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Effects of Commercial Harvest on Shovelnose Sturgeon Populations in the Upper Mississippi River

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Abstract

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Keywords

Upper Mississippi River, shovelnose sturgeon, sustainability, commercial harvest

Disciplines

Agribusiness | Aquaculture and Fisheries | Environmental Indicators and Impact Assessment | Natural Resources Management and Policy | Sustainability

Comments

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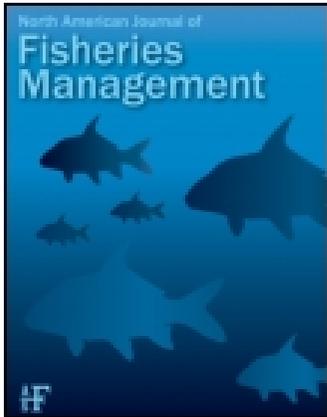
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Abstract.—Shovelnose sturgeon *Scaphirhynchus platyrhynchus* have become an increasingly important commercial species in the upper Mississippi River (UMR) because of the collapse of foreign sturgeon (family Acipenseridae) populations and bans on imported caviar. In response to concerns about the sustainability of the commercial shovelnose sturgeon fishery in the UMR, we undertook this study to describe the demographics of the shovelnose sturgeon population and evaluate the influence of commercial harvest on shovelnose sturgeon populations in the UMR. A total of 1,682 shovelnose sturgeon were collected from eight study pools in 2006 and 2007 (Pools 4, 7, 9, 11, 13, 14, 16, and 18). Shovelnose sturgeon from upstream pools generally had greater lengths, weights, and ages than those from downstream pools. Additionally, mortality estimates were lower in upstream pools (Pools 4, 7, 9, and 11) than in downstream pools (Pools 13, 14, 16, and 18). Linear regression suggested that the slower growth of shovelnose sturgeon is a consequence of commercial harvest in the UMR. Modeling of potential management scenarios suggested that a 685-mm minimum length limit is necessary to prevent growth and recruitment overfishing of shovelnose sturgeon in the UMR.

Sturgeons (Acipenseridae) are slow-growing, long-lived, late-maturing fish that do not spawn annually (Birstein 1993; Boreman 1997). Because of these factors, sturgeons are vulnerable to human activities such as flow and temperature alterations, changes in sediment dynamics, overfishing, and pollution (Birstein 1993; Boreman 1997). Birstein (1993) reported that nearly all Eurasian sturgeon species have declined; some populations have experienced local extinctions, and more species face a similar plight. Of the eight sturgeon species native to North America, six are listed as endangered, threatened, or of special concern (Williams et al. 1989).

Three species of river sturgeon (genus *Scaphirhynchus*) are present in North America, including the shovelnose sturgeon *S. platyrhynchus*, pallid sturgeon *S. albus*, and Alabama sturgeon *S. suttkusi*. Pallid sturgeon and Alabama sturgeon have experienced significant declines in distribution and abundance; both are federally listed as endangered species.

Although shovelnose sturgeon are the most abundant and widespread of the river sturgeons, commercial harvest and alterations to large river habitats have reduced their distribution and abundance (Bailey and Cross 1954; Birstein 1993; Boreman 1997; Keenlyne 1997). Carlson et al. (1985) state that shovelnose sturgeon were classified as extirpated or at risk of extirpation in 50% of the states within their native distribution. In other states where shovelnose sturgeon are native, they have either declined in abundance or their status is unknown (Keenlyne 1997). Shovelnose sturgeon have been extirpated from the Rio Grande River and from upstream reaches of many large western and midwestern rivers, where habitat has been altered and movement has been blocked by water development activities (Keenlyne 1997).

Historically, shovelnose sturgeon were considered a nuisance by commercial fisherman because the high densities of them decreased the efficiency of nets used to capture lake sturgeon *Acipenser fulvescens* (Barnickol and Starrett 1951; Moos 1978). Destruction of shovelnose sturgeon was common during this time: thousands were caught in nets and burned to “clean” the area of shovelnose sturgeon (Carufel 1953). Not until the early 1900s did shovelnose sturgeon become

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commercially important and markets developed for their meat and roe (i.e., eggs). In addition to roe, which was highly valued as caviar, the smoked flesh was considered one of the finest fish products from the Mississippi River (Coker 1930). Currently, shovelnose sturgeon roe, often sold under the name “American Hackleback,” retails for around US\$770 per kilogram, whereas smoked flesh sells for about \$9 per kilogram.

Because of collapsing sturgeon populations in the Caspian, Black, and Adriatic seas (Birstein 1993; Keenlyne 1997; Colombo et al. 2007), commercial fishing pressure on shovelnose sturgeon for their roe is expected to increase, raising concerns about the sustainability of the populations of these fish in the United States. From 1997 to 2003, the harvest of shovelnose sturgeon flesh more than doubled in Iowa waters (from 6,859 kg to 15,996 kg; M. Marron, Wisconsin Department of Natural Resources [DNR], personal communication). In 2004, the Iowa DNR reported that the total harvest of shovelnose sturgeon roe by licensed commercial harvesters was 1,492 kg. In 2005, harvest increased to 1,595 kg, valued at approximately \$158,000 (G. Jones, Iowa DNR, personal communication). In response to concerns about the increasing harvest of shovelnose sturgeon, in August 2006 Iowa enacted a 685- to 864-mm harvestable slot in Iowa–Wisconsin border waters and a 685-mm minimum length limit in Iowa–Illinois border waters. Before implementation of these regulations, Iowa had no length restrictions for shovelnose sturgeon harvest. However, Iowa is not the only state in the upper Mississippi River (UMR) basin with concerns about increased commercial harvest of shovelnose sturgeon. Harvest by licensed Illinois fisherman has increased almost 10-fold since the late 1990s in Pools 12–26. In Wisconsin, commercial harvest has tripled since 2001 (P. Short, Wisconsin DNR, personal communication).

Shovelnose sturgeon are considered to be the least vulnerable of the North American sturgeons to commercial harvest owing to their relatively early age of maturation and fast growth (Keenlyne 1997; Morrow et al. 1998). Quist et al. (2002) reported that exploitation rates of 20% on the Missouri River could affect size structure and lifetime egg production of shovelnose sturgeon and that restrictive harvest regulations (e.g., length limits) could reduce the effects of harvest on shovelnose sturgeon populations. Similarly, Colombo et al. (2007) suggested that current harvest regulations were not adequate to prevent the overfishing of shovelnose sturgeon populations in the middle Mississippi River. Although these studies have provided important insight on the management of shovelnose sturgeon, they were conducted on populations outside

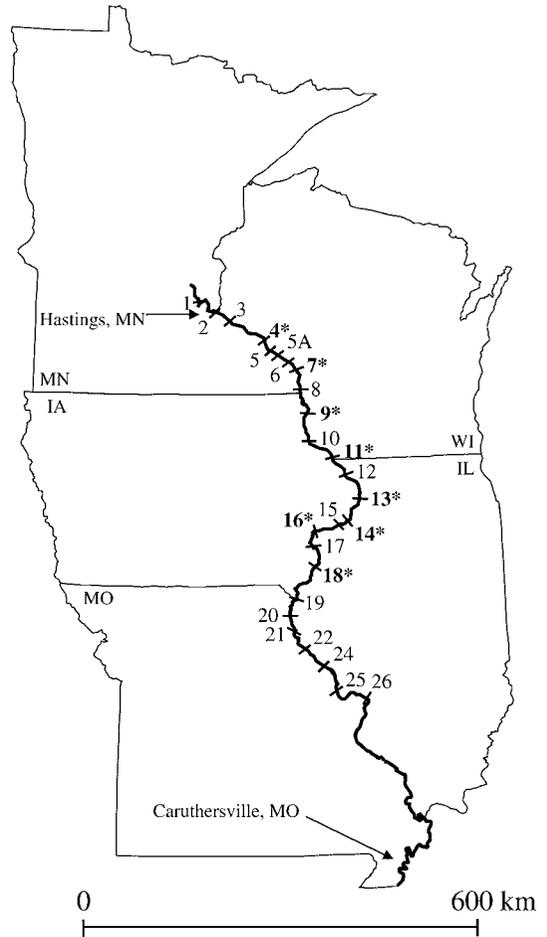


FIGURE 1.—Upper Mississippi River with numbers indicating locks and dams. Bold numbers with asterisks designate pools included in the study of shovelnose sturgeon populations (e.g., Pool 13 is upstream of Lock and Dam 13).

of the UMR. In response to increasing harvests of shovelnose sturgeon, similar insight is needed to guide management of the commercial shovelnose sturgeon fishery in the UMR. The objectives of this study were to describe population parameters (e.g., length and age structure, mortality, growth, sex ratios) and evaluate different management scenarios for shovelnose sturgeon populations in the UMR.

