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Population Characteristics and Assessment of Overfishing for an Exploited Paddlefish Population in the Lower Tennessee River

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Abstract.—Paddlefish *Polyodon spathula* (n = 576) were collected from Kentucky Lake, Kentucky–Tennessee, with experimental gill nets in 2003–2004 to assess population characteristics and the potential for commercial overfishing. Additional data were collected from 1,039 paddlefish caught by commercial gillnetters in this impoundment. Since the most recent study in 1991, size and age structure have been reduced and annual mortality has tripled. In the 1991 study, 37% of the fish collected were older than the maximum age we observed (age 11), and in 2003 annual mortality for paddlefish age 7 and older was high (A = 68%). Natural mortality is presumably low (<10%) for paddlefish; therefore, exploitation in recent years is high. Estimates of total annual mortality were negatively related to river discharge in the years preceding each estimate. The number of paddlefish harvested since 1999 was also negatively related to river discharge because gill nets cannot be easily deployed when discharge exceeds approximately 850 m^3/s. Large females spawn annually because all females longer than 1,034 mm eye−fork length (EFL) were gravid. No mature females were protected by the current 864-mm minimum EFL limit. At a low natural mortality rate, higher size limits when exploitation was high (40–70%) increased simulated flesh yields by 10–20%. Even at low levels of exploitation (21%), spawning potential ratios (SPRs) under the current 864-mm minimum EFL size limit fell below 20%. If the size limit was raised to 1,016 mm EFL, the population could withstand up to 62% exploitation before the SPR falls below 20%. An analysis of annual mortality caps indicated that the best way to increase the average size of harvested fish is to increase the minimum size limit. Recruitment overfishing probably occurs during drought years; however, variation in river discharge has prevented the population from being exploited at unsustainable rates in the past.

Paddlefish *Polyodon spathula* was once abundant in the Mississippi River drainage basin and several other tributaries of the Gulf of Mexico (Combs 1982). By the 1980s, many populations had declined as a result of dam construction, industrial pollution, and overexploitation (both legal and illegal) by commercial and recreational fishers (Carlson and Bonislawsky 1981). In 1995, under the auspices of the Mississippi Interstate Cooperative Resource Association, what was once a largely ignored resource became the focus of interstate efforts to study, conserve, and ultimately rebuild stocks of paddlefish throughout their historic range.

Tennessee is one of only six states that allow the commercial harvest of paddlefish, and over half of U.S. commercially harvested paddlefish comes from Tennessee waters (Hoffnagle and Timmons 1989; Timmons and Hughbanks 2000). On average, 80% of Tennessee's paddlefish harvest comes from Kentucky Lake on the lower Tennessee River, making it the largest paddlefish fishery in the world (R. Todd, Tennessee Wildlife Resource Agency [TWRA], personal communication). Paddlefish have been harvested from Kentucky Lake since its impoundment in 1944, but significant harvest did not occur until the early 1970s, when paddlefish roe became an acceptable substitute for caviar (i.e., sturgeon *Acipenser* spp. and European sturgeon *Huso huso*). Wholesale paddlefish roe prices in Tennessee steadily increased from less than US$77/kg in 1973 (in 2004

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dollars) to about $110/kg in 2004 (D. Blackwelder, commercial fisher, personal communication).

Until recently, there were few regulations on the harvest of paddlefish in Tennessee. In 1998, TWRA prohibited entanglement gear with bar-measure mesh less than 152 mm and required all commercial fishers who sold paddlefish to obtain a free permit (in addition to a $125 commercial fishing license) and report their catches. In addition, commercial fish markets in Tennessee were required to record the number of paddlefish and the weight of flesh and eggs they purchased from commercial fishers. Despite these regulations, a liberal minimum length limit (864 mm eye−fork length[EFL]), a long commercial fishing season (15 November to 23 April) that encompasses the paddlefish spawning migrations, and an unlimited-entry fishery make overexploitation of paddlefish a distinct possibility in Kentucky Lake.

Under certain conditions, paddlefish can be easily overfished in a commercial gill-net fishery. Paddlefish are especially vulnerable to entanglement gear when they congregate in spawning areas below dams (Pasch and Alexander 1986). High flows induce paddlefish to migrate to spawning areas (Zigler et al. 1999; Paukert and Fisher 2001b), but it is difficult for fishers targeting mature females to deploy and retrieve gill nets in high flows. Fluctuating flows (i.e., regularly alternating periods of high and low discharge) in a regulated system such as Kentucky Lake create conditions that are favorable to commercial fishing with gill nets.

Impounding large rivers such as the Tennessee River can hamper paddlefish recruitment (Purkett 1961; Russell 1986; Scarnecchia et al. 1996) and make it difficult for populations to recover after periods of heavy exploitation. The creation of reservoirs inundates habitat required by paddlefish for spawning and egg incubation (Hoxmeier and DeVries 1996), although adults can thrive in lentic environments (Russell 1986). Regulated river discharges often fail to mimic natural flow regimes that provide important cues for paddlefish spawning (Unkenholz 1986). Even if flows are sufficient for spawning, dams may obstruct paddlefish migration and force them to spawn in inferior habitats (Southall and Hubert 1984; Unkenholz 1986; Runstrom et al. 2001).

Late maturation also contributes to the effects of dams on the recovery of a population after a period of heavy exploitation. Female paddlefish often do not become sexually mature until age 7 or later (Hoyt 1984; Reed et al. 1992). In Kentucky Lake, some age-6 males and age-8 females were sexually mature, but 100% maturity of a year-class was not achieved until age 12 for males and age 16 for females (Timmons and Hughbanks 2000). Paddlefish grow relatively fast, so they often recruit into a fishery before they are sexually mature. In 1991, the average age at recruitment in Kentucky Lake was 9.7 years (males) and 11.1 years (females), and many fish were not sexually mature (Timmons and Hughbanks 2000). Early recruitment to the fishery and late maturation make paddlefish especially susceptible to recruitment overfishing (Pasch and Alexander 1986).

The reported harvest of paddlefish in Kentucky Lake dropped 66% between 2000 and 2003 (R. Todd, personal communication) despite the fact that roe prices received by fishers remained fairly stable over the same period (D. Blackwelder, personal communication). The steep decline in catch suggested that the Kentucky Lake stock was being overfished, particularly when fishing effort and demand for flesh and roe were presumably high. Previous studies on Kentucky Lake reported classic signs of overexploitation, such as high mortality, a comparatively young population, and few large females (Bronte and Johnson 1985; Hoffnagle and Timmons 1989). The Division of Scientific Authority of the U.S. Fish and Wildlife Service (USFWS), which regulates paddlefish roe exports, voiced concerns in 2002 that paddlefish in Kentucky Lake were being overfished. Therefore, the objectives of this study were to (1) estimate the size and age structure of the paddlefish population in Kentucky Lake; (2) investigate reasons for recent harvest declines; and (3) assess the likelihood that the paddlefish population in Kentucky Lake was suffering from growth or recruitment overfishing.

