

Potential Influence of Harvest on Shovelnose Sturgeon Populations in the Missouri River System

MICHAEL C. QUIST* AND CHRISTOPHER S. GUY

*Kansas Cooperative Fish and Wildlife Research Unit,¹
Kansas State University, 205 Leasure Hall,
Manhattan, Kansas 66506, USA*

MARK A. PEGG²

*Iowa Cooperative Fish and Wildlife Research Unit,³
Department of Animal Ecology, Iowa State University,
11 Science II, Ames, Iowa 50011, USA*

PATRICK J. BRAATEN⁴

*Kansas Cooperative Fish and Wildlife Research Unit,
Kansas State University, 205 Leasure Hall,
Manhattan, Kansas 66506, USA*

CLAY L. PIERCE

*Iowa Cooperative Fish and Wildlife Research Unit,
Department of Animal Ecology, Iowa State University,
11 Science II, Ames, Iowa 50011, USA*

VINCENT H. TRAVNICHEK

*Missouri Department of Conservation, Conservation Research Center,
1110 South College Avenue, Columbia, Missouri 65201, USA*

Abstract.—The collapse of the European and Asian caviar industry has raised concern about the overexploitation of shovelnose sturgeon *Scaphirhynchus platyrhynchus* in the Missouri River. Unfortunately, little is known about the potential effects of harvest on the population dynamics of this species. Therefore, this study was conducted to describe the population characteristics (e.g., growth, longevity, and mortality) and to determine the influence of exploitation and harvest regulations (minimum length limits) on the yield, size structure, and egg production of shovelnose sturgeon from three sites in the Missouri River using a Beverton–Holt equilibrium model. Despite differences in the population characteristics (e.g., growth and longevity) of shovelnose sturgeon among sites, all populations responded similarly to harvest at the conditional natural mortality rates (death rate in the absence of harvest) used in our simulations (i.e., 5% and 20%). Our simulations of yield indicated that growth overfishing (i.e., shovelnose sturgeon being harvested before reaching their full growth potential) occurred with and without length limits at low conditional natural mortality rates in all populations. At a higher conditional natural mortality rate, only a 508-mm (fork length) minimum length limit prevented growth overfishing. Size structure (relative stock density of preferred-length fish [RSD-P]; ≥ 510 mm) was highly sensitive to exploitation and was reduced up to 87% in simulations without a harvest restriction or with a 406-mm length limit. A 508-mm length limit prevented RSD-P from declining more than 18% in all simulations. As with size structure, maximum lifetime egg production was reduced up to 74% at low exploitation rates ($\leq 20\%$), indicating the

* Corresponding author: mcquist@ksu.edu

¹ The Unit is jointly sponsored by the U.S. Geological Survey, Biological Resources Division; Kansas Department of Wildlife and Parks; Kansas State University; and the Wildlife Management Institute.

² Present address: Illinois River Biological Station, Illinois Natural History Survey, 704 North Schrader, Havana, Illinois 62644, USA.

³ The Unit is jointly sponsored by the U.S. Geological Survey, Biological Resources Division; Iowa Department of Natural Resources; Iowa State University; and the Wildlife Management Institute.

⁴ Present address: U.S. Geological Survey, Biological Resources Division, East Kansas, Fort Peck, Montana 59223, USA.

Received April 3, 2001; accepted October 17, 2001

potential for recruitment overfishing. A 508-mm length limit prevented the proportion of maximum lifetime egg production from reaching 20% in all populations, except at the uppermost site (upstream of Fort Peck Lake, Montana). Although shovelnose sturgeon are thought to be more resilient to exploitation than the other sturgeon species, these results suggest that shovelnose sturgeon are sensitive to low levels of exploitation. We believe that a proactive approach to their management is warranted due to their current status and possible threats in the future.

Sturgeons (Acipenseridae) are dominated by large, far-ranging species that are vulnerable to human activities due to their unique reproductive biology, long life span, and high susceptibility to harvest (Birstein 1993; Boreman 1997). Nearly all European and Asian sturgeons are endangered, and several species (e.g., Amu Darya shovelnose sturgeon *Pseudoscaphirhynchus kaufmanni*) will likely become extinct in the near future (Birstein 1993). Although North American sturgeon populations appear more stable than those in Europe and Asia, over 65% of the North American species are categorized as endangered, threatened, or of special concern (Williams et al. 1989). The status of sturgeons illustrates the need to better understand the effects of harvest on their populations for proper management and conservation.

Shovelnose sturgeon *Scaphirhynchus platyrhynchus* are the smallest of the North American sturgeon species and are indigenous to the Mississippi and Missouri river systems (Bailey and Cross 1954; Lee et al. 1980). Although these fish are one of the most widespread sturgeons in North America, their distribution and abundance have been significantly reduced over the last 100 years due to habitat alterations, water pollution, and overharvest (Keenlyne 1997). For example, shovelnose sturgeon are classified as extirpated or at risk in 50% of the states within their native distribution. In the remaining states, shovelnose sturgeon populations have either declined during the past 60 years or their population status is unknown. Despite these concerning trends, shovelnose sturgeon are still one of the few sturgeons that can be commercially harvested in North America (Carlson et al. 1985; Keenlyne 1997).

The current status of sturgeon populations from the Caspian, Black, and Adriatic seas (Birstein 1993) has raised concern that the exploitation of shovelnose sturgeon may increase due to the increasing demand for and value of caviar. In the late 1800s, shovelnose sturgeon were undesirable for commercial harvest and were often considered a nuisance to those commercially fishing for lake sturgeon *Acipenser fulvescens* (Carlander 1954; Moos 1978). However, by 1900, shovelnose sturgeon became an important commercial species

when markets developed for their meat and eggs (Coker 1930; Barnickol and Starrett 1951; Moos 1978). Currently, shovelnose sturgeon are commercially harvested in seven states throughout the Missouri and Mississippi river system, with most harvests occurring in the Mississippi River (Keenlyne 1997), and with most fisheries using trammel or gill nets to target shovelnose sturgeon for their flesh and eggs. The harvest of shovelnose sturgeon in the Missouri River has been relatively low until recent years. In the state of Missouri, for example, the commercial harvest of shovelnose sturgeon from the Missouri River was less than 1,400 kg/year prior to the early 1980s; this increased rapidly, however, and peaked at about 8,000 kg in 1987 (V. H. Travnichek, unpublished data). While the commercial harvest of shovelnose sturgeon declined to 325 kg in 1994, during the past 5 years it has increased to about 500 kg/year. The level of sport harvest is generally unknown, but most states speculate that recreational harvest is low (Keenlyne 1997).

Previous studies indicate that North American sturgeons are highly sensitive to fishing mortality (Rieman and Beamesderfer 1990; Boreman 1997). Rieman and Beamesderfer (1990) estimated that exploitation rates higher than 15% could lead to a collapse of the Columbia River white sturgeon *A. transmontanus* fishery and suggested that conservative management was needed to protect the species. Similarly, Boreman (1997) found that increasing the total annual mortality of shortnose sturgeon *A. brevirostrum* from 12% to 16% resulted in an estimated 50% reduction in potential lifetime egg production. Furthermore, restricting fishing mortality may be the only tool available for managers to protect and restore sturgeon populations (Boreman 1997). Considerable information has been published on the ecology and life history of shovelnose sturgeon; however, we currently have little knowledge on how their populations would respond to varying harvest rates.

