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Age Structure of the Yellowstone–Sakakawea Paddlefish Stock, 1963–1993, in Relation to Reservoir History

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Abstract.—Current and historical age structure information on the Yellowstone–Sakakawea stock of paddlefish *Polyodon spathula* is reviewed in relation to the completion of Garrison Dam in 1953 and the subsequent filling of Lake Sakakawea, a 156,000-ha impoundment on the Missouri River. Paddlefish abundance increased greatly after the closure of Garrison Dam, and the first large group of paddlefish (nearly all males) migrated up the Yellowstone River to Intake, Montana, in 1962–1963. By the mid-1970s, after the gradual filling of the reservoir (1954–1966), both females and males had fully recruited to the Intake fishery, and more females were harvested than males. By the 1980s, older females predominated in the harvest. Based on age determination in 1991–1993, the stock has continued to age, from a mean of 10.3 years in 1964–1965 to 14.8 in 1974, 20.3 in 1985, and 23.5 in 1992. In 1993, however, mean ages of paddlefish at Intake decreased by 2 years for males and 3.3 years for females. In 1991 and 1992, males from Intake were characterized by bimodal age distributions with ages ranging from 7 to 40 (means, 18.4 and 17.8, respectively); females demonstrated unimodal age distributions and ranged in age from 10 to 42 (means, 25.5 and 26.1). Males commonly matured at age 9, but females almost never matured before age 15. The oldest paddlefish encountered was a 14-kg male caught in 1985 and estimated to be 55 years old. Although substantial recruitment has occurred within the past decade (as indicated by recruitment of 9–11-year-old males to the fishery in 1991–1993) and reproduction appears to have occurred in 1991 and 1993 (based upon counts of young-of-the-year in Lake Sakakawea), the age structure suggests that recruitment may be less in recent years than in the years soon after the reservoir was closed and filled. A conservative harvest is called for until it is clear that reproduction is adequate to sustain the stock and the fishery.

The Yellowstone–Sakakawea stock of paddlefish *Polyodon spathula* supports important recreational snag fisheries in eastern Montana and western North Dakota (Scarnecchia et al. 1995). Fish of this stock rear in Lake Sakakawea, a main-stem impoundment on the Missouri River. Mature fish become vulnerable to harvest during spawning migrations up the Missouri River to the tailwaters of Fort Peck Dam and up the Yellowstone River to Intake, a low-head diversion dam 27 km downriver from Glendive, Montana (Figure 1).

This stock, in contrast with most other paddlefish stocks throughout the species' range (Carlson and Bonislawsky 1981; Gengerke 1986) has evidently increased in numbers in the past 40 years. A significant fishery for the stock first developed at Intake in 1962 (Robinson 1966), 9 years after the closure of Garrison Dam in 1953 created Lake Sakakawea. Since 1962, the annual harvest of paddlefish at Intake has typically ranged between 1,000 and 5,000 fish. North Dakota's paddlefish fishery began in 1977, and occurs mainly at the confluence of the Missouri and Yellowstone rivers (the Confluence). Harvest has increased substantially since the 1980s; total harvest in 1993 was more than 2,000 fish.

During the years of these fisheries, the age structure of the stock has been monitored sporadically through collection and interpretation of dentaries (lower jaw bones), the most commonly used method of age determination for this species (Adams 1931, 1942). No attempt has been made to relate long-term age structure changes to the changing habitat features in Lake Sakakawea. The objectives of this paper are to review past efforts at age determination, report on the age structure of the stock

