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Maturation and Reproduction of Shovelnose Sturgeon in the Middle Mississippi River

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Abstract.—Shovelnose sturgeon *Scaphirhynchus platorynchus* in the middle Mississippi River provide one of the last commercially viable sturgeon fisheries in the world, yet their maturation and reproduction have not been linked. During 2005 and 2006, we sampled adult and age-0 shovelnose sturgeon to link age at maturation, the timing and periodicity of spawning, age-0 sturgeon production, and the resulting age-0 growth rates. Age at maturity was later than previous estimates, the minimum age of first maturation being 8 years for males and 9 years for females. Total egg count was slightly lower than previously reported (mean = 29,573 per female; SE = 2,472). Males and females typically spawned every 2 and 3 years, respectively. Peaks in mature fish coincided with rising river stages and water temperatures at which shovelnose sturgeon probably spawn. Peaks in spent adults followed. Age-0 shovelnose sturgeon occurred during June and July 2005 and May and June 2006, confirming successful spawning. Age-0 sturgeon grew between 0.69 and 1.69 mm total length/d; four distinct weekly cohorts occurred each year. During fall 2006, females contained ripe eggs, males were milting, and a single age-0 sturgeon (total length = 55 mm) was captured, suggesting that shovelnose sturgeon spawn during fall as well as spring. Management must consider the protracted nature of spawning within seasons as well as differences in spawning activity between seasons.

Some of the most valuable freshwater commercial species are sturgeon and paddlefish (order Acipenseriformes). Given the susceptibility of this group, it is also considered to be among the most endangered and threatened of all fishes (Ludwig et al. 2002; Pikitch et al. 2005). Of the 27 extant species, all are characterized by limited adult abundance and most are threatened (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 this and other European and Asian sturgeon fisheries, increased pressure has shifted towards the smaller North American species, such as the shovelnose sturgeon *Scaphirhynchus platorynchus* (Quist et al. 2002; Pikitch et al. 2005; Colombo et al. 2007a). With much commercial effort being diverted towards the shovelnose sturgeon population in some reaches of the Mississippi River and continued habitat alterations occurring throughout the entire river system, a thorough understanding of its life history is needed (Keenlyne 1997; Colombo et al. 2007a).

Shovelnose sturgeon are one of North America's (and perhaps the world's) most abundant sturgeons. The native distribution of shovelnose sturgeon extends from the upper basins of the Missouri and Mississippi river systems to the confluence of the Gulf of Mexico (Keenlyne 1997). Previous research suggests that shovelnose sturgeon spawning commences in early spring (i.e., April) at a water temperature of 16.9°C and concludes during summer (i.e., end of June) at 20.5°C (Keenlyne 1997). Furthermore, shovelnose sturgeon have similar reproductive requirements as other sturgeon species, such as abiotic cues triggering spawning during the spring or fall, gravel or rock substrate spawning grounds, and multiple years between spawning intervals (Billard and Lecointre 2001; Williamson 2003). However, in contrast to other sturgeons, the small size of shovelnose sturgeon leads to earlier age at maturation (5–7 years), faster growth rates, shorter life spans (generally less than 15 years), and lower fecundity (Keenlyne 1997; Billard and Lecointre 2001; Williamson 2003). These unique traits for a sturgeon species may allow shovelnose sturgeon to better tolerate large changes in population dynamics (e.g., variable recruitment), perhaps requiring different management tactics. As noted above, much information on shovelnose sturgeon life history exists; however, more information on the reproductive ecology and its implications for recruitment are needed to effectively manage shovelnose sturgeon fisheries.

