

UNDERSTANDING HOW HARVEST INFLUENCES THE LIFE HISTORY
AND DEMOGRAPHICS OF SHOVELNOSE STURGEON IN THE MIDDLE
MISSISSIPPI RIVER

by

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TITLE: Understanding How Harvest Influences the Life History and Demographics of Shovelnose Sturgeon in the Middle Mississippi River

MAJOR PROFESSORS: James E. Garvey and Brooks M. Burr

Shovelnose sturgeon *Scaphirhynchus platyrhynchus* in the Middle Mississippi River is one of the last commercially viable sturgeon populations in the world. To determine whether commercial harvest of the black-egg (sexually mature) females is impacting this population, information regarding sex-specific demographics and the reproductive life history is required. Adult shovelnose sturgeon were sampled using gill nets (5-cm bar mesh) monthly during February 2005 through July 2006 at three sites on the Middle Mississippi River between Cairo, IL and St. Louis, MO; (RKM: 201-198; 191-188, and RKM 127-124). Of all shovelnose sturgeon sampled, 363 were females and 416 were males, deviating from 1:1 ($p=0.06$). Sex-specific length frequency distributions differed ($p=0.03$) with females having a larger median fork length (614 mm). Compared to historical data, the population shifted towards longer fish, and somatic growth declined. The population also shifted towards older fish with reduced recruitment. Age at maturity was later than previously reported, with females maturing at a mean age of 10.5 years and males at 9 years of age. Total egg count was slightly lower than previously reported with a mean of 29,573/female. However, the spawning cycle had not changed with most males and females

spawning every 2 and 3 years, respectively. Larval sturgeon were also sampled to link age at maturation, timing and periodicity of spawning, and larval growth rates. Larval sturgeon occurred during June and July of 2005 and May and June of 2006, confirming successful spawning. Larval sturgeon grew between 0.69 to 1.69 mm total length per day among four distinct cohorts produced each year. For the first time for this population, sturgeon were found to spawn during the fall. Fall sturgeon contained ripe eggs with polarization indexes (PIs) <0.05 ; larval sturgeon were collected thereafter. The population structure is changing likely due to increased commercial harvest perhaps coupled with poor habitat conditions. The life history strategy, which is similar to other sturgeon, likely places this species at risk of overharvest.

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CHAPTER ONE

CHANGING DEMOGRAPHICS OF STURGEON IN THE MIDDLE MISSISSIPPI RIVER: POTENTIAL HARVEST RESPONSES

ABSTRACT

To determine whether shovelnose sturgeon *Scaphirhynchus platorynchus* populations are changing due to commercial overharvest of black-egg (sexually mature) females, I require seasonal information regarding sex-specific population demographics. I sampled shovelnose sturgeon using gill nets (5-cm bar mesh) monthly during February 2005 through June 2006 at three sites on the Middle Mississippi River between Cairo, IL and St. Louis, MO; (RKM: 201-198; 191-188; and RKM 127-124). Of all shovelnose sturgeon sampled, 363 were females and 416 males, deviating from 1:1 ($p=0.06$). Annual mortality was 44%. Sex-specific length-frequency distributions differed ($p=0.03$) with females having a larger median fork length (614 mm). Compared to historical data, the population shifted towards longer fish, and somatic growth declined. The population shifted towards older fish with reduced recruitment. Age at maturity was later than previously reported, with females maturing at a mean age of 10.5 years and males at 9 years of age. Population structure is changing, likely due to increased commercial harvest perhaps coupled with poor habitat conditions.

INTRODUCTION

Globally, the status of most sturgeon populations is either imperiled or unknown. Of the 27 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. However, this value also leaves these species susceptible to overharvest of females. These long-lived late maturing species are unable to compensate for intense harvest and when coinciding 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 species that can be legally harvested in the world.

Shovelnose sturgeon appear to be more resilient to harvest than other sturgeon species, being relatively small and perhaps less commercially valuable (Carlander 1954). Shovelnose sturgeon are thought to mature at a 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 more stable than their European and Asian counterparts, its distribution and abundance have been reduced 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) 309, St. Louis, MO to RKM 0, Cairo, IL. In 2001 commercial harvest of shovelnose sturgeon flesh in the MMR reached a historical high (Colombo et al. 2007a). By 2000, this

population appeared to be responding to harvest and habitat alteration with low population growth and high mortality relative to other sturgeon populations (Jackson 2004). 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 signs of growth and recruitment over-fishing (Colombo et al. 2007a).

Little is known about the autecology and population dynamics of this species. Age structure, growth patterns, and mortality rates can reveal potential effects of habitat changes over decades (Everett et al. 2003) and also evaluate vulnerability to overharvest (Morrow et al. 1998). Because female sturgeon are harvested preferentially, I examined sex-specific age structure, growth, and mortality rates. I compared these data to historical data sets collected from the same sampling areas to assess trends in population structure over time.

METHODS

Commercial Harvest

During the spring of 2004, length data were collected on fish being harvested for roe by a commercial fisherman on three sampling trips conducted within our sampling reach (Rob Maher, Illinois Department of Natural Resources). These data were reviewed and used to compile a length frequency distribution to represent the individuals that were being removed from the population. The mean, median, and mode were calculated in order to compare the commercial harvest data to our adult sampling length-frequency data.

Stratified Random Adult Sampling

Standardized sampling of shovelnose sturgeon occurred during November through April, 2002 through 2005. Stationary bottom set gill nets [5.08 centimeter bar mesh, 45.7 meters long, 3.05 meters deep] were set at randomly selected sites, stratified by habitat type in the MMR. Fork length (FL, 1 mm) and wet weight (0.1 g) were quantified for each fish. The left pectoral ray was removed from all fish and later used to determine the age of each specimen. These data were used to compare yearly length and age-frequency distributions across years, with mean and mode reported for each year.

Directed Repeated Adult Sampling

In addition to the annual random sampling, directed monthly collection of shovelnose sturgeon occurred during February 2005 through June 2006, using the same stationary bottom set gill nets. Six nets were set for 24 hours on the seam of wingdikes at Modoc, IL (RKM 201-198), Chester, IL (RKM 191-188), and Grand Tower, IL (RKM 127-124) due to known high densities of shovelnose sturgeon in these areas. Lengths, weights, and rays were collected as before. Water temperature, conductivity, dissolved oxygen, and pH were collected at the surface for each sampling trip with a Quanta Hydrolab water quality meter. Daily river stage height was determined from the United States Geological Services (USGS) gauging station at Chester, IL.

Each month, a subsample of the first 20 sturgeon collected at each site was preserved on wet ice and taken back to the lab. A mid-ventral incision was made from the anus through the pelvic girdle, exposing the gonads. The gonads from each sturgeon were photographed and the digital images were later used to categorize the samples into stages of development based on the index from Colombo et al. (2007b).

Catch was quantified as fish per net night and was compared to season using an ANOVA and river stage and water temperature using Pearson's Correlation and significance was determined using and alpha (α) value of 0.05 for all statistical comparisons. Length-frequency graphs were constructed for both sexes with mean, median and mode reported. Kolmogorov-Smirnov test was used to determine if distributions were sex-specific. Sex-specific length-weight regressions and relative weight calculations were compiled to determine the condition of the population. Relative weight can also be used to monitor influences of environmental change or human manipulations over time (Ney 1999) and was defined as:

$$W_r = \frac{W}{W_s} \times 100$$

where W is the observed weight and W_s is the length-specific standard weight values for the species. Relative weight values were calculated using the length specific standard weight (W_s) equation determined by Quist et al. (1998):

$$\log_{10} W_s = -6.287 + 3.330 \log_{10} FL.$$

Age and Growth

Pectoral fins rays were placed in coin envelopes and dried. Three sections were cut from the basal portion of each fin ray using a Buhler Isomet® low speed saw. Each section, increasing in width (0.635mm, 0.6858mm, and 0.7366mm) was secured to a slide using cyanoacrylate. Cross sections were examined independently by two readers using a stereomicroscope under 7-45x magnification. Under transmitted light, a pair of opaque (growth) and translucent bands was considered an annulus (Everett et al. 2003). The annuli were counted from the nucleus to the apex of each section. This method has been

validated for Atlantic sturgeon (Secor et al. 1997), lake sturgeon (Rossiter et al. 1995), and white sturgeon (Brennan and Cailliet 1989) and is the most precise method for aging the shovelnose sturgeon (Jackson et al. 2007). When readers disagreed, they examined the cross sections together to reach an agreement.

Precision between independent readers was assessed using average percent error (Beamish and Fournier 1981) and coefficient of variation (Chang 1982) for the shovelnose sturgeon collected in the directed repeated sampling in 2005 and 2006.

Average percent error (APE) was defined as:

$$APE_j = 100x \frac{1}{R} \sum_{i=1}^R \frac{|X_{ij} - X_j|}{X_j}$$

where X_{ij} was the i th age determination of the j th fish, X_j was the mean age of the j th fish, and R was the number of times each fish was aged. When APE_j was averaged across many fish, it became an index of average percent error (Campana et al. 1995). The coefficient of variation (CV):

$$CV_j = 100x \frac{\sqrt{\frac{\sum_{i=1}^R (X_{ij} - X_j)^2}{R-1}}}{X_j}$$

was expressed as the ratio of the standard deviation of age estimates to the mean, where X_{ij} was the i th age determination of the j th fish, X_j was the mean estimated age of the j th fish, and R was the number of times each fish was aged (Chang 1982). This formula yielded a single index value for each ray; when the individual values were averaged a mean coefficient of variation was generated giving an estimate of precision. Age bias plots were constructed to visualize reader precision, in which the mean estimated age of one reader was plotted against the second reader's set of estimated ages for each age class

(Campana et al. 1995). Using linear regression, precision could be tested. If the agreement was perfect the slope of the line would equal one.

Growth curves for the population and also sex specific growth curves were calculated using FAST (Fishery Analysis and Simulation Tools) software (Slipke and Maceina 2000). Growth in length was assessed using a von Bertalanffy model:

$$L_t = L_\infty [1 - e^{(-K(t-t_0))}]$$

where L_∞ is the theoretic maximum length, K is the Brody growth coefficient, t_0 is the predicted age at which length is zero (Ricker 1975). Differences in sex-specific growth curves were evaluated using the residual sums of squares method (Chen et al. 2002).

Mortality

A catch curve analysis was used to quantify mortality rates for the population as a whole and sex-specific. The catch curve analysis equation:

$$\log_e(N_t) = \log_e(N_o) - Z(t)$$

where N_t is the number alive at time t , N_o is the number alive initially (at time t_o), Z is total mortality or instantaneous total mortality rate, and t is the time elapsed since t_o , is used to calculate the total instantaneous mortality rate (Ricker 1975). The equation is simply a linear regression in which the natural log of abundance of fish at age (y) is regressed against age (x) (Ricker 1975). A weighted regression was used to reduce any bias that may occur due to reduced relative abundance of older individuals in the population (Slipke and Maceina 2000). The declining slope of this regression equation represents the instantaneous mortality estimate (Z), which is used to determine total annual mortality (A) using this equation:

$$A = 1 - e^{-Z}$$

for the population and sex specific mortality rates. Sex-specific catch curve slopes were tested for homogeneity (test for interaction in ANCOVA) to determine if annual mortality differed among sexes.

RESULTS

Of the 557 shovelnose sturgeon captured by the commercial fisherman in 2004, 139 were harvested for eggs. The harvested shovelnose sturgeon FL ranged from 400 mm to 760 mm, with a median FL of 654 mm. A total of 3518 shovelnose sturgeon were captured during the stratified random sampling in 2002 through 2005, with the median FL ranging from 591 mm in 2002 to 616 mm in 2005. During the 18 month directed sampling completed during 2005 through 2006, a total of 1725 shovelnose sturgeon were collected, with a median FL of 621 mm. The length-frequency distributions of shovelnose sturgeon collected during 2002 through 2006 shifted in median FL towards larger fish and the distribution transformed from normally distributed to negatively skewed and truncated toward fish in the 600-700 mm range (Figure 1). The length distribution of the commercial harvest shovelnose sturgeon illustrated that larger mature females were targeted with the modal FL being 690 mm (Figure 1).

Of the 1725 shovelnose sturgeon collected in 2005 through 2006, 792 were brought back to the lab for analysis. The subsample contained 415 males, 363 females, and 14 that were either intersexuals or unidentifiable. Thus, the sex ratio was 1.14 males: 1 female ($\chi^2 = 3.48$, $df = 1$, $p = 0.06$). Catch declined by year, with the mean catch in 2005 being 9.06 fish per net night, which decreased to 3.05 fish per net night in 2006 (T

= 4.21, $df = 253$, $p < 0.0001$). Catch was related to season (ANOVA $F = 3.92$, $df = 45$, $p = 0.014$) and weakly, positively correlated with river stage ($r = 0.34$, $df = 45$, $p = 0.02$), but unrelated to water temperature ($r = 0.025$, $df = 45$, $p = 0.87$).