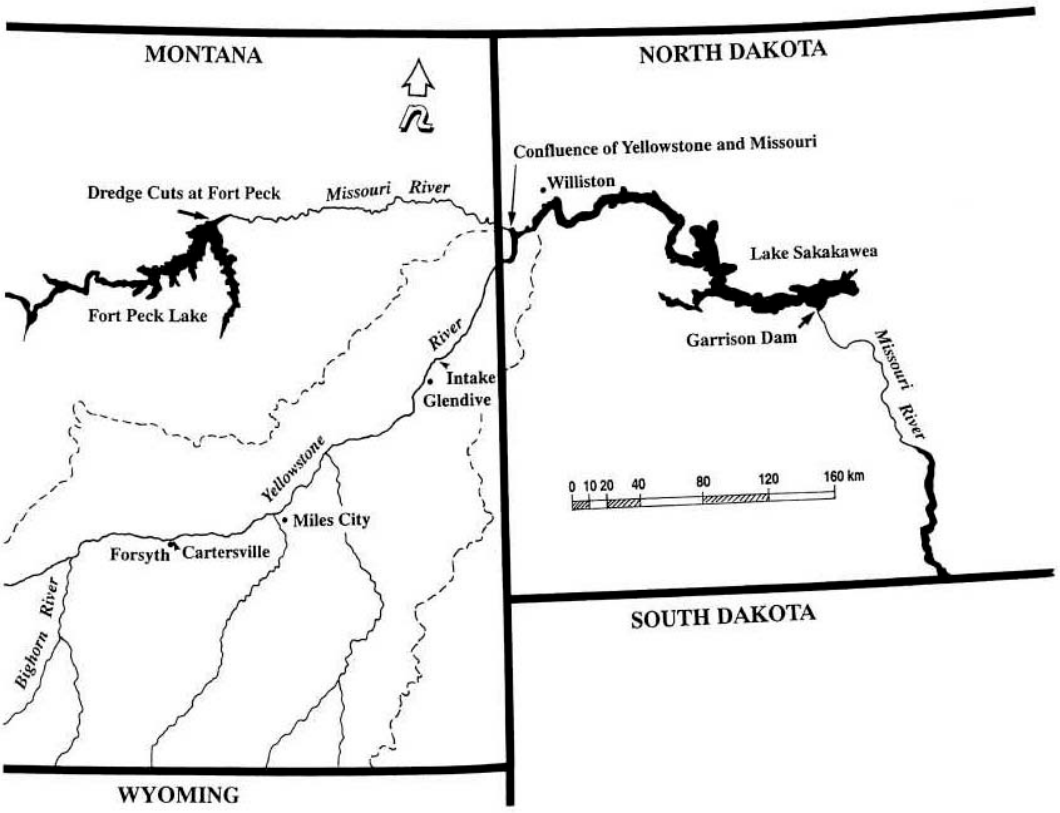

FIGURE 1.—Lower Yellowstone River and Lake Sakakawea, Montana and North Dakota.

over 1991–1993, and relate changes in age structure to relevant environmental conditions in the reservoir.

Study Site

The lower Yellowstone River extends approximately 630 km from the mouth of the Bighorn River to its confluence with the Missouri River, approximately 40 km southwest of Williston, North Dakota (Figure 1). Haddix and Estes (1976) and Graham et al. (1979) reviewed the physical, chemical, and biological characteristics of the lower Yellowstone River. Although the main stem is unregulated, two low-head irrigation diversion dams impede fish migrations at Cartersville (near Forsyth) and at Intake (near Glendive). After the Yellowstone River's confluence with the Missouri River, the Missouri River flows freely until it empties into Lake Sakakawea, a distance of from 24 to 80 km, depending on Lake Sakakawea's level. Lake Sakakawea, the largest of the Missouri River main-stem reservoirs, is 320 km long and has a maximum surface elevation of 565.4 m above sea level, an area of 156,000 ha, and a storage capacity of more than 30 billion cubic meters. High rates of sediment deposition (an average of 32 million cubic meters per year), mainly from the Yellowstone River, result in shallow, turbid water in the upper portion of the reservoir (Power et al. 1994). After closure of the dam in 1953, the reservoir filled gradually from 1954 to 1966. It reached full pool in 1967 and remained full until 1976. From 1977 to 1988 the reservoir level underwent periodic fluctuations; in 1988, it dropped well below full pool and remained low until mid-1993. Heavy precipitation throughout the Great Plains in 1993 and retention of water in the reservoirs to avoid downriver flooding resulted in a rapid rise in the reservoir level in mid-1993 (Figure 2).