Our objective was to better understand the reproductive ecology of shovelnose sturgeon in the middle

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TABLE 1.—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 a small amount of testicular fat
	MI	Yellow tubular testis in a 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 a small amount of fat
	FI	Ovarian folds with a large amount of fat
	FII	Small white to yellow oocytes
	FIII	Yellow to green eggs
	FIV	Black eggs
	FV	Spawning female
	FVI	Spent or recovering female, translucent ovary with atretic oocytes

Mississippi River (MMR), which extends between the confluences of the Ohio and Missouri rivers. Adult shovelnose sturgeon were sampled to determine age at maturation and periodicity of spawning. Age-0 shovelnose sturgeon were collected to determine the timing of spawning and to quantify age-0 growth rates in the MMR. These data will provide maturation and recruitment parameters that are required for stock assessment and population models.

Methods

Directed repeated adult sampling.—To quantify reproductive status of adult shovelnose sturgeon in the MMR, fish were sampled monthly during February 2005 through June 2006 using stationary bottom-set gill nets (5.08-cm-bar mesh, 45.70 m long, 3.05 m deep). During each month, six nets were set for 24 h off the tips of wing dikes, parallel to the flow in an area of converging water velocities at Modoc, Illinois (river kilometer [RKM] 201–198, measuring from the confluence of the Ohio River), Chester, Illinois (RKM 191–188), and Grand Tower, Illinois (RKM 127–124). These locations were chosen based on prior knowledge of high shovelnose sturgeon densities in these areas. Fork length (FL), the most precise length measurement for adults, was measured to the nearest 1 mm and weight was measured to the nearest 0.1 g for each fish. The left pectoral ray was removed from all fish and later used to estimate age. Water temperature was collected at the surface during each sampling trip. Daily river stage height was determined from the U.S. Geological Services gauging station at Chester, Illinois.

Each month, a subsample of the first 20 shovelnose sturgeon collected at each site was preserved on wet ice and taken back to the laboratory. A midventral 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 100 times the gonad and gonadal fat weight divided by the total body weight. All gonads were fixed in a 10% solution of neutral buffered formalin. The digital images of the gonads were later used to categorize each fish into developmental stages based on Colombo et al. (2007b; Table 1). Using the proportion of each stage by season in combination with age data, we estimated the periodicity of spawning intervals. Egg quantity within black egg (stage FIV) females was quantified by removing five 1-g 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 FL, weight, GSI, egg count, and relative egg size were present for stage FIV sturgeon. Significance was determined using an alpha value of 0.05 for all comparisons.

Aging.—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 (Buhler, Ltd., Lake Bluff, Illinois). Each section, increasing in width (0.64, 0.69, and 0.74 mm), was secured to a slide using cyanoacrylate. Cross sections were examined independently by two readers using a stereomicroscope under 7–45× 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 *Acipenser oxyrinchus* (Secor et al. 1997), lake sturgeon *A. fulvescens* (Rossiter et al. 1995), and white sturgeon *A. transmontanus* (Brennan and Cailliet 1989), and is the most precise method for aging shovelnose sturgeon (Jackson et al. 2007). When readers disagreed, they examined the cross sections together to reach an agreement; if no agreement was reached, the sample was discarded.

TABLE 2.—Sex- and stage-specific FL and age ranges for shovelnose sturgeon collected from February 2005 through June 2006 in the middle Mississippi River.

	FL (mm)				Age (years)			
Stage	Minimum	Maximum	Mean	SE	Minimum	Maximum	Mean	SE
				Males				
Mv	319	598	480	10.61	3	13	6.4	5.14
MI	457	786	595	4.55	6	18	9.7	5.78
MII	531	762	635	2.93	8	19	12.0	5.48
MIII	549	743	632	4.15	8	18	12.0	5.20
				Females				
Fv	344	599	492	7.91	4	12	6.5	4.71
FI	506	738	607	4.33	7	17	10.8	5.17
FII	574	761	641	4.98	9	16	12.2	4.58
FIII	592	760	655	6.29	10	16	12.9	4.45
FIV	559	767	665	5.18	9	22	13.3	6.03
FVI	549	723	641	5.25	10	17	12.5	4.81

Age-0 sampling.—To determine the timing and duration of successful spawning, age-0 sturgeon were collected at sites within the MMR using a mini-Missouri trawl during June and July 2005 as well as May through August 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 m at the headrope to 0.46 m at the midsection and the cod end (Herzog et al. 2005). The headrope with floats and a chained footrope are tied to otter boards (40.6 × 22.86 cm, weighing 8.20 kg). Each trawl was towed in a downstream direction along the bottom contours of the river using 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, the majority of the effort being concentrated at island tips at about 3-m depth. All fish were kept in an ice slurry and brought back to the laboratory.