This study was conducted to describe differences in population characteristics and to determine the effects of fishing mortality on shovelnose sturgeon in the Missouri River. We used a modeling approach to determine the effects of harvest

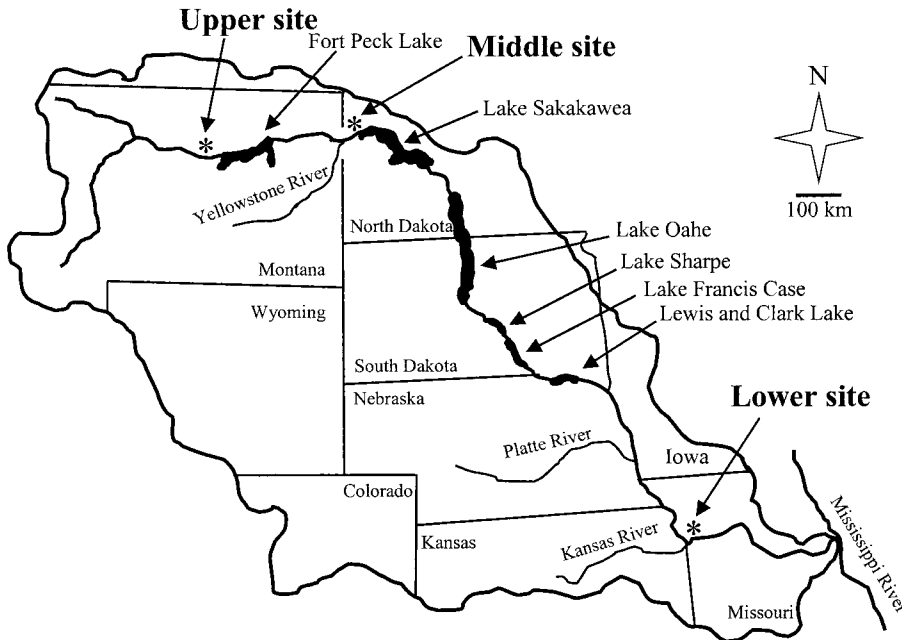


FIGURE 1.—Locations of the shovelnose sturgeon populations (upper, middle, and lower) from the Missouri River that were used in our analysis.

on yield, size structure, and reproductive potential, and we examined the utility of minimum length limits under varying harvest regimes.

Methods

Population characteristics.—Information on shovelnose sturgeon populations was obtained by sampling three sites (upper, middle, and lower) in the Missouri River during 1996, 1997, and 1998 (Figure 1). The upper site is characterized by relatively natural flow and temperature regimes (Braaten 2000; Pegg 2000). Although the middle site is located in the upper portion of the Missouri River and is in close proximity to the upper site, it has altered flow and temperature regimes due to hypolimnetic releases from Fort Peck Dam. The lower site represents the channelized Missouri River where the flow regime is highly modified, but the temperature regime is relatively natural. All fish used in this analysis were sampled during late summer and early fall using bottom-drifting trammel nets (22.9 m long, with a 2.4-m-deep inner wall of 25-mm-bar mesh and 1.8-m-deep outer walls of 203-mm-bar mesh). For a complete description of study sites and methodologies see Young et al. (1997), Braaten (2000), and Pegg (2000).

Fork length (mm) and weight (g) were measured

for all fish and the marginal right pectoral fin ray was collected from 10 fish per centimeter length-group at each site for age and growth analysis. Transverse sections (0.3–0.5 mm thick) were removed from the distal portion of the cartilaginous ray. Annuli were measured with the aid of a dissecting microscope coupled with an image analysis system following the guidelines of Carrier (1951) and Brennan and Cailliet (1989). The use of fin rays is a widely accepted technique for aging sturgeons (Zweiacker 1967; Dadswell 1979; Keenlyne and Jenkins 1993; Beamesderfer et al. 1995; Morrow et al. 1998) and has been validated for lake sturgeon (Rossiter et al. 1995) and shovelnose sturgeon (Helms 1974). Mean back-calculated length at age was estimated using the direct proportion method (DeVries and Frie 1996). Because shovelnose sturgeon are a long-lived species, we only back-calculated lengths to the most recent annulus. A von Bertalanffy growth function was also used to describe the growth of shovelnose sturgeon:

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

where L_t = length at time t , L_∞ = the theoretical maximum length, K = the growth coefficient (the rate at which fish approach L_∞), and t_0 = the time when length would theoretically equal 0 mm.

TABLE 1.—Parameter estimates used in population simulations of shovelnose sturgeon from the Missouri River. The numbers in parentheses are standard errors.

Variable	Description	Population		
		Upper	Middle	Lower
β_0	Intercept of the regression of weight on length ^a	−6.29 (0.24)	−6.29 (0.19)	−6.00 (0.08)
β_1	Slope of the regression weight on length ^a	3.34 (0.09)	3.33 (0.07)	3.19 (0.03)
L_∞	Theoretical maximum length (mm) ^b	660 (14.25)	660 (14.25)	660 (14.25)
K	Growth coefficient (rate at which fish approach L_∞)	0.273 (0.03)	0.168 (0.01)	0.191 (0.007)
t_0	Time when length would theoretically be equal to 0 (years) ^b	−0.269 (0.04)	−0.269 (0.04)	−0.269 (0.04)
Age _{max}	Maximum age of sampled fish (years)	33	28	17

^a Variable was log₁₀ transformed.
^b Standardized L_∞ and t_0 values were obtained by fitting a pooled von Bertalanffy growth model.

First, we fitted a growth model for fish within each population to investigate differences in growth among populations. For our population simulations (see Methods below), we also fitted a growth model using the pooled age and growth information from all populations ($L_t = 660 \cdot \{1 - e^{-0.211 \cdot [t - (-0.269)]}\}$; $r^2 = 0.97$, $P = 0.0001$). We then fitted growth functions to obtain population-specific growth coefficients (K) using standardized L_∞ (i.e., 660 mm) and t_0 (i.e., −0.269 years) values from the pooled model similar to the technique used by Beamesderfer et al. (1995). The predicted values from these models were very similar to the observed mean back-calculated lengths at age in each of the populations (r^2 varied from 0.97 to 0.98; $P \leq 0.0001$). We attempted to fit models using the longest fish in our sample (994 mm); however, the results did not provide an adequate fit to the observed data.

The size structure of each population was assessed by calculating the proportional stock density ($PSD = 100 \cdot [\text{number of fish} \geq 380 \text{ mm}] / [\text{number of fish} \geq 250 \text{ mm}]$) and relative stock density ($RSD = 100 \cdot [\text{number of fish} \geq \text{specified length}] / [\text{number of fish} \geq 250 \text{ mm}]$) of preferred-length (RSD-P; 510 mm) and memorable-length (RSD-M; 640 mm) shovelnose sturgeon (Quist et al. 1998). We estimated the total annual mortality of age-5 to age-15 shovelnose sturgeon by fitting catch curves to each population (Ricker 1975). The number of fish older than age 10 from the upper and middle sites varied between zero and three individuals at each age. Thus, regressions of log_e-transformed number on age resulted in a poor fit for both the upper ($r^2 = 0.0001$, $P = 0.93$) and middle ($r^2 = 0.005$, $P = 0.77$) sites compared with that for the lower population ($r^2 = 0.61$, $P = 0.002$). Therefore, we used Heincke’s method to estimate total annual mortality (A ; Everhart et al. 1975),

$$A = 1 - [(n - n_0) \cdot n^{-1}],$$

where n is the total of all age frequencies in the sample (including the first fully recruited age) and n_0 is the frequency of the first fully recruited age. Parameter estimates from the length–weight relationships and von Bertalanffy growth equations were obtained using SAS (SAS Institute 1996) and were then used in our population simulations (Table 1).