The mean FL and weight of females captured during the 2005 through 2006 sampling (mean \pm SE) was 615 ± 4 mm (Figure 2) and 998 ± 9 g, respectively. Male sturgeon had a mean fork length of 609 ± 3 mm (Figure 2) and a mean weight of 936 ± 15 g. Sex-specific length-frequency distributions differed (KS = 0.06, $df = 769$, $p = 0.02$) with females having a greater median fork length. Weight-length regressions were [\log_{10} weight = $3.4497(\log_{10}$ length) – 6.6457] ($R^2 = 0.92$) for females and [\log_{10} weight = $3.3205(\log_{10}$ length) – 6.2953] ($R^2 = 0.90$) for males (Figure 3). Mean relative weight values were for females 96, and 94 for males.

Age and Growth

Two hundred and eighty-three shovelnose sturgeon collected during 2002 through 2003 were aged and compared to the age-frequency distributions of the 740 that were aged from the 2005 through 2006 sampling. The comparison of the age-frequency distributions showed a shift towards older fish with mean age in 2002 being 7.6 years and in 2006 11.3 years in age (Figure 4). The age-frequency distributions also converted from a positively skewed distribution to being normally distributed.

Of the 740 shovelnose sturgeon aged from the 2005 through 2006 sampling; 337 were females and 389 were males with the remaining 14 being intersexuals. Female shovelnose sturgeon ages ranged between 4 and 22 years of age with a mean age of 11.2, while males ranged between 3 and 19 years of age with a mean age of 10.9. Females became sexually mature within the range of 9 to 12 years of age (mean age of maturity

10.5) and males matured at 8 to 10 years of age (mean age of maturity 9) (Figure 5). Between reader percent agreement was high with 88% exact agreement, 10% agreement within 1 annulus, and 2% within 2 annuli. Precision was high with an APE of 0.7% and a CV of 1.1 for the entire sample. Bias was not apparent in age estimates according to the age bias plot; however the slope (0.982) did slightly differ from one (Figure 6).

The von Bertalanffy growth equations for the MMR shovelnose sturgeon population were estimated and compared among years and sexes (Table 1). In 2002-2003 the population reached a larger L_{∞} and the Brody growth coefficient was greater than in 2005-2006 ($F = 6.72$, $df = 27$, $p = 0.0016$). When somatic growth was broken down by age class for each year of data, a decrease in mean fork length at age was observed between 2002-2003 and 2005-2006 over all age classes (Figure 7). The sex-specific von Bertalanffy growth curves differed ($F = 5.72$, $df = 27$, $p = 0.0036$) with males reaching the L_{∞} at a slightly quicker rate, but females having the larger L_{∞} (Figure 8 A). During the years in which the females were becoming sexually mature, the males attained a larger size; however after maturity was reached, females became larger (Figure 8 B).

Mortality

The catch curve analyses for instantaneous mortality rates were based on fish age 12 and older for both males and females. The pooled instantaneous mortality rate for both years and sexes was 0.60 ($r^2 = 96$, $df = 8$, $p = <0.0001$) or 45% annual mortality. The instantaneous mortality rate for females in the population was 0.58 ($r^2 = 0.86$, $df = 7$, $p = .0005$; 44.3% annual) and 0.59 for males ($r^2 = 0.93$, $df = 7$, $p = 0.0001$; 44.8% annual). Catch curve regressions were tested for homogeneity of slopes, but did not differ.

DISCUSSION

In the MMR, the shovelnose sturgeon population is changing demographically over time. I suggest that these changes are due to increased harvest and habitat change. All of the observed changes are characteristic of exploited fisheries experiencing a lack of spawning activity and poor recruitment. Habitat alterations can further reduce reproductive success, by reducing available spawning habitat, impeding access to required habitat, and reducing environmental cues that prompt spawning.

The sex ratio for the shovelnose sturgeon population in the MMR was 1:1 in 2002-2003 (Colombo et al. 2007b); however increased harvest in recent years may be responsible for the shift to a skewed sex ratio with more males. The sex ratio of a sturgeon population at equilibrium should be 1:1 (Trencia et al. 2002, Apperson and Wakkinen 1993, Alberta Sustainable Resource Development 2002), but the ratio may deviate on a local level due to differential distributions, activities, or movements of males and females. These natural effects on sex ratios were likely not important given our unbiased, standardized sampling effort, which was identical to that of Colombo et al. (2007b). More likely, sex ratio changed at the population scale due to changes in sex-specific growth, mortality, and longevity through selective harvest (Sandovy 1996). In many fisheries the sex ratio shifts toward predominately males due to high fishing pressure directed towards mature females or large-sized individuals which are typically females (Bruch 1999, Kamukuru and Mgaya 2004). The preferential harvest of females not only affects the sex ratio of the population, but also can negatively affect the reproductive success of the population, which reduces recruitment.

Evidence of reduced reproductive success and recruitment in the MMR can be seen in shifting length and age-frequencies. Sex-specific length distributions showed a pattern that is common among sturgeon species, with females growing larger (Everett et al. 2003). This pattern was not previously seen in the MMR population; Colombo et al. (2007b) reported no sex-specific differences in length-frequencies. However, as the removal of females likely has increased through harvest, it makes sense that the surviving females would enhance growth to compensate. Comparing length and age distributions at the population level between 2002 through 2006, it appears that fewer recruits are being produced. Thus, the removal of mature females by commercial harvest is likely leading to decreased reproductive success, which indirectly has a negative impact on recruitment leading to reduced abundance of smaller fish. Colombo et al. (2007a) found a similar pattern in that year class strength was negatively related to harvest. This increased tipping of the length and age structure towards older individuals has been reported in other sturgeon populations as an effect of substantial loss in reproduction due to increased exploitation and habitat degradation blocking migrations to spawning grounds (Khodorevskaya et al. 1997).

Increased harvest appears to be contributing to increased mortality. Colombo et al. (2007a) concluded that the pooled annual mortality rate for years 2000 through 2003 was 37%. With just a few years passing, the pooled mortality rate for 2005 and 2006 has risen to 45%. In this same time period standardized catch rates have declined relative to historical levels (Colombo et al. 2007a).

Changes in growth and maturation of commercial fish stocks over time have been well documented (Law 2000); specifically size-selective harvest causes adaptive changes

in life history traits related to body size such as modified length and age at maturity (Conover and Munch 2002). These changes can often be immediate consequences of shifts in the physical environment, the biotic environment, the prevailing patterns of fishing, or any combination of these (Law 2000). The most common response is earlier maturation and increased growth due to reduced intraspecific competition (Weatherly 1972, Beacham 1983, Law 2000), which allows fish to reproduce before being harvested (Gardmark et al. 2003). The converse appears to be happening in the MMR. Shovelnose sturgeon are thought to reach maturity at age 5 for males and age 7 for females (Helms 1974, Hurley and Nickum 1984) while MMR sturgeon matured later. A possible explanation is that sturgeon that are maturing early are being selected for by commercial fishers (Law 2000). In sturgeon populations, females do not recruit to the fishery until they become sexually mature. It is advantageous for fish to mature at a later age and larger size in populations that are mainly harvested for mature adults (Ernande et al. 2003) and when fishing primarily takes place on spawning grounds (Law 2000). In both cases, increased mortality due to fishing makes it beneficial to grow larger and older before maturing.

The sex-specific growth curves strategically make sense, with males attaining the theoretical maximum length quicker than females, but females reaching a larger maximum length. However, all year classes have experienced a similar deceleration in somatic growth through time, with a consistent shift in length at age. Similar trends have been previously seen in populations in which harvest was selective for larger-sized individuals, the growth rate of the surviving individuals declines and smaller sizes occur (Walsh et al. 2006). In addition, 2005 and 2006 were atypically low water years in the

MMR and this may have reduced growth rates across all ages through some climatic mechanism (e.g., high temperatures or reduced food).

One of the major factors impeding the understanding of what is truly occurring within the shovelnose sturgeon population in the MMR is the difficulty of teasing apart the actual contribution of each possible factor such as harvest, habitat degradation, and climate. Habitat has not been greatly altered in the past decade, with the exception of low water levels in 2005 and 2006, which likely affected growth but probably not longer-term population characters such as survival and recruitment. Thus, on the basis of these data, I suggest that the current harvest of mature females is negatively affecting the reproductive capacity of the shovelnose sturgeon population. It appears that the population is aging, recruitment is not sufficient to replace those being removed, and the majority of those fish remaining are male due to females being harvested after maturation.

A major goal of fisheries science is to conserve the available resources, and 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 only continue to decline. One possible strategy to conserve the population is to impose conservative length limits, such as a minimum harvestable size of 685 mm FL, which was 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 these types of areas could be protected at the appropriate times, a majority of the mature females may be allowed to spawn. A temporary ban on harvest may also be successful as it has in other sturgeon populations (Pikitch et al. 2005), but the signs of recovery may not be seen for many years. The best management plan for sturgeon population recovery will probably be a combination of regulations and restrictive harvest with strict enforcement and monitoring.

Table 1. Von Bertalanffy parameters estimated for the Middle Mississippi River shovelnose sturgeon population in 2002-2003 and 2005-2006, and also sex-specific parameters 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

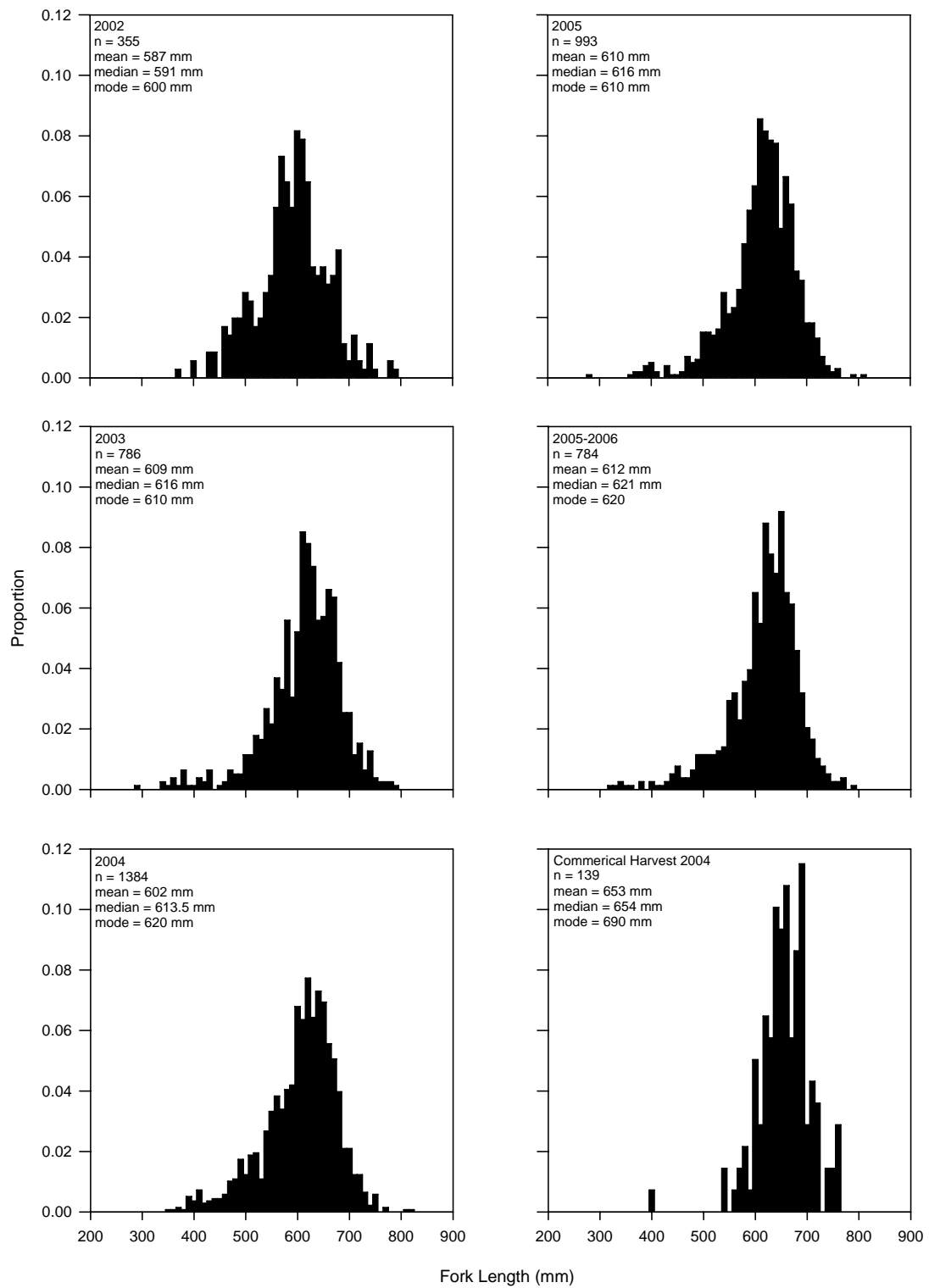


Figure 1. Length-frequency distributions of the shovelnose sturgeon population in the Middle Mississippi River by year and commercially harvested shovelnose sturgeon from one sample in 2004.

