and St Louis, Missouri, we used catch as a function of effort based on winter standardized sampling conducted during January–February 1995 through 2001. Shovelnose sturgeon were sampled from randomly selected historically productive wing-dike, channel-training structures on the unimpounded river, each year using 51 mm bar monofilament mesh gill nets that were 46 m long and 3 m deep. Effort was standardized as fish per net night and a mean for each year was calculated.

Population demographics

Shovelnose sturgeon were captured from randomly selected sites in the MMR using 51 mm bar mesh during 2002 and 2003. All shovelnose sturgeon were measured to the nearest mm fork length and weighed to the nearest gram. For age analysis, a 25 mm section of the right pectoral fin was removed from an area proximal to the origin of the ray. Because pallid sturgeon are rare, numerous methods were employed to sample them. We employed baited trot lines, 51 mm and 76 mm gill nets, a Missouri trawl, and commercial fishers. Any capture pallid was weighed, measured and numerous morphometric and meristic measurements were made for species identification (Wills et al., 2002). A 25 mm section of the right pectoral fin was removed from all pallid sturgeon for age analysis as well.

Age, growth, and mortality

Fin rays were sectioned using a Buhler Isomet® slow speed saw. Three 600-um sections were mounted to glass slides and aged to the nearest annulus at 7–45× magnification under a stereomicroscope. Annuli were determined to be the light bands when transmitted light was used; areas of growth showed up as dark bands with transmitted light. Fish were aged by two readers independently. Disagreements were resolved by reaching a consensus. If a consensus could not be reached, the spine was discarded. Pallid sturgeon fin rays were processed in the same fashion as the shovelnose sturgeon.

Mortality rates were quantified for both the pallid and shovelnose sturgeon using analysis of catch curves. To reduce the amount of bias created by an influential observation in the catch curve, we used weighted regression, which deflates the importance of rare old fish (Slipke and Maceina, 2000). The declining slope of the catch curve reflects instantaneous mortality (Z). This estimate of Z was used to determine the total annual mortality (A) from the equation $A = 1 - e^{-Z}$. For pallid and shovelnose sturgeon, catch curves were generated by summing the number of fish caught per age-class across years. This method mitigates the bias created by variability in recruitment inherent in the catch curve (Ricker, 1975).

Shovelnose sturgeon growth was assessed using a von Bertalanffy model, using the length at capture as a measure of length at age. The von Bertalanffy model assumes the form $L_t = L_\infty (1 - e^{-K(t-t_0)})$, where, L_t is the length at time t, L_∞ is the theoretic maximum length, K is the growth constant, t is time of concern and t_0 is the age at which length is zero. These parameters can be used to compare growth among populations.

Year-class strength

The residuals generated from each catch curve regression provided an index of cohort strength (Maceina, 1997; Sammons et al., 2002). Points that fall above the regression line indicate strong annual cohorts (i.e. a generation with high recruitment to the population) and points that fall below the line indicate weaker than average year classes (Maceina, 1997; Sammons et al., 2002). These residuals can then be used to determine those factors that contribute to year-class strength. Because previous research suggested that harvest was more important to cohort abundance than were abiotic factors (e.g. discharge) in shovelnose sturgeon (Jackson, 2004), we used harvest as the sole independent variable. Harvest for the upper Mississippi River was determined from the commercial reports submitted by Illinois and Missouri commercial fishers. To determine if the relative strength of the different year-classes (i.e. strong and weak) was maintained among samples we used pairwise correlations between years.

Simulation modeling

The commercially exploited shovelnose sturgeon population of the MMR was modeled using the Beverton-Holt equilibrium yield model (Ricker, 1975) in the yield per recruit function in Fishery Analysis and Simulation Tools (FAST) software (Slipke and Maceina, 2000). The FAST yield per recruit model is actually a modification of the original Beverton-Holt model (Ricker, 1975; Slipke et al., 2002), but it is similar to the yield model of other programs (Quist et al., 2002). The Beverton-Holt yield per recruit estimates yield using the following formula (Slipke and Maceina, 2000):

$$Y = \frac{FN_t\, e^{Zr}\, W_\infty}{K}[\beta(X,P,Q)] - [\beta(X_1,P,Q)], \qquad (1)$$

where F = instantaneous fishing mortality; N_t = the number of recruits entering the fishery at some time t; Z = instantaneous mortality rate; r = time to recruitment ($t_r - t_0$); W_∞ = maximum theoretic weight estimated from L_∞ and the weight length regression; K = the Brody growth constant from the von Bertalanffy model; β = the incomplete beta function; $X = e^{-Kr}$; $X_1 = e^{-K(\text{Max Age}-t_0)}$, Max Age is the maximum age from the sample; $P = Z/K$; Q = slope of the weight length regression + 1.

Several parameters are needed to run the simulation models using FAST. Information regarding the growth, longevity, and weight length regression was calculated from the data collected during this study (Table 1). For the minimum length limits we used 550, 610, and 685 mm coinciding with the current (no limit), proposed (IL, KY, MO, TN), and conservative length limits, respectively (Table 1).

To generate an estimate of conditional natural mortality (natural mortality rate when no fishing mortality occurs), a mortality estimate similar to the unexploited shovelnose sturgeon population in the Missouri River was used (3–7%; Quist et al., 2002). To estimate how yield was affected by harvest we modeled the populations over varying conditional fishing mortality. The lowest minimum conditional fishing mortality was 0%, coinciding with an unexploited fishery, and the population was modeled to a high of 90% fishing mortality (Table 1). For the yield per recruit models, the inflection point in the conditional fishing mortality yield plot was considered above which growth overfishing occurs. The 10% rule ($F_{0.1}$ = fishing mortality that leads to a slope 10% of the slope at F = 0; King, 1995) was used to determine the level of mortality that maintained a sustainable fishery (Hilborn and Walters, 1992; Haddon, 2001; King, 1995). The 10% rule is more conservative than F_{max} and has been shown robust to maintain sustainability (Hilborn and Walters, 1992; Haddon, 2001; King, 1995).

Table 1
Selected population demographics and parameters used to simulate effect of harvest on shovelnose sturgeon (*Scaphirhynchus platorynchus*) in MMR

Parameter	IN and IL
Von Bertalanffy growth parameters	
L_∞	792 mm
K	0.16
t_0	−1.54
Conditional natural mortality	0.05, 0.10
Conditional fishing mortality	0.0–0.90
Log (weight): log(length) coefficients	$a = -10.98$; $b = 2.85$
Age at sexual maturity	5.5
Fecundity: length relationship	$m = 2.77$; $b = -3.174$
Percent of females spawning	
5.5–6 year olds[a]	50%
7–18 year olds[a]	25%
Maximum age	18.2
Minimum length limits	550; 610; 685 mm

[a] From Colombo (2004).

The effect of harvest on the reproductive potential of the population was estimated by simulating the spawning potential ratio (SPR). The SPR has been used extensively in marine systems (Goodyear, 1993) and has recently been used to determine the point of recruitment overfishing in freshwater systems (Quist et al., 2002; Slipke et al., 2002). The SPR estimates the number of eggs produced in an exploited fishery compared to an unexploited one by estimating the fecundity potential of the recruits using the formula (Goodyear, 1993):

$$P = \sum_{i=1}^{n} E_i \prod_{j=0}^{t=1} S_{ij} \qquad (2)$$

where n = number of ages in an unfished population; E_i = the mean fecundity of females of age i; $S_{ij} = e^{-(F_{ij}+M_{ij})}$, the density-independent annual survival probabilities of females age i when age j; F_{ij} = instantaneous fishing mortality rate of females age i when age j; and M_{ij} = instantaneous natural mortality rate of females age i when age j.

Calculation of SPR requires information on age at sexual maturation, an estimate of length to fecundity, and percentage of females spawning annually, all derived from Colombo (2004) (Table 1). We used a threshold level of 40% SPR to produce a sustainable fishery. A critical level of 30% (i.e. allowing fish to meet 30% of their maximum expected reproductive potential) was set as the minimum level of SPR necessary to avoid recruitment overfishing (Goodyear, 1993).

Results

Commercial harvest

Harvest of shovelnose sturgeon in the Mississippi River reached historically high levels during 2001 (Fig. 1). Harvest of shovelnose sturgeon was related to decreasing harvest from the Russian sturgeon species caviar fisheries (Fig. 2).

Adult density

Standardized winter catch rates of shovelnose sturgeon in gill nets during 1997 through 2001 declined exponentially as basin-wide harvest increased (Fig. 3). Pallid sturgeon catch rates were too low to estimate their abundance using a standardized scheme. Although standardized sampling suggests an impact of harvest on adult shovelnose sturgeon numbers, a separate approach is necessary to evaluate historical effects on reproduction.

Mortality and growth

Annual percent mortality rates for shovelnose sturgeon were estimated by quantifying the rate of decline in annual cohorts through time with independently derived annual samples. Rates were 42% for 2000 (ln frequency = 9.73–0.568 × age, $r^2 = 0.92$, $P < 0.001$), 31% for 2002 (ln frequency = 5.90–0.374 × age, $r^2 = 0.94$, $P < 0.001$), 35% for 2003 (ln frequency = 7.77–0.452 × age, $r^2 = 0.86$, $P < 0.004$), and pooled 37% (ln frequency = 9.14–0.47 × age, $r^2 = 0.92$, $P < 0.001$). By pooling cohort abundances across sampling

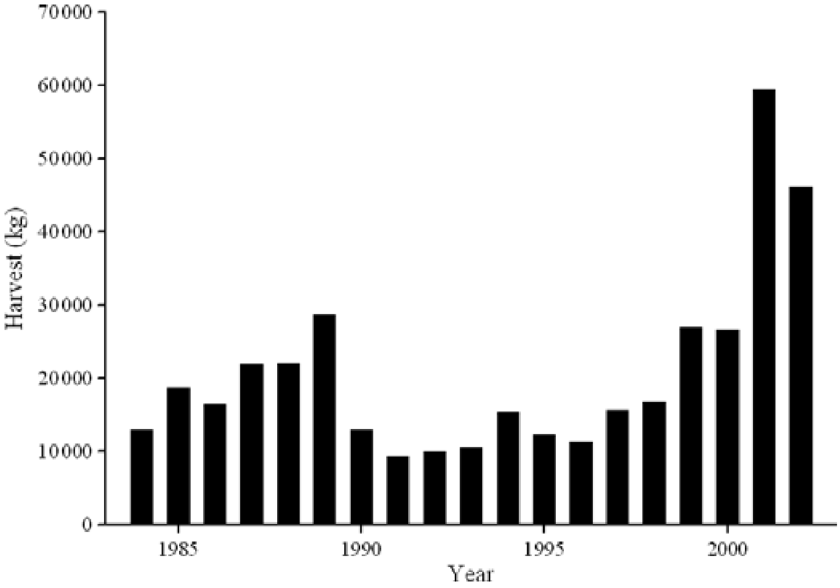

Fig. 1. Harvest of shovelnose sturgeon (*Scaphirhynchus platorynchus*) flesh by Illinois and Missouri fishers in the upper Mississippi River system (i.e. entire border of the state) from 1984 to 2002

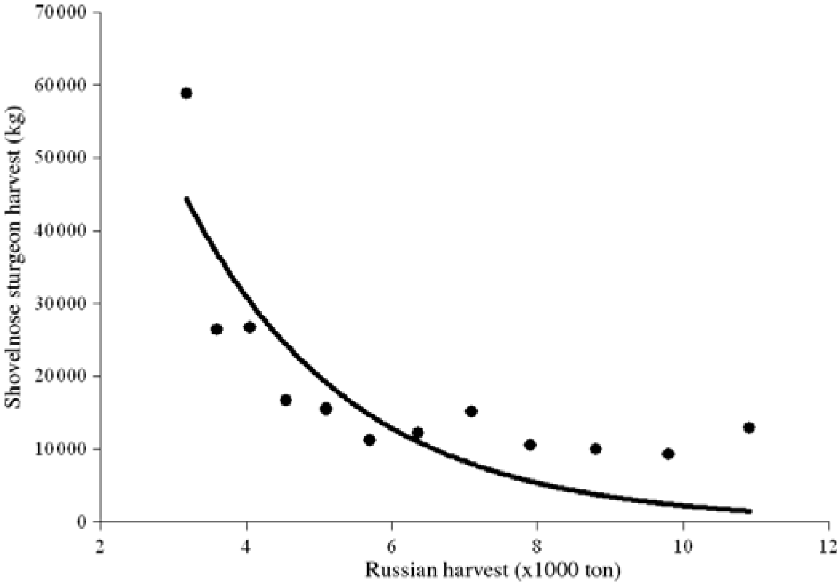

Fig. 2. Relationship between harvest of Russian sturgeon species and harvest of shovelnose sturgeon in the Upper Mississippi River from 1990 through 2002. *Ln* (shovelnose) = 11.68–1.12 Ln (Russian), $r^2 = 0.68$, $P < 0.001$

years, we quantified pallid sturgeon annual mortality to be 37% (ln frequency = 7.08–0.465 × age, $r^2 = 0.95$, $P < 0.001$).

The Brody growth constant of the shovelnose sturgeon population in the MMR was similar to that of other sturgeon populations (Table 1; Morrow et al., 1998; Quist et al., 2002). However, the theoretic maximum length was higher (Table 1); this may be attributable to the reduced density due to commercial exploitation leading to a higher L_∞ (Beverton, 1992; Lorenzen, 1996; Shin and Rochet, 1998).

Year-class strength

Analyzing residual deviations from the average regression line of age vs relative abundance in an unbiased population sample may reflect the relative success of annual cohorts (Maceina, 1997; Sammons et al., 2002). There was a high degree of correlation among the different samples (2000–2002: $r = 0.89$, 2000–2003: $r = 0.83$, 2002–2003: $r = 0.97$) suggesting the different samples provided a similar picture of year class strength. Positive deviations occurred during years of low harvest and negative deviations during high harvest (Fig. 4, 2000: year-class strength = $0.702–5 \times 10^{-5} \times$ harvest, $r^2 = 0.72$, $P < 0.05$; 2002: year-class strength = $1.003–7 \times 10^{-5} \times$ harvest, $r^2 = 0.73$, $P < 0.05$; 2003: year class strength = $0.917–6 \times 10^{-5} \times$ harvest, $r^2 = 0.74$, $P < 0.05$), suggesting a negative impact of harvest on the ultimate success (i.e. recruitment to adulthood) of annual cohorts. Furthermore, from these equations the level of harvest that allowed for an average year class was determined to be 14536 (±380) kg.

Simulation modeling

Under the lower estimate of natural mortality (*cm* = 5%), with harvest being limited only by age at maturity and gear selectivity, the population reached F_{max} at a conditional fishing mortality of 26% (Fig. 5), well below the current level of annual mortality. The level of annual mortality that could be sustained ($F_{0.1}$) with no management was 16% (Fig. 5). Using the proposed minimum length limit of 610 mm, the population reached F_{max} at 35% fishing mortality (Fig. 5); the population was sustainable at a fishing mortality of 20% (Fig. 5). With a

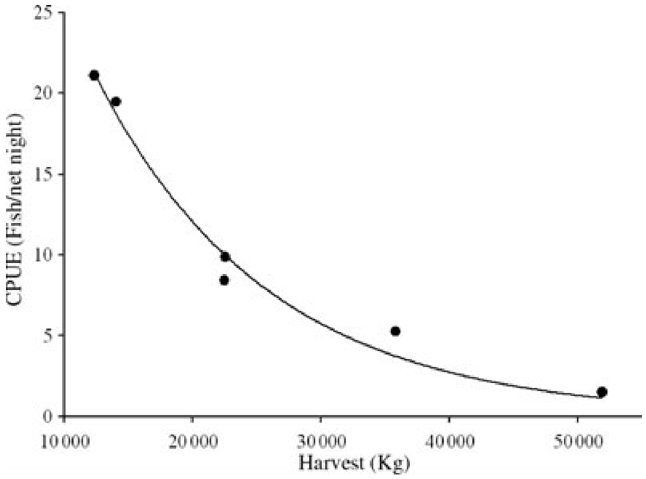

Fig. 3. Adult abundance of shovelnose sturgeon (*Scaphirhynchus platorynchus*) as a function of Mississippi River shovelnose sturgeon harvest by Illinois and Missouri commercial fishers. $\mathrm{CPUE} = 53.062e^{(-0.0001\mathrm{Harvest})}$, $r^2 = 0.981$, $\mathrm{P} = 0.0001$

685 mm minimum length limit, $\mathrm{F}_{\max}$ was not reached until fishing mortality reached 67% (Fig. 5) and the population remained sustainable until mortality reached 33% (Fig. 5). At a higher estimate for conditional natural mortality (*cm* = 10%) yield per recruit for all management options was approximately 36% lower at $\mathrm{F}_{\max}$ than at natural mortality of 5% (Fig. 5). However, there was an increase in the level of fishing mortality before $\mathrm{F}_{\max}$ was reached.

With no minimum length limit and a conditional mortality rate of 5% the spawning potential ratio of the population fell below 40% at a fishing mortality of 15% (Fig. 6) and below 30% at 20% annual mortality (Fig. 6). At the same level of natural mortality with the proposed minimum length limit (610 mm), the population fell below the 40% threshold in SPR at a fishing mortality rate of 21% (Fig. 6) and below the critical 30% threshold at 30% fishing mortality (Fig. 6). With the more conservative length limit (685 mm), the threshold SPR of 40% was not reached until conditional fishing mortality reached 69% (Fig. 6) and the critical threshold SPR was not reached over the entire range of mortalities for which the population was modeled (Fig. 6). Similar results were seen with the higher natural mortality rate (10%), the exception being that the threshold SPR (40%) was not reached under the conservative length limit (Fig. 6). When the results of the yield per recruit modeling are compared to the SPR modeling it becomes apparent that these populations experience a reduction in SPR below the critical threshold (30%) at mortalities similar to those of $\mathrm{F}_{\max}$. This suggests that the more conservative $\mathrm{F}_{0.1}$ be used as a target for management rather than $\mathrm{F}_{\max}$.

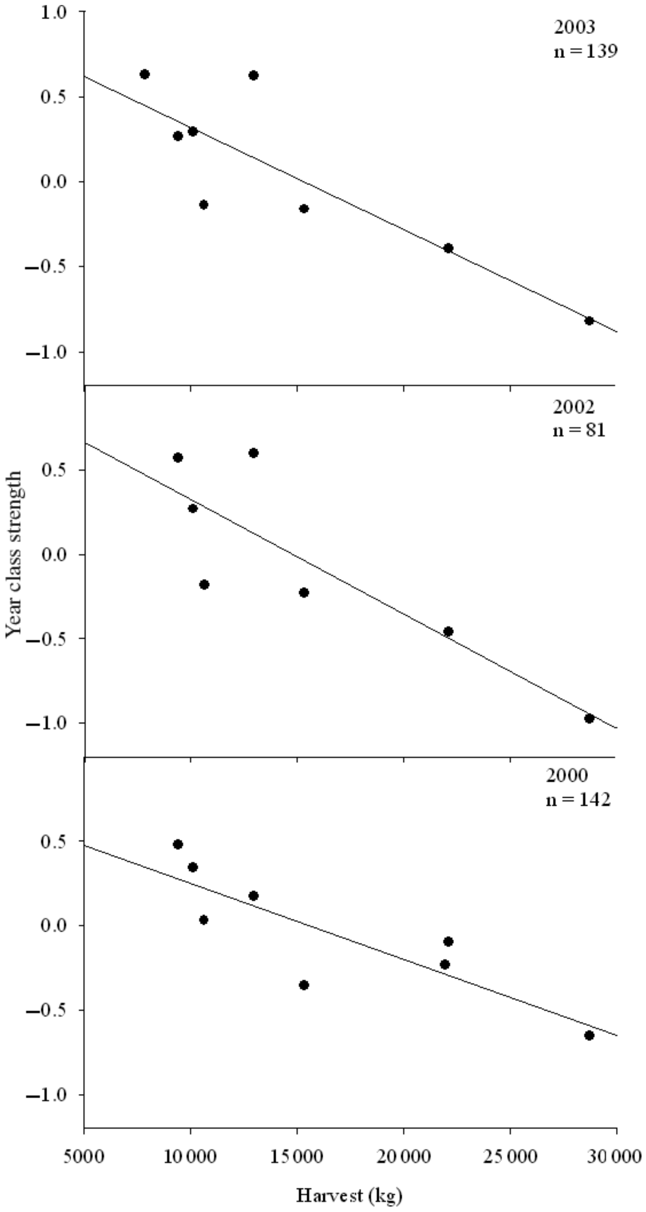

Fig. 4. Relationship between Mississippi River harvest by Illinois and Missouri commercial fishers and year-class strength as derived from residuals from catch-curves for shovelnose sturgeon (*Scaphirhynchus platorynchus*) sampled during 2003 ($r^2 = 0.73$, $\mathrm{P} < 0.05$), 2002 ($r^2 = 0.74$, $\mathrm{P} < 0.05$) and 2000 ($r^2 = 0.72$, $\mathrm{P} < 0.05$). Value of 0 indicates no deviation from average abundance of an annual cohort. Positive and negative values indicate strong and weak cohorts in the population, respectively

Discussion

In our view, these results provide compelling, albeit correlative, support for a harvest effect on the population of shovelnose sturgeon in the MMR. Harvest is directly impacting adult abundances and indirectly affecting reproductive success, ultimately influencing the contribution of cohorts to population size. Given that sturgeon do not become fully vulnerable to standardized sampling gear and commercial harvest until age 6 or greater, a considerable lag exists between the impact of the fishery on cohort abundance and the apparent response of the population documented by both biologists and fishers. These lags may be responsible for the apparently sudden decline in many fish populations after years of sustained but high harvest (Fromentin and Fonteneau, 2001). The apparent decline in standing stock that we documented coupled with a succession of weak year classes may well cause a large decline in future catch rates. Although we cannot tease apart the contribution of harvest to observed annual mortality rates, it is probable that these rates are largely driven by harvest, given that sturgeon mature late in life and are long-lived (Birnstein, 1993; Billard and Lecointre, 2001; Secor et al., 2002). Annual mortality rates of shovelnose sturgeon in the unharvested middle Missouri River (3%; Quist et al., 2002), harvested lower Missouri River (20%; Quist et al., 2002), and historically harvested lower Mississippi River

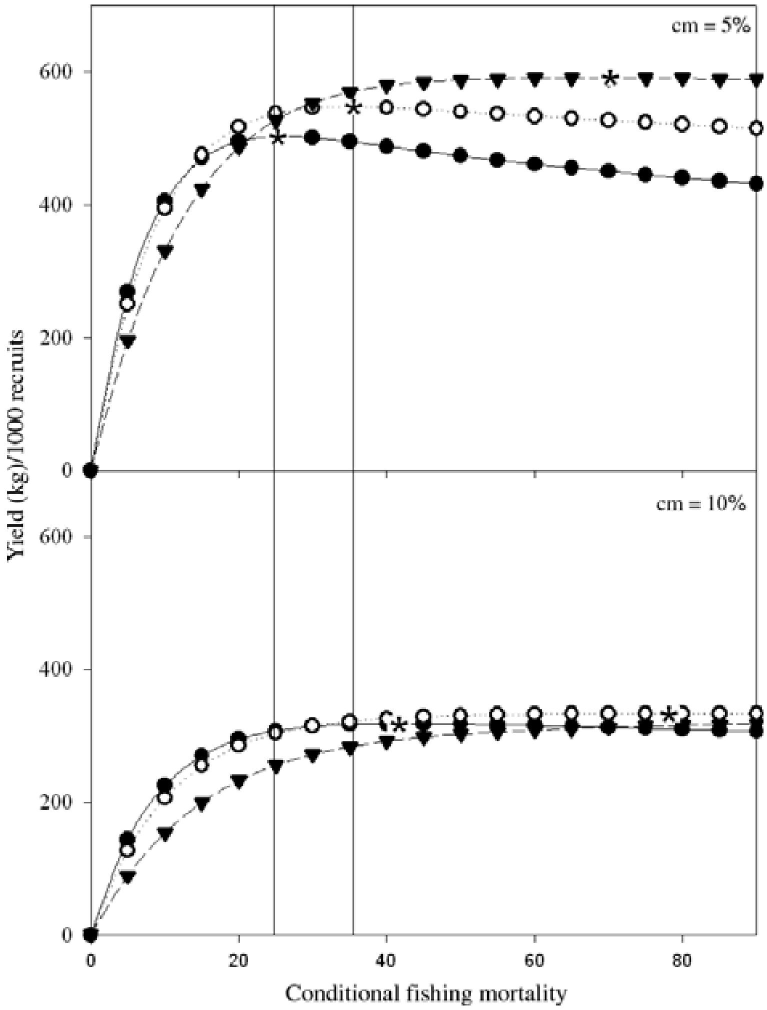

Fig. 5. Simulated yield per 1000 recruits for shovelnose sturgeon (*Scaphirhynchus platorynchus*) population in middle Mississippi River under three different length limits: no limit (-550 mm), dark circles; proposed (610 -mm), open circles; conservative (685 mm), dark triangles; and two different conditional natural mortalities (*cm*), 5% top graph and 10% bottom graph. Vertical lines denote range of current level of harvest. Asterisks – denote F_{max}

(20%; Morrow et al., 1998) were considerably lower than found in this study (37%). This suggests that harvest has caused an increase in the mortality rate of the population.

The strong association between harvest and annual cohort size is likely related to removal of mature, ovigerous females from the upper Mississippi River fishery as they are staging to spawn. Similar reproductive aggregations and strong spawning migrations are found in other taxa that have experienced collapse, including Pacific salmon (Nehlsen et al., 1997) and Atlantic cod (Fogarty et al., 2001). Although strong anecdotal evidence exists for the location of spawning aggregations in the upper Mississippi River, the actual location or locations of successful spawning contributing to annual cohorts is unknown. If spawning habitat is limited or adult movement through impoundments of the upper river is impeded, then harvest effects are likely to be exacerbated on remaining viable areas.

Modeling suggested at the current level of harvest with no regulations that the population is theoretically experiencing both growth and recruitment overfishing. With the proposed state limitation change to a 610 mm minimum length limit, there is still a propensity for the population to become overfished at similar mortality rates to what it is currently experiencing. Further recruitment overfishing would also be occurring. With a more conservative minimum length limit (i.e. 685 mm) the population theoretically could withstand an increase in harvest. Modeling also suggested with a higher natural morality rate that the stock could withstand a higher level of fishing mortality before reaching either $F_{0.1}$ or F_{max}. However, the yield per recruit at all levels of fishing mortality is lower when modeled with a lower natural mortality rate.

The population reproductive potential of shovelnose sturgeon in the MMR is strongly affected by harvest. This suggests that the population has the propensity to experience recruitment overfishing with moderate increases in harvest. Similar results were seen with other populations of shovelnose sturgeon (Quist et al., 2002) and white sturgeon (Boreman, 1997). This is primarily due to the life history of sturgeon (i.e. late maturation and intermittent spawning). As this is one of the last harvestable sturgeon populations it is advisable to be conservative in management practices so that in the face of increased demand the population remains sustainable.

Annual mortality rates of pallid sturgeon were similar to those of its congener. During an intensive four-year sampling effort in which many individuals were recaptured, no pallid sturgeon sampled by our crews was beyond 15 years of age. In the northern Missouri River, pallid sturgeon reach 60 years of age with very low annual mortality (Krentz et al., 2001). Although little is known about the age of maturity in pallid sturgeon, our initial analysis of these data suggests that females do not become mature until 9 years of age. Thus, harvest of large, mature individuals, whether intentional or not, may be contributing to the mortality rates we have quantified. Given the rarity of this species and the lack of

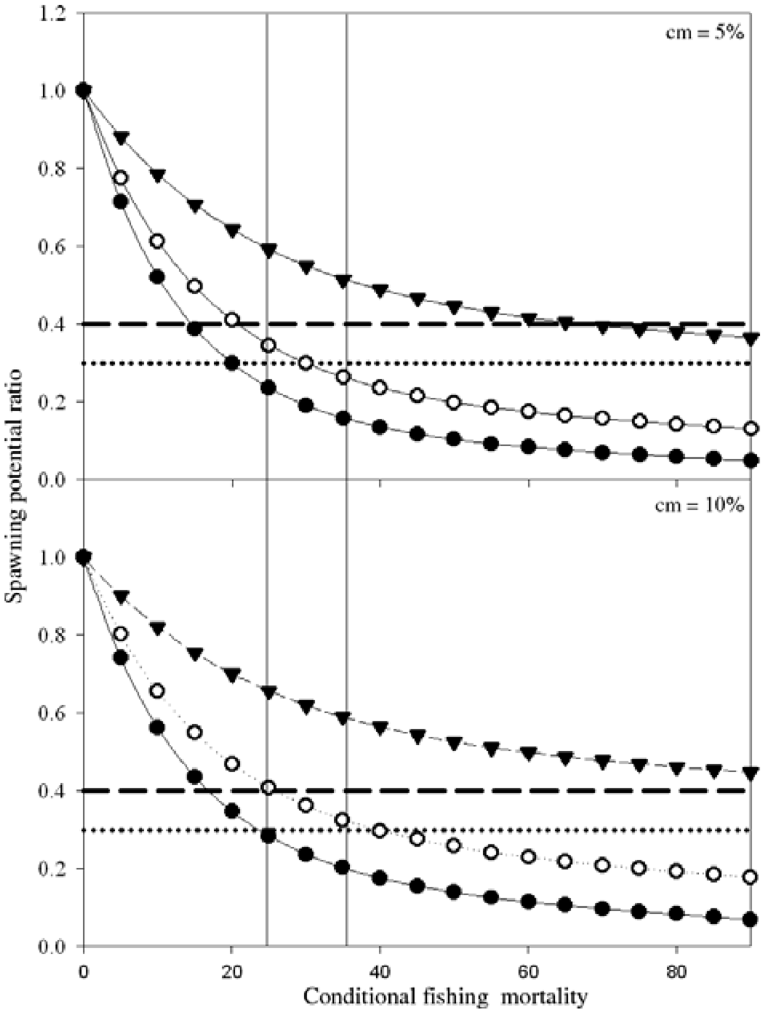

Fig. 6. Simulated spawning potential ratio for shovelnose sturgeon (*Scaphirhynchus platorynchus*) population in middle Mississippi River under three different length limits: no limit (550 - mm), dark circles; proposed (610 mm), open circles; conservative (685 mm), dark triangles; and two different conditional natural mortalities (*cm*), 5% top graph and 10% bottom graph. Horizontal dashed line represents threshold SPR of 40%; horizontal dotted line represents critical SPR of 30%. Vertical lines denote range of current level of harvest

apparent reproduction in most of its range, the potential relationship between harvest and reproduction for shovelnose sturgeon may also hold for this species, hastening its decline. Other sources of mortality beyond senescence are likely rare for adults. However, entrainment by barges may contribute to mortality in the river, reducing juvenile and adult survival (Killgore et al., 2001; Gutreuter et al., 2003).

Although fisheries ecology has often failed to isolate clear patterns between fishing activities and population dynamics, these strong patterns from a notoriously variable river ecosystem provide suggestive evidence that harvest of adults is directly affecting production of future generations. Although harvest has been largely unregulated in the past, some size-dependent and seasonal regulations have been proposed by the states in 2005 to reduce the potential impact of harvest on shovelnose sturgeon. However, the interaction between spawning habitat availability and harvest is far from understood. Given that the proposed regulations do not restrict the number of individuals harvested, the recently increasing trend in domestic harvest may cause shovelnose sturgeon to become commercially extinct and perhaps extirpated within the center of its range. Further, current recovery efforts underway for the endangered pallid sturgeon may be jeopardized.

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References

Beverton, R. J. H., 1992: Patterns of reproductive strategy parameters in some marine teleost fishes. J. Fish Biol. **41,** 137–160.

Beverton, R. J. H.; Holt, S. J., 1957: On the dynamics of exploited fish populations. Chapman and Hall, London.

Billard, R.; Lecointre, G., 2001: Biology and conservation of sturgeon and paddlefish. Rev. Fish Biol. Fish. **10,** 355–392.

Birnstein, V. J., 1993: Sturgeon and paddlefishes: threatened fishes in need of conservation. Conservat. Biol. **7,** 779–787.

Boreman, J., 1997: Sensitivity of North American sturgeon and paddlefish to fishing mortality. Environ. Biol. Fish. **48,** 773–787.

Botsford, L. W.; Castilla, J. C.; Peterson, C. H., 1997: The management of fisheries and marine ecosystems. Science **277,** 509–515.

Brennan, J. S.; Cailliet, G. M., 1989: Comparative age-determination techniques for white sturgeon in California. Trans. Am. Fish. Soc. **118,** 296–310.

Colombo, R. E., 2004: Reproductive demographics and early life history of the shovelnose sturgeon (*Scaphirhynchus platorynchus*). Ms Thesis, Southern Illinois University, Carbondale, IL.

Fabrizio, M. C.; Richards, R. A., 1996: Commercial fisheries surveys. In: Fisheries techniques, 2nd edn. B. R. Murphy and D. W. Willis (Eds). American Fisheries Society, Bethesda, Maryland, pp. 625–646.

Fogarty, M. J.; Myers, R. A.; Bowen, K. G., 2001: Recruitment of cod and haddock in the North Atlantic: a comparative analysis. ICES J. Mar. Sci. **58,** 952–961.

Fromentin, J. M.; Fonteneau, A., 2001: Fishing effects and life history traits: a case study comparing tropical versus temperate tunas. Fish. Res. **53,** 133–150.

Goodyear, C. P., 1993: Spawning stock biomass per recruit in fisheries management: foundation and current use. Can. Spec. Publ. Fish. Aquat. Sci. **120,** 67–81.

Gutreuter, S.; Dettmers, J. M.; Wahl, D. H., 2003: Estimating mortality rates of adult fish from entrainment through the propellers of river towboats. Trans. Am. Fish. Soc. **132,** 646–661.

Haddon, M., 2001: Modeling and quantitative methods in fisheries. Chapman and Hall, CRC Press, Boca Raton, FL.

Herzog, D., 2002: Open river field station report for January 2002. Missouri Department of Conservation, Fisheries Research, Assessment and Monitoring Section, Open River Field Station, Cape Girardeau, Missouri.

Hilborn, R.; Walters, C. J., 1992: Quantitative fisheries stock assessment: choice, dynamics and uncertainty. Chapman and Hall, London, England.

Houde, E. D., 1987: Fish early life dynamics and recruitment variability. Am. Fish. Soc. Symp. **2,** 17–29.