Growth of each age-0 sturgeon was estimated by first measuring total length (TL, mm), which is the most precise measurement for young sturgeons. Growth rates for each year then were estimated using methods from 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 then calculated. Linear regression was used to estimate relative growth rates for each weekly cohort (Braaten and Fuller 2007). Slopes were tested for homogeneity (test for interaction in analysis of covariance) to determine whether growth rates differed among weekly cohorts.

Additional fall sampling.—A high proportion of both mature male and female sturgeon in October 2005 followed by a peak in spent male and female sturgeon in January 2006 prompted additional fall sampling in 2006. Although standard sampling ceased in June 2006, shovelnose sturgeon adults were collected during September, October, and November 2006 using the same methods as described above. To determine whether eggs were near or at spawning condition, eggs were collected from FIV females and stored in balanced salt solution. The eggs were then boiled for 10 min, allowing the yolk to harden and fixing the position of the germinal vesicle. Boiled eggs were stored in buffered formalin, 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 (Detlaff et al. 1993). For sturgeon, females that are good candidates for spawning will have a PI of less than 0.07 (Detlaff et al. 1993). Trawling for age-0 fish also was conducted during October and November 2006 using the same methods as described above.

Results

Reproductive Demographics

Four hundred fifteen adult male shovelnose sturgeon between 319- and 786-mm FL were sampled. All stages (Mv–MII) described by Colombo et al. (2007b) occurred in addition to milting males and the MIII stage (spent male; Table 1). Each stage had a wide range of FLs and ages (Table 2). Mean GSI differed between stages except for MI and MIII, Mv (mean GSI = 1.03; SE = 0.13) being lower and MII (mean GSI = 3.09; SE = 0.14) being greater than all others ($F_{3,\,411} = 27.13$; $P < 0.0001$). Ages were estimated for 389 fish, ages ranging between 3 and 19 years. Male sturgeon had a modal age of 12 years and a mean age of 10.9 years (SE = 0.14; Figure 1). Males became sexually mature between ages 8 and 10 years (minimum age of first maturation = 8 years). The male reproductive cycle appeared to be completed between 1 and 2 years. With 61% of the males becoming mature in a given year, the 2-year cycle is apparently most common in the MMR. Male sturgeon spend about 6–7 years in the Mv stage before they become an MI, then they spend 1–2 years developing into a mature male (MII) and spawn.

Three hundred sixty-three females were captured, ranging from 344- to 767-mm FL. All stages except for spawning females (FV) occurred (Table 1). Female stages also varied in FL and age (Table 2). The mean GSI differed between all stages except for Fv and FVI ($F_{5,\ 357} = 183.94$; $P < 0.0001$). Mean GSI increased throughout the first five stages (Fv = 1.20, SE = 0.10; to FIV = 13.11, SE = 0.54), followed by a decrease after spawning (FVI = 2.18, SE = 0.41). The 337 sturgeon that could be aged ranged from 4 to 22 years. Female sturgeon had a modal age of 12 years and a mean age of 11.2 years (SE = 0.16; Figure 1). Females became sexually mature between ages 9 and 11 years (minimum age of first maturation = 9 years). Female shovelnose sturgeon apparently spawn every 3–4 years as 27% of females were in spawning condition each year. Female sturgeon transform from the Fv to the FI stage after about 7–8 years, spend about 2 or 3 years in stage FI, then progress through FII and FIII within the next year. Within the following year, females then transition through the FIV stage and become running ripe (FV) during the spawning season.