Study Area

The UMR is defined by the Upper Mississippi River Conservation Committee as the 1,490-km portion of the Mississippi between Hastings, Minnesota, and Caruthersville, Missouri (Pitlo and Rasmussen 2004; Figure 1). Before large-scale channelization began in 1816, the UMR was characterized as having deep pools separated

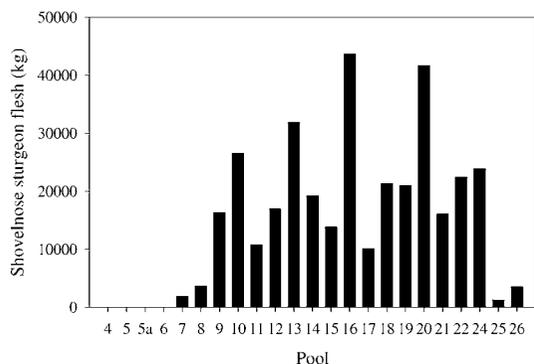


FIGURE 2.—Reported shovelnose sturgeon commercial flesh harvest by pool in the upper Mississippi River from 1995 to 2005.

by shallow rapids (Hurley et al. 1987). The first modifications to the Mississippi River involved removal of simple snags and debris from the river's main channel to improve navigation. Over the last 150 years, several additional habitat modifications have occurred. The depth of the navigation channel was increased from 1.4 m in 1878 to 1.8 m in 1907. During the 1930s, the U.S. Army Corps of Engineers further increased the depth of the navigation channel by constructing a series of locks and dams, as well as over 3,100 wing dams to divert current into the main channel. Along the Iowa border 11 locks and dams serve to maintain a navigation channel of at least 2.7 m in depth and 122 m in width (Hurley et al. 1987). Commercial traffic on the river was also enhanced by closing chutes and backwaters, dredging, and stabilizing banks through revetment (Pitlo and Rasmussen 2004).

We selected eight pools representing a diversity of habitats and a variety of shovelnose sturgeon harvest rates as study pools (Pools 4, 7, 9, 11, 13, 14, 16, and 18; Figure 1). The two pools most upstream (Pools 4 and 7) are north of the Iowa–Minnesota border, where shovelnose sturgeon harvest is limited to recreational anglers and commercial trot-line harvesters. Thus, exploitation of shovelnose sturgeon in Pools 4 and 7 is probably very low. Commercial harvest of shovelnose sturgeon in Wisconsin–Minnesota border waters is regulated by a 635-mm minimum length limit. The Iowa–Minnesota border intersects Pool 9 approximately 8 km downstream of Lock and Dam 8. Downstream of the Iowa–Minnesota border, harvest of shovelnose sturgeon by using traditional commercial fishing gear (e.g., entanglement gear, hoop nets, and trot lines) is allowed and regulated by a 685- to 864-mm harvestable slot limit. The Wisconsin–Illinois border intersects Pool 12 near Dubuque, Iowa. In Iowa waters, the shovelnose sturgeon fishery is regulated with a 685-

mm minimum length limit. However, the Illinois regulation for commercial harvest of shovelnose sturgeon is a more liberal 610- to 813-mm harvestable slot limit. Shovelnose sturgeon harvest has traditionally increased downstream of this location (Figure 2). Although the lower bound of the Illinois slot limit is 610 mm, commercial harvesters are not allowed to possess shovelnose sturgeon less than 685 mm (i.e., the Iowa minimum length limit for commercial shovelnose sturgeon harvest) in Iowa waters.

Methods

Fish collection.—Shovelnose sturgeon were sampled with 30.5-m drifted trammel nets consisting of 13.6-kg lead-core line and 12.7-mm foam-core float line. Consistent with standard trammel nets used in the UMR, nets were constructed with three panels of mesh. The outer wallings were 1.8-m-deep panels with 304.8-mm bar-measure mesh (number 9 multifilament nylon twine). A single 2.4-m-deep panel of inner mesh was constructed of 50.8-mm bar-measure mesh (number 139 multifilament nylon twine). Wooden “mules” were attached to both ends of the net to help the net drift more efficiently and to prevent the net from closing while deployed. Trammel nets were drifted downstream perpendicular to the thalweg and were generally fished in main channel, channel border, and tailwater habitats. Shovelnose sturgeon were collected in mid- to late summer to avoid sampling bias associated with aggregations of spawning fish.

All shovelnose sturgeon were measured to the nearest millimeter (fork length; FL) and weighed to the nearest gram. In six of the study pools (Pools 9, 11, 13, 14, 16, and 18), 100 randomly selected shovelnose sturgeon were euthanatized with a lethal dose of tricaine methanesulfonate (MS-222; Argent, Redmond, Washington) to obtain information on age and length at maturity, gonad weight, and sex ratio. The fish were identified as male or female, and gonads from stage-V females (Moos 1978) were preserved in formalin and transported to the laboratory. We removed a marginal pectoral fin ray from 10 shovelnose sturgeon per 1-cm length-group per pool, using methods described by Koch et al. (2008). Fin rays were placed in a numbered coin envelope and air-dried for at least 1 week before being mounted and sectioned.

Laboratory methods and data analysis.—Fin rays were cleaned of residual tissue and mounted in epoxy in preparation for sectioning (Koch and Quist 2007). Encapsulated fin rays were sectioned with a Buehler Isomet low-speed saw (Buehler, Lake Bluff, Illinois). Three 0.6-mm-thick cross sections were removed from the region immediately distal to the conspicuous curve near the articulating process of the fin ray (Koch et al.

2008). Three sections were taken from each fin ray to ensure at least one section of high readability was available for age and growth analyses. We estimated the ages of the fish from which the fin ray sections were taken by using a compound light microscope equipped with a camera linked to an image analysis system (Image-Pro Plus; Media Cybernetics, Silver Spring, Maryland). The ages of a subsample of 203 shovelnose sturgeon fin rays were independently estimated by three readers to assess the precision of the age estimates. Exact agreement between experienced readers (Koch et al. 2008) was 75%; agreement within 1 year was 94%. All remaining fin ray sections were aged by one reader. Annuli were measured from all fin rays. Mean back-calculated lengths (MBCL) at age were estimated by using the Dahl–Lea method (DeVries and Frie 1996), that is,

$$L_i = L_c \cdot (R_i/R_c),$$

where L_i is the length at annulus i , L_c is the length at capture, R_i is the fin ray radius at annulus i , and R_c is the fin ray radius at capture. A von Bertalanffy growth function was also used to describe the growth of shovelnose sturgeon, namely,

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

where L_t is the length at time t , L_∞ is the theoretical maximum length, K is the growth coefficient (the rate at which fish approach L_∞), and t_0 is the time when length would theoretically equal 0 mm. Fecundity was estimated by weighing and counting three subsamples of eggs from each third of both preserved ovaries (i.e., 18 subsamples per fish). The number of eggs per gram for each subsample was calculated and averaged for each third of each ovary. The resulting average eggs per gram was then multiplied by the weight of each respective third and summed for each ovary to obtain a total estimate of fecundity for each ovary. The estimates for each ovary were summed to obtain a total fecundity estimate for each fish. Nonlinear regression was used to develop a fecundity–length equation. Mean relative weight (W_r ; Anderson and Neumann 1996) was calculated to evaluate the somatic condition of the shovelnose sturgeon in each study pool. Relative weight was calculated as

$$W_r = 100 \cdot (W/W_s),$$

where W is the observed weight and W_s is the length-specific standard weight for the species. The standard weight of shovelnose sturgeon was estimated by the equation

$$\log_{10} W_s = -6.287 + 3.330 \cdot (\log_{10} \text{FL}),$$

where FL is fork length in millimeters (Quist et al. 1998). To assess the size structure of the shovelnose sturgeon sampled from each pool, we used proportional size distributions (PSDs; Anderson and Neumann 1996; Guy et al. 2007; Neumann and Allen 2007). Proportional size distribution was calculated as the number of fish greater than or equal to quality length (380 mm) divided by the number of fish greater than or equal to stock length (250 mm; Quist et al. 1998). Additional PSD indices were calculated as the number of fish at or above a specified length divided by the number of stock-length fish. Specified lengths included preferred (PSD-P; 510 mm), memorable (PSD-M; 640 mm), and trophy lengths (PSD-T; 810 mm; Quist et al. 1998). Subsampled age data were extrapolated to the entire sample by using an age–length key (DeVries and Frie 1996). Using the resulting age structure data, we estimated the total annual mortality (A) of age-6 and older shovelnose sturgeon with a weighted catch curve (Ricker 1975; Van Den Avyle and Hayward 1999; Miranda and Bettoli 2007).

Differences in size structure, sex ratio, MBCL at age, and mean W_r were examined for all study pools. Differences in size structure and sex ratios among pools were analyzed using chi-square analysis (Neumann and Allen 2007). Mean back-calculated length at age 5 and mean W_r were compared among pools by analysis of variance (ANOVA). A difference in MBCL at age 5 of male and female shovelnose sturgeon was analyzed with a Student's t -test. Pairwise comparisons (i.e., between pools) of MBCL at age and W_r were analyzed by using least-squares means. Statistical analyses were performed in SAS (SAS Institute 2003) with $\alpha = 0.05$.