Jackson, N. D., 2004: Age, growth and mortality of shovelnose sturgeon, *Scaphirhynchus platorhynchus*, in the Middle Mississippi and Lower Wabash Rivers, Illinois. Ms Thesis, Southern Illinois University, Carbondale, IL.

Keenlyne, K. D., 1997: Life history and status of the shovelnose sturgeon, *Scaphirhynchus platorynchus*. In: Sturgeon biodiversity and conservation. V. J. Birnstein, J. A. Waldman and W. E. Bemis (Eds). Kluwer Academic Publishers, Dordrecht, NL. pp. 291–298.

Killgore, K. J.; Maynord, S. T.; Chan, M. D.; Morgan, R. P. II, 2001: Evaluation of propeller-induced mortality on early life stages of selected fish species. N. Am. J. Fish. Manage. **21,** 947–955.

King, M., 1995: Fisheries biology, assessment and management. Fishing news books. Iowa State University Press, Ames, IA.

Koslow, J. A., 1992: Fecundity and the stock-recruitment relationship. Can. J. Fish. Aquat. Sci. **49,** 210–217.

Koslow, J. A.; Thompson, K. R.; Silvert, W., 1987: Recruitment to northwest Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) stocks: influence of stock size and climate. Can. J. Fish. Aquat. Sci. **44,** 26–39.

Krentz, S.; King, W.; Hellman, S.; Wilson, R., 2001: 2001 summary report of work conducted by the Missouri River FWMAO on Missouri-Yellowstone River's Pallid Sturgeon. U.S. Fish and Wildlife Service, Missouri River FWMAO, Bismarck, ND.

Lorenzen, K., 1996: A simple von Bertalanffy model for density-dependent growth in extensive aquaculture with an application to common carp (*Cyprinus carpio*). Aquaculture **142,** 191–205.

Maceina, M. J., 1997: Simple application of using residuals from catch curve regressions to assess year-class strength in fishes. Fish. Res. **32,** 115–121.

Maceina, M. J.; Ozen, O.; Allen, M. S.; Smith, S. M., 1998: Use of equilibrium yield models to evaluate length limits for crappies in Weiss Lake, Alabama. N. Am. J. Fish. Manage. **18,** 66–75.

Morrow, J. V., Jr; Kirk, J. P.; Killgore, K. J.; George, S. G., 1998: Age, growth, and mortality of shovelnose sturgeon in the lower Mississippi River. N. Am. J. Fish. Manage. **18,** 725–730.

Myers, R. A., 2001: Stock and recruitment: generalizations about maximum reproductive rate, density dependence, and variability using meta-analytic approaches. ICES J. Mar. Sci. **58,** 937–951.

Nehlsen, W.; Williams, J. E.; Lichatowich, J. A., 1997: Pacific salmon at the crossroads: stocks at risk from California, Oregon, Idaho, and Washington. Fisheries **16,** 4–21.

Pala, C., 2005: Ban on beluga sturgeon caviar points to sturgeon's worldwide decline. Science **310,** 37.

Pikitch, E. K.; Doukakis, P.; Lauck, L.; Charkrabarty, P.; Erickson, D. L., 2005: Status, trends and management of sturgeon and paddlefish fisheries. Fish & Fisheries **6,** 233–265.

Quinn, T. J.; Deriso, R. B., 1999: Quantitative fish dynamics. Oxford University Press, New York.

Quist, M. C.; Guy, C. S.; Pegg, M. A.; Braaten, P. J.; Pierce, C. L.; Travnichek, V. H., 2002: Potential influence of harvest on shovelnose sturgeon populations from the Missouri River System. N. Am. J. Fish. Manage. **22,** 537–549.

Ricker, W. E., 1975: Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. **1975,** 382 pp.

Rossiter, A.; Noakes, D. G. L.; Beamish, F. W. H., 1995: Validation of age estimation for the lake sturgeon. Trans. Am. Fish. Soc. **124,** 777–781.

Sammons, S. M.; Bettoli, P. W.; Isermann, D. A.; Churchill, T. N., 2002: Recruitment variation of crappies in response to hydrology of Tennessee reservoirs. N. Am. J. Fish. Manage. **22,** 1393–1398.

Secor, D. H.; Anders, P. J.; Van Winkle, W.; Dixon, D. A., 2002: Can we study sturgeon to extinction? What we know and don't know about the conservation of North American sturgeon. In: Biology, management and protection of North American sturgeon. W. Van Winkle, P. J. Anders, D. H. Secor and D. A. Dixon, (Eds). American Fisheries Society, Bethesda, MD.

Shin, Y. L.; Rochet, M. J., 1998: A model for phenotypic plasticity of North Sea herring growth in relation to trophic conditions. Aquat. Living Res. **11,** 315–324.

Slipke, J. W.; Maceina, M. J., 2000: Fisheries analysis and simulation tools (FAST) user's guide. Auburn University, Auburn, AL.

Slipke, J. W.; Murphy, A. D.; Pitlo, J.; Maceina, M. J., 2002: Use of the spawning potential ratio for the upper Mississippi River channel catfish fishery. N. Am. J. Fish. Manage. **22,** 1295–1300.

Vitousek, P. M.; Mooney, H. M.; Lubcheno, J. A.; Melillo, J. M., 1997: Human domination of earth's ecosystems. Science **277,** 494–499.

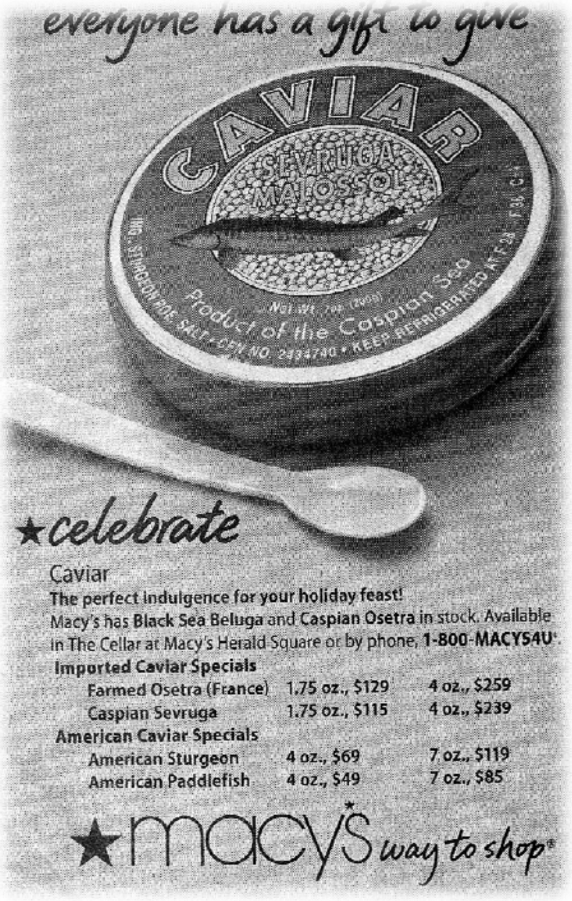
Whiteman, K. W.; Travnichek, V. H.; Wildhaber, M. L.; DeLonay, A.; Papoulias, D.; Tillett, D., 2004: Age estimation for shovelnose sturgeon: a cautionary note based on annulus formation in pectoral fin rays. N. Am. J. Fish. Manage. **24,** 731–734.

Williams, J. E.; Johnson, J. E.; Hendrickson, D. A.; Contreras-Balderas, S.; Williams, J. D.; Navarro-Mendoza, M.; McAllister, P. E.; Deacon, J. E., 1987: Fishes of North America endangered, threatened or of special concern. Fisheries **14,** 2–20.

Wills, P. S.; Sheehan, R. J.; Heidinger, R.; Sloss, B. L.; Clevenstine, R., 2002: Differentiation of pallid sturgeon and shovelnose sturgeon using an index based on meristics and morphometrics. In: Biology, management, and protection of North American sturgeon. W. Van Winkle, P. J. Anders, D. H. Secor and D. A. Dixon (Eds). American Fisheries Society Symp. 28, Bethesda, MD, pp. 249–258.

Author's address: James E. Garvey, Department of Zoology, Fisheries and Illinois Aquaculture Center, Southern Illinois University, Carbondale, IL 62901, USA.
E-mail: jgarvey@siu.edu

CHAPTER 8: COMPARATIVE AGE AND GROWTH



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Age and growth of pallid sturgeon in the free-flowing Mississippi River

K. J. Killgore, J. J. Hoover, J. P. Kirk, S. G. George, B. R. Lewis and C. E. Murphy

U. S. Army Engineer Research and Development Center, Environmental Laboratory, Vicksburg, MS 39180, USA

Summary

Trotlines were used to capture pallid sturgeon in the free-flowing Mississippi River, which extends from the Gulf of Mexico to the mouth of the Missouri River. Trotlines were baited with worms, and set overnight usually along the channel border. The pectoral fin rays of 165 pallid sturgeon caught in the Mississippi River were aged; 118 were from the lower Mississippi River (LMR) between the Gulf and mouth of the Ohio River, and 47 were from the middle Mississippi River (MMR) between the mouths of the Ohio and Missouri rivers. Initial agreement within ±1 year between two readers ranged from 53% for the LMR specimens, which were read first, to 84% for the MMR. Final age was agreed upon by both readers. For LMR pallid sturgeon, final age estimates ranged from 3 to 21 years with a mean (±SD) of 11.0 ± 4.7. For MMR pallid sturgeon, final age estimates ranged from 5 to 14 years with a mean of 9.5 ± 2.1. Seven pallid sturgeon marked with coded wire tags (CWT), indicating hatchery origin, were collected in the MMR. Age estimates for CWT fish were 7–8 years representing 1997 stocked fish, and 11–12 years representing 1992 progeny stocked in 1994. Von Bertalanffy growth equations for length indicated that pallid sturgeon in the MMR had higher growth rates for a given age than pallid sturgeon in the LMR. However, there were no significant differences (ANOVA, $P > 0.5$) in the length–weight relationships between reaches. In the LMR, pallid sturgeon fully recruited to trotlines at age 11 and instantaneous total mortality (Z; slope of catch curve) was estimated at −0.12 ($n = 10$ year classes, $r^2 = 0.55$, $P = 0.01$). Of the 118 sectioned rays from the LMR, 28 could not be reliably aged (only one section from the MMR could not be aged). Therefore, age was predicted from length using the von Bertalanffy equation. The catch curve was re-calculated using the predicted ages of the 28 pallid sturgeon in the LMR resulting in $Z = -0.07$. In the MMR, pallid sturgeon fully recruited to trotlines at age 9 and Z was estimated at −0.36 ($n = 6$ year classes, $r^2 = 0.67$, $P = 0.04$), which was significantly higher (ANOVA, $P = 0.04$) than the LMR estimate. Higher mortality in the MMR may be due to habitat limitations compared to a larger, more diverse channel in the LMR, and incidental take of larger, older individuals during commercial harvesting of shovelnose sturgeon. Commercial take of shovelnose does not occur in the LMR except in the northern portion of the reach. Considering the presence of pallid sturgeon with CWT, recruitment of older individuals in the MMR may have been influenced by stocking a decade earlier. Management strategies for this endangered species should consider the differences in mortality rates among reaches, the impacts of commercial fishing on recovery of pallid sturgeon in the MMR, and the long-term effects of hatchery fish now recruiting into the free-flowing Mississippi River.

Introduction

Pallid sturgeon (*Scaphiryhnchus albus*) are long-lived fish with a broad distribution in the Mississippi River basin. They occur throughout the Missouri River, albeit at low abundance, including the impounded reaches above Gavin's Point Dam and the lower Missouri River (Bailey and Cross, 1954; Dryer and Sandvol, 1993). Information on age and growth of pallid sturgeon are based principally on observations of adults in the Missouri River. Individuals from the northern part of the range are known to attain 167 cm total length (TL) and 31 kg, although adults 53–88 cm TL are probably typical (Carlander, 1969; Lee, 1980; Kallemeyn, 1983). Age of one individual in the upper Missouri River measuring 140 cm (fork length, FL) and 17 kg was estimated at 41 years; pallid sturgeon probably attain greater ages than this (Keenlyne et al., 1992). However, age and growth of pallid sturgeon in the free-flowing Mississippi River below the mouth of the Missouri River remain undocumented.

Recent studies of pallid sturgeon in the free-flowing Mississippi River indicate latitudinal differences in morphology (Murphy et al., 2007) and larger average sizes of individuals in the Middle Mississippi River between the mouths of the Ohio and Missouri rivers (Killgore et al., 2007). It may be that fish tend to live longer and achieve greater sizes with increasing latitude (Garvey and Marschall, 2003). Latitudinal gradients in age and growth of pallid sturgeon would have implications for distinguishing this species from the closely related shovelnose sturgeon (*S. platorynchus*), both of which undergo allometric growth of taxonomic features (Murphy et al., 2007). Furthermore, stocking pallid sturgeon is an ongoing practice for enhancing recovery of the species. Using brood stock from disparate geographic areas for stocking elsewhere may impact the genetic integrity of local populations. More importantly, if recovery of populations is recognized based on year-class strength and longevity of individuals, managers must consider differences in age and growth throughout the range of the species.

The age of a sturgeon is typically determined by counting the number of annuli of the sectioned pectoral fin ray read under magnification (Helms, 1974; Carlson et al., 1985; Morrow et al., 1998; Everett et al., 2003). Aging bias, or disagreement among readers on the individual age of a fish, has been documented for sturgeon aged with rays (Hurley et al., 2004; Whiteman et al., 2004). However, pectoral fin rays are the only aging structures that can be removed without harming the fish (Parsons et al., 2003), and aging data are necessary to evaluate demographic patterns throughout the range of this federally endangered species.

A 6-year study of pallid sturgeon in the free-flowing Mississippi River was completed in 2005. One of the principal objectives was to age each pallid sturgeon captured during the

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study. This article summarizes the age-length distribution of pallid sturgeon and estimates their instantaneous rates of total mortality (Z) in two different reaches of the free-flowing Mississippi River.

Materials and methods

From 2000 to 2006, pallid sturgeon were captured with trotlines in the free-flowing Mississippi River extending 1847 river kilometers (rkm) from its mouth at the Gulf of Mexico upstream to the mouth of the Missouri River (Killgore et al., 2007). Data were separated into two reaches for analytical purposes: lower Mississippi River (LMR) below the mouth of the Ohio River, and middle Mississippi River (MMR) between the mouths of the Ohio and Missouri rivers. A unique feature of the MMR is the chain of rocks (COR) at rkm 1839.5, a naturally occurring low water dam, reinforced with concrete and rip-rap, which is the only obstruction (at low water) to upstream movement of sturgeon and other fish in the MMR and LMR.

For each pallid sturgeon captured, FL and weight were measured, additional morphometric measurements and meristic counts were taken to verify species designation *a posteriori* as described by Murphy et al. (2007), and a non-encrypted PIT (passive integrated transponder) tag was inserted at the base of the dorsal fin. Beginning in the autumn of 2004, all sturgeon were scanned for coded wire tags (CWT) to determine if individuals were of hatchery origin. Prior to release, an approximately 12-mm segment of the anterior-most fin ray, usually the right ray, was removed. The segment was taken proximal to the body of the fish (approximately 5 mm from body surface) using wire cutters (for small fish with relatively thin rays) or a Dremel® rotary tool (for larger fish with relatively thick rays). This technique was intended to remove a usable segment of the oldest part of the ray while preserving normal articulation and most of the anterior edge of the fin. Sturgeon handled in this manner retain normal hydrodynamic function (Parsons et al., 2003).

The ray segment was air dried and later cut perpendicularly on a Buehler Isomet® slow speed saw into a 0.46–0.58 mm section; two sections were cut from each ray. Sections were mounted on a microscope slide using clear fingernail polish and labeled with a unique identification number (typically the number of the PIT tag implanted in that fish). All sections were examined by readers using a binocular microscope and variable magnification with light transmitted from the bottom through the section.

Fish were aged by counting each concentric continuous band, beginning with the first (resembling a star), and ending with the last (just inside the margin of the ray). Bands were translucent or clear and appeared 'raised'. They alternated with darker, frequently wider bands that appear 'recessed'. Separation (and discrimination) of bands was greatest at the posterior lobes of the ray. The pattern of a thin light zone followed by a darker zone was used to define each annulus (except at the margin of the section). Determining age was problematic when the light (translucent) zones were incomplete, doubled (or grooved), or indistinct. In some cases, the band(s) could be traced around the section to determine whether they originated as individual or as multiple structures. In other cases, the slide was reversed and examined from the opposite surface. If the count could not be determined reliably, the second section of the same fin ray was examined, and the process repeated. To minimize bias in age determinations, readings were done with no data on the size of the individual fish.

Sectioned rays were read independently by two people with prior training in recognizing diagnostic features of the annuli. If counts were identical, age was accepted. If counts differed by 1 year, fish were assigned the higher age. This was based on the conservative assumption that a reader was more likely to underestimate age by overlooking a partly-obscured section (e.g. near the edge of the cross-section) than to overestimate age by counting an anomaly or artifact (e.g. false annulus). If counts differed by 2 years or more, sections were re-examined and read collaboratively with a third reader. Those sections which were difficult to read and readers lacked consensus on number of annuli were evaluated separately.

Data for all years were combined for analysis. Rarity of pallid sturgeon precluded demographic analysis for separate years or seasons, adjusting age estimates for the time of annulus formation relative to time of capture, or tracking of individual year classes. However, cursory examination of age distributions among study years did not show differences in year-class strength. Therefore, we assumed that recruitment, growth, and mortality were similar among all years of the study.

A von Bertalanffy growth equation (Von Bertalanffy, 1938) using the Gulland modification (Ricker, 1975) was calculated for fork length (FL) as follows:

$$\mathrm{FL} = L_\infty(1 - \mathrm{e}^{-K(t-t_0)})$$

where L_∞ is the mean asymptotic FL (mm), t is age (years), t_0 is the hypothetical age at length 0, and K is the Brody growth coefficient. A weight–length relationship was estimated after Ricker (1975) as follows: $\log_{10}(\mathrm{W}) = \log_{10}\mathrm{a} + \mathrm{b}(\log_{10}\mathrm{FL})$ with weight (W) measured in grams, length FL measured in millimeters, $\log_{10}\mathrm{a}$ is the y-axis intercept, and b is the slope of the equation. The instantaneous mortality rate (Z) was estimated with a catch curve, and this value was converted into the annual mortality rate (Ricker, 1975). Catch curves were generated from the linear regression of the $\log_{10}$ number of individuals per year class (Ricker, 1975). The slopes of the regression lines among the reaches for both the weight–length relationships and the catch curves were statistically compared using analysis of co-variance with log-transformed values. Statistical Analysis System (SAS) was used for all calculations (Version 9.1, SAS Institute, NC, USA).

Results

A total of 165 spine sections, 118 from the LMR and 47 from the MMR, were read independently by two readers. For LMR sections, eight were deleted initially because of major impairments in the quality. During the second reading, 20 more were deleted because annulus counts varied by more than 6 years after repeated attempts to reach agreement. Mean (±SD) FL (mm) of deleted sections was 730 ± 79 and the range was 540–892. This resulted in a total sample size of 90 sections for the LMR. MMR sections were read after completing all counts for LMR sections, and therefore, readers had the benefit of this experience. Only one section (FL = 995 mm) was deleted for MMR pallid sturgeon, resulting in a total sample size of 46.

Initial agreement between readers differed substantially for LMR spines (Table 1). Readers agreed on the same age 21% of the time, and 33% differed by 1 year. In contrast, readers agreed on the counts within 1 year or >83% of the time for MMR spines. For counts that differed by one or more, both primary readers along with a third reader viewed the sections together to determine a final age estimate. For LMR sections, final age estimates ranged from 3 to 21 years with a mean (±SD) of 11.0 ± 4.7 (Fig. 1). For MMR sections, final age

Table 1
Percent agreement of the initial annulus counts between two readers for pallid sturgeon rays, lower (LMR, n = 90) and middle (MMR, n = 46) Mississippi River

	Percent agreement of annulus counts within				
Reach	± 0	± 1	± 2	± 3	> ± 4
LMR	21	33	23	15	8
MMR	44	40	10	5	2

estimates ranged from 5 to 14 years with a mean of 9.5 ± 2.1. A total of seven pallid sturgeon were collected in the MMR that contained CWT. Age estimates for these fish were 7–8 and 11–12 years with a mean of 9.7 ± 2.2.

Von Bertalanffy growth equation parameters for length were $L_\infty = 847.6$ mm FL (SE = 23), $t_0 = -1.307$ (SE = 0.75), and $K = 0.1609$ (SE = 0.0247). For MMR spines, growth equation parameters for length were $L_\infty = 890.2$ mm FL (SE = 139.5), $t_0 = -1.5843$ (SE = 5.7131), and $K = 0.1802$ (SE = 0.1853). Pallid sturgeon in the MMR grew faster and attained greater length for a given age compared to pallid sturgeon in the LMR (Fig. 2). However, differences in growth rates were negligible in older individuals.

A weight–length relationship was calculated for all pallid sturgeon captured during the study with data pooled across sampling years. Sample size was 226, including 169 fish from the LMR and 57 for the MMR (Fig. 3). Scatter plots indicated that COR pallid sturgeon, which included all CWT sturgeon, had a different weight–length relationship than the other two reaches and were evaluated separately. However, ANOVA indicated no significant ($P > 0.5$) difference in the slopes of the three log-linear regression lines. Although not statistically significant, several observations were made on length–weight relationships among reaches. MMR pallid sturgeon have the propensity to reach heavier weights (>4 kg). All pallid sturgeon caught at the COR, however, were more slender than their MMR counterparts. Of the 29 pallid sturgeon caught at the COR not designated with CWT, 48% were caught in spring (mostly April) and 52% were caught during autumn (late November–early December). Of the seven CWT pallid sturgeon, 71% were caught in late November–early December and the remaining in March.

In the LMR, pallid sturgeon fully recruited to trotlines at age 11 (Fig. 1). In the MMR, we assumed that pallid sturgeon fully recruited to trotlines at age nine even though peak abundance occurred at age 10. However, these two ages differed by only one individual. Mortality estimates would increase if recruitment was assumed to be at age 10. Instantaneous rate of total mortality (Z) in the LMR was estimated at −0.12 ($r^2 = 0.55$, $P = 0.01$) which yields an annual rate of total mortality of 11% (Ricker, 1975). Using von Bertalanffy growth equation parameters, age was calculated for LMR sections that could not be reliably aged under magnification (n = 28). The length of three of these pallid sturgeon exceeded L_∞ and were assigned the next highest age actually calculated (25 years). When these sections were included in the catch curve, Z was estimated at −0.08 ($r^2 = 0.90$, $P = 0.002$) which yields an annual rate of total mortality of 7%. In the MMR, instantaneous rate of total mortality was estimated at −0.36 ($r^2 = 0.67$, $P = 0.04$) which yields an annual rate of total mortality of 30%.

Discussion

Relatively high disagreement in initial age estimates has been noted in other studies of pallid and shovelnose sturgeon. In the Missouri River, between-reader agreement of pallid sturgeon age was 46.9% (Hurley et al., 2004). For shovelnose sturgeon, two readers agreed on the same age only 18% of the time (Whiteman et al., 2004). Similarly, readers agreed 31.5% on the exact ages of shovelnose sturgeon in the lower Mississippi River (Morrow et al., 1998). These studies, and our own experience, indicate that difficulty in reading pallid sturgeon rays was caused by damaged sections, anomalous annuli, and compressed annuli on the anterior fin ray margin of older fish. However, our study also indicates that agreement can be reached on most fin ray sections once lower quality sections are removed from the data base, and that experience in reading pallid sturgeon fin rays increases agreement between readers. We did not notice a difference in the readability of high quality rays between the LMR and the MMR sturgeon, and we assumed that sturgeon in the southern latitudes produce annuli similarly to those in the northern latitudes. However, the time of annulus formation was not determined in this study, although slower growth may occur in the summer when pallid sturgeon are inactive (Killgore et al., 2007). We had only one validated spine from a pallid sturgeon caught in the LMR with an external floy tag indicating hatchery origin (Killgore et al., 2002). Two readers blindly aged this fish to be 5-years old, which was correct based on release from the hatchery and date of recapture. Ages may vary by 1 or 2 years among readers, but a certain level of error should be acceptable for long-lived species considering the importance of age data in management of pallid sturgeon.

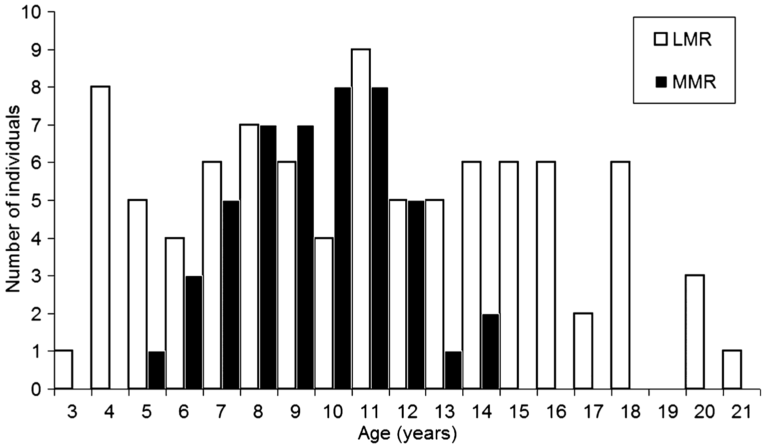

Fig. 1. Age distribution of pallid sturgeon in the lower Mississippi River (LMR) and middle Mississippi River (MMR)

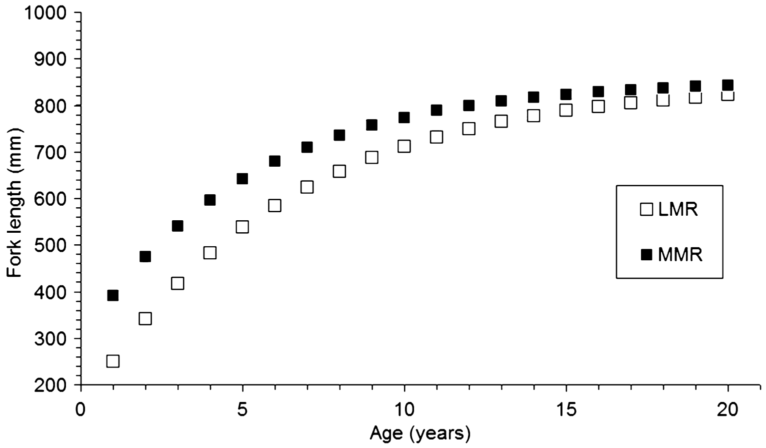

Fig. 2. Growth curves for pallid sturgeon in the lower Mississippi River (LMR), and middle Mississippi River (MMR)

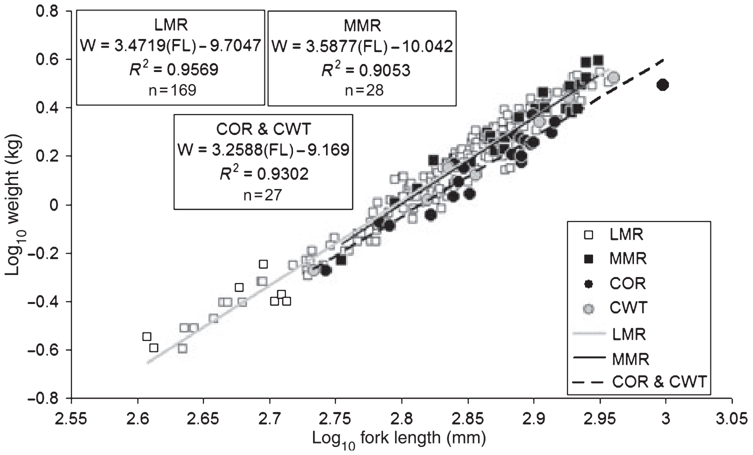

Fig. 3. Weight–length relation for pallid sturgeon in the lower Mississippi River (LMR), middle Mississippi River without chain-of-rocks (MMR), and all individuals caught only at the chain-of-rocks (COR) which includes those with coded wire tags (CWT)

Mortality rate of pallid sturgeon in the MMR ($Z = -0.36$) was triple that of LMR ($Z = -0.12$). High mortality rate ($Z = -0.36$) of pallid sturgeon in the MMR has also been noted in a recent study (Colombo et al., 2007). Differences in habitat between the two reaches may account for part of this disparity. The LMR has fewer dikes per kilometer of river and a much larger channel than the MMR (Killgore et al., 2007). Therefore, the reduced influence of river training structures in the LMR as well as the greater availability of channel and channel border habitat typically used by pallid sturgeon may enhance survival.

Incidental take during commercial fishing operations may be another reason for higher mortality in the MMR. Commercial fishing for shovelnose sturgeon has been closed in the LMR for over 10 years except for states in the northern portion of the reach (Kentucky, Missouri, and Tennessee), all of which have restricted harvest regulations and comprise only 25% of the total length of the LMR. In contrast, commercial fishing for shovelnose in the MMR is intensive (Colombo et al., 2007). Incidental take of pallid sturgeon during commercial fishing operations may be one reason older individuals (> 14 years) are not being caught in the MMR, thus leading to higher mortality rate estimates. Absence of older fish in the MMR was also noted almost 30 years ago. Maximum age of 11 pallid sturgeon caught in the Mississippi and lower Missouri Rivers in 1978–1979 was 14 years during a time of continuing commercial fishing (Carlson and Pflieger, 1981). Recently, take of pallid sturgeon by commercial fishermen has been documented by law enforcement agencies (e.g. Jeff Quinn, Arkansas Game and Fish Commission, 2006, pers. comm.).

The COR harbors a seemingly different size group of pallid sturgeon, which are relatively abundant at this location compared to other reaches in the free-flowing Mississippi River (Killgore et al., 2007). In this study, all pallid sturgeon caught at the COR, including hatchery fish (CWT), were less heavy for their size than their MMR counterparts. We can speculate that pallid sturgeon captured at the COR had recently spawned (spring collections) or undergone long migrations (spring and autumn) resulting in a decrease in weight. Regardless, the collective information on the unique characteristics of the sturgeon population and habitat at the COR support development of specific management strategies for this unusual location near the upstream terminus of the free-flowing Mississippi River.

We were unable to differentiate sex and this likely contributed to only moderate squared correlation coefficients ($R^2 < 0.68$) of the catch curves. Carlson et al. (1985) reported that females outnumbered males 2 : 1 throughout the Missouri and Mississippi Rivers, and females are generally larger than males at a given age. Age of sexual maturity is 5–7 for males, 9–12 for females, but first spawning may not begin until age 15–17 or later (Keenlyne and Jenkins, 1993). Therefore, the absence of older fish in the MMR and the increased demand for caviar may result in higher mortality rates of females.

The age distribution in the LMR indicates strong year classes of pallid sturgeon, beginning at age four, being recruited into the population and older age classes are present up to 21 years. This differs from the upper Missouri where pallid sturgeon are not naturally recruiting, but are comprised of older individuals that can reach ages greater than 50 years (Dryer and Sandvol, 1993). The larger sizes and older individuals in the Missouri River, compared to the LMR, suggest latitudinal variation in growth and longevity. Latitudinal differences in morphology and relative abundance of pallid sturgeon have also been reported (Killgore et al., 2007; Murphy et al., 2007).

Based on trotline catches, the MMR age distribution lacked younger fish suggesting reduced recruitment compared to the LMR. In the MMR, strong year classes begin to appear at age eight and persisted through age 11. Coincidentally, the seven pallid sturgeon with CWT were comprised of older individuals (7–8 and 11–12 years). Pallid sturgeon were first stocked in the lower Missouri River and MMR in 1994 when individuals were approximately 2 years old (Krentz et al., 2005), which corresponds to the 12-year old pallid sturgeon collected with a CWT in 2004. Killgore et al. (2007) reported that CWT fish comprised 47% of pallid sturgeon caught in the MMR during a period when all fish were routinely scanned. This proportion of CWT fish does not account for tag loss, if any. Therefore, the abundance and age of CWT fish may be evidence that recruitment of older fish in the MMR is now being influenced by release of hatchery fish years earlier.

The pallid sturgeon population in the MMR is influenced by multiple factors that contribute to uncertainty in recovery. These factors include the increasing presence of hatchery fish in the MMR, unknown movement patterns between the MMR, LMR, and Missouri River, and the growing demand for domestic caviar. Despite the uncertainty in the MMR, our study does indicate low mortality and self-recruiting populations of pallid sturgeon in the LMR. Latitudinal and site-specific differences in weight–length relationships among the LMR, MMR, COR, and CWT fish were not documented, although the average size of pallid sturgeon in the MMR is higher compared to the LMR (Killgore et al., 2007). Differences in mortality between the two reaches suggest that management and recovery options may differ. The LMR may serve as an unexploited reference population with low mortality, whereas the MMR is an exploited population with high mortality. Ultimately, a better understanding of long-term population trends in both reaches of the free-flowing Mississippi River will depend on reproductive success, which is the focus of ongoing studies of pallid sturgeon.

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References

Bailey, R. M.; Cross, F. B., 1954: River sturgeons of the American genus Scaphirhynchus: characters, distribution, and synonomy. Pap. Mich. Acad. Sci. Art Lett. **39,** 169–208.

Carlander, K. D., 1969: Handbook of freshwater fishery biology, Volume 1. Iowa State University Press, Ames, IA, 752 pp.

Carlson, D. M.; Pflieger, W. L., 1981: Abundance and life history of the lake, pallid, and shovelnose sturgeons in Missouri. Missouri Department of Conservation, Columbia, MO, 59 pp.

Carlson, D. M.; Pflieger, W. L.; Trial, L.; Haverland, P. S., 1985: Distribution, biology, and hybridization of *Scaphirhynchus albus* and *S. platorynchus* in the Missouri and Mississippi Rivers. Environ. Biol. Fishes **14,** 51–59.

Colombo, R. E.; Garvey, J. E.; Jackson, N. D.; Koch, B. T.; Brooks, R.; Herzog, D. P.; Hrabik, R. A.; Spier, T. W., 2007: Harvest of Mississippi river sturgeon drives abundance and reproductive success: a harbinger of collapse. Report to St Louis District, Corps of Engineers, St Louis, MO.

Dryer, M. P.; Sandvol, A. J., 1993: Recovery plan for the pallid sturgeon (*Scaphirhynchus albus*). U.S. Fish and Wildlife Service, Denver, CO, 55 pp.