Study Area

Kentucky Lake is a mainstream impoundment of the Tennessee River located in western Tennessee and Kentucky (Figure 1). Impounded in 1944 by Kentucky Dam at river kilometer (rkm) 35 (measuring from its confluence with the Ohio River), this 296-km-long reservoir is a eutrophic impoundment that covers 64,870 ha at full pool and has a mean depth of 5.4 m. Water levels usually fluctuate about 1.5 m between winter and summer pools. Water discharged from Pickwick Dam, the upstream boundary at rkm 331, flows north through Kentucky Lake. Kentucky and Pickwick dams have navigation locks, power generators, and floodgates that are controlled by the Tennessee

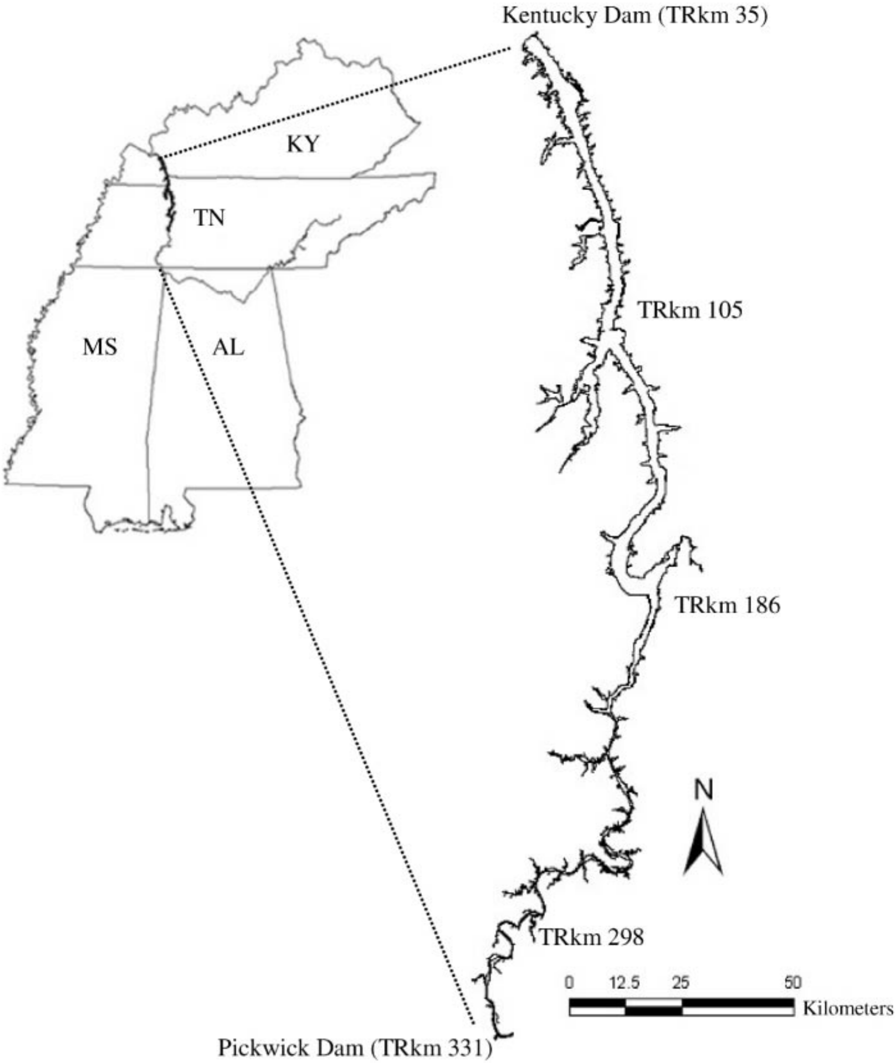

FIGURE 1.—Map of Kentucky Lake, a mainstream impoundment on the lower Tennessee River, where population characteristics and the potential for commercial overfishing were assessed for an exploited paddlefish population in 2003–2004. The numerical values are river kilometers along the Tennessee River.

Valley Authority. Kentucky Lake is riverine upstream of (south half) and lacustrine downstream of (north half) rkm 186. All riverine habitat and the upper half of lacustrine habitat lie within Tennessee; the remainder of lacustrine habitat and Kentucky Dam are located in Kentucky.

Methods

Data collection.—Paddlefish were collected in the riverine and lacustrine regions of Kentucky Lake between rkm 105 and rkm 298 before (5 September to 2 November 2003) and after (20 April to 3 May 2004) Tennessee's commercial fishing season. A cooperative interaction with experienced commercial fishers gave us access to ''traditional ecological knowledge'' (Price and Rulifson 2004) and allowed us to collect paddlefish in a range of habitat types, flow regimes, and seasons. Horizontal, experimental monofilament gill nets (3.6 × 128 m, tied down to 2.4 m; and 9.1 × 91 m, tied down to 7.6 m) with six panels of 89-, 102-, 127-, 152-, 178-, and 203-mm-bar measure mesh were fished overnight. During the 2002–2003 and 2003–2004 commercial fishing seasons, commercial fishers were occasionally accompanied and their catch was observed to collect additional data for certain analyses (e.g., creating an age–length key). Although individual gill nets varied in length (55.0–114.0 m) and depth (6.1–9.1 m), most Kentucky Lake paddlefish fishers used horizontal multifilament gill nets with 152-mm-bar measure mesh.

Weight (nearest 0.25 kg), EFL (mm), sex, and maturity were recorded for each paddlefish. Sex and maturity were determined by examining gonads. Immature males had long, wavy, tubular gonads that were slightly gray; females had pinkish, lamellar gonads that were highly convoluted (Russell 1986). Females with partially developed or immature ova (usually white or mottled) were also categorized as immature. Fish were classified as mature if testes were large and swollen or ovaries contained large (2–3 mm diameter) dark eggs (Bronte and Johnson 1985).

Ovaries were excised from all females and weighed (nearest 0.1 g). A subsample of eggs was collected from at least six locations that spanned the length and depth of each mature ovary. Each subsample was weighed and preserved with a 5% unbuffered formalin solution (Markle 1984). Twenty-five randomly selected eggs from the pooled subsample of each ovary were measured (maximum diameter, nearest 0.01 mm). The eggs in each subsample were weighed (nearest 0.001 g), counted, and fecundity was estimated through extrapolation (Reed et al. 1992). Relative fecundity was determined by calculating the number of eggs per kilogram of body weight (Hoxmeier and DeVries 1997).

Dentary bones of at least 5 male and 5 female paddlefish per 25-mm EFL group were removed for age estimation. Dentary bones were submersed in a 10:90 solution of all® laundry detergent and water and heated to 43°C for 14 h to loosen flesh adhering to the bones. After cleaning, the dentary bones were soaked in a 50:50 solution of ammonia and water for 5 h and then a 50:50 solution of ethanol and water for 24 h (R. Todd, personal communication). After drying, five sections (~0.5 mm thick) were obtained from the left dentary bone 10 mm posterior to the mesial bend with a Buehler Isomet low-speed saw (Buehler Ltd., Lake Bluff, Illinois; Scarnecchia et al. 1996; Lein and DeVries 1998). The senior author estimated age for each set of sections in two independent readings. Annuli were counted (Adams 1942) without knowledge of fish size or sex with a microprojector at 40× magnification. When discrepancies occurred between the first and second readings, those sections were read a third time. Two of the three readings always agreed; therefore, the modal age was assigned (Hoxmeier and DeVries 1997). Ages were then assigned to unaged fish with an age–length key.

Data analysis.—Length-frequency (25-mm groups) and age-frequency histograms were constructed to visually assess size and age structure of the population. Size and age structure were estimated from the paddlefish catch in experimental gill nets before spawning migrations began. Spatial and temporal differences between ratios of males to females and immature fish to mature fish were tested with the chi-square statistic. Mean ages were compared between sexes with *t*-tests.

The annual paddlefish harvest from Kentucky Lake in 1999–2003 (data from TWRA annual harvest reports) was regressed against the number of fishable days each season using linear regression. Typically, commercial fishers will not deploy their nets in Kentucky Lake when discharge from Pickwick Dam exceeds about 850 m^3/s because nets will encounter too much debris and not fish properly (D. Blackwelder, personal communication); therefore, a fishable day was assumed to be any day during the commercial paddlefish season with a mean discharge from Pickwick Dam of 850 m^3/s or less.