Review of Past Studies: 1963–1989

Stock expansion and reservoir filling in the 1950s and 1960s.—Robinson (1966) sampled paddlefish for dentaries at Intake during the May–June fishing seasons of 1964 and 1965, soon after the first large

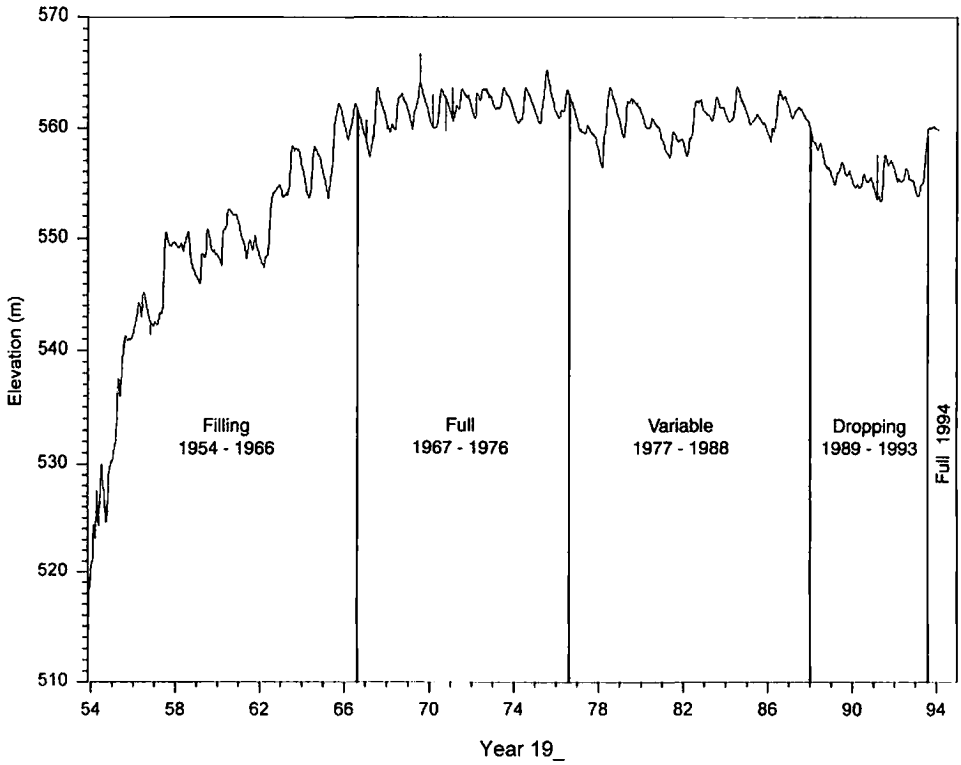

FIGURE 2.—Elevation (meters above mean sea level) of Lake Sakakawea, 1953–1993.

run of paddlefish up the Yellowstone River in 1962. More than 90% of these fish were less than 15 years old (Figure 3a). The three most common ages were 9, 10, and 11 years, which corresponded to brood years 1954–1956, the period immediately after the closure of Garrison Dam (Figure 2). More than 97% of the fish harvested were males. Evidently the males of these strong year-classes matured earlier than the females and recruited to the fishery at a younger age. The hypothesis that the population increased is consistent with paddlefish commercial catch statistics from Lake Sakakawea. Power et al. (1994) reported that 21 paddlefish caught with nets in the reservoir in 1954 weighed an average of only 65 grams and that 13 paddlefish caught in 1955 averaged only 87 grams. These fish would have been young-of-the-year. The first significant catches in the reservoir occurred in 1961 when the mean weight of 779 paddlefish caught was 3.5 kg.

Full recruitment of both sexes and a full reservoir in the 1970s.—Rehwinkel (1978) reported that 503 male paddlefish sampled in 1974 ranged in age from 9 to 26 years (mean, 13), with ages 11 and 12 the most common (Figure 3b). A sample of 478 females ranged in age from 15 to 20 years (mean, 18), with ages 17 and 18 the most common (Figure 3b). Females sampled by Rehwinkel (1978) evidently first recruited to the fishery at age 15 and did not fully recruit until perhaps age 17 or 18. These females were evidently the first female recruits produced from the large postimpoundment year-classes 15 to 20 years earlier (1954–1958). Whereas more than 90% of paddlefish creeled in 1964–1965 had been males, only 56% of the fish creeled in 1973 were males (Stewart 1994). By 1974, females harvested at Intake began to outnumber males, and the predominance of females persisted until 1993 (Stewart 1994; Figure 4).