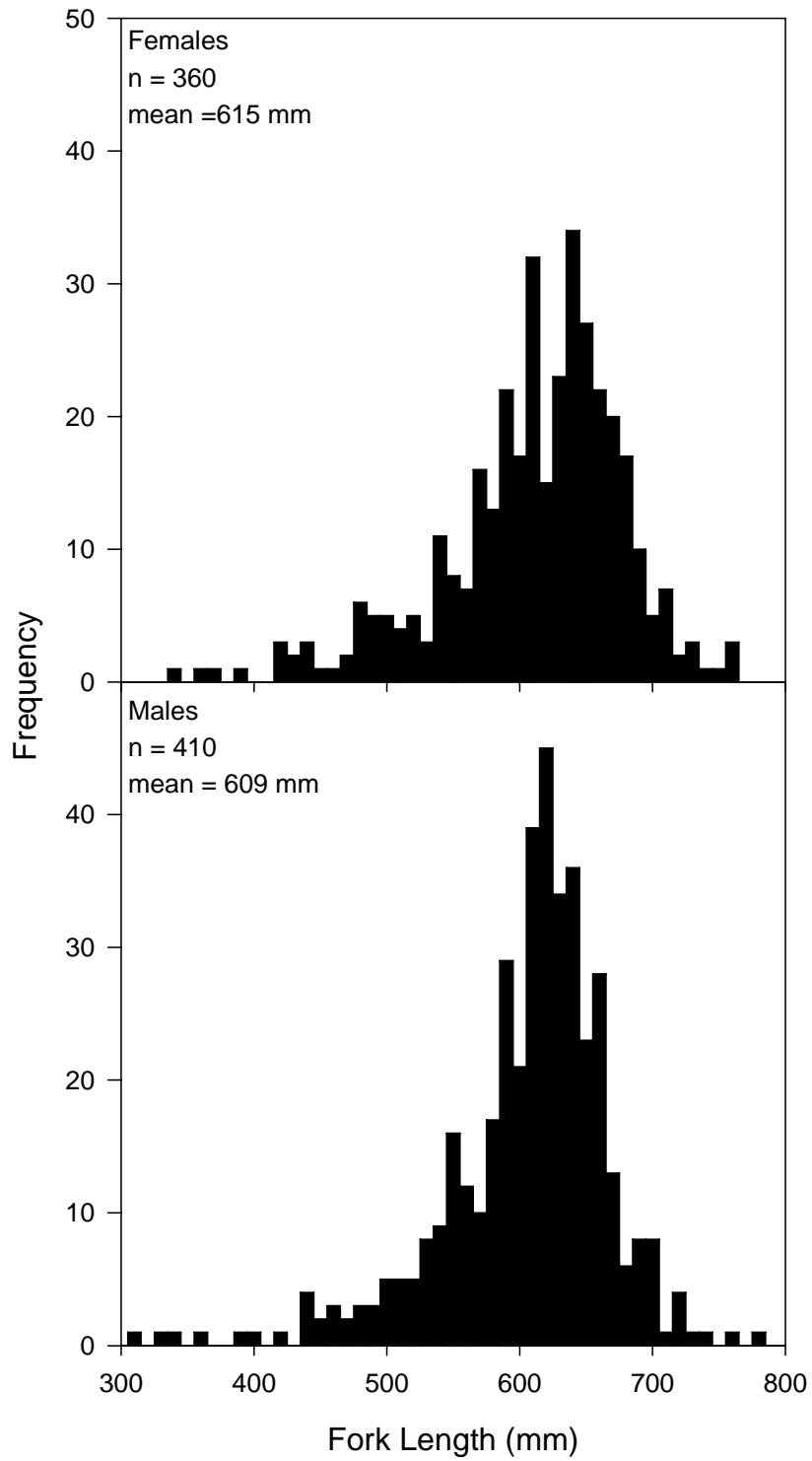


Figure 2. Sex-specific length-frequency distributions of shovelnose sturgeon in the Middle Mississippi River during 2005 through 2006.

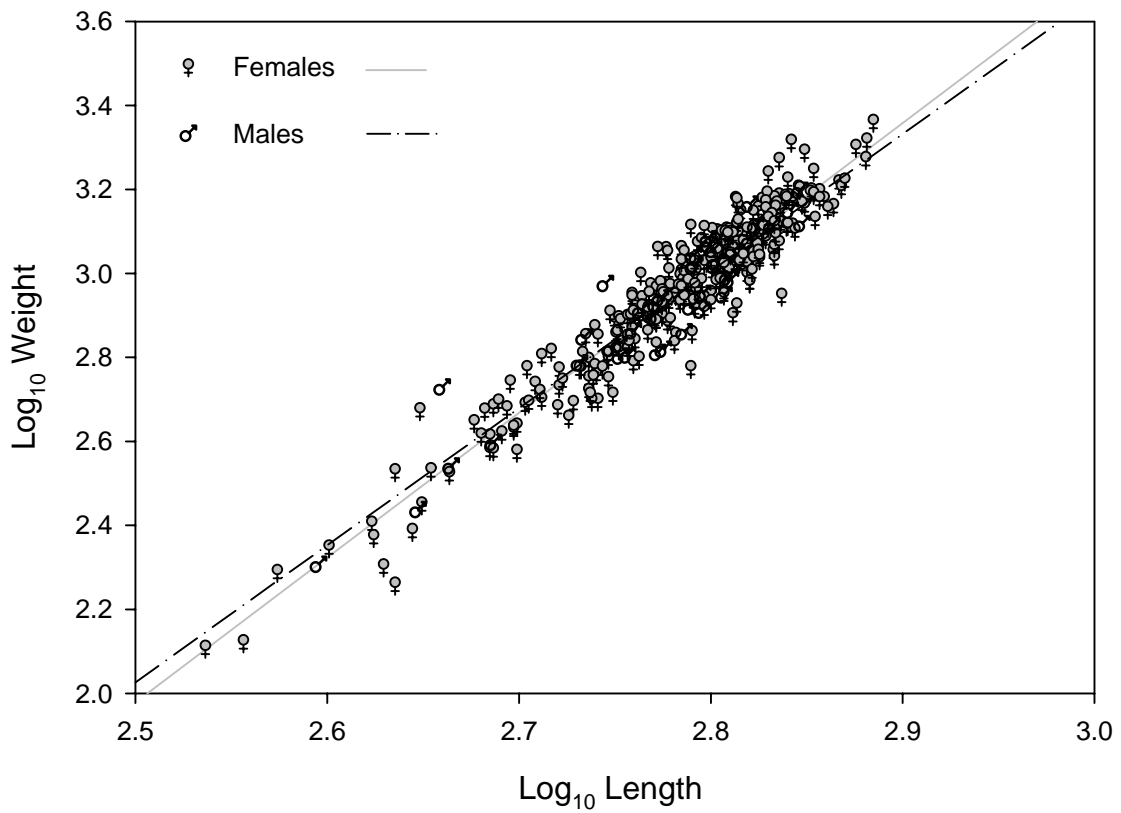


Figure 3. Length-weight relationship of shovelnose sturgeon in the Middle Mississippi River during 2005 through 2006. Solid line representing females ($R^2 = 0.92$) and dashed line representing males ($R^2 = 0.90$).

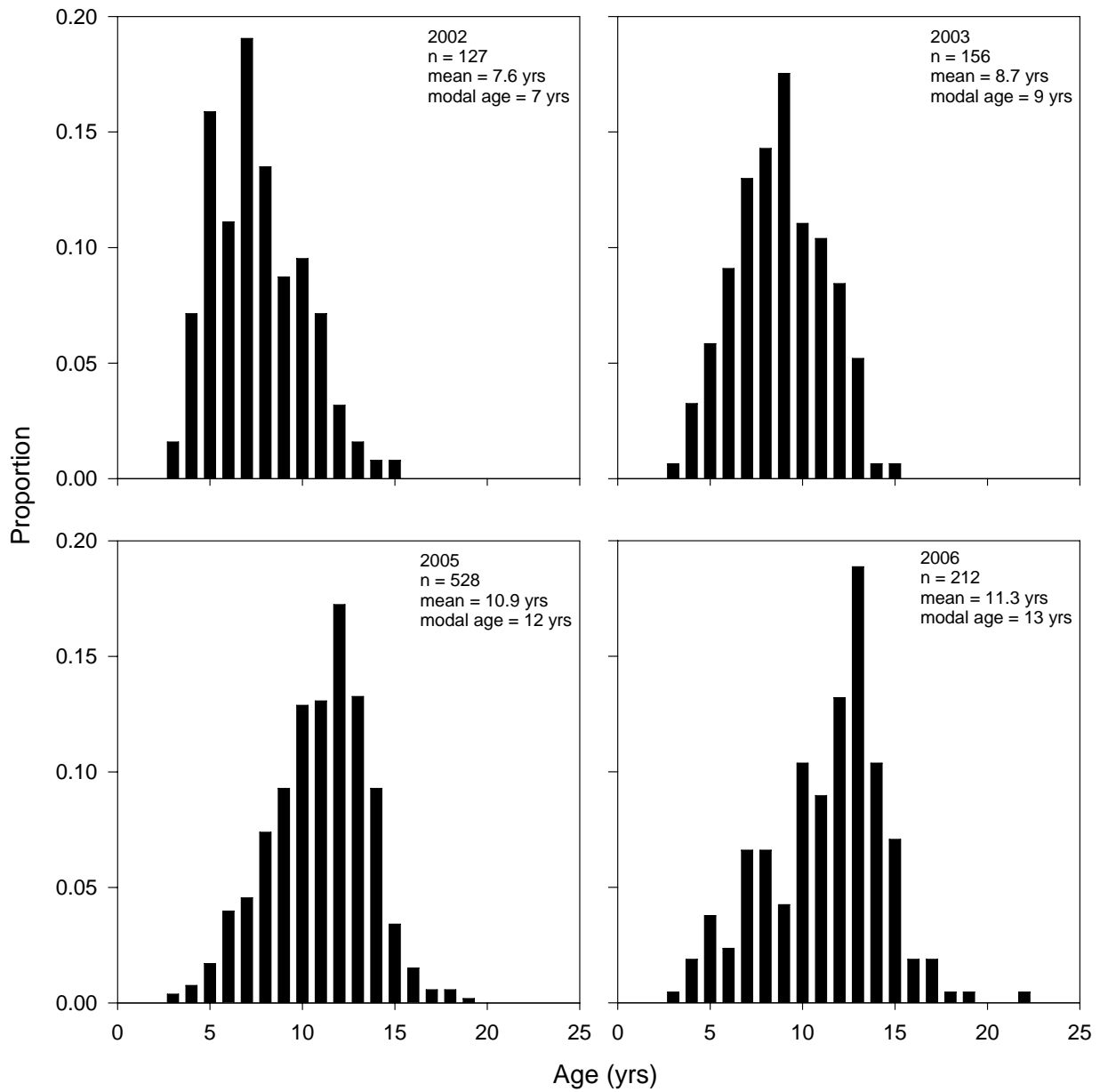


Figure 4. Age-frequency distributions for the shovelnose sturgeon population in the Middle Mississippi River from 2002 to 2006.