The natural logarithm of catch from each age-class in the preseason sample was plotted against age to construct a catch curve. The age at full recruitment was considered the age at which the catch curve began to descend. Instantaneous total annual mortality (Z) was derived from the slope of the descending limb of the catch curve and transformed into an interval annual mortality rate ($A = 1—e^{-Z}$). Bronte and Johnson (1985), Hoffnagle and Timmons (1989), and Timmons and Hughbanks (2000) estimated annual mortality from ages that were fully recruited (>age 6) into the fishery in their 1980, 1985, and 1991 studies, respectively. Their estimates and the annual mortality estimate from this study were regressed against total discharge from Pickwick Dam each fishing season for the years preceding each study. We assumed that natural mortality would remain constant; thus, variation in total mortality would reflect different levels of exploitation.

The yield-per-recruit option in Fisheries Analyses and Simulation Tools (FAST) software (developed by researchers at Auburn University and available at www.fisheries.org/cus/) was used to determine whether growth overfishing was occurring. This option uses the Jones (1957) modification of the Beverton–Holt equilibrium yield equation to calculate yield (Ricker 1975). Yields (kilograms of flesh per 1,000 recruits) were simulated for the current size limit (864 mm EFL) and two size limits (965 and 1,016 mm EFL) that would protect approximately 33% and 50% of the mature females sampled in this study, respectively. This simulation used the *y*-intercept and slope from the $\log_{10}$(EFL)–$\log_{10}$(weight) regression model, von Bertalanffy growth parameters (L_{inf}, K, and t_0), and hypothetical fishing and natural mortality rates. Data on the largest (1,220 mm) and oldest (age 21) paddlefish collected by Timmons and Hughbanks (2000) in their 1991 study on Kentucky Lake were included in the von Bertalanffy growth model. In the unfished South Cross Creek subimpoundment on the Cumberland River, Tennessee, natural mortality of paddlefish was less than 9% (Boone and Timmons 1995), and Timmons and Hughbanks (2000) suggested that natural mortality was low (8%) for paddlefish in Kentucky Lake. Therefore, yield was simulated with a conditional natural mortality rate of 8%. Conditional fishing mortality rates from 10% to 70% were used to simulate yield over a wide range of exploitation levels.

A maturation schedule for females was formulated by determining the percentage of mature fish in each size- (25-mm EFL groups) and age-class. Female paddlefish maturity was indexed with the gonadosomatic index (GSI; Irwin and Bettoli 1995):

$$\text{OW} \times 100/(\text{WT} - \text{OW}),$$

where OW is ovary weight and WT is body weight. Relations among GSI, ovary weight, mean egg diameter, fecundity, and the EFL and weight of paddlefish were described with linear regression models. With age- and length-specific fecundity data and a maturation schedule, the spawning potential ratio (SPR; Goodyear 1993) was simulated as

$$\text{SPR} = P_{\text{EXPLOITED}}/P_{\text{UNEXPLOITED}},$$

where P (potential recruit fecundity) represents the lifetime production of eggs by the average recruit in an exploited and unexploited population.

Miranda (2002) defined mortality caps as thresholds of mortality above which management objectives can no longer be met. Mortality caps can be used to identify which length objectives are practical and to forewarn managers when mortality is too high. Annual mortality caps were estimated for the current minimum EFL limit (864 mm) and the two potential minimum EFL limits discussed above (965 mm and 1,016 mm) with parameters (K and L_{inf}) from the von Bertalanffy growth model and Miranda's (2002) equation, as follows:

$$Z = K \times [(L_{\text{inf}} - L_{\text{mean}}) \times (L_{\text{mean}} - L_x)^{-1}],$$

where L_{mean} represents the desired mean EFL of harvested fish (i.e., management objective) and L_x is the minimum EFL at which fish are vulnerable to harvest (minimum EFL limit). Length objectives (L_{mean}) have not been set for Kentucky Lake paddlefish; therefore, Z was estimated over a range of L_{mean} (L_x to L_{inf}) for each EFL limit and subsequently transformed into A.

Programs written for the Statistical Analysis System (SAS Institute 2001) were used for all statistical analyses. All tests were considered significant at $\alpha \leq 0.05$.

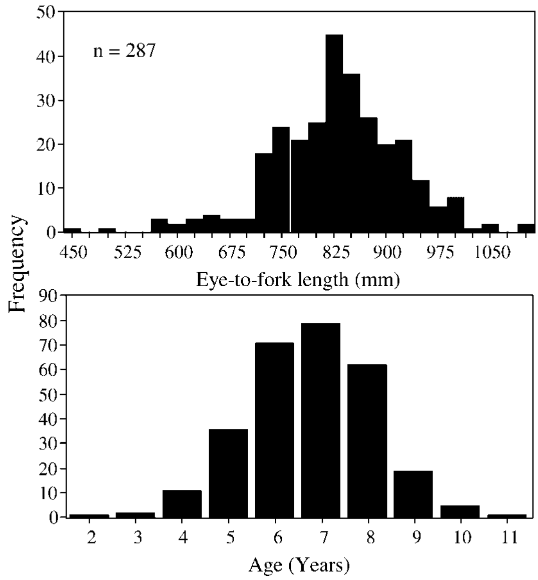

FIGURE 2.—Length-frequency (top; 25-mm intervals) and age-frequency (bottom) distribution of paddlefish collected with experimental gill nets from Kentucky Lake during the fall of 2003.

Results

Although 576 paddlefish were collected with experimental gill nets, our length-frequency and age-frequency histograms (Figure 2) represent only paddlefish collected in the preseason sample (n = 287) because we observed distinct spatial and temporal differences in the distribution of paddlefish throughout Kentucky Lake. Specifically, the ratios of mature to immature and males to females varied spatially in the postseason sample. Before the commercial fishing season began (September–October 2003), the percentages of males that were mature

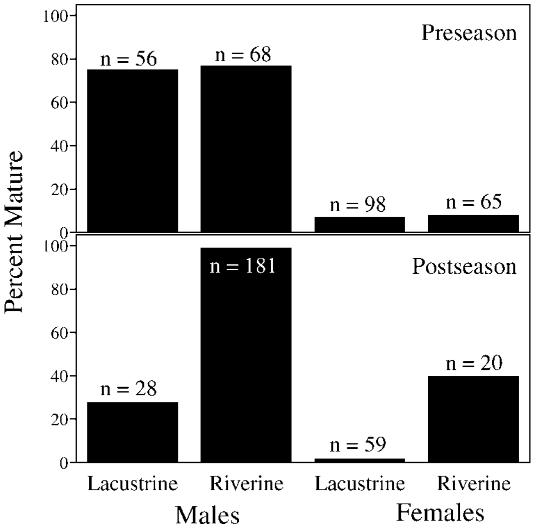

FIGURE 3.—Percentage of paddlefish of each sex that were mature in two regions of Kentucky Lake before and after the 2003 commercial paddlefish fishing season.

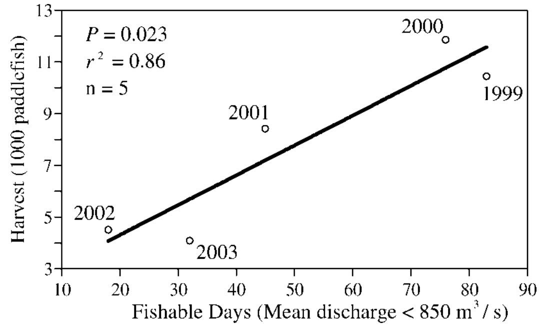

FIGURE 4.—Number of days when mean discharge from Pickwick Dam was less than 850 m^3/s (fishable days) versus total paddlefish harvest from Kentucky Lake, during five commercial paddlefish fishing seasons.