Population simulations.—The effects of minimum length limits on the harvest of shovelnose sturgeon were simulated by using a Beverton–Holt yield-per-recruit model. Yield per recruit (Y) was estimated with the following equation (Slipke and Maceina 2001):

$$Y = (F \times N_t \times e^{Zr} \times W_\infty) \times K^{-1} \times [\beta(X, P, Q)] - [\beta(X_1, P, Q)],$$

where F is the instantaneous rate of fishing mortality; $N_t = N_0 \cdot e^{-M(t-t_0)}$; the number of recruits entering the fishery at some minimum length at time t ; N_0 is the initial population size; M is the instantaneous rate of natural mortality; t_r is the age of recruitment to the fishery; $r = (t_r - t_0)$; the time to recruit to the fishery; t_0 is the age when length would theoretically be 0 mm from the von Bertalanffy model; Z is the instantaneous rate of total mortality ($F + M$); W_∞ is the asymptotic weight, derived from the length–weight relationship and L_∞ ; β is the incomplete beta function, $X = e^{-Kr}$; K

is the growth coefficient from the von Bertalanffy model; $X_1 = e^{-K(\text{Age}_{\text{max}} - t_0)}$; Age_{max} is the maximum age from the sample; $P = Z/K$; and Q is $1 +$ the slope of the length–weight relationship.

In addition to information on growth, maximum age, and length–weight relationships, the rates of conditional natural mortality (*cm*, i.e., the mortality that would occur in the absence of fishing mortality) and conditional fishing mortality (*cf*, i.e., the mortality attributable to fishing in absence of natural mortality) were specified in the models. Previous research has estimated low rates (e.g., less than 10%) of total annual mortality of shovelnose sturgeon in unexploited reaches of the Missouri River (Quist et al. 2002). Colombo et al. (2007) estimated natural mortality rates of 10% in the middle Mississippi River. Accordingly, we conducted harvest simulations with a *cm* of 10%. Conditional fishing mortality was modeled at levels varying from 0% to 90%. Simulations were conducted for five different minimum length limits (250, 535, 610, 685, and 710 mm). The 250-mm length limit represented a scenario of unregulated harvest, being the approximate length of the smallest shovelnose sturgeon collected in commercial gears. The 535-mm length limit represents the approximate length at which shovelnose sturgeon in the UMR are fully recruited to commercial gear. The 610- and 685-mm length limits are the current minimum lengths for commercial harvest of shovelnose sturgeon in Illinois and Iowa, respectively. Additionally, we evaluated a 710-mm length limit as a more restrictive regulation than currently exists in the UMR. Yield was plotted against exploitation to evaluate the likelihood of growth overfishing. Growth overfishing occurs when yield decreases with increasing levels of exploitation because fish are harvested before they are able to realize their full growth potential (Slipke and Maceina 2001).

We also examined the potential for recruitment overfishing. Recruitment overfishing occurs when fish are harvested from a population before they are able to replace themselves, thus leading to population decline and possible stock collapse. Recruitment overfishing is traditionally examined by assessing the reproductive potential of an exploited population relative to that of an unexploited population (Goodyear 1993; Mace and Sissenwine 1993). The spawning potential ratio (SPR) represents the proportion of lifetime egg production of an exploited population compared with that of an unexploited population. It is calculated as

$$SPR = 100 \cdot (P_{\text{exploited}} / P_{\text{unexploited}}),$$

where the lifetime egg production (P) of a cohort of recruits is calculated from the formula

$$P = \sum_{i=1}^n E_i \prod_{j=0}^{t=1} S_{ij},$$

where n is the number of ages in an unexploited population; E_i is the mean fecundity of females of age i , $S_{ij} = e^{-(F_{ij} + M_{ij})}$, the density-dependent annual survival probabilities of females of age i when age j , F_{ij} is the instantaneous fishing mortality of females of age i when age j , and M_{ij} is the instantaneous natural mortality of females of age i when age j . An unexploited population has an SPR of 100, and SPR decreases as the population is exploited. Spawning potential ratios were analyzed at different levels of exploitation in response to the five aforementioned minimum length limits. Some researchers suggest that an SPR for a population should be maintained above 20% or 30% to avoid recruitment overfishing (e.g., Goodyear 1993; Slipke et al. 2002). However, Colombo et al. (2007) suggested the possibility of increasing the theoretical recruitment overfishing threshold of shovelnose sturgeon populations to an SPR of 40%. Accordingly, we considered a threshold of 40% as the minimum SPR to prevent recruitment overfishing in the current study. Simulations of yield and SPR were analyzed for each of the study pools by using pool-specific population parameter estimates. In addition, study-wide models (hereafter termed pooled models) were evaluated by using pooled population parameter estimates (e.g., von Bertalanffy parameters) from throughout the study area.

Scientists have raised concerns about age and growth data obtained from shovelnose sturgeon fin rays (Morrow et al. 1998; Whiteman et al. 2004). Although the agreement among readers was relatively high for the fish used in this study, variation in age and growth parameter estimates was evaluated to provide insight into the potential effects of aging errors. Specifically, we maintained the maximum ages at values 2 and 5 years above and below the maximum observed ages of the shovelnose sturgeon in our study while holding all other parameters constant. Similarly, growth estimates were manipulated by increasing and decreasing all MBCL at age by 5% and 10%, again holding all other parameters constant. We performed these analyses using pooled models only. All simulations were analyzed with an initial population of 1,000 recruits by using Fisheries Analysis and Simulation Tools (FAST) software, version 2.1 (Slipke and Maceina 2001).

Results

Population Characteristics

In all, 1,682 shovelnose sturgeon were sampled from the eight study pools during 2006 and 2007. These fish

TABLE 1.—Population parameters of shovelnose sturgeon sampled from eight pools in the upper Mississippi River, 2006–2007. Size structure indices include the overall proportional size distribution (PSD) and those of preferred- (PSD-P), memorabile- (PSD-M), and trophy-length (PSD-T) fish. Total annual mortality is for age-6 and older shovelnose sturgeon. Growth parameters include the mean back-calculated length at age 5 (MBCL-5), as well as the asymptotic maximum length (L_{∞}), growth coefficient (K), and time when length theoretically equals 0 mm (t_0) from von Bertalanffy growth models. Pools with the same lowercase letter were not significantly different ($P < 0.05$).

Parameter	Pool							
	4	7	9	11	13	14	16	18
<i>N</i>	122	155	203	303	198	162	214	325
Size structure								
PSD	100 z	100 z	100 z	100 z	99 z	92 x	100 z	98 y
PSD-P	100 z	100 z	100 z	95 y	78 x	75 x	93 y	93 y
PSD-M	87 z	44 x	58 y	36 xw	21 v	23 v	17 v	32 w
PSD-T	0 z	0 z	0 z	2 z	0 z	0 z	0 z	1 z
Total annual mortality (%)	23	27	22	23	34	25	32	30
Growth								
MBCL-5 (SE)	538 (4.7) y	544 (3.7) y	541 (3.3) y	533 (3.2) y	534 (5.3) y	559 (5.2) z	492 (4.3) w	523 (3.9) x
L_{∞}	738	741	759	789	729	756	681	760
K	0.275	0.258	0.241	0.198	0.258	0.261	0.252	0.218
t_0	0.229	0.023	-0.009	-0.425	-0.024	0.002	-0.088	-0.249
Sex ratio (female : male)			1.6:1 zy	1.2:1 yx	2.1:1 z	0.9:1 x	1.1:1 yx	1.8:1 zy
Relative weight (SE)	91.6 (0.7) y	91.7 (0.6) y	94.3 (0.7) zy	91.3 (0.6) x	86.6 (0.6) w	91.1 (0.8) x	89.6 (0.7) x	96.3 (0.6) z

varied from 233 to 850 mm FL and weighed from 67 to 3,394 g. The shovelnose sturgeon from Pool 4 had the greatest lengths (684 ± 3.8 mm [mean \pm SE]); those from Pools 13 (569 ± 5.4 mm) and 14 (569 ± 8.3 mm) had the lowest lengths. Size structure indices were generally higher in upstream pools (Pools 4, 7, and 9) because these samples included no small (<530 mm) shovelnose sturgeon (Table 1). For example, PSD-P was significantly higher ($\chi^2 = 7.72$, $df = 1$, $P = 0.005$) in Pools 4, 7, and 9 than in the other pools. Smaller shovelnose sturgeon (<530 mm) were present in the samples from all other study pools but represented less than 16% of the total catch.