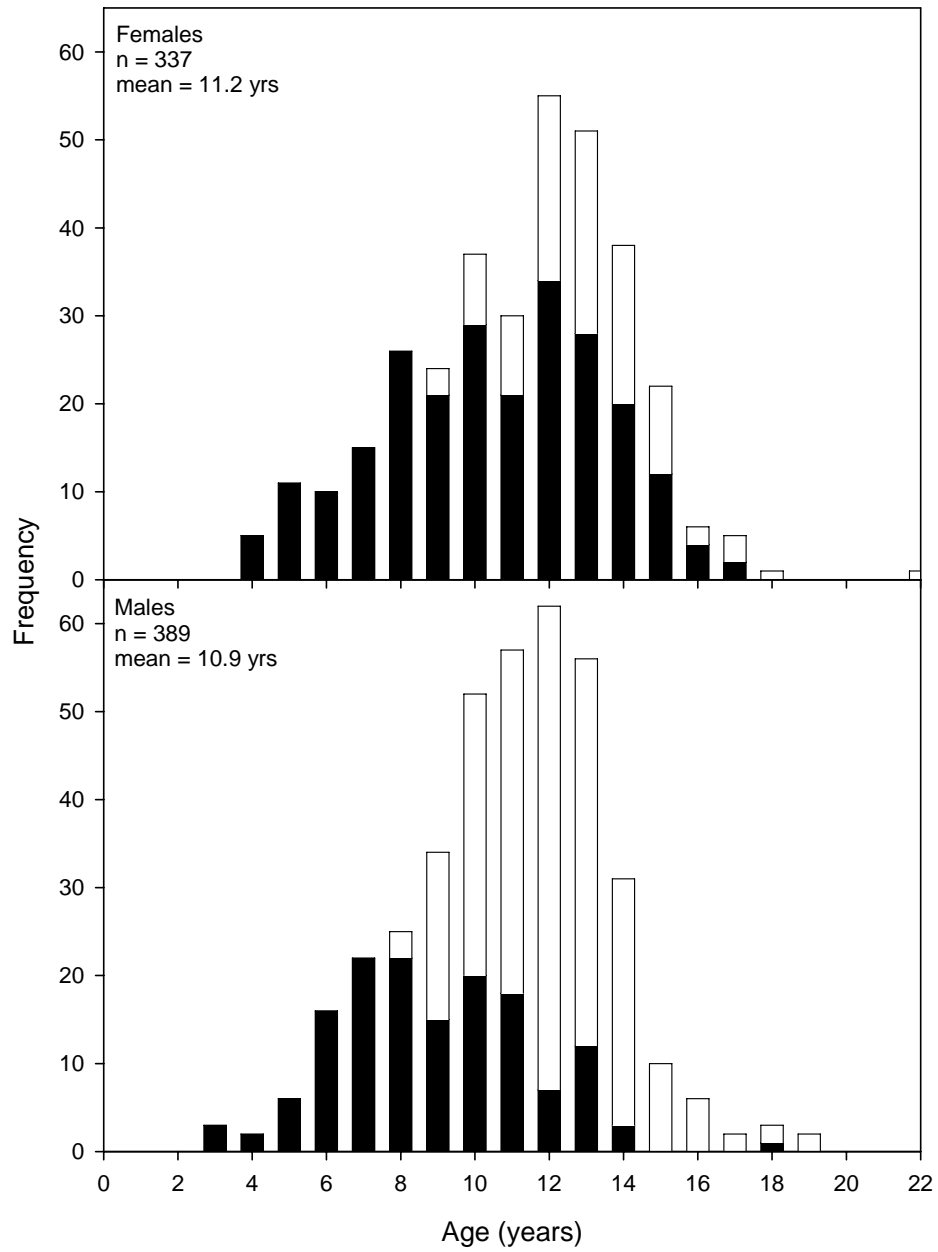


Figure 5. Sex-specific age-frequency distributions for shovelnose sturgeon in the Middle Mississippi River during 2005 through 2006. Black portion of bars showing immature individuals and white portion of bars representing the mature individuals.

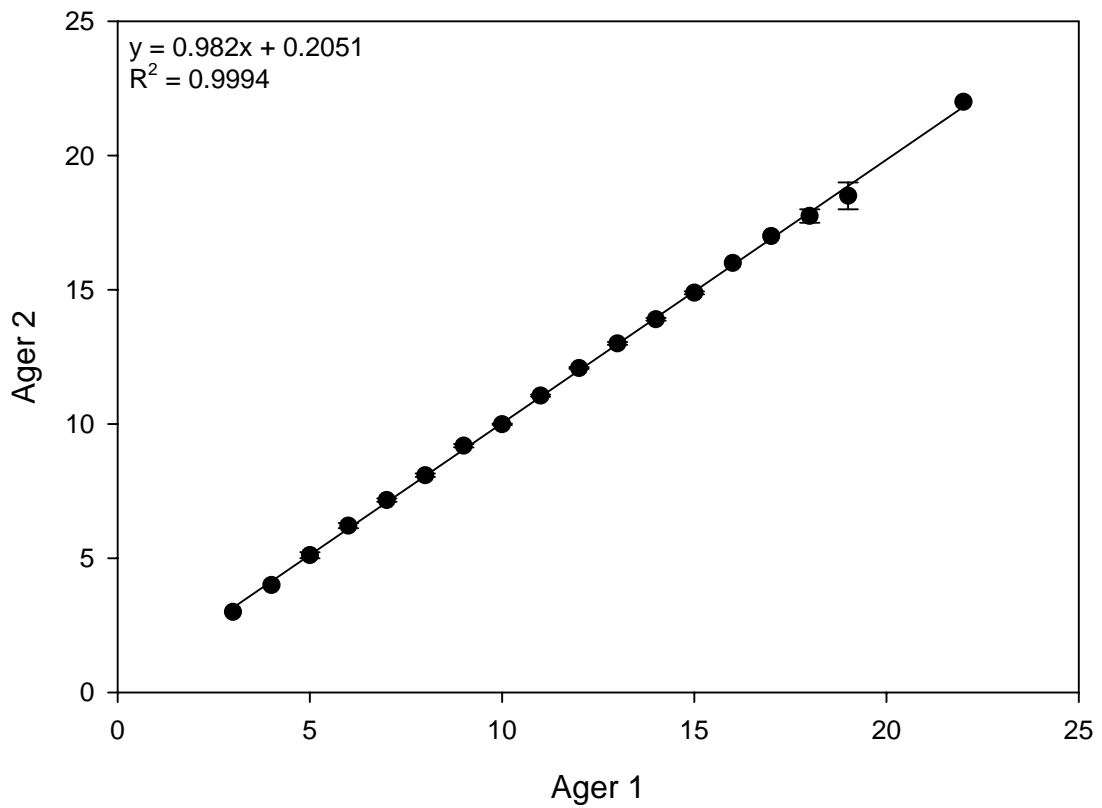


Figure 6. Linear regression analysis of age bias between independent readers. Age estimates are plotted as the mean age estimate by ager 2 for the age classes of ager 1 for shovelnose sturgeon collected in the Middle Mississippi River during 2005 through 2006. Error bars represent 95% confidence intervals. The slope of the regression line did differ from one due to minimal variation in the data.

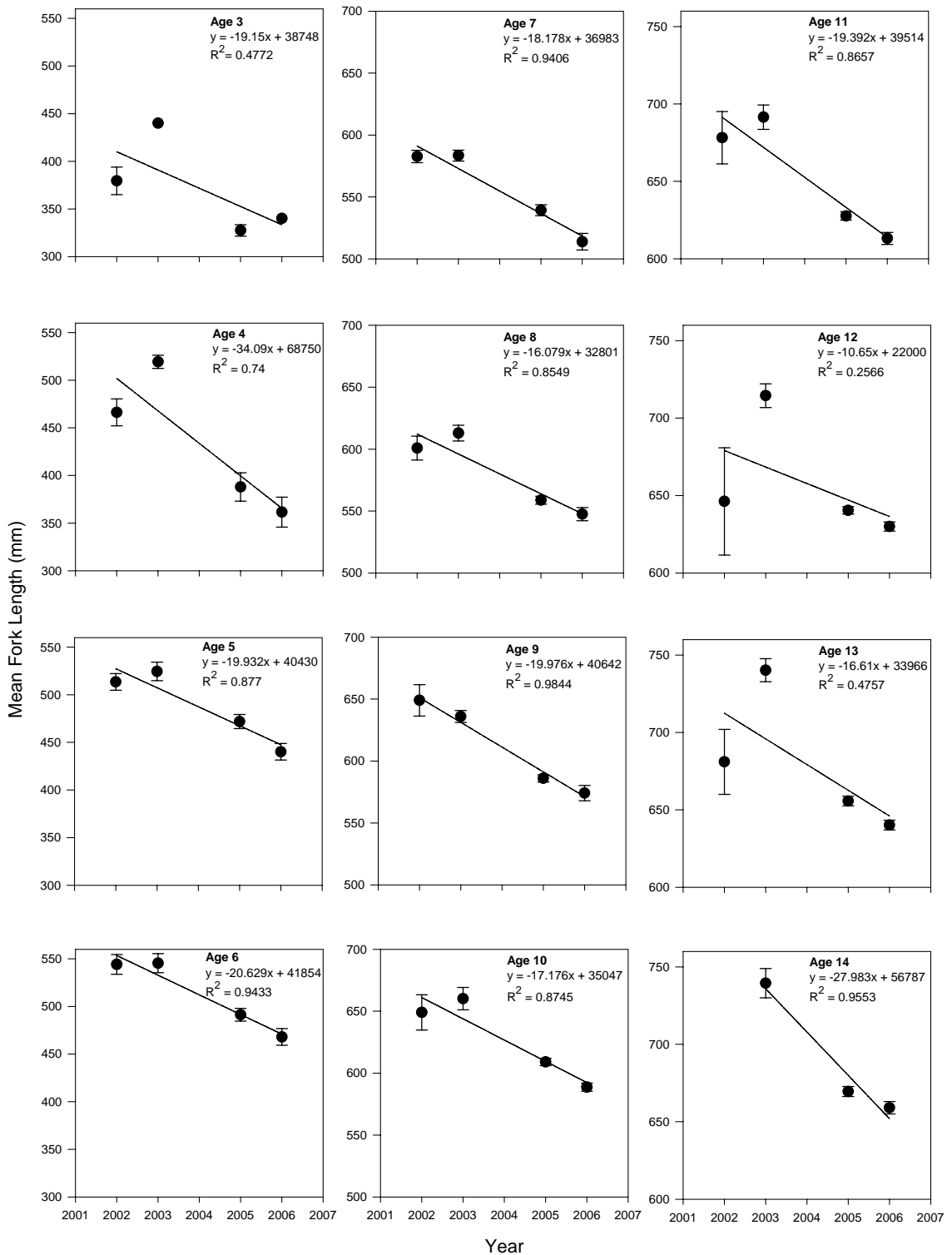


Figure 7. Mean fork length with error bars (standard error) of each age class by year. Note different scales on the y-axis.

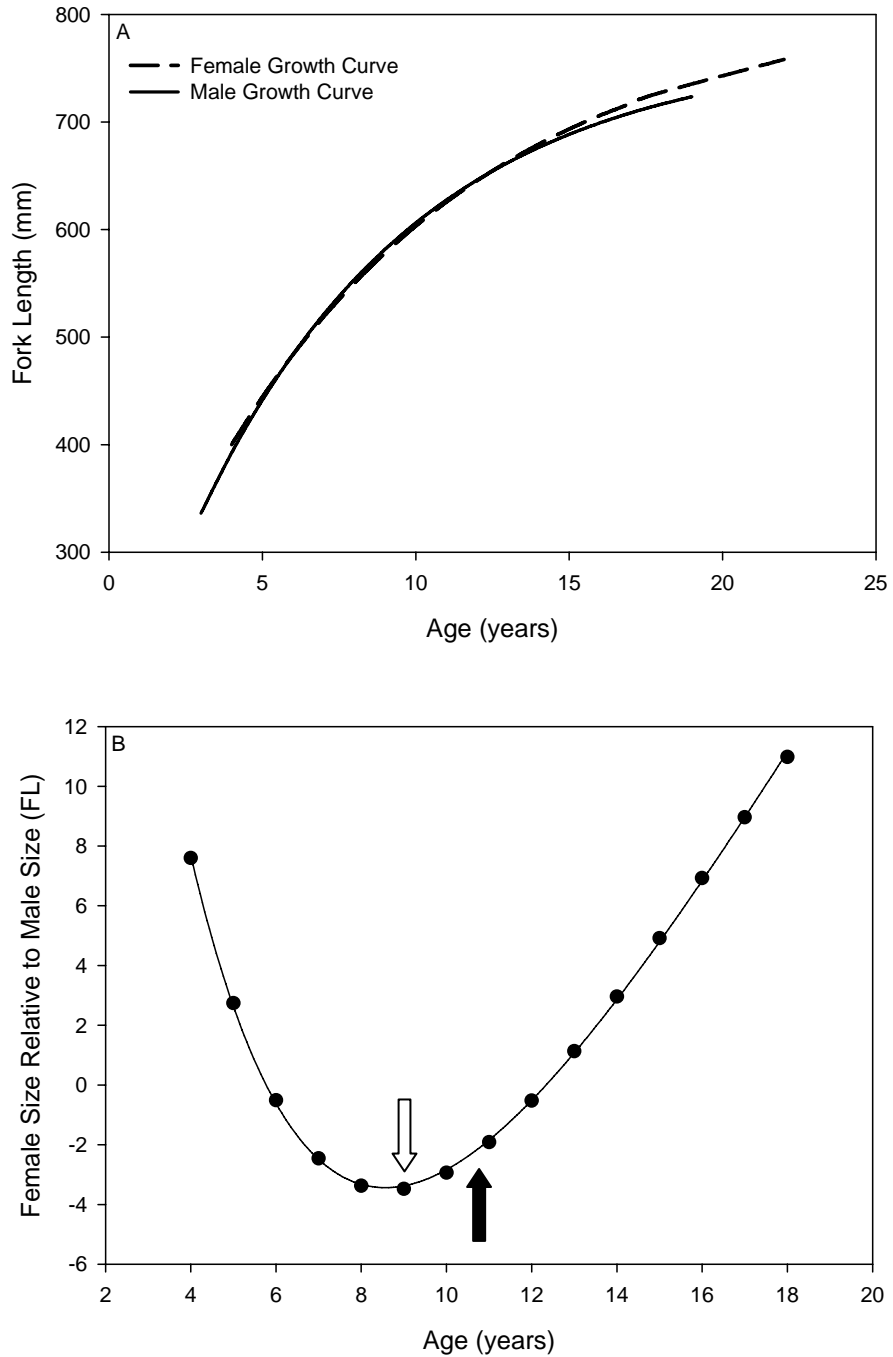


Figure 8. A. Von Bertalanffy growth curves representing female (dashed line) and male (solid line) growth in the Middle Mississippi River shovelnose sturgeon population collected during 2005 through 2006. B. A plot of the relative size of females to males at a specific age using the predicted lengths from the von Bertalanffy growth curves. The white arrow represents the mean age of maturity for males and the black arrow indicates the mean age of maturity for females.