(76% lacustrine, 78% riverine) did not vary ($\chi^2 = 0.04$; df = 1; $P = 0.849$) between the two reaches of Kentucky Lake (Figure 3). Similarly, the percentages of females that were mature were almost identical (7% lacustrine, 8% riverine; $\chi^2 = 0.02$; df = 1; $P = 0.895$) in both reaches of the reservoir before the season began. In contrast, the same percentages differed ($\chi^2 \geq 21.7$; df = 1; $P < 0.001$) after the season ended in April–May 2004. Sex ratios in the riverine (1.05 males:1 females) and lacustrine (0.57 males:1 females) reaches differed ($\chi^2 = 6.3$; df = 1; $P = 0.012$) before the season began; it was assumed that the pooled sex ratio (i.e., both reservoir regions; 0.76 males : 1 females) accurately reflected the sex ratio of this population. After the season ended, the difference in sex ratios in the riverine (9.05 males : 1 females) and lacustrine (0.49 males : 1 females) reaches was more pronounced ($\chi^2 = 100.5$; df = 1; $P < 0.001$). Few mature males and almost no mature females remained downstream in the lacustrine reach of Kentucky Lake at the end of the spring spawning season.

The 66% decrease in paddlefish harvest between 2000 and 2003 was probably more a function of variable discharge from Pickwick Dam than stock collapse. During the past 30 years, the amount of water discharged through Pickwick Dam each commercial paddlefish fishing season has varied more than fourfold. There was a strong positive relation between the number of fishable days in each commercial fishing season and the number of paddlefish harvested from Kentucky Lake ($n = 5$; $P < 0.023$; $r^2 = 0.86$; Figure 4). Those 5 years (1999–2003) encompassed drought years as well as years of average and slightly above-average discharges.

The age structure of Kentucky Lake's paddlefish stock reflected a young population. The 661 paddlefish that were aged ranged from 398 to 1,238 mm EFL and represented ages 2–11. Repeatability (i.e., assigning the same age for each of the two readings) was 66%. Most (96%) discrepancies between readings did not exceed 1 year, and discrepancies never exceeded 3 years. Females (mean age = 7.2 years, range = 3–11 years) were significantly older on average ($t = 6.03$, df = 283, $P < 0.001$) than males (mean age = 6.3 years, range = 2–9 years). Age 7 was considered the age at full recruitment based on the catch curve.

Paddlefish in Kentucky Lake experienced high mortality. Instantaneous annual mortality (Z) was 1.126, which equates to an interval annual mortality rate (A) of 68%. There was essentially no deviation ($r^2 = 0.95$) of points about the catch curve. Annual mortality estimates (from this study and studies in 1980, 1985, and 1991) and mean discharges from Pickwick Dam during the previous 1, 2, 3, 4, and 5 seasons were negatively correlated ($r^2 = 0.58$–0.96), and mean discharges during the previous two and three seasons were significant ($P < 0.05$) predictors of annual mortality.

The relationship between EFL (398–1,238 mm) and weight (750–29,250 g) was best described by the equation

$$\log_{10}(\text{weight}) = -5.711 + 3.307 \log_{10}(\text{EFL})$$

$$(n = 978, P < 0.001, \text{ and } r^2 = 0.87).$$

TABLE 1.—Maturity, mean eye–fork length (EFL; mm), and mean weight (kg) by age-class and sex for paddlefish collected with experimental gill nets from Kentucky Lake, 2003–2004.

	Males				Females				All fish	
Age	No.	% Mature	Mean EFL	Mean weight	No.	% Mature	Mean EFL	Mean weight	Mean EFL	Mean weight
3	1	0	632	4.5	3	0	542	2.3	565	2.9
4	7	43	701	6.4	7	0	646	4.4	667	5.3
5	48	77	804	8.1	11	0	705	5.5	786	7.6
6	79	84	813	8.0	50	0	812	9.2	813	8.4
7	119	92	837	8.6	54	0	864	11.4	846	9.5
8	33	97	889	10.4	77	5	926	14.5	915	13.3
9	39	82	866	9.7	27	26	977	17.0	912	12.7
10	4	50	883	10.8	11	82	980	16.5	954	14.9
11	0				2	50	1,065	23.4	1,065	23.4

The von Bertalanffy model closely fit observed mean lengths at age and was best described by the equation

$$\mathrm{EFL}_t = 1{,}279 \cdot [1 - e^{-0.131(t-1.527)}],$$

where t is age. The model predicted that paddlefish took 7.1years to reach legal size (i.e., 864 mm EFL), 8.0 years to reach 914 mm EFL, 9.2 years to reach 965 mm EFL, and 10.6 years to reach 1,016 mm EFL.

Mature females represented a small fraction of the population. Four percent of the paddlefish collected before the 2003–2004 season began and 8% of the paddlefish caught by commercial fishers during the 2002–2003 and 2003–2004 seasons were mature females. Males began to mature earlier (age 4; 452 mm EFL; 6.0 kg) than females (age 8; 885 mm EFL; 10.0 kg). There was no age-class of either sex in which all of the individuals were mature, but at least 50% of the age-5 males and age-10 females were mature (Table 1). One age-11 female was not mature; however, all females (n = 21) equal to or longer than 1,034 mm EFL were mature. As EFL increased from 885 mm to 1,034 mm, the proportion of mature females in each 25-mm group increased; that is, 29% of females between 926 mm and 950 mm were mature and 61% of females between 1,001 mm and 1,025 mm were mature.

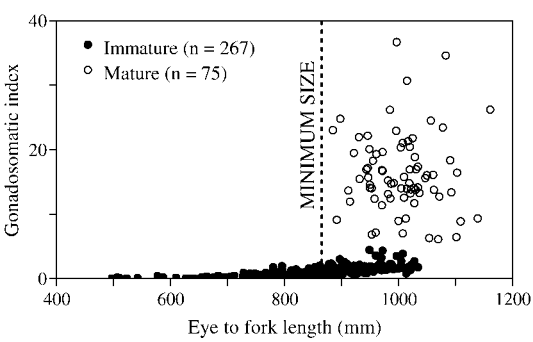

FIGURE 5.—Gonadosomatic index values versus eye−fork lengths (EFLs) for immature and mature female paddlefish collected immediately before and during the 2002–2003 and 2003–2004 commercial paddlefish fishing seasons (15 November to 23 April) in Kentucky Lake. The dashed line represents the current EFL minimum of 864 mm.

No mature females collected during this study were protected by the current minimum size limit (864 mm EFL; Figure 5). Female GSI values were positively correlated to EFL (r^2 = 0.54; P < 0.0001). Minimum EFL limits of 914 mm, 965 mm, and 1,016 mm would have protected 7, 29, and 58% of the mature females from harvest, respectively. The GSI values for mature females ranged from 6.1% to 36.7% and there was little adipose tissue associated with mature ovaries. GSI values for immature females ranged from 0.1% to 4.4%, but gonads were usually attached to large, fat bodies that represented as much as 12% of somatic body weight.