Population simulations.—We used the software program Fishery Analyses and Simulation Tools (FAST), developed by Slipke and Maceina (2000), to model the effects of harvest and minimum length limits on shovelnose sturgeon populations. The program uses the Jones modification of the Beverton–Holt equilibrium model to estimate yield and is similar to other commonly used simulation models (e.g., GIFSIM; Taylor 1981). Previous versions of this model can be found in Allen and Miranda (1995) and Maceina et al. (1998b). The model estimates yield (Y) using the following equation:

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

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

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

The software program FAST allows users to model different rates of exploitation by inputting variable conditional natural mortality (cm; the death rate due to natural causes in the absence of fishing mortality) and conditional fishing mortality rates (cf; the exploitation rate in the absence of natural mortality). These values are used to estimate $F (= -\log_e[1 - \text{cf}])$ and $M (= -\log_e[1 - \text{cm}])$ and are then used in the equilibrium model (Slipke and Maceina 2000). Because the total annual mortality of shovelnose sturgeon is low in the Missouri River system, we modeled fixed rates of $\text{cm} = 5\%$ and 20% . The program FAST only allows the input of cf and cm, not exploitation; therefore, we manipulated cf to obtain exploitation rates from 0% to 90%. All simulations were conducted with an initial population size of 1,000 recruits.

In addition to assessing yield, we investigated the effects of harvest on size structure (RSD-P) and spawning potential ratio (SPR). Goodyear (1993) provides a detailed review of SPR. The potential recruit fecundity (P) is defined as the number of eggs that could be produced by an average recruit in the population (assuming density-dependent growth and survival do not occur). Potential fecundity is determined as

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

where n = the number of ages in an unfished population; E_i = the mean fecundity of females of age i ; $S_{ij} = e^{-(F_{ij}+M_{ij})}$, the density-dependent annual survival probabilities of females of age i when age j ; F_{ij} = the instantaneous fishing mortality rate of females of age i when age j ; and M_{ij} = the instantaneous natural mortality rate of females of age i when age j .

The SPR ($= 100 \cdot [P_{\text{fished}}/P_{\text{unfished}}]$) has a maximum value of 100 and declines toward 0 as exploitation increases. To prevent the harvest of spawners below the replacement level of their progeny, Goodyear (1993) recommends maintaining SPR values that are at least 20% of the maximum (when $\text{cf} = 0$). In order to estimate SPR for the study populations, we used the linear fecundity–length relationship (number of eggs = $23.4 \cdot [\text{length}] - 2,798.8$) presented in Zweiacker (1967) to estimate average egg production. We assumed that fish were sexually mature at age 5 and that populations exhibited a 50:50 sex ratio

(Zweiacker 1967; Helms 1974; Moos 1978). We also assumed that 50% of the females spawned in a given year because shovelnose sturgeon spawn every 2–3 years (Moos 1978).

The utility of minimum length limits was assessed by comparing model predictions of yield, size structure, and SPR without harvest restrictions with estimates having a 406-mm (16-in) or 508-mm (20-in) minimum length limit. We selected 250 mm (10 in) to represent the harvest of shovelnose sturgeon without a length limit because it is unlikely that fish smaller than 250 mm would be harvested by either commercial or recreational anglers. In addition, it is unlikely that fish smaller than 250 mm would be collected in the gears (primarily gill and trammel nets) commonly used to commercially harvest shovelnose sturgeon (Quist and Guy 1999). We selected a 406-mm length limit because it represents the approximate length (440 mm) at sexual maturity in the Missouri River (Zweiacker 1967; Moos 1978). The 508-mm minimum length limit was selected because most adult fish from the sampled populations would be available for harvest under these restrictions, and it represents a length close to preferred length. Additionally, if length limits were much greater than 508 mm, few fish would be available for harvest, except in the population upstream of Fort Peck Lake.

Results

Population Characteristics

Three hundred and eighty-five shovelnose sturgeon were collected, with lengths varying from 124 to 994 mm (Figure 2). Size structure (i.e., PSD, RSD-P, and RSD-M) was highest in the upper population followed by the middle and lower sites. Most sampled fish (79%) were greater than 500 mm and less than 5% were greater than 800 mm or less than 200 mm. The length–weight relationships indicated that the weights of fish from the upper and middle sites were similar for a given length (Figure 2). Conversely, shovelnose sturgeon from the lower site were lighter for a given length compared to the other populations.

The growth of shovelnose sturgeon was fastest in the upper population, followed by the lower and middle sites (Figure 3). This trend was most dramatic after age 6 when mean back-calculated length at age 6 was 576, 470, and 445 mm for the upper, lower, and middle sites, respectively. When we fitted growth models using a standardized L_{∞} and t_0 , the growth coefficients (Table 1) conformed