CHAPTER TWO

DEFINING A LIFE HISTORY STRATEGY FOR SHOVELNOSE STURGEON IN THE MIDDLE MISSISSIPPI RIVER

ABSTRACT

Shovelnose sturgeon *Scaphirhynchus platorynchus* in the Middle Mississippi River is one of the last commercially viable sturgeon populations in the world, yet its basic life history strategy is unknown. I sampled adult and larval shovelnose sturgeon to link age at maturation, timing and periodicity of spawning, and larval growth rates. Age at maturity was later than shown previously, with males becoming sexually mature at age 9 and females at 10.5 years. Total egg count was slightly lower than previously reported with a mean of 29,573/female. Similar to previous reports, most males and females spawned every 2 and 3 years, respectively. Larval shovelnose sturgeon occurred during June and July of 2005 and May and June of 2006, confirming successful spawning. Larval sturgeon grew between 0.69 to 1.69 mm total length per day among four distinct cohorts produced each year. For the first time for this population, sturgeon were found to spawn during the fall. Fall sturgeon contained ripe eggs with polarization indexes (PIs) <0.05 ; larval sturgeon was collected thereafter. This life history strategy is similar to those of other sturgeon and likely places this species at risk to overharvest.

INTRODUCTION

Life history theory attempts to predict population responses to changes in reproduction, growth, and mortality, thus providing insight into vulnerability to

disturbances in the environment, mortality rates due to harvest, and recruitment variability. Winemiller and Rose (1992) proposed a triangular continuum of life history strategies for fishes with three endpoints: (1) opportunistic - small, rapidly maturing, short-lived fish with high reproductive effort, low batch fecundity, and low investment per offspring, (2) equilibrium - intermediate size fish that often exhibit parental care with moderate to long generation time, low reproductive effort, low batch fecundity, and high investment per offspring, and (3) periodic - large, late-maturing, long-lived fish with moderate reproductive effort, high batch fecundity, and low investment per offspring. Models such as those proposed by Winemiller and Rose (1992) increase our ability to develop management and conservation practices.

The high intrinsic rate (r) of population growth of opportunistic fishes (Winemiller and Rose 1992, Rochet et al. 2000, Winemiller 2005), allows them to resist frequent habitat disturbances and high adult mortality (Winemiller and Rose 1992). Because equilibrium strategists depend on density-dependent factors to control population size, they are less vulnerable to environmental variability and harvest (Rochet et al. 2000, Winemiller 2005). Species with a periodic life history are vulnerable to exploitation because they rely on predictable environmental cues and must have long life spans to allow reproductive effort to be spread over multiple years (Winemiller and Rose 1992, Rochet et al. 2000). These traits not only cause populations to be adversely affected by increased adult mortality (Rochet et al. 2000), but also small differences in mortality of early life stages have potential to greatly influence the stock abundance (Winemiller 2005). Because a majority of our commercially and economically important species are periodic strategists (Winemiller and Rose 1992, Winemiller 2005), it is

important to gain information on their reproductive biology so that I can better understand their population dynamics.

Some of the most valuable commercial species are sturgeon and paddlefish in the order Acipenseriformes, which typically fall in the periodic endpoint. Given the susceptibility of this group, it is also considered to be among the most endangered and threatened (Ludwig et al. 2002, Pikitch et al. 2005). Of the 27 extant species, all are characterized by limited adult abundance and most are threatened with only a few exceptions (Billard and Lecointre 2001, Pikitch et al. 2005). The Caspian Sea sturgeon fishery has long produced the majority of the caviar traded internationally, but with the collapse of these European and Asian sturgeon fisheries appearing imminent, increased pressure has shifted towards the smaller North American species, such as the shovelnose sturgeon (*Scaphirhynchus platyrhynchus*) (Quist et al. 2002, Pikitch et al. 2005, Colombo et al. 2007a). The Winemiller and Rose life history model may provide some guidance as to how shovelnose sturgeon populations will respond to increased harvest and how to better manage these populations before they reach the imperiled status. However, sturgeon population demographics and reproductive characteristics vary greatly between geographical ranges and among species, so guidelines for one species may not benefit another. For example, the Winemiller and Rose model used large sturgeon, but it is possible that small sturgeon such as the shovelnose sturgeon may have a different suite of tactics.

Most sturgeon show some basic spawning characteristics such as environmental cues triggering spawning during the spring over gravel or rock substrates, with multiple years between spawning intervals (Billard and Lecointre 2001, Williamson 2003).

However the small size of shovelnose sturgeon leads to earlier age at maturation, higher growth rates, shorter life spans, and lower fecundity than other sturgeon (Keenlyne 1997, Billard and Lecointre 2001, Williamson 2003). These traits that deviate from most other sturgeon may place shovelnose sturgeon farther from the periodic endpoint and closer to the opportunistic end of the continuum, perhaps requiring different management tactics.

The objective of this study was to quantify the duration and timing of life stages of the shovelnose sturgeon in the Middle Mississippi River (MMR). Adult shovelnose sturgeon were sampled to determine age at maturation and periodicity of spawning. Larval shovelnose sturgeon were collected to determine the timing of spawning and to quantify larval growth rates in the MMR. Collecting data on the reproductive biology of the shovelnose sturgeon will provide the parameters that are required for stock assessment and population models.

METHODS

Directed Repeated Adult Sampling

To quantify reproductive status of adults, shovelnose sturgeon were sampled monthly during February 2005 through June 2006, using stationary bottom set gill nets [5.08 centimeter bar mesh, 45.7 meters long, 3.05 meters deep]. During each month, six nets were set for 24 hours off the tips of wingdikes, parallel to the flow in an area of converging water velocities at Modoc, IL (RKM 201-198), Chester, IL (RKM 191-188), and Grand Tower, IL (RKM 127-124) due to known high densities of shovelnose sturgeon in these areas. Fork length (FL, 1 mm) and wet mass (0.1 g) were quantified for each fish. The left pectoral ray was removed from all fish and later used to determine

age. Water temperature, conductivity, dissolved oxygen, and pH were collected at the surface for each sampling trip with a Quanta Hydrolab water quality meter. Daily river stage height was determined from the United States Geological Services (USGS) gauging station at Chester, IL.

Each month, a subsample of the first 20 sturgeon collected at each site was preserved on wet ice and taken back to the lab. A mid-ventral incision was made from the anus through the pelvic girdle, exposing the gonads. The gonads from each sturgeon were photographed, removed, and weighed to calculate gonadosomatic index (GSI), which is defined as the gonad and gonadal fat wet weight divided by the total body wet weight and then multiplied by 100. All gonads were fixed in 10% neutral buffered formalin. The digital images of the gonads were later used to categorize the samples into the stages of development based on the index from Colombo et al. (2007b). Egg quantity within black egg (Stage FIV) females was quantified by removing five, 1-gram samples per ovary and counting eggs in each subsample. The mean egg count for each ovary was multiplied by the weight of both ovaries to estimate total egg quantity (Crim and Glebe 1990). Linear regression was used to determine whether relationships among fork length, weight, GSI, egg count, and relative egg size were present for FIV sturgeon.

Aging

Pectoral fins rays were placed in coin envelopes and dried to determine age, so that age at maturation could be established. Three sections were cut from the basal portion of each fin ray using a Buhler Isomet® low speed saw. Each section, increasing in width (0.635mm, 0.6858mm, and 0.7366mm) was secured to a slide using cyanoacrylate. Cross sections were examined independently by two readers using a

stereomicroscope under 7-45x magnification. Under transmitted light, a pair of opaque (growth) and translucent bands was considered an annulus (Everett et al. 2003). The annuli were counted from the nucleus to the apex of each section. This method has been validated for Atlantic sturgeon (Secor et al. 1997), lake sturgeon (Rossiter et al. 1995), and white sturgeon (Brennan and Cailliet 1989) and is the most precise method for aging the shovelnose sturgeon (Jackson et al. 2007). When readers disagreed, they examined the cross sections together to reach an agreement.

Larval and Juvenile Sampling

In order to determine the timing and duration of successful spawning, sturgeon larvae and juveniles were collected at sites within the MMR reach using a mini-Missouri trawl during June and July of 2005 as well as May through August of 2006. The mini-Missouri trawl is a two-layer, balloon trawl with a cover of 4.76 mm delta style mesh and an inner trawl body of 17.46 mm bar mesh. The trawl narrows from 2.44 meters at the head rope to 0.46 meters at the mid-section and the cod end (Herzog et al. 2005). The head rope with floats and a chained foot rope are tied to otter boards [40.6 cm x 22.86 cm, weighing 8.2 kg]. The trawl is towed (in reverse) along the bottom contours of the river with 22.86 m tow lines tied to each side of the bow of the boat. Three minute trawls were made around islands and in side channels, with the majority of the effort being concentrated at island tips at about 3 m depth. Larvae were kept in an ice slurry and brought back to the lab.

The total length (mm, TL) of each larval sturgeon was measured and a digital image was captured. Growth rates for each year were estimated, using similar methods to Braaten and Fuller (2007). Length-frequency histograms for each sampling week were

generated and cohorts were assigned to groups of fish with similar length modes progressing throughout the sampling period. For each sampling week, the mean length of each weekly cohort was calculated. Regression was used to estimate relative growth rates for each weekly cohort (Braaten and Fuller 2007). The slopes were tested for homogeneity (test for interaction in ANCOVA) to determine whether growth rates differed among cohorts.

Additional Fall Sampling

The increased proportion of both mature male and female sturgeon in October 2005 followed by an increased proportion of spent male and female sturgeon in January of 2006, prompted additional fall sampling in 2006. Although standard sampling ceased in June 2006, shovelnose sturgeon adults also were collected during September, October and November in 2006. The first twenty fish were brought back to the lab and data were collected as before. Egg samples also were collected from the FIV females and stored in balanced salt solution. The eggs were then boiled for 10 minutes allowing the yolk to harden and fixing the position of the germinal vesicle. After boiling, the eggs were stored in buffered formalin. Eggs were then bisected with a razor blade along the animal-vegetal axis and examined under a dissecting microscope. The distance of the germinal vesicle from the inner border of the oocyte chorion and oocyte diameter was used to calculate the polarization index (PI) for each sample. The PI (an indicator of oocyte ripeness) is the distance of the germinal vesicle from the chorion divided by the egg diameter (Dettlaff et al. 1993). Trawling for larval fish also was conducted during October and November of 2006.

RESULTS

Male Reproductive Demographics

Four hundred fifteen adult male shovelnose sturgeon, ranging from 319 to 786 mm FL, were sampled. All stages (Mv – MII) described by Colombo et al. (2007b) occurred in addition to running ripe males and the MIII stage (spent male) (Table 2). Each stage had a wide range of fork lengths and ages (Table 3). Mean GSI differed between stages except for MI and MIII, with Mv being lower and MII being greater than all others ($F_{3, 411} = 27.13$, $p < 0.0001$) (Figure 9). Ages were determined for 389 fish, with ages ranging from 3 to 19 years. Male sturgeon had a modal age of 12 years and a mean age of 10.9 years (Figure 10). Males become sexually mature between ages 8 to 10 years (mean age at maturity 9 years of age).