Predominance of large, older females and a dropping reservoir level in the 1980s.—Sex ratios (Figure 4) and weight distributions of paddlefish indicated that large, older females were the predominant sex contributing to the catch at Intake throughout the 1980s. Mean weight of female paddlefish at Intake rose slowly but consistently throughout the decade (Figure 5). The 221 paddlefish dentaries aged by Stewart (1987) were subsequently recut and reaged in 1992 with more ad-

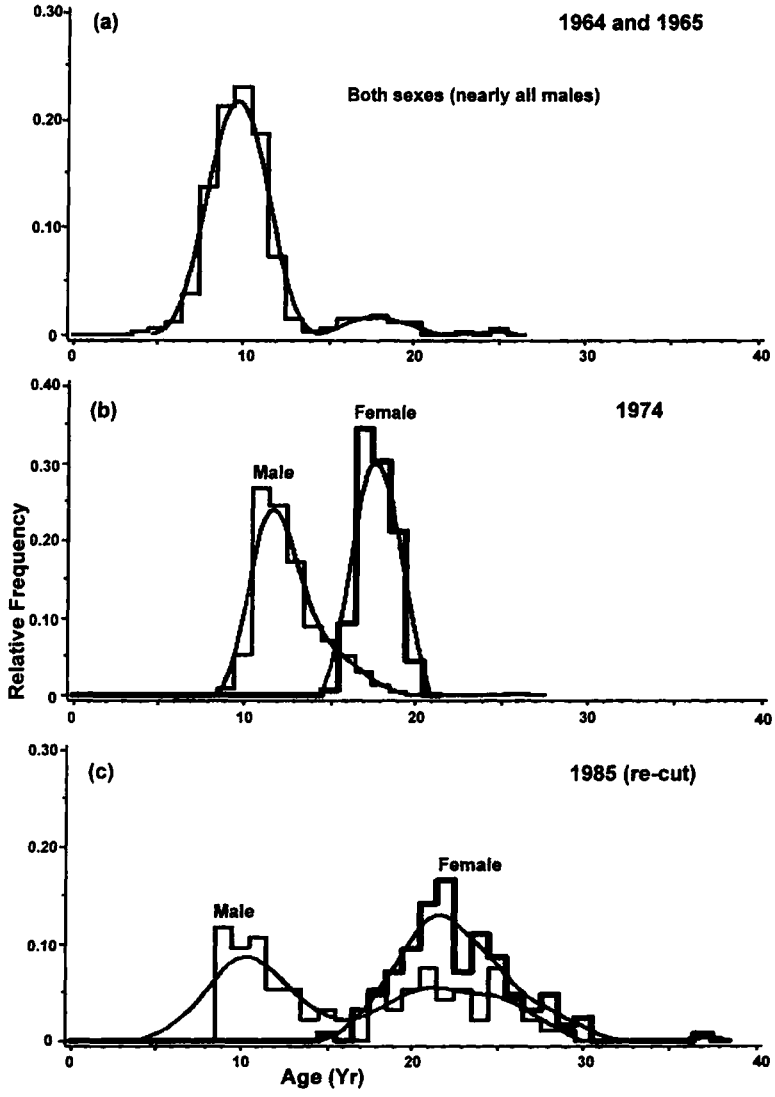

FIGURE 3.—Age distribution of paddlefish in (a) 1964 and 1965 (N = 343 fish; Robinson 1966), (b) 1974 (N = 503 males, N = 478 females; Rehwinkel 1978), and (c) 1985 (N = 94 males, N = 127 females) for recut and reaged samples originally aged by Stewart (1987). Smoothed curves were generated by the spline method available in PROC PLOT (SAS Institute 1987).

vanced dentary sectioning and reading equipment. Ninety-four males ranged in age from 9 to 29 years (mean, 17; with one fish aged 55); the most common ages were 9, 11, 21, and 25 years. Females (127) ranged in age from 15 to 30 years (mean, 23; with one fish at 37); the most common ages were 21 and 22 (Figure 3c). These female-predominated catches occurred when reservoir levels were generally slightly below full pool in the mid-1980s and considerably below full pool in the late 1980s (Figure 2).