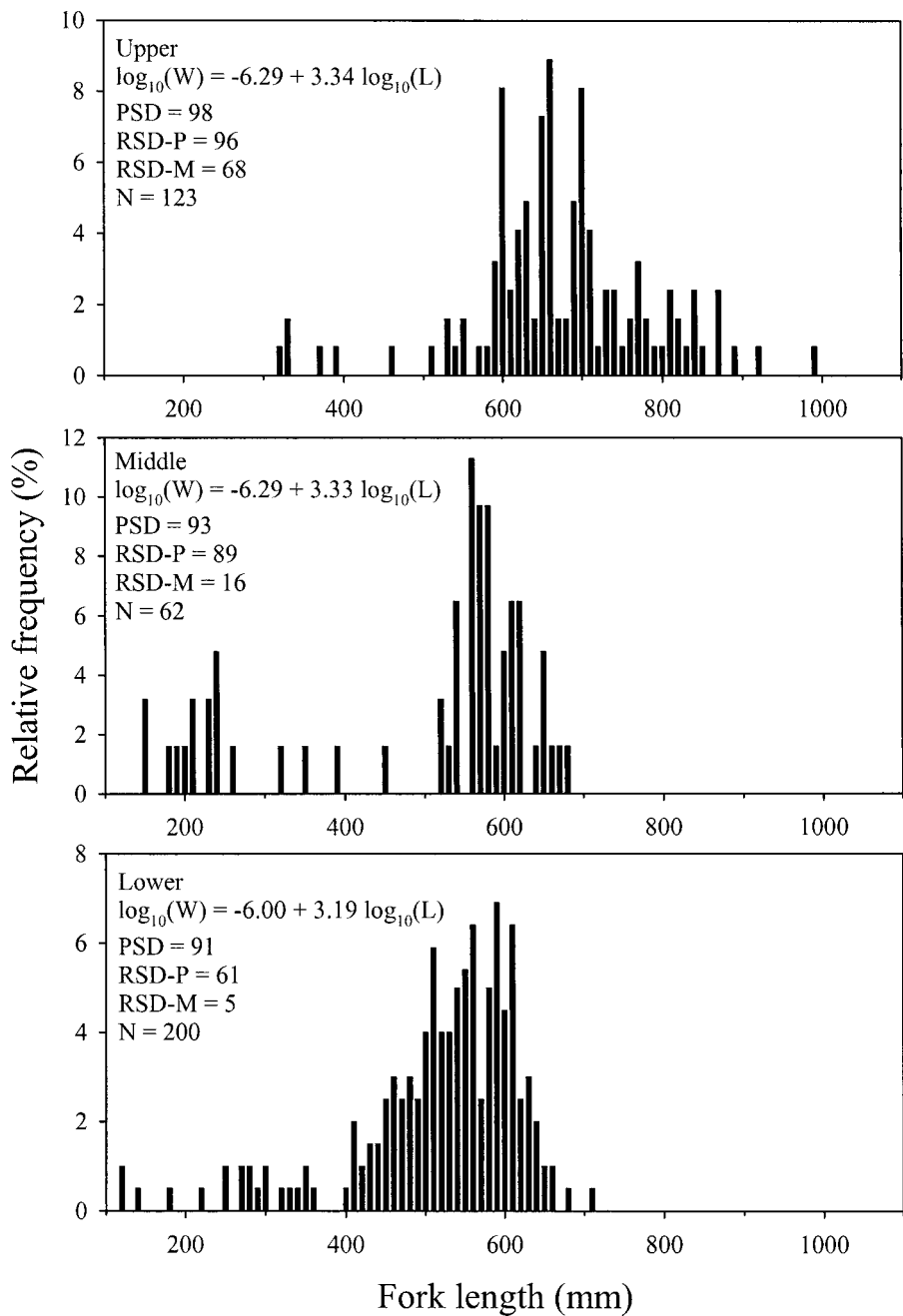


FIGURE 2.—Length frequency histograms, length–weight (L–W) relationships ($r^2 > 0.95$, $P \leq 0.001$ for all populations), size structure indices (proportional stock density [PSD]; relative stock density of preferred-length [RSD-P] and memorable-length [RSD-M] fish; see text for complete description), and sample size (N) for shovelnose sturgeon sampled from the Missouri River.

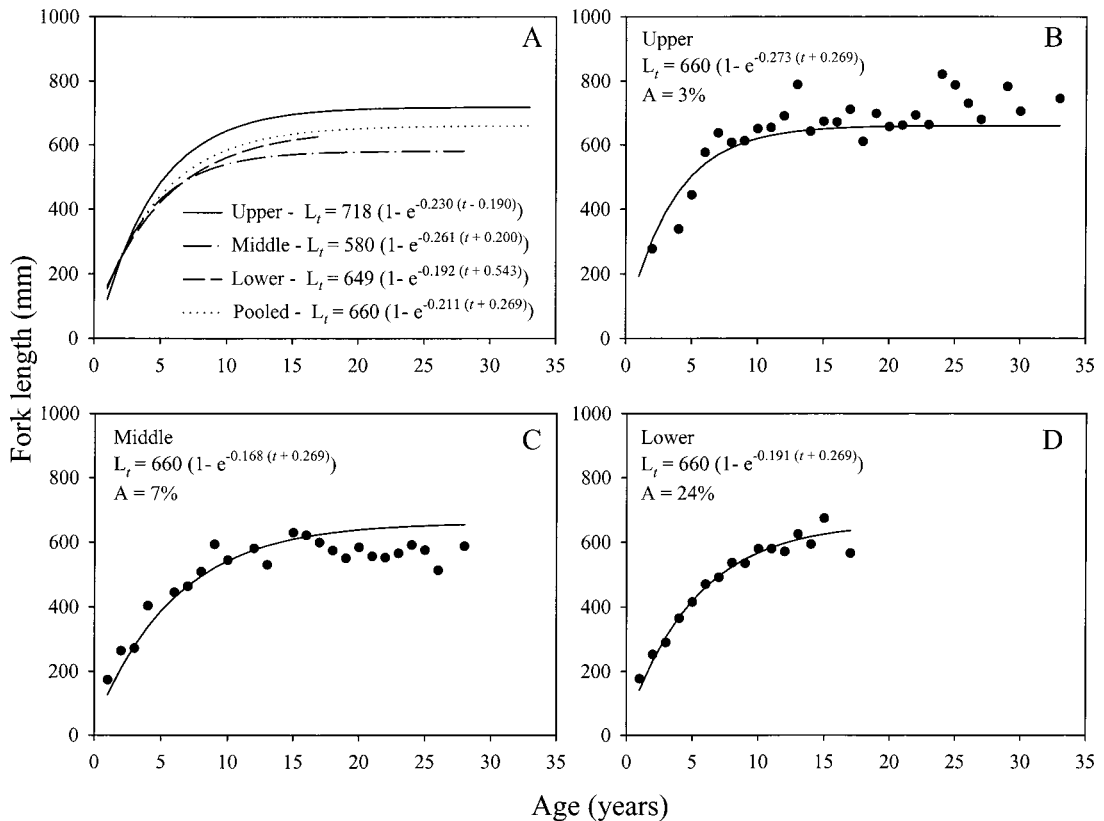


FIGURE 3.—Estimated von Bertalanffy growth equations (A) for each of the shovelnose sturgeon populations sampled from the Missouri River and (B–D) for the three individual populations as fitted using a standardized L_∞ and t_0 . The solid circles in panels B–D represent mean back-calculated lengths at age; A represents total annual mortality. See text for complete description of variables and statistical results.

to the observed mean back-calculated lengths at age. Shovelnose sturgeon from the upper and middle sites experienced higher longevity (Age_{max} : upper = 33 years, middle = 28 years) and lower total annual mortality compared with fish from the lower Missouri River ($\text{Age}_{\text{max}} = 17$ years; Figure 3).

Population Simulations

Yield

Predicted yields with harvest restrictions were generally higher than in simulations without harvest regulations (Figure 4). Predicted yield was higher in the upper population than at the other sites, especially at low levels of exploitation. At $\text{cm} = 5\%$ (most likely similar to the upper and middle sites), we found that yields declined with increasing exploitation with no limit or with a 406-mm length limit. Predicted maximum yields with

a 508-mm length limit occurred at 20–30% exploitation.

At a higher conditional natural mortality rate ($\text{cm} = 20\%$), predicted yields were approximately three times lower than at $\text{cm} = 5\%$ (Figure 4). Similar to the case with $\text{cm} = 5\%$, yields were generally lower without a length restriction. Without length limits, yield peaked at 20% exploitation and then declined. With a 406-mm minimum length limit, maximum yield occurred at exploitation rates of 30–50%. With a 508-mm minimum length limit, yield increased with increasing exploitation.