Female Reproductive Demographics

Only 363 females were captured, representing a smaller proportion of the sample. Female sturgeon ranged in size from 344 to 767 mm FL. All stages except for running ripe (FV) were captured (Table 2). Female stages also varied in FL and age (Table 3). The mean GSI differed between all stages except for Fv and FVI ($F_{5, 357} = 183.94$, $p < 0.0001$) (Figure 11). Three hundred thirty seven female sturgeon were aged, with ages ranging from 4 to 22 years. Female sturgeon had a modal age of 12 years and a mean age of 11.2 years (Figure 10). Females became sexually mature between ages 9 and 11 years (mean age at maturity 10.5 years of age).

Total Egg Count

The mean (\pm SE) total egg count of FIV shovelnose sturgeon was 29573 ± 2472 eggs ($n = 40$), or 21.7 ± 1.29 eggs per gram of fish wet weight. The total number of eggs was positively related to wet weight ($p < 0.001$, $r^2 = 0.48$) (Figure 12). No other relationships occurred among fecundity, fork length, GSI, and relative egg size.

Timing and Periodicity of Spawning

Mature (FIV and MII) shovelnose sturgeon, peaked during March and April 2005, October 2005, and April 2006 (Figure 13). These peaks coincided with conditions believed necessary for successful spawning. The peak in the proportion of mature sturgeon was followed by peaks in proportion of spent (FVI and MIII) shovelnose sturgeon with a lag time of about one or two months during May through June 2005, January 2006, and June 2006 (Figure 13).

Mature ovaries comprised 13% of the total body weight with a mean GSI of 13.11%, while the mature testes only accounted for 3% of the body weight with a mean GSI of 3.09%. All stages for both males and females were present during all seasons. However, only 61% of males and 27% of females were mature.

Larval and Juvenile Sampling

Larval and juvenile sturgeon were collected in June and July of 2005 and May and June of 2006 (Figure 14). A total of 130 and 39 larval and juvenile shovelnose sturgeon were collected during 2005 and 2006, respectively. In 2005, individuals were collected on eleven sampling days during June 8th through July 7th. In 2006, individuals were collected on eleven sampling days during May 8th through June 22nd.

Relative growth rates were estimated for the larval sturgeon in 2005 and 2006. The relative growth rates were based on four weekly cohorts each year. In 2005 the growth rates (\pm 95% confidence intervals) of weekly cohort 1 (1.28 mm per day, 0.86 – 1.69), weekly cohort 2 (1.34 mm per day, 1.22 – 1.44), weekly cohort 3 (1.38 mm per day, 1.3 – 1.46), and weekly cohort 4 (1.28 mm per day, 1.17 – 1.38) did not differ ($p = 0.594$) (Figure 15). For 2006, again the growth rates for each weekly cohort were not different ($p = 0.699$) (weekly cohort 1: 1.27 mm per day, 1.12 – 1.42), (weekly cohort 2: 1.14 mm per day, 0.98 – 1.32), (weekly cohort 3: 1.21 mm per day, 1.01 – 1.42), and (weekly cohort 4: 1.35 mm per day, 0.69 – 2.01) (Figure 15).

Evidence of Fall Spawning

Eggs of three fall sturgeon collected in September and October had PIs < 0.05 , meaning the eggs were ripe and good candidates for spawning. During September, a milting male occurred. Additional trawling was inhibited by low water, but in November 2006 I collected a 55-mm TL larval sturgeon.

DISCUSSION

While shovelnose sturgeon may be smaller and mature earlier than some other sturgeon species, their reproductive biology appears to fall into the periodic life history strategy. Shovelnose sturgeon gonadal development was similar to that of other sturgeon species. All stages described by Colombo et al. (2007b) were collected and identified with the exception of FV (running ripe females) and I additionally found spent males (MIII). Similar to other sturgeon species, shovelnose sturgeon do not spawn annually, having multiple years between spawning intervals. Using the proportion of each stage by

season in combination with age data, models for the periodicity of spawning intervals were developed. The male reproductive cycle is completed in one to two years. The abundance of each stage in a given year indicates that the two-year cycle is more common. Male sturgeon spend about 6 to 7 years in the Mv stage before they become an MI, then they spend 1 to 2 years developing into a mature male (MII) and spawn (Figure 16). Female shovelnose spawn every three to four years. The three-year cycle is most common. Female sturgeon transform from the Fv to the FI stage after about 7 to 8 years, spend about 2 or 3 years in stage FI, then progress through FII and FIII within the next year and a half. From the FIV stage, which can last 4 to 6 months, which then becomes running ripe (FV) during the spawning season (Figure 16).

Previous research in the Mississippi and Missouri Rivers suggested that shovelnose sturgeon matured at age 5 (males) and 7 (females) (Helms 1974, Moos 1978, Hurley and Nickum 1984). However, our results (males: 9 and females: 10.5) coupled with a recent study in the Wabash River (females: 9) (Kennedy et al. 2005), show evidence that these populations are now reaching maturity at later ages. A possible explanation for this could be the increased harvest seen in recent years (Colombo et al. 2007a). Because sex and size-specific harvest can increase age at maturity (Law 2000, Conover and Munch 2002, Ernande et al. 2003) these changes may be due to the recent increase in shovelnose sturgeon harvest. Size selective harvest also can reduce fecundity (Conover and Munch 2002), which is supported by a decline in mean fecundity estimates from 32,562 in 1974 (Helms 1974) to 29,573 in 2005 and 2006. Shovelnose sturgeon were once assumed to be more resilient to harvest than other sturgeon species due to smaller size, earlier maturation, and shorter life spans (Carlander 1954, Morrow et al.

1998). However the MMR shovelnose sturgeon population may now be showing negative impacts of harvest similar to other exploited sturgeon populations.

As seen in other periodic species, shovelnose sturgeon spawning seems to be cued by annual or seasonal variations in environmental conditions. Three major peaks occurred in the proportions of mature fish, two in the spring of each year and one in the fall of 2005. However all peaks coincided with rising river stages and water temperatures that approached or included the 16.9 to 20.5 °C range at which shovelnose sturgeon are believed to spawn. These peaks were then followed by peaks in spent adults and larval shovelnose sturgeon, suggesting that successful spawning occurred. With a periodic strategy, fish can delay maturation so that they are more likely to reproduce when environmental conditions are optimal for the growth and survival of larval and juvenile fish (Winemiller and Rose 1992). Based on the reproductive demographics for shovelnose sturgeon in the MMR it appears that females have a longer reproductive cycle than male sturgeon, similar to other sturgeon. With the ovaries on average comprising a larger percentage of the total body weight, this prolonged reproductive cycle in females may be expected. Female shovelnose sturgeon appear to favor a three year cycle that allows a third of the mature females to reproduce any given year, similar to many other sturgeon species in the same geographical range (Williamson 2003). With only a fraction of the fish reproducing each year, this allows reproductive output to be allocated across multiple years and some individuals to reproduce successfully despite long periods of unfavorable conditions (Winemiller 2005). This tactic of “bet-hedging” enhances adult survivorship in suboptimal conditions and allows the reproductive effort to be spread over many years, so that increased recruitment during a year of optimal conditions will

compensate for years with reduced juvenile survivorship (Winemiller and Rose 1992). However if the environmental conditions are suboptimal for many years or adult mortality increases, reproductive success will be reduced.

Based on all the evidence, I believe that harvest may be selecting individuals that spawn in the fall when conditions are similar to those that occur during the spring. This phenomenon has been observed in other exploited sturgeon populations, such as the Atlantic sturgeon (*Acipenser oxyrinchus oxyrinchus*) (Collins et al. 2000), Gulf sturgeon (*Acipenser oxyrinchus desotoi*) (Sulak and Clugston 1998), and a number of Eurasian species (Berg 1959). Indeed additional sampling in fall 2005 produced milting males as well as females with eggs in spawning condition. If I apply the growth rates found in 2005 and 2006, the one larval shovelnose sturgeon collected during November 2006 was spawned in September.

This study has provided current information on the reproductive biology of shovelnose sturgeon in the Middle Mississippi River as well as some evidence of possible fall spawning; however, gaps still remain. The best possible management for periodic species, such as the shovelnose sturgeon, is to maintain some critical density of adult stock and to protect spawners and spawning habitat during the reproductive period. In order to implement this type of management, spawning areas in the MMR must be identified and possibly more effort should be focused on determining whether both spring and fall spawning cohorts exist. If these information gaps could be filled, maintaining this crucial density of adult stocks by protecting the spawning habitat during the spawning periods, conservation of the MMR shovelnose sturgeon population is not only possible, but may also allow commercial harvest to persist.

Table 2 Stages of gonadal development of the shovelnose sturgeon (modified from Colombo et al. 2007b).

Sex	Stage	Description
Male	Mv	Virgin male, pink ribbon like testis embedded in small amount of testicular fat
	MI	Yellow tubular testis in large amount of fat
	MII	Large pink testis in reduced amount of fat
	MIII	Spent male, compressed red/pink testis
Female	Fv	Virgin female, small well ordered ovarian folds with small amount of fat
	FI	Ovarian folds with large amount of fat
	FII	Small white to yellow oocytes
	FIII	Yellow to green eggs
	FIV	Black eggs
	FV	Spawning female
	FVI	Spent female or recovering, translucent ovary with atretic oocytes

Table 3. Sex and stage specific fork length and age ranges for shovelnose sturgeon collected from February 2005 through June 2006.

Sex/Stage	Fork Length (mm)			Age (years)		
	Minimum	Maximum	Mean	Minimum	Maximum	Mean
Mv	319	598	480	3	13	6.4
MI	457	786	595	6	18	9.7
MII	531	762	635	8	19	12
MIII	549	743	632	8	18	12
Fv	344	599	492	4	12	6.5
FI	506	738	607	7	17	10.8
FII	574	761	641	9	16	12.2
FIII	592	760	655	10	16	12.9
FIV	559	767	665	9	22	13.3
FVI	549	723	641	10	17	12.5

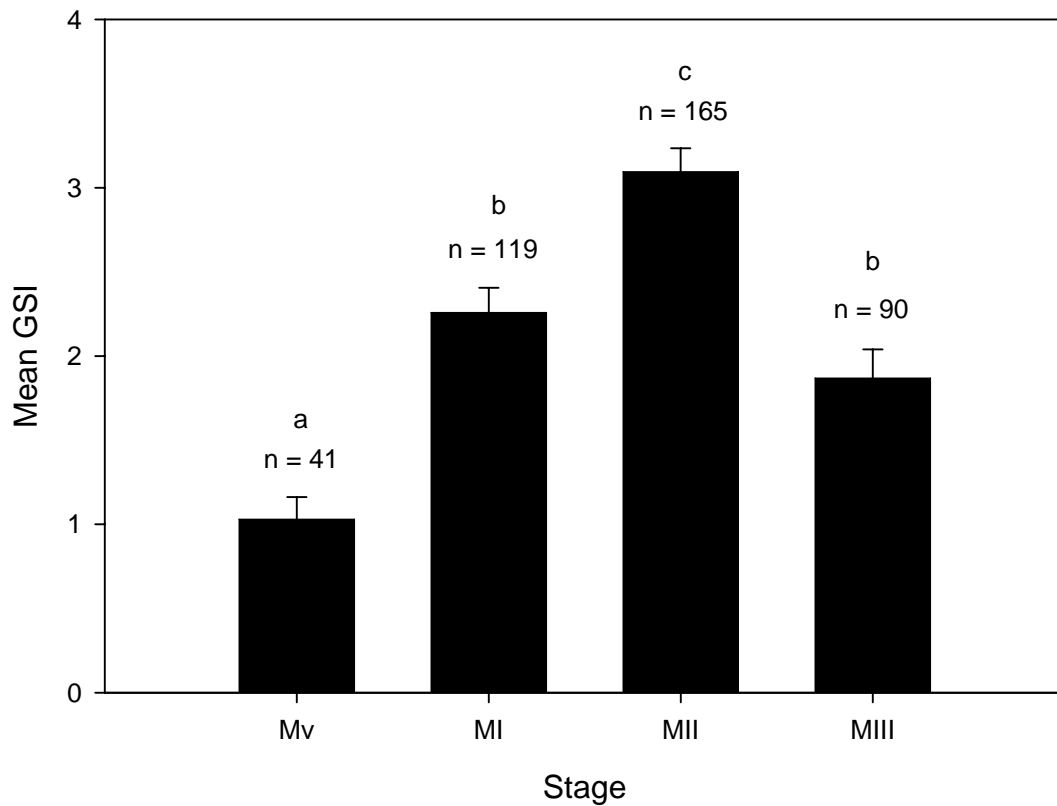


Figure 9. Mean GSI for each stage of the male shovelnose sturgeon gonadal development in the Middle Mississippi River during 2005 through 2006 with standard error and sample size above each error bar. (Different letters represent significantly different means, at $p < 0.05$).

