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ARTICLE

Demographics and Management of the Isolated Upper Missouri River Paddlefish Stock of Fort Peck Reservoir, Montana

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Abstract
Paddlefish *Polyodon spathula* inhabiting Fort Peck Reservoir and the upper Missouri River, Montana, are members of the northern-most and western-most isolated group of the species. These isolated fish support a recreational, river-based snag fishery on migratory adults. We provide population demographics for the Fort Peck Paddlefish stock, including age structure, growth, reproductive success, recruitment, and population trends developed from creel surveys, adult fish tagging, and reservoir surveys of age-0 and age-1 fish over the period 1992–2020. Of 5,108 fish (2,560 males; 2,558 females), mean annual male age ranged from 18.5 to 21.5 years; mean age of females ranged from 24.3 to 30.8 years. Males did not mature until at least 9–12 years, whereas females did not mature until at least ages 16–19. Females were longer and much heavier than males at a given age and throughout adult life. Males exhibited both annual and biennial spawning, whereas almost no females showed consecutive-year spawning but commonly showed biennial spawning. Annual survival rates estimated from cumulative catch curves were 85% for males and 88% for females. Low counts of age-0 and age-1 fish in the reservoir as well as the modest numbers of young male recruits to the fishery indicate that the Fort Peck stock is characterized by a fairly steady but modest recruitment. This isolated stock continues to be managed as a recreational fishery with harvest while maintaining adult population size, sex, and age structure consistent with its recruitment.

The Paddlefish *Polyodon spathula*, an ancient, filter-feeding zooplanktivore of the Mississippi and Missouri River drainages (Russell 1986; Grande and Bemis 1991; Jennings and Zigler 2009), has declined in abundance in many portions of its range in the past century as a result of dams (Hoover et al. 2019), large-river habitat alterations (Sparrowe 1986), and overfishing (Bettoli et al. 2009). Peripheral declines (i.e., edges of the native range) have been especially obvious (Gengerke 1986). In peripheral locations, initial numbers were often lower than in

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core areas of abundance, and extirpation has sometimes resulted (e.g., North Carolina, New York, Pennsylvania; Bettoli et al. 2019).

In the pre-dam era, Paddlefish had largely unimpeded access to the large river corridors, enabling the species to undertake long migrations (2,000 km or more; Russell 1986; Jennings and Zigler 2009; Tripp et al. 2019), disperse, and colonize many habitats. The dams of the mid-20th century, including the main-stem Pick–Sloan dams of the Missouri River (Ridgeway 1955; Hart 1957), have partially—and in some cases completely—isolated groups of fish into stock-like components (Hesse et al. 1989; Galat et al. 2005). One result has been a reduction in downriver movements except during spill events at dams (e.g., Garrison Dam, North Dakota; Hoover et al. 2019). Upriver movements have typically been more seriously impeded (Sparrowe 1986; Tripp et al. 2019).

The Paddlefish inhabiting Fort Peck Reservoir and the upper Missouri River, Montana, are members of the northern-most and western-most isolated group of the species (Brown 1951; Bowersox 2004). This Paddlefish stock (hereafter, "the Fort Peck stock") is the remnant population of fish that formerly, in the pre-dam era, migrated freely up and down the Missouri River. After closure of Fort Peck Dam in 1937 (Fort Peck Reunion Committee 1977), Fort Peck Reservoir provided newly flooded rearing habitat for the species (Nagel 2017) in an arid region (Bowman 1931).

Little information was available on the Fort Peck Paddlefish stock before a late-1970s study by Berg (1981). However, trophic upsurge associated with reservoir filling probably increased stock numbers beyond pre-dam levels in the years following 1940. Such a population expansion after reservoir filling occurred in the better-monitored Yellowstone–Sakakawea stock, the next stock downriver, after the filling of Lake Sakakawea (Scarnecchia and Stewart 1996; Scarnecchia et al. 2009). Efforts at population estimation for the Fort Peck stock have included recent Jolly–Seber estimates with POPAN parameterization by Glassic et al. (2020) as well as Schnabel multiple mark–recapture estimates (D. L. Scarnecchia and coworkers, University of Idaho, unpublished data). Both approaches indicate a stock size for 2016–2020 of between 12,000 and 25,000 adult fish. Little evidence is available to suggest strong changes in abundance in the past three decades. The naturally reproducing Fort Peck stock is known for its large individuals (Montana record weight, 64.6 kg; https://units.fisheries.org/montana/science/species-of-concern/species-status/Paddlefish/) and continues to support a modest, steady, and increasingly popular recreational snag fishery (Scarnecchia and Gilge 2000; Scarnecchia et al. 2008, 2021). The fishery has historically occurred upriver of the reservoir, primarily from mid-March through early June, on migrating, sexually mature fish. These fish ascend the Missouri River from Fort Peck Reservoir prior to spawning (Miller and Scarnecchia 2008, 2011; Miller and Scarnecchia 2011). Regulations and seasons have varied over the decades, generally becoming more restrictive (Scarnecchia et al. 2021). Annual harvests have typically ranged between 300 and 900 fish; in recent years, harvest has been less than 500 fish (Scarnecchia et al. 2008, 2021). As of 2021, Montana Fish, Wildlife and Parks (MFWP) manages the fishery under a lottery draw system, with a limit of one harvested fish per successful lottery angler, with immediate high-grading allowed. The number of harvest tags annually allocated is designed to result in a harvest of about 500 fish (Scarnecchia et al. 2021). Historical estimated natural and harvest mortality rates based on recoveries of jaw-tagged fish have been low (1973–1986, harvest rates of 1.5–3.5%: Needham and Gilge 1986; harvest rates of 2.6% for females, 2.9% for males: Glassic et al. 2020; annual total survival $S =$ 0.92 for females, 0.82 for males: Glassic et al. 2020).

The Fort Peck Paddlefish stock presents unusual conservation challenges. The stock is vulnerable to overharvest (Boreman 1997), habitat changes (Gerken and Paukert 2009; Jennings and Zigler 2009), a lack of natural genetic introgression from downriver and resultant bottlenecking (Schwemm et al. 2019), and other human influences (Hoover et al. 2019). No hatchery-produced fish have been stocked (Scarnecchia et al. 2021); sustainability is dependent on successful recruitment of wild fish hatched from spawning in the river above Fort Peck Reservoir.

For long-lived species such as the Paddlefish, effective management must be based on reliable information on a variety of life history characteristics (Musick 1999). Sound management is of added importance because of increasing interest in Paddlefish snagging (Scarnecchia et al. 2008; Nagel 2017) and potential illegal harvest for the species' caviar (De Meulenaer and Raymakers 1996; Williamson 2003). As part of MFWP's management plan for this stock (Scarnecchia et al. 2021), key informational needs for stock population assessment include estimates of abundance (Glassic et al. 2020), sex-specific age structure, growth rates, reproduction, and recruitment (Scarnecchia et al. 2014, 2019a, 2019b).

The objective of this paper is to provide population demographics for the Fort Peck Paddlefish stock, including age structure, growth, reproduction, recruitment, abundance trends, and the recreational fishery. These results are interpreted in the broader context of previously published Paddlefish life histories elsewhere and the observed differences between northern and southern latitude stocks (e.g., Montana and North Dakota versus Oklahoma) and their differential metabolic demands (Scarnecchia et al. 2007, 2011). Information is then related to current and future management of this isolated stock.