Everett, S. R.; Scarnecchia, D. L.; Power, G. J.; Williams, C. J., 2003: Comparison of age and growth of shovelnose sturgeon in the Missouri and Yellowstone Rivers. North Am. J. Fish. Manage. **23,** 230–240.

Garvey, J. E.; Marschall, E. A., 2003: Understanding latitudinal trends in fish body size through models of optimal seasonal energy allocation. Can. J. Fish. Aquat. Sci. **60,** 938–948.

Helms, D. R., 1974: Age and growth of shovelnose sturgeon, *Scaphirhynchus platorynchus* (Rafinesque), in the Mississippi River. Proceedings of the Iowa Acad. Sci. **81,** 73–75.

Hurley, K. L.; Sheehan, R. J.; Heidinger, R. C., 2004: Accuracy and precision of age estimates for pallid sturgeon from pectoral fin rays. North Am. J. Fish. Manage. **24,** 715–718.

Kallemeyn, L., 1983: Status of the pallid sturgeon. Fisheries **8,** 3–9.

Keenlyne, K. D.; Jenkins, L. G., 1993: Age at sexual maturity of the pallid sturgeon. Trans. Am. Fish. Soc. **122,** 393–396.

Keenlyne, K. D.; Grossman, E. M.; Jenkins, L. G., 1992: Fecundity of the pallid sturgeon. Trans. Am. Fish. Soc. **121,** 139–140.

Killgore, K. J.; Hoover, J. J.; Hrabik, R. A, 2002: Pallid sturgeon captured four years after its release. Am. Curr. **28,** 30.

Killgore, K. J.; Hoover, J. J.; George, S. G.; Lewis, B. L.; Murphy, C. E.; Lancaster, W. E., 2007: Distribution, relative abundance, and movements of pallid sturgeon in the free-flowing Mississippi River. J. Appl. Ichthyol. **23,** 476–483**.**

Krentz, S; Holm, R.; Bollig, H.; Dean, J.; Rhodes, M.; Hendrix, D.; Heidrich, G.; Krise, B., 2005: Pallid sturgeon spawning and stocking summary report, 1992–2004. U.S. Fish and Wildlife Service, Bismark, ND. (Available at: http://www.fws.gov/filedownloads/ftp%5Fregion6%5Fupload/George%20Jordan/Pallid%20Sturgeon/) (last accessed 12 April 2007)**.**

Lee, D. S., 1980: *Scaphirhynchus albus* (Forbes and Richardson), pallid sturgeon. pp. 43. In: D. S. Lee, et al. (ed.). Atlas of North American Freshwater Fishes, North Carolina State Museum of Natural History. Publication #1980–12 of the North Carolina Biological Survey, Raleigh, NC, pp. 854**.**

Morrow, J. V.; Kirk, J. P.; Killgore, K. J.; George, S. G., 1998: Age, growth and mortality of shovelnose sturgeon in the Lower Mississippi River. North Am. J. Fish. Manage. **18,** 725–730.

Murphy, C. E.; Hoover, J. J.; George, S. G.; Killgore, K. J., 2007: Morphometric variation among river sturgeons (*Scaphirhynchus* spp.) of the middle and lower Mississippi River. J. Appl. Ichthyol. **23,** 313–323**.**

Parsons, G. R.; Hoover, J. J.; Killgore, K. J., 2003: Effect of pectoral fin ray removal on station-holding ability of shovelnose sturgeon. North Am. J. Fish. Manage. **23,** 742–747.

Ricker, W. E., 1975: Computations and interpretation of biological statistics of fish populations. Fisheries Research Board of Canada Bulletin **191,** 382 pp**.**

Von Bertalanffy, L., 1938: A quantitative theory of organic growth. Hum. Biol. **10,** 181–213.

Whiteman, K. W.; Travnichek, V. H.; Wildhaber, M. L.; DeLonay, A.; Papoulias, D.; Tillett, D., 2004: Age estimation for shovelnose sturgeon: a cautionary note based on annulus formation in pectoral fin rays. North Am. J. Fish. Manage. **24,** 731–734.

Author's address: K. Jack Killgore, Engineer Research and Development Center, Environmental Laboratory, 3909 Halls Ferry Road, EE-A, Vicksburg, MS 39180, USA.
E-mail: jack.killgore@erdc.usace.army.mil

CHAPTER 9: ANOMOLIES

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Types and occurrence of morphological anomalies in *Scaphirhynchus* spp. of the Middle and Lower Mississippi River

By C. E. Murphy, J. J. Hoover, S. G. George, B. R. Lewis and K. J. Killgore

United States Army Corps of Engineers, Engineer Research and Development Center, Vicksburg, MS, USA

Summary

Sturgeon specimens encountered in the wild that exhibit visible signs of gross physical trauma often look to the naked eye to be in otherwise good condition. Visible morphological anomalies were observed in 9.1% of 176 pallid (*Scaphirhynchus albus*) and 4.6% of 4904 shovelnose (*Scaphirhynchus platorynchus*) sturgeon specimens captured in the Middle (mouth of Missouri River to mouth of Ohio River) and Lower (below mouth of Ohio River) Mississippi River from 1997 to 2004. Frequencies among the types of anomalies differed between the lower and middle river reaches. In the lower river, deformities from foreign objects (typically rubber bands) comprised almost one-third of anomalies observed and may have contributed to other types of anterior injury which, if combined, would comprise the majority of lower river anomalies. In the middle river, nearly half of the observed anomalies involved damage to the caudal peduncle, usually a missing tail. Power regressions from length–weight relationships were compared for anomalous and non-anomalous specimens and demonstrated no significant disparity, verifying the resiliency of river sturgeons.

Introduction

Sturgeons belong to an ancient and robust group of fishes whose form has withstood the tests of evolutionary time and environmental pressure. With an armor of sharp bony scutes, large sturdy pectoral fins, tough skin and ventrally-flattened body, sturgeon are the 'tanks' of the big river benthos. Their conservative life history traits of slow maturation, slow respiration, slow metabolism and infrequent reproduction have served them well over geologic time scales (Secor et al., 2002). It has been suggested that sturgeon benthophagy offered a feeding specialization unique among early Mesozoic fishes (Bemis et al., 1997) and, although they share this niche in modern times, sturgeon remain its oldest and most resolute occupants. In this case, evolutionary pressure has conserved an ancient system because it works.

The same traits that have enabled sturgeon to survive two geologic eras, however, have increased their susceptibility to more recent anthropogenic disturbances. For example, the long-term recruitment system that ensures sturgeon population persistence over decades under natural pressures cannot withstand the short-term pressures of over-fishing or loss of spawning habitat (Boreman, 1997; Secor et al., 2002). Their slow, predictable migrations make them highly susceptible to certain fishing practices such as 'snasts' and weirs (Boreman, 1997; Saffron, 2002). The same rough exterior and bony scutes that protect sturgeon from predation and other external hazards appear to prevent escape from attachment of foreign objects such as rubber bands or monofilament. As individuals, however, sturgeons are still robust and resilient creatures able to survive extreme morphological deformity, significant physical injury, and substantial loss of sensory tissue.

This paper examines the occurrence of morphological anomalies among pallid and shovelnose sturgeon populations in the Middle and Lower Mississippi River (MMR and LMR, respectively), confirms the physical resiliency of *Scaphirhynchus* spp., and highlights some of the more peculiar anthropogenic factors affecting them.

Materials and methods

A total of 176 (130 LMR, 46 MMR) pallid and 4904 (2818 LMR, 2086 MMR) shovelnose sturgeon specimens was collected throughout the Middle (Upper Rkm 322–0) and Lower (Lower Rkm 953.5–250) Mississippi River from 1997 to 2004. These collections were part of two ongoing studies in the MMR and LMR, respectively, on the life history of *Scaphirhynchus* spp. The majority of specimens were captured using 91-m trotlines carrying 60 2/0 hooks baited with Canadian night crawlers. Trotlines were chosen because they target large benthic species, cause minimal bleeding, and do not inhibit respiration. Trotlines were used for 97% of the samples taken in the MMR and 62% of the samples taken in the LMR. Other gear types used were 27-m experimental mesh gillnets, 5-m otter trawl and Missouri-trawl (Herzog et al., 2005) (MMR total sample n = 312; LMR n = 1301). Anomalous specimens were measured, weighed, photographed and qualitative descriptions of visible anomalies were noted. Fork length was recorded for all specimens, but weight was recorded for only one-third (1645 of 4679 individuals) of the non-anomalous shovelnose sturgeon due to high numbers and field processing time. All specimens were tagged and released after processing.

Overt external morphological deformities, injuries, or abnormalities were considered anomalies for the purposes of this study. Anomaly descriptions were consolidated into six categories by anatomical location and type for purposes of analysis: (i) no visible anomalies, (ii) band or foreign object encircling specimen, or scar from foreign object, (iii) broken or injured caudal peduncle, (iv) rostrum deformity, (v) pectoral fin deformity, (vi) other anomalies occurring at low frequencies. Accurate fork length measurements could not be obtained for specimens with broken tails due to the lack of appropriate anatomical landmarks. Lengths were measured from snout tip to the 'end' of the fish. This incongruity confounded the comparison of length–weight relationships for those specimens

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(see Results). Foreign objects found on or embedded in specimen tissues were removed and some were set aside for future examination.

In sturgeon, as in other fish, sexual maturity, season, age, and gender are factors which affect 'condition' or degree of well-being (Carlander, 1969). These factors varied in the specimens used in this study. As an alternative to calculating coefficient of condition, the relative robustness of a population can be detected from a length–weight regression in which relatively robust fish exceed the average weight at a given length and relatively skinny fish weigh less than average (Williams, 2000). Using the power function ($y = ax^b$), where y is weight (g), x is fork length (cm), and a and b are parameters (Nielsen and Johnson, 1983), length–weight relationships were compared among normal and anomalous pallid and shovelnose specimens, and type-frequencies were compared between the Lower and Middle reaches of the Mississippi River.

Results

Length–weight relationships were compared for anomalous and non-anomalous specimens of each species for which both measurements were recorded. Power regressions were highly correlated ($R^2 > 0.91$) and significant ($P < 0.0001$) among non-anomalous specimens for both pallid ($n = 159$) and shovelnose sturgeon ($n = 1645$). The length–weight relationships for specimens in each of the anomaly categories were compared to the non-anomalous specimens for shovelnose and pallid sturgeon, respectively (Figs 1 and 2). Power regressions among specimens for four anomaly categories ('other' excluded) varied and were more weakly correlated ($R^2 < 0.88$), but were significant ($P < 0.008$) and did not plot outside the distribution of non-anomalous specimens (Figs 3 and 4).

Considering the power function ($W = aL^b$), Nielsen and Johnson (1983) states that $b < 3.0$ represents fish that become less rotund as length increases, and $b > 3.0$ represents fish that become more rotund as length increases. As expected, shovelnose sturgeon with broken tails yielded the greatest deviation ($b = 1.71$) from the non-anomalous model ($b = 3.29$) (Fig. 3). These specimens fell to the left of the model (i.e. length short for their weight) because true fork length could not be measured for fish with no tails. In pallid sturgeon, specimens with injuries from embedded foreign objects ($b = 2.87$) tended to fall to the right of the non-anomalous model ($b = 3.38$), indicating low weight for their length (Fig. 4). This regression, however, was based on four observations, none of which plotted outside the non-anomalous distribution, and was not significant ($P = 0.09$). Pallid sturgeon specimens in the other anomaly categories were too few in number to develop statistically significant models.

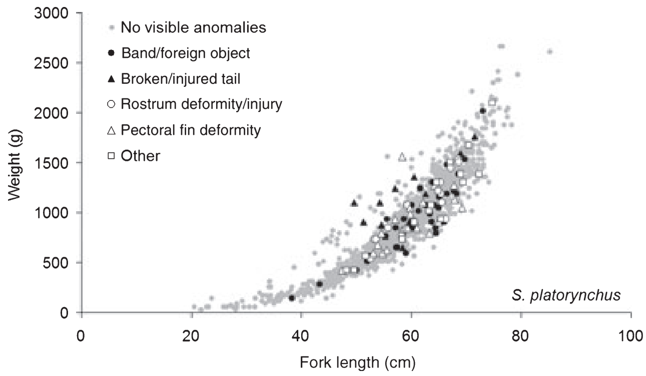

Fig. 1. Length–weight relationships among shovelnose (*Scaphirhynchus platorynchus*) specimens with and without anomalies

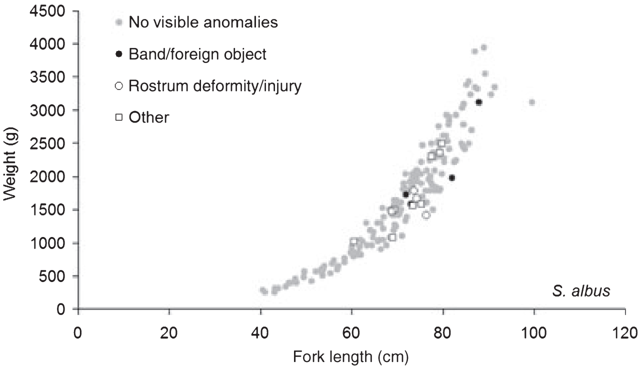

Fig. 2. Length–weight relationships among pallid (*Scaphirhynchus albus*) specimens with and without anomalies

Visible anomalies of shovelnose sturgeon were observed in 5.4% and 3.4% of LMR and MMR individuals, respectively. Visible anomalies were observed in 7.6% and 13.0% of pallid sturgeon specimens from the LMR and MMR, respectively. Distribution of anomalous specimens within the five anomaly categories varied in the Lower and Middle river reaches (Fig. 5). In the LMR, deformities resulting from embedded foreign objects (e.g. rubber bands, oil rings, gaskets, monofilament, gillnetting, and plastic rings) comprised over 29% of the anomalies observed. Embedded objects may have contributed to other types of anterior injury including notch in rostrum, deformed eyes, deformed or missing barbels, damaged dorsal scutes and reduced or deformed pectoral fins. This combined group would comprise the majority of the lower river anomalies. In the MMR, injury to the caudal peduncle, usually a broken tail, accounted for 47% of the anomalies observed. Embedded objects and deformities of the rostrum and pectoral fins were also observed in MMR sturgeon, comprising 19%, 9% and 4% of anomalies, respectively. Anomalies classified as 'other' included abnormal eye-size, bifurcated barbel tips, small (< 2.5 cm) abdominal incision scars presumably from 'egg-checking' by caviar fishermen (William Lancaster, personal communication), missing scutes and other abnormalities whose frequencies were not statistically significant.

Discussion

Sturgeon have a long history of susceptibility to anthropogenic disturbances. They 'exhibit unusual combinations of morphology, habits and life history characteristics, which make them highly vulnerable to impacts from human activities' (Boreman, 1997). Concerns have been raised about habitat loss, fishing mortality and migration interruption (Secor et al., 2002). Considering that sturgeon have been heavily exploited in the West since the early 19th century (Saffron, 2002), conservation has been long overdue. Steps are being taken to better understand the nature of these fish in order to address these issues of larger scope, but other, more subtle pressures exist that, when exerted on an already taxed population, may augment the ill-effects of anthropogenic intrusion.

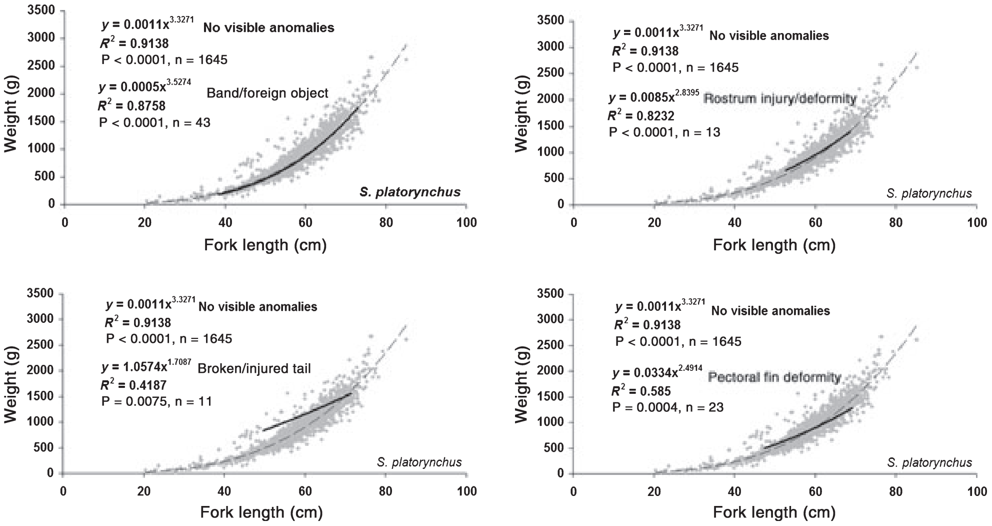

Fig. 3. Power regressions for shovelnose (*Scaphirhynchus platorynchus*) with anomalies (heavy solid lines) vs no anomalies (dashed lines)

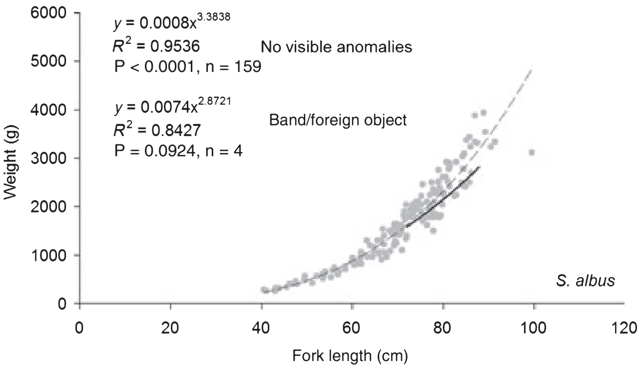

Fig. 4. Power regressions for pallids (*Scaphirhynchus albus*) with anomalies (heavy solid line) versus no anomalies (dashed line)

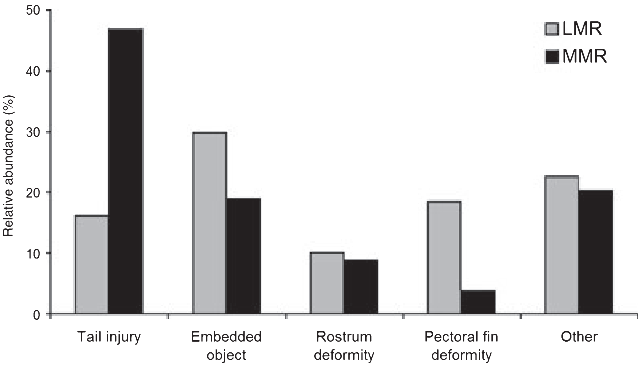

Fig. 5. Relative abundance (% total anomalous specimens) of types of anomalies observed in LMR and MMR sturgeon

Fig. 6. Severely deformed rostrum of shovelnose sturgeon (*Scaphirhynchus platorynchus*) captured in LMR in November 2000 and observed in laboratory flume

Feeding behavior and locomotion were periodically observed in three anomalous shovelnose sturgeon specimens collected from Togo Bendway (Lower Rkm 666) on 29 November 2000 and transported to a Ferguson flume (Baker et al., 1994) at the Engineer Research and Development Center in Vicksburg, MS, USA. Specimen 1 (52.9-cm fork length) had only two barbels on its 'hare-lipped' rostrum, which appeared to have grown proximally around a central cleft, causing invagination of the rostral tissue (Fig. 6). It exhibited swimming behaviors similar to other adult sturgeon kept in the flume and was observed to be more visually oriented (i.e. faster eye movement and quicker response to visual stimuli) than the other two specimens. Specimen 2 (42.3 cm 'total' length) had lost its caudal peduncle posterior to the dorsal and anal fins. Swimming behavior for this specimen was abnormal (i.e. swimming labored, mostly short bursts at a 45° angle, frequently resting on bottom). Specimen 3 (46.0 cm 'total' length) had lost its caudal peduncle posterior to the dorsal and anal fins, but also exhibited spinal kyphosis along the midback anterior to the origin of the dorsal fin. This specimen consequently rested on the bottom of the tank in a tripod fashion, with the two pectoral fins and the anal fin facilitating movement along the bottom. Specimen 3 never began to eat and died after 76 days in captivity. Specimens 1 and 2 began eating bloodworms and shrimp chunks after 109 days in captivity. Interestingly, even with little or no sensory function in the rostrum, Specimen 1 was able to find food just as easily as the specimen with an intact rostrum. One explanation could be that the food was not live and detection, therefore, was purely olfactory.

Foreign objects found on fish have piqued ichthyologic interests since the early 20th century (Gudger and Hoffmann, 1931). The commonness of rubber bands on sturgeon was documented in 1997 in the Lower Mississippi River, St Lawrence estuary, Kennebec River and Atchafalaya Basin (Mississippi Interstate Cooperative Resource Association (MICRA), 1997). 'Banding' may occur when sturgeon, especially those < 130-cm long (Mississippi Interstate Cooperative Resource Association (MICRA), 1997; this study) swim into the semi-buoyant rubber band, gasket or ring while searching for food along the river bottom. The possibility exists that the band may be a crude 'tag' placed deliberately by fisherman (Mississippi Interstate Cooperative Resource Association (MICRA), 1997), but the variety of materials and locations along the anterior portion of the body suggest auto-entrapment. There is no question, however, that banding causes severe damage and morphological deformity (Fig. 7) as the fish outgrows its 'collar'. Depending on the placement of the embedded object, damage ranges from 'notching' of the rostrum and loss of barbels to broken dorsal scutes and possibly deformed pectoral fins. Because of the widespread occurrence and disfiguring results of this type of anomaly, it has the potential to cause significant mortality in the species (Mississippi Interstate Cooperative Resource Association (MICRA), 1997). This study, however, demonstrates that length–weight relationships did not significantly differ between anomalous and non-anomalous sturgeon specimens. Mortality, therefore, probably would not be associated with wasting.

Not well-documented but equally significant is the prevalence of injuries to the caudal peduncle in *Scaphirhynchus* spp. Sturgeon in this genus have a long, slender and precariously brittle peduncle compared to the thick, muscular peduncle of those in the genus *Acipenser*, such as the lake sturgeon (*Acipenser fulvescens*), which is also found in the Mississippi River. Shovelnose and pallid sturgeon, therefore, may be morphologically predisposed to this type of injury, which comprised nearly half of the physical anomalies (or one in every 56 shovelnose) observed in the MMR. Possible causes of peduncle injury are not clear. Although this anomaly was observed throughout the LMR and MMR, it was most frequent (1.1% of shovelnose) below the Chain of Rocks low water dam 27 (Upper Rkm 306). Sturgeon tend to congregate below this natural barrier and broken tails may be the result of contact injury with other sturgeon, injury from large benthic predators such as blue catfish (*Ictalurus furcatus*) or contact injury from foreign objects. Although fish with no tail appear capable of maneuvering for mundane activities such as feeding and changing position in the water column (previously mentioned laboratory observations), it is unknown whether they can perform short-term survival maneuvers such as evading predators or long-term maneuvers such as spawning migration. Recapture data from anomalous tagged fish could provide clues to some of these questions.

Fig. 7. Embedded rubber band and associated tissue damage to rostrum of shovelnose sturgeon (*Scaphirhynchus platorynchus*)

This study is only a cursory examination of the prevalence and effects of morphological anomalies in shovelnose and pallid sturgeon populations of the Mississippi River. The length–weight comparisons between anomalous and non-anomalous fish herein reveal the tenacity of individuals, but also elucidate an alarming statistic. Nearly one in every 20 sturgeon exhibits signs of physical trauma. This study literally only scratches the surface of the effects of this type of distress on individual sturgeon and does not provide any clues as to the long-term effects on spawning potential or immune response. The anomalous specimens brought to the laboratory demonstrated that severely deformed fish are able to maneuver and find food, but may be more sensitive to stress. A study of spawning potential, stress hormone levels or susceptibility to disease in *Scaphirhynchus* specimens with morphological anomalies may reveal more long-term effects in both individuals and populations.

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References

Baker, J. A.; Killgore, K. J.; Foster, S., 1994: Population variation in spawning current speed selection in the blacktail shiner (*Cyprinella venusta*). Env. Biol. Fish. **134,** 28–36.

Bemis, W. E.; Findeis, E. K.; Grande, L., 1997: An overview of Acipenseriformes. Env. Biol. Fish. **48,** 25–71.

Boreman, J., 1997: Sensitivity of North American sturgeons and paddlefish to fishing mortality. Env. Biol. Fish. **48,** 399–405.

Carlander, K. D., 1969: Handbook of freshwater fishery biology, Vol. 1. Iowa State University Press, Ames, IO, USA, 752 pp.

Gudger, E. W.; Hoffmann, W. H., 1931: A shark encircled with a rubber automobile tire. Sci. Monthly **46,** 281–285.

Herzog, D. P.; Barko, V. A.; Scheibe, J. S.; Hrabik, R. A.; Ostendorf, D. E., 2005: Efficacy of a benthic trawl for sampling small-bodied fishes in large river systems. North Am. J. Fish. Manage. **25,** 594–603.

Mississippi Interstate Cooperative Resource Association (MICRA), 1997: Sturgeon and rubber bands. River Crossings **6,** 3.

Nielsen, L. A.; Johnson, D. L., 1983: Fisheries techniques. Am. Fish. Soc. Publ., Bethesda, MD, USA, 468 pp.

Saffron, I., 2002: Caviar: the strange history and uncertain future of the world's most coveted delicacy. Broadway Books, New York, 270 pp.

Secor, D. H.; Anders, P. J.; Van Winkle, W.; Dixon, D. A., 2002: Can we study sturgeons to extinction? What we do and don't know about the conservation of North American sturgeons. Am. Fish. Soc. Symp. **28,** 3–10**.**

Williams, J. E., 2000: The coefficient of condition of fish. In: Manual of fisheries survey methods II: With periodic updates. J. C. Schneider (Ed.) Michigan Dept. Nat. Res., Fisheries Special Report 25, Ann Arbor, MI, USA.

Author's address: Catherine E. Murphy, United States Army Corps of Engineers, Engineer Research and Development Center, 3909 Halls Ferry Road, EE-A, Vicksburg, MS 39180, USA.
E-mail: cmurphy@jayacorp.com

CHAPTER 10: DIETS

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Diet of shovelnose sturgeon and pallid sturgeon in the free-flowing Mississippi River

By J. J. Hoover, S. G. George and K. J. Killgore

United States Army Engineer Research and Development Center, Vicksburg, MS, USA

Summary

Gut contents of shovelnose and pallid sturgeon from the lower and middle Mississippi River were obtained by colonic flushing, a safe and easily implemented alternative to gastric lavage. Diets of both species were dominated numerically by immature Trichoptera, Ephemeroptera, and Diptera. Primary prey, based on volume, for shovelnose sturgeon were Trichoptera, and for pallid sturgeon were various fishes. Geographic and seasonal nuances in diet were observed for both species, but the general dichotomy of shovelnose sturgeon as browser on invertebrates and pallid sturgeon as predator on fishes did not change. Data indicate that both species require hard substrates for feeding. Data demonstrate that colonic flushing is an effective technique for describing diet and inferring ecological and behavioral information about sturgeon.

Introduction

Data on the diet of the commercially harvested shovelnose sturgeon (*Scaphirhynchus platorynchus*) and the endangered pallid sturgeon (*S. albus*) can provide useful information on habitat (e.g., substrates for foraging) and for ecological models (e.g., bioenergetics). Morphological similarity of the two species [Murphy et al., (in press)], local management of shovelnose sturgeon, and federal protection of pallid sturgeon, however, preclude traditional 'destructive' sampling to obtain gut contents for comparative studies. Non-destructive techniques, notably stomach flushing or gastric lavage, have been used previously on ganoid fishes, but with mixed outcomes. Thus, questions exist about the safety of gastric lavage on species such as pallid sturgeon and its utility for biologists.

Field studies using gastric lavage on bowfin gave good representation of gut contents, but large food particles sometimes became lodged in the esophagus (Ashley and Rachels, 1999). This risk would be shared by river sturgeons feeding on large crustaceans and fishes. High mortality in sturgeon (i.e., 33%) subjected to gastric lavage has been reported and attributed to internal injury (Sprague et al., 1993). Ruptured swim bladders and bleeding from the vent have been observed. Use of anesthesia, and small flexible lavage tubing provided better results for the fish but handling time increased to 20 min and water volumes required for sample recovery were variable (Haley, 1998). In addition, gut contents were not obtained from as many as 20% of fish examined in some field studies (Haley, 1998; Brooking et al., 2000). In experiments with captive sturgeon, gastric lavage, even when properly performed, resulted in long-term effects, such as weight reductions (Brosse et al., 2002). Field studies of shovelnose sturgeon and pallid sturgeon in the Missouri River employed gastric lavage but no stomach contents were obtained from 26% of the shovelnose sturgeon and 30% of the pallid sturgeon (Gerrity, 2005). Gastric lavage, in general, requires researchers to exercise high levels of effort, subjects fish to potentially significant stress and injury, and fails to produce a usable sample 20–30% of the time.

An alternative to gastric lavage is colonic flushing (i.e., the use of enemas). Instead of introducing water through the mouth and into the stomach to obtain recently eaten food, water is introduced through the anus and into the lower intestinal tract to obtain feces. This procedure reduces or eliminates risk of injuring or infusing the swim bladder and of dislodging large particles of undigested food. It is also a more 'natural' technique, inducing a frequent and gentle physiological function (i.e., defecation) rather than an infrequent and stressful function (i.e., regurgitation). Colonic flushing has not been widely practiced however, and the recovery of a sample of sufficient quality and quantity from sturgeon has not been demonstrated. Herein we report on the use of colonic flushing in field studies of shovelnose and pallid sturgeon in the lower Mississippi River (LMR) and middle Mississippi River (MMR) to describe interspecific, geographic, and seasonal differences in food habits and to infer ecological differences between the two species.

Materials and methods

Fish were obtained during 'spring' (Mar–May) and 'winter' (Dec–Feb) surveys of pallid sturgeon during the period 2002–2005 [Killgore et al., (in press)]. Fish were collected primarily by trotline; some specimens were collected in gillnets. Collections were made in the LMR from Rivermile 155 (St James, LA) to Rivermile 855 (Caruthersville, MO), in the MMR from Rivermile 1 (Cairo, IL) to Rivermile 190 (Granite City, IL). The downstream boundary of the MMR occurs at the confluence of the Mississippi River with the Ohio River and is designated as Rivermile 0. It corresponds to Rivermile 954 when reaches of the MMR are numbered sequentially from the LMR.

Identifications of river sturgeon were made in the field based on a suite of qualitative characters: position and length of barbels, development of barbel filaments, oral lobe papillae, and ventral squamation (Forbes and Richardson, 1905; Bailey and Cross, 1954). Identifications were subsequently confirmed from detailed morphometric analyses [Murphy et al., (in press)]. Fork length of fish was measured to the nearest mm using a measuring board, and weight to the nearest ounce using a top-loaded scale. Beginning in autumn 2004, all fish were scanned for coded wire tags to determine whether or not they were hatchery-reared fish.

Principal effort was made to obtain samples from pallid sturgeon since only that species is rare and federally endangered and since dietary data are available for only a few specimens (e.g., Carlson et al., 1985). Gut contents of pallid sturgeon were taken whenever field conditions and logistic constraints permitted. Samples from shovelnose sturgeon were also taken if they were obtained on the same trotline or gillnet as a pallid sturgeon.

The colonic flushing apparatus consists of a 500 ml screw top wash bottle (Nalgene) fitted with a 41 cm, 3.3 mm urethral catheter commonly used in verterinary medicine (# 701017, Kendall Company, Mansfield, MA). The catheter is soft and flexible and includes features which make it especially useful for colonic flushing: funnel shaped end (for easy attachment to wash bottle), two 'eyes' (for increased dispersal of water and reduced pressure of an individual jet), and a rounded, closed tip (to minimize likelihood of gut puncture). The bottle is filled with river water and the end gently inserted 30–50 mm through the anus and into the colon. The bottle is gently squeezed in short pulses, and feces expelled into a dissecting pan. The colon is flushed until the expelled water is clear. All materials (solid feces, flushed liquid) is poured into a 500 ml sample jar and preserved in 5% formalin. The technique requires <1 min, typically 15–30 s.

Samples were identified by date, locality (rivermile), and size and weight of fish. Size and weight of fish (converted to grams) were later used to quantify robustness of individual fish, or condition (Carlander, 1969). Condition was calculated as:

$$K_{FL} = \frac{W(10^5)}{FL^3}$$

in which W = weight in grams and FL = fork length in mm.

In the laboratory, supernatant from the samples was decanted and the sample poured into a graduated cylinder 100 ml or smaller (size depending on volume of sample). It was allowed to settle for a minimum of 1 h, or until all remaining supernatant was clear of suspended particles. Solid volume was recorded to the nearest 0.1–0.5 ml. Samples were then stained with Rose Bengal and poured into a white enamel pan. All solid components were picked, sorted, classified, and enumerated. Plant materials and minerals were identified to the lowest distinguishable category, animals to the lowest practical taxon (e.g., order, family). Sometimes whole animals were obtained, facilitating identification, but more often prey were represented by fragments, necessitating identification from isolated body parts. Ephemeroptera (mayfly) nymphs were identified from legs, mandibular structures, and segments of caudal cerci. Trichoptera (caddisfly) larvae were identified from head capsules, sclerites, and legs. Diptera (fly) larvae were identified from head capsules. Fishes were identified from bones: jaws, pharyngeal teeth, gill arches and vertebrae.

Whole organisms were counted, and fragments sorted according to taxon. Number of individuals represented by fragments of a given taxon was determined by counting all parts (e.g., head capsules, legs, sclerites), dividing total number of each part by the number of parts/prey (e.g., 1 for head capsule, 6 for legs, 3 for sclerites), and recording the highest value obtained. Because whole plants were not consumed and because it was impossible to know how many plant fibers, seeds, or sand grains were ingested as a 'unit', plant and mineral components were assigned a count of '1' for any sample in which they occurred. This may underestimate relative percentages of gut contents, but since these materials are presumed non-nutritive, they should not be assigned high dietary value. Remaining unconsolidated material was examined under 10–40× magnification and the process of identification and enumeration repeated. Processing time varied depending on food volume and number of prey obtained; time ranged from 1 to 8 h per sample, with 4 h being typical.