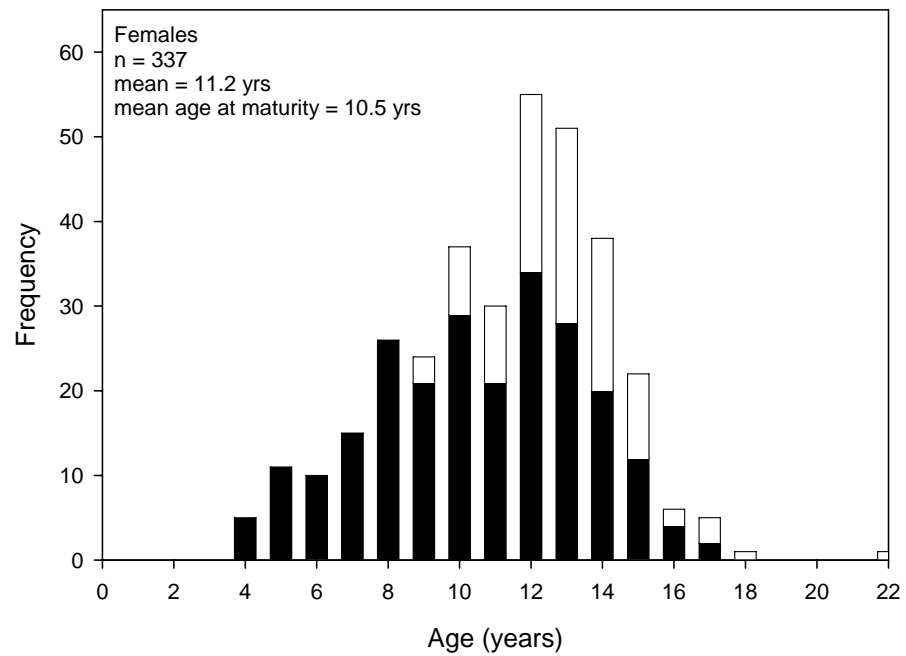
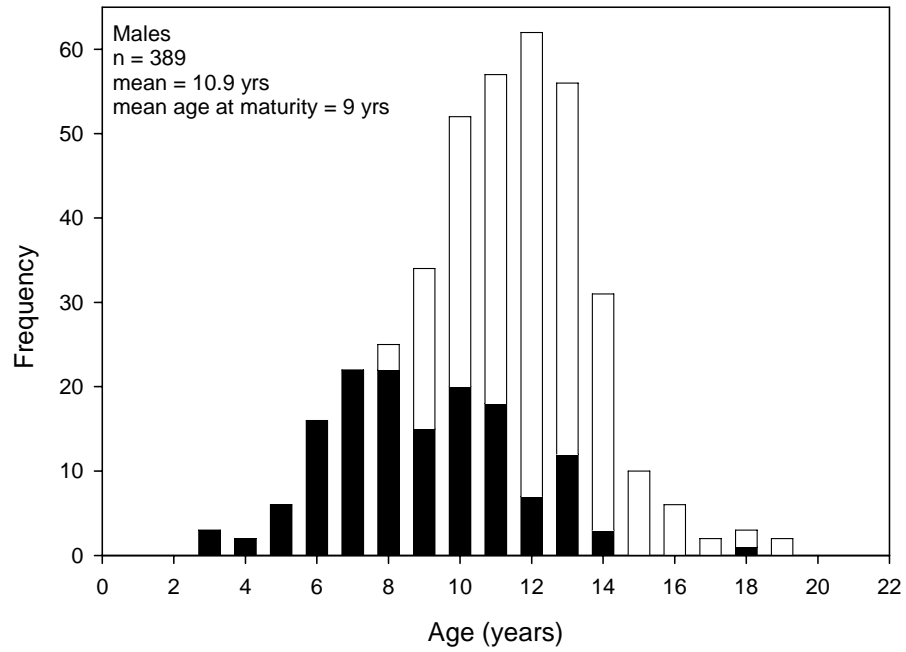


Figure 10. Age-frequency distributions for male (top) and female (bottom) shovelnose sturgeon in the Middle Mississippi River during 2005 through 2006. Black portion of bars showing immature individuals and white portion of bars representing the mature individuals.

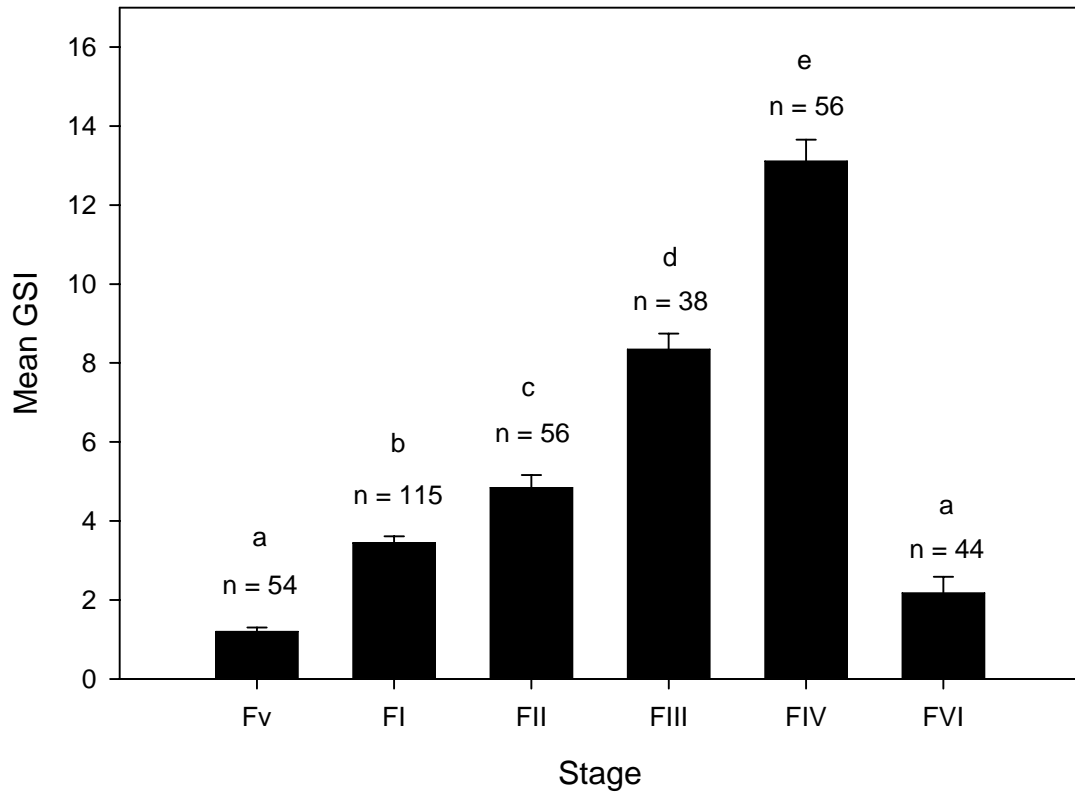


Figure 11. Mean GSI for each stage of the female shovelnose sturgeon gonadal development in the Middle Mississippi River during 2005 and 2006 with standard error and sample size above each error bar. (Different letters represent significantly different means at $p < 0.05$)

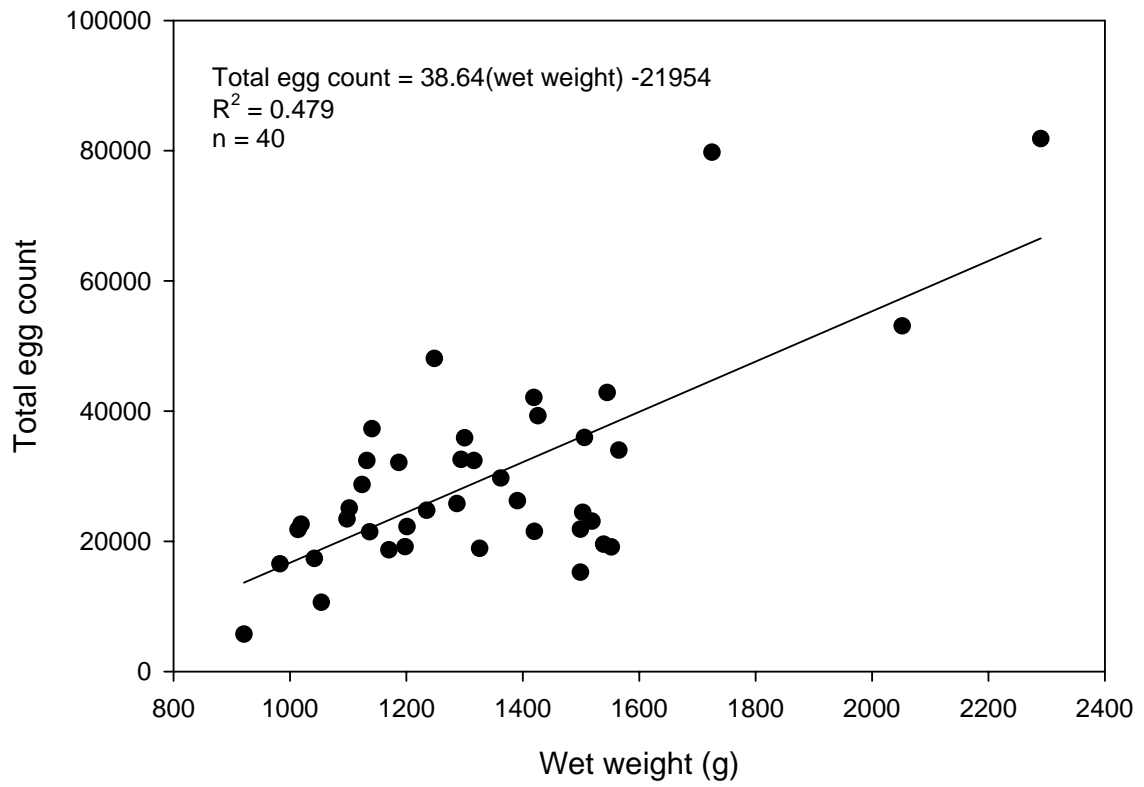


Figure 12. Total egg count –wet weight relationship of female black egg shovelnose sturgeon in the Middle Mississippi River during 2005 and 2006 ($R^2 = 0.48$).

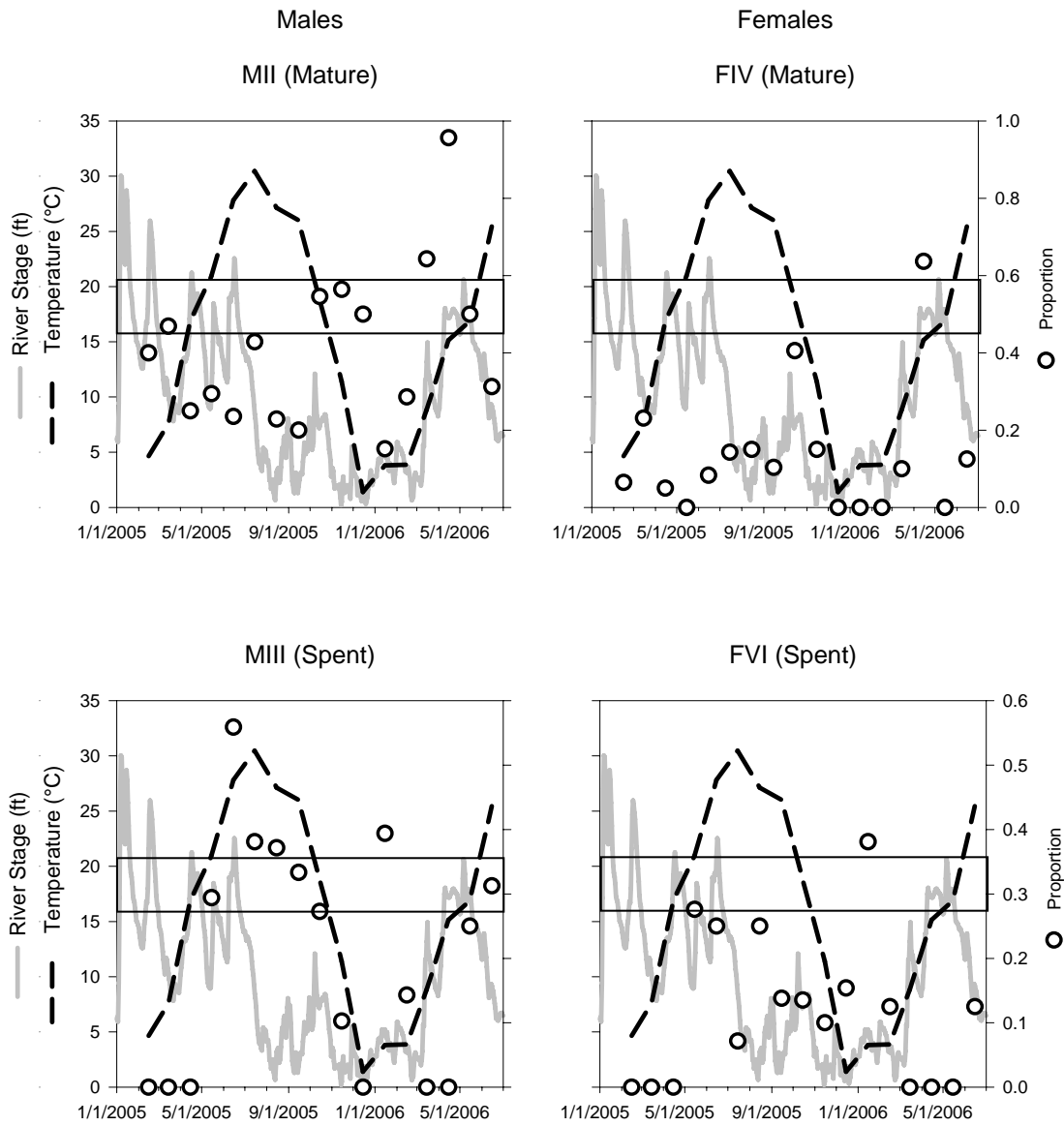


Figure 13. Proportion of mature (top) and spent (bottom) males (left) and females (right) plotted against river stage (gray solid) and water temperature (black dash). The black box includes the optimal spawning temperatures for shovelnose sturgeon.