Size Structure

The predicted size structure (i.e., RSD-P) of shovelnose sturgeon populations was sensitive to changes in exploitation and harvest restrictions (Figure 5). Without harvest regulations or with a 406-mm minimum length limit, RSD-P declined

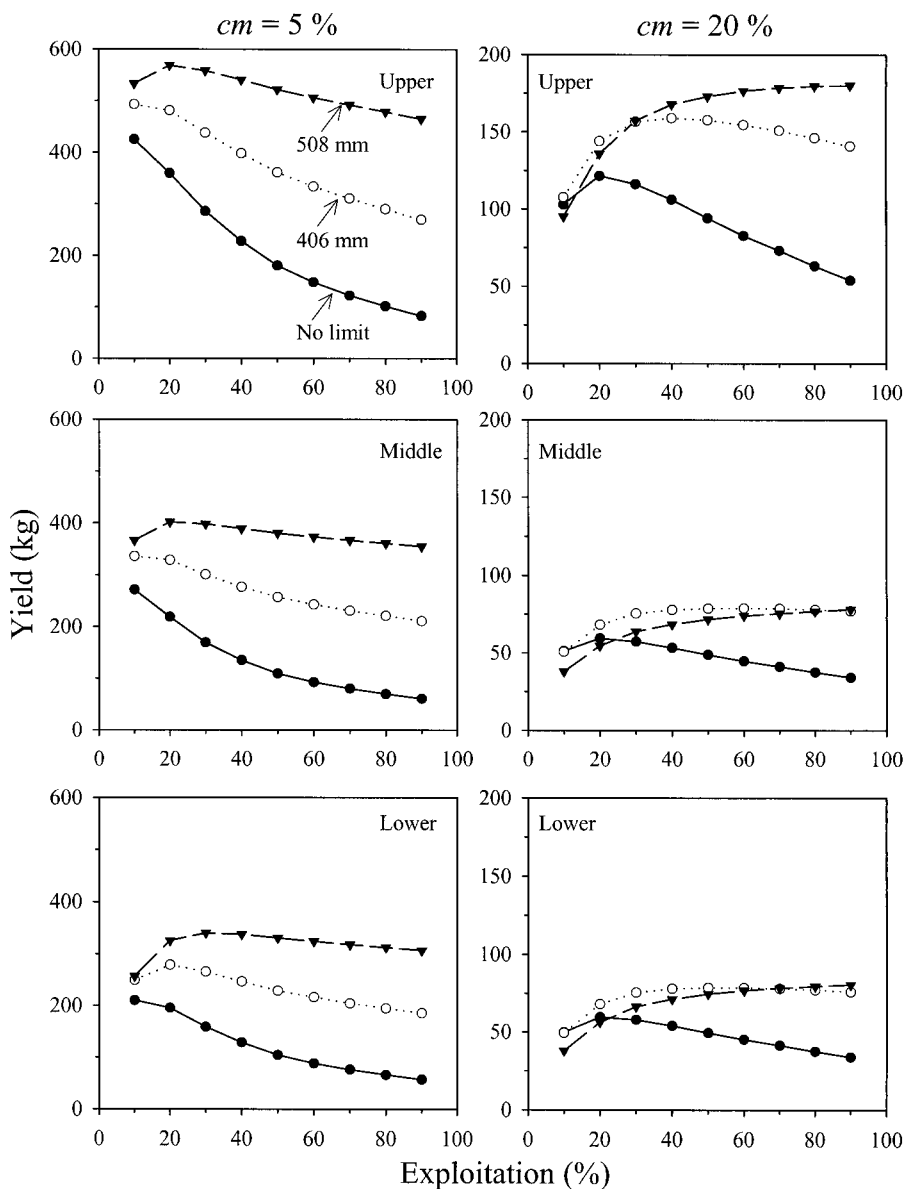


FIGURE 4.—Simulated yields for shovelnose sturgeon populations in the Missouri River with conditional natural mortality rates (cm) of 5% and 20%. The simulations were conducted with no minimum length limit, with a 406-mm minimum length limit, and with a 508-mm minimum length limit. Note that the scale for yield differs between the 5% and 20% cm graphs.

rapidly with increasing exploitation. For example, at $cm = 5\%$ and no length limit, RSD-P declined by 60–73% when exploitation was 20%, and 75–87% when exploitation was 30%. Similar results were obtained when we modeled the response with $cm = 20\%$. Our simulations predicted that a 508-mm length limit would prevent RSD-P from de-

creasing more than 18% at both conditional natural mortality rates.

Spawning Potential Ratio

Similar to RSD-P, SPR was highly sensitive to harvest (Figure 6). At $cm = 5\%$ and no length limit, potential lifetime egg production was re-

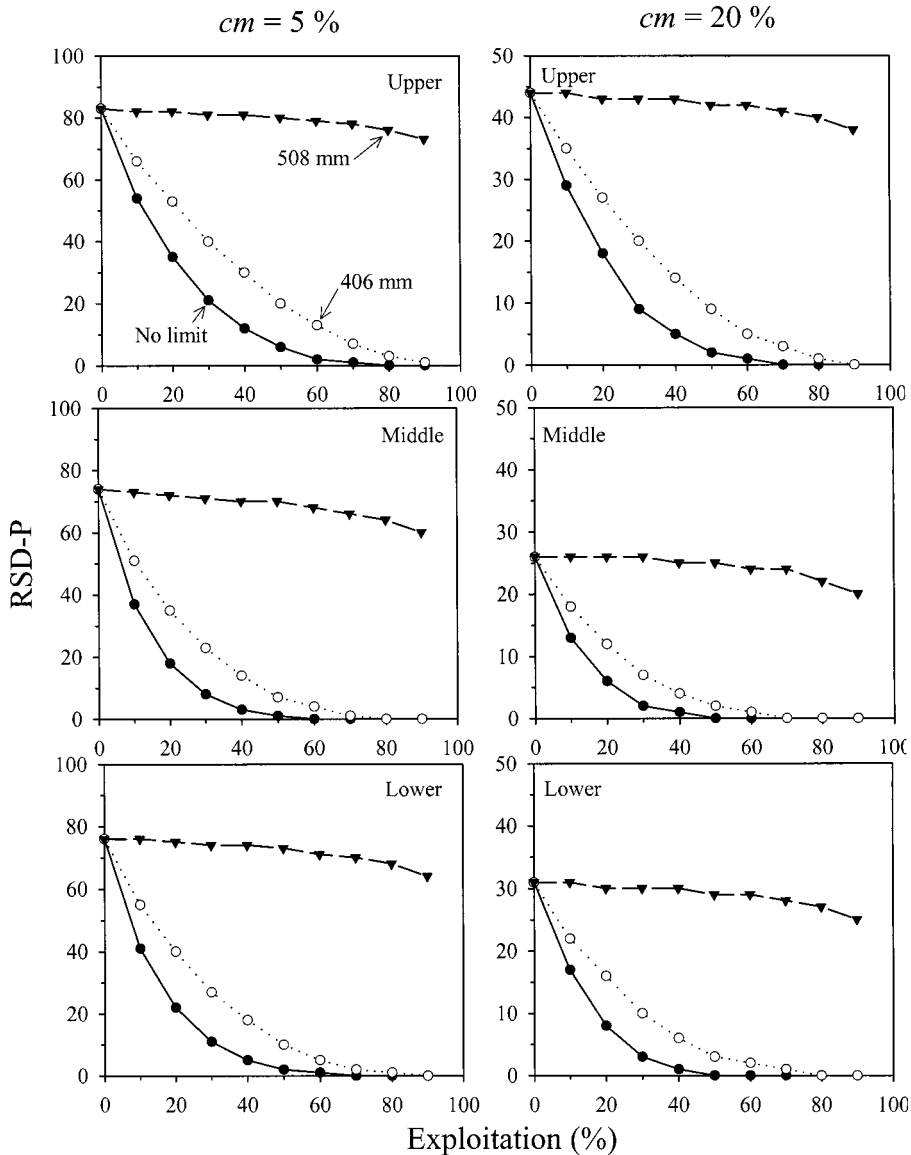


FIGURE 5.—Simulated relative stock densities of preferred-length (RSD-P; see text for complete description) shovelnose sturgeon populations in the Missouri River with conditional natural mortality rates (cm) of 5% and 20%. See the caption to Figure 4 for additional details.