Fecundity was estimated for 75 mature females (885–1,161 mm EFL; 10.5–29.0 kg) and the fecundity of similar-sized paddlefish was highly variable. The number of eggs per female ranged from 109,048–504,112 (mean = 279,256; SE = 9,590) and relative fecundities ranged from 9,281–26,374 eggs/kg body weight (mean = 16,381; SE = 417). The relationship between fecundity and body size was best described by the equation

$$\log_{10}(\text{fecundity}) = 4.282 + 0.937 \log_{10}(\text{weight})$$

$$(P < 0.0001 \text{ and } r^2 = 0.48), \quad \text{and}$$

$$\log_{10}(\text{fecundity}) = -4.284 + 3.236 \log_{10}(\text{EFL})$$

$$(P < 0.0001 \text{ and } r^2 = 0.38).$$

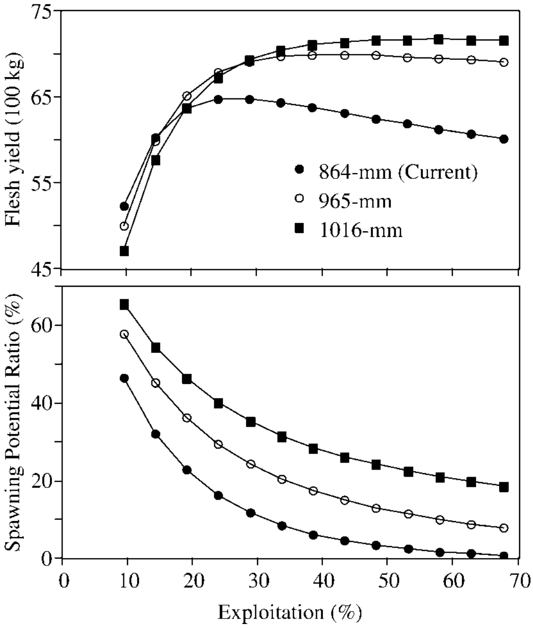

FIGURE 6.—Predicted paddlefish flesh yield (per 1,000 recruits; top) and spawning potential ratio (bottom) versus exploitation for three different minimum length limits in Kentucky Lake in 2003–2004.

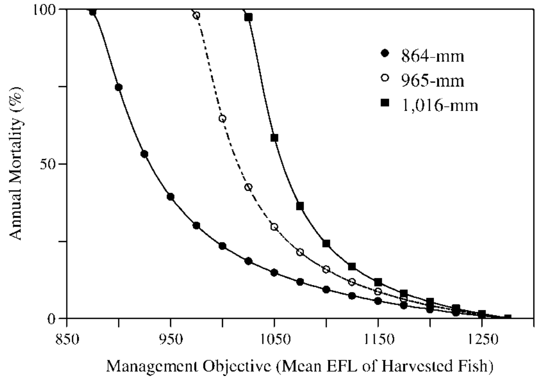

FIGURE 7.—Annual mortality caps versus target mean eye–fork length (EFL) of harvested paddlefish for three minimum EFL limits in Kentucky Lake.

Total ovary weights ranged from 0.957 to 4.884 kg (mean = 2.310 kg; SE = 0.093 kg). Log_{10} EFL and weight were significant ($P < 0.005$) predictors of ovary weight, but each variable explained little of the variation ($r^2 = 0.21$ and 0.10, respectively). Egg diameters ranged from 1.3 to 3.2 mm (mean = 2.33 mm; SE = 0.01 mm) and mean egg diameter for individual fish ranged from 1.6 to 2.7 mm (mean = 2.33 mm; SE = 0.03 mm). There was a weak positive relationship between mean egg diameter and body weight ($P < 0.01$; $r^2 = 0.15$), but not EFL ($P = 0.34$; $r^2 = 0.01$).

Simulation modeling suggested modest growth overfishing under the current 864-mm minimum EFL limit. When exploitation was high (40–70%), increasing the minimum EFL limit from 864 mm to either 965 mm or 1,016 mm increased simulated flesh yields by 10–15% and 12–20%, respectively (Figure 6); however, these size limits did not increase flesh yields at low (<20%) levels of exploitation.

Simulated SPRs were very low for Kentucky Lake's paddlefish stock. Under the current 864-mm minimum EFL limit, SPR values ranged between 1% and 46% when exploitation rates ranged from 10% to 70% (Figure 6). Increasing the minimum size limit to 965 mm or 1,016 mm increased the SPR to 7–57% and 18–65%, respectively. Under the 864-mm minimum EFL limit, SPR values fell below 20% when exploitation rates exceeded 21%. If the size limit was raised to 965 mm, this population could theoretically withstand exploitation rates as high as 35% before the SPR value fell below 20%. A 1,016-mm size limit allowed the simulated population to withstand exploitation rates as high as 62% before the SPR fell below 20%.

Total annual mortality would have to be extremely low ($A \leq 17\%$) under the current size limit if our objective was to increase the mean length of harvested fish (919 mm in 2003) to the length at which all females are mature (i.e., 1,034 mm EFL and longer; Figure 7). If the minimum size limit was increased from 864 mm to 965 mm or 1,016 mm, annual mortality caps could be much higher (37% and 83%, respectively) and still allow that same target size to be achieved. If the target size was more conservative (e.g., the length at which approximately 50% of females are mature; 965 mm EFL), exploitation and total mortality would still need to be low ($A \leq 33\%$) to achieve that target if the population was managed with the current size limit.

Discussion

Our results suggest that growth and recruitment overfishing probably occur during seasons when discharge is low, but the population is afforded temporary relief from overfishing during high-water years. Though not directly comparable, a similar negative relationship between catch and discharge was observed in the recreational tailwater trout (i.e., *Oncorhynchus* spp. and *Salmo* spp.) fishery below Bull Shoals Reservoir, Arkansas (Aggus et al. 1979), because high discharges reduced angling effort. Although weather and subsequent discharge could be affecting paddlefish movements in Kentucky Lake, we believe the relationship between harvest and discharge is the result of reduced effort when fishing conditions were unfavorable (i.e., river discharges were high). Similarly, river stage influenced the commercial catch of several species in the Amazon River, Peru, by altering the accessibility of certain waters (De Jesús and Kohler 2004).

The relationship between paddlefish harvest and discharge from Pickwick Dam indicates that the reason for the recent decline in paddlefish harvest was probably related to effort, not abundance. This relationship also resolves, in part, a question that had been posed by TWRA biologists for many years: Why was the estimated exploitation rate for paddlefish in 1991 so low (14%; Timmons and Hughbanks 2000), yet most investigators (Bronte and Johnson 1985; Hoffnagle and Timmons 1989) had concluded that the same population was being overfished? Pickwick Dam discharges were higher during the 1991 fishing season than they were when the other studies were conducted (1980, 1985, and 2003). We predict that fishing effort and harvest were low in 1991 compared with what the fishery experiences during drier seasons.

Maximum weight and age in this study were lower than those observed in 1991, suggesting that heavy exploitation in recent years has led to reduced size and age structure of the Kentucky Lake paddlefish stock. Reduced size and age structures observed in our study have also been observed in commercially exploited paddlefish stocks elsewhere (Hoyt 1984; Alexander et al. 1987). Previous studies on Kentucky Lake suggest that the paddlefish stock was also heavily exploited in the early 1980s. Maximum size and age in 1980 (age 14, 1,020 mm EFL, 22.7 kg; Bronte and Johnson 1985) and 1985 (age 16, 1,060 mm EFL, 18.2 kg; Hoffnagle and Timmons 1989) were similar to what was observed in this study, but Timmons and Hughbanks (2000) collected fish as large as 1,220 mm (34.0 kg) and as old as age 21 in 1991. Similarly, 37% of the fish collected in 1991, but less than 5% in 1980 and 1985, were older than maximum age in our study. The reduced size and age structure in the early 1980s was probably a result of low flows and subsequent high harvests before those studies were conducted. In contrast, flows before Timmons and Hughbanks's (2000) study in 1991 were relatively high, which probably made it difficult for fishers to deploy and retrieve nets. High flows in the late 1980s probably allowed the stock to recover from a period of high exploitation; conversely, favorable netting conditions in recent years probably resulted in another period of heavy exploitation preceding our study.