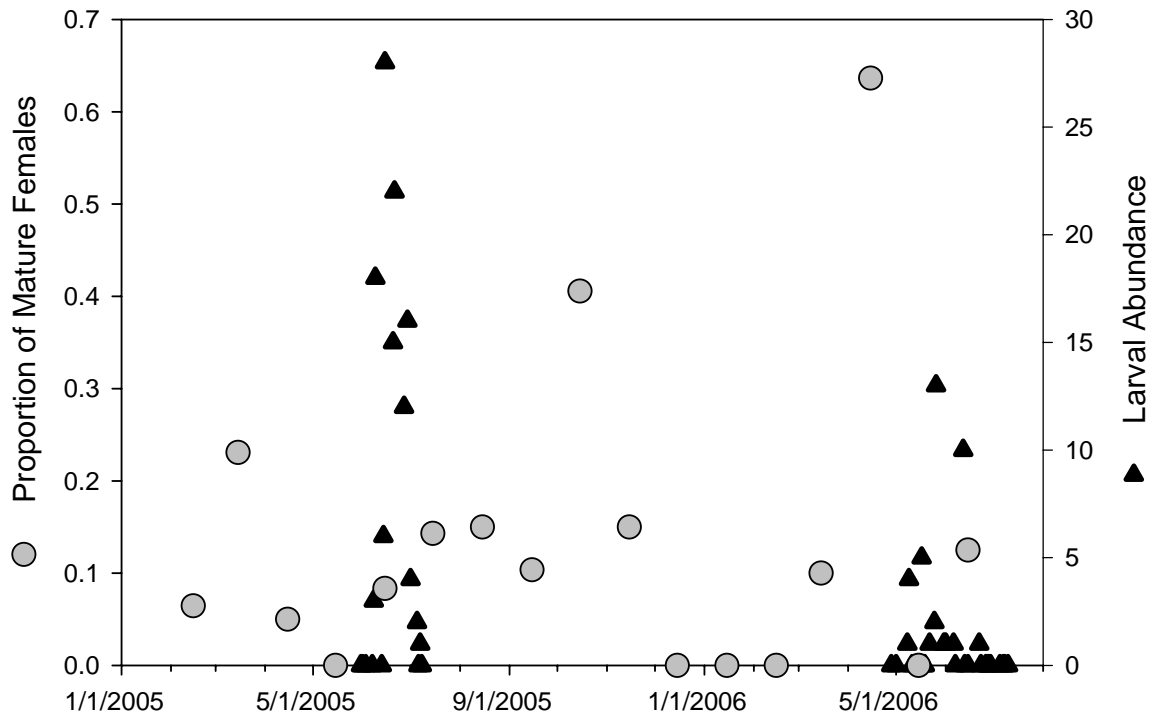


Figure 14. Proportion of mature female shovelnose sturgeon (circles) with larval abundance (triangles) during 2005 and 2006 in the Middle Mississippi River.

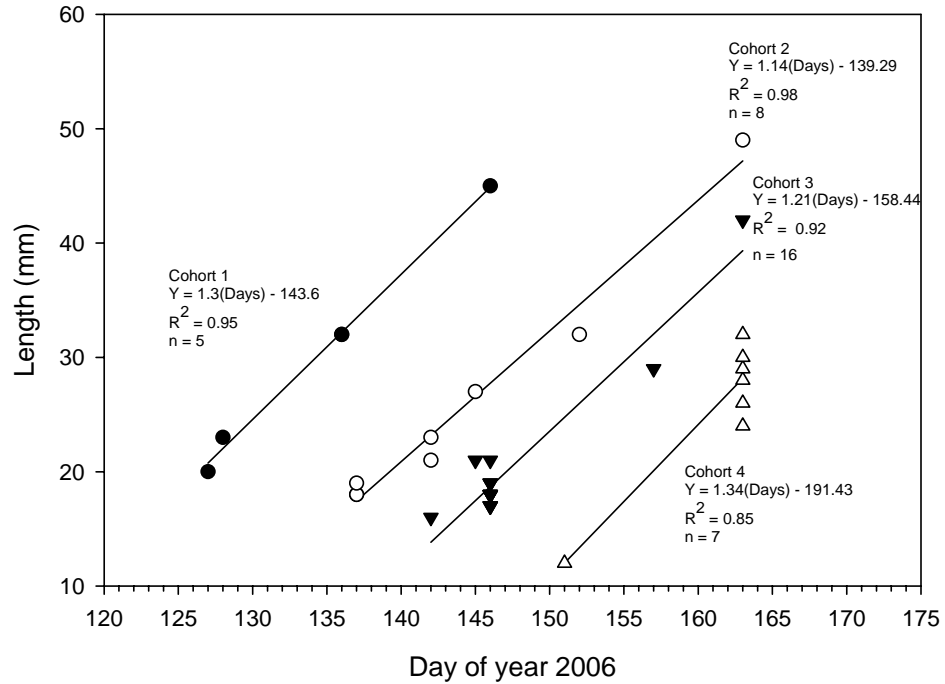
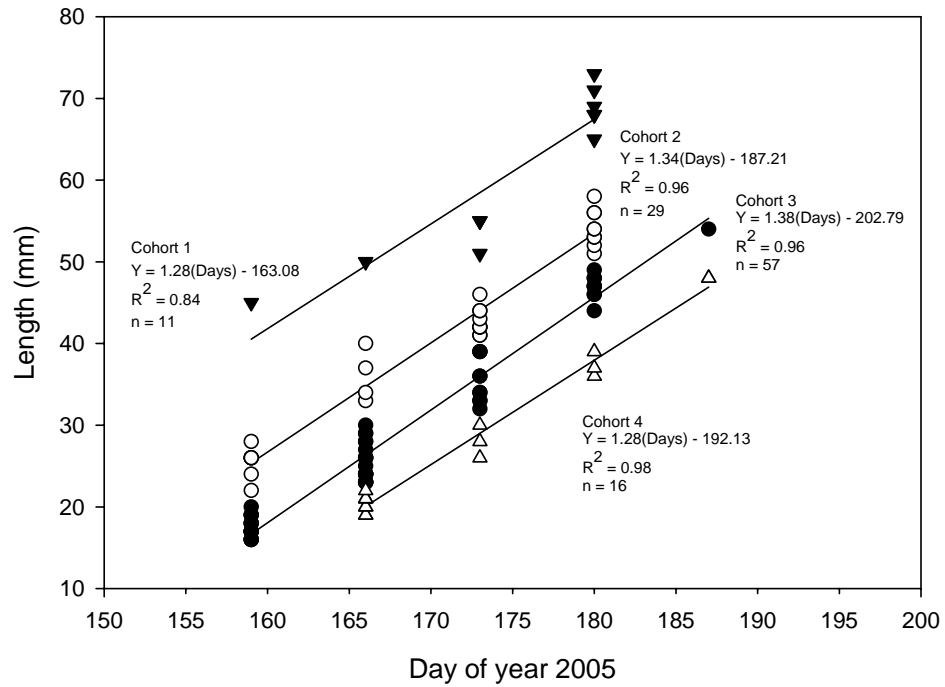


Figure 15. Linear relationship of length (mm) and day of the year for cohorts of larval and young of the year shovelnose sturgeon in the Middle Mississippi River during 2005 (top) and 2006 (bottom).

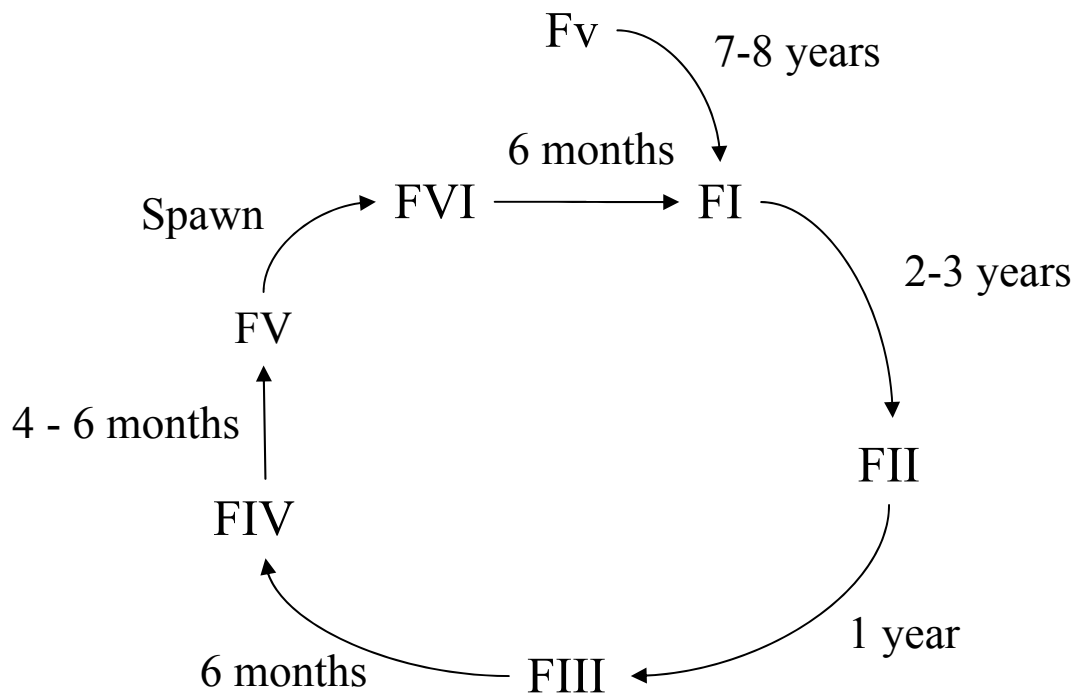
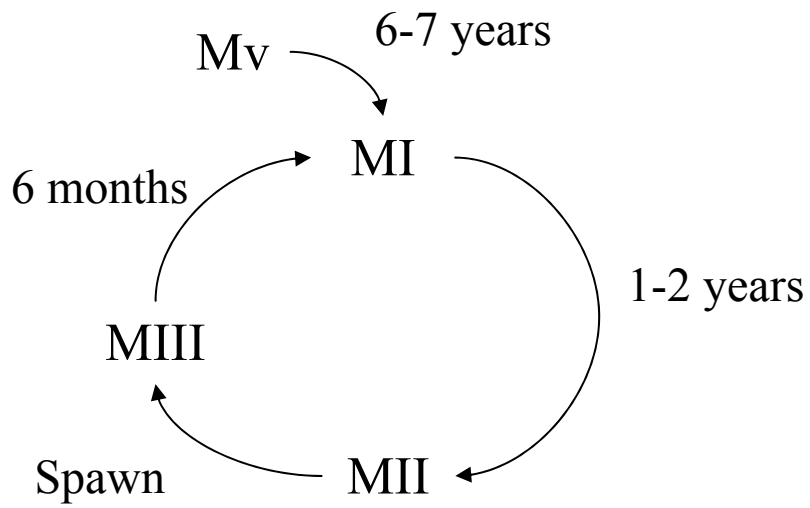


Figure 16. The reproductive cycle of male (top) and female (bottom) shovelnose sturgeon in the Middle Mississippi River.

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