Differences among sample variables (i.e., size and condition of fish, solid volume and number of prey in sample) were described using means and standard deviations (SAS, 1987). Because of special concern for stocked fish, sample variables for hatchery-reared pallid sturgeon were compared to those for the general population of pallid sturgeon in the middle Mississippi River using independent group *t*-tests.

Diets were described using simple frequency based analyses of separate prey taxa among samples (SAS, 1987). Because pallid sturgeon fed on prey ranging in size over multiple orders of magnitude and in numbers ranging over multiplicative factors, numerical descriptors alone were inadequate to represent relative importance of different prey. Prey numbers, therefore, were converted to approximate prey volume (mm^3) by multiplying number times a representative value of volume for that prey. Because prey size can not yet be determined empirically from artifacts in feces, representative prey sizes were determined from standard references on invertebrate size (e.g., Pennak, 1978) and from sizes of fish in trawls (unpublished data).

Size of invertebrates was converted to volume using appropriate formula for geometric figures most closely approximating shape of the organism (e.g., ellipsoids for adult beetles, right circular cylinders for some minnows). For invertebrates, values ranged from <100 mm^3 for small taxa (e.g., Hydropsychidae, Chironomidae), 200–1000 mm^3 for medium size taxa (e.g., Ephemeroptera, most Coleoptera, terrestrial insects), to >2500 mm^3 for large taxa (e.g., Mollusca, Decapoda). Volumetric values for fish prey were determined by measuring water displacement of fish in a graduated cylinder. Values ranged from <1000 mm^3 for speckled chub (*Macrhybopsis aestivalis*), 3000–5000 mm^3 for larger minnows, and 10 000–20 000 mm^3 for other fishes. Volume of plant parts was arbitrarily designated as 1000 mm^3, comparable to a single medium-sized invertebrate. This value was compatible with observer estimates of plant volumes (minimal in all samples) and would be expected from incidental ingestion of invertebrate tubes and cases or occasional loose particles of vegetation. Values of '0' were assigned to mineral components since they were presumed non-nutritive. Volumetric data were expressed as percentages of total calculated volume of ingested material.

Relationships between locality (in rivermiles) of individual fish (i.e., one independent variable) and size of sturgeon, as fork length and condition, and sample material, as volume and prey number (i.e., four dependent variables) were described using Pearson product moment correlation analysis (SAS, 1987). This provided a correlation coefficient, *r*, and probability of error, p. To reduce likelihood of spurious correlations (i.e., those occurring by chance alone) occurring in a large number of simultaneous comparisons, a sequential Bonferroni adjustment was applied to each P-value (Rice, 1989). This adjustment compensated for the number of simultaneous tests within each group of comparisons (i.e., each species of sturgeon). Compared with the 'individual significance method', the 'simultaneous inference method' reduces number of significant correlations among variables, is considered more conservative and more powerful. We selected an overall significance level of $\alpha = 0.05$. Significance level for individual correlations was calculated as $\alpha/(1 + k–i)$, in which k = number of tests and i = rank of each P-value within

Table 1
Characteristics of samples and fish used in diet study. Values are means (and standard deviation) for the lower (LMR) and middle Mississippi River (MMR)

	Shovelnose sturgeon		Pallid sturgeon		Hatchery pallid sturgeon
	LMR	MMR	LMR	MMR	MMR
Number of samples	22	23	31	39	7
Volume of sample, ml	9.6 (10.1)	2.7 (3.6)	12.6 (10.1)	3.5 (5.5)	6.6 (7.9)
Number of prey	46.8 (68.5)	15.2 (23.4)	30.1 (37.2)	9.0 (11.0)	18.7 (22.1)
Fork length of fish, mm	631 (78.1)	668 (67.0)	673 (86)	767 (84)	738 (125.4)
Condition of fish, K_{FL}	0.44 (0.05)	0.42 (0.07)	0.43 (0.05)	0.42 (0.07)	0.40 (0.05)

the group of tests. A group of tests was defined as all correlations calculated for each species. For any correlation coefficient, if $p_i < \alpha/(1 + k-i)$, that value was considered significant.

Results

Samples were taken from 122 fish: 45 shovelnose sturgeon and 77 pallid sturgeon (Table 1). Seven specimens of pallid sturgeon from the MMR carried coded wire tags indicating that they were hatchery-reared sturgeon. Data from these fish were analyzed separately. Sturgeon from all populations were comparable in size, but mean sizes of individuals of both species in the LMR were slightly smaller than those in the MMR. Coefficient of condition was comparable among groups.

'Empty' samples obtained by colonic flushing were infrequent and were not associated with characteristics of the fish (i.e., species, size) or collection (i.e., location, season). Only 11 samples (9%) contained no identifiable prey. The majority of the empty samples (i.e., seven of the 11 with no identifiable prey) contained very small quantities of solid material (<0.5 ml) and none were represented by more than 1.5 ml of solid material. Empty samples were obtained from shovelnose sturgeon (4 fish) and pallid sturgeon (7 fish), from fish in the LMR (3 fish) and MMR (8 fish), and during spring (6 fish) and winter (5 fish). Shovelnose sturgeon with no identifiable prey ranged in size from 541 to 691 mm FL, pallid sturgeon from 568 to 870 mm FL. The lack of identifiable material and low sample volume suggested that those fish probably defecated just prior to sampling.

Mean sample volumes ranged from 2.7 to 12.6 ml of solid material (Table 1). Maximum sample volume was 43 ml of solid material. Mean prey number ranged from 9 to 47 prey/fish. Maximum prey number was 241 prey/fish. Sample volume and number of prey were significantly higher for both species in the LMR than in the MMR ($P < 0.05$). In the MMR, samples obtained from hatchery-reared pallid sturgeon were similar to those from the general population. There were no significant differences in sample volume ($t = 1.32$, $P = 0.166$), number of prey ($t = 1.13$, $P = 0.297$), fork length of fish ($t = -0.80$. $P = 0.430$), or condition of fish ($t = -0.66$, $P = 0.514$).

Diets were comprised of more than 30 taxa of organisms including mollusks, crustaceans, aquatic insects, and fishes (Table 2). Aquatic insects were diverse (7 orders, >12 families) but were dominated numerically by three aquatic insect taxa that were abundant in all groups of samples. Larval Hydropsychidae (common netspinner caddisflies) were the primary prey (5.1–24.4 individuals/sample) in all groups of sturgeon. Nymphs of Ephemeridae (burrowing mayflies) were found in lower numbers (0.4–8.4 individuals/sample). Larval Chironomidae (midges) were third in abundance (0.3–4.8 individuals/sample). Fish were frequently encountered in the diet of pallid sturgeon (0.5–2.3 individuals/sample) and were comprised of at least three families: Cyprinidae (minnows), Sciaenidae (freshwater drum), and Clupeidae (shad). They were often not identifiable to lower species because they were represented only by scales, vertebrae, and/or lenses. Of the identifiable remains, many were *Macrhybopsis* (chubs), including *M. aestivalis* (speckled chub) and *M. storeriana* (silver chub). Other prey were infrequent in occurrence. Although number of sturgeon sampled were comparable in the LMR and MMR, diversity of prey was substantially higher in the LMR with more than 10 additional taxa recorded than for MMR counterparts. This was probably an artifact of the greater sample volume (and prey number) obtained from LMR fish.

In terms of food volume, shovelnose sturgeon were benthic or drift-feeding invertivores and pallid sturgeon were piscivores (Table 2). Hydropsychidae, Ephemeridae, and Chironomidae collectively comprised 66% of the diet of shovelnose sturgeon and only 11–16% of pallid sturgeon. Fish were not eaten by shovelnose sturgeon and comprised 60–74% of the diet of pallid sturgeon. River prawn (*Macrobrachium ohione*) was rarely eaten by either species, but due to its large size, comprised 7–14% of the diet by volume for all groups of sturgeon except shovelnose sturgeon in the MMR which did not feed on the crustacean.

Despite interspecific and geographic variation in diet composition, both sturgeon species within each river segment, showed similar seasonal responses (Table 3). Shovelnose sturgeon and pallid sturgeon in the LMR both showed greater feeding on Trichoptera and Ephemeroptera in the winter than in the spring, but in the MMR showed reduced feeding on those same taxa. Both species in the LMR fed on a greater diversity of prey in the winter than in the spring. For pallid sturgeon, fish were the volumetrically dominant component of the diet ($>52\%$) in both populations and during both seasons. Because of the low sample size, seasonal variation in hatchery reared pallid sturgeon was not quantified.

Only two of the correlations between locality (rivermile) and fish characteristics were statistically significant (shovelnose sturgeon fork length in the LMR in spring, pallid sturgeon condition in the MMR in spring), but pattern of coefficients (including non-significant values) suggest seasonal trends in fish movements that may be associated with feeding (Table 4). Both shovelnose sturgeon and pallid sturgeon sampled in the spring were larger and more robust in the upper reaches of the LMR ($r > 0.60$, $P < 0.04$), and more robust in the lower reaches of the MMR ($r = -0.55$, $P = 0.08$). No such trend was apparent for winter samples. There were no significant correlations between locality and sample characteristics, but there was a trend for shovelnose sturgeon from the lower reaches of the MMR to contain greater quantities of food than fish from the upper reaches ($r < -0.60$, $P < 0.07$).

Table 2
Diets of Mississippi River sturgeon: mean number of prey (and percentage of total food volume). A 'T' indicates trace quantities (mean numbers < 0.1 individuals/sample and volume < 0.1%)

	Shovelnose sturgeon		Pallid sturgeon		Hatchery pallid sturgeon
	LMR	MMR	LMR	MMR	MMR
Nematoda	0.1 [T]		T [T]	T [T]	1.4 [T]
Dresseina	T [2.2]	T [7.9]		T [2.6]	
Corbicula	T [2.2]				
Copepoda	T [T]				
Cladocera			T [T]		0.1 [T]
Isopoda			0.1 [T]	T [T]	
Amphipoda	2.8 [4.5]		1.0 [0.7]		
Decapoda (*Macrobrachium ohione*)	0.1 [11.5]		0.3 [14.4]	T [7.0]	0.1 [10.5]
Ephemeridae (*Hexagenia* sp.)	8.4 [30.2]	0.4 [5.4]	4.1 [6.4]	1.1 [4.2]	1.0 [2.1]
Ephemeroptera (unknown)		T [0.6]	T [T]	T [0.1]	
Anisoptera			0.2 [1.0]		
Odonata (unknown)	T [0.6]			T [0.8]	0.1 [1.2]
Hemiptera (Corixidae)	0.1 [0.4]		0.1 [0.2]		
Haliplidae	0.1 [0.1]		T [T]		
Dytiscidae	0.1 [1.2]		0.2 [0.6]		
Coleoptera (unknown)	0.2 [1.9]	0.5 [16.9]	0.3 [1.0]	T [0.7]	0.4 [2.1]
Hydropyschidae	24.4 [33.1]	11.6 [59.8]	14.7 [8.8]	5.1 [7.4]	12 [9.5]
Trichoptera (unknown)			0.2 [0.1]		0.1 [0.1]
Lepidoptera			T [0.2]		
Chironomidae	4.8 [2.8]	0.6 [1.3]	4.0 [1.0]	0.7 [0.4]	0.3 [0.1]
Ceratopogonidae	2.3 [1.3]	0.2 [0.4]	1.2 [0.3]	0.1 [T]	0.1 [T]
Culicidae (*Chaoborous*)	T		0.1 [T]		
Simuliidae	2.7 [1.6]				
Stratiomyidae	T		T [T]		
Diptera (unknown)		0.2 [0.7]	0.2 [0.1]	0.6 [T]	
Arthropoda (terrestrial)	0.3 [7.3]		0.5 [3.4]		
Clupeidae (unknown)			0.1 [5.8]		
Macrhybopsis aestivalis			0.2 [1.3]	0.1 [1.7]	0.7 [6.3]
Macrhybopsis storeriana			0.1 [7.2]	T [1.4]	0.6 [16.9]
Cyprinidae (unknown)			0.1 [1.4]	T [2.8]	0.3 [8.5]
Non-perciform			0.2 [6.0]	0.3 [23.5]	
Aplodinotus grunniens			T [4.2]	T [8.1]	
Perciform (unknown)			0.1 [7.2]		0.1 [14.1]
Fish (unknown)			0.7 [26.5]	0.2 [35.3]	0.6 [28.2]
Vegetation (seeds, wood)	0.4 [0.8]	1.1 [7.0]	0.6 [0.4]	0.2 [0.4]	0.2 [0.3]
Coal			T		
Sand	0.5	0.6	0.3	0.5	0.3
Gravel				T	
Total number prey	46.8	15.2	30.1	9.0	18.7

Discussion

Colonic flushing was an effective technique for sampling diets of sturgeon. We observed no complications during and immediately after processing. All recovered quickly from handling and showed no signs of distress. Sample recovery by colonic flushing in 91% of fish (both species) is higher than reported values for gastric lavage in 74% of shovelnose sturgeon and 70% of pallid sturgeon (Gerrity, 2005). Shortcomings of colonic flushing include increased processing time, taxonomic uncertainty, and the difficulty of reconstructing relative importance of prey for individual fish (e.g., volumetrically, gravimetrically) due to the advanced state of digestion.

Difficulties associated with colonic flushing can be addressed by a taphonomic approach to prey identification. Forensic scientists and archaeologists are often required to identify and estimate the sizes of animals from a few, randomly preserved bone fragments (e.g., Olsen, 1968; Paloumpis, 1989). Some ichthyologists have used a similar approach to diet reconstruction by estimating mass of individual prey using preditive models and measurements of digestion-resistant structures, such as head capsules (e.g., Rakocinski, 1991; Wilkins, 1992). To allow us to identify fishes more precisely, and estimate their volumetric or caloric contribution to the diet of pallid sturgeon, we are now skeletonizing fishes of ingestible size (< 200 mm TL) collected with pallid sturgeon. Fishes are fileted in the field, bottled in river water, and allowed to decompose. Disarticulated skeletons are extracted and retained for comparisons with fish parts removed from sturgeon guts. When series for both collections are sufficiently large, it should be possible to identify fishes, determine sizes, and estimate their relative value to the nutrition of pallid sturgeon more precisely.

Hatchery-reared pallid sturgeon in the MMR were comparable to the general population in size and condition (Table 1) and in diet (Table 2). Both groups of fish ate comparable quantities (i.e., relative volumes) of fish (74 vs 73%) Trichoptera (12 vs 8%), Decapoda (10 vs 7%), and Ephemeroptera (2 vs 4%). Based on sizes and ages of the fish collected, they are most likely individuals stocked in 1994 and 1997 (Krentz et al., 2005). Similarities between hatchery-reared and general population pallid sturgeon may reflect comparable behavior and physiology of the two groups. It may also indicate simple food availability. The majority of pallid sturgeon from the MMR, and all of the hatchery-reared pallid sturgeon, were collected at a single site: Chain of Rocks, near Granite City, Illinois. Similarities may also be an indication that a substantial portion of the pallid sturgeon population consists of hatchery-reared fish. We did not begin scanning for coded wire tags until late in the study and fish captured earlier would have gone undetected and classified as part of the general population.

Table 3
Seasonal variation in diets of pallid sturgeon in the Mississippi River. Numbers are percentage of total food volume

	Shovelnose sturgeon				Pallid sturgeon			
	LMR		MMR		LMR		MMR	
	Spring	Winter	Spring	Winter	Spring	Winter	Spring	Winter
Mollusca		5.2		15.0			3.1	
Crustacea	38.4	11.6			12.2	16.4	8.3	
Ephemeroptera	19.8	32.3	8.9	3.4		7.4	5.0	
Odonata		0.8			4.4	1.5	0.9	
Hemiptera		0.5				0.3		
Trichoptera	23.9	35.0	66.5	53.9	3.0	11.5	8.0	4.1
Coleoptera	2.3	3.3	11.9	21.2	0.8	1.9	0.8	
Lepidoptera						0.3		
Diptera	7.5	5.5	3.7	1.2	0.6	1.9	0.6	0.3
Terrestrial invertebrates	4.7	5.5			1.6	5.8	3.8	
Total invertebrates	96.6	99.7	91.0	94.7	22.6	47.0	30.5	4.4
Clupeidae						8.3		
Macrhybopsis spp.						12.2	1.0	15.4
Cyprinidae (other and unknown)					2.4	1.0	3.3	
Fish (other and unknown)					74.6	31.0	64.6	80.2
Total fish	0.0	0.0	0.0	0.0	77.0	52.5	68.9	95.6
Vegetation	3.3	0.3	9.0	5.3	0.2	0.5	0.4	0.0

Table 4
Correlation analysis for locality of sturgeon samples (rivermile) and characteristics of sturgeon (fork length, condition of individual fish) and of sample material (solid volume, total number of prey in individual sample). Values are Pearson correlation coefficients, *r* (with associated probability values, P). Significance (*) was determined by assuming a group-wise $\alpha < 0.05$ and performing a sequential Bonferroni adjustment on individual P-values (Rice, 1989)

	Shovelnose sturgeon				Pallid sturgeon			
	LMR		MMR		LMR		MMR	
Variable	Spring	Winter	Spring	Winter	Spring	Winter	Spring	Winter
Fork length	+0.97*(<0.0001)	+0.07 (0.823)	−0.08 (0.77)	−0.47 (0.201)	+0.70 (0.016)	+0.04 (0.867)	−0.28 (0.133)	0.46 (0.256)
Condition	+0.70 (0.025)	−0.12 (0.706)	−0.60 (0.07)	+0.24 (0.526)	+0.64 (0.035)	−0.11 (0.651)	−0.57* (0.0008)	−0.62 (0.097)
Volume	+0.38 (0.312)	+0.16 (0.611)	−0.28 (0.33)	−0.73 (0.027)	+0.32 (0.334)	+0.18 (0.442)	−0.15 (0.403)	−0.53 (0.175)
Total Prey	+0.57 (0.088)	+0.20 (0.53)	−0.29 (0.316)	−0.64 (0.064)	+0.43 (0.190)	+0.20 (0.40)	0.10 (0.575)	−0.30 (0.475)

After scanning became a regular part of our field protocol, we collected 15 pallid sturgeon, seven of which were hatchery-reared. This suggests that nearly half of the fish at this location could be stocked.

Data obtained for these specimens were similar to those previously published for populations in lower and upper reaches of the Missouri River (Carlson et al., 1985; Gerrity, 2005). In those studies, shovelnose sturgeon and pallid sturgeon both fed on aquatic insects and pallid sturgeon alone fed on fish. For shovelnose sturgeon, Trichoptera were volumetrically dominant in the lower river, and Diptera were gravimetrically dominant in the upper river. For pallid sturgeon in both populations, fish were volumetrically and/or gravimetrically the primary food. Our data confirm the importance of Trichoptera to shovelnose sturgeon, and minnows and other fishes to pallid sturgeon (Table 2). High frequencies and/or volumes of certain invertebrate taxa indicate the importance of substrates that are soft (e.g., *Hexagenia* sp., *Macrobrachium ohione*), hard (e.g., Hydropsychidae), and diverse (e.g., Chironomidae) as feeding grounds by both species of sturgeon.

Numerical preponderance of Trichoptera in the diets of both sturgeon, however, suggest that hard surfaces are critical feeding habitat in the Mississippi River. This habitat may be provided by naturally occurring gravel deposits or by man-made surfaces such as stone dikes (e.g., Payne and Miller, 1996). Such substrates may be used as feeding surfaces by shovelnose sturgeon and by pallid sturgeon. They may also be important to pallid sturgeon as feeding grounds and cover for prey. Shad, silver chub, and freshwater drum, on which pallid sturgeon feed, are all common to abundant on revetted banks of the Mississippi River (Baker et al., 1991).

Our data also show that shovelnose sturgeon and pallid sturgeon exhibit comparable geographic (Table 2) and seasonal (Table 3) variation in the amounts eaten of certain prey, notably Trichoptera and Ephemeroptera. In addition, there may be similar patterns in long-range movements – such as spring migrations of larger, more robust fish to the upper LMR and lower MMR, possibly for spawning but also to feed (Table 4). Gross interspecific differences in diet, however, indicate overriding differences in feeding behavior – shovelnose sturgeon are benthic or drift-feeding browsers and pallid sturgeon are piscivores. This fundamental difference in their biology suggests that effective conservation of both species will require separate management strategies.

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References

Ashley, K. W.; Rachels, R. T., 1999: Food habits of bowfin in the Black and Lumber Rivers, North Carolina. Proc. Ann. Conf. Southeast. Assoc. Fish and Wildl. Agencies **53,** 50–60.

Bailey, R. M.; Cross, F. B., 1954: River sturgeons of the American genus *Scaphirhynchus*. Characters, distribution, and synonymy. Pap. Mich. Acad. Sci. Arts Lett. **39,** 169–208.

Baker, J. A.; Killgore, K. J.; Kasul, R. L., 1991: Aquatic habitats and fish communities of the lower Mississippi River. Rev. Aquatic Sci. **3,** 313–356.

Brooking, T. E.; VanDeValk, A. J.; Rudstam, L. G., 2000: Growth, habitat use, and diet of re-introduced lake sturgeon in Oneida Lake, New York. [Abstract]. In: Update on Lake Sturgeon in New York State Waters, Abstracts and Meeting Summary. T. E. Brooking (Ed.). Cornell University, Bridgeport, NY, USA, 17 pp.

Brosse, L.; Dumont, P.; Lepage, M.; Rochard, E., 2002: Evaluation of a gastric lavage method for sturgeons. N. Am. J. Fish. Manage. **22,** 955–960.

Carlander, K. D., 1969: Handbook of freshwater fishery biology – life history data on freshwater fishes of the United States and Canada, exclusive of the Perciformes, Volume 1. The Iowa State University Press, Ames, Iowa, USA, 752 pp.

Carlson, D. M.; Pflieger, W. L.; Trial, L.; Haverland, P. S., 1985: Distribution, biology, and hybridization of *Scaphirhynchus albus* and *S. platorynchus* in the Missouri and Mississippi Rivers. Env. Biol. Fishes. **14,** 51–59.

Forbes, S. A.; Richardson, R. E., 1905: On a new species of shovelnose sturgeon from the Mississippi River. Bull. Ill. State Lab. Nat. Hist. **7,** 37–44.

Gerrity, P. C., 2005: Habitat use, diet, and growth of hatchery-reared juvenile pallid sturgeon and indigenous shovelnose sturgeon in the Missouri River above Fort Peck Reservoir. MS thesis, Montana State University, Bozeman, MT, USA.

Haley, N., 1998: A gastric lavage technique for characterizing the diets of sturgeons. N. Am. J. Fish. Manage. **18,** 978–981.

Killgore, K. J.; Hoover, J. J.; George, S. G.; Murphy, S. G.; Lewis, B. R.; Lancaster, W. E., 2007: Distribution and abundance of pallid sturgeon in the free-flowing Mississippi River. J. Appl. Ichthyol. **23,** 476–483.

Krentz, S.; Holm, R.; Bollig, H.; Dean, J.; Rhodes, M.; Hendrix, D.; Heidrich, G.; Krise, B., 2005. Pallid sturgeon spawning and stocking summary report: 1992–2004. Unpublished report, U.S. Fish and Wildlife Service, Bismarck, ND, USA, 40 pp.

Murphy, C. E.; Hoover, J. J.; George, S. G.; Killgore, K. J., 2007: Morphometric variation among *Scaphirhynchus* of the midldle and lower Mississippi River. J. Appl. Ichthyol. **23,** 313–323.

Olsen, S. J., 1968: Fish, amphibian, and reptile remains from archaeological sites. Part 1: Southeastern and Southwestern United States. Pap. Peabody Mus. Archaeol. Ethnol. **56,** 1–137.

Paloumpis, A. A., 1989: Osteology of the bowfin *Amia calva* Linnaeus. Occ. Pap. Inst. Fla. Stud. Tampa, FL, USA, 34 pp.

Payne, B. S.; Miller, A. C., 1996: Life history and production of filter-feeding insects on stone dikes in the lower Mississippi River. Hydrobiologia **319,** 93–102.

Pennak, R. W., 1978: Fresh-water invertebrates of the United States, 2nd edn. John Wiley and Sons, New York, NY, USA, 803 pp.

Rakocinski, C. F., 1991: Prey-size relationships and feeding tactics of primitive stream-dwelling darters. Can. J. Fish. Aquat. Sci. **48,** 681–693.

Rice, W. R., 1989: Analyzing tables of statistical tests. Evolution **43,** 223–225.

SAS, 1987: SAS/STAT Guide for personal computers, Version 6 edition. SAS Institute, Inc., Cary, NC, USA, 1028 pp.

Sprague, C. R.; Beckman, L. G.; Duke, S. D., 1993: Prey selection by juvenile white sturgeon in reservoirs of the Columbia River. In: Status and habitat requirements of the white sturgeon populations in the Columbia River downstream from McNary Dam, Vol. 2. Final Report to Bonneville Power Administration. R. C. Beamsderfer, A. A. Nigro (Eds). Oregon Department of Fish and Wildlife, Portland, OR, pp. 229–243.

Wilkins, S. D., 1992: Life history of the least madtom (Ictaluridae: *Noturus hildebrandi*) from Bayou Pierre, MS. MS thesis, The University of Southern Mississippi, Hattiesburg, MS, USA.

Author's address: Jan Jeffrey Hoover, U.S. Army Engineer Research and Development Center, Waterways Experiment Station, Vicksburg, MS 39180-6199, USA.
E-mail: jan.j.hoover@erdc.usace.army.mil

CHAPTER 11: DECLINING RECRUITMENT AND GROWTH

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[Note]

Declining Recruitment and Growth of Shovelnose Sturgeon in the Middle Mississippi River: Implications for Conservation

SARA J. TRIPP, ROBERT E. COLOMBO, AND JAMES E. GARVEY*

Fisheries and Illinois Aquaculture Center, Department of Zoology,
Southern Illinois University, Carbondale, Illinois 62901, USA

Abstract.—To determine how populations of shovelnose sturgeon *Scaphirhynchus platorynchus* are changing and may respond to poor environmental conditions, current commercial harvest of black-egg (sexually mature) females, and incidental mortality of males, we require annual information about sex-specific age structure as it relates to the recruitment of new cohorts. We sampled shovelnose sturgeon by use of gill nets (5-cm bar mesh) monthly during 2002–2006 in the Middle Mississippi River between Cairo, Illinois, and St. Louis, Missouri. We compared patterns of size and age structure over time and projected age structure and population size into the future. Sex ratio in 2005–2006 was 1.14:1.00 (416 males and 363 females; $P = 0.06$), deviating from the 1:1 ratio that occurred in 2002–2003. Annual mortality increased from 37% in 2002–2003 to 44% by 2005–2006. Female shovelnose sturgeon were larger than males. Across years, the population shifted toward longer, older fish, and growth in length declined. Recruitment declined through time (29% per year). If these trends continue and if immigration from nonharvested populations is limited, population density may decline by an order of magnitude within one decade. Under current conditions, resilience to harvest and environmental perturbations is probably limited.

Of the 25 extant sturgeon species, all are characterized by limited adult abundance and most are threatened (Pikitch et al. 2005). The order Acipenseriformes includes some of the most economically valuable freshwater species due to their ability to produce black caviar. The high economic value also leaves these species susceptible to the overharvest of females. Long-lived, late-maturing species are unable to compensate for intense harvest; when overharvest coincides with habitat degradation, the fishery collapses (Billard and Lecointre 2001; Ludwig et al. 2002; Secor et al. 2002). World catch of sturgeon is currently at its lowest level in recent decades (Billard and Lecointre 2001). With the recent collapse of the Caspian Sea fisheries (Birstein 1993; Billard and Lecointre 2001; Pikitch et al. 2005), fishing pressure has shifted toward North American species, such as the shovelnose sturgeon *Scaphirhynchus platorynchus*, which is one of the few sturgeon species in the world that can be legally harvested.

Shovelnose sturgeon may be more resilient to harvest than other sturgeons because they are relatively small and, until recently, were less commercially valuable (Carlander 1954). Shovelnose sturgeon are thought to mature at the relatively early age of 5–7 years (Helms 1974; Farbee 1979), which may enable them to better withstand fishing pressure (Morrow et al. 1998). Although shovelnose sturgeon populations appear to be more stable than their European and Asian counterparts, their distribution and abundance have declined over the last century due to habitat alteration, water pollution, and overharvest (Bailey and Cross 1954; Hurley and Nickum 1984; Keenlyne 1997; Morrow et al. 1998).

Commercial fishing is currently legal in both Missouri and Illinois and occurs in the Middle Mississippi River (MMR), which extends from river kilometer (rkm) 313.8 at St. Louis, Missouri, to rkm 0 at Cairo, Illinois. In 2001, commercial harvest of shovelnose sturgeon flesh in the MMR reached a historical maximum and was increasing exponentially (Colombo et al. 2007a). No harvest data beyond 2001 are yet available from the resource agencies. However, market pressure appears to be increasing, and processed shovelnose sturgeon roe fetched US$900 per pound as of February 2009 (based on an internet search for caviar; www.petrossian.com). By 2000, the MMR population appeared to be responding to harvest and habitat alteration with low population growth and high mortality relative to other sturgeon populations in unharvested reaches of the Mississippi River (Jackson 2004; Killgore et al. 2007). Using data collected from 2002 and 2003, Colombo et al. (2007a) found that adult abundance declined with increased harvest and year-class strength also was negatively related to harvest; both are signs of growth and recruitment overfishing (Colombo et al. 2007a).

Continual monitoring, identification of trends, and forecasting of responses are essential for sound management of fisheries. We quantified age structure of shovelnose sturgeon over a 5-year period and assessed how recruitment and sex ratio were changing through time. We also collected data from a commer-

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* Corresponding author: jgarvey@siu.edu

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cial fisher to estimate sex-specific patterns and rates of harvest. Presence of a stable age structure (i.e., constant numbers of individuals in each cohort during each year) and an unchanging sex ratio despite variable environmental conditions would indicate some resiliency of the population to ongoing commercial harvest and changing environmental conditions. Conversely, changes in age structure, mortality, and sex ratio may interact with harvest and environmental variation to affect population dynamics.

Methods

The MMR extends from the mouth of the Missouri River (rkm 313.8) at St. Louis to the confluence with the Ohio River at Cairo (rkm 0). The MMR is free flowing and unimpounded but is restricted to its channel by wing dikes and revetments used to aid navigation (Pflieger 1997). These channel-training structures reduce natural fluvial processes that once created variable seasonal habitats and provided necessary in-channel and off-channel spawning and nursery habitats for many species (Sheehan and Rasmussen 1999).

During spring 2004, fork lengths (FLs; mm) and sex of shovelnose sturgeon harvested for roe or released by a single commercial fisher were quantified on three trips conducted within our sampling reach (rkm 309–300; Illinois Department of Natural Resources, unpublished data). Harvest rate and the mean and median of fish caught were calculated to compare the commercial harvest data with the length-frequency data from our adult sampling.

We sampled shovelnose sturgeon during 2002–2006, although our sampling protocol differed through time. Standardized, stratified random sampling of shovelnose sturgeon occurred during November–April of 2002–2005; some of these data (2002–2003) are summarized by Colombo et al. (2007a). Stationary, bottom-set gill nets (5.08-cm bar mesh, 45 m long, 3 m deep) were placed at randomly selected sites stratified by habitat type (channel border, wing dike, island tip, and side channel) in the MMR. Given that random sampling was inefficient and size structure did not appear to differ among habitats (Garvey et al. 2006), we sampled monthly during February 2005 through June 2006 at sites where catch rates were high (hereafter, directed sampling). During each month, six nets were set for 24 h on the seam of wing dikes at Modoc (rkm 201–198), Chester (rkm 191–188), and Grand Tower, Illinois (rkm 127–124). Fork length and wet weight (nearest 0.1 g) were quantified for each fish. During all years except 2004, the left pectoral fin ray was removed from each fish and was later used to determine fish age (Jackson et al. 2007). Pectoral fin rays were dried, and three cross sections (0.64, 0.69, and 0.74 mm) were secured to a slide using cyanoacrylate. Cross sections were examined independently by two readers. A pair of opaque (growth) and translucent bands was considered an annulus (Everett et al. 2003; Jackson et al. 2007). When readers disagreed, they examined the cross sections together to reach an agreement. Annual length- and age-frequency distributions were compared across years; mean and mode were calculated for each year.

During each month in 2005–2006, the first 20 shovelnose sturgeon collected at each site were preserved on wet ice and taken back to the laboratory for anatomical determination of sex (not possible from external examination), maturation status (Colombo et al. 2007b), and weight (g wet mass). Means and medians were identified for both sexes. Mean lengths of males and females were compared among years using a one-way analysis of variance (ANOVA). A Kolmogorov–Smirnov (KS) test was used to compare length distributions between sexes. Chi-square analysis was used to determine whether the sex ratio deviated from 1:1. For all tests, the significance level was 0.10.

Growth curves in length for the population and sex-specific growth curves during 2002, 2003, 2005, and 2006 were calculated using von Bertalanffy models in Fishery Analysis and Simulation Tools software (Slipke and Maceina 2000). Differences in sex-specific growth curves were evaluated using the residual sum-of-squares method (Chen et al. 1992).

A catch curve analysis for fish at the declining portion of the log-transformed curve was used to quantify mortality rates for males and females (Ricker 1975). A weighted linear regression of log-transformed data was used to reduce any bias that may have occurred due to reduced relative abundance of older individuals in the population (Slipke and Maceina 2000). The declining slope of this regression equation represented the instantaneous mortality for the population and sex-specific mortality rates. Sex-specific catch curve slopes were tested for homogeneity (test for interaction in analysis of covariance) to determine whether mortality differed among sexes and years.

Adult shovelnose sturgeon appeared to fully recruit to our sampling gear by age 8. We regressed $\log_e$ transformed relative abundance of this age-class against each year to estimate the percent decline in recruitment during 2002–2006 (i.e., from the slope of the linear regression). From this, we used our estimate of annual mortality, the relative proportion of fish in each age-class in 2006, and our estimate of declining recruitment (i.e., percent decline per year) to predict how population age structure might change in the future. In addition, we used a population estimate of adult shovelnose sturgeon in the MMR (160,000 fish; Garvey et al. 2006) to determine how the density of the population might change as recruitment declined, assuming no immigration.

Results

All of the 557 shovelnose sturgeon captured by the commercial fisher in 2004 were checked for eggs; 25% of these fish were harvested for eggs. Fish without black eggs were released. Mean (±SD) size of fish harvested was 653 ± 49 mm FL (median = 654 mm FL).