STUDY SITE

Fort Peck Paddlefish inhabit the Missouri River system of Montana from Fort Peck Dam westward as far as Morony Dam, 24 km downstream of Great Falls (Figure 1). The riverine portion from Morony Dam to the reservoir headwaters is approximately 336 km, depending on reservoir elevation. Two major tributaries enter the river within this reach: the Marias River and the Judith River (Figure 1). The semi-arid climate is highly variable and prone to periodic drought (Bowman 1931), which is reflected in variable annual river discharges and reservoir elevations. Runoff in the area of the Missouri River above Fort Peck Dam is associated with snowmelt and typically peaks in June. Mean monthly discharge in the Missouri River at the Virgelle gauging station (U.S. Geological Survey station 10040101) over the period 1935–2019 has been highest in June (mean, 470.1 m^3/s), followed by May (mean, 362.5 m^3/s) and July (mean, 279.2 m^3/s). Discharge in June above Fort Peck Reservoir averages 1.42 times that at Culbertson, between Wolf Point and the Missouri–Yellowstone River confluence (Figure 1), as a result of regulation from Fort Peck Dam. This amount is only about 50% of that in the lower Yellowstone River at Sidney. Since 1990, June flows have been highest in the periods 1995–1997, 2008–2011, and 2018, similar to high-flow years in the Yellowstone River (Scarnecchia et al. 2021).

Fort Peck Reservoir, which began filling with the completion of the dam in 1937 (Anonymous 1936; Fort Peck

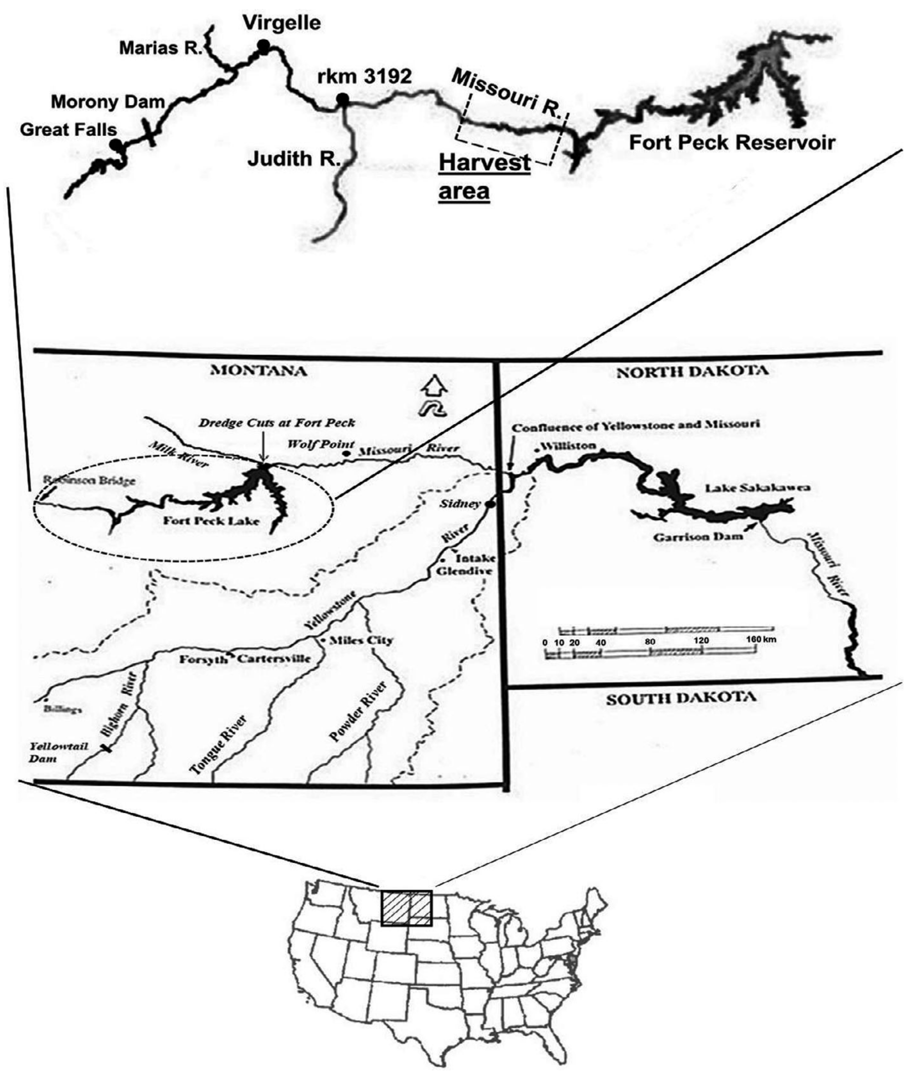

FIGURE 1. Map of the Missouri River and lower Yellowstone River basins in eastern Montana. The area occupied by the Fort Peck Paddlefish stock is circled. The uppermost panel is a close-up of the realm and harvest area of the Fort Peck Paddlefish stock. The area in the Yellowstone River and Missouri River below Fort Peck Dam (Montana–North Dakota) is occupied by the Yellowstone–Sakakawea stock mentioned frequently in comparisons in the text.

Reunion Committee 1977; USACE 1987), is the fifth-largest reservoir in the United States at 202 km long, 980 km^2 in area, and about 2,400 km of shoreline at maximum normal operating pool. It drains an area of 26,418 km^2. Although the reservoir stores more than 23×10^9 m^3 of water at a maximum operating pool of 684.7 m above mean sea level, elevations in the reservoir have typically resulted in lower water levels lying within the Annual Flood Control and Multiple Use Zone and the Carryover Multiple Use Zone (during drought). Fort Peck Reservoir has had two periods of years of low elevation associated with major droughts since 1985, with the second drought period (2003–2008) also being more intense (Figure 2).

Berg (1981) reported 49 species of fish representing 14 families in the combined river and reservoir areas. The river reach utilized by migratory Paddlefish consists of two fishery zones. The upper reach from Morony Dam to the mouth of the Marias River is a coldwater/warmwater transitional zone, with Sauger *Sander canadensis* as the predominant game fish. The warmwater zone used more frequently by Paddlefish extends from the mouth of the Marias River downstream to the headwaters of Fort Peck Reservoir (Berg 1981; Figure 1). In the lower portions of the warmwater zone (Cow Island, Fred Robinson Bridge, and Turkey Joe), the river is characterized by a wide, meandering channel with shifting sandbars, islands, side channels, and backwaters (Gardner and Berg 1980). Substrate in the Fred Robinson Bridge area consists of mainly gravel with some sand.

Several fish species may interact with Paddlefish rearing in Fort Peck Reservoir, including Walleye *S. vitreus*, Northern Pike *Esox lucius*, and Cisco *Coregonus artedi* (Mullins 1991; Dalbey et al. 2012). Cisco abundance has fluctuated widely since their introduction in 1984. Although the Cisco has been credited with improving the prey base and condition for Walleye and perhaps other species (MFWP 2002), it is a zooplanktivore (Mullins 1991) with similar dietary preferences as the Paddlefish (Russell 1986).