Total Egg Count

The mean total egg count of FIV shovelnose sturgeon was 29,573 eggs (SE = 2,472; range = 5,733–81,842; $N = 40$) and the mean number of eggs per gram of fish body weight was 21.7 (SE = 1.29; range = 6.22–46.23; $N = 40$). The total number of eggs was positively related to weight ($P < 0.001$, $r^2 = 0.48$) and relative egg size ($P < 0.001$; $r^2 = 0.78$). Relationships of egg count with fork length ($P = 0.004$; $r^2 = 0.20$) and GSI ($P = 0.009$; $r^2 = 0.18$) were weakly positive.

Timing of Spawning

Mature (FIV and MII) shovelnose sturgeon peaked during March and April 2005, October 2005, and April 2006 (Figure 2). The peak in the proportion of mature shovelnose sturgeon was followed by peaks in proportion of spent (FVI and MIII) shovelnose sturgeon, a lag time of 1–2 months occurring during May through June 2005, January 2006, and June 2006 (Figure 2). All peaks in mature shovelnose sturgeon coincided with rising river stages and water temperatures that approached or included the 16.9–20.5°C range are represented by the black box in Figure 2.

Age-0 Sampling

Age-0 sturgeon were collected during June through July 2005 ($N = 130$) and May through June 2006 ($N = 39$). In 2005, individuals were collected on 11 sampling days during June 8 through July 7. In 2006, individuals were collected on 11 sampling days during May 8 through June 22.

Relative growth rates of age-0 sturgeon for 2005 and 2006 were based on weekly cohorts that occurred throughout the sampling period. In 2005, the growth rates of weekly cohort 1 (1.28 mm/d; 95% confidence interval, 0.86–1.69), weekly cohort 2 (1.34 mm/d; 1.22–1.44), weekly cohort 3 (1.38 mm/d; 1.3–1.46), and weekly cohort 4 (1.28 mm/d; 1.17–1.38) did not differ ($F_{7,\ 105} = 608.08$, $P = 0.59$; Figure 3). During 2006, the growth rates for each weekly cohorts were not different ($F_{7,\ 38} = 77.34$; $P = 0.699$). The growth rates were as follows: weekly cohort 1 (1.27 mm/d; 1.12–1.42), weekly cohort 2 (1.14 mm/d; 0.98–1.32), weekly cohort 3 (1.21 mm/d; 1.01–1.42), and weekly cohort 4 (1.35 mm/d; 0.69–2.01; Figure 3).

Evidence of Fall Spawning

Eggs within three shovelnose sturgeon collected during September and October had PIs less than 0.05, meaning the eggs were ripe and good candidates for spawning. During September, milting males occurred. Trawling success during fall 2006 was limited by low water, but in November 2006 we collected a 55-mm TL age-0 sturgeon.

Discussion

While shovelnose sturgeon may be smaller and mature earlier than most sturgeon species, including the closely related and sympatric pallid sturgeon *S. albus*, patterns of gonadal development were similar to those of other sturgeon species. All stages described by Colombo et al. (2007b) were collected and identified with the exception of FV (running ripe females); spent males also occurred (MIII). The absence of running ripe females probably occurred because this is a relatively short stage and perhaps these females were being removed by targeted roe harvest. Shovelnose sturgeon did not appear to spawn annually, having multiple years between spawning intervals (Moos 1978); this holds important implications for population dynamics.

Previous sampling in the Mississippi and Missouri rivers suggested that shovelnose sturgeon matured at age 5 (males) and 7 (females; Helms 1974; Moos 1978;