The mean FL of shovelnose sturgeon differed among years; the FL in 2002 was smaller than those in all other years, and the FL in 2004 was lower than those in 2005–2006 (ANOVA: $F = 10.13$; df = 4, 4,306; $P < 0.0001$). Mean (±SD) FLs were as follows: 587 ± 69 mm in 2002 ($n = 355$; median = 591 mm), 609 ± 70 mm in 2003 ($n = 786$; median = 616 mm), 602 ± 69 mm in 2004 ($n = 1{,}384$; median = 614 mm), 610 ± 64 mm in 2005 ($n = 993$; median = 616 mm), and 612 ± 67 mm during directed sampling in 2005–2006 ($n = 1{,}384$; median = 621 mm). The length-frequency distributions of shovelnose sturgeon collected during 2002–2006 shifted in median and mean FL toward larger fish, and the distribution transformed from normally distributed to negatively skewed and truncated beyond 600 mm.

During 2005 and 2006, 792 shovelnose sturgeon were subsampled to determine sex. The subsample consisted of 415 males, 363 females, and 14 fish that were either intersexual or unidentifiable. This male : female sex ratio of 1.14:1.00 deviated from 1:1 ($\chi^2 = 3.48$, df = 1, $P = 0.06$). The mean (±SD) FL and weight of females captured during 2005–2006 were 615 ± 76 mm and 998 ± 171 g, respectively. Male shovelnose sturgeon had a mean FL of 609 ± 60 mm and a mean mass of 936 ± 305 g. Length-frequency distributions differed between sexes (KS test statistic = 0.06, df = 769, $P = 0.02$): females had a greater mean FL and a more truncated distribution than males.

Age distributions changed during 2002, 2003, 2005, and 2006. Bias (i.e., indicated by a slope different than 1.0) was not apparent in our age estimates according to an age bias plot between readers. Age-frequency distributions shifted toward older fish; mean age was 7.6 years in 2002 and 11.3 years in 2006 (Figure 1). The age-frequency distributions also changed from positively skewed to normal (Figure 1). The rightward shift in age-frequency distributions was not driven by specific cohorts growing through time (Figure 1); rather, fundamental changes in the distribution (i.e., declining number of recruits) appeared to be occurring.

Age of female shovelnose sturgeon ranged between 4 and 22 years (mean ± SD = 11.2 ± 3.0 years), while that of males ranged between 3 and 19 years (mean ± SD = 10.9 ± 2.7 years). Females became sexually mature at 9–12 years (age at first maturation = 9 years), and males matured at 8–10 years (age at first maturation = 8 years; Figure 2). At ages when females became sexually mature, the males attained larger sizes than did the females; however, after maturity was reached, females achieved larger sizes than males of the same age (Figure 2).

Population growth patterns differed among years and sexes (Table 1). The population reached a larger asymptotic length L_∞ and the von Bertalanffy growth coefficient was greater in 2002–2003 than in 2005–2006 ($F = 6.72$, df = 1, 27, $P = 0.0016$; Table 1). When somatic growth was examined by age-class for each year of data, a decrease in mean FL at age occurred between 2002–2003 and 2005–2006 for all age-classes (Figure 3). The sex-specific von Bertalanffy growth curves differed ($F = 5.72$; df = 1, 27; $P = 0.0036$); males reached L_∞ at a slightly faster rate, but females attained a larger L_∞ (Table 1).

Mortalities were estimated based on fish that were 7 and 9 years and older during stratified random sampling in 2002 and 2003. The instantaneous mortality rate was 0.40 in 2002 ($r^2 = 93$, df = 8, $P < 0.0001$; 33% annual mortality) and 0.51 in 2003 ($r^2 = 81$, df = 6, $P = 0.006$; 40% annual mortality). For directed sampling (2005–2006), the instantaneous mortality rates were based on fish of age 12 and older because younger fish were rare in the catch. The combined instantaneous mortality rate for directed sampling (both sexes) was 0.60 ($r^2 = 96$, df = 8, $P < 0.0001$; 45% annual mortality). The instantaneous mortality rate during this time was 0.58 for females ($r^2 = 0.86$, df = 7, $P = 0.0005$; 44.3% annual mortality) and 0.59 for males ($r^2 = 0.93$, df = 7, $P < 0.0001$; 44.8% annual mortality). Catch curve regressions were tested for homogeneity of slopes but did not differ among sexes. Instantaneous mortality rates only differed between 2002 and the directed sampling of 2005–2006 ($F = 117$; df = 3, 13; $P = 0.002$).

The relative number of fish within the age-8 cohort declined between 2002 and 2006 ($r^2 = 0.94$, df = 3, $P < 0.002$; slope = 29% annual decline). Assuming a starting density of 160,000 shovelnose sturgeon in 2006, a 44% annual mortality rate, and a 29% annual decline in recruitment, we predicted that the number of fish of age 8 and older would decline to 3,200 individuals by 2016.

Discussion

The shovelnose sturgeon population appears to be changing demographically over time in the MMR; such

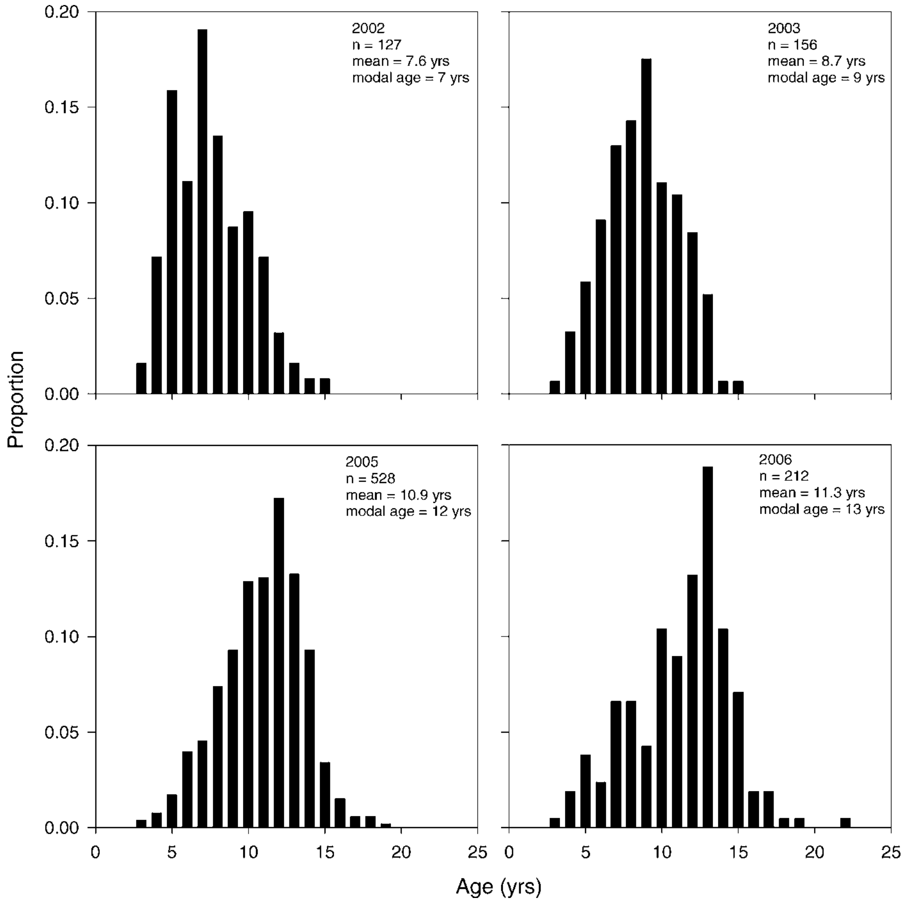


FIGURE 1.—Age-frequency distributions of the shovelnose sturgeon population in the Middle Mississippi River during 2002, 2003, 2005, and 2006.

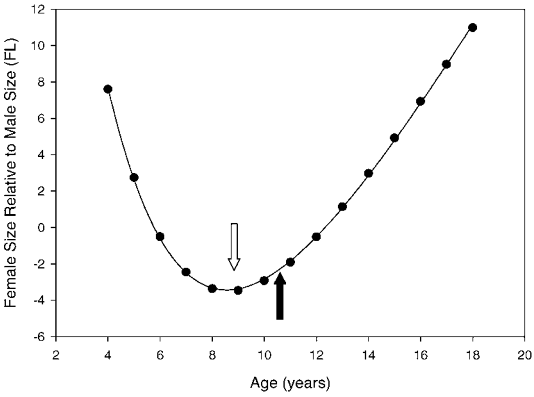


FIGURE 2.—Difference in predicted fork length (FL; mm) at each age between female and male shovelnose sturgeon in the Middle Mississippi River; predicted FLs were derived from von Bertalanffy growth curves (see Table 1). Median age at maturity for males (unshaded arrow) and females (black shaded arrow) is indicated.

changes should not be occurring so rapidly in a long-lived, slow-growing, late-maturing species with expected stable population structure (Winemiller and Rose 1992). Regardless of the underlying mechanisms, our very simple analysis of these monitoring data suggests that the resident population in the MMR is on a declining trajectory because mortality is increasing,

TABLE 1.—Von Bertalanffy parameters (L_∞ = asymptotic length, mm; k = growth coefficient; t_0 = age [years] at a length of zero) estimated for the shovelnose sturgeon population sampled in the Middle Mississippi River during 2002–2003 and 2005–2006, and sex-specific parameter estimates for the 2005–2006 sample.

Year	Level	L_∞	k	t_0	n
2002–2003	Population	792.31	0.16	−1.54	283
2005–2006	Population	781.31	0.13	−1.23	726
	Male only	770.78	0.14	−1.13	389
	Female only	811.52	0.11	−1.99	337

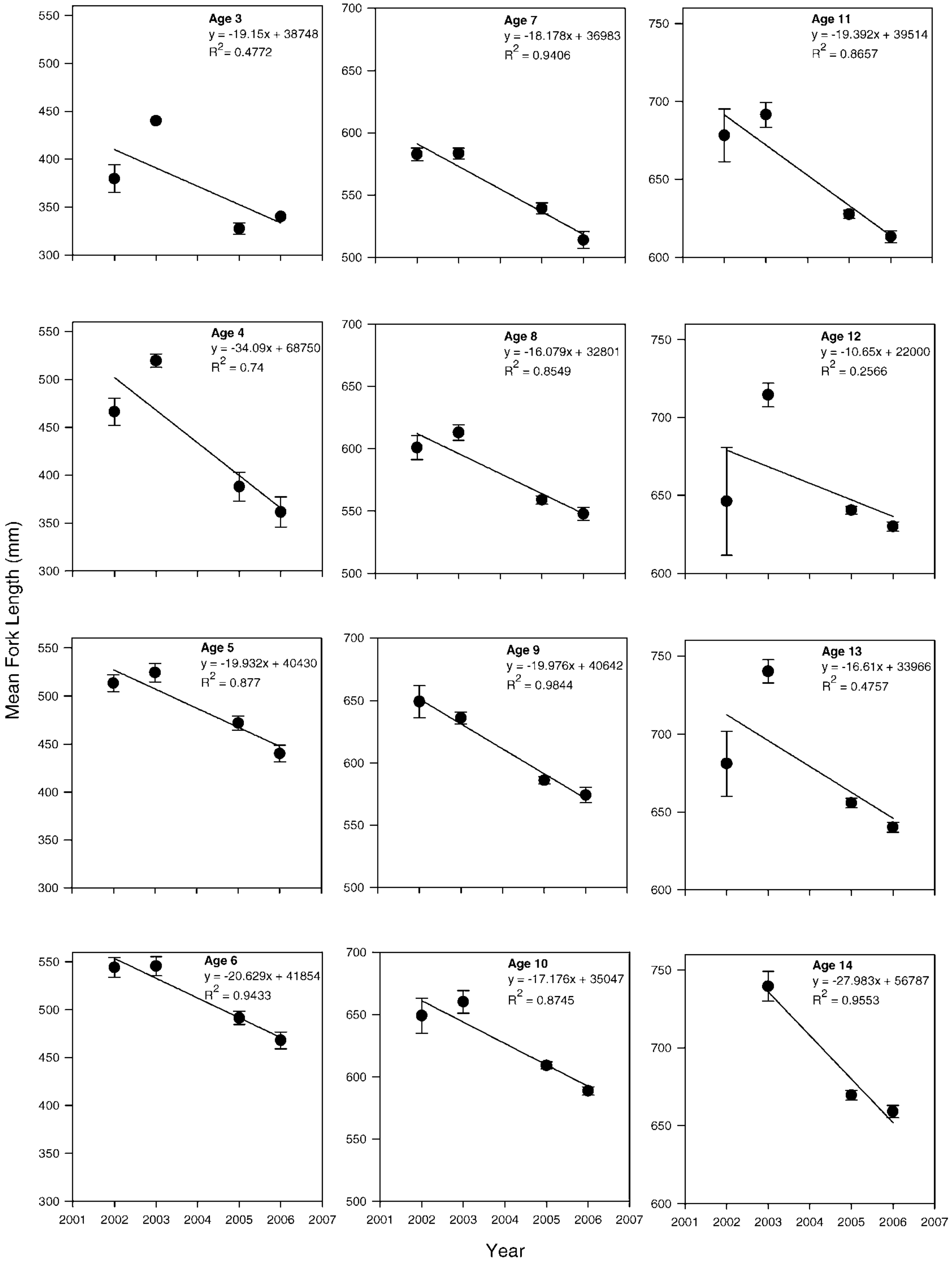


FIGURE 3.—Mean (±SE) fork length (mm) of shovelnose sturgeon from each age-class in the Middle Mississippi River during 2002, 2003, 2005, and 2006. Note that the *y*-axis scale differs among panels.

recruitment is declining, and somatic growth rates are declining. Without management intervention in the form of reduced mortality or perhaps improved habitat, this research supports previous analyses that the population will decline (Colombo et al. 2007a) and may be following the same fate as many harvested sturgeon populations (Pikitch et al. 2005). Of course, predicted declines could be ameliorated by other factors, such as immigration from other populations, a reversal of recruitment trends, and increased growth rates.

Recruitment changes that were reflected by the 8-year-old cohorts through time may be due to increased harvest in the MMR that began occurring in the late 1990s, when these fish were hatched (Colombo et al. 2007a). These observed changes are characteristic of exploited fisheries experiencing a lack of spawning activity due to removal of spawning females (see Colombo et al. 2007a). To date, we know of only five potential spawning areas in the MMR, and aggregations of spawning adults are probably vulnerable in these areas (Garvey et al. 2006). Reproductive females are probably being selectively harvested on the purported spawning grounds during the October–May harvest season (Bettoli et al. 2009). Further support of the selective loss of females due to their harvest, with negative consequences for reproduction and recruitment, is reflected in the sex ratio that deviated from the 1:1 ratio observed in the MMR during 2002–2003 (Colombo et al. 2007b). We found that females became larger on average than did males after maturation; thus, females have a higher likelihood of being harvested by size-selective gear in the MMR, perhaps increasing their risk of harvest. Our estimate of 25% commercial harvest for females with black eggs further supports the assertion that harvest of females is intensive.

Although our estimate of sex ratio suggests differential mortality between females and males, our population-level analysis indicates that total annual mortality is increasing for both sexes. Harvest is probably contributing to this increase, given that the mortality rates we quantified far exceed those of unharvested shovelnose sturgeon populations (<10%; Quist et al. 2002; Jackson 2004; Killgore et al. 2007). Males and nonreproductive females may be experiencing harvest mortality because of increased incidental effects. All fish that were collected by the commercial fisher were checked for eggs; this involves making an incision in the body wall to determine sex and maturity. This invasive procedure may increase handling mortality of both sexes in the field. The question remains whether the changing sex ratios or population-level mortality rates from catch curves are more sensitive in estimating changes in sex-specific demographics of the population.

Declining population-level growth in length through time may have been partly attributable to an unusually dry period during 2005 and 2006, which perhaps reduced foraging success or increased temperature-dependent metabolic costs. Because growth affects body size, condition, fecundity, and reproductive success, we might expect that future recruitment will be curtailed by these conditions. Habitat in the MMR is probably not ideal given the many navigation-related alterations that might produce further negative effects on recruitment success.

A major goal of fisheries science is to conserve available resources; in the case of sturgeon populations, this means that recruitment must be successful and spawning stocks must be preserved. However, if current harvest and habitat degradation persist, spawning and recruitment success will continue to decline, with negative consequences for population growth. One possible strategy to conserve the shovelnose sturgeon population is to impose conservative length limits, as suggested by Colombo et al. (2007a), to allow the population to withstand harvest. Limits on length, gear, and catch can be very effective when coupled with strict enforcement and close monitoring (Williamson 2003), but such regulations are difficult to enforce, particularly on such a large system, and may not be the best option. Although specific spawning areas have not been located in the MMR, aggregations occur at specific locations during the spawning season. If such areas could be protected at the appropriate times, spawning by a majority of the mature females is possible. Enhancement and perhaps an increase in these spawning areas may relax the purported recruitment bottleneck. A temporary ban on harvest may also be successful as it has been for other sturgeon populations (Pikitch et al. 2005), but the signs of recovery may not be seen for many years. The best management plan for shovelnose sturgeon population recovery will probably be a combination of regulations and restrictive harvest with strict enforcement and monitoring. On a longer time scale, identifying whether successful spawning is limited by habitat and responds positively to habitat restoration will be important for allowing populations to resist harvest and environmental perturbations.

Acknowledgments

We thank the Illinois Department of Natural Resources for collecting and supplying the commercial harvest data. Special thanks to Mike Hill for assistance in field collection and aging of all shovelnose sturgeon and to Quinton Phelps for assistance in manuscript preparation; we are also grateful to P. Beck, R. Echols, D. Knuth, A. Lohmeyer, A. Plauck, and D. Schultz for assistance with field collection. Funding for this research was provided by the U.S. Army Corps of Engineers St. Louis District. Thomas Keevin was particularly helpful during this process.

References

Bailey, R. M., and F. B. Cross. 1954. River sturgeons of the American genus *Scaphirhynchus*: characters, distribution, and synonymy. Papers of the Michigan Academy of Science, Arts, and Letters 39:169–208.

Bettoli, P. W., M. Castro-Yerty, G. D. Scholten, and E. J. Heist. 2009. Bycatch of the endangered pallid sturgeon (*Scaphirhynchus albus*) in a commercial fishery for shovelnose sturgeon (*S. platorynchus*). Journal of Applied Ichthyology 25:1–4.

Billard, R., and G. Lecointre. 2001. Biology and conservation of sturgeon and paddlefish. Reviews in Fish Biology and Fisheries 10:355–392.

Birstein, V. J. 1993. Sturgeons and paddlefish: threatened fishes in need of conservation. Conservation Biology 7:773–787.

Carlander, H. B. 1954. History of fish and fishing in the upper Mississippi River. Upper Mississippi River Conservation Commission, Rock Island, Illinois.

Chen, Y., D. A. Jackson, and H. H. Harvey. 1992. A comparison of von Bertalanffy and polynomial functions in modeling fish growth data. Canadian Journal of Fisheries and Aquatic Sciences 49:1228–1235.

Colombo, R. E., J. E. Garvey, N. D. Jackson, B. T. Koch, R. Brooks, D. P. Herzog, R. A. Hrabik, and T. W. Spier. 2007a. Harvest of Mississippi River sturgeon drives abundance and reproductive success: a harbinger of collapse? Journal of Applied Ichthyology 23:444–451.

Colombo, R. E., J. E. Garvey, and P. S. Wills. 2007b. Gonadal development and sex-specific demographics of the shovelnose sturgeon (*Scaphirhynchus platorynchus*) in the Middle Mississippi River. Journal of Applied Ichthyology 23:420–427.

Everett, S. R., D. L. Scarnecchia, G. J. Power, and C. J. Williams. 2003. Comparison of age and growth of shovelnose sturgeon in the Missouri and Yellowstone rivers. North American Journal of Fisheries Management 23:230–240.

Farbee, G. B. 1979. Life histories of important sport and commercial fishes of the upper Mississippi River, shovelnose sturgeon. Pages 41–68 *in* Jerry L. Rasussen, editor. A compendium of fishery information on the upper Mississippi River, 2nd edition. Upper Mississippi River Conservation Committee, Rock Island, Illinois.

Garvey, J. E., E. J. Heist, R. C. Brooks, D. P. Herzog, R. A. Hrabik, and K. J. Killgore. 2006. Current status of the pallid sturgeon (*Scaphirhynchus albus*) in the Middle Mississippi River: habitat, movement, and demographics. Final Report to U.S. Army Corps of Engineers St. Louis District, St. Louis, Missouri.

Helms, D. R. 1974. Shovelnose sturgeon in the Mississippi River, Iowa. Iowa Fisheries Research Technical Series 74–3. Iowa Conservation Commission, Des Moines.

Hurley, S. T., and J. G. Nickum. 1984. Spawning and early life history of shovelnose sturgeon. Iowa Cooperative Fish and Wildlife Research Unit, Iowa State University, Project Segment 2–399-R-1, Completion Report. Iowa State University, Ames.

Jackson, N. D. 2004. Age, growth, and mortality of shovelnose sturgeon, *Scaphirhynchus platorynchus*, in the Middle Mississippi River and lower Wabash River, Illinois. Master's thesis. University of Southern Illinois, Carbondale.

Jackson, N. D., J. E. Garvey, and R. E. Colombo. 2007. Comparing aging precision of calcified structures in shovelnose sturgeon. Journal of Applied Ichthyology 23:525–528.

Keenlyne, K. D. 1997. Life history and status of the shovelnose sturgeon, *Scaphirhynchus platorynchus*. Environmental Biology of Fishes 48:291–298.

Killgore, K. J., J. J. Hoover, J. P. Kirk, S. G. George, B. R. Lewis, and C. E. Murphy. 2007. Age and growth of pallid sturgeon in the free-flowing Mississippi River. Journal of Applied Ichthyology 23:452–456.

Ludwig, A., L. Dubus, and I. Jenneckens. 2002. A molecular approach to control the international trade in black caviar. International Review of Hydrobiology 87:661–674.

Morrow, J. V., J. P. Kirk, K. J. Killgore, and S. G. George. 1998. Age, growth, and mortality of shovelnose sturgeon in the lower Mississippi River. North American Journal of Fisheries Management 18:725–730.

Pflieger, W. L. 1997. The fishes of Missouri, 2nd edition. Missouri Department of Conservation, Jefferson City.

Pikitch, E. K., P. Doukakis, L. Lauck, P. Charkrabarty, and D. L. Erickson. 2005. Status, trends and management of sturgeon and paddlefish fisheries. Fish and Fisheries 6:233–265.

Quist, M. C., C. S. Guy, M. A. Pegg, P. J. Braaten, C. L. Pierce, and V. H. Travnichek. 2002. Potential influence of harvest on shovelnose sturgeon in the Missouri River System. North American Journal of Fisheries Management 22:537–549.

Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Bulletin of the Fisheries Research Board of Canada 191.

Secor, D. H., P. J. Anders, W. Van Winkle, and D. A. Dixon. 2002. Can we study sturgeon to extinction? What we know and don't know about the conservation of North American sturgeon. Pages 183–189 *in* W. Van Winkle, P. J. Anders, D. H. Secor, and D. A. Dixon, editors. Biology, management, and protection of North American sturgeon. American Fisheries Society, Bethesda, Maryland.

Sheehan, R. J., and J. L. Rasmussen. 1999. Large rivers. Pages 529–559 *in* C. C. Kohler and W. A. Hubert, editors. Inland fisheries management in North America, 2nd edition. American Fisheries Society, Bethesda, Maryland.

Slipke, J. W., and M. J. Maceina. 2000. Fisheries Analysis and Simulation Tools (FAST) user's guide. Auburn University, Auburn, Alabama.

Williamson, D. F. 2003. Caviar and conservation: status, management, and trade of North American sturgeon and paddlefish. TRAFFIC North America, Washington, D.C.

Winemiller, K. O., and K. A. Rose. 1992. Patterns of life-history diversification in North American fishes: implications for population regulation. Canadian Journal of Fisheries and Aquatic Sciences 49:2196–2218.

CHAPTER 12: COMMENTS AND RESPONSES

United States Department of the Interior

FISH AND WILDLIFE SERVICE
Bishop Henry Whipple Federal Building
1 Federal Drive
Fort Snelling, MN 55111-4056

IN REPLY REFER TO:

FWS/R3/ES-TE

MAR 22 2007

Mr. Joseph P. Kellet
Deputy District Engineer for Planning,
St. Louis District
U.S. Army Corps of Engineers
1222 Spruce Street
St. Louis, Missouri 63103-2833

Dear Mr. Kellet:

We have received and reviewed the draft document "Current Status of the Pallid Sturgeon (*Scaphirhynchus albus*) in the Middle Mississippi River: Habitat, Movement, and Demographics" (Draft Report). This four year study was conducted to partially fulfill the requirements of the Reasonable and Prudent Alternative in the Fish and Wildlife Service's Biological Opinion for Operation and Maintenance of the 9-Foot Navigation Channel on the Upper Mississippi River. We wish to commend the Army Corps of Engineers (Corps) for this significant undertaking. The information obtained will prove invaluable as we progress toward development of the Pallid Sturgeon Conservation and Restoration Plan for the Middle Mississippi River (MMR).

Our review of the subject document was coordinated by our Ecological Services office in Marion, Illinois and included peer review by various pallid sturgeon and fisheries experts. Within this letter we will provide general comments. Specific comments from reviewers are provided as an attachment. We received numerous specific editorial and stylistic comments on "marked-up" documents. These will be provided under a separate cover from our Marion, Illinois Ecological Services office.

One of the main goals of the habitat study as described in the Biological Opinion is to identify habitat variables and related factors that limit pallid sturgeon population growth and distribution in the MMR, in particular focusing on spawning and larval/juvenile life stages. However, it is apparent that the research conducted focused primarily on adults. While the information on adult pallid sturgeon is useful, and will serve to help direct pallid sturgeon conservation in the MMR, information on early life stages is critical. We are aware that extensive trawling occurred to sample for early life stages of pallid sturgeon. The report notes that no pallid sturgeon less than 40 centimeters (cm) in size were collected, however, it was assumed that all sturgeon less than 12 cm in size were shovelnose sturgeon. Shovelnose sturgeon sizes ranged from 1 – 105 cm, indicating that the gear used was capable of collecting smaller size classes. The report should separately summarize the data collected for early life stages of both shovelnose sturgeon and pallid sturgeon, and discuss the reasons why there is not representation of pallid sturgeon less than 40 cm in size (e.g., lack of early life stages, misidentification, etc.) . Finally, if possible, information on habitat restoration measures that would benefit early life stages of pallid sturgeon and additional research needed to better characterize habitat needs should be provided.

The Draft Report contains numerous separate independent reports, many of which focus on shovelnose sturgeon. The information in the Draft Report should concentrate on information and data that pertain to conservation and management of pallid sturgeon, including the information that tests accepted paradigms concerning hybridization and recruitment of pallid sturgeon (e.g., morphometric and genetic studies). Some of the individual reports should be refocused to specifically address demographics of pallid sturgeon, including the accuracy and precision of aging pallid sturgeon. Reports that pertain exclusively to shovelnose sturgeon would be more appropriate to other forums.

One of the research objectives was to evaluate pallid sturgeon food preferences by comparing utilized prey with available prey. This information is lacking in the diet section of the report. We recommend this information be added, if available, or request some explanation as to why this research was not conducted.

It is sometimes difficult to assess whether the results in the Draft Report are statistically significant. We recommend P-values and N numbers be provided for all statistical analyses. Care should be used in using the term "statistically" such that it applies to significant findings and not just qualitative observations.

The telemetry results in the report indicate movement of pallid sturgeon into both the Lower Missouri River and the Lower Mississippi River. This is not surprising as pallid sturgeon are known to make long distance migrations. The relative size distribution of smaller pallid sturgeon occurring in the Lower Mississippi River may be indicative of this area being important for pallid sturgeon growth and recruitment. As such, it is important that both the Fish and Wildlife Service and the Army Corps of Engineers be cognizant of the movement of these fish between river systems and various jurisdictional boundaries. As you are aware, there are already significant habitat restoration and population monitoring efforts underway in the Lower Missouri River. The work the St. Louis District is undertaking in the Middle Mississippi River complements these efforts. We recommend the St. Louis District continue to coordinate their efforts among the various Corps Districts in both river systems to ensure consistency and information sharing that will contribute to the recovery of the species. In particular, we encourage the St. Louis District to work with the various Districts along the Lower Mississippi River to advocate similar habitat restoration and population monitoring efforts. The Pallid Sturgeon Habitat and Conservation Plan being developed for the Middle Mississippi River can serve as a template for similar efforts in the Lower Mississippi River.

Finally, we recognize the significance of the mortality estimates for pallid sturgeon in the MMR. The Mississippi Interstate Cooperative Resource Association (MICRA) paddlefish/sturgeon committee will be meeting in January 2007, to discuss shovelnose sturgeon commercial harvest and pallid sturgeon protection. Fish and Wildlife Service staff will participate in this meeting and will continue to work with the states to resolve issues concerning the incidental and illegal harvest of pallid sturgeon.

Thank you for the opportunity to review the Draft Report. Again, we complement the Corps for this extraordinary effort that will greatly contribute to the conservation and long-term management of endangered pallid sturgeon. Ms. Joyce Collins (618-997-3344 x340) of the Marion, Illinois Ecological Services office is available for further coordination regarding the Draft Report and to address questions regarding these comments.

Sincerely,

Robert Kraka

for Wendi Weber
Ecological Services
Assistant Regional Director

Enclosure:
Specific Comments

SPECIFIC COMMENTS – Draft Report "Current Status of the Pallid Sturgeon (*Scaphirhynchus albus*) in the Middle Mississippi River: Habitat, Movement, and Demographics"

REVIEWER 1

1. Title Page – Not to authors: All in all, this is a great report, full of much needed and useful information!

2. Page 2, second bullet – Here is why pallid to shovelnose ratios can be very misleading. The way this is written it could be interpreted by some to mean that pallid numbers (based on CPUE) are greater downstream than they are upstream. However, pallid numbers were not significantly different when reach B was compared to COR (Killgore et al. this paper) and I would like more information on the statistics regarding the data and the test for normality (see comment in Killgore et al. this paper).

Yet shovelnose sturgeon numbers appear to be what are increasing in the latitudinal fashion (less down and more up) with a mean CPUE being lowest in Reach B and greatest at the COR. This could suggest that the lower most reaches of the LMR are not preferred for shovelnose and thus the ratios do little to reflect pallid sturgeon prevalence. I realize the ratios are often reported in the literature, but want to caution that comparing ratios from one area to the next can be misleading. Studying ratio trends within an area through time likely is a more useful index.

3. Page 10, 1st full paragraph, last sentence – There is also seasonal influences that can explain size gradation like migration of larger adults. Was seasonal variation evaluated at all sample sites and were all sample sites sampled during all seasons?

4. Page 12, 1st full paragraph, 1st sentence – See note above. IF catches at COR were seasonally influenced this could skew length frequency observations.

5. Page 20, 1st full paragraph, 5th sentence – Recommend deleting the word "continuing" in this sentence.

6. Page 27, Table 2 – It may be useful to include a column that is the entire MMR as well as reporting the statistics along with the MMR sans CR and CR.

Also, reporting p-values for statistical tests when mean CPUE were compared would be useful for readers.

7. Page 44, 5th complete sentence – Recommend editing this sentence as follows: "Accordingly, several Mississippi River basin states have restricted harvest regulations (e.g., Illinois, Iowa, Kentucky, Missouri, Tennessee, and Wisconsin) or have closed commercial harvest to all sturgeon species in the Mississippi River (e.g., Arkansas, Louisiana, and Mississippi) to ensure that some sexually mature fish remain **in** the system."

8. Page 83, Abstract, 9th sentence – This sentence is a little unclear. Was pallid sturgeon abundance greater below that Atchafalaya than the COR? Maybe it should be reworded to state: Pallid sturgeon abundance was higher at both the COR and Atchafalaya to New Orleans study areas than the other sites (P–).

9. Page 84, Introduction, 1st paragraph, 6th sentence – Most collections of pallid sturgeon in Montana and the Dakotas were/are from inter-reservoir reaches of the Missouri River not from reservoirs themselves. Where pallid sturgeon are collected from the reservoirs, they typically are associated with the more riverine habitats of these reservoirs, i.e., below the dam outlet structures where more lotic like conditions prevail.

10. Page 84, Introduction 1st paragraph, last sentence Constant et al. (1997) did not perform a population estimate and thus the conclusion of their reporting a large population may be a little misleading. Constant et al. (1997) report a density in the Atchafalaya that is as high as densities recorded elsewhere in the species range. However, the density figure could be biased upwards as sampling below the ORCS was in conjunction with artificial flow manipulation that may result in concentrating fishes.

11. Page 85, 1st full paragraph, 2nd sentence – Hurley et al. (2004) report that pallid sturgeon were most often found in main channel habitats, but they indicate that pallid sturgeon demonstrated a negative selection for main channel habitats. Koch et al. (this paper) indicate nearly identical results. Pallid sturgeon exhibits a negative selection for main channel habitats. It appears misleading in this sentence to state that pallid sturgeon prefer main channel environments.

12. Page 85, 1st full paragraph, 3rd sentence – In this context, regulation seems to imply flow regulation, however all anthropogenic modifications likely are attributable to the species' decline. Anthropogenic modifications that maintain main channel habitats at the expense of other habitat types likely should be identified also.

13. Page 86, top of page, last sentence – See above comment. Hurley et al. (2004) and Koch et al, (this paper) did not document a selection for main channel habitats by pallid sturgeon. Likely pallid sturgeon were most often found in the main channel as a result of this being the most abundant habitat type. Both Hurley et al. (2004) and Koch et al. (this paper) identified that pallid sturgeon demonstrated a negative selection for main channel habitats.

14. Page 88, full paragraph, 7th sentence – This seems odd that it is naturally occurring yet reinforced with concrete and rip-rap. Was the crest height increased as a result of this anthropogenic modification to a natural geomorphic feature?

15. Page 90, 1st paragraph, last sentence Does this mean that each reach (A-E) received comparable effort? That is, was each reach sampled with comparable trot line sets among each season and were seasonal differences analyzed with no significance being found allowing you to combine seasons?

16. Page 91, 1st full paragraph, last sentence – Earlier in the report it indicates that scanning for coded wire tags was not standard practice until fall 2004 (see page 18).