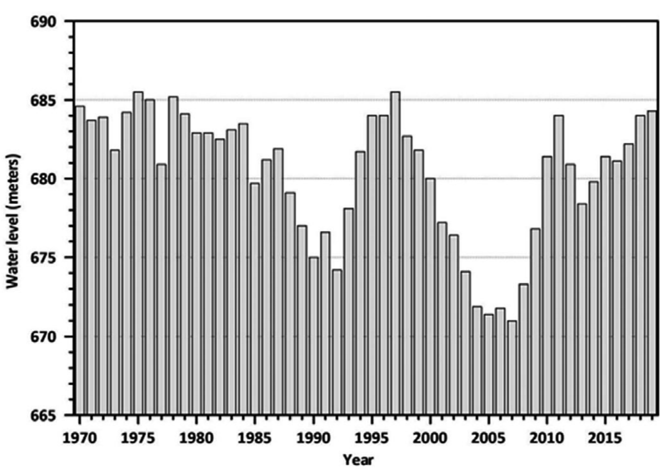

FIGURE 2. Mean monthly elevation in August, Fort Peck Reservoir, Montana, 1970–2019.

METHODS

Roving and access site creel surveys of the recreational fishery above Fort Peck Reservoir were conducted by MFWP over the years 1992–2020 and provided the data for analysis. On-site surveys provided biological information on harvested fish as well as angler demographic data. Paddlefish dentaries were also collected from harvested fish for age estimation (Adams 1942; Scarnecchia et al. 2006). On-site data were not collected in 1997, 1999, 2001, 2003, or 2004. Most harvested Paddlefish were sampled over the period of mid-March through mid-June. Information collected from individual Paddlefish included date and location of capture, body length (BL; from front of eye to fork of caudal fin [Ruelle and Hudson 1977], measured to the nearest 2.5-cm interval), weight (to the nearest 0.45-kg interval), and sex. Sex was determined from inspection of the internal body cavity (Scarnecchia et al. 2007).

Age and growth.— Dentaries (lower jawbones) used for age determination were removed with diagonal pliers; cleaned of excess tissue; placed in individually numbered, permeable envelopes; and allowed to dry. In the laboratory, dentaries were cleaned of all attached tissue by using a standard protocol similar to that described by Faust and Scholten (2017) and were sectioned with a diamond-edged blade on a Buehler Isomet low-speed saw; ages were estimated with a Biosonics Optical Pattern Recognition System or Image-Pro software using a double-blind method (Scarnecchia et al. 2006). Sections were interpreted for age without knowledge of fish size or sex, except insofar as smaller fish tended to have smaller-diameter sections. Age validation was not possible for the Fort Peck stock because no Paddlefish of this stock were of known age, although validation of ages through age 25 has been confirmed for the Yellowstone–Sakakawea stock immediately downriver (through age 10: Scarnecchia et al. 2006; through age 23: Scarnecchia et al. 2019a). Thin cross sections of dentaries from the two stocks are nearly identical and much more straightforward to interpret than sections from most Paddlefish stocks downriver in the Mississippi River basin, which have more halo bands (Scarnecchia et al. 2011).

Relations between BL and age and between weight and age were characterized separately by sex using von Bertalanffy growth curves, expressed as $L(t) = L_\infty\left[e^{-K(\mathrm{Age}-t_0)}\right]$, where L is length, L_∞ is the asymptotic length, Age is fish age in years, K is the curvature parameter, and t_0 is the initial condition parameter (Ricker 1975; Moreau 1987; Chen et al. 1992). The length–weight (W) relation was expressed as $W = aL^b$, where a and b are parameters. In weight-converted form, the relation between weight and age is expressed as

$$W = W_\infty \left[1 - e^{-K(\text{Age}-t_0)}\right]^b,$$

where W is weight, W_∞ is the asymptotic weight, Age is fish age in years, K is the curvature parameter, and t_0 is the initial condition parameter (Moreau 1987).

Postmaturation growth of all fish was also estimated by comparing BLs and weights of fish at the time of tagging and recapture. We hypothesized that once fish were mature, and especially after reaching their prime reproduction period, little or no growth in BL or weight would occur (Scarnecchia et al. 2007). To test this hypothesis, mean percent change in weight (W_{MPC}) was compared among individual fish that were tagged and recaptured at least 4 years apart. In a further analysis, this calculation was also conducted strictly for a group of fish determined from age assessment at the time of harvest to be older males (age 20 and older) and older females (age 25 and older). The differences in weight at tagging (W_T) and weight at recapture (W_R) over each time interval $t_R - t_T$ (i.e., years between tagging [T] and recapture [R]) for each fish were expressed as W_{MPC} in the expression

$$W_R = W_T(1 + \frac{W_{\text{MPC}}}{100})^{(t_R - t_T)}.$$

Reproductive periodicity.— Reproductive periodicity of males and females was determined from the pattern of jaw tag recoveries by year for the first few years after tagging (i.e., number of years to the first peaks in returns; Scarnecchia et al. 2007). Results were compared with estimated reproductive periodicity based on upriver migratory patterns of radio-tagged Paddlefish (Miller and Scarnecchia 2011).

Mortality rates.— Total instantaneous mortality rates (Z) of fully recruited male and female Paddlefish were estimated with catch curves (Ricker 1975), expressed as Z, the negative slope of a plot between the natural logarithm of the numbers caught (ln[N]) versus age (Age) for fully recruited ages. Annual survival S was calculated as $S = e^{-Z}$; annual mortality rate A was calculated as $A = 1 - S$. To smooth out the annual variations in recruitment, a composite catch curve was calculated for all available years (all but 5 years over the period 1992–2020) by sex. The catch curves were fitted by regression methods, and slopes of curves were compared using PROC GLM in SAS (SAS Institute 2012), with sex (male or female) as a class variable. The null hypothesis was that mortality rates for males and females did not differ; $P < 0.05$ was required for significance.

Recruitment.— Estimates of reproductive and recruitment success are based on two counts: surface visual counts of advanced age-0 fish and age-1 and older fish along transects in the upper end of Fort Peck Reservoir in July and August (S. E. Miller, University of Idaho, Moscow, unpublished). Boats (two-person crew) traveling at 8 km/h along the transects were used to enumerate age-0 Paddlefish. Fish feeding in the water column are startled by the boat, and their attempts to flee drive them to the surface, where they are enumerated within 10 m of each side of the boat (Fredericks and Scarnecchia 1997). Fish can frequently also be captured with dip nets (Scarnecchia and Ryckman 1997). Counts were conducted each year over the period 1997–2020. Owing to extreme water level fluctuations and other logistical factors, standard counts along transects were not feasible each year. For those reasons, estimates are assumed to be only approximate indicators of reproductive success and year-class strength (Scarnecchia et al. 2021).

RESULTS

Age and Growth

Over the period 1992–2020, 2,560 male Paddlefish were aged. Mean male age by year varied from 15.5 to 23.4 years; in nearly all years, however, mean age was between 18.5 and 21.5 years (Table 1). No harvested fish were aged less than age 8. Males at least 30 years old constituted 8.3% of the fish. Males at least 40 years old were found in 11 years, and the oldest male was aged at 59 years. Males typically showed broad spacing of annuli in their first 6–8 years, followed by much closer spacing as the fish started to undergo sexual maturation (Figure 3A). Annuli became progressively closer together as fish aged (Figure 3B).