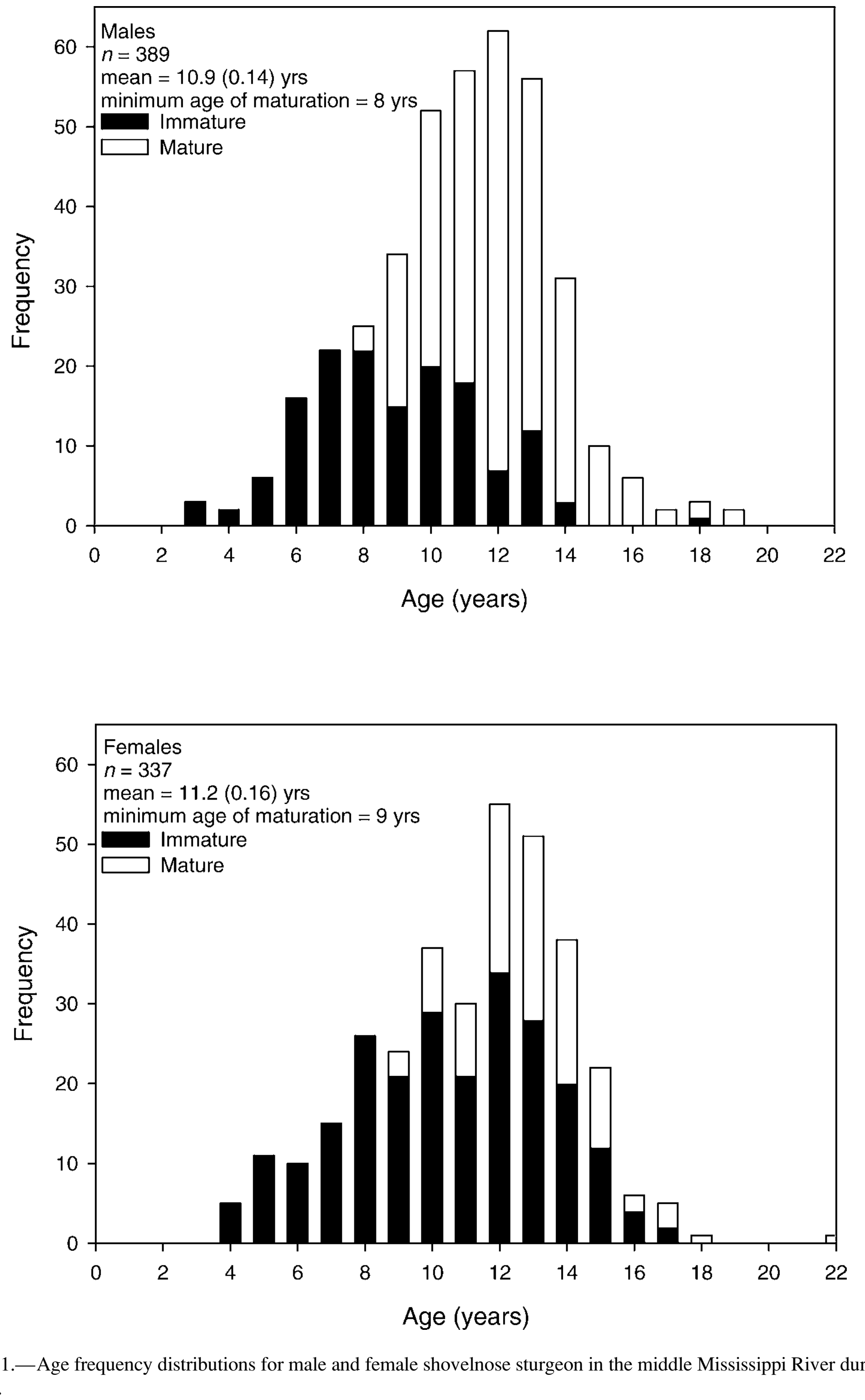

FIGURE 1.—Age frequency distributions for male and female shovelnose sturgeon in the middle Mississippi River during 2005 and 2006.