Maximum ages of other southern paddlefish stocks were comparable (≤age 14) to the maximum age that we observed in Kentucky Lake (Reed et al. 1992; Lein and DeVries 1998; Paukert and Fisher 2001a). However, maximum ages of 25–30 years are common in lightly exploited paddlefish fisheries in northern latitudes (Purkett 1963; Robinson 1966; Rosen et al. 1982; Elser 1986), and the oldest paddlefish on record, collected from the Yellowstone River, Montana, in 1985, was estimated to be age 55 (Scarnecchia et al. 1996).

Males matured as early as age 6 and females as early as age 8 in this study, which was similar to the results of previous studies on Kentucky Lake (Bronte and Johnson 1985; Hoffnagle and Timmons 1989; Timmons and Hughbanks 2000). Age at first maturity is similar in most systems (Adams 1942; Hoyt 1984; Reed et al. 1992); however, Gengerke (1978) observed mature males and females in the upper Mississippi River as young as ages 4 and 6, respectively.

This study found evidence that contradicts the premise of others (e.g., Meyer 1960; Hoyt 1984; Russell 1986) that mature female paddlefish require more than 1 year to become gravid. Although no age-class was represented solely by mature fish, all females longer than 1,034 mm EFL were mature. Length at first maturity (885–1,034 mm EFL) varied for female paddlefish, but once they were mature they probably became gravid each year. If mature females did not spawn annually, ungravid females longer than 1,034 mm EFL should have been collected; their absence suggests that females became gravid as a function of EFL more so than age. Similarly, other researchers have observed gravid paddlefish in consecutive years in aquaculture ponds (S. Mims, Kentucky State University, personal communication).

The relative abundance of mature females in the population in 1980, 1985, and 1991 was probably lower than what was reported. Previous researchers reported that mature females made up 4% of the catch in 1980 (Bronte and Johnson 1985), 7% in 1985 (Hoffnagle and Timmons 1989), and 13% in 1991 (Timmons and Hughbanks 2000). These studies were based on paddlefish collected from the riverine reach of Kentucky Lake during the spawning run. In our study, the relative abundance of mature females in the gill-net samples was higher in the riverine reach during the spawning period (8%) than it was before the season began (4%).

The relative fecundity of the 75 mature paddlefish that we observed was within the broad range reported by others. On a per-kilogram basis, Kentucky Lake paddlefish were 73% more fecund than paddlefish in Louisiana (Reed et al. 1992), close to 18% less fecund than paddlefish in the Alabama River drainage (Hoxmeier and DeVries 1997; Lein and DeVries 1998), and had nearly identical fecundities to fish in the upper Mississippi River (Gengerke 1978).

Examination of age and size structure data indicated that mortality rates were high after paddlefish were fully recruited to the fishery. Total annual mortality in this study (68%) was nearly identical to that reported in 1985 (69%; Hoffnagle and Timmons 1989), but higher than 1980 and 1991 estimates (44% in 1980, Bronte and Johnson 1985; 22% in 1991, Timmons and Hughbanks 2000). Annual mortality estimates reflect the additive effects of exploitation because natural mortality is usually less than 10% for paddlefish (Timmons and Hughbanks 2000). The inverse relation between annual mortality estimates and mean discharge during the three seasons preceding each study suggests that exploitation (and total mortality) is highly variable and influenced by the amount of water discharged from Pickwick Dam.

Simulated flesh yields for Kentucky Lake's paddlefish stock suggested that modest growth overfishing was occurring because increasing the minimum size limit increased flesh yields over a wide range of exploitation rates above 20%. We believe that exploitation in recent years was much higher than 20%, despite the fact that Timmons and Hughbanks (2000) estimated exploitation in 1991 (not corrected for tag loss, nonreporting, or mortality associated with tagging) at only 14%. In that study, flows were average or above average the 3 years preceding their sampling, and fishing pressure was presumed to be low. If natural mortality is less than 10%, recent exploitation rates probably exceeded 50% given the high annual mortality rate we observed.

None of the mature females we collected were protected by the current minimum size limit. Recruitment overfishing is a distinct possibility in Kentucky Lake because females reached legal size (864 mm EFL) at an average age of 7.1 years, which is younger than the age at first maturity (age 8). Increasing the minimum length limit would delay the average age at recruitment by 2.1 years under a 965-mm EFL limit and by 3.5 years under a 1,016-mm EFL limit. Delaying the age at recruitment would allow some mature females to spawn at least once before becoming vulnerable to harvest, which is probably desirable because the number of spawning females might limit subsequent paddlefish abundance (Scarnecchia et al. 1989).

Paddlefish may reach legal size in Kentucky Lake before they mature, but it is improbable that immature fish will be caught if they do not leave the lacustrine reaches of the reservoir, where we observed little commercial fishing activity. Immature females represented less than 5% of all paddlefish we observed in the riverine section of the reservoir during the 2002–2003 and 2003–2004 commercial seasons. Purkett (1961), Hageman et al. (1988), and Lein and DeVries (1998) also reported low relative abundance of immature fish in spawning areas. In the lower Alabama River, immature paddlefish from channel and backwater habitats accompanied spawning fish during spring migrations, but immature fish in oxbow habitats did not (Hoxmeier and DeVries 1997). This study and previous studies on Kentucky Lake were not designed to compare the relative abundances of mature and immature fish by reservoir reach; therefore, further monitoring of the commercial catch is necessary to confirm that most immature females do not migrate upriver. If the management objective is to reduce fishing mortality of immature females, gill netting could be banned in the lacustrine portions of the reservoir if immature females normally do not migrate upriver. If immature females occasionally migrate upriver with spawning fish, it would be necessary to increase the minimum EFL limit to protect them and reduce the likelihood of recruitment overfishing.

Goodyear (1993) suggested that SPRs should be maintained above 20–30% to prevent recruitment overfishing in most fish populations. Although minimum SPRs necessary to prevent overfishing for nest-building species are probably lower, 20–30% is probably a reasonable minimum SPR for a species that leaves its eggs unattended (Slipke et al. 2002). According to the SPR model, recruitment overfishing in Kentucky Lake's paddlefish population is occurring when exploitation exceeds 20%. Coincidentally, previous studies have suggested exploitation higher than 15–20% should be considered excessive for paddlefish stocks (Combs 1982; Pasch and Alexander 1986). Exploitation in Kentucky Lake probably exceeds 20% most seasons and may have been as high as 50–60% in the years immediately preceding our study. Although minimum SPRs for paddlefish and other freshwater species are not well defined and are still being investigated (Slipke and Maceina 2001), an exploitation rate of 50% corresponds with a SPR value of only 3% under the current minimum EFL limit.

Spawning potential ratios less than 10% have been associated with stock declines in heavily fished populations. The collapse of the striped bass *Morone saxatilis* fishery in the Chesapeake Bay in the late 1980s was associated with predicted SPR values of less than 10% (Slipke and Maceina 2001). Slipke et al. (2002) reported that declining yields and catch of channel catfish *Ictalurus punctatus* in the upper Mississippi River were associated with predicted SPR values of 3–12%. In both situations, populations recovered after minimum length limits were increased. Manooch et al. (1998) suggested SPRs would increase in a red snapper *Lutjanus campechanus* fishery if fishers would comply with minimum size regulations enacted to delay the age at entry into the fishery. Increasing the minimum EFL limits for paddlefish in Kentucky Lake to 965 mm or higher would allow the population to experience high exploitation with little risk to the fishery.