The oldest shovelnose sturgeon were generally found in samples from upstream pools. The maximum age for shovelnose sturgeon was 17 years, observed in samples from Pools 7 and 9. The minimum age of shovelnose sturgeon sampled was 1 year; this age-group was observed only in Pool 13. Samples from Pools 13 and 14 contained a high proportion of young shovelnose sturgeon. For example, age-4 and younger shovelnose sturgeon made up at least 55% of the samples from Pools 13 and 14, whereas the proportion of age-4 and younger shovelnose sturgeon in the other study pools never exceeded 30%. Estimates of total annual mortality varied from 21% in Pool 9 to 34% in Pool 13 and were generally lower in upstream pools (Table 1).

Although the growth of shovelnose sturgeon was similar among pools, significant differences in MBCL at age 5 were detected between pools ($F_{7, 1248} = 21.12$; $P = 0.0001$; Table 1). For instance, MBCL at age 5 was significantly lower for shovelnose sturgeon from Pool

16 than for fish from all other pools ($P = 0.0001$), whereas MBCL at age 5 for fish in Pool 14 was significantly higher ($P = 0.01$) than that for all other pools. In addition to having a shorter length at age 5, the shovelnose sturgeon from Pool 16 appeared to grow at a slower rate throughout their life. No difference was observed between growth (e.g., MBCL at age 5) of male and female shovelnose sturgeon ($t = 0.29$; $df = 456$; $P = 0.77$). The pooled von Bertalanffy growth equation for shovelnose sturgeon was $L_t = 767(1 - e^{-0.219[t+0.2016]})$.

The sex ratio of the shovelnose sturgeon was skewed toward females (Table 1). Fifty-eight percent of all sacrificed shovelnose sturgeon ($N = 600$) were female (1.4 females : 1 male). Females outnumbered males in five of the six study pools where shovelnose sturgeon were sacrificed, and in three of these pools the sex ratio was greater than 1.5. Pool 13 had the highest ratio (2.1), whereas Pool 14 had the only ratio that was below 1 (0.9).

Mean W_r varied by pool from 86.6 (SE=0.6) to 96.3 (SE = 0.6; Table 1), and the overall mean W_r of shovelnose sturgeon in the study area was 91.9 (SE = 0.2). Although shovelnose sturgeon populations in the study area were in good condition, significant differences in mean W_r were observed ($F_{7, 1647} = 21.72$; $P = 0.0001$). The mean W_r of the shovelnose sturgeon in Pool 13 was significantly lower than that of the fish in all other pools ($P = 0.0405$). The shovelnose sturgeon from Pools 9 (94.2 ± 0.7) and 18 (96.3 ± 0.8) had the highest mean W_r . The length–weight relationship ($R^2 = 0.96$; $P < 0.001$) for all shovelnose sturgeon in the UMR was $\text{weight} = -6.882(\text{length})^{3.530}$.

Six hundred shovelnose sturgeon from among the study pools were sacrificed for further study. Thirty-two of these fish were stage-V female shovelnose sturgeon, varying from 570 to 770 mm. Fecundity varied from 20,120 to 66,303 among fish and averaged 34,908 eggs per female (SE = 2,183). The equation ($R^2 = 0.62$; $P < 0.001$) for the fecundity-length relationship was: fecundity = $5 \times 10^{-7}(\text{FL})^{3.821}$. The numbers of stage-V females collected were not sufficient to compare fecundity estimates between pools. Nearly all of the gravid females were greater than 615 mm; only one gravid female less than 600 mm was collected. Although the youngest mature female (i.e., as indicated by black eggs or spent ovaries) shovelnose sturgeon was age 6, most (i.e., 97%) female shovelnose sturgeon were mature at age 7 or older. Males appeared to mature at age 5; however, distinguishing mature testes from immature testes was often difficult because of the season when fish were sampled.

Population Simulations

Simulated yields from the Beverton-Holt yield-per-recruit model were generally highest in upstream study pools (Figure 3). Changes in yield in response to the simulated minimum length limits were similar among pools. At low levels of exploitation, the highest yields occurred with a minimum length limit of 535 or 610 mm. The patterns of yield were similar between the 685- and 710-mm length limits; at all levels of exploitation, however, yields were higher for a 685-mm length limit than for a 710-mm length limit. The potential for growth overfishing was evident with the three least-restrictive minimum length limits. Yield generally began decreasing in response to a 535-mm length limit at an exploitation rate of about 30%. In simulations with a 610-mm length limit, growth overfishing became evident at exploitation levels above 40%. Only the three most conservative minimum length limits were evaluated for Pool 16 because the asymptotic length from the von Bertalanffy growth model (681 mm) was less than 685 mm. The results of the pooled model were similar to those from the individual study pools, in which growth overfishing would probably occur with the three least-restrictive length limits (Figure 4).

The response of the yield to changes in growth and maximum age was variable, especially when restrictive length limits were simulated (Figure 5). Increasing growth and maximum age had a positive effect on yield, whereas decreasing growth and maximum age reduced yield. Although yield estimates were dependent on maximum age and growth estimates, patterns used to assess the likelihood of growth overfishing were consistent with models that used observed data. In

the simulation using observed data, only the two most restrictive minimum length limits prevented growth overfishing at all levels of exploitation. The only scenario that changed when growth or maximum age was altered was with the 610-mm minimum length limit. On the basis of observed data, the 610-mm length limit protected fish from growth overfishing; however, decreasing growth by 10% led to growth overfishing with a 610-mm length limit.

As with yield, SPR followed consistent patterns among study pools (Figure 6). Generally, SPR approached or decreased to 40% for the three most liberal length limits at exploitation levels of 20% or lower. Spawning potential ratio did not decrease to levels below 40% for the two most restrictive length limits, except at high levels of exploitation. Spawning potential ratio was generally higher at a given level of exploitation in populations with lower L_{∞} values (e.g., Pools 13 and 16). For example, SPR was 79% in Pool 13 at an exploitation of 20% with a 685-mm length limit. In Pool 9, SPR was 66% at the same level of exploitation. The SPRs estimated with a 685-mm minimum length limit were approximately 20% higher at 10% exploitation than those estimated with a 610-mm length limit. At exploitation rates of 30%, the SPR was nearly twice that observed with a 610-mm minimum length limit. Theoretical maximum length, sex ratio, and maximum length all are factors that influence the lifetime egg production in a given pool. The highest maximum lifetime egg production was 25.2×10^6 eggs (Pool 9) and the lowest was 11.5×10^6 eggs (Pool 16). Once again, only the three least-restrictive length limits were evaluated for Pool 16. In the pooled model, SPR was above 40% at all levels of exploitation with the two most-restrictive minimum length limits (Figure 7). Spawning potential ratio decreased to below 40% at approximately 20% exploitation or less with the three least-restrictive regulations, suggesting that recruitment overfishing of shovelnose sturgeon is possible at relatively low levels of exploitation.

As with yield, SPR was sensitive to changes in maximum age and growth (Figure 8). The greatest effects were observed in simulations with the most restrictive minimum length limits. Increasing maximum age decreased SPR. For example, in the simulation of a 685-mm minimum length limit at an exploitation rate of 30%, decreasing the maximum age by 5 years increased SPR by 26%, whereas increasing the maximum age by 5 years decreased SPR by 12%. Increasing growth had a negative effect on SPR, because shovelnose sturgeon were recruited to the commercial fishery at a younger age. This increased