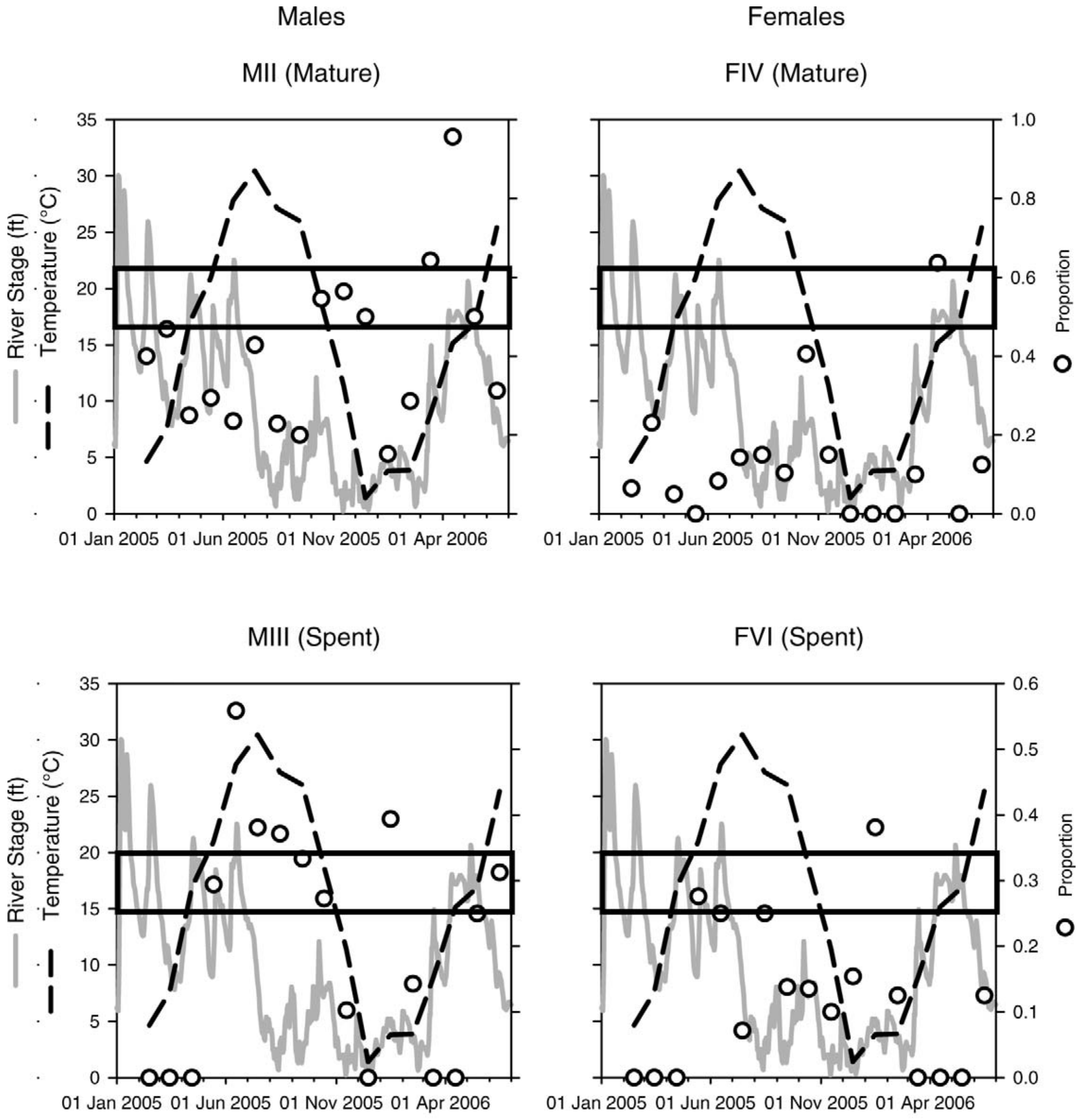

FIGURE 2.—Proportion of mature and spent shovelnose sturgeon males and females plotted against river stage and water temperature in the middle Mississippi River. The black boxes depicts the range of known spawning temperatures (16.9°–20.5°C) for shovelnose sturgeon.