Over the period 1992–2020, 2,558 female Paddlefish were aged. In every year, mean age of females was older than that for males and varied from 24.3 to 30.8 years (Table 1). The youngest harvested females found were age 12. Older females were more prevalent than males; nearly one-third (33.2%) of females were at least 30 years old. Females at least 40 years old were found in all 24 years sampled, and the oldest females (in 2013 and 2019) were aged at 65 years. Males did not mature and ascend the river until at least ages 9–12, whereas females typically did not mature and ascend the river until at least ages 16–19. Unlike males, females more commonly showed wide spacing of annuli past 10 years, with closer spacing in the ages 15–20 associated with sexual maturation (Figure 4A). As with males, annuli of female fish became progressively closer together as fish aged, especially in the oldest females (Figure 4B).

TABLE 1. Age (years) summary for harvested Paddlefish of the Fort Peck stock, Montana, 1992–2020. Data were not collected in 1997, 1999, 2001, 2003, or 2004.

	Male Paddlefish						Female Paddlefish					
Year	*N* of fish	Mean age (years)	% fish <16 years	% fish ≥30 years	*N* of fish ≥30 years	Max age (years)	*N* of fish	Mean age (years)	% fish <16 years	% fish ≥30 years	*N* of fish ≥30 years	Max age (years)
1992	15	21.3	20.0	6.7	1	33	29	29.5	3.5	55.2	16	44
1993	159	18.1	39.0	5.0	8	35	101	26.3	2.0	34.7	35	45
1994	139	15.5	56.1	4.3	6	38	240	26.0	3.8	32.9	79	44
1995	346	19.8	30.9	9.0	31	41	194	28.0	0.5	36.6	71	51
1996	125	20.5	24.8	12.0	15	40	220	26.9	1.8	32.3	71	47
1998	49	21.2	18.4	12.2	6	38	76	27.3	1.3	30.3	23	53
2000	85	19.1	38.8	11.8	10	38	68	24.3	2.9	27.9	19	48
2002	208	20.0	23.0	9.1	19	48	150	26.4	0.0	24.7	37	50
2005	126	21.8	23.0	11.1	14	59[a]	74	28.9	0.0	33.8	25	52
2006	127	19.7	32.3	9.4	12	52	111	26.9	5.4	30.6	34	56
2007	57	17.7	31.6	0.0	0	28	70	28.6	0.0	35.7	25	50
2008	96	19.7	28.1	9.4	9	44	87	28.6	0.0	38.0	33	56
2009	109	17.2	48.6	6.4	7	42	103	25.9	1.0	24.3	25	54
2010	77	19.0	40.3	9.1	7	37	70	25.3	7.1	24.3	17	53
2011	128	19.5	37.5	5.5	7	49	168	26.5	3.6	26.2	44	58
2012	107	20.1	32.7	6.5	7	52	89	28.1	0.0	38.2	34	52
2013	56	23.4	7.1	17.9	10	53	79	30.8	0.0	46.8	37	65[b]
2014	104	21.1	10.6	10.6	11	37	74	30.8	0.0	27.0	20	50
2015	65	20.8	18.5	10.8	7	46	86	30.5	0.0	50.0	43	59
2016	93	18.1	28.0	1.1	1	30	119	25.6	1.7	27.7	33	48
2017	97	20.9	17.5	10.3	10	36	108	29.8	0.0	38.9	42	60
2018	59	21.3	18.6	11.9	7	39	66	28.7	0.0	40.9	27	48
2019	55	19.0	25.5	3.6	2	37	99	27.2	0.0	26.3	26	65[b]
2020	78	20.2	19.2	6.4	5	36	77	29.5	1.3	42.9	33	56
Total	2,560				212		2,558				849	
% age ≥30 years					8.3						33.2	

[a]Observed maximum male Paddlefish age.
[b]Observed maximum female Paddlefish age.

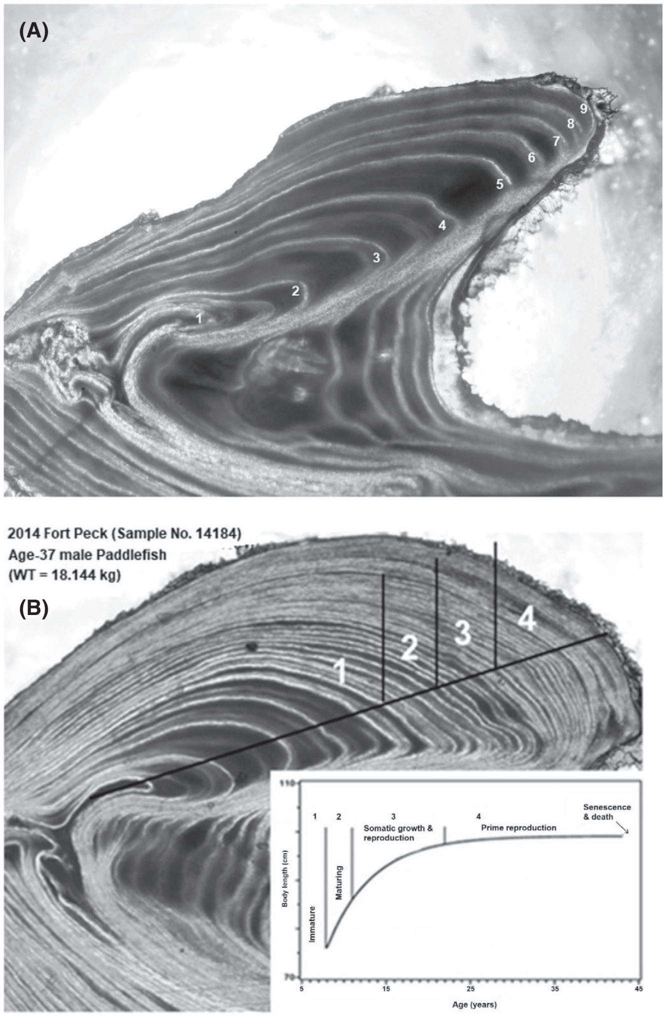

FIGURE 3. **(A)** Example of age determination for a young male Paddlefish (Fort Peck stock, Montana; sample number 20041; 2020). The male was age 9, with a body length of 864 mm and weight of 13.608 kg. Annuli are marked. **(B)** Example of an older male Paddlefish shows rapid growth in its immature phase (stage 1), slowing growth following initiation of sexual maturation (stage 2), slower growth during the growth and reproduction phase (stage 3), and much slower growth during the prime reproduction phase (stage 4). Stages 1–4 and approximate positions along the von Bertalanffy growth curve are patterned after Scarnecchia et al. (2007).