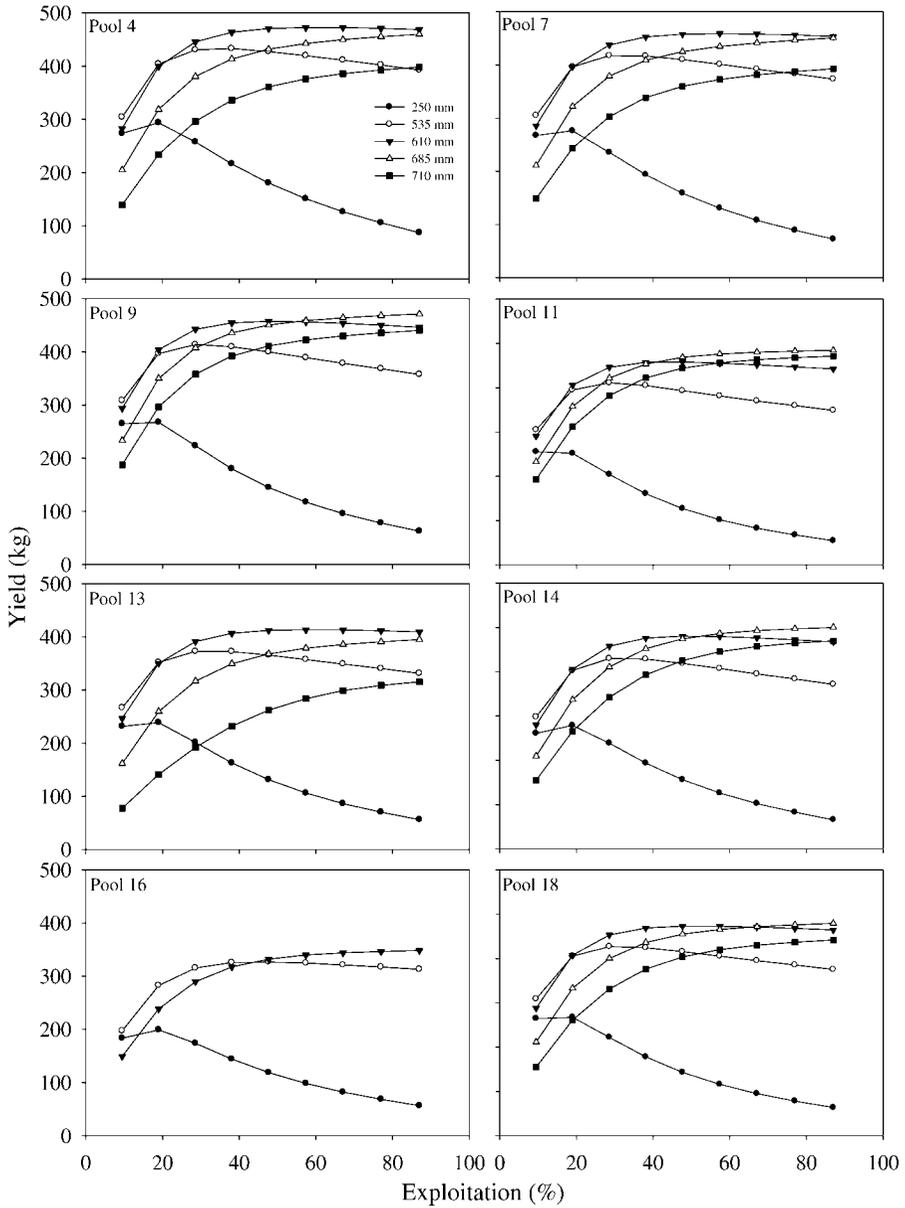


FIGURE 3.—Simulated yields for selected shovelnose sturgeon populations in the upper Mississippi River with a conditional natural mortality of 10%. The simulations were conducted with five different minimum length limits except in the case of Pool 16, for which only three minimum length limits were simulated because the 685- and 710-mm length limits exceeded the asymptotic maximum length of the fish in the pool.

harvest of younger shovelnose sturgeon decreased lifetime egg production.

Discussion

The mean length and size structure of shovelnose sturgeon were generally highest for upstream populations in the UMR. Several factors may be responsible

for this pattern. Larger fish in upstream pools may be the result of relatively low harvest of shovelnose sturgeon, such that fish can live to older ages and grow to a larger size. The absence of small shovelnose sturgeon (i.e., <530 mm) in upstream study pools was of particular interest because it might indicate a lack of recruitment. Such a scenario is unlikely, however,

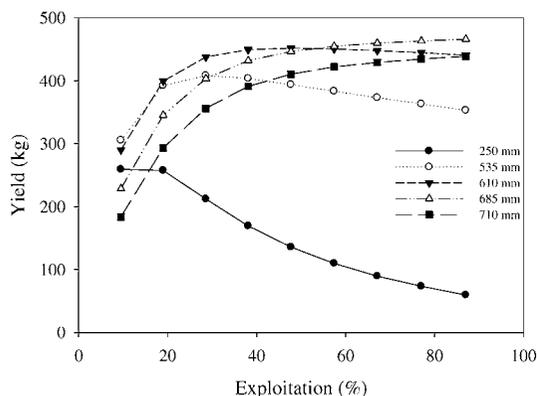


FIGURE 4.—Simulated yields for the combined shovelnose sturgeon populations in the upper Mississippi River with a conditional natural mortality of 10%.

because small shovelnose sturgeon were sampled in the tailwaters of Pool 4 with otter trawls during 2006 (J. Meerbeek, Minnesota DNR, personal communication). The paucity of small shovelnose sturgeon in our samples from upstream pools is most likely a result of sampling bias. Trammel nets were drifted primarily in tailwater habitats in Pools 4, 7, and 9 because of a lack of flow in other portions of the pool. In other study pools, there was usually sufficient current to drift trammel nets in main-channel and channel border habitats, areas that may be more suitable for small shovelnose sturgeon. It should be noted, however, that small shovelnose sturgeon were collected in the tailwaters of three of the downstream study pools (Pools 13, 14, and 18). Other studies have also reported difficulties sampling small shovelnose sturgeon, resulting in high size structure indices reported for shovelnose sturgeon populations. For instance, Quist et al. (1998) analyzed data from 32 populations of shovelnose sturgeon and reported that 31 populations had a PSD greater than 79. Kennedy et al. (2007) reported a PSD of 100 and PSD-M of 81 for shovelnose sturgeon in the Wabash River, Indiana, where shovelnose sturgeon smaller than 550 mm represented only 0.2% of the total sample. Hamel and Steffensen (2007) reported that no gear (e.g., gill nets, trammel nets, otter trawls) was effective at sampling shovelnose sturgeon less than 380 mm FL in the Missouri River; however, some researchers have had success sampling shovelnose sturgeon of less than 250 mm, using otter trawls (Plauck et al. 2008; Utrup et al. 2008).

Many studies have documented the longevity of shovelnose sturgeon. Quist et al. (2002) reported that in the southern portion of the shovelnose sturgeon's distribution, maximum ages vary from 12 to 16 years.

Our data corroborate these findings, the maximum observed ages varying from 14 to 17 in the UMR. Shovelnose sturgeon as old as 30 years have been observed in the Wabash River, Indiana (Kennedy et al. 2007), and 43 years old in the upper Missouri River (Everett et al. 2003). Lower maximum ages of shovelnose sturgeon in the UMR may be the result of harvest, because the Missouri and Wabash rivers have relatively low levels of exploitation (Quist et al. 2002; Kennedy and Sutton 2007). Although our results may have been confounded by sampling bias, age structures of shovelnose sturgeon populations were skewed towards older individuals in the upstream pools. In addition to possibly affecting maximum age, harvest requirements may contribute to differences in the age structure of shovelnose sturgeon populations. For example, the Wisconsin-Illinois border intersects the upstream reaches of Pool 12. Downstream of this point, the regulation for shovelnose sturgeon changes from a 685–864-mm harvestable slot in Iowa-Wisconsin waters to a 685-mm minimum length limit in Iowa waters and a 610–813-mm harvestable slot in Illinois waters. From 1995 to 2005, an average of 17,866 kg of shovelnose sturgeon was harvested from Pools 9, 10, and 11 (i.e., pools north of Illinois). In pools bordering Illinois (i.e., Pools 12–19), harvest was 24% higher (22,229 kg). Our results indicate that in the four study pools upstream of the Illinois border, 34% of age-6 and older shovelnose sturgeon were older than age 10. In the four study pools downstream this point, only 17% of age-6 shovelnose sturgeon were older than age 10. These results indicate that restrictive length limits may affect age structures of shovelnose sturgeon by allowing fish to reach older ages.

Mortality rates of shovelnose sturgeon are variable throughout North America and are most likely influenced by anthropogenic factors such as commercial harvest and habitat alterations (Quist et al. 2002; Jackson 2004). Quist et al. (2002) reported total annual mortality rates of approximately 10% from commercially unexploited reaches of the upper and middle Missouri River, whereas estimates of total annual mortality from the Mississippi River vary from 20% (lower Mississippi River; Morrow et al. 1998) to 41% (middle Mississippi River; Jackson 2004). Our results indicate that mortality rates of shovelnose sturgeon were higher in downstream study pools. Pools 13 and 16 had the highest observed mortality rates in the study. Interestingly, harvest records from 1995 to 2005 also indicate that Pools 13 and 16 had the highest shovelnose sturgeon harvest of any study pool.