duced by 51–74% when exploitation was increased from 0% to 10%. A further increase in exploitation to 20% resulted in an additional loss of 16–22% of the maximum lifetime egg production. In addition, populations exhibited SPR values below 20% once exploitation reached 20% with no harvest restrictions. While a 406-mm length limit had little effect on SPR at the upper site, it prevented SPR from reaching 20% of the maximum potential until 30–40% exploitation in the other popula-

tions. The most restrictive length limit prevented SPR from reaching 20% in all populations except the upper site.

At $cm = 20\%$ and no length limit, SPR was decreased by 50–56% at 10% exploitation (Figure 6). Spawning potential ratio was reduced below 20% of the maximum potential egg production once exploitation reached 30% for all populations with no harvest restrictions. With a 406-mm length limit, estimated egg production was 20% of the

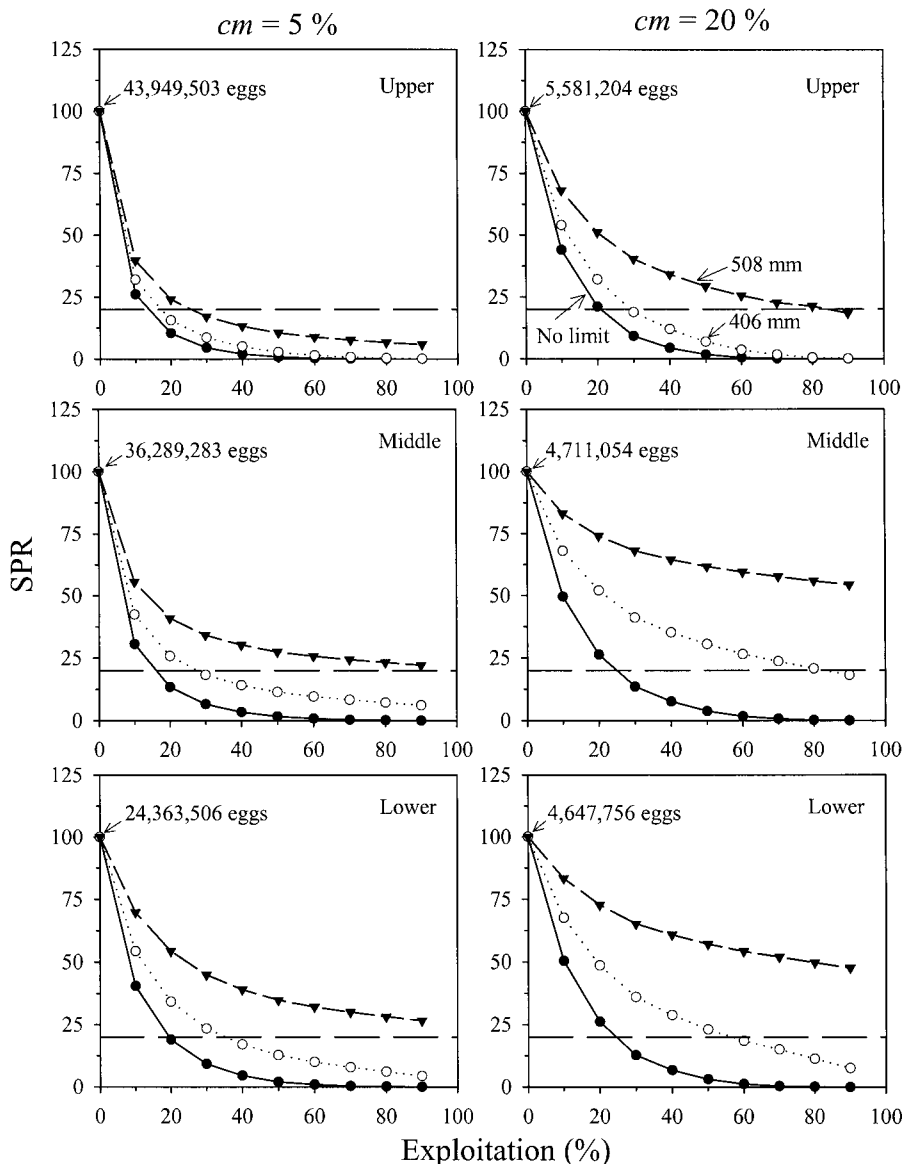


FIGURE 6.—Simulated spawning potential ratios (SPRs) for shovelnose sturgeon populations in the Missouri River with conditional natural mortality rates (cm) of 5% and 20%. The maximum lifetime egg production is also provided for each population, with the horizontal dashed line representing an 80% reduction in maximum potential lifetime egg production.

maximum potential at 30% exploitation in the upper site, 60% at the lower site, and 80–90% exploitation at the middle site. A 508-mm length limit prevented SPR from reaching 40% in the middle and lower sites at all levels of exploitation. Our simulations predicted that SPR would reach 20% only at high exploitation rates at the upper site.

The SPR appeared less sensitive to exploitation

at higher conditional natural mortality rates. However, equal SPR values do not mean that egg production was equal. Potential lifetime fecundity at the upper site was 45.9×10^6 eggs at $cm = 5\%$ and only 5.6×10^6 eggs at $cm = 20\%$ (Figure 6).

Discussion

Shovelnose sturgeon in the uppermost portion of the Missouri River exhibited faster growth,

greater longevity, and lower total annual mortality than the other populations examined in this study. These results are consistent with our current knowledge of shovelnose sturgeon populations in the Missouri, Mississippi, and Kansas rivers. Shovelnose sturgeon in the upper Missouri River are generally larger than fish from the lower portion of the river and are heavier for a given length (Quist et al. 1998). For example, Quist et al. (1998) found that relative weight ($W_r = 100 \cdot \text{weight}/\text{length-specific standard weight}$) varied on a longitudinal gradient in the Missouri River, with the highest W_r values found in the upper river. We are unaware of any previous studies that have determined total annual mortality of shovelnose sturgeon in the upper portions of the Missouri River; however, their longevity indicates that total annual mortality must be extremely low. Shovelnose sturgeon from the lower site exhibited reduced longevity and higher total annual mortality when compared with the upper and middle populations. The maximum age of shovelnose sturgeon from the southern portion of their distribution varies from 12 to 16 years (Helms 1974; Morrow et al. 1998; Quist and Guy 1999), and total annual mortality rates are around 20% (Morrow et al. 1998; M. C. Quist, unpublished information). Although shovelnose sturgeon from the middle site exhibited population characteristics (i.e., length-weight relations and maximum age) similar to the upper site, their growth was less than that of the uppermost population. It is likely that the altered flow and temperature regimes influenced the growth of fish in this population (Pegg 2000).