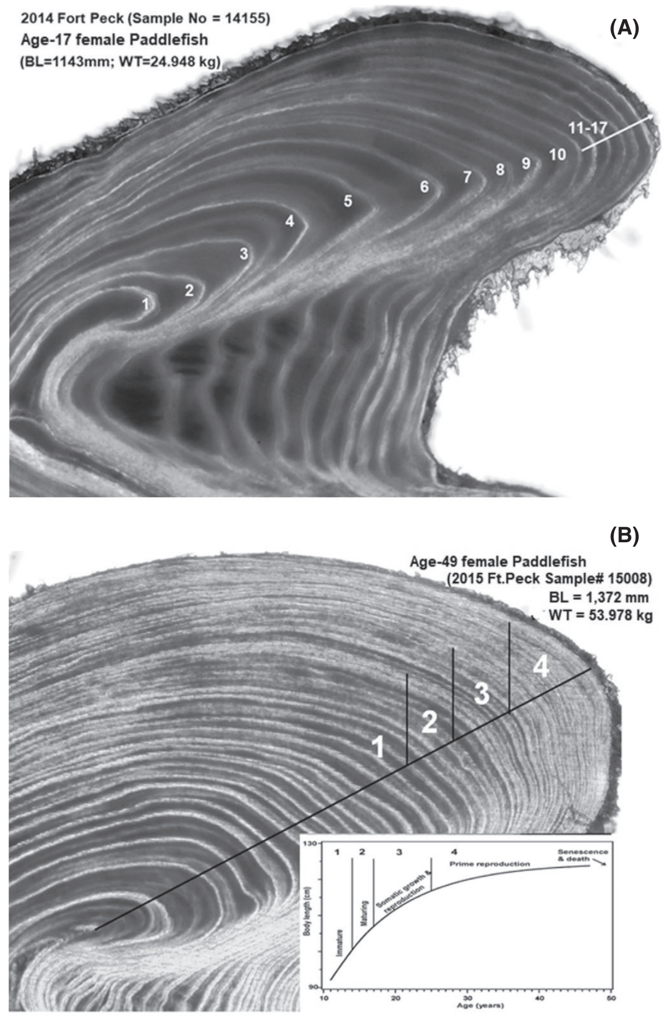

FIGURE 4. **(A)** Example of age determination for a young female Paddlefish (BL = body length; WT = weight). Annuli are marked. **(B)** Example of an older female Paddlefish shows rapid growth in its immature phase (stage 1), slowing growth following initiation of sexual maturation (stage 2), slower growth during the growth and reproduction phase (stage 3), and much slower growth during the prime reproduction phase (stage 4). Stages 1–4 and approximate positions along the von Bertalanffy growth curve are patterned after Scarnecchia et al. (2007).

Von Bertalanffy growth curves indicated that females were much larger than males over comparable ages in terms of BL (Figure 5) and weight (Figure 6). Males and females also diverged from each other in BL and weight as the fish aged (Figures 5, 6). The curves approaching asymptotes were consistent with the increasingly closer spacing of annuli on the dentary sections (Figures 3B, 4B).

Tagged fish that were recaptured at least 4 years later did not always increase in weight. Although both male and female fish tended to be heavier upon recapture, a substantial fraction of both male and female fish commonly lost weight as they aged (Figure 7A, B). Among all recovered fish, the number of fish showing a mean percent increase in weight of at least 0.5% since tagging compared to the number of fish showing a mean percent decrease in weight of at least 0.5% was 2.58 to 1 for males and 4.42 to 1 for females. Among the fish that were tagged at older ages (20 and older for males; 25 and older for females), fish increased in weight even less and were more likely to lose weight between capture and tagging than fish that were tagged and recaptured at younger ages. Among this subset of older fish, the number of fish showing a mean percent increase in weight of at least 0.5%

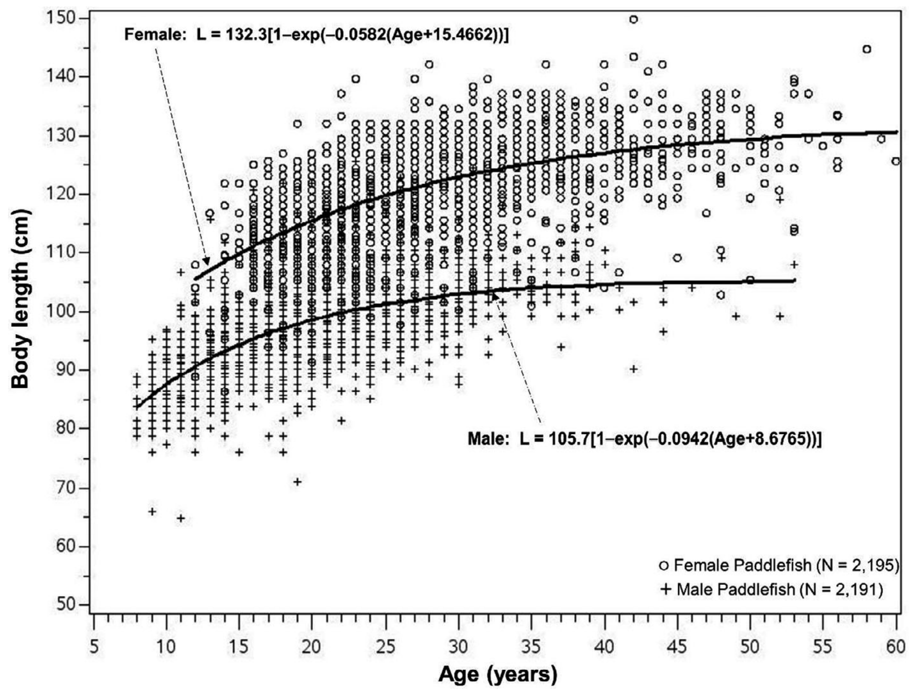

FIGURE 5. Composite von Bertalanffy growth curves for male and female Paddlefish of the Fort Peck stock, Montana, 1992–2020. Dotted lines and arrows identify the two fitted lines.

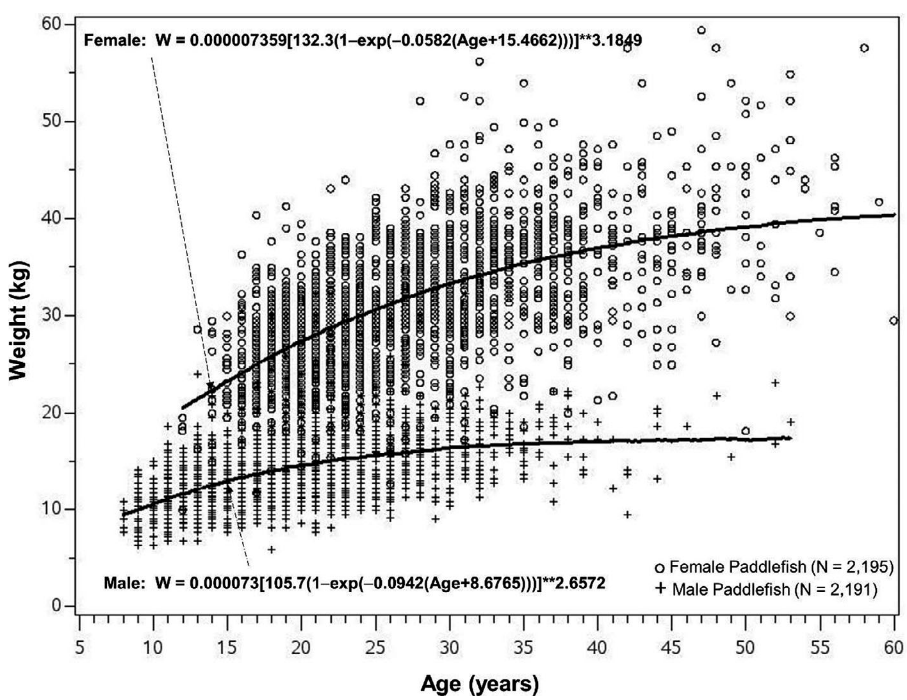

FIGURE 6. Composite weight-converted von Bertalanffy growth curves for male and female Paddlefish of the Fort Peck stock, Montana, 1992–2020. Dotted lines and arrows identify the two fitted lines.