Growth is another population characteristic of shovelnose sturgeon that varies throughout their distribution. The mean back-calculated length at age

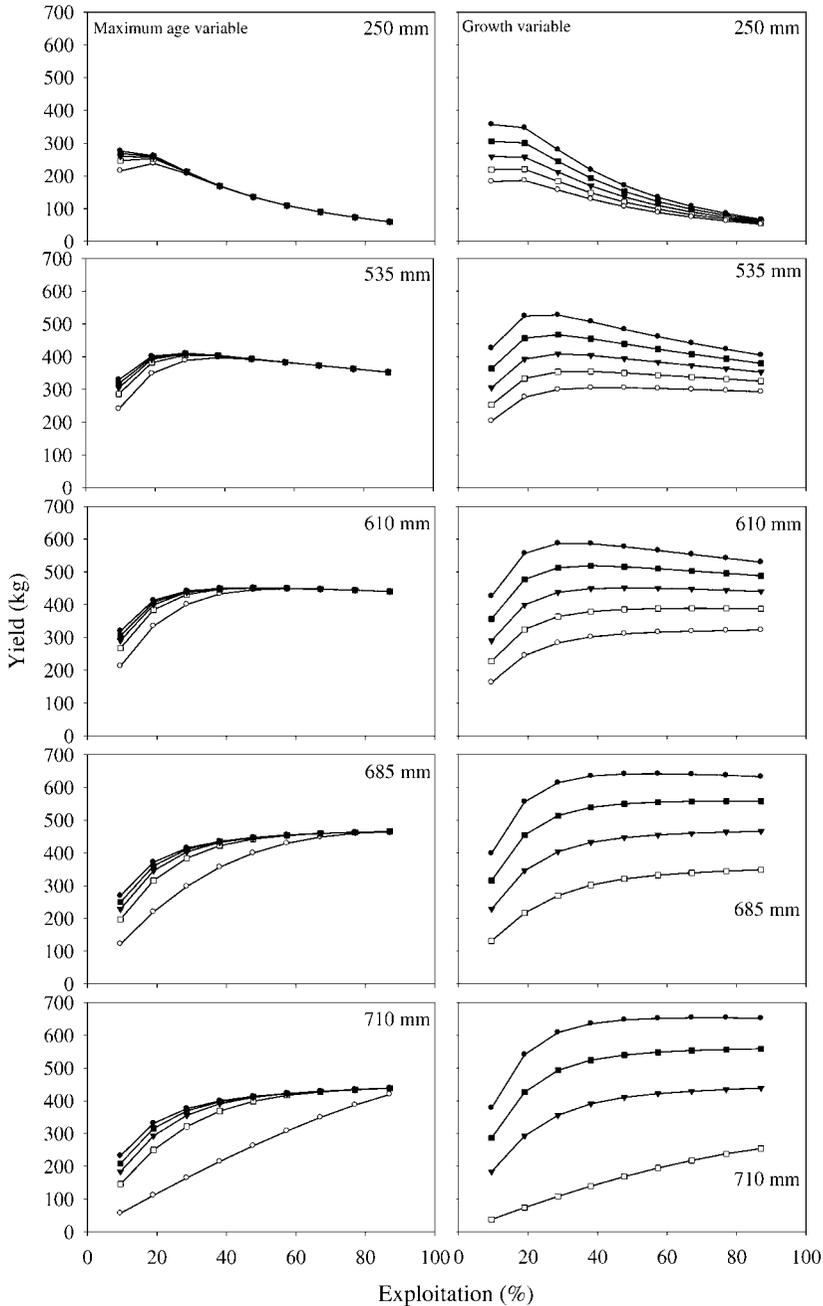


FIGURE 5.—Simulated yields for shovelnose sturgeon in the upper Mississippi River with a conditional natural mortality rate of 10%. Each row represents a different minimum length limit. The panels on the left present the results of models in which the maximum age was varied. In each simulation the middle line (solid triangles) represents yields calculated using the observed maximum age of 17 years; the two lines above it represent yields calculated with maximum ages of 19 (solid squares) and 22 years (solid circles), and the two lines below it represent yields calculated with maximum ages of 15 (open squares) and 12 years (open circles). The panels on the right present the results of models in which growth was varied. The middle line (solid triangles) represents yields calculated using the observed growth parameters; the two lines above it represent yields calculated with 5% (solid squares) and 10% higher growth (solid circles); the two lines below it represent yields calculated with 5% (open squares) and 10% lower growth (open circles). Note that there are no simulations representing 10% lower growth for the 685- and 710-mm minimum length limits, as such growth would cause the asymptotic maximum length to be less than the limit.

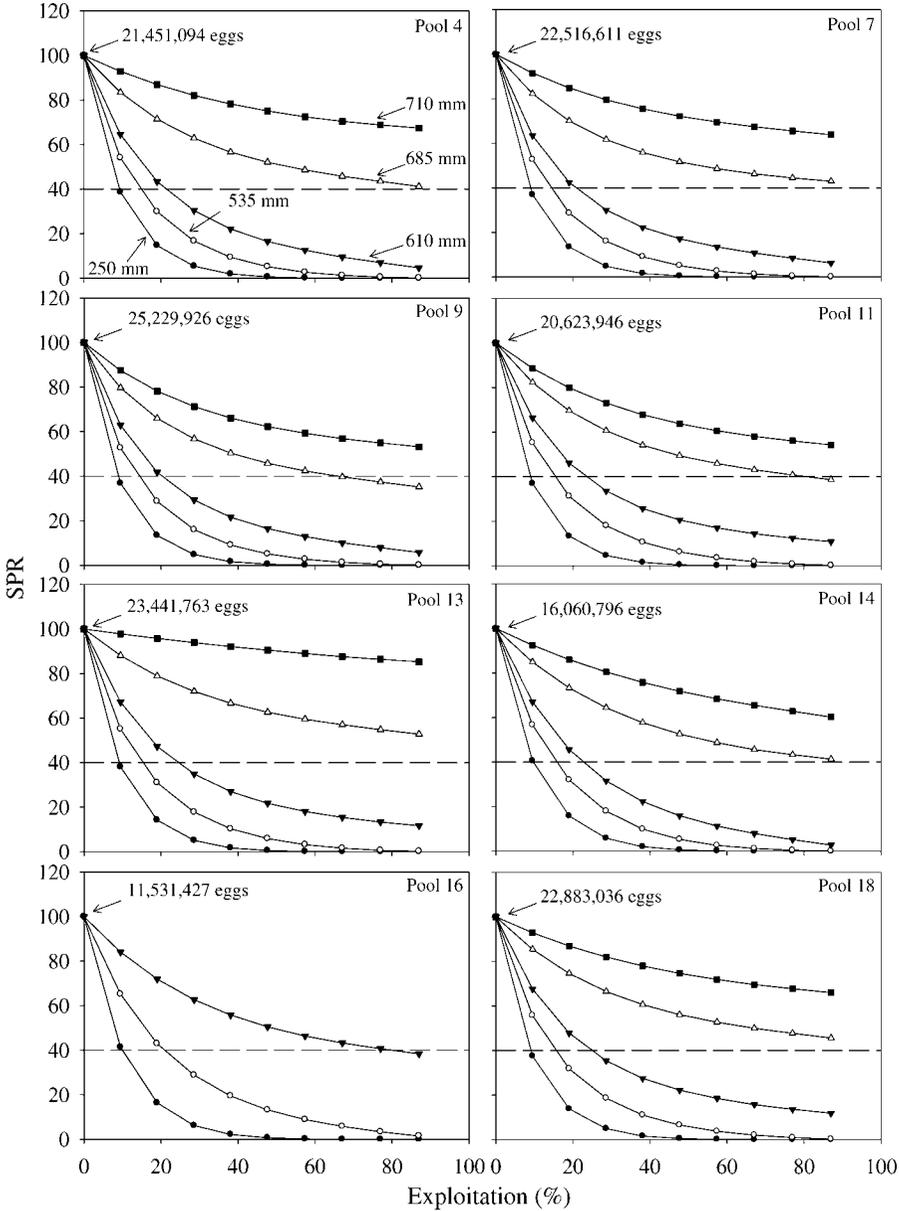


FIGURE 6.—Simulated spawning potential ratios (SPRs) for selected shovelnose sturgeon populations in the upper Mississippi River in response to five minimum length limits. Each simulation assumed a conditional natural mortality rate of 10%. The maximum lifetime egg production is also provided for each pool. The horizontal dashed lines represent the recruitment overfishing threshold of 40%. Only three minimum length limits were simulated for Pool 16 because the 685- and 710-mm minimum length limits exceeded the asymptotic maximum length of the shovelnose sturgeon in that pool.