Hurley and Nickum 1984). However, our results (males = 8 years; females = 9 years) show evidence that these populations are now reaching maturity at later ages. Harvest occurs on shovelnose sturgeon in this reach (Colombo et al. 2007a). Loss of rapidly growing, early-maturing fish to selective harvest (especially ripe females) may cause late-maturing, slow-growing individuals to be more prevalent (Ernande et al. 2003). Of course, a more comprehensive time series, coupled with sound harvest data, are needed to identify harvest as the primary mechanism for this pattern (Conover and Munch 2002).

As it is for many other fishes, shovelnose sturgeon spawning is apparently cued by unique annual or seasonal environmental conditions. Three major peaks occurred in mature fish: two peaks in the spring of each year, and one in fall 2005. All peaks coincided with rising river stages and water temperatures that

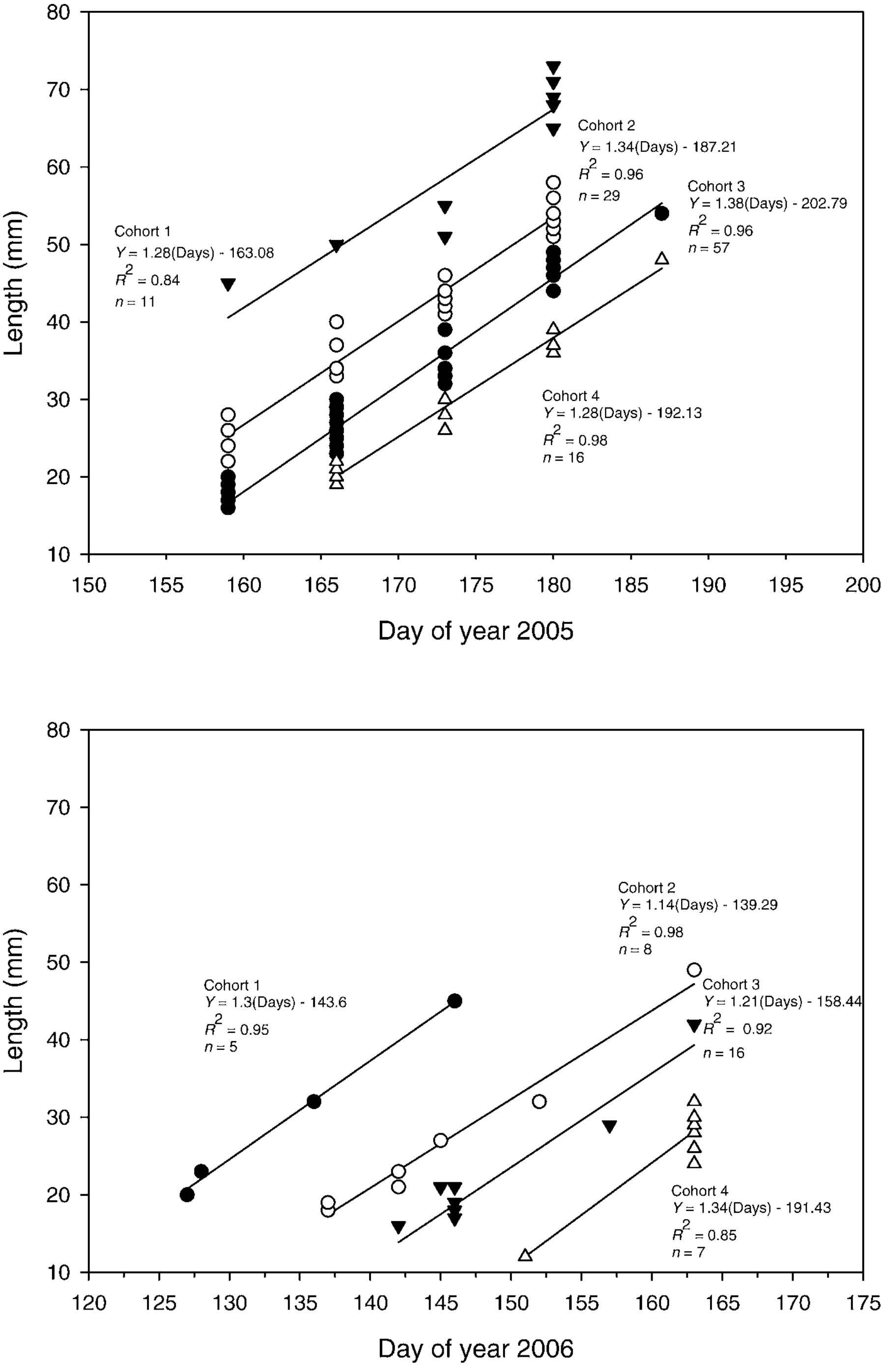

FIGURE 3.—Linear relationships between total length and day of the year for four cohorts of age-0 shovelnose sturgeon in the middle Mississippi River during 2005 and 2006.

approached or included the 16.9–20.5°C range at which shovelnose sturgeon are believed to spawn (Keenlyne 1997). These peaks were then followed by peaks in spent adults and age-0 shovelnose sturgeon, suggesting that successful spawning occurred. We suspect that shovelnose sturgeon, like many other species, delay maturation so that they are more likely to reproduce when environmental conditions are conducive for the growth and survival of age-0 and juvenile fish (Winemiller and Rose 1992).

Our results confirm that female shovelnose sturgeon in the MMR have a longer, more complex reproductive cycle than males, similar to other sturgeon species. Because ovaries comprise a high percentage of the total body weight and require a considerable energetic investment, a prolonged reproductive cycle in females may be expected. Similar to many other sturgeon species in the same geographical range (Williamson 2003), only about a third of the mature females reproduce any given year. This cycle allows reproductive output to be allocated across multiple years, allowing some individuals to reproduce successfully despite occasional periods of unfavorable conditions (Winemiller 2005). In unharvested populations, adult shovelnose sturgeon may live more than 15 years and have multiple spawning opportunities. This form of reproductive "bet hedging" may