Recent Investigations: 1991–1993

Between 1991 and 1993, dentaries were collected from 4,448 paddlefish, 93% from Intake and 7% from the Confluence and nearby sites. Dentaries were removed with diagonal pliers, and excess skin was peeled off. Cleaning and sectioning of dentaries followed, with minor changes, procedures outlined by Reed (1989). Dentaries were sectioned with a diamond-edged blade on a Buehler Isomet low-speed saw. Two sections 0.635 mm thick were obtained 10 mm posterior to the point

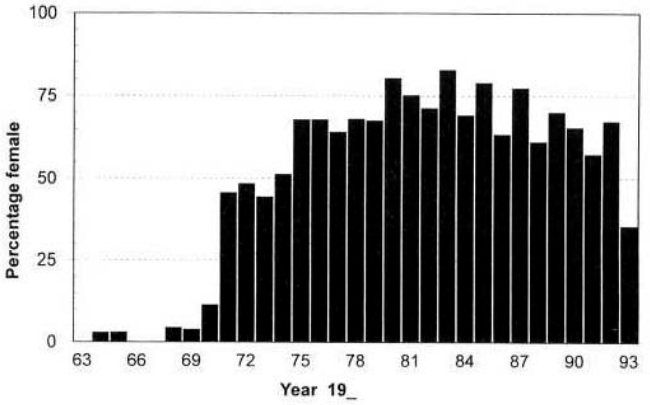

FIGURE 4.—Percentage of female paddlefish in Intake catch, 1963–1993.

of greatest curvature (Reed 1989; Reed et al. 1992). Sections to be aged were immersed in glycerine and interpreted for age by counting annual bands with the aid of a Biosonics Optical Pattern Recognition System (OPRS). Samples were interpreted without knowledge of the size or sex of the fish, except insofar as smaller fish tended to have smaller diameter sections. Annuli were counted along the long axis of the mesial arm. Age validation was not possible because no paddlefish were of known age.

Results

Intake

In 1991, male paddlefish ranged in age from 7 to 40 years (mean, 18.4). Females ranged from 14 to 42 years (mean, 25.5). Although 205 of the 721 males in 1991 were between age 7 and age 13, the youngest females were age 14, which indicated a considerably older age at maturity for the females (and hence delayed migration pattern and delayed vulnerability to harvest). Age-frequency distributions for the sexes also differed: males had a bimodal distribution with a minor peak at about age 9 and a higher peak at age 21, whereas females had a unimodal distribution with the peak at age 26 (Figure 6a).

Age distributions in 1992 were similar to those in 1991. Males ranged in age from 7 to 33 years (mean, 17.8), or 0.6 year younger than in 1991. Females ranged from 10 to 40 years (mean, 26.1), or 0.6 year older than in 1991. Although 79 of the 219 males were aged 7–13, only one of the 471 females was under age 14. As in 1991, males had a bimodal age distribution with the highest peak at age 21, whereas females had a unimodal peak at age 27 (Figure 6b).

In 1993, for the first time in nearly 20 years, the harvest at Intake was predominantly males. The age structure also differed from those in 1991 and 1992. Males ranged in age from 6 to 35 years, (mean, 15.8), two years younger than in 1992. Females ranged in age from 9 to 38 years (mean, 22.8), 3.3 years younger than in 1992 (Figure 6c). Mean weight of aged males was the same in 1992 (11.5 kg) as in 1993 (11.5 kg), but mean weights of aged females dropped by 0.7 kg in 1993 (26.5 kg) from 1992 (27.2 kg).

North Dakota

Although there were fewer samples from North Dakota than from Intake, results from their analysis were in general agreement with results from Intake (except for 1993). In 1991, 74 males ranged in age from 9 to 37 years (mean, 21); 54 females ranged in age from 17 to 33 (mean, 24). In 1992, 19 males ranged in age from 9 to 33 years (mean, 22); 22 females ranged from 19 to 34 (mean, 24). In 1993, 48 males ranged from 9 to 29 years (mean, 18); 72 females ranged from 16 to 35 (mean, 25). Mean age of both males and females in North Dakota in 1993 was 2.2 years higher than at Intake and was similar to the mean ages recorded at Intake in 1991 and 1992. As with the Intake samples, females did not recruit until 6–10 years after males, and few fish were old enough to have hatched before the 1953 closure of Garrison Dam.