17. Page 91, end of page – The results of the Shapiro-Wik test should be reported here. Were the CPUE data normally and independently distributed (NID)? If not, did the log transformation result in the data being NID? If the data were not NID, the non-parametric Kruskal-Wallace test may be more appropriate here.

18. Page 92, end of page, 4th sentence – The percent of lake sturgeon that contain CWT's is blank. This should be filled in.

19. Page 94, 1st paragraph, 4th sentence – Were the data explored to see if there was a significant seasonal interaction?

20. Page 94, 1st paragraph, last sentence – According to table 2, significantly fewer shovelnose sturgeon were collected in this reach (Reach B). This is an inherent problem with trot-line data in that once a fish is hooked, the ability of additional fish to be collected goes to zero on that hook. So if there truly are fewer shovelnose in this reach, one would expect a higher ratio even with a small population of pallid sturgeon being present.

21. Page 97, top of page   The first documented case of a pallid sturgeon occurring in the Obion River is Interesting!

22. Page 97, top of page, last sentence – Does this really indicate a high retention rate of floy spaghetti tags? To me a high retention rate would be demonstrated by a substantial portion of tagged fish retaining the tag for several years or more. This single fish seems to suggest that floy tags may remain for many years but does not necessarily indicate a high retention rate. See next paragraph where there were several recaptures with only a CWT being detected.

23. Page 97, 1st full paragraph, 5th sentence – Were not all fish scanned for CWT's in 2006?

24. Page 109, Table 2 – Why was the MMR divided into two reaches for the analysis? Study Reach E is designated as the MMR from the Ohio to the Missouri confluence. The results and comparisons should be reported as such for reach E. Dissecting reach E for further exploratory analysis should be in a separate table or at the very least the reach E analysis should be included in this table prior to the MMR w/o COR and COR columns.

24. Page 109, Table 2, bottom of page – The Pallid:Shovelnose ratio for COR should be 1:77.

25. Page 110, Table 3 – Same comment as above. Please report Reach E results in this table.

26. Page 117, 1st full paragraph – What was the frequency of tracking, i.e., were the fish tracked daily, weekly, etc.? Was the entire reach tracked? Were fish randomly selected for tracking?

27. Page 118, top of page – Any concerns about autocorrelation with weekly and bi-weekly sampling?

28. Page 123, top of page, 4th sentence – Multiple relocations of the same fish can inflate sample size. How was this addressed in movement and habitat analysis? Were samples collected far enough apart (time wise) that they were considered independent?

29. Page 246, top of page, last sentence – Check this reference. Ray et al. is not included in this MMR report. Likely should be Ray et al. (In Press).

30. Page 265 Add Ray et al. citation.

31. Page 303, Acknowledgements, 1st sentence -- This should be Region 3 not Section 3.

32. Page 337, top of page, 4th complete sentence – How were the known hatchery fish (either from brood stock collected above Gavins Point or the other Blind Pony spawned fish) factored into this analysis?

33. Page 339, top of page, 2nd full sentence Not sure about the wording in this sentence.

REVIEWER 2

Review: Pallid sturgeon movement and habitat selection in the middle Mississippi River 2003-2005.

The authors should better describe triangulation procedures used to locate sturgeon. Can they provide estimates of accuracy and evaluate the potential effects on ancillary data habitat data and habitat classifications?

To aid the reader, the authors should provide clear definitions of habitat classifications and associated acronyms, preferably in a table.

The methods do not mention purpose objectives and methods for either the hourly survey (Figure 7) or the ADCP surveys (Table 11; Appendix B). Did these portions of the study result in useful information?

Do the authors feel their habitat classifications adequately provide the information needed to manage pallid sturgeon habitat? Is there a need for more fine scale data such as they apparently gathered with the ADCP, or are macrohabitats satisfactory?

There are several questions in regard to the analyses of movement data. Fish are clearly the experimental unit here (individual fish behave differently--observations on individual fish are not independent). Should models account for fish attributes such as size and sex that might be important influences on movement? Also, how were the buoy detections used in this analyses? There is a bias associated with movement rates derived from active tracking (via boat search) and versus passive (via buoy) relocation. The authors might consider comparing and reporting seasonal and annual home range (e.g., linear river km) estimates, which are probably more relevant information for management than movement rates that are strongly influenced by time intervals between locations.

In my opinion, the authors could better tie their information together in the discussion and to provide some context and relevance to potential management actions, and recommendations/prioritization of data needs for future studies. Do we have the information needed to identify any habitat bottlenecks or develop habitat suitability models? Given the new information, what are appropriate management scales?

The bar graphs (Figures 15-18) contain substantial redundancy because each graph includes the same availability. The authors should consider combining each set of graphs into a single graph using patterned bars (e.g., different patterns for each season in Figure 18) to facilitate comparisons. Because individual fish are the experimental unit, mean percentages and error bars of use by fish would be more appropriate than lumped data so that the reader can judge variability.

Certain sturgeon movements are loosely labeled pre-spawn or post-spawn throughout the report, but the criterion, which is based on information from sturgeon life history and water temperature observations from other systems, for that hypothesis is not laid out until near the end of the report. The rationale and definition for "pre-spawn" and "post-spawn" should be laid out before applying those terms to specific movements in the report.

Other minor concerns and editorial suggestions are noted on the hardcopy of the text. TO BE PROVIDED UNDER SEPARATE COVER.

REVIEWER 3

Overall, this work on the MMR and LMR makes a substantial advance in terms of the knowledge on the topics addressed. Not being certain if management suggestions should be purposefully provided by the authors, or rather if those data and data gaps that they consider to be instructive to management decisions should simply be stressed, some statements might be tempered. Clarification of some wording and inclusion of additional detail are needed in order for the Chapters to be complete and soundness of data to be judged. (Some of this would be addressed in the peer reviews for journals.) Citation format should be consistent between chapters, as should capitalizations (e.g. pallid versus Pallid), plural use (e.g. sturgeon[s] or gear[s]) and acronym usage.

Throughout the document, referring to "we" and "our" were changed to a less personal approach, and providing *P* values is suggested. At times it is difficult to assess whether results stated are statistically significant or simply observations, as sometimes "statistically" is used. Suggest not using this terminology, and highlight only if it is a "trend" that is noted. This way of writing casts doubt on whether or not results being reported have been statistically analyzed; this is easily corrected with more attention to the use of terms.

Here is a summary of my comments per chapter, and please know many of the critical bits are marked on the pages themselves. TO BE PROVIDED UNDER SEPARATE COVER.

Executive Summary. This is a critical chapter and it will be the one to which most people refer, therefore a bit more attention to detail is needed.

1. The N numbers should be included, as much as possible, throughout the chapter.
2. Mention how individuals were tracked and how "hatchery products" were determined.
3. Mention how species were defined – upon which particular morphomeristic index/ices? Wills et al. 2001 only?
4. Temper last paragraph on page 4, or provide data collected to justify the statement.
5. Provide N numbers for the numbers of sturgeon that were identified morphomeristically and tested genetically.
6. The chapter could be logically divided based on the subsequent chapters.
7. Specificity of some of the Tables may not be appropriate for inclusion in an Executive Summary chapter.
8. Figure 1 appears to not be representative of what is in the text. What are the stars? Where are the Missouri and Ohio Rivers?
9. Figure 2 is confusing in that what is below the top line in not in accord with life stage. Suggest removing top line and making cells out of the table below. Could move that top line to text and refer to Figure 2.
10. For Figure 9, how many individuals does one point represent?

Chapter I. Sampling Techniques. This information is useful baseline information for sampling. See several suggestions on rewriting.

1. The abstract should be rewritten according to the suggestions provided on the hardcopy. There are not definitions of indicator variables, CPUE, P values should be given.
2. There are additional references, beyond Colombo in Review [can and "in review" be used in this Report] that should be included regarding declines of sturgeon stocks.
3. Detailed information on sexual maturities (page 44) is not appropriate for this Chapter's Introduction.
4. In Methods, it is critical to describe how species were identified.
5. Provide better descriptors of size/volume/lengths of MMR and UMR.
6. What is "ground-truthing"? (page 46)
7. Provide a flow chart for the reader to easily understand, and not have to diagram for themselves, the sampling design. See suggestion. Add emphases as appropriate.
8. As previous months per season are given, provide the same for Spring 2005 (page 47).
9. Suggest additional subheadings for Methods: Habitat Types, Experimental Design, Gear Types, Data Analyses.
10. As the order of presentation of results does not follow methods presentation, suggest adding sentence "Results are presented per species."
11. Citation possible missing from text: Birstein, Moos.
12. Change Table 1 heading to "Numbers of sampling efforts and sturgeon captured (in parentheses) with gear types of 2002-2005 from the Middle Mississippi River.
13. In Table 2 write out CPUE and change heading as suggested.
14. For Tables 3-6, write out headings.
15. For Table 7, footnote part of heading.
16. For Figure 1, need to identify acronyms and if this is a real location.
17. Figure 2 and 3 legends are missing "per fork length".

18. Suggest including a figure that shows actual river miles.

Chapter 2. Size and Abundance. This chapter provides important data for all MR biologists. It was easier to follow than the previous 2 chapters.

1. Throughout, there is a reference to "current publication" that does not make sense. If this Report is to be finalized following the publication of that chapter, it would make sense to leave it as a placeholder, but only then.
2. Significance values should be included in the Abstract.
3. In the abstract (and as appropriate throughout), "catch" and "abundance" are two terms that need definition.
4. At the end of the abstract, which river reaches are being discussed needs to be defined – just lower and middle?
5. In the abstract, include more information/results that lead to the decision that the MR can be divided into 5 or 6 reaches.
6. Nice table on page 89 – needs title, though.
7. Again, as in Chapter 1, in Methods, it is critical to describe how species were identified.
8. Use of "replication" and "standard efforts" need description – page 90, first paragraph.
9. Suggest adding percentages of totals of species caught in MMR and LMR on page 92 – see suggestions provided on hardcopy.
10. Use of CWT on page 92 not yet provided confusing phrase there.
11. Ross citation is 2000 or 2001?
12. Gear are not techniques, so be careful with terms.
13. In the definition of the Reaches (pages 100-102), the language needs to be more equitable and less subjective with regard to which "have management potential." For example, based on the results provided, it would appear that Reach 2 would have the highest management potential, but that is not stated.
14. Fisk citation out of place in Lit Cited.
15. Dryer citation needs a USFWS report number.
16. Keenlyne and Jenkins 1993 may not be in text.
17. Moos – cannot cite an unpublished dissertation. What is that?
18. Table 1 heading confusing. See comments.
19. Headings for Tables 2 and 3 are too long. Need both shortening and clarification. Move parts to text, if need be.

REVIEWER 4

We commented on all chapters of the Garvey et al. draft manuscript on pallid sturgeon in the Middle Mississippi River except chapter 9 (just ran out of time). What a wealth of information! Congratulations to all those who contributed to this effort. We found most chapters well written and all chapters informative. All chapters had editorial mistakes that will need to be addressed. Chapter 3 also had many mistakes that had to be reconciled before our review could continue (identified many of the mistakes below) and had other more major issues. Thank you for the opportunity to review.

Executive Summary

Pg. 38 If the sampling effort was relatively consistent through the years, it looks like a strong year class moving through that has grown to a length that is more susceptible to the gear. If you have other evidence to support declining production of young, it would be helpful. Other interpretation would be that fishers got more efficient at collecting older individuals (looks more like greater number of older fish caught than decrease in young fish) or got more efficient at aging older fish. Just appears to be more related to greater number of older fish than lower numbers of young fish. If this case is made stronger in chapter 6, then more of that case should be presented in the Executive Summary as this is what most people will read, particularly given the large size of the entire report. Standing alone, this figure could have multiple interpretations beyond what is presented.

Pg. 2 and 12 – COR is referred to as a 'destination' with little made of Low Water Dam 27 as a barrier based on documented passing of 3 fish. Could well be that COR is a major impediment and only a small number of fish passed despite many fish unsuccessfully attempting to pass. It may be a destination but might be less of a destination and more an impediment while being no more of a destination then any of the other 4 areas where pallids congregated in the spawning season. Much the way Mel Price L&D is causing great numbers of fish to congregate relative to LD22 despite the fact that some fish pass (some fish passing is different than all or most of the fish attempting to pass being successful). Also, would it be possible to relate possible passage to other river stages (put the 16 ft at the St. Louis gauge in perspective – how high is 16 ft – is it a major water even or routine spring level -- is it likely pallids could pass at 12 or 14 ft?).

Chapter 3 (more 'editorial' comments included than for other chapters)

Needs thorough editorial review to make it easier for a review of content. Current mistakes add confusion that must be reconciled by reviewer.

Figures showing 'observed movements' Because each of these data points is a discrete observation with no information about what the fish did between observations, no lines should be used to connect the data points. Certainly there are limitations to the time available to track fish but it is very possible that there were major movements missed, minor jaunts missed, or even diurnal movements each day for a number of fish. It would be most appropriate to acknowledge the lack of information between trips by omitting the line.

Pg. 117 – Why wasn't telemetry a high priority from 2002-2004?

Pg. 119 Several undefined terms – DOQ, WDU, WDS, WDSD.

Pg. 127-32 – Difficult to follow 'habitat use' section. Adding to the presentation of the first chi-square results might help to clarify that one and all following. Very well may be demonstrating ignorance of the type of analysis but found it very difficult to follow other than that pallids selected for wing dikes.

Pg. 135 Movement cues paragraph 1 states that water levels and temps increased concurrently in 2004 and 2005 but Figure 3 indicates that during April 2004 that water levels dropped while temperature increased. Dropping water levels in 2004 would be a good argument for temperature as the driving factor (along with stable flow during rising temps in 2003 as presented).

Pg 136 Lines 1-3 – Looks more like pallids were increasingly active from about 11-17 degrees with peak activity around 15 degrees based on Figs. 2-5. If there is better data available to justify the temperature ranges you reported, then it should be presented.

Pg 143 Line 1 Undefined acronyms MCB and CBD.

Pg 140-44 – Future focus should occur on each of these 5 important areas.

Pg 146 First sentence of last paragraph – undefined terms ITU, TTD, TM.

Pg 156-57 – Didn't see references in text to Tables 2 and 3 (at least not between references to Tables 1 and 4).

Pg 173-74 – Figures say 2003 and 2004 while captions are all 2005.

Pg 180 – Red shading blocks out data beneath – use transparent shading.

Pg 159-60 – Discrepancy in max. upriver of 16,883 in Table 5 and 19,408 in Table 6.

Pg. 161 – Cumulative frequency and % just add confusion; don't see the benefit or need for cumulative results.

Pg166 – Should it be discharge for all three rather than water level for chi-square 2 and comparison)?

Pg. 170 Caption refers to sinuosity but table presents temperature.

Pg. 184 – BWD appears to equal 13.8% in chart but not in figure caption.

Pg. 187 – Introduced 'WD Seam' on chart which doesn't match caption and adds confusion.

Pg. 191-223 – Much was made of movements but little of the lack of movement observed for about 20 fish that moved very little if any. Do they just sit tight for extended periods? Do you suspect some mortality? If they do stay put, did many of these stationary fish go right back to their site of capture following release? What can we learn about these stationary fish?

Pg. 225-232 – Most profiles show fish in 20-40 or 40-60 cm/sec. with a few in 60-80 or 80-100. Regardless of the average, it looks as if pallids are regularly found in flows lower than the ~90 cm/sec reported. Is the average flow is misleading because of some fish that were found in very high flows? Perhaps displaying a histogram or other chart to show the actual number of fish in each flow category would be helpful (even if average isn't skewed, it would be helpful to know that fish use a variety of flows). It would also be helpful to know more about the doplar profiling and how that information was gathered, used, analyzed. Also, even if a very accurate value can be obtained from the profiling, is it reasonable to carry that accuracy over to the fish given the location of a particular fish is not exact and flows can be very different depending on where the 'x' is put on the map. Would it be more realistic to report the data as 0-50 cm/sec, 50-100, 100-150, etc. given this uncertainty (sure the unit can give precise measurements but is that accuracy really appropriate given the uncertainty of each fish's location?

Pg. 234-42 – Each Figure or caption needs to indicate what each color or markings represent on the bars.

Chapter 5

Pg. 303 Acknowledgement should be to USFWS 'Region' 3 rather than 'Section' 3.

REVIEWER 5

The purpose of the report was to summarize a three year study designed to characterize habitat for pallid sturgeon in the middle Mississippi River (MMR) and to establish baseline population information for the species in this reach of river. This was a daunting task to accomplish, given that prior to this effort there was virtually no information on pallid sturgeon in the Mississippi River. At the time the study was designed, the prevailing consensus was that pallid sturgeon was extremely rare in all reaches of the Mississippi River, and it was being severely affected by recruitment failure and extreme levels of hybridization with shovelnose sturgeon. Therefore, the Garvey *et al.* report had to not only adapt or develop collecting and monitoring techniques to the extreme habitat conditions found in the MR, but also had to address basic systematic issues such as taxonomy and genetics in order to test accepted paradigms.

In general, I found that the main points presented in the Executive Summary (pp. 2-4) were supported by, and descriptive of the data in the individual chapters. In the discussion of Major Results, there is some confusion on pg 10: "Maximum length of trotlined pallid sturgeon increased from 620mm mean FL to 756 mm FL…" According to the table cited (Table 3; Chapter 2), these are *mean lengths*. (Is there such a thing as maximum mean length? Guess there could be a mean maximum length, but these sizes sound more like mean lengths...) I think it is also interesting to note that in the table cited, minimum length of pallid sturgeon (but not shovelnose) decreased progressively in the reaches below Chain of Rocks. This suggests, among other possibilities, that the LMR may be a destination for growth and development of pallid from upper reaches.

The chapters present much information we have heard about in the past few years, and it's good to see it finally laid out with the data. This includes the first evidence of preferred staging/spawning areas, spawning migrations, possible site fidelity, genetic distinction, morphological variation, and impacts of commercial fishing.

At the top of pg 21, the statement is made: "We have collected larvae and small juveniles in our trawling (Chapter 1), of which some have been confirmed to be pure pallids." I speed read Chapter 1 several times and could not find support for this statement. In fact, to the best I can determine, only 3 pallids were reported collected in trawls and these measured 46-73 cm. I do know that Herzog et al. *have* collected YOY pallid by trawl in the Missouri reach of the Lower Mississippi River (Herzog *et al.* 2005), but could find no reference in Chapter 1. Maybe it is there and I'm missing it. Perhaps it was left out because it was not a part of the comparison study, but this data should be noted in Chapter 1, and summarized some way in Chapter 6, Demographics and Mortality. It is also possible that larval and YOY pallid captured in the LMR were spawned in the MMR, again raising the possibility of the LMR as a location of critical importance to the MMR pallid population.

Other evidence ties conservation of MMR pallid directly to the LMR. For example, the 2002-05 study showed apparent spawning movements, including telemetered fish moving out of the MMR after spawning into the LMR. Herzog and others have continued monitoring during 2006, and apparently many, if not most, pallid tagged in the MMR moved downriver. As noted above, the minimum size of pallid decreases downstream into Louisiana, suggesting the lower river may be important in recruitment and growth. In addition, the absence of legal caviar harvest in most of the LMR allows fish to survive longer and, unless captured during spawning runs, contribute more to recruitment. Guess what struck me is the amount of evidence linking MMR pallid populations to the LMR. For any future pallid sturgeon/MMR conservation plan to be credible, it must consider and include actions, habitat, and pallid populations in the LMR. (of course you knew I'd say that...but the data also supports it) Regarding commercial fishing, this report provides strong evidence that eliminating illegal or incidental commercial harvest is the fastest, most cost-effective conservation measure that could be taken for pallid sturgeon at this time.

Sorry I don't have time to really provide a critical review, but most chapters will be published in credible journals, and they will get a much better review than I could ever provide. I'd like to see stronger recommendations at the end to include:
1) Dealing with effects of commercial caviar harvest,
2) more ideas and suggestions on future studies such as identification of spawning areas and recruitment levels, and pallid movement throughout the river; and, 3) more emphasis on tying pallid conservation in the MMR to the LOMO and LMR

REVIEWER 6

1.) General - Would be good, if possible, to compare some of the results of habitat use, etc. with some of the work on the Missouri River to see differences/similarities. I think all the monitoring crews have at least 1-2 reports on the web by now, and I know USGS has at least one year's worth of telemetry data on the Missouri River.

2.) Specific comments:

Pg. 83 - I don't quite follow the second to the last sentence on that page. The higher and statistically the same has me confused. Could this be reworded to be clearer?

Pg. 100 - May want to use term other than RPMA. The recovery team is looking at those now and is tossing around a slightly different approach/term. Using another term would avoid confusion, and also may help better characterize what these areas are - I assume the intent is focused on looking at similar management opportunities in these areas, rather than implying they may have discrete populations. Yes? No? The actions in any one of these proposed units may well affect the same fish as they move throughout the river.

Pg. 126 - Suggest clarifying what is meant by post-spawn movement. Is that the condition of that fish - i.e., checked similar to USGS work on the Missouri River? or movement after inferred spawning window? or movement after assumed spawning migration, etc.

Pg. 136 - Double check Paragamian and Kruse 2001 - Lit. Cit. only lists et al. 2001.

Pg. 137 - Double check spelling on Sulag - Lit. Cit has Sulak. need global replace.....

Pg. 138 - Was there an attempt to relate the spawning condition of the fish (reported later in the document) to the timing and movements of these fish?

Pg. 140 - The text states the fish were not found to congregate with one another. On the Missouri, multiple pallids are often caught at one site. (Possible social implications/influence on habitat use). Nice opportunity to compare/contrast patterns. Are more the 1 PS found on same trotlines? etc.?

Pg. 141 - Do we have genetics on these fish? If so are they all from the MMR "group"?

Pg. 153 - Add USACE. 1999. Cited on page 119.

Pg. 359 - Were the fish that were figured into the mortality figures all presumed/verified wild origin pallids?

pg. 363 - What is the confidence in the PS mortality figure compared to the SNS estimate? Seems like there is far more SNS to work with.

pg. 463 - I'm surprised at the low level of agreement between paired fin rays. What does this mean for the accuracy of the method? How does one know if they are using the fin with the most accurate annuli? Not a real problem in old fish, but could make a big difference in young fish.

REVIEWER 7

EXECUTIVE SUMMARY

1. General Comment - A discussion of the results of sampling for early life stages (larvae/juveniles) should be included separately in the report. It appears that the habitat data, CPUE, etc. for these individuals is lumped together with the information for sub-adults and adults.

2. General Comment – Information on dietary preferences of pallid sturgeon and the implications of diet to pallid sturgeon restoration and conservation in the MMR is lacking in the

Executive Summary. Additionally, one of the objectives of the study was to determine food preferences by comparing utilized prey with available prey. This appears lacking in the report.

3. Page 3, 4th bullet – The actual calculated mortality rate for pallid sturgeon should be reported.

4. Page 5, Justification and Approach, 1st paragraph, 3rd sentence – The citation should be USFWS 2000.

5. Page 5, Justification and Approach, 1st paragraph, 5th sentence – The study was in response to the issuance of the Fish and Wildlife Service's Final Biological Opinion for Operation and Maintenance of the 9-Foot Navigation Channel on the Upper Mississippi River (USFWS 2000). This should be corrected.

6. Page 6, 1st full paragraph, 1st sentence – The study purpose was to quantify habitat characteristics for all life stages, not just adult pallid sturgeon. Information on larvae and juvenile pallid sturgeon is lacking in the report.

7. Page 9, top of page – Much of the funding for the genetic studies was provided by the U.S. Fish and Wildlife Service.

8. Page 9, Major Results, General, 7th sentence – What was the accuracy and precision associated with aging the 75 pallid sturgeon. This would be worthwhile information for this report.

9. Page 12, 1st full paragraph, 2nd sentence – The information provided does not present a clear picture that the Low Water Dam 27 does not present a barrier to fish movement. Although three fish were able to pass the dam at 16 feet St. Louis Gage, were other fish unable to do so. How does this river stage relate to normal or average conditions during the spring?

10. Page 12, 1st full paragraph, 6th sentence – Statements concerning spring aggregations at the confluence of major tributaries (Meramec River and Kaskaskia River) seem inconsistent with information on page 11 that states that tributary mouths were never used by tagged adult fish. Some explanation would be warranted.

11. Page 16, 2nd paragraph, 4th sentence – This sentence requires some clarification. Pallid sturgeon harvest is illegal everywhere. Shovelnose sturgeon harvest is still legal in the Kentucky and Tennessee portions of the Lower Mississippi River.

12. Page 21, 1st full paragraph, 1st sentence – Data on larvae and juveniles is lacking in the report. The information indicates that no pallid sturgeon <40 cm in size were collected.

13. Page 21, 2nd paragraph, 1st sentence – Change "know" to "known".

14. Page 27, Table 2 – The information for the entire MMR Reach should be reported in this table prior to a breakout of information for the MMR without COR and the COR alone.

CHAPTER 1

1. General Question What are the results of the genetic testing of larval sturgeon? It is a concern that all sturgeon < 12 cm were classified as shovelnose sturgeon. How does this impact any subsequent analysis?

2. Page 43, Top of page, 3rd complete sentence These results identify that higher numbers of pallid sturgeon were collected in wing dike, channel borders near wing dikes and island tip habitats than in other habitat types. This data is contradictory to statements in the Executive Summary and Chapter 3 which indicate pallid sturgeon did not use island tip habitats.

3. Page 52, top of page, 2nd complete sentence – What was the bias, if any, associated with identifying all *Scaphirhynchus* spp. less than 12 cm FL as shovelnose sturgeon?

4. Page 58, top of page, sixth sentence – For random sampling from 2003-3004, the CPUE in tributary mouths was 0. How can this be reconciled with data in Chapter 3 that indicates pallid sturgeon congregate at the confluence of major tributaries?

5. Page 59, top of page, 5th complete sentence – For random sampling from 2004-2005, the only habitat that correlated with CPUE was island tip where CPUE was greatest (CPUE = 0.016). How can this data be reconciled with statements in the Executive Summary and Chapter 3 which indicate pallid sturgeon did not use island tip habitats?

6. Page 60, top of page, 3rd complete sentence – For directed sampling from 2004-2005, only island tips were correlated with CPUE (CPUE = 0.035). How can this data be reconciled with statements in the Executive Summary and Chapter 3 which indicate pallid sturgeon did not use island tip habitat.

7. Page 61 – What was the mean and median lengths of pallid sturgeon. Why were no pallid sturgeon ≤ 44 cm FL collected as the data indicate that shovelnose sturgeon lengths ranged from 1 – 105 cm FL.

8. Page 62, bottom of page – Why did directed sampling in 2004-2005 only occur in the spring?

9. Page 63, last sentence How does classifying all *Scaphirhynchus* spp. < 12 cm bias this statement? If commercial harvest is limiting recruitment of pallid sturgeon because of the lack of small fish in the 4.87 m trawl, would shovelnose sturgeon not be affected in the same manner? Yet the 4.87 m trawl collected many small shovelnose sturgeon? Does available length at age data indicate shovelnose sturgeon grow slower than pallid sturgeon? Are there other explanations for the lack of small pallid sturgeon in the samples?

10. Page 64, 2nd sentence The highest pallid sturgeon CPUE was at channel borders with dikes and island tip habitats, while lowest CPUE was at open channel borders and tributary mouths. How can these results be reconciled with information in the Executive Summary and Chapter 3 which indicate that sturgeon did not use island tip habitats and that sturgeon congregated at the confluence of major tributaries?

11. Page 68, 5th citation – Correct spelling of the word "Assessment".

CHAPTER 2

1. General Comment – The 57 pallid sturgeon collected with trotlines by CERC should be pooled with the 79 pallid sturgeon collected by SIUC and MoDOC for analysis of demographics and habitat use, including size distribution information and comparisons with shovelnose sturgeon.

2. Page 84, bottom of page – This should be the "un-impounded Upper Mississippi River, also called the Middle Mississippi River"....

3. Page 85, 2nd complete sentence – Add "impounded" to Upper Mississippi River.

4. Page 85 – This would appear to be an inaccurate statement regarding pallid sturgeon habitat preferences. Hurley et al. (2004) report that pallid sturgeon demonstrated a negative selection for main channel habitat. Koch et al. (this paper) indicate nearly identical results. Hurley et al. (2004) indicate a positive selection (preference) for main channel border, downstream island tips, between wing-dam and wing-dam tip habitats.

5. Page 86, 1st full paragraph, 4th sentence The reference study was conducted in response to the Biological Opinion for Operation and Maintenance of the 9-Foot Navigation Channel, USFWS 2000, not the cited Biological Opinion.

6. Page 88, last sentence – The Chain of Rocks reach is a complex of natural rock/riffle habitat. However, the Chain of Rocks low water dam is not a natural structure, but was constructed by the Corps of Engineers to maintain water levels for navigation upriver to Mel Price Locks and Dam. This should be clarified.

7. Page 90, bottom of page – "Hertzog" should be changed to Herzog to correct the spelling.

8. Page 92, top of page – Were any of the shovelnose sturgeon scanned for coded wire tags?

9. Page 92, bottom of page – The percentage of lake sturgeon containing coded wire tags should be provided.

10. Page 93, top of page – The rkm should be identified for captures of Stonecats (e.g., "locations between rkm 576 and ???").

11. Page 94, 1st paragraph – Based on data in Table 2, it appears that the higher ratio of pallid sturgeon to shovelnose sturgeon at the Chain of Rocks can be attributed to the large number of shovelnose sturgeon that aggregate there, although it also appears that pallid sturgeon also aggregate at that location. What is the likelihood that the Low Water Dam may be preventing passage of these fish to upstream spawning locations?

12. Page 94, 2nd paragraph, 5th sentence – This sentence would indicate the mean length of shovelnose sturgeon was statistically the same in three reaches, not two as stated. However, the data in Table 3, if labeled correctly would support two reaches being statistically the same. This should be clarified.

13. Page 94, 2nd paragraph – It is interesting to note that similar to data in Chapter 1, the smallest pallid sturgeon captured with trotlines was 40.5 cm FL, while the smallest shovelnose sturgeon collected was 26.5 cm FL. It does not appear that the gear is biased to only larger (e.g., > 40 cm FL) sturgeon. Thus, what would explain the lack of capturing pallid sturgeon < 40 cm FL? Is it possible that the character indices are not distinguishing pallid sturgeon and shovelnose sturgeon at lengths less than 40 cm FL?

14. Page 96, 1st full paragraph – Do the results of this analysis hold true when the pallid sturgeon collected by SIUC and MoDOC are included?

15. Page 97, top of page – The recapture of one hatchery released sturgeon with a floy tag does not indicate an overall high retention rate of these tags for all the fish released.

16. Page 105, 6th citation – "Hertzog" should be changed to "Herzog" to correct the spelling.

17. Page 107, 3rd citation – This citation is incorrect. The correct citation is: U.S. Fish and Wildlife Service. 2000. Final Biological Opinion for the Operation and Maintenance of the 9-Foot Navigation Channel on the Upper Mississippi River. Prepared by U.S. Fish and Wildlife Service Rock Island Field Office, Rock Island, Illinois; Marion Sub-Office, Marion, Illinois; Twin Cities Field Office, Bloomington, Minnesota, USA.

16. Page 110, Table 3 – Why were data for non-targeted sites excluded from this analysis?

CHAPTER 3

1. General Comment - This chapter contains habitat data based on telemetered fish. All habitat and movement data should be evaluated together to give a better understanding of pallid sturgeon habitat use and movement (e.g., combine telemetry data, trotline data, catch-per-unit-effort data, trawling data, etc. to give the full picture).

2. General Question – How were data from fish with many relocations compared to fish with only a few locations (e.g., some fish with many locations could bias the data)? Habitat selectivity could be biased with some fish using many different types of habitats and with many relocations versus some fish using few types of habitat or with few locations. It appears that all relocations were pooled together for the analysis.

3. Page 115, 1st paragraph, last sentence – Recommend changing "establishment" to "conservation" as the MMR already has an established population of pallid sturgeon.

4. Page 120, Top of Page Corps of Engineers bathymetry maps of 2001 are of a better resolution than the 1999 maps. It is recommended that these maps be used for determining the area of each macrohabitat.

5. Page 122, top of page Habitat selectivity should be analyzed to determine differences based on age, size or sex.

6. Page 123, top of page, 5th sentence – Appendix has movement data for 63 pallid sturgeon. The document states that 612 locations were recorded for 84 sturgeon. Where are the data for the remaining 21 sturgeon?

7. Pages 123-124 – How do the observed movement patterns correlate with prior telemetry studies in the MMR (e.g., Hurley et al. 2004). Are there any different patterns revealed by considering the size, age or sex of the fish?

8. Page 127, 1st full paragraph, 2nd sentence – This indicates multiple locations of pallid sturgeon at the Meremac River confluence and the Kaskaskia River confluence. However, the Executive Summary states that pallid sturgeon were not located in tributary mouths. While the mapping used with the telemetry data probably classified those fish congregating that the confluence of major rivers as occurring in the main channel, the tributaries are the apparent reason for the congregations. This is an important factor for consideration.

9. Pages 127-132 This habitat use doesn't include habitat data for fish collected through trawling, trotlines, or other methods? All the data should be analyzed in order to best determine habitat use (preference or selectivity) for pallid sturgeon.

10. Page 128, top of page 2nd full sentence – This indicates that pallids were rarely in water levels less than 3-m deep (2% of the time). However, Table 10 indicates pallid sturgeon occurred in water levels 0-3 m in depth 14% of the time.

11. Page 128, top of page 3rd full sentence – This states that pallid sturgeon frequented habitats where velocities averaged 90 cm/sec. However the ADCP profiles in Appendix B would indicate pallid sturgeon in areas with velocities generally less than 80 cm/sec and most in areas with velocities 20-60 cm/sec.

12. Page 128, 1st full paragraph, 2nd sentence – This states that pallid sturgeon were never found on island tips. However, in Chapter 1, during random and directed sampling in 2004-2005 island tip habitat was correlated with CPUE. This would indicate a significant degree of use of island tip habitats. The results of the telemetry study would seem to be based on the very small percentage of island tip and tributary mouth habitat occurring on the habitat classification maps, making the probability of relocating pallid sturgeon in these habitats extremely low (e.g., unlikely to occur). As mentioned above for tributary mouths, it is likely that pallid sturgeon are using the habitat structure associated with the presence of islands (e.g., island tips), but these relocations are classified as occurring in the main channel. This should be explained in the report.