5 of shovelnose sturgeon varies from 576 mm in the upper Missouri River to 470 mm in the lower Missouri River (Quist et al. 2002). Everett et al. (2003) reported that growth of shovelnose sturgeon was significantly greater in the Yellowstone River than in the upper Missouri River. Our results indicate similar spatial

differences in growth of shovelnose sturgeon. Possible explanations for differences in growth include habitat quality, prey availability, and density-dependent interactions (i.e., competition). Everett et al. (2003) suggested that alterations in hydrology may account for spatial differences in shovelnose sturgeon growth

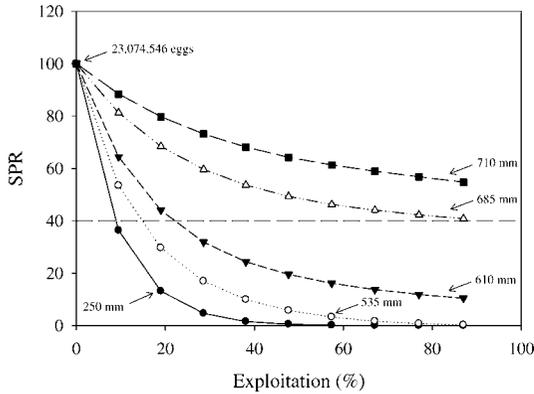


FIGURE 7.—Simulated spawning potential ratios (SPRs) for the shovelnose sturgeon populations in the upper Mississippi River in response to five minimum length limits. See Figure 6 for additional details.

between the Missouri and Yellowstone rivers. Modde and Schmulbach (1977) indicated that shovelnose sturgeon had lower condition factors during periods of high discharge because increased velocities mobilized food items and reduced aggregations of prey. High harvest rates may also influence the growth estimates of shovelnose sturgeon; because commercial harvesters select the largest, fastest-growing individuals, the result is a population dominated by slow-growing fish. If harvesters are selecting the fastest-growing shovelnose sturgeon from each age-class, back-calculated lengths at age would be smaller for older individuals than for younger individuals (i.e., Lee's phenomenon; Ricker 1975; DeVries and Frie 1996). We examined this further by compiling MBCL at age 1 for each age-class in each pool (Figure 9). A primary explanation for Lee's phenomenon is that slow-growing individuals in a cohort are less vulnerable to fishing mortality because they do not recruit to fishing gear as early as the fast-growing individuals (Ricker 1975; DeVries and Frie 1996). Our results appear to support this hypothesis; we saw no evidence of Lee's phenomenon in the pools with low exploitation (i.e., Pools 4 and 7). In contrast, significant decreasing trends in the MBCL at age 1 of older fish was observed in all other study pools except for Pool 18.

Few studies have evaluated the sex ratios of shovelnose sturgeon populations, and those that have provide few consistencies. Colombo et al. (2007) found a sex ratio of 1:1 in the middle Mississippi River. In contrast, Jackson (2004) reported that only 20% of shovelnose sturgeon sampled from the middle Mississippi River were females. Jackson (2004) contended that this estimate was confounded by concentrations of

spawning fish, because many female fish had already been harvested from the area immediately before sampling. Kennedy (2005) estimated a female to male ratio of 0.6:1 (i.e., 36% female) in the Wabash River. In the UMR, a higher proportion of males might be expected, given a fishery targeted at females. Our results, however, indicate that sex ratios were skewed toward females. In three of the six study pools where sex ratios were evaluated, the female to male ratio was above 1.5. Although a skewed sex ratio could be an artifact of sampling bias, the fact that our sampling was conducted in multiple pools and over a large time span makes such bias unlikely. Regardless, the large proportion of females in shovelnose sturgeon populations may be evidence of a mechanism to balance the sex ratio of spawning fish. Previous research suggests female shovelnose sturgeon have a spawning periodicity of 3 years, whereas males spawn approximately every 2 years (Moos 1978). Thus, females would have to make up approximately 60% of the population to maintain an annual spawning ratio of one female to one male.

No clear spatial patterns in condition (i.e., mean W_r) of shovelnose sturgeon populations were observed in the UMR. Quist et al. (1998) reported that shovelnose sturgeon W_r values varied longitudinally in the Missouri River, populations from upstream reaches exhibiting higher W_r than downstream populations. Quist et al. (1998) suggested a target W_r of 80–90 for shovelnose sturgeon populations not in the upper Missouri River. All mean W_r s of shovelnose sturgeon for pools in our study area either fell within or exceeded this range, suggesting that the shovelnose sturgeon in the UMR are in good condition. Mean W_r for shovelnose sturgeon from the UMR were generally higher than those reported from the Missouri River. Hamel and Steffensen (2007) reported a mean W_r of 82 for shovelnose sturgeon in a reach of the Missouri River from Gavin's Point Dam to the confluence of the Platte River. In the lower Missouri River, Utrup et al. (2008) and Plauck et al. (2008) reported mean W_r values near 90.

Size at maturity is highly variable throughout the distribution of shovelnose sturgeon. In slower growing populations, such as those from the Missouri and White rivers, female shovelnose sturgeon become sexually mature as small as 414 mm (Zweiacker 1967; L. Holt, Arkansas Game and Fish Commission, personal communication). Our data indicate that most female shovelnose sturgeon in the UMR mature at approximately 615 mm and age 7. Correspondingly, Monson and Greenback (1947) and Helms (1974) suggested that female shovelnose sturgeon in the UMR mature between 615 and 635 mm and at age 7. Based on the

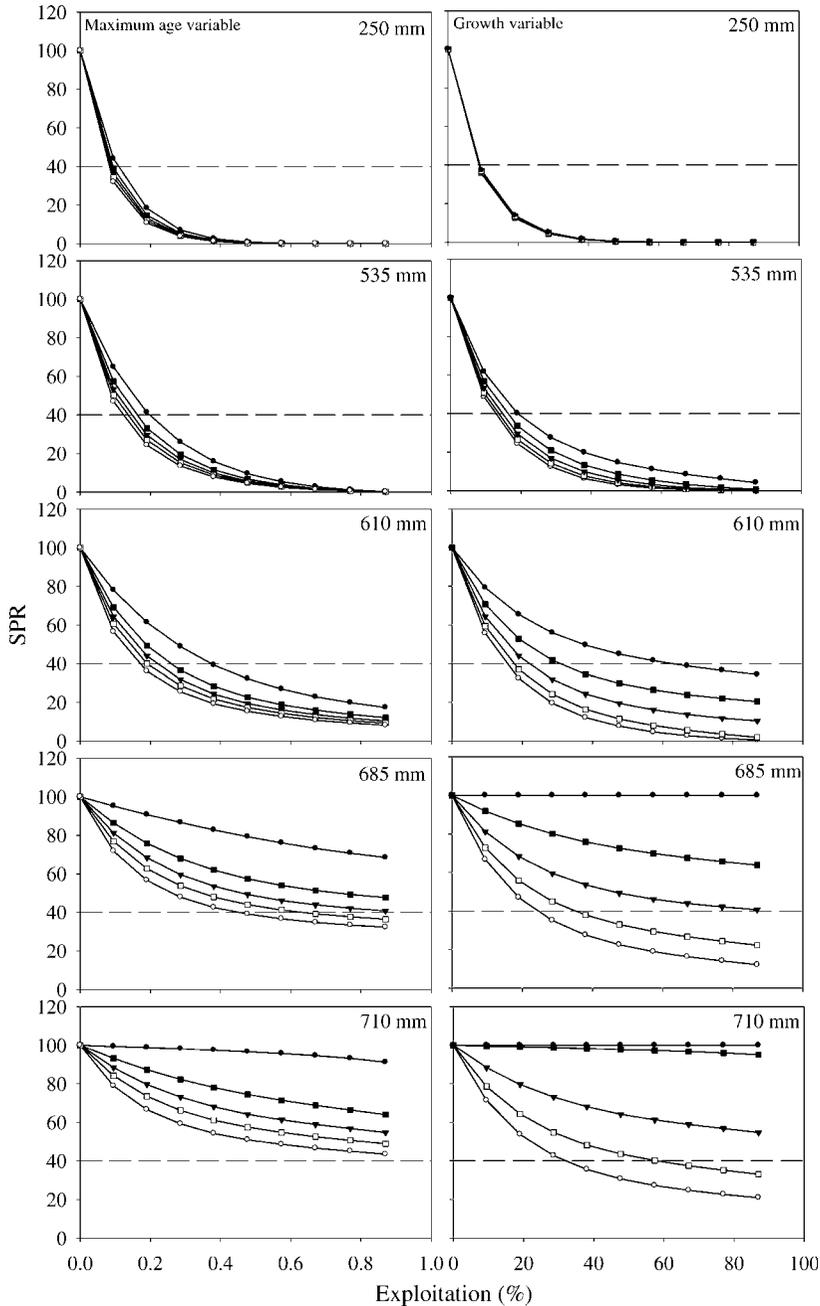


FIGURE 8.—Simulated yields for the combined shovelnose sturgeon populations in the upper Mississippi River with a conditional natural mortality rate of 10%. Each row represents a different minimum length limit. The horizontal dashed lines represent the recruitment overfishing threshold of 40%. The panels on the left present the results of models in which the maximum age was varied. The middle line (triangles) represents spawning potential ratios (SPRs) calculated from the observed maximum age of 17 years; the two lines above it represent SPRs calculated with maximum ages of 15 (solid squares) and 12 years (solid circles), and the two lines below it represent SPRs calculated with maximum ages of 19 (open squares) and 22 years (open circles). The panels on the right present the results of models in which growth was varied. The middle line (triangles) represents SPRs calculated from the observed growth parameters; the two lines above it represent SPRs calculated with 5% (solid squares) and 10% lower growth (solid circles), and the two lines below it represent SPRs calculated with 5% (open squares) and 10% higher growth (open circles).