Age Structure in Relation to Stage of Reservoir

Nearly 60% of the females captured in 1991 and 1992 were hatched in years when the reservoir was filling (1954–1966; Figure 2; Table 1). In contrast, in 1993, lower mean ages and mean weights of

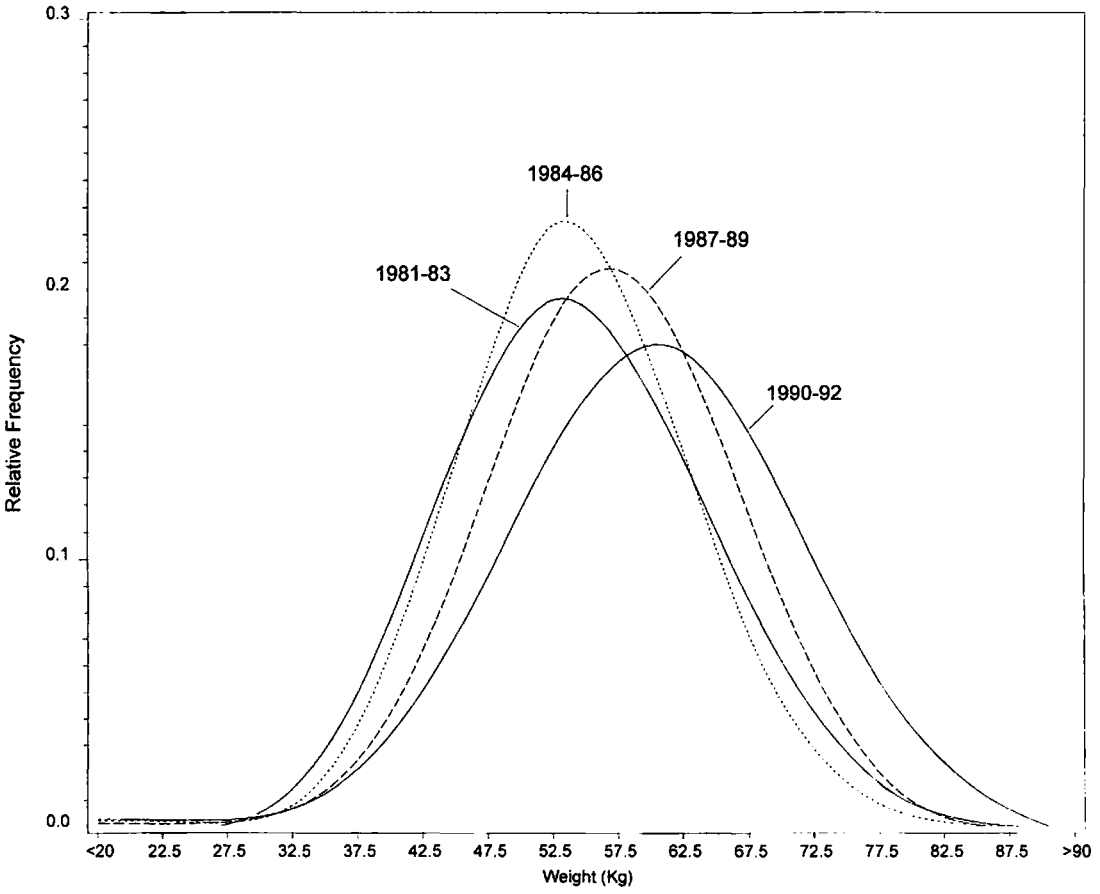

FIGURE 5.—Approximated weight distributions of female paddlefish harvested at Intake in 3-year intervals, 1981–1992.

females indicated that only about 24% of those fish were produced during these years. A high percentage of males caught in 1991–1993 derived from brood years when the reservoir was full (1967–1976), and by 1993, young males from the year-classes 1977–1988 constituted half of all males aged.