13. Page 128-129 – Are there any differences in selectivity between sexes, sizes or age class?

14. Page 129-130 – Are the percentages of observations biased by multiple observations of some fish? How does river stage affect the results (e.g., are all habitats equally available at all river stages)? For example, side channels were used most often during spring. However, were these available (accessible) during summer, spring and fall and not used or unavailable to fish.

15. Pages 130-131 – Did the differences in habitat selectivity occur as a result of some habitat types being unavailable at certain water levels? Was this considered in the analysis?

16. Page 140, 1st full paragraph, 4th sentence This notes that study fish were not found to congregate. However, page 12 of the Executive Summary notes that spring aggregations did occur. What is the distinction here?

17. Page 141, 2nd complete sentence – Add the word "dam" following "lowhead".

18. Page 145, bottom of page, 4th sentence – Change "bodies" to "bodied".

19. Page 149, top of page, 2nd full sentence – Does the diet data for pallid sturgeon support this assumption (e.g., do pallid sturgeon feed on more invertebrates during the summer months compared to the rest of the year)?

20. Page 172, Figure 1 The WTU habitat type is not identified in the figure. The acronyms WD and WT are not described in the text.

21. Pages 173 and 174, Figures 2 and 3 The graphs are labeled 2003 and 2004, but the caption states 2005 as the year.

22. Page 185, Figure 14 – It should be noted that not all habitat types are available during all seasons.

23. Page 186, Figure 15 – These figures show all habitat types to be equally available during all seasons. A more accurate picture could be presented if the habitat available was adjusted for each season based on average river stages.

24. Pages 234-236, Figures C-1 to C-3 – There appears to be significant between year differences in habitat use indicated by these figures. For example, during winter 2003 wind dike habitats were used almost exclusively, however, this use dropped significantly in winter 2004. In summer 2003 wing dike habitats were not used, however, these habitats were used to a great extent in summer 2004. Can these yearly differences in habitat use be explained?

25. Pages 239-241, Figures C-6 to C-8 – Same comment as above. There appear to be significant between year differences in habitat use indicated by these figures. Can these differences in habitat use be explained?

CHAPTER 4

1. General Comment – What role does the results of this study play in *Scaphirhynchus* spp. management, particularly in the MMR? What adjustments, if any, to current management need tobe made? What is the probability that smaller pallid sturgeon are being misidentified as shovelnose sturgeon?

2. Page 245, Introduction, 3rd Sentence The U.S. Fish and Wildlife Service (2004) citation should be changed as follows: "U.S. Fish and Wildlife Service's Final Biological Opinion for the Operation and Maintenance of the 9-Foot Navigation Channel on the Upper Mississippi River System (USFWS 2000)".

3. Page 266, 8th citation – Delete this citation and modify per above comment.

CHAPTER 5

1. Page 291, top of page – It appears something is missing from this sentence (e.g., "based on a ?? and a morphological character index").

2. Page 303, Acknowledgements – Section 3 should be changed to Region 3.

3. Page 336, 1st full paragraph, last sentence – Change "form" to "from".

CHAPTER 6

1. This chapter contains very little demographic information for the pallid sturgeon. In addition to the instantaneous rate of mortality, the report should also provide information on the density of pallid sturgeon, age (range, mean, etc.), length at age relationship and spawning potential ratio. Some discussion should be provided as to how these data compare to the LMR and the Missouri River pallid sturgeon. A discussion of factors that may be influencing pallid sturgeon demographics is appropriate and should be included, however, the information regarding mortality of shovelnose sturgeon and the efficacy of regulation changes for shovelnose sturgeon is better suited to another forum. We recommend the chapter be revised to place the emphasis on reporting data for pallid sturgeon.

2. Page 358, top of page, last sentence – The pallid sturgeon pectoral fin ray collection protocol for this study specified that a 4-11mm section would be removed. Did the removal of a 25-mm section from pallid sturgeon occur, or is this a typographical error? Information on the process, accuracy, precision and results of aging pallid sturgeon should be presented. Were any adverse effects observed for recaptures?

3. Page 358, Age, Growth and Mortality, 1st paragraph - How many pallid sturgeon rays were discarded? Pallid sturgeon growth should be assessed and reported. Some discussion is warranted regarding how the accuracy and precision of age estimates may affect calculated growth and mortality rates.

4. Page 359, Year Class Strength What other independent variables may be influencing year class strength in pallid sturgeon?

5. Page 362, Adult Density, last sentence - Population estimates for pallid sturgeon should be provided here with an explanation of how the estimate was derived.

CHAPTER 7

1. General Comment – This paper pertains solely to shovelnose sturgeon. Some discussion as to how this information pertains to pallid sturgeon restoration and conservation should be included. Otherwise, this chapter should be omitted from this report.

2. Page 391, top of page, 4th sentence There is some evidence that shovelnose sturgeon and/or pallid sturgeon also spawn in late summer or early fall based on collections of very small sturgeon during these timeframes.

CHAPTER 8

1. General Comment - A second part of the diet study was to determine prey selectivity, versus abundance, by sampling macroinvertebrates where pallid sturgeon were captured. Where are the results of this effort? How can data in this study assist in development of the Conservation and Restoration Plan for pallid sturgeon in the MMR?

2. Page 410, Table 1 – Relative weight should be determined for these pallid sturgeon so their condition can be compared to pallid sturgeon in other parts of the range. Were there any differences in feeding habits between sex, size or age of these fish?

3. Page 411, top of page and page 412, Table 2 – As discussed, winter samples of prey from the MMR were exceptionally low in numbers in diversity. However, the condition factor for these fish was not significantly different from the fish in the LMR. What could explain such a low number of prey being taken in the winter in the MMR? Is there any correlation between the numbers or diversity of prey eaten and length or weight of pallid sturgeon? Are there any long-term implications of not feeding well in winter?

CHAPTER 9

1. General Comment – While the information in this paper may be useful, it is more suitable to other publications and not this report.

2. Page 421, 2nd paragraph, 10th sentence – Delete "of they".

3. Page 422, Results, 1st paragraph, 1st sentence – This appears to be a run-on sentence.

CHAPTER 10

1. General comment - Data on aging of pallid sturgeon is lacking. Information on the process, accuracy, precision and results of aging pallid sturgeon should be presented unless otherwise discussed in the report. Otherwise, this chapter is more appropriate in other forums.

REVIEWER 8

1. General Comment -- I think what you guys put together is commendable and sets a great example of teamwork for those of us involved in this process.

2. Page 408, Introduction, 2nd paragraph, 3rd sentence – This sentence is awkward. An editorial change would be appropriate. Either "would not be obtained" or "were not obtained".

Illinois Department of
Natural Resources
One Natural Resources Way • Springfield, Illinois 62702-1271
217.785.0075 • http://dnr.state.il.us

Rod R. Blagojevich, Governor
[redacted]
Sam Flood, Acting Director

January 19, 2007

Mr. Lewis F. Setliff III
Colonel, U.S. Army
District Engineer
Department of the Army
St. Louis District, Corps of Engineers
1222 Spruce Street
St. Louis, Missouri 63103-2833

Dear Colonel Setliff:

I am in receipt of your November 9, 2006 request for the State of Illinois, Department of Natural Resources to provide a technical review and comment on the draft document entitled, "Current Status of the Pallid Sturgeon in the Middle Mississippi River: Habitat, Movement, and Demographics". I appreciate the opportunity to participate in your project and review draft documents produced by study contractors.

Members of my staff who have extensive experience with the fisheries resources of the Mississippi River, both from management and research perspectives, have provided some additional relevant fisheries information and detailed technical comments concerning the draft document for your consideration. I would like to make some prefacing comments about Illinois DNR fisheries management activities and the draft document which are important to know before reading the remainder of my comments and subsequent technical review comments provided by Illinois DNR fisheries staff.

The Illinois DNR remains committed to protection of the pallid sturgeon and their known habitats in the Illinois portion of the Mississippi River. Sportfishing and commercial fishing activities in Illinois waters are regulated in order to insure the long-term sustainability of all sturgeon populations, including the recovery of the pallid sturgeon.

As a result, the Illinois DNR has previously taken extraordinary measures to protect pallid sturgeon and provide for their recovery by prohibiting the harvest of pallid sturgeon by Illinois regulation for both sport and commercial fishing. Any pallid sturgeon incidentally taken by sport or commercial fishermen, must be immediately returned to the water unharmed. In addition, by Illinois Revised Statute, *515 ILCS 5/15-105* commercial fishermen may not be within 300 yards of the dams on the Mississippi River thereby providing a "fish refuge" for pallids below each dam which concentrates sturgeon at certain times of the year. Further, large river tributaries to the Mississippi River (such as the Rock River) serve as major "fish refuges and spawning areas" for sturgeon and commercial fishing is prohibited in most river tributaries (except for the Illinois River).

In 2007, the new sportfishing season regulations prohibit snagging of any fish below the Chain of Rocks dam near Alton, Illinois. This area has been identified as one of the most heavily used areas by spawning sturgeon. Both Illinois and Missouri will be implementing the regulation. Also, Illinois and Missouri are implementing a 24"-32" harvest slot-length limit for commercial harvest of shovelnose sturgeon in the shared waters of the Mississippi River.

Shovelnose less than 24" and greater than 32" in eye to fork length are protected and must be returned immediately to the water unharmed.

Concerning the draft report, I would summarize my views on the substance of the document as follows.

1. The science presented did not support the conclusions reached by the authors that sturgeon are declining in the middle Mississippi River (open river). Data from the Illinois DNR for the Illinois portion of the open river demonstrates that harvest levels are very low, relatively steady year to year and are not increasing.

2. Need a baseline population level for pallid sturgeon to enable the authors to determine if pallids are less or more abundant now and measure the progress made by protection activities implemented by States and Federal government agencies.

3. Investigations are needed into other possible factors (different than commercial harvest) which may be contributing (either positively or negatively) to the long-term sustainability and recovery (need target level of abundance) of the pallid sturgeon (such as flow rates, sedimentation, navigation traffic, or contaminants). What measures could be implemented by the States and Federal government agencies to meet the target levels of recovery for the pallid sturgeon?

4. Need an assessment of available spawning habitat. Is it adequate for meeting the recovery target or does more spawning habitat need to be developed?

5. I cannot reach the same conclusion from the data presented in the draft document as stated in your letter that either illegal or incidental commercial harvest may be a major factor limiting the potential to recover the species in the Middle Mississippi River.

Finally, I believe that the authors of the draft document have made every effort to meet the goals of the research project and generally made strides in furthering the base knowledge on the pallid sturgeon in the Middle Mississippi River. The greatest weakness of the draft document is that many of the conclusions reached were not supported by the data presented. I am sure substantial revisions will be necessary for the document to be useable by the U.S. Army Corps.

If you have any question concerning my comments and the technical review comments, please contact me or Mr. Mike Conlin, Director of the Office of Resource Conservation.

Sincerely,

Sam Flood

Sam Flood
Acting Director

Cc: Mike Conlin, Director
Office of Resource Conservation

General comments:

No where in the report is there any mention of uncertainty or error associated with the data presented. This does not bode well for the conclusions drawn and many of these chapters would not withstand critical peer-review.

With that said, some of the data presented here is provocative and could be representative of a fish population that is in trouble. In particular, the life history of sturgeon make them very prone to collapse (late maturity, low fecundity, high market value for caviar, variable river conditions). Other possible alternatives (not just commercial harvest) should be investigated for their contribution to annual mortality of pallid sturgeon.

Fishing and loss or degradation of spawning and juvenile rearing habitat are *additive* to this problem. Fish populations collapse due to an insufficient number of adults (overharvest) and/or poor juvenile survivorship (habitat degradation, etc.).

Specific comments by page follows:

Page 2—Where are records of historic pallid sturgeon abundances? Was their *there* a historic gradient in abundance in the MS river? Lee et al. said they were rare compared to shovelnoses in *1978!*They were also rare in the early *1900's. Is* the gradient caused by fishing? Fishing may have something to do with it.

Page 3 — Mortality estimates are highly uncertain (remember here that pallids may represent a species that is more prone to collapse due to their life histories)

Page 3 — Little faith in the population estimates presented. How can you calculate this for the river? Confidence intervals?

Page 4—Here and throughout, the author's are drawing conclusions from shovelnose sturgeon. Is this acceptable?

Page 4—Not many fishes show a stock-recruitment relationship that is meaningful. Why would sturgeon differ? Shovelnose may be showing depensatory dynamics, can this be transferred to pallid?

Page 6 — Do we have any indications for past abundances of pallids? This is really important. Is this just a rare species that doesn't occur at super high abundances (with that said, is three years of data sufficient?)

Page 9 -- What were the confidence intervals on the pallid sturgeon population estimate with 143 captures and 4 recaps? Obviously a low population, but not a lot of confidence in that. Pallids were all large. More suggestive of problems with spawning and rearing habitat as opposed to recruitment overfishing of adults. Or gear bias. Ratios of shovelnose to pallids seem high, but aren't abnormal according to Lee et al.

Page 10 -- All fish were 5-15 years old and presumably reproductive? Again, seems like juvenile bottleneck, not overfishing -- no asymptotic length may suggest cropping of largest individuals, but you can calculate the asymptotic length for pallids using Ford-Walford plots. Using this method the asymptotic length is about 900 mm

Page 10 – Were there any gear types that focused on larger or smaller pallids?

Page 13 – Suggests intersexuals as potential cause of decline. What does this have to do with overfishing?

Page 14 – Bold, but true. Sturgeon have a life history making them very prone to collapse. Especially, the choice not to spawn every year. Populations collapse for two reasons. Not enough adults, poor juvenile survivorship, or both.

Page 15 – What is this index of annual year class strength and the harvest of shovelnose? The index may be reliable if they calculated the catch curves with any certainty. The harvest of shovelnose needs to be standardized.

Page 15 – In past 5 years, age structure has increased with no year classes. This is too short of time to determine collapse. Many fish do this. But, is a red flag.

Page 16 – Mortality rate same for pallids as shovelnose? Coincidence? They only aged 75 individuals over 10 age classes. This can be highly variable. And, no young fish were represented.

Page 16-17 – What about Lee's phenomenon? If pallid #'s are declining, is there not a concomitant decrease in age at maturity and increase in growth rates?

Page 17 – Using the upper mortality rate for shovelnose PE's is precautionary. Not necessarily right.

Page 18 – High variability in the pallid PE

Page 19 – It took 10 years for hatchery pallids to recruit to "their" gears. Suggestive of not sampling for small pallids. Gear bias.

Page 19 – Admission that little historical data exists for pallids and historical low abundances.

Page 21 – How do you figure that a stock-recruit model will help you predict anything when spawning is erratic?

Page 33 – This sort of L-F distribution could be very representative of a gear-bias towards larger fish.

Page 34 – Is sexual size dimorphism in pallid sturgeon evident ?

Page 34 – Asymptotic length can be estimated from data using a Ford-Walford plot. It's around 900 mm. That's not precise because I don't have the data, but it could be done. In any case, the growth relationship they have shown is not linear.

Page 36 – Yes, moving upstream to spawn. Why is it unlikely that the barrier dam is causing the population troubles?

Page 37 -- Really curious. How do you estimate year class strength from catch curves? Where is this shown? References? Needs a lot more explanation and justification. Where do the sample sizes come from? They don't match up with data points in the regression. N = 3 years is not a good sample size for an analysis like this.

Page 38 — There is nothing abnormal about this figure in fish populations at all, especially over 4 years. Could mean several things. Gill nets didn't target young fishes Recruitment is variable (big surprise). Where did all of the fish come from in 2005? Increased effort? Again, gear bias potential Not enough information given variability of the river.

Page 39 — Again, could be size-selective harvest or gear bias towards medium-sized individuals

Chapter 1

Page 42 — Why were the authors willing to be wrong 15 times out of 100 in your statistical analyses? Although not a rule, p = 0.05 is generally more acceptable.

Page 43 --- Smaller meshes did catch smaller shovelnose. Are these comparable?

Page 44 -— Makes great claim for sexually dimorphic growth due to age at maturity. Overharvest could be a huge factor. In a collapsing population, we might expect to see all females over time. Unless, harvest is focusing upon them. Very interesting. Do female pallids live longer than male pallids?

Page 51 — Why was sturgeon CPUE used as a predictor variable and not a response variable? Why p = 0.15 for inclusion? Indicator variables are your predictors here!

Page 52 — Is it right to assume that individuals less than 12 cm are all shovelnoses? This will surely make all the data look like there are no small pallids out there.

Page 53 --- Flawed multiple regression statistical analysis. Why wasn't Mallow's Cp, AIC, or maximum likelihood used to calculate best model? Penalization for more parameters. Lots of parameters here.- Low correlation explained Where do interaction terms come from when the main predictor is not included in the model itself? This statistical test says nothing. Multicolinearity issues?

Page 54 — Same problem as above. How do you even interpret the interactions? Do they add much to the model? Low p-values are simply a function of sample sizes!

Page 63 — The conclusions of this page are not supported by the data in many areas. Last sentence is not supported. Speculation!

Page 74 — As seen here, additional parameters are adding nothing to the model. This needs to be accounted for in a statistical test. See Draper's book.

Page 80-81 --- Indeed, no small pallid sturgeon were captured, in contrast to shovelnoses.

Chapter 2

Page 83 — The trotlines only seem to target larger sturgeon. Is their on ontogenetic diet shift in sturgeon such that trotlines are ineffective for catching small fish? Are hook sizes to large to target smaller sturgeon?

Page 84 — Pallid sturgeon is listed as historically being low in abundance. Only 250 observations in a 70 year period!

Page 85 — Statement suggests that there are many variables causing declines in pallid numbers.

Page 92 — More pallids were captured in the LMR compared to the MMR. Vice versa for shovelnose. What are the regulations on sturgeon in the LMR states? Since several LMR states have closed the sturgeon fishery, this may be suggestive of overfishing. But, shovelnose seem to be doing fine in the MMR (open river portion).

Page 94 – A 265 mm shovelnose was captured by trotline. Nothing smaller than 405 mm for pallids on trotlines.

Page 95 – Ratios of pallids:shovelnoses are not out of the ordinary

Page 108 – All common names should be lower case. The scientific name for walleye is *Sander vitreus* and for sauger *Sander canadensis*.

Chapter 3

Page 120 – This method may not adequately characterize movement (telemetry). The time between marking locations may be too long if there are short term movements.

Page 121 – Why Bonferroni? How many comparisons? Why alpha = 0.10?

Page 121 – Using AIC is the proper way to select model

Page 133 – life history for collapse, SSD

Page 138 – More suggestion of SSD, males spawning longer

Page 142 – Protecting COR seems reasonable

Pallid sturgeon are already offered protection at the COR. They appear to be doing quite well under the current regulations at this site. In my opinion, no further commercial fishing restrictions are necessary at this site!

Chapter 4

Page 244 -- If this report is about pallids, why is there so much inference from other sturgeon? How do we know that hybridization has not always occurred?

Page 244 -- Morphological variation is less downstream in MR. Author's suggesting that hybridization is a consequence of overfishing in MMR?

Page 247 -- Again, this difficulty of identifying young specimens and assuming they are shovelnoses. Until we can actually identify young, how can any claims be made about lack of reproduction. 10 year old pallids have to come from somewhere. Page 250 – Were the pallids collected from the hatchery genetically proven to be true pallids?

Page 260 -- How are multivariate analyses going to help identification in the field? They don't. Difficult to interpret.

Page 261 -- Better method, but not functional

Page 261-262 – Conflicting views. 261 suggests more hybrids in higher abundance populations. 262 says higher morphological variance is indicative of hybridization in smaller populations of MMR.
Morphometric = measured variables, Meristic = counted variables

Chapter 5 -- no comments

Chapter 6

Page 353 – In general, harvested populations respond with better than average recruitment. Stock-recruitment relationships have been around for some time. Yet, sturgeon are different beasts.

Page 353 – Commercial harvest of shovelnose is not increasing in the middle MR (open river portion) see Illinois DNR figure 1 and 2 at end of these comments. Are populations going down? What is this based on? PE's? How long of a trend?

Page 353 – How can the authors say that cohort strength is going down when they can't effectively sample juveniles?

Page 354 – This statement is plain false. Most stocks are fine or maintained at about 50% of historic abundances. Exactly the way they are managed to be.

Page 354 – Collapse is caused by not enough adults, poor juvenile survivorship, or BOTH! Not just overfishing. And, depensation has not really been observed in fish stocks

Page 355 — Yes, you can determine Z from this, but how have you calculate the proportions of each age class with any amount of accuracy given that mark-recapture PE's for shovelnose or pallids are very uncertain? There is huge uncertainty in estimating Z accurately, especially for rivers. This problem should be bounded, not a certainty.

Page 356 – Yes, perhaps true again and referenced. But, how did you determine any sort of frequency in age classes? CPUE? This can't be used but for either directed or random effort. These values cannot be taken as accurate.

Page 356 – Are marine fisheries SPR's comparable to sturgeon? Probably not. Maybe for sharks. Other marine fishes likely mature faster and are more fecund.

Page 357 – Why would you use winter directed gill net sampling to estimate abundances when it results in the lowest CPUE of any season? How would your results look if you used summer, fall, spring CPUE? This needs to be acknowledged. Further, gill net CPUE will be a very poor measure of actual abundances.

Page 358 – What were your sample sizes for developing the catch curves? How did you estimate young fish abundances when you don't capture them? Lots of questions about this analysis. Need to see the data and catch curves.

Page 359 – This is not a reflection of what mortality rates are! You need to know the actual frequencies of each age class and the variability around those estimates. Plus, by combining years, you are assuming that mortality is a constant among years which is usually not the case.

Page 359 – What units were commercial harvest presented in? Biomass, #'s, what? CPUE? Harvest is presented in kg. This creates more flaws. You can't use this. Yes, this looks like harvest is increasing, but how many are out there? You need to standardize this by effort, river mile, ha, or a proportion of the current population. This can be really misleading. In most fisheries, harvest correlates positively with density. Therefore, you may simply be seeing compensatory recruitment dynamics as presented here. Higher adult abundances with decreases in juvenile survivorship, not the other way around.

Page 362 – You cannot say that shovelnose harvest increased without some standardization. This will confound the results. In general, harvest increases with fish density. Not the other way around unless technology or focusing on key areas is a major issue. Needs to be standardized by effort.

Page 362 – Are 5 data points and years sufficient to determine that abundances have declined? Winter CPUE will already provide low numbers and CPUE is not a measure of abundances. Basin-wide harvest needs to be standardized. How many fish were actually caught? How many were aged to determine mortality rates? How did the authors even estimate mortality rates for young age classes. None were caught. Having that missing gap in the age frequencies MAY artificially inflate your annual mortality rate.

Page 363 — The statement about a higher Linf due to commercial exploitation is completely unfounded and not supported by the data.

Page 363 — Again harvest needs to be standardized or you cannot draw any conclusions. This is like saying there are more salmon in Lake Superior compared to Lake Michigan. Of course there might be! But, how do densities compare? That is the true metric, just like mortality rate or fishing rate.

Page 364 — Fishing mortality rate cannot be determined from total harvest without an estimate of effort or abundance.

Page 365 — Basically tries to justify that the author can't say anything about young age classes. This is very important.

Page 365 — Of course mortality rates are going to be lower if there is lower harvest.

Page 366 — how did the author estimate the current level of harvest? It is not standardized. Impossible.

Page 366 — There are big questions about Lee's phenomenon in all of this. At different growth rates, maturation schedules will be different.

Page 367 — The last paragraph states shovelnose sturgeon harvest has been largely unregulated. Not true for Illinois waters.

Page 372 — Natural mortality rates this high seem unreasonable for sturgeon. Is the proportion of females spawning something that is currently peer-reviewed?

Page 373 — This is a significant regression when the year 2001 is included (a significant increase). Year 2001 is an outlier. When removed, the regression is no longer significant. What are harvest rates for 2003-2006? Why weren't those data included?

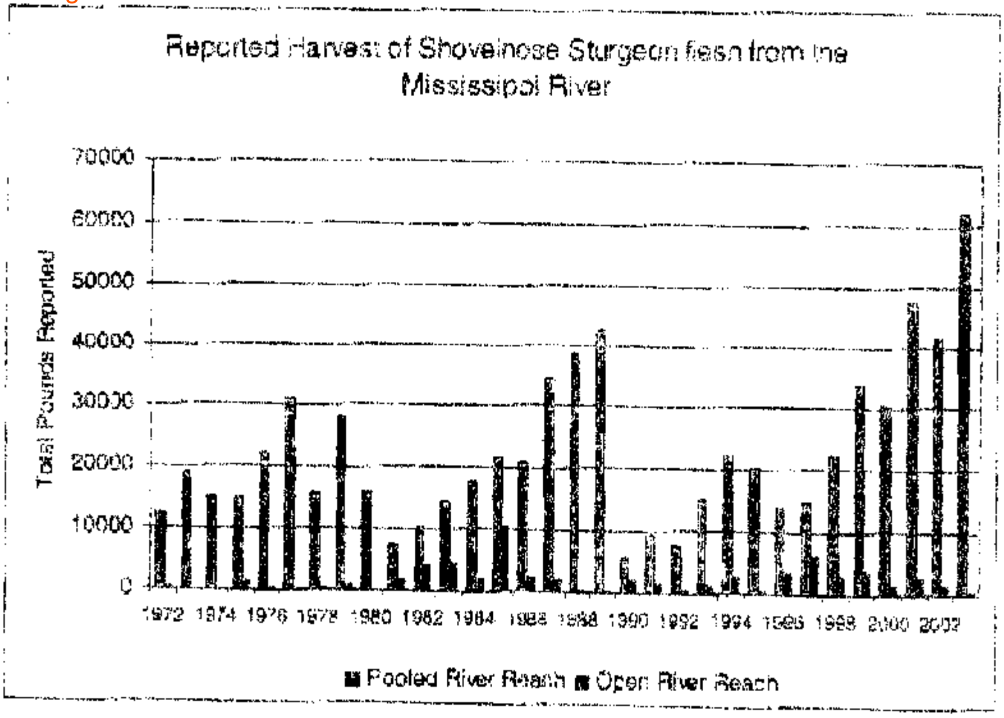
Page 375 — Why would harvest be down in years when abundances are high? This could very well be the opposite pattern. There should be more harvest when abundances are higher. This is standard fisheries stuff. This is likely more a reflection of an inaccurate measure of ambient sturgeon abundances.

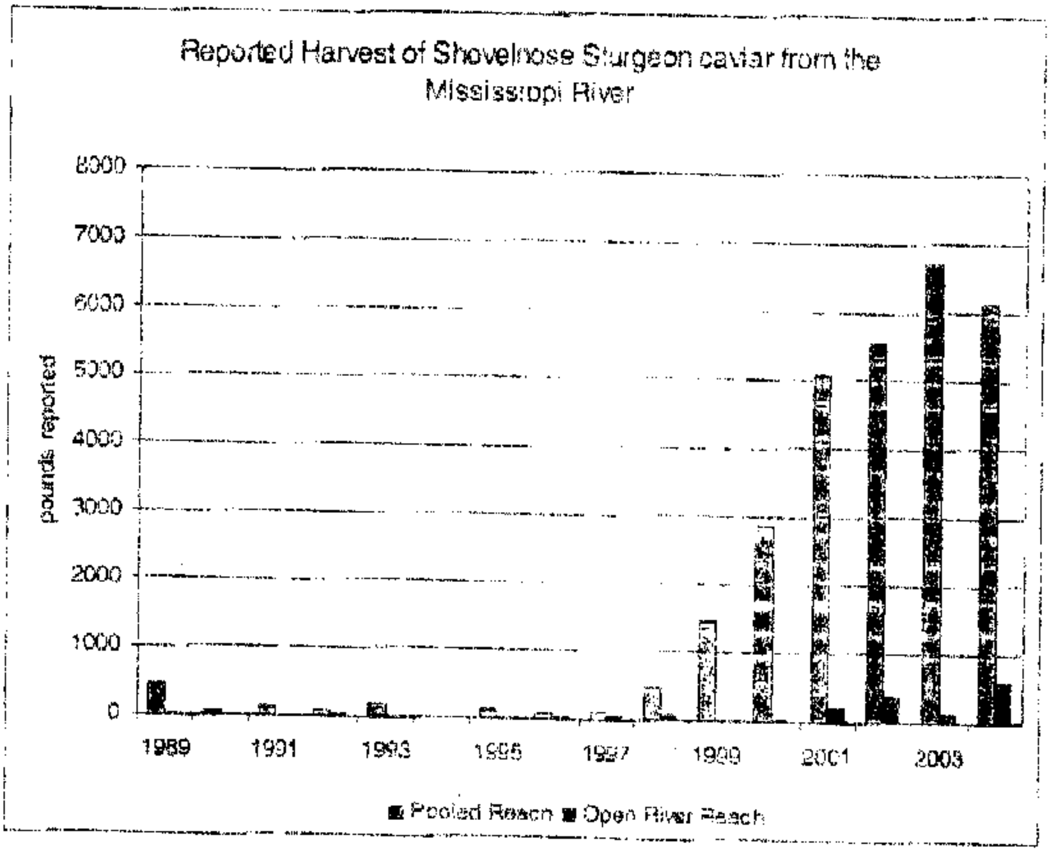
Chapter 7

Page 380 — The claim that sturgeon harvest has increased is tenuous. It is not standardized or supported by the data in the draft report.

(see ILDNR figure 1 and 2 for additional information). Open river harvest of shovelnose sturgeon flesh remains with the annual variation of harvest data over the past 25 years. No trend in flesh harvest – remaining steady. Only about 5-10% of total annual harvest of sturgeon flesh from Mississippi River comes from the open river portion. Pallid sturgeon occur in the open river below the Missouri River. Pooled portion of the Mississippi River is generally accepted to be outside of the normal range of the Pallid Sturgeon.

ILDNR Figures 1 and 2. Taken from annual commercial harvest records.





Page 380 — High likelihood that this species is sexually size dimorphic.

Page 381 — Sex ratios of 4:1 male:female may not be a bad thing if sturgeon are sexually dimorphic. Highly skewed male sex ratios are generally observed in very healthy fish populations. Problems arise when sex ratios are skewed to females due to SSD. This may not be the case for sturgeon though because females are targeted.

Page 384 — What's the problem? Sex ratios are 1:1.

This concludes our technical review comments. This research effort is a good beginning, but efforts to resolve issues needs to continue.

Headquarters
2901 West Truman Boulevard, P.O. Box 180, Jefferson City, Missouri 65102-0180
Telephone: 573/751-4115 ▲ Missouri Relay Center: 1-800-735-2966 (TDD)

JOHN D. HOSKINS, Director

June 6, 2007

Dr. Thomas Keevin
USACOE, St. Louis District
1222 Spruce Street
St. Louis, Missouri 63103-2833

Dear Dr. Keevin:

Thank you for the opportunity to review the draft document "Current Status of the Pallid Sturgeon (*Scaphirhynchus albus*) in the Middle Mississippi River: Habitat, Movement and Demographics." While the work documented in this draft report was required as part of the Biological Opinion issued for navigation channel maintenance, we recognize and appreciate the extensive efforts of the U.S. Army Corps of Engineers (Corps) to gather scientific information on this species. The Missouri Department of Conservation (Department) is very interested in the long-term survival of the pallid sturgeon and the scientific results of the four-year study presented in the draft document will aid in further development of management and research needs for the pallid sturgeon.

The draft document summarizes existing knowledge and identifies information gaps that still need to be addressed for successful management of the pallid sturgeon. As you know, Department personnel participated in preparing several of the document's chapters. Therefore, our comments on the draft document are few and relate primarily to future actions using this information and to certain knowledge gaps identified within the text.

We understand that one of the next steps of the Corps, as part of the issued Biological Opinion, is to develop a conservation and restoration plan for the pallid sturgeon. We anticipate that many, if not all, of the knowledge gaps identified in the draft document will be incorporated into the plan, with tasks identified to address each gap. Building upon the efforts and results of the studies included in the draft document will help target those areas of greatest information need. Department staff familiar with this species and its management will continue to participate in the recovery of this species and aid in the development of the required conservation and restoration plan.

As identified in the draft document (i.e., Figure 2), there are major knowledge gaps for pallid sturgeon reproduction and these gaps are critical for developing a recovery plan. The Department agrees that addressing these knowledge gaps is vitally important to maintaining pallid sturgeon in the Middle Mississippi River. We need to better understand where spawning and rearing occurs, the quality and availability of existing spawning habitat, and factors necessary for successful pallid sturgeon reproduction and recruitment. Additional studies in these areas are necessary for developing a successful conservation strategy. Once we better understand the areas and factors necessary for spawning and rearing success, actions to eliminate or reduce disturbance during critical periods can be identified, developed and implemented. However, we do not recommend waiting for this information before proceeding with the conservation and restoration plan. This information and other information needs and studies should instead be developed concurrently with the plan, and incorporated into the plan as the information becomes available.

Another information gap is understanding intra- and inter-basin movement of pallid sturgeon. Telemetry arrays for tracking the movement of tagged fish should be expanded and enhanced. Additional efforts should be directed at tracking mature females to better understand movements associated with spawning.

The Department stands ready to continue efforts with the Corps, and other river partners, to learn more about the pallid sturgeon in the Middle Mississippi River and to successfully manage for its continued existence. Mr. Dave Herzog and Mr. Robert Hrabik of the Department's Resource Science Division will continue to be the Department's primary contacts for sturgeon studies.

Sincerely,

JANET STERNBURG
POLICY COORDINATOR

c: Mr. Steve Eder, Mr. Ron Dent, Mr. Robert Hrabik, Mr. Dave Herzog, Ms. Peggy Horner

Responses to US Fish and Wildlife Service (FWS) Comments:

1. *"Marked up" drafts are made available.* Response: We used these marked up documents from FWS to improve the presentation and clarity of the various chapters in the report, most of which are now published articles.

2. *Trawling included young fish, yet the report did not focus on the habitat associations of these individuals.* Response: The primary goal of the funded research in this report was to identify habitat needs of adult pallid sturgeon, because technology at the time allowed us to only verify species using morphomeristic characters. This was not plausible for young sturgeon. Since then, with guidance from the FWS and fiscal support from the US Army Corps of Engineers (Corps) St Louis District, we have begun processing these young fish for genetics. We also conducted a pilot study in 2008 to collect randomly stratified data specifically for young sturgeon, which the previous study did not do.