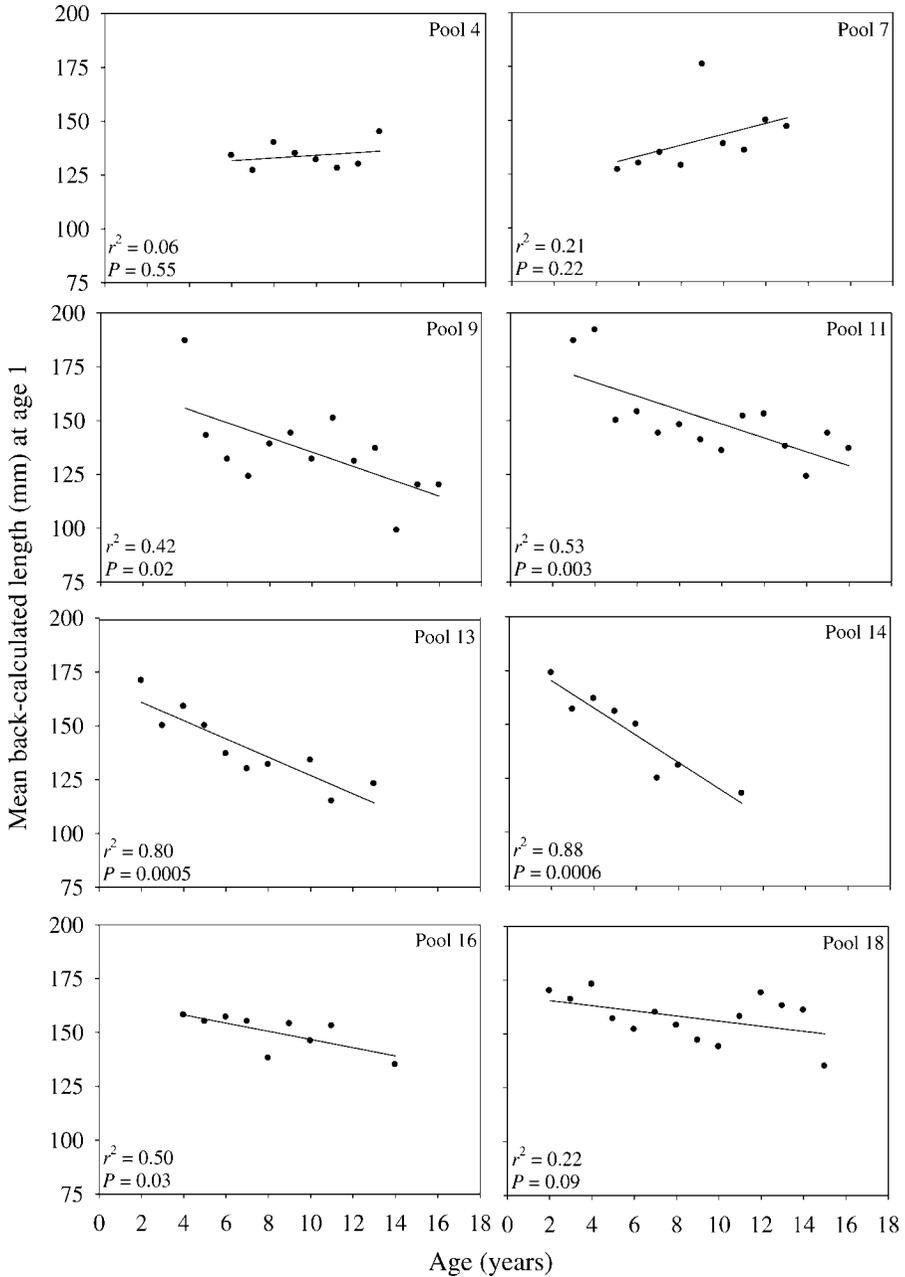


FIGURE 9.—Mean back-calculated lengths at age 1 for different shovelnose sturgeon age-classes sampled from eight pools of the upper Mississippi River, 2006–2007.

historical literature, size- or age-at-maturity does not appear to have changed substantially over the last several decades.

In all study pools except Pool 16, population simulations showed the potential for growth overfishing with simulated minimum length limits less than 685 mm. More restrictive length limits allowed shovelnose

sturgeon to realize a larger proportion of their growth potential before harvest. Increasing minimum length limits beyond 685 mm reduced yield because individuals died naturally instead of being harvested. Our results are concordant with the results of previous research on shovelnose sturgeon populations in the middle Mississippi River. Colombo et al. (2007)

reported that a 610-mm minimum length limit was not sufficient to prevent growth overfishing in the middle Mississippi River and thus recommended the implementation of a 685-mm minimum length limit.

Although the consequences of growth overfishing are important to consider, recruitment overfishing is a much greater concern, as it can lead to population decline and extirpation. Our simulations indicate the potential for recruitment overfishing at exploitation levels of 20% and greater with a 610-mm length limit. Increasing the minimum length limit for shovelnose sturgeon harvest to 685 mm could prevent recruitment overfishing in the UMR as SPR increased to levels above the minimum thresholds (i.e., 20–40%) suggested by previous research (e.g., Goodyear 1993; Colombo et al. 2007). Given the unique and complex reproductive ecology of shovelnose sturgeon, researchers have suggested higher SPR thresholds for assessing recruitment overfishing. Quist et al. (2002) suggested the possibility of a minimum SPR target value of 40–50%, which would further support the argument for more restrictive regulations for harvesting shovelnose sturgeon in the UMR. A conservative approach to shovelnose sturgeon harvest may be warranted to increase the reproductive potential of populations in the UMR.

Yield was more sensitive to changes in growth than to changes in maximum age in our simulations. In a given simulation, the potential for growth overfishing was not altered by changes in growth and maximum age except for the 610-mm length limit with a 10% decrease in growth. Therefore, although estimates of yield may differ as a result of aging error, the conclusions regarding growth overfishing remain consistent. Spawning potential ratio was also sensitive to changes in growth and maximum age. Increasing maximum age resulted in lower SPR values because more eggs were produced over the recruits' lifetime in the simulated unexploited population. Decreasing maximum age had the opposite effect on SPR. If we underestimated maximum age by 5 years (i.e., a 29% change in maximum age), SPR did not decrease to levels below 40% until exploitation reached 35% with a 610-mm length limit. In the original model, SPR reached 40% at 20% exploitation. In the simulations of the two most restrictive length limits, SPR did not decrease to levels below 40% when maximum age was altered until the highest levels of exploitation were included. As such, a 685-mm or longer minimum length limit is still recommended if errors in maximum age occur. Simulated errors in growth also affected SPR. Increasing growth decreased the amount of time required for shovelnose sturgeon to recruit to the commercial fishery. As a result, more fish were

harvested earlier in life, thus decreasing egg production. Conversely, decreasing growth increased SPR and allowed shovelnose sturgeon to reach reproductive age well before they were recruited to the fishery. Spawning potential ratio was more affected by varying growth in scenarios where more restrictive length limits were evaluated. At 30% exploitation with a 535-mm length, decreasing growth by 10% increased SPR from 17% to 28%, whereas in the 610-mm length limit simulation, SPR increased from 32% to 56%. In the 685-mm simulation performed with observed data, SPR does not fall below 40% until high levels of exploitation. When growth is increased by 5% and 10%, SPR decreases to levels below 40% at exploitation levels of 35% and 25%, respectively. Age-validation studies conducted on white sturgeon *A. transmontanus* and pallid sturgeon (e.g., Rien and Beamesderfer 1994; Paragamian and Beamesderfer 2003; Hurley et al. 2004) indicate that true ages are underestimated when pectoral fin rays are used for aging. Although age estimates have not been validated for shovelnose sturgeon, any aging errors will probably be underestimates of age. Such errors would result in lower SPR, whereas simulated yields may be increased. Despite these considerations, a 685-mm or longer minimum length limit would still be recommended to prevent recruitment overfishing.

Many studies have shown longitudinal differences in the population parameters of shovelnose sturgeon. The current study corroborated these findings, as significant differences were found among pools with regard to size and age structure, mortality, growth, condition, and sex ratios. Although some movement of shovelnose sturgeon between navigation pools of the UMR has been documented (Hurley 1983), this study suggests that local effects such as harvest may influence population parameters of shovelnose sturgeon. In light of the recent increase in shovelnose sturgeon exploitation, our results indicate that the implementation of a basin-wide 685-mm or longer length limit on shovelnose sturgeon harvest is needed to provide a sustainable shovelnose sturgeon fishery. A 685-mm minimum length limit approximately doubles the SPR values relative to those estimated with a 610-mm length limit. Although analyses examining yield and SPR are sensitive to errors in input parameters, simulations suggest that more restrictive harvest regulations (i.e., 685-mm length limit) are prudent in management of the species. Additionally, our results are corroborated by research from the middle Mississippi River (i.e., Colombo et al. 2007), which also reports that current regulations (i.e., 610-mm length limit) are not sufficient to prevent growth and recruitment overfishing. As such, sturgeon populations should be monitored

closely, and similar analyses should be conducted in the future to ensure the sustainability of the shovelnose sturgeon fishery.

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