The approach we used to estimate mortality caps should be valid because important assumptions appear to have been met. Two important assumptions (mortality is constant over time and recruitment is constant or varies randomly) were met because there was very little discrepancy between observed and predicted catches at age in the catch curve, suggesting consistent mortality and recruitment (Maceina 1997). The growth curve fit the data on observed lengths at age reasonably well; therefore, we have no reason to believe that another assumption (growth is constant and adequately described by the von Bertalanffy model) was violated. Two other important assumptions (only lengths fully recruited into the gear are monitored and the sampling gear adequately represents age and size structure of the population) require that the fishing gear adequately sampled the population. Pasch et al. (1980) and Paukert and Fisher (1999) concluded that experimental gill nets with mesh sizes ranging from 102 to 152 mm would adequately sample all paddlefish larger than 400 mm EFL, and we used those and other mesh sizes to capture paddlefish.

Merely reducing mortality of fish vulnerable to the gear cannot increase the mean size of harvested paddlefish. For example, the 17% mortality cap necessary to meet a 1,034-mm mean EFL objective would allow very little exploitation if this commercial fishery operated under the current minimum EFL limit. A more feasible approach to increase the EFL of harvested fish would be to increase the minimum EFL limits. Similarly, Quist et al. (2004) noted that a 500-mm mean length objective was unrealistic for walleye *Sander vitreus* in Kansas reservoirs unless the minimum length limit was increased from 381 mm to 457 mm total length. The mortality cap analysis provided additional support for potential regulation changes suggested by our yield and SPR simulations; however, the benefits of increasing the minimum size limit will not be realized if bycatch mortality of sublegal fish is high.

Bycatch mortality in the Kentucky Lake fishery may be high at certain times of the year. Nearly all (92%) of the paddlefish we captured in experimental gill nets were dead when water temperatures exceeded 21°C. Conversely, mortality was low (<15%) when water temperatures were less than 18°C. High initial or delayed mortality of the bycatch will confound efforts to protect Kentucky Lake paddlefish from overfishing through the use of minimum EFL limits and are the subject of ongoing investigations.

Commercial fishing has reduced paddlefish stocks throughout history. Stocks in Mississippi, Louisiana, and Wisconsin were depleted after a few years of intensive seine fishing in the early 1900s (Stockard 1907; Alexander 1914; Coker 1930). Paddlefish catches declined so severely in Norris Reservoir, Tennessee (e.g., the 1960 catch was only 8% of the 1958 catch), that commercial fishing was permanently terminated in 1960 (Carroll et al. 1963), although poor recruitment may have contributed to the stock collapse. Alexander and McDonough (1983) noted a severe decline in the number of age-0 paddlefish impinged at the Gallatin Steam Electric Plant on Old Hickory Lake, Tennessee, after heavy exploitation in the late 1970s. Again, poor recruitment resulting from impounding the Cumberland River may have contributed to stock collapse in Old Hickory Lake. The Alabama Department of Conservation and Natural Resources suspected that paddlefish in Alabama waters of the Tennessee River were being overfished and implemented a moratorium on paddlefish harvest in 1988. Five years later, Hoxmeier and DeVries (1996) collected no paddlefish in those waters and hypothesized that the population had not recovered from previous overexploitation.

Considering the high harvest that regularly occurs, it is remarkable that Kentucky Lake's paddlefish stock has not met a similar fate as the stocks immediately upriver in Alabama.

Commercial fishing is not exclusively responsible for paddlefish population declines in other locales; however, the negative impacts of other, uncontrollable factors (e.g., dams and pollution) on reproduction and age-0 survival can be offset by reducing fishing mortality (Boreman 1997). Our study suggests that Kentucky Lake's paddlefish population is overfished during dry seasons and that current regulations do little to restrict harvest or protect mature females. Fortunately, during years of high rainfall and high discharges, this population is afforded temporary relief from bouts of high exploitation. However, the ability of this stock to sustain high exploitation may be compromised if national or international demand for paddlefish caviar increases, an extended drought occurs, or both situations develop. A developing market for smoked paddlefish flesh may also increase the likelihood that the stock will experience growth and recruitment overfishing, particularly if fishers target immature fish that remain downlake in areas amenable to netting during all discharge regimes.

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References

Adams, L. A. 1942. Age determination and rate of growth in *Polyodon spathula*, by means of the growth rings of the otoliths and dentary bone. American Midland Naturalist 28:617–630.

Aggus, L. R., D. I. Morais, and R. F. Baker. 1979. Evaluation of the trout fishery in the tailwater of Bull Shoals reservoir, Arkansas, 1971–73. Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies 31(1977):565–573.

Alexander, C. M., and T. A. McDonough. 1983. Effect of water conditions during spawning on paddlefish year-class strength in Old Hickory Reservoir, Tennessee. Tennessee Valley Authority, Office of Natural Resources, Division of Air and Water Resources, Progress Report, Knoxville, Tennessee.

Alexander, C. M., A. I. Myhr III, and J. L. Wilson. 1987. Harvest potential of paddlefish stocks in Watts Bar Reservoir, Tennessee. Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies 39(1985):45–55.

Alexander, M. L. 1914. The paddlefish (*Polyodon spathula*). Transactions of the American Fisheries Society 44:34–39.

Boone, E. A., Jr., and T. J. Timmons. 1995. Density and natural mortality of paddlefish, *Polyodon spathula*, in an unfished Cumberland River subimpoundment, South Cross Creek Reservoir, Tennessee. Journal of Freshwater Ecology 10:421–431.

Boreman, J. 1997. Sensitivity of North American sturgeons and paddlefish to fishing mortality. Environmental Biology of Fishes 48:399–406.

Bronte, C. R., and D. W. Johnson. 1985. Growth of paddlefish in two mainstream reservoirs with reference to commercial harvest. Transactions of the Kentucky Academy of Science 46:28–31.

Carlson, D. M., and P. S. Bonislawsky. 1981. The paddlefish (*Polyodon spathula*) fisheries of the midwestern United States. Fisheries 6(2):17–22.

Carroll, B. B., G. E. Hall, and R. D. Bishop. 1963. Three seasons of rough fish removal at Norris Reservoir, Tennessee. Transactions of the American Fisheries Society 92:356–364.

Coker, R. E. 1930. Studies of common fishes of the Mississippi River at Keokuk. U.S. Bureau of Fisheries Bulletin 45:141–225.

Combs, D. L. 1982. Angler exploitation of paddlefish in the Neosho River, Oklahoma. North American Journal of Fisheries Management 4:334–342.

De Jesús, M. J., and C. C. Kohler. 2004. The commercial fishery of the Peruvian Amazon. Fisheries 29(4): 10–16.

Elser, A. A. 1986. An overview of current management practices for paddlefish fisheries. Pages 62–67 *in* J. G. Dillard, L. K. Graham, and T. R. Russell, editors. The paddlefish: status, management, and propagation. American Fisheries Society, North Central Division, Special Publication Number 7, Columbia, Missouri.

Gengerke, T. W. 1978. Paddlefish investigations. Iowa Conservation Commission, Fisheries Section, Commercial Fisheries Investigation Project 2-255-R, Completion Report, Des Moines.

Goodyear, C. P. 1993. Spawning stock biomass per recruit in fisheries management: foundation and current use. Pages 67–71 *in* S. J. Smith, J. J. Hunt, and D. Rivard, editors. Risk evaluation and biological reference points for fisheries management. Canadian Special Publication of Fisheries and Aquatic Sciences 120.