Most studies that have examined the growth of shovelnose sturgeon have been conducted in the Mississippi River or in the lower Missouri River systems (Helms 1974; Carlson et al. 1985; Morrow et al. 1998). We are aware of only one other study that has fit a von Bertalanffy growth equation to shovelnose growth data. Morrow et al. (1998) estimated a K of 0.213 for shovelnose sturgeon in the Mississippi River, which is quite similar to the estimates obtained in our study. These values are much higher than K estimates for other North American sturgeon species such as shortnose sturgeon (0.047–0.063; Dadswell 1979) and white sturgeon (0.020–0.040; Kohlhorst et al. 1980; Beamesderfer et al. 1995). Morrow et al. (1998) suggested that the higher K estimates for shovelnose sturgeon likely reflect differences in reproductive biology. Shortnose sturgeon and white sturgeon reach sexual maturity at 10–25 years (Dadswell 1979; Chapman 1989; Beamesderfer et al. 1995;

Boreman 1997), whereas shovelnose sturgeon generally mature at age 5 (Zweiacker 1967; Moos 1978). In our study, growth of shovelnose sturgeon was rapid up to age 5–8 and declined rapidly thereafter in all populations. Similar results have been reported across the distribution of shovelnose sturgeon (Fogle 1963; Zweiacker 1967; Christensen 1975; Morrow et al. 1998; Quist and Guy 1999). Morrow et al. (1998) suggested that shovelnose sturgeon are probably the least vulnerable of the North American sturgeons to exploitation due to their early age at maturation and comparatively fast growth. Despite the differences in population dynamics among Missouri River shovelnose sturgeon, our simulation models suggest that they are sensitive to exploitation.

In nearly all the simulations, we observed the potential for growth overfishing (Maceina et al. 1998a; Slipke and Maceina 2000). This occurs when a large portion of the population is harvested before their full growth potential is realized. This was especially evident in simulations with low conditional natural mortality ($cm = 5\%$) and without restrictive harvest regulations. When we increased conditional natural mortality ($cm = 20\%$), only the most restrictive length limit (508 mm) prevented growth overfishing.

For all populations, size structure (i.e., RSD-P) and egg production declined rapidly with increasing exploitation. Although these simulations have not been previously applied to shovelnose sturgeon populations, our results are similar to those reported for other species. For example, Maceina et al. (1998a) investigated the effects of harvest on the size structure of saugers *Stizostedion canadense* in the Tennessee River, Alabama, and found that RSD-P declined with increased exploitation. However, their model predicted that a minimum-length limit (356 mm total length) would prevent substantial reductions in the number of preferred-length saugers. We found similar results in our study where harvest regulations limited the reductions in size structure with increased exploitation.

Our simulations indicated that even low exploitation rates risk recruitment overfishing, which can be expected to substantially reduce the yield of shovelnose sturgeon and can also risk population persistence. Estimates of population egg production at various harvest rates provide an index of the potential for recruitment overfishing (Prager et al. 1987; Goodyear 1993). If we adopt a target value of $SPR = 20\%$, we would likely observe recruitment overfishing without a length limit. If

we adopt a more conservative approach with a target value of $SPR = 40\text{--}50\%$, the no-length-limit model suggests that recruitment overfishing may occur at exploitation rates of 10% or less. Only the 508-mm length limit would provide a measure of protection. Similar results were reported by Boreman (1997) who found that a fishing mortality rate (F) of 5–6% resulted in a 50% reduction in lifetime egg production of white sturgeon and Atlantic sturgeon *Acipenser oxyrinchus*.

It is important to note that our simulations predicted lower yield, size structure, and absolute egg production with increased conditional natural mortality, regardless of exploitation. Habitat modifications (e.g., impoundments) may cause adverse changes in the reproductive biology of sturgeon such as lower fecundity, growth, spawning success, and recruitment (Artyukhin et al. 1978; Votinov and Kas'yanov 1978). This further illustrates our need to better understand the effects of human-induced changes on sturgeon population dynamics and suggests that changes in natural mortality through anthropogenic activities may influence the ability of shovelnose sturgeon to withstand exploitation. Therefore, management objectives and harvest regulations may vary if shovelnose sturgeon population characteristics change.

Acknowledgments

We thank Lee Bergstedt, Chuck Berry, Doug Dieterman, David Galat, Mike Ruggles, Dennis Scarnecchia, Tim Welker, Bob White, Mark Wildhaber, Brad Young, and the rest of the Missouri River Benthic Fishes Consortium for helping in the data collection and design. We also thank the numerous field and laboratory technicians who helped sample and section fin rays. Michael Maceina provided technical assistance with FAST. Helpful comments on an earlier version of the manuscript were provided by Charles Bronte, Ronald Bruch, Carolyn Griswold, Michael Maceina, and one anonymous reviewer. Direct and indirect support was provided by the U.S. Corps of Engineers; U.S. Bureau of Reclamation; U.S. Environmental Protection Agency; U.S. Fish and Wildlife Service; U.S. Geological Survey; Kansas Department of Wildlife and Parks; Iowa Department of Natural Resources; Missouri Department of Conservation; Montana Department of Fish, Wildlife and Parks; Nebraska Game and Parks Commission; North Dakota Game and Fish Department; and South Dakota Department of Game, Fish and Parks.

References

- Allen, M. S., and L. W. Miranda. 1995. An evaluation of the value of harvest restrictions in managing crappie fisheries. *North American Journal of Fisheries Management* 15:766–772.
- Artyukhin, Y. K., A. D. Sukhoparova, and L. G. Fimukhira. 1978. The gonads of sturgeon, *Acipenser guldenstädti*, in the zone below the dam of the Volgograd water engineering system. *Journal of Ichthyology* 19:912–923.
- Bailey, R. M., and F. B. Cross. 1954. River sturgeons of the American genus *Scaphirhynchus*: characters, distribution and synonymy. *Papers of the Michigan Academy of Science, Arts and Letters* 39:169–209.
- Barnickol, P. G., and W. C. Starrett. 1951. Commercial and sport fishes of the Mississippi River between Caruthersville, Missouri, and Dubuque, Iowa. *Illinois Natural History Survey Bulletin* 25:267–350.
- Beamesderfer, R. C. P., T. A. Rien, and A. A. Nigro. 1995. Differences in the dynamics and potential production of impounded and unimpounded white sturgeon populations in the lower Columbia River. *Transactions of the American Fisheries Society* 124: 857–872.
- Birstein, V. J. 1993. Sturgeons and paddlefishes: threatened fishes in need of conservation. *Conservation Biology* 7:773–787.
- Boreman, J. 1997. Sensitivity of North American sturgeons and paddlefish to fishing mortality. *Environmental Biology of Fishes* 48:399–405.
- Braaten, P. J. 2000. Growth of fishes in the Missouri River and lower Yellowstone River and factors influencing recruitment of freshwater drum in the lower channelized Missouri River. Doctoral dissertation. Kansas State University, Manhattan.
- Brennan, J. S., and G. M. Cailliet. 1989. Comparative age-determination techniques for white sturgeon in California. *Transactions of the American Fisheries Society* 118:296–310.
- Carlander, K. D. 1954. History of fish and fishing in the upper Mississippi River. Upper Mississippi River Conservation Commission, Rock Island, Illinois.
- Carlson, D. M., W. L. Pflieger, L. Trial, and P. S. Haverland. 1985. Distribution, biology, and hybridization of *Scaphirhynchus albus* and *S. platyrhynchus* in the Missouri and Mississippi rivers. *Environmental Biology of Fishes* 14:51–59.
- Chapman, F. A. 1989. Sexual maturation and reproductive parameters of wild and domestic stocks of white sturgeon (*Acipenser transmontanus*). Doctoral dissertation. University of California, Davis.
- Christensen, L. M. 1975. The shovelnose sturgeon, *Scaphirhynchus platyrhynchus* (Rafinesque) in the Red Cedar-Chippewa River system, Wisconsin. Wisconsin Department of Natural Resources, Research Report 82, Madison.
- Coker, R. E. 1930. Studies of common fishes of the Mississippi River at Keokuk. *U.S. Bureau of Fisheries Bulletin* 45:141–225.
- Currier, J. P. 1951. The use of pectoral fin rays for determining age of sturgeon and other species of fish. *Canadian Fish Culturist* 11:10–18.