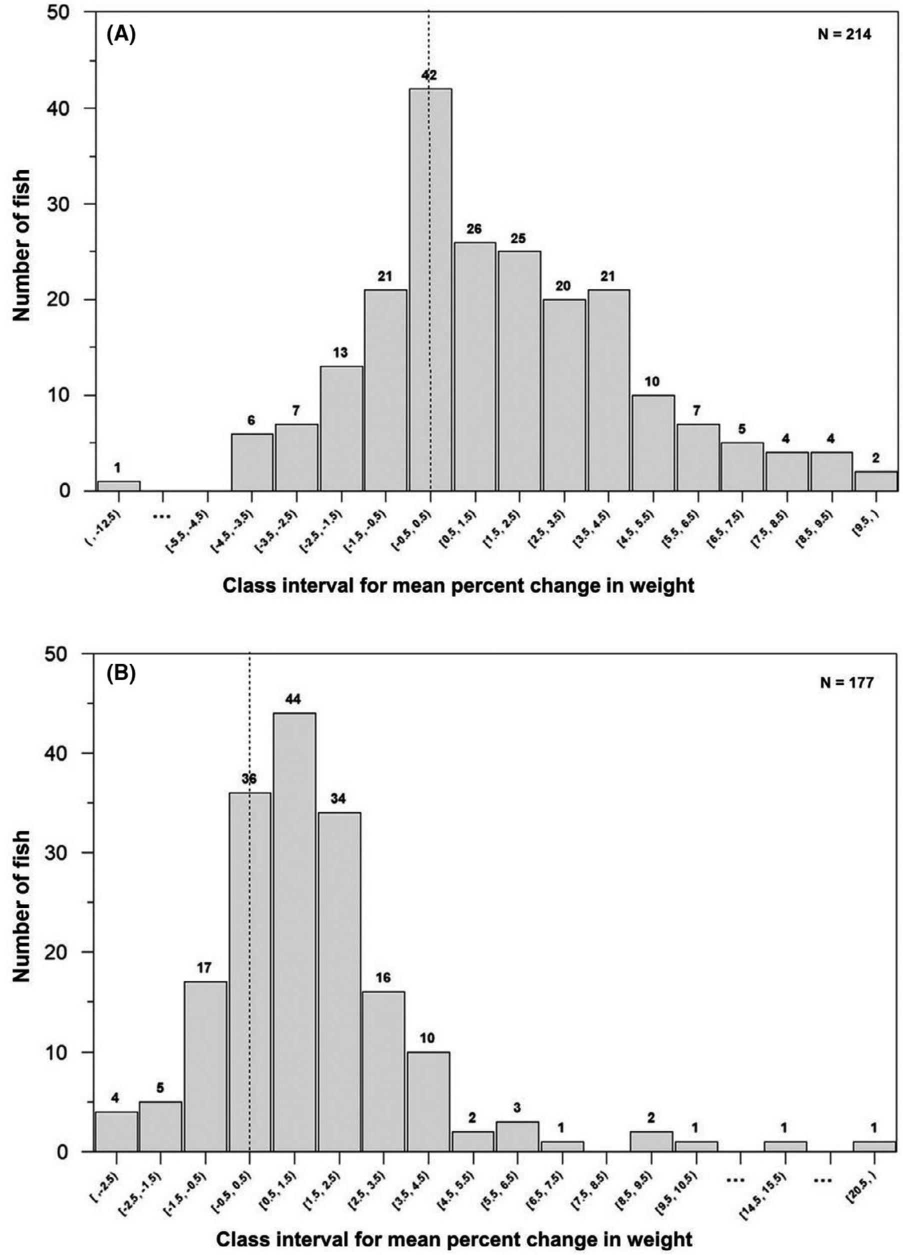

FIGURE 7. Numbers of fish by mean percent change in weight between tagging and recapture for all fish tagged and recaptured at least 4 years apart: **(A)** male Paddlefish and **(B)** female Paddlefish of the Fort Peck stock, Montana. The dotted line indicates no change in weight.

since tagging compared to the number of fish showing a mean percent decrease in weight of at least 0.5% was 1.90 to 1 for males and 2.89 to 1 for females (Figure 8A, B). This result was also consistent with the closer spacing of annuli in the older fish, associated with slower growth as the fish aged (Figures 3B, 4B).

Reproductive Periodicity

Frequency distribution of the number of years between jaw tagging and recovery also provides insight into reproductive periodicity. For males, large numbers of fish tagged in a particular year were recaptured the following year and 3 years later, with the maximum recoveries occurring 2 years after tagging. The pattern was indicative of a mixture of annual and biennial spawners. For females, a different pattern emerged; almost no fish tagged in a particular year were recaptured the following year, but large numbers were recaptured 2 years after tagging and every other year thereafter for 22 years, strongly indicative of a dominant biennial reproductive periodicity (Figure 9A, B).