Discussion

Age Structure Relative to Other Localities

The Yellowstone–Sakakawea paddlefish stock consisted of older (commonly 25–35-year-old), later-maturing fish (at least 9 years for males, 15 years for females) than reported in most other locations. Gengerke (1978) reported that only one of 787 paddlefish in Iowa's portion of the Mississippi River was older than age 20; male fish of that stock matured as young as age 4, and females as young as age 6. In the Osage River, Missouri, Purkett (1963) and Russell (1986) reported paddlefish commonly reaching 25 years and some as old as 30. In more southerly and more heavily exploited populations, maximum age observed is evidently lower. In Lake Ponchartrain, Louisiana, Reed et al. (1992) found paddlefish only up to age 14. None of the above stocks exhibit the old age of the Yellowstone–Sakakawea stock, in which fish exceeding 25 years of age are abundant and fish exceeding 30 are not uncommon. The oldest fish found thus far, a 14-kg male caught in 1985 and estimated to be 55 years old, is, to our knowledge, the oldest paddlefish reported anywhere. A few fish have exceeded age 40, even in the presence of considerable annual harvest.

Accuracy of Age Determination

If ages of old fish are underestimated, as occurs for old white sturgeon *Acipenser transmontanus* (Rien and Beamesderfer 1994) and other fishes (Beamish and McFarland 1987), 40-year-old pad-

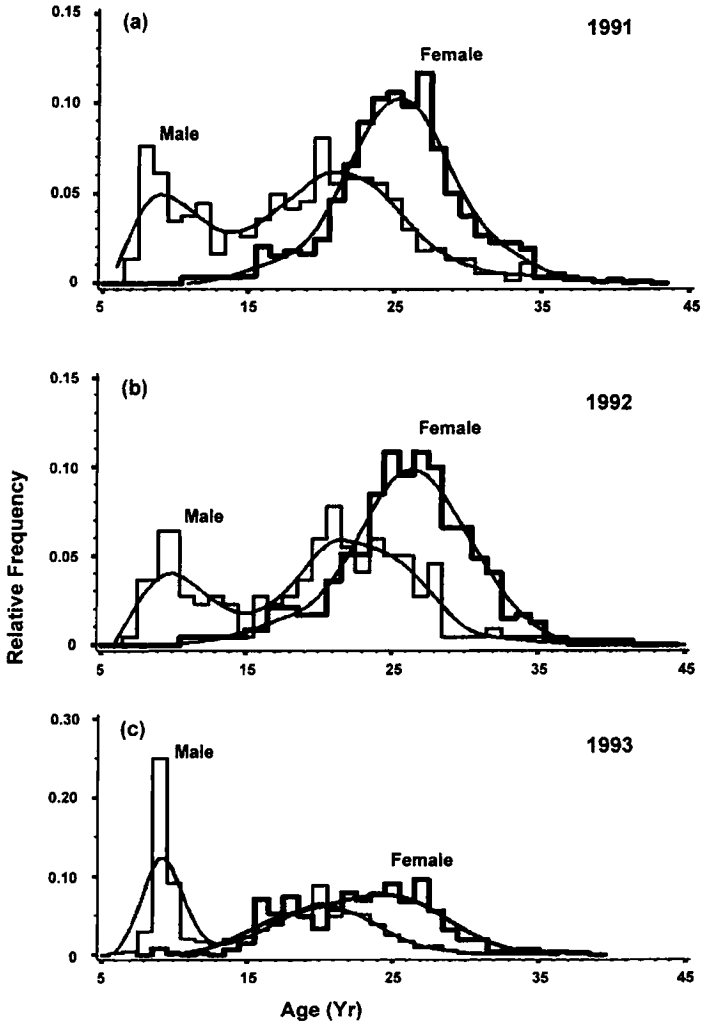

FIGURE 6.—Age distribution of (a) 721 male and 975 female paddlefish sampled at Intake in 1991, (b) 219 male and 471 female paddlefish in 1992, and (c) 1,144 male and 672 female paddlefish in 1993. Smoothed curves were generated by the spline method available in PROC PLOT (SAS Institute 1987).

TABLE 1.—Percentages of male (M) and female (F) paddlefish caught at Intake, Montana, from 1991 to 1993, according to their year-class and relation to reservoir water levels: pre-1954 = before reservoir; 1954–1966 = reservoir filling; 1967–1976 = reservoir full; 1977–1988 = variable reservoir, full, or slightly below full.