- Dadswell, M. J. 1979. Biology and population characteristics of the shortnose sturgeon, *Acipenser brevirostrum* LeSueur 1818 (Osteichthyes: Acipenseridae), in the Saint John Estuary, New Brunswick, Canada. *Canadian Journal of Zoology* 57:2186–2210.
- DeVries, D. R., and R. V. Frie. 1996. Determination of age and growth. Pages 483–512 in B. R. Murphy and D. W. Willis, editors. *Fisheries techniques*, 2nd edition. American Fisheries Society, Bethesda, Maryland.
- Everhart, W. H., A. W. Eipper, and W. D. Youngs. 1975. *Principles of fishery science*. Cornell University Press, Ithaca, New York.
- Fogle, N. E. 1963. Report of fisheries investigations during the fifth year of impoundment of Oahe Reservoir, South Dakota, 1962. South Dakota Department of Game, Fish, and Parks, Project F-1-R-12, Jobs 10, 11, and 12, Pierre.
- Goodyear, C. P. 1993. Spawning stock biomass per recruit in fisheries management: foundation and current use. *Canadian Special Publication of Fisheries and Aquatic Sciences* 120:67–81.
- Helms, D. 1974. Shovelnose sturgeon in the Mississippi River, Iowa. Iowa Conservation Commission, Iowa Fisheries Research Technical Series 74-3, Des Moines.
- Keenlyne, K. D. 1997. Life history and status of the shovelnose sturgeon, *Scaphirhynchus platyrhynchus*. *Environmental Biology of Fishes* 48:291–298.
- Keenlyne, K. D., and L. G. Jenkins. 1993. Age and sexual maturity of the pallid sturgeon. *Transactions of the American Fisheries Society* 122:393–396.
- Kohlhorst, D. W., L. W. Miller, and J. J. Orsi. 1980. Age and growth of white sturgeon collected in the Sacramento-San Joaquin Estuary, California: 1965–1970 and 1973–1976. *California Fish and Game* 66: 83–95.
- Lee, D. S., C. R. Gilbert, C. H. Hocutt, R. E. Jenkins, D. E. McAllister, and J. R. Stauffer. 1980. *Atlas of North American freshwater fishes*. North Carolina Museum of Natural History, Raleigh.
- Maceina, M. J., P. W. Bettoli, S. D. Finely, and V. J. DiCenzo. 1998a. Analysis of the sauger fishery with simulated effects of a minimum size limit in the Tennessee River of Alabama. *North American Journal of Fisheries Management* 18:66–75.
- Maceina, M. J., O. Ozen, M. S. Allen, and S. M. Smith. 1998b. Use of equilibrium yield models to evaluate length limits for crappies in Weiss Lake, Alabama. *North American Journal of Fisheries Management* 18:854–863.
- Moos, R. E. 1978. Movement and reproduction of shovelnose sturgeon, *Scaphirhynchus platyrhynchus* (Rafinesque), in the Missouri River, South Dakota. Doctoral dissertation. University of South Dakota, Vermillion.
- Morrow, J. V., Jr., J. P. Kirk, K. J. Killgore, and S. G. George. 1998. Age, growth, and mortality of shovelnose sturgeon in the lower Mississippi River. *North American Journal of Fisheries Management* 18:725–730.
- Pegg, M. A. 2000. Hydrological variation along the Missouri River and its effect on the fish community. Doctoral dissertation. Iowa State University, Ames.
- Prager, M. H., J. F. O'Brien, and S. B. Saila. 1987. Using lifetime fecundity to compare management strategies: a case history for striped bass. *North American Journal of Fisheries Management* 7:403–409.
- Quist, M. C., and C. S. Guy. 1999. Spatial variation in population characteristics of shovelnose sturgeon in the Kansas River. *Prairie Naturalist* 31:65–74.
- Quist, M. C., C. S. Guy, and P. J. Braaten. 1998. Standard weight (W_s) equation and length categories for shovelnose sturgeon. *North American Journal of Fisheries Management* 18:992–997.
- Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. *Fisheries Research Board of Canada Bulletin* 191.
- Rieman, B. E., and R. C. Beamesderfer. 1990. White sturgeon in the lower Columbia River: is the stock overexploited? *North American Journal of Fisheries Management* 10:388–396.
- Rossiter, A., D. G. L. Noakes, and F. W. H. Beamish. 1995. Validation of age estimation for the lake sturgeon. *Transactions of the American Fisheries Society* 124:777–781.
- SAS Institute. 1996. *SAS statistics user's guide*. SAS Institute, Cary, North Carolina.
- Slipke, J. W., and M. J. Maceina. 2000. *Fishery analyses and simulation tools (FAST)*. Auburn University, Department of Fisheries and Applied Aquacultures, Agricultural Experiment Station, Auburn, Alabama.
- Taylor, C. J. 1981. A generalized inland fishery simulator for management biologists. *North American Journal of Fisheries Management* 1:60–72.
- Votinov, N. P., and V. P. Kas'yanov. 1978. The ecology and reproductive efficiency of the Siberian sturgeon, *Acipenser baeri* in the Ob as affected by hydraulic engineering works. *Journal of Ichthyology* 18:20–29.
- Williams, J. E., J. E. Johnson, D. A. Hendrickson, S. Contreras-Balderas, J. D. Williams, M. Navarro-Mendoza, D. E. McAllister, and J. E. Deacon. 1989. Fishes of North America endangered, threatened, or of special concern: 1989. *Fisheries* 14(6):2–20.
- Young, B. A., T. L. Welker, M. L. Wildhaber, C. R. Berry, and D. Scarnecchia, editors. 1997. *Population structure and habitat use of benthic fishes along the Missouri and lower Yellowstone rivers*. 1997 Annual Report of the Missouri River Benthic Fish Study PD-95-5832 to the U.S. Army Corps of Engineers and the U.S. Bureau of Reclamation, Kansas City, Missouri.
- Zweifel, P. L. 1967. Aspects of the life history of the shovelnose sturgeon, *Scaphirhynchus platyrhynchus* (Rafinesque) in the Missouri River. Master's thesis. University of South Dakota, Vermillion.