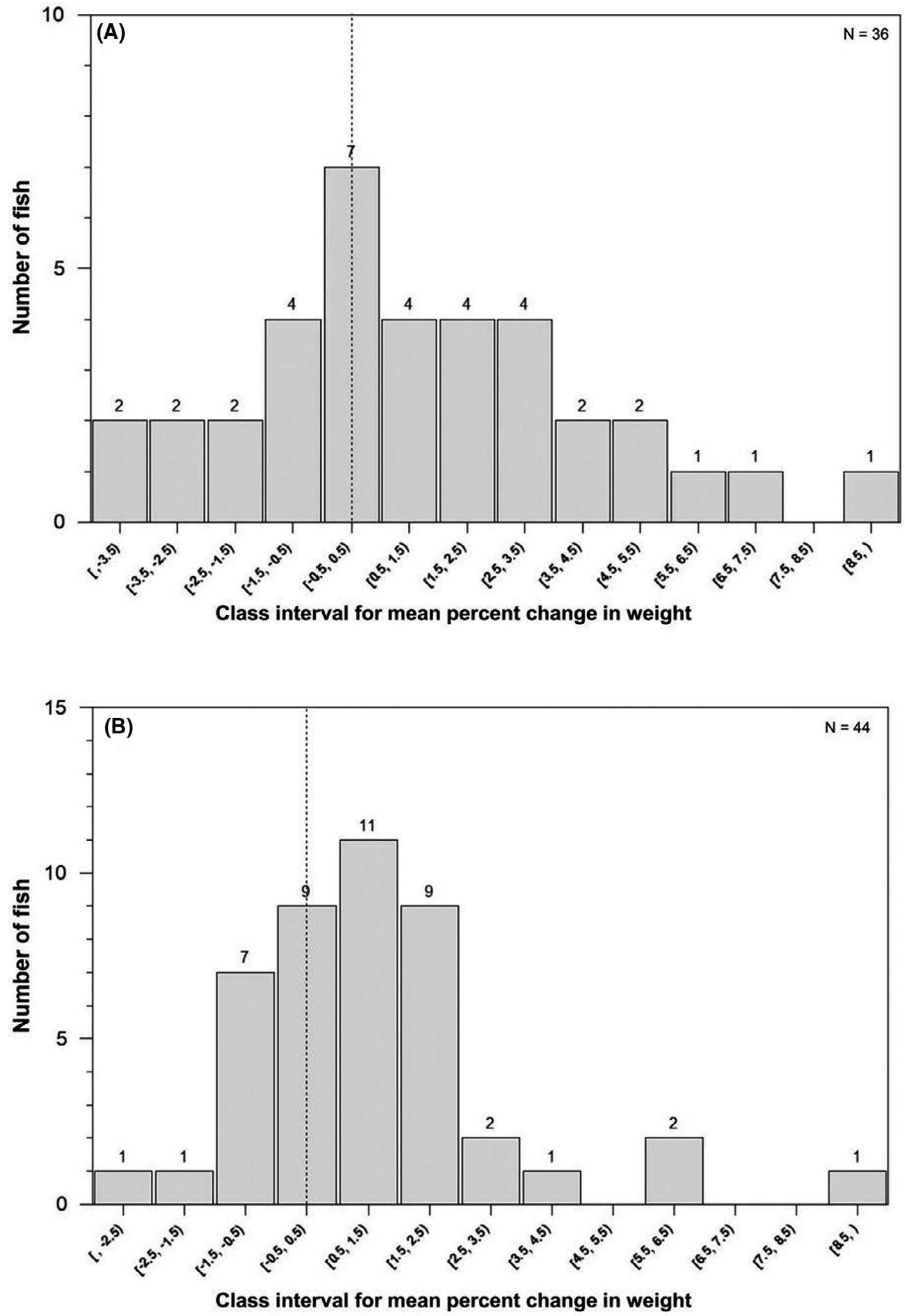

FIGURE 8. Numbers of fish by mean percent change in weight between tagging and recapture for fish tagged and recaptured at least 4 years apart: **(A)** age-20 and older male Paddlefish and **(B)** age-25 and older female Paddlefish of the Fort Peck stock, Montana. The dotted line indicates no change in weight.

Mortality Rates

Catch curves showed distinct differences between males and females. The regression plot for males (age 15 and older) was expressed as $\ln(N) = 8.20109 - 0.16346 \cdot \text{Age}$; the regression plot for females was expressed as $\ln(N) = 8.20143 - 0.12661 \cdot \text{Age}$. Instantaneous rate of total mortality (Z) was 0.163 for males and 0.127 for females. For males, S was 0.85 and A was 0.15. For females, S was 0.88 and A was 0.12 (Figure 10). The negative slope of the catch curve for males was significantly greater than that for females ($T = 4.52$, $P < 0.0001$).

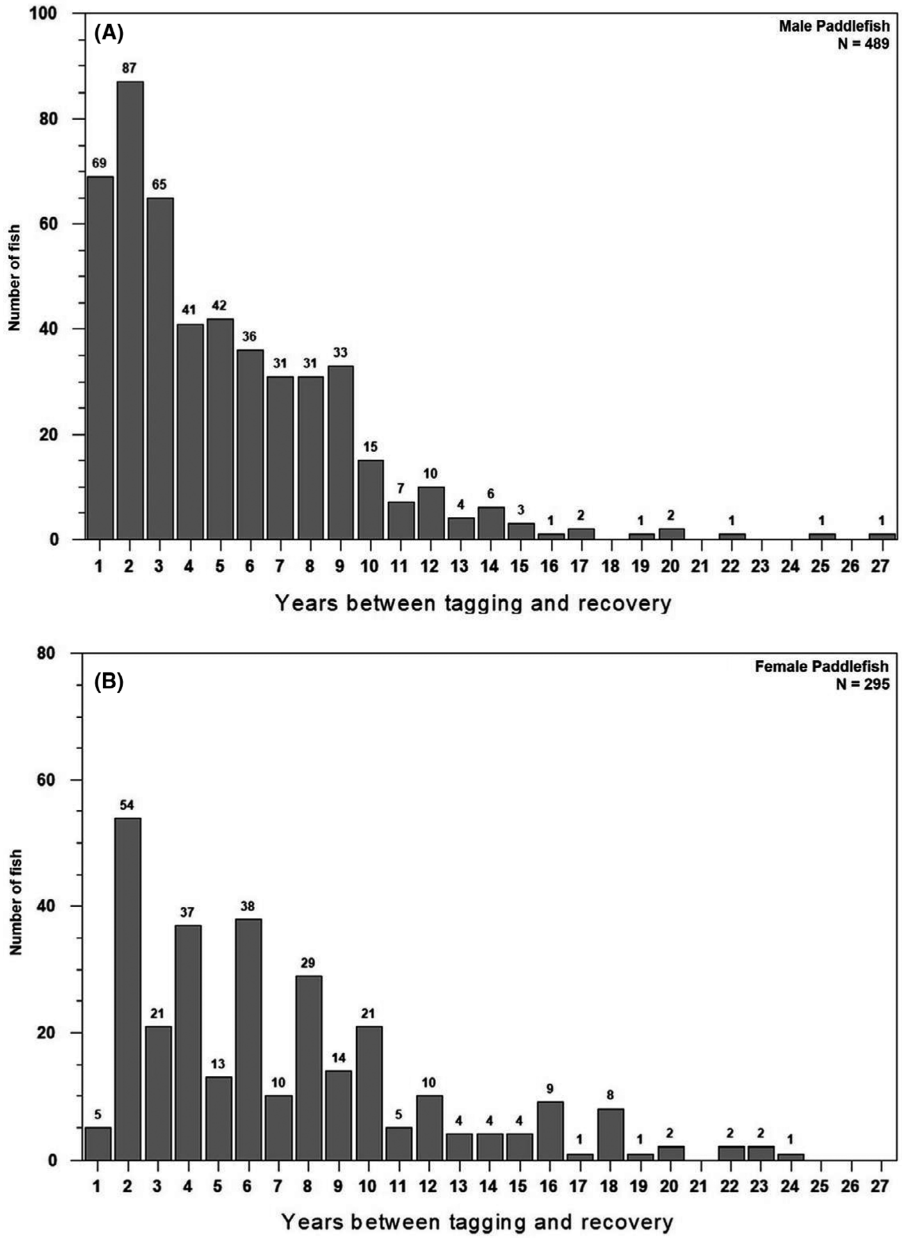

FIGURE 9. Number of years between tagging and recovery for **(A)** adult male and **(B)** adult female Paddlefish of the Fort Peck stock, Montana.

Recruitment

Counts of age-0 Paddlefish in transects were measurable in 1997 (113) and 1998 (97) but declined steadily to near zero by 2007, associated with drought and declining water levels in Fort Peck Reservoir. Since 2007, the only measurable numbers of fish observed were in 2008 and 2011, the 2 years of highest June flows and also years of increasing (2008) and high (2011) reservoir levels (Figures 2, 11). High subadult numbers in years following the high counts of age-0 fish were also apparent as indicators of recruitment (Figure 11). For example, high counts of subadults in 2013 followed high counts of age-0 fish in the 2011 cohort (Figure 11).