Hageman, J. R., D. C. Timpe, and R. D. Hoyt. 1988. The biology of paddlefish in Lake Cumberland, Kentucky. Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies 40(1986):237–248.

Hoffnagle, T. L., and T. J. Timmons. 1989. Age, growth, and catch analysis of the commercially exploited paddlefish population in Kentucky Lake, Kentucky−Tennessee. North American Journal of Fisheries Management 9:316–326.

Hoxmeier, R. J. H., and D. R. DeVries. 1996. Status of paddlefish in the Alabama waters of the Tennessee River. North American Journal of Fisheries Management 16:935–938.

Hoxmeier, R. J. H., and D. R. DeVries. 1997. Habitat use, diet, and population structure of adult and juvenile paddlefish in the lower Alabama River. Transactions of the American Fisheries Society 126: 288–301.

Hoyt, R. D. 1984. Population dynamics and biology of the paddlefish, *Polyodon spathula*, in Lake Cumberland. Department of Biology, Western Kentucky University, Project Completion Report 2-388-R, Bowling Green.

Irwin, E. R., and P. W. Bettoli. 1995. Introduced clupeids in a southern reservoir: more evidence for system-specific reproductive styles. Environmental Biology of Fishes 42:151–159.

Jones, R. 1957. A much simplified version of the full yield equation. International Commission for Northwest Atlantic Fisheries, International Council for the Exploration of the Sea, and Food and Agriculture Organization of the United Nations, Document P.21, Lisbon.

Lein, G. M., and D. R. DeVries. 1998. Paddlefish in the Alabama river drainage: population characteristics and the adult spawning migration. Transactions of the American Fisheries Society 127:441–454.

Maceina, M. J. 1997. Simple application of using residuals from catch-curve regressions to assess year-class strength in fish. Fisheries Research 32:115–121.

Manooch, C. S., III, J. C. Potts, D. S. Vaughn, and M. L. Burton. 1998. Population assessment of the red snapper from the southeastern United States. Fisheries Research 38:19–32.

Markle, D. F. 1984. Phosphate-buffered formalin for long-term preservation of formalin-fixed ichthyoplankton. Copeia 1984:525–528.

Meyer, F. P. 1960. Life history of *Marsipomtera hastata* and the biology of its host, *Polyodon spathula*. Iowa State University Press, Ames.

Miranda, L. E. 2002. Establishing size-based mortality caps. North American Journal of Fisheries Management 22:433–440.

Pasch, R. W., and C. M. Alexander. 1986. Effects of commercial fishing on paddlefish populations. Pages 46–53 *in* J. G. Dillard, L. K. Graham, and T. R. Russell, editors. The paddlefish: status, management, and propagation. American Fisheries Society, North Central Division, Special Publication Number 7, Bethesda, Maryland.

Pasch, R. W., P. A. Hackney, and J. A. Holbrook II. 1980. Ecology of paddlefish in Old Hickory Reservoir, Tennessee, with emphasis on first-year life history. Transactions of the American Fisheries Society 109:157–167.

Paukert, C. P., and W. L. Fisher. 1999. Evaluation of paddlefish length distributions and catch rates in three mesh sizes of gill nets. North American Journal of Fisheries Management 19:599–603.

Paukert, C. P., and W. L. Fisher. 2001a. Characteristics of paddlefish in a southwestern U.S. reservoir, with comparisons of lentic and lotic populations. Transactions of the American Fisheries Society 130:634–643.

Paukert, C. P., and W. L. Fisher. 2001b. Spring movements of paddlefish in a prairie reservoir system. Journal of Freshwater Ecology 16:113–124.

Price, A. B., and R. A. Rulifson. 2004. Use of traditional ecological knowledge to reduce striped bass bycatch in the Currituck Sound white perch gill-net fishery. North American Journal of Fisheries Management 24:785–792.

Purkett, C. A., Jr. 1961. Reproduction and early development of the paddlefish. Transactions of the American Fisheries Society 90:125–129.

Purkett, C. A., Jr. 1963. The paddlefish fishery of the Osage river and the Lake of the Ozarks, Missouri. Transactions of the American Fisheries Society 92: 239–244.

Quist, M. C., J. L. Stephen, C. S. Guy, and R. D. Schultz. 2004. Age structure and mortality of walleyes in Kansas reservoirs: use of mortality caps to establish realistic management objectives. North American Journal of Fisheries Management 24:990–1002.

Reed, B. C., W. E. Kelso, and D. A. Rutherford. 1992. Growth, fecundity, and mortality of paddlefish in Louisiana. Transactions of the American Fisheries Society 121:378–384.

Ricker, W. E. 1975. Computation and interpretation of biological statistics in fish populations. Fisheries Research Board of Canada Bulletin 191.

Robinson, J. W. 1966. Observations on the life history, movement, and harvest of the paddlefish, *Polyodon spathula*, in Montana. Proceedings of the Montana Academy of Science 26:33–44.

Rosen, R. A., D. C. Hales, and D. G. Unkenholz. 1982. Biology and exploitation of paddlefish in the Missouri River below Gavin's Point Dam. Transactions of the American Fisheries Society 111:216–222.

Runstrom, A. L., B. Vondracek, and C. A. Jennings. 2001. Population statistics for paddlefish in the Wisconsin River. Transactions of the American Fisheries Society 130:546–556.

Russell, T. R. 1986. The biology and life history of the paddlefish: a review. Pages 2–21 *in* J. G. Dillard, L. K. Graham, and T. R. Russell, editors. The paddlefish: status, management, and propagation. American Fisheries Society, North Central Division, Special Publication 7, Columbia, Missouri.
SAS Institute. 2001. SAS/STAT® user's guide, Version 8. 2. SAS Institute, Cary, North Carolina.
Scarnecchia, D. L., T. W. Gengerke, and C. T. Moen. 1989. Rationale for a harvest slot limit for paddlefish in the upper Mississippi River. North American Journal of Fisheries Management 9:477–487.
Scarnecchia, D. L., P. A. Stewart, and G. J. Power. 1996. Age structure of the Yellowstone−Sakakawea paddlefish stock, 1963–1993, in relation to reservoir history. Transactions of the American Fisheries Society 125:291–299.
Slipke, J. W., and M. J. Maceina. 2001. Fishery Analysis and Simulation Tools (FAST), version 1. 1. Department of Fisheries and Allied Aquaculture, Auburn University, Auburn, Alabama.
Slipke, J. W., A. D. Martin, J. Pitlo, Jr., and M. J. Maceina. 2002. Use of the spawning potential ratio for the upper Mississippi River channel catfish fishery. North American Journal of Fisheries Management 22:1295–1300.
Southall, P. D., and W. A. Hubert. 1984. Habitat use by adult paddlefish in the upper Mississippi River. Transactions of the American Fisheries Society 113: 125–131.
Stockard, C. R. 1907. Observations on the natural history of *Polyodon spathula*. American Naturalist 41: 753–766.
Timmons, T. J., and T. A. Hughbanks. 2000. Exploitation and mortality of paddlefish in the lower Tennessee and Cumberland rivers. Transactions of the American Fisheries Society 129:1171–1180.
Unkenholz, D. G. 1986. Effects of dams and other habitat alterations on paddlefish sport fisheries. Pages 54–61 *in* J. G. Dillard, L. K. Graham, and T. R. Russell, editors. The paddlefish: status, management, and propagation. American Fisheries Society, North Central Division, Special Publication 7, Columbia, Missouri.
Zigler, S. J., M. R. Dewey, and B. C. Knights. 1999. Diel movement and habitat use by paddlefish in Navigation Pool 8 of the upper Mississippi River. North American Journal of Fisheries Management 19:180–187.