enhance population stability by increasing recruitment during a year of favorable conditions, thus compensating for years with reduced age-0 survivorship (Warner and Chesson 1985; Winemiller and Rose 1992; Garvey et al. 2002). However, if the environmental conditions for spawning are poor for many contiguous years or adult mortality increases across years, long-term reproductive success will be reduced.

Shovelnose sturgeon reproduction appears to be protracted into the fall or bimodal (i.e., spring and fall peaks) when fall environmental conditions are similar to those that occur during the spring. Our sampling in fall 2005 produced milting males as well as females with eggs in spawning condition. Furthermore, based on our estimated growth rates, the age-0 shovelnose sturgeon collected during November 2006 was probably spawned in September. Fall reproduction occurs in other sturgeon populations, such as the Atlantic sturgeon (Collins et al. 2000), Gulf sturgeon *A. oxyrinchus desotoi* (Sulak and Clugston 1998), and a number of Eurasian species (Berg 1959). Fall spawning occurs in other populations of shovelnose sturgeon as well (R. A. Hrabik, unpublished data). The question remains about the relative contribution of fall-spawned cohorts to the population (see Garvey et al. 2002), and whether this is an alternate spawning strategy in the population.

Some potentially novel trends appear to be occurring in the MMR, including later maturation and perhaps an increased prevalence of fall spawning. These phenomena have not been previously documented in the MMR. The best possible management practice for shovelnose sturgeon is to thoroughly understand all life history characteristics and apply this knowledge to policy. For example, understanding how recruitment varies among years is critical for developing sound assessment models. More effort should be focused on determining the relative magnitude of spring and fall spawning cohorts. Trends through time must continue to be captured. With this type of information, we could identify effective seasons by which reproduction could be protected from commercial fishing. By understanding the length and age of maturation, we also can implement effective length limits that will allow for a sustainable fishery. If these information gaps could be filled, we may quantitatively assess the sustainability of the MMR shovelnose sturgeon fishery.

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