3. *Many of the independent reports in the draft report focused on shovelnose sturgeon. Refocus on pallid sturgeon.* Response: The research was conducted to focus on the habitat associations of pallid sturgeon. This is the centerpiece of the report and indeed focuses primarily on pallid sturgeon. In addition, we amassed data on the demographics of both species. First, we are not proponents of using shovelnose sturgeon as a surrogate for pallid sturgeon. However, we can derive some important information about the status of pallid sturgeon by comparing key characteristics of the population to those of their close congener. The primary goal of the Executive Summary plus several contributing chapters is to identify the trajectory of the populations' growth and mortality. For example, knowing that shovelnose sturgeon and pallid sturgeon have similar mortality rates in the MMR, as compared to the unfished lower Mississippi River, we deduced that harvest of adults, primarily females is a significant threat to the recovery of the species.

4. *One of the research objectives was to evaluate pallid sturgeon food preferences by comparing consumed prey to that in the environment.* Response: Identifying prey availability is a difficult, expensive, and time-consuming task. This is further complicated by the fact that adult pallid sturgeon captured at one location may have been feeding in a different location. Our limited resources at the time were devoted to collecting and identifying diets from adult pallids in a non-obtrusive manner, culminating in a publication (and related chapter in this report). We have begun to quantify habitat specific invertebrate distributions in 2008 and will begin to link this to diet patterns/habitat quality in the future.

5. *It is sometimes difficult to assess whether the results are statistically significant*. Response: This is particularly a pertinent concern for the gear-specific comparison including pallid, shovelnose, and lake sturgeon. This chapter has culminated in report that is being revised for publication. It shows that our extensive sampling effort was insufficient in power to compare pallid sturgeon abundance estimates in a statistically significant fashion. Basically, we established an important truth: pallid sturgeon are rare and conventional, randomized sampling will not provide necessary information about habitat use. Also important, we established putative ratios between pallid and shovelnose. Given that we were able to

adequately sample shovelnose sturgeon and estimate their density using multiple techniques, we could estimate pallid population size from this approach.

6. *Better coordinate telemetry efforts with other portions of the pallid sturgeon range beyond MMR*. Response: We recognize the importance of movement of pallid sturgeon into the lower Mississippi River and the Missouri River and have attempted to quantify this in our habitat use and movement chapter and manuscript. Currently, resources are unavailable in the Lower Mississippi River to maintain a coordinated monitoring effort with telemetry. Our group could not afford to use the telemetry technology being used in the Missouri River. Until these issues are resolved, it will be difficult to assess the degree of interconnectedness occurring among reaches.

7. *We recognize the significance of the mortality estimate…* Response: We continue to point out that the major factor probably limiting pallid sturgeon recovery is a lack of females producing young fish. However, if this threat abates, then we need to provide information about how young and surviving adults may find available habitat.

Specific Comments:

REVIEWER 1:

1. *All in all this a great report, full of much needed and useful information.* Response: We try our best.

2. *…pallid to shovelnose ratios can be very misleading.* Response: Agreed. We now emphasize that ratios do not reflect density.

3. *Seasonal influence on patterns?* Response: We tested this further with a power analysis and found that we had insufficient power using the combination of gears in our sampling.

4. *Seasonal differences in catch may skew results.* Response: True. We have insufficient power to say this, although our catch rates were typically highest in spring.

5. *Delete continuing.* Response: Done.

6. *Include column with entire MMR.* Response: The problem with this is that we feel that the Chain of Rocks is so atypical, that information from this area skews inferences we make about the entire reach. In other words, including data from the Chain in our entire MMR estimate may be misleading.

7. *Modify sentence (p. 44).* Response: This chapter has been completely rewritten.

8. *Was pallid sturgeon abundance greater below the Atchafalya than the COR?* Response: This chapter is now a published article. The abstract now says specifically that the abundances were statistically the same.

9. *Most collections from upper Missouri River are from inter-reservoir reaches not the reservoirs themselves.* Response: Noted and clarified.

10. *The density figure may be biased upward due to artificial flow manipulation.* Response: Noted. This statement from Constant et al. (1997) was meant to provide a starting point for reach comparisons. The abundance estimates from this paper are the first to provide a standardized comparison among reaches.

11. *It appears misleading to state that pallid sturgeon prefer main channel environments.* Response: We disagree. They do not “prefer” certain categories of the main channel. However, we have no evidence that they frequent tributaries or other extrachannel areas (e.g., backwater lakes). This is a main channel dweller, although they prefer certain structures in this environment.

12. *Regulation seems to imply flow regulation…* Response: More detail is now provided.

13. *Likely pallid sturgeon are found in the main channel as a result of this being the most abundant habitat.* Response: See our comment to point 11.

14. *Seems odd that it is naturally occurring yet reinforced…* Response: We do not know how the modifications to Chain of Rocks has affected hydrology. However, this turbulent part of the river is very unique and a sturgeon haven.

15. *Does this mean that each reach had comparable effort…* Response: Distribution of effort is in Table 3.

16. *Earlier in the report it indicates that scanning for coded wire tags until fall 2004…* Response: For the specific trotlining effort outlined in this chapter, all fish were scanned. This was not the case for other sampling.

17. *Did the log transform end up in normally distributed data?* Response: Yes.

18. *Lake sturgeon % CWT missing.* Response: Fixed.

19. *Were the data explored to see if there was a significant seasonal interaction?* Response: We had insufficient statistical power to compare the proportions this way.

20. *Table2 may be biased by trotlines. Trotlines tend to bias proportions.* Response: Perhaps. However, our trotlines were never saturated with fish (i.e., nearly all hooks used), thus this problem was probably not an issue.

21. *Obion River pallid is interesting.* Response: Agreed.

22. *High retention of floy tags?* Response: We took this out.

23. *Were not all fish scanned for CWTs in 2006?* Response: They were. But pallids were not specifically caught in the MMR in 2006.

24. *Why was the MMR divided into two reaches?* Response: As noted before, it would be misleading to lump the Chain of Rocks with the remainder of the river. They are simply distinct geomorphologically and biologically.

25. *Pallid:shovelnose ratio incorrect.* Response: fixed.

26. *What was the frequency of tracking?* Response: This chapter has been entirely rewritten, although the original, more inclusive text also is still available. We attempted to track weekly during spring and every 2 weeks the remainder of the year. We tried to cover the entire MMR during each sampling effort.

27. *Any concerns about autocorrelation?* Response: Individuals were treated as replicates. By definition, their behavior is correlated within subjects. This must be taken into account when interpreting the results.

28. *Multiple relocations can inflate sample size.* Response: Agreed. Only a single location per fish per day was used.

29. *Ray et al?* Response: Not included in the final draft.

30. Same as 29.

31. *Should be Region 3.* Response: We missed this in the final publication. Apologies.

32. *How were hatchery fish factored into this?* Response: They were not included in analysis.

33. Wording has been changed.

REVIEWER 2

1. *Authors should better describe triangulation procedures.* Response: Agreed. We modified this information in the text of the manuscript/chapter.

2. *Clear definitions of habitat classifications.* Response: Done in text of manuscript.

3. *Methods do not mention purpose or objectives for hourly survey or adcp. Did they result in useful information?* Response: We now address this in the report. Of course, yes.

4. *Do the authors feel their habitat classifications adequately provide the information needed to manage habitat?* Response: That is a tough question. We are limited by the Cobb classification index we used at the outset. In the refined manuscript now also included with the report, we also explore proximity to known bottom features such as gravel bars. In the Executive Summary, we now posit this issue. Ultimately, the entire range needs similar definitions for management and recovery.

5. *Several questions about movement data.* Response: We have addressed these in the refined manuscript that is associated with the more comprehensive chapter. We separate our analyses in to those done with manual tracking and with automated receivers. The reviewer asks for annual home range. We rarely had data available spanning that time frame.

6. *The authors could better tie their results to management options*. Response: In the manuscript draft, we provide more detailed information about purported habitat needs, specifically as related to

spawning habitat. The issue is that adult densities are so rare that the few individuals do not seem to be limited by habitat at this juncture. Not until adult densities increase will be able to bracket the relative quality of habitat by linking distributions of adults to their condition.

7. *The bar graphs could be combined*. Response: We provided all possible scenarios for comparison. The synthesized (combined) data are in the manuscript draft.

8. *Use of pre- versus post-spawn descriptions unclear.* Response: We assume that after fish complete moving upstream (or occasionally downstream) in spring and temperatures exceed the purported temperature when fish have spawned. In the manuscript draft, we better explain that this is supposition and requires more information.

REVIEWER 3

Stylistic congruence among chapters needed. Response: All of the chapters are now published or formatted for publishing. So, we have made the chapters comparable in style and format.

Make the writing less personal (i.e., strip first person, active voice) and provide statistics. Response: We follow conventional scientific writing style. As for statistical treatment of data, we make this as clear as possible in all chapters (of which most are now published) as well as the Executive Summary.

Executive Summary Comments:

1. *Sample sizes need to be included throughout Executive Summary.* Done.

2. *How many individuals tracked in Executive Summary.* Done.

3. *Mention how many species were defined. Only Wills et al used?* Done.

4. *Temper last paragraph on p. 4*. We now provide an additional citation of research supporting this idea.

5. *Provide Ns for genetically and morphomeristically identified sturgeon.* Done.

6. *Executive summary could logically be divided into the same organization as the Chapters.* We now provide specific reference to the Chapters. It is important to note, however, that some of the material in this summary synthesizes across all chapters and thus is difficult to categorize in this fashion.

7. *Tables in Executive Summary are too specific.* These data are important to telling the synthetic story in this section and need to be included.

8. *Figure 1 does not represent the text.* We have improved the captions to make this more informative.

9. *Figure 2 is confusing.* We have refurbished this diagram with improved caption.

10. *For Figure 9, How many individuals per point.* The y-axis defines this as total per class.

Chapter 1 – This chapter has been completed rewritten. All comments are addressed.

Chapter 2 – This chapter is now a publication (Killgore et al. 2007).

REVIEWER 4

The pattern of declining recruitment appears to be driven by one strong year class moving through. We address this in both Colombo et al. 2007a and later in Tripp et al. 2009, both of which are published chapters in the report. We have verified that the numbers of fish entering the gear vulnerability appear to be declining each year.

Chain of Rocks is referred to as a destination….could be a barrier. We address this pretty extensively now in the Executive Summary. Could be either. Needs more research.

Chapter 3 – We have completely rewritten this chapter and added additional information. The previous version of the chapter remains as an appendix because it contains far more detail than the revised chapter.

Figures showing "observed movements". These data are now in the appendix, not the revised chapter. Indeed, they are only for the record, and not intended to be synthetic. However, in the revised chapter we now recognize that the data are discrete. We also only include one observation per date for each fish to avoid overrepresenting some individuals.

Why wasn't telemetry a high priority from 2002-2004? We were initially tasked with using randomized sampling with several gears to determine habitat preference. By 2004, we realized we simply did not have the resources to accomplish this effectively (Chapter 1).

Several undefined terms. All taken care of in the revised chapter.

Difficult to follow habitat use section. Again, we revised the analysis in the new chapter.

Dropping water levels in 2004 would be a good argument for temperature as the driving movement (plus stable flow). Good point. IN the revised chapter, we use AIC analysis to show that a combination of increased flow plus temperature is the best predictor of movement.

Looks like pallids increase activity with temperatures of about 11-17 degrees. We now explore this more explicitly in the revised chapter (by month). Actually, movement was high in summer (downstream mostly).

Specific comments. All are addressed in the revised draft.

What about the stationary fish? In the revised chapter, we point this out. We also note this occurrence in the Executive Summary.

Average flow of pallids? Part of the problem with this analysis is that we are unsure of the true depth of the adults when profiling flow. In the revised chapter, we avoid making this statement. Also, we strike this from the Executive Summary. Better data are required.

REVIEWER 5.

Maximum length is confusing. Indeed, we were in error. Changed in Executive Summary.

Interesting to note that pallids became smaller as farther south. Could be due to young moving into lower river? Very interesting point. However, we have compared length at age between reaches and found that individuals that are the same age are smaller in southern reaches.

Not much information about young pallids. We erred in referring to Chapter 1 about this. This has been the focus of current research.

Deal more with caviar harvest. We attempt to make a strong point about this in the report. Added Tripp et al. 2009, which further suggests that strong regulation (or closure) is needed.

Strengthen ties with the lower Mississippi River. We cannot lose focus that this report is by the FWS's requirement and assessment of issues in the MMR. However, we do make the point that movement between basins is common.

REVIEWER 6.

Compare to Missouri River work. We do now tip our hat to the research being done in this basin. However, access to published information for pallid sturgeon has been tough. We do cite the life history model and the unpublished data being amassed currently.

Many of the specific comments by this reviewer no longer apply because the sections have been completely rewritten.

Clarify what is meant by post spawn movement. In the revised draft, we are careful to point out that this is simply supposition based on the downstream drift following upstream movement. IN fact, it is likely that most of the pallids we tracked did not spawn at all during this time.

Were the fish in mortality estimates presumed wild caught fish? Yes.

What is the confidence in pallid sturgeon mortality estimates? The statistics account for the difference in sample size. The fact that two independent groups derived similar estimates using different gear increase our confidence.

Low level of agreement between paired fin rays. For short lived fish, this would be a problem. However, for the life span of pallids, the error is likely blurred. Also, we have some unpublished data that suggest that pallid fin rays are more accurate and precise than shovelnose rays.

REVIEWER 7.

Executive Summary

1. *Separate analysis for young sturgeon?* We missed this in the analysis. Indeed, trawling (Chapter 1) did generate small fish. However, the genetic tools have just become available to identify them to

species. Since this report was reviewed, research has been conducted on these young fish and will be provided in a separate report (Phelps et al. submitted manuscript to Transactions of the American Fisheries Society).

2. *Diet preferences?* The chapter on diet content is included, which confirmed that piscivory was important. Diet availability was never a goal in the original scope of work for this project. However, since then, SIUC has sampled and analyzed habitat-specific food availability, which will be available in a future report.

3. *Actual calculated mortality rate should be reported*. Done.

4. *Citation should be USFWS 2000.* Done.

5. *The study was in response to…* Done.

6. *The study purpose was to quantify habitat for all life stages.* Unfortunately, the original scope was focused on adults. We have since focused continued work on young fish.

7. *Much of the funding for genetic studies was provided by the USFWS.* Noted.

8. *What was the accuracy and precision for aging?* Figure 9 shows that we were able to explain 73% of the variance in the mortality estimate. As for precision, we had good agreement between readers (noted in the Executive Summary). As for accuracy, we do note in the Executive Summary that we were able to age known age pallid sturgeon.

9. *How does 16 feet relate to spring water levels at COR?* We make a pretty strong argument that the lowhead as a barrier issue is yet unresolved.

10. *Fish aggregate at tributaries but then we never say they are used.* Good point. Pallids never moved into tributaries. However, during spawning, they appear to hang in the main river in vicinity of these areas.

11. *Harvest needs clarification.* Done.

12. *Data on young fish are lacking*. Indeed, we had no idea whether small fish were pallids in our samples. Recent research is rectifying this and will emerge in another report.

13. *Change "know".* Done.

14. *Table 2. Entire information for MMR should be considered before breaking out COR.* See Killgore et al. 2007 for an argument why we should refrain from doing this. COR is so different from the remainder of MMR that pooling it generally with the remainder of the reach would be misleading.

Chapter 1. As noted earlier, this chapter has been completely rewritten and reanalyzed. Thus all comments specifically for this chapter are not necessarily applicable. We do provide a few general answers:

1. *What are results of genetic testing of larvae?* This is just occurring and not included in the report. A preliminary screen suggests a ratio of about 1 pallid to 100 shovelnose.

2. *Pallid sturgeon were collected at island tips with sampling but not found with telemetry.* We have recast Chapter 1 to note that we had insufficient power to say much about pallid location with our sampling. It is quite likely that they use island tips, but the telemetry research confirms that regular use occurs near wing dikes.

3. *What is the bias for identifying small sturgeon?* The morphomeristic indexes don't work for small fish (see Murphy et al. 2007).

4. *Catch in tributary mouths is zero.* However, they do occur near tributaries in the main river.

5-6. *Island tips were correlated with abundance in sampling.* The statistical approach we used was incorrect (a p value of 0.15 is unacceptable) and the chapter has been recast. However, we do not doubt that island tips are used and point this out in the Executive Summary and in the Appendix to Chapter 1.

7. *Why were no small pallids collected?* As noted earlier, we were unable to identify them to species.

8-9. *Why was directed sampling only in spring?* We knew that catch rates were highest during this time, presumably because the pallid sturgeon are more active.

10. *Highest sturgeon CPUE was in areas that don't match the telemetry information.* Again, low power is the problem.

CHAPTER 2

1. *The 57 pallid sturgeon collected with trotlines should be combined with the SIUC/MDC data.* Good point. This would increase power. However, our methods were so very different that it would be comparing very different data sets. These fish are combined in the telemetry effort, where the meaningful habitat use results derive.

2-3. The distinction between the Upper Mississippi River and the Middle Mississippi River can be considered semantics. However, in our view the MMR is unique in that it is greatly influenced by the Missouri River and behaves differently.

4. *Need to clarify the apparent contradiction between Hurley et al. and Koch et al.* Hurley et al. has some serious limitations which we outline in Chapter 3.

5. The cited Biological Opinion has been changed in the text.

6. *The lowhead dam at Chain of Rocks is not a natural structure.* We have clarified.

7. *Hertzog.* We missed that before publication. Sorry Dave.

8. *Were any shovelnose sturgeon scanned?* No.

9. *The percentage of lake sturgeon containing coded wire tags should be provided.* They were not regularly scanned. We assumed all were stocked.

10. *Stonecats?* We didn't feel this relevant, given the focus on pallid sturgeon.

11. *What is the likelihood that Chain of Rocks is a barrier?* We address this in the Executive Summary. Maybe, but probably not. This chapter can't speculate without considering the telemetry data in Chapter 3.

12. Table 3 was clarified.

13. *Lack of capture of pallid sturgeon?* As noted earlier, lack of the proper tools to identify them.

14. *Do the results hold true when combining data with SIU and MDC?* Can't do this reliably (see above).

15. *High retention rates with one fish?* Good point, addressed.

16. Again, sorry Dave.

17. We have modified the citation.

18. *Non targeted sites excluded?* As noted earlier, this was a completely different effort and not directly comparable.

CHAPTER 3.

1. *All data should be combined (telemetered and sampling) to provide better habitat data.* We do this in the Executive Summary, which we now call the "synthesis".

2. *Relocations - few versus many.* We handle this by averaging data for fish to one location per sampling trip. All fish are similarly represented in the data set. This is clear in the revised chapter.

3. *Change establishment to conservation.* This has been addressed in the revised draft.

4. *2001 bathymetry maps are better.* We were analyzing data based on a variety of information including the bathymetry maps. The resolution is sufficient for the analysis we were conducting.

5. *Habitat selectivity should be based on sex, age, size.* We had insufficient power to break our analyses into the level of detail. However, we do provide specific detail about movement of the few black-egg females we tracked.

6. *Where are data for remaining 21 sturgeon?* These sturgeon were relocated insufficient times to produce a reasonable time series.

7. *How compare to Hurley's data?* Revised version addresses this.

8. *Tributary mouths versus tributary aggregations.* We have already addressed this in previous responses.

9. *The habitat does not include the habitat from sampling?* Correct. Addressed in the Synthesis of the report.

10. *Table is incorrect on depth selection.* This is changed and corrected in the revised chapter.

11. *Velocity data incongruent.* Right. We have modified in the text.

12. *Island tips.* Again, we have modified to be more accurate.

13. *Differences among sizes, sexes, etc.* Again, insufficient power to detect.

14. *Are seasonal differences apparent?* Yes. The new version includes this.

15. *Habitat selectivity due to water level?* We consider this in the new version of the chapter.

16. *Fish not found to aggregate but Executive Summary says that they do.* The statement in the Executive Summary is based on anecdotal observations with side scan SONAR. Also, the term aggregation here simply refers to the fact that the destinations were similar, not that the fish were found close to each other at the same time.

17. *Add dam.* Done.

18. *Change bodies.* Done.

19. *Do diet data support assumption?* No seasonal pattern was evident. Again, low power hampered fine scale resolution.

20. *WTU?* Defined in Figure 1.

21. *2003 and 2004 wrong.* Fixed.

22-23. *It should be noted that not all habitat are available during all seasons.* Done.

24 -25. *Good points.* These issues can only be addressed with access to a data set that determines how connectivity changes with river stage.

CHAPTER 4.

1. *What role does this play?* This is addressed in the Synthesis at the start of the report.

2. *Wrong citation.* Missed before publication. Apologies.

CHAPTER 5.

Specific comments addressed before publication.

CHAPTER 6.

1. *This chapter contains very little demographic information for pallid sturgeon.* We do this in the synthesis section at the beginning of the report.

2. *Pallid fin ray removal.* Fin rays were removed as per Recovery Team approvals. No negative effects were noted in the few recaptures that occurred.

3. *Age and growth information.* This is included in the synthesis section at the start of the report.

4. *Year class strength.* We are unsure what independent variables to put into the model at this juncture. We know it is not discharge per se…but that it may play some role. As we note in the Executive Summary/synthesis, long-term data on reproductive success is needed to better understand the process.

5. *Population estimate.* It is explained, up front, in the “synthesis”.

CHAPTER 7.

Paper removed.

CHAPTER 8.

1. *A second part of the diet study was to determine prey selectivity.* We do not recall this being in the original Scope of Work. However, we are in the process of quantifying prey availability which will be presented in a separate report.

2. *Relative weight should be determined.* The only source for this condition index is an unpublished report by Keenlyne and Evenson. In this report, it is unclear how they developed their standard weight equation; we therefore are unable to determine what this number represents about condition. We had insufficient power to examine patterns at the sex, size or age specific level.

3. *Seasonal differences?* We need to be careful about elucidating seasonal differences in this paper. Much variation occurred and only one significant correlation occurred between condition and stomach content. More diet information is clearly needed.

CHAPTER 9.

Has been deleted.

CHAPTER 10.

Has been deleted.

Responses to Illinois Department of Natural Resources Comments:

Mr. Flood, Director of Natural Resources at the time of the review, noted that Illinois was taking extraordinary measures to prevent incidental take of pallid sturgeon. We commend this agency in their efforts to address increased harvest of shovelnose and perhaps pallid sturgeon (see concerns addressed by Betolli et al. 2009) in the river. However, we have amassed a fair amount of information implicating harvest to have at least some impact on the pallid sturgeon, although we have toned down our conclusions in the Executive Summary. There are now publications spread across three peer-reviewed journals (Transactions of the American Fisheries Society, North American Journal of Fisheries Management, and Journal of Applied Ichthyology) that suggest that harvest is having some impact and that current harvest (with the regulations in place and enforced) is neither sustainable for shovelnose nor pallid sturgeon.

Specific responses:

Page 2 – Where is the record of historic pallid abundances? Good point. As we note in the Executive Summary, this is the first attempt to compile some baseline data for future comparisons.

Page 3 – Mortality estimates are highly uncertain. Actually, our estimates derive from multiple independently derived sources and are quite congruous. This suggests that we are touching upon some accurate estimate.

Page 3 – Little faith in population estimates. Later in the Executive Summary, we provide information about how these were derived with error estimates. Again, we used multiple lines of evidence and derived similar densities. We do provide the caveat that these estimates are likely attributable to adult fish only.

Page 4- Here and there authors make conclusions from shovelnose sturgeon. We try to make it clear when we are doing this. And it is only for mechanisms that would affect both species similarly.

Page 4 – Not many fish show a stock recruitment relationship that is meaningful. On the contrary, Garvey et al. 2009 point out that in many stock recruitment relationships, tangible threshold changes in the relationship between adults and offspring occur. Sturgeon may be a candidate.

Page 5 – Do we have any indications of past abundances of pallids? No.

Page 10 – Multiple gear types were employed (2 and 3 inch mesh gillnets, 3 trawls, and trotlines). The trotlines, 3” gillnets, and larger trawls were deployed to target larger fish, 2” gillnets should capture moderate to large fish, and the smallest trawl was used to target larvae and juveniles. Implementing the multiple gear types should allow for an adequate representation of the actual length-frequency distribution of the population.

Page 13 – Suggests intersexuals as a potential cause of decline. What does this have to do with harvest? Nothing. We were noting that other problems than harvest could be involved. Although hermaphroditism is a problem, with only 7% of the sample showing this trait, we believe that it may have an impact on decline, but the impact may be negligible.

Page 14 – Sturgeon have a life history making them more prone to collapse. We agree and judging by other sturgeon populations this occurs, but we would also include that lack of production due to poor reproductive success not juvenile survivorship is impacting the lack of recruitment.

Page 15 – What is this index? Catch-curve residual approach using methods by Maceina (1997) and Sammons et al. (2002) is the generally accepted method for determining mortality. There is no method of standardization because the IL commercial fishermen are not required to record effort. Biomass is the important issue and harvest biomass has increased without effort recorded. We do know that the amount of flesh and caviar has steadily increased since 1990, however we have unbiased catch data from winter samples in which CPUE has declined.

Page 15 – Age structure has increased with no year classes. We agree, given our data; however this is not the only evidence of collapse, just one piece. Since fish recruit to the gear around age 6, we are seeing what has happened from 1995-2001, which is a larger time scale than it seems.

Page 16 – Mortality rates the same as for shovelnose? Mortality is estimated from only those year classes where mortality is constant. Catch curve analysis is based on descending limb of the catch curve starting at age 9. Catch curve mortality estimation is standard fisheries assessment. Also in area where commercial harvest of shovelnose sturgeon is not allowed, such as the Upper Missouri River and Lower Mississippi River, pallid mortality has been estimated as being only 7%.

Page 16-17 – What about Lee's phenomenon? Lee's phenomenon suggests that as density dependent competition is reduced due to decreased abundance, then age at maturity will decrease and growth rates will increase; however we are suggesting that the opposite effect is actually occurring (see Tripp et al. 2009, now in print). Regardless of age at maturity and growth rates, if pallid numbers are declining, then steps need to be taken to protect the remaining population.

Page 17 – Using the upper mortality rate for shovelnose PE's is precautionary. We did not use the upper mortality rates, we used a combined mortality rate over the years of the study. This mitigates the assumption of equal year class, thus reducing the variability in mortality rate estimation. For further information see Ricker 1975.

Page 18 – High variability in the pallid PE. Obviously, due to low abundance and catchability.

Page 19 – Gear bias. Every gear has bias, this is why we used six different gear types. We are now in the process of identifying small pallid sturgeon captured in trawls using genetics.

Page 19 – Admission that little historical data exist for pallids and historical low abundances. "Illinois government officials are required to manage, protect, and sustain Illinois's natural and cultural resources," from IDNR website. We are a bit concerned why the IDNR is not questioning (1) why this species is rare and (2) how we preserve its abundance.

Page 21 – How do you figure a stock-recruit model will help? Sturgeon are K-strategists when not exploited, suggesting relatively equal and consistent year class strength (Winemiller 1992). Therefore with a stock-recruitment model we could estimate maximum sustainable yield with information on stock size.

Page 33 – This sort of distribution would be representative of a bias toward larger fish. Again we are using six different gear types and a stratified random sampling design, which is the best method of getting a representative length-frequency distribution without knowing the “true population”.

Page 34 – Any dimorphism? A discriminate function analysis failed to separate sturgeon sexes based on seven different traits (Tripp unpublished data), so at this point there seems to be no dimorphic traits.

Page 34 – Asymptotic length can be estimated using a For Walford plot. We attempted to fit a von Bertalanffy growth curve using non-linear regression; however the maximum likelihood estimator could not estimate the parameters needed in von Bertalanffy. Are you suggesting that Ford-Walford plots are more accurate? Refer to figure 4 on page 34 – It appears that the growth relationship is linear.

Page 36 – Why is it unlikely that the barrier dam is causing the population troubles. We have evidence that fish are passing over the dam. Additional information amassed during the past couple of years (Fish Passage project; http://fishdata.siu.edu/move.htm) supports this.

Page 37 – How do you estimate year class strength from catch curves? Refer to the comment about page 15 for references. When harvest is high, year class strength is low showing that harvest impacts year class strength. What is being missed, we are recreating year classes from 12-14 years in the past. Regardless of sample size, they are independent samples and they all show the same trend.

Page 38 – There is really nothing abnormal in this figure. Normal populations do not shift in age structure (Leslie 1942). Changes in age structure indicate a fundamental change in the population.

Page 39 – Could be a bias toward medium sized individuals. The first complaint dealing with gear selectivity was a gear biased towards larger fish, now medium sized individuals. We can only do the best with the information we have.

Chapter 1 – All comments associated with this chapter have been addressed by completely rewriting the chapter. See previous responses to comments.

Chapter 2 –

Page 83 - The trotlines only seem to target larger fish. Indeed. See Chapter 1, revised.

Page 84 – Pallid sturgeon is listed as historically being low in abundance. We think we know why. Adult pallid sturgeon occupy swifter waters that probably were not targeted by many fishermen in the past.

Page 85 – Statement suggests that there are many variables causing declines. We do not disagree.

Page 92 – More pallids caught in the LMR compared to the MMR. Opposite for shovelnose. Interesting point.

Page 94 – We agree that trotlines are good for sampling shovelnose but not pallids. This has to do with the placement of the trotlines as well as the actual gear.

Page 95 – Ratio of pallids to shovelnose do not seem to be out of the ordinary. Right. It is the potentially declining absolute abundance of both species which is the concern.

Page 108 – All common names should be lower case. OK.

Chapter 3 –

Page 120 – Telemetry may not adequately characterize movement. That is why we added the VR2 system to the river.

Page 121 – Why alpha 0.10? Power always is an issue. When dealing with the conservation of a species, it is always better to err on the side of making decisions with a higher error rate than risking a negative effect.

Page 121 – Using AIC is proper way to select a model. Yes. See revised chapter.

Page 142- Seems reasonable protecting at COR. Yes.

Chapter 4 –

Page 244 – If this report is about pallids, why so much inference from other sturgeon? We might argue that hybridization is a natural phenomenon. We will have to see with future research.

Page 247 – Difficult to identify young sturgeons. We recognize and are working on this issue with genetics.

Page 260 – How are multivariate analyses going to help in the field? They won’t.

Page 261-262 - Conflicting views. This is addressed in the revised, published version.

Chapter 5 – No comments

Chapter 6

Page 353 –Harvested populations respond with better reproduction. Yet, sturgeon are different beasts. We agree sturgeon are different, particularly given the focus on reproductive females.

Page 353 – Commercial harvest in the open-river portion is not increasing. This may be the case, but overall in the Mississippi River harvest is increasing. Our recent research in the Upper Mississippi River indicates that more mixing occurs between the pools and the open river than expected…so the populations are linked.

Page 353 – How can the authors say year class strength is declining when they can’t sample juveniles? The method used recreated the year-classes 7-15 years ago and does not deal with juveniles.

Page 354 – This statement is plain false. We disagree. If you believe this is false see Botsford et al. 1997 (Science). Post et al. 2002 as well. We are talking both commercial and potentially recreational fisheries.

Page 353 & 356 – How can authors say that cohort strength is going down when they can't effectively sample juveniles? Catch curve is the generally accepted method for estimating instantaneous mortality, see Ricker 1975. This is the catch curve residuals method (Maceina 1997).

Page 356 – Are marine SPRs comparable to sturgeon. Probably not. We realize this but Slipke found Spawning Potential Ratios similar to what we report for catfish in the Upper Mississippi River.

Page 357 – Why would you use winter CPUE? Winter catch data were used because at this time the population is at admixture. Summer actually produces the lowest catch rates (see Chapter 1). CPUE has been shown to produce indices that correspond to abundance (hundreds of papers). We are looking at the trends in winter data and only winter data.

Page 358 – What were your sample sizes for developing catch curves? Sample sizes were 81-142 depending on the year. Only fish that recruit to the gear were used in the estimate. Refer to Maceina 1997 and Sammons 2002.

Page 359 – This is not a reflection of what mortality rates are! See page 17 comments.

Page 359 – What units were harvest presented in? Harvest was presented in biomass. Based on the figures provided by the reviewer, harvest is increasing. Effort has to remain constant in order for harvest to correlate with density; however if effort is increasing harvest can also increase with a reduction in density.

Page 362 – You cannot say that shovelnose harvest increased without some standardization. Based on the figure provided, there was an increase from 40 – 60 kg, whether or not there was an increase in effort, harvest has increased. Commercial fishermen are focusing on key areas, mainly areas in which they are congregating prior to spawning.

Page 362 – Are 5 data points and years sufficient to say that abundances have declined? There are six data points and the regression was highly significant, suggesting a decline in standardized catch with increasing harvest.

Page 363 – The statement about a higher Linf due to commercial exploitation in completely unfounded. See Beverton 1992, Lorenzen 1996, Chen and Rochet 1998 for examples on how this can occur.

Page 363 – Refer to page 362 comment. The true metric in N which is the population size.

Page 364 – Fishing mortality rates cannot be determined from total harvest. True. However, commercial fishermen do not report effort. We have estimates of natural mortality rates in similar areas; therefore any increase in mortality would be attributed to fishing.

Page 365 – Of course, mortality rates are going to be lower with no harvest. We agree, we cannot say anything about the young fish because we cannot sample the smaller fish, as in the case of many fish species.

Page 365 – The 30% difference seems high. We estimated current levels of fishing mortality not harvest (in biomass). Theoretically yes, however unless compensation is perfect, then this can not maintain the fishery.

Page 366 – There are problems with Lees Phenomenon in all this. Perhaps.

Page 367 – The last paragraph states that the fishery is unregulated. We do agree that there are non-species specific commercial regulations in the Mississippi River. And we commend IL on passing length regulations.

Page 372 – Natural mortality rates this high seem unreasonable for sturgeon. Natural mortality of 5 – 10 % is not high, but well within the limits for unfished populations reported by Quist et al. 2002. Yes, proportion of females is in Journal of Applied Ichthyology.

Page 373 – Year 2001 is an outlier. 2001 is not an outlier, both x and y were measured without error and at the time of writing this paper 2003-2006 commercial harvest data were not available.

Page 375 – Why would harvest be down in years when abundances were high? The standard for this type of fisheries related question effort needs to remain the same.

Chapter 7

Page 380 – The claim that sturgeon harvest has increased is tenuous. Total harvest (biomass) has increased regardless of effort.

Page 380 – High likelihood that this species is sexually size dimorphic. No; length-frequency distributions were not significantly different between males and females.

Page 381 – At this point we do not see any sexually dimorphic traits. There are instances where populations are skewed towards males and are healthy, however females drive population growth.

Page 384 – Current sex ratios are not 1:1, they are skewed towards males.