Year of catch	Year-class group and sex							
	Pre-1954		1954–1966		1967–1976		1977–1988	
	M	F	M	F	M	F	M	F
1991	<1	<1	18	59	51	40	31	<1
1992	0	<1	15	58	46	41	39	<1
1993	0	0	3	24	46	66	50	10

dlefish may be more common than it appears, based on our aging technique. Under-aging of older paddlefish is a distinct possibility because the outer annuli on fish 20 years and older are commonly spaced closely together. Although age validation (Beamish and McFarland 1983) is an obvious need for this species, it will only be possible in the near term through tagging fish of known ages, and then only for young recruits.

Age Structure, Reservoir Level, and Stock Status

The Yellowstone–Sakakawea stock has continued to age since 1953, when Garrison Dam created

Lake Sakakawea. Mean age of paddlefish at Intake has increased from 10.3 years in 1964–1965 (Robinson 1966) to 14.8 in 1974 (Rehwinkel 1978), 20.3 in 1985, and 23.5 in 1992. Despite years of harvest, old female paddlefish still constitute a significant fraction of the harvest. The predominance of old females hatched in the years of reservoir filling (1954–1966) and immediately thereafter indicate that these early years were often successful for paddlefish reproduction, and the resulting recruits have supported a fishery for more than 30 years.

Although reproduction and recruitment are occurring, as evidenced by young-of-the-year in Lake Sakakawea in 1991–1993 (Fredericks 1994) and by the presence of 7–14-year-old males in the 1993 harvest (Figure 6), the age structure indicates that recruitment may be less in recent years than just after the reservoir was closed and filled. The positive effects of trophic upsurge in the years immediately after reservoir construction on reproduction and recruitment of fish stocks are well documented (Baranov 1966; Ostrofsky and Duthie 1978; Kimmel and Groeger 1986). In Lake Francis Case (South Dakota), another Missouri River reservoir, Gasaway (1970) reported that postimpoundment growth of 13 species of fish initially increased after impoundment but later decreased. Neel (1967) reported that from 1954–1958, phytoplankton density in Lake Sakakawea peaked in 1956, the second summer after dam closure, and declined greatly in 1957 and 1958. For female paddlefish that recruit to the fishery 15–20 years after birth, any such upsurge effects would not be evident for many years after the initial strong year-classes and a decade or more after the effects would have dissipated for shorter-lived fishes. In addition, the gradual, 13–14-year filling of Lake Sakakawea may have resulted in more gradual trophic changes than if it had filled over a much shorter period. For this reason, the entire filling period (1954–1966) and perhaps some years afterward could be viewed as the upsurge phase of the reservoir. Most of the large females that supported the paddlefishery in 1991–1993 may have been hatched during conditions of upsurge-related productivity that were not sustainable over the long term. Also, any underestimation of ages of either males or females would result in even higher percentages of older males and females being hatched during the earlier years of Lake Sakakawea's existence.

Little direct information exists, however, on the ecological conditions in Lake Sakakawea during the early years as they would relate to survival of young-of-the-year paddlefish. During the early to mid-1960s (the latter part of the filling period), a strong fishery for northern pike *Esox lucius* developed as a result of the excellent spawning conditions created by recently flooded vegetation. This fishery remained strong until the early 1970s. After the reservoir had filled, a more stable water level and significant shore erosion resulted, by 1979–1980, in strong year-classes of walleye *Stizostedion vitreum* and sauger *Stizostedion canadense*. A nationally renowned fishery existed for these species in the mid-1980s (Power et al. 1994). Natural reproduction of walleye waned as reservoir water levels fell during the mid-1980s, which led to stocking of large numbers of walleyes. Although walleyes and saugers are known predators of paddlefish in Lake Sakakawea (Mero 1992), the effects of these changes in predator abundance on paddlefish are unknown. In the last two decades, much of the upper end of Lake Sakakawea has become filled with silt, producing increasingly shallow, turbid habitat. More information is needed on factors affecting annual year-class strength of paddlefish, and, in particular, on reservoir habitat conditions and the resulting abundance of other species.

The importance of the upper end of Lake Sakakawea and the Missouri River near the Confluence to the reproduction and recruitment of paddlefish is also uncertain. The rapid refilling of Lake Sakakawea which occurred in 1993 may provide information on the effects of reservoir aging and water levels on paddlefish reproduction and recruitment. Until reservoir productivity and reproduction and recruitment of paddlefish are shown to be adequate to sustain the stock and fishery, conservative harvest regulations are warranted.

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