DISCUSSION

Age, Growth, and Life History Stages

Several demographic aspects of the Fort Peck Paddlefish, including large individual fish size (sometimes

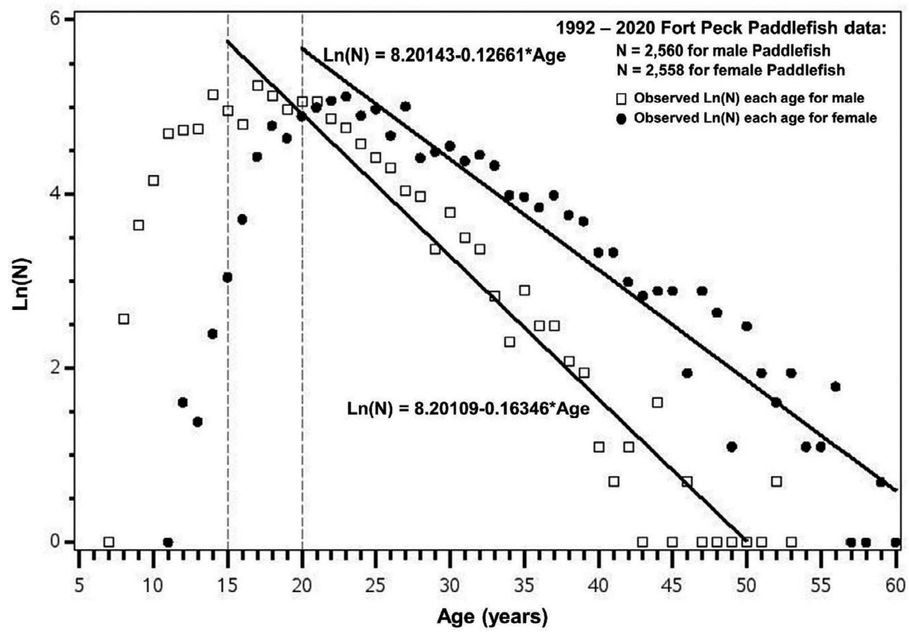

FIGURE 10. Composite catch curves for male and female Paddlefish of the Fort Peck stock, Montana, over the period 1992–2020; *N* refers to the total number of individual fish aged. Regression lines are based on age 15 and older for males or age 20 and older for females.

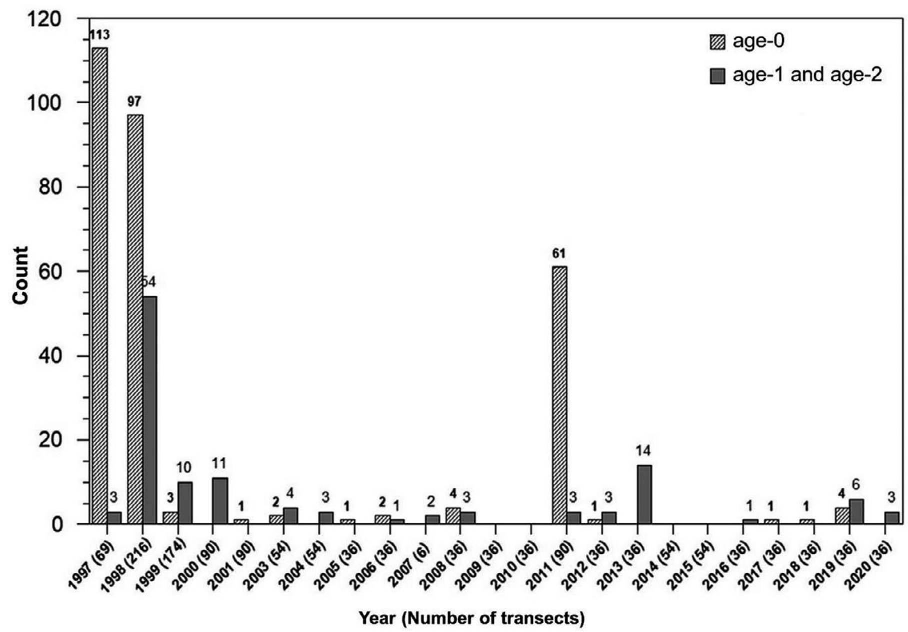

FIGURE 11. Counts of age-0 and subadult (mostly age-1 and age-2) Paddlefish along transects for the Fort Peck stock, Montana, by year (1997–2020).

exceeding 50 kg), late age at maturity (typically at least 9–10 years for males and 16–18 years for females), marked sexual size dimorphism (females much larger than males), slow or negative growth in weight among the oldest, largest fish of both sexes, and a long life span (exceeding 60 years; Scarnecchia et al. 2007, 2019a), are very similar to the demographic aspects of the Yellowstone–Sakakawea stock, the next stock downriver (Scarnecchia et al. 2007, 2019a). Results from Fort Peck Paddlefish are also consistent in pattern, age, and approximate duration with the specific life stages of Yellowstone–Sakakawea Paddlefish stock that have been identified (Scarnecchia et al. 2007). Yellowstone–Sakakawea Paddlefish were characterized as having five stages: (1) immature, (2) maturing, (3) somatic growth and reproduction, (4) prime reproduction, and (5) senescence to death. The five stages involved differential growth, fecundity, spawning periodicity, and fat accumulation (Scarnecchia et al. 2007, 2011). Prime spawning fish tended to minimize their time of gonadal recrudescence, grow little in body weight, store less fat than younger recruited fish, and put more energy into fecundity and reproduction (Scarnecchia et al. 2007). The Fort Peck stock also shows a dominant 2-year reproductive periodicity, a protracted life history, and a long life span that is more typical of northerly stocks, as opposed to the more compressed life history and shorter life span of more southerly stocks (Scarnecchia et al. 2011). Southerly stocks show less protracted life history stages, less sexual size dimorphism, more annual spawning of both sexes, and life spans commonly half as long (Scarnecchia et al. 2011). The differences among northern and southern stocks were interpreted in terms of the metabolic theory of ecology (Brown et al. 2004; Charnov and Gillooly 2004), the high natural metabolic rate of Paddlefish compared to sturgeons and many other fishes, and the higher metabolic rate at higher temperatures in southern latitudes (Scarnecchia et al. 2011).

Reproductive Periodicity

The reproductive periodicity as indicated by tag recoveries (males: 1–2 years; females: almost never 1 year but mostly 2 years) is consistent with movements of radio-tagged Paddlefish of the Fort Peck stock based on past radiotelemetry studies (Gardner and Berg 1980; Wiedenheft 1992; Miller and Scarnecchia 2011; Miller et al. 2011). Over a 4-year period, Miller and Scarnecchia (2011) tracked 80 radio-tagged fish for more than 1 year and found that at least 46 fish (34 males and 12 females) were repeat migrants (i.e., migrated more than once at some time during the 4-year period). Males had a shorter migration periodicity (mean, 1.5 years) than females (mean, 2.3 years), similar to the periodicity of the Yellowstone–Sakakawea stock (Scarnecchia et al. 2007). A longer gonadal recrudescence period for females than males is associated with delayed maturation and higher costs of reproduction for females (Scarnecchia et al. 2007). A longer gonadal recrudescence period for northern stocks (Montana and North Dakota) than southern stocks (Oklahoma) has also been linked to lower metabolic rates in the north (Scarnecchia et al. 2011).

Mortality Rates

The low total annual mortality rates observed in this study ($A = 15\%$ for males and 12% for females, including harvest) are very similar to the low rates for the stock estimated from jaw tag recoveries (18% for males and 8% for females; Glassic et al. 2020). In both studies, females had higher survival. The significantly higher female total survival found here would be expected with their later maturation and resulting delayed and less frequent upriver spawning migration subjecting them to fishing. With the lack of a mandatory retention regulation, it is expected that the lower mortality of females early in their lives (e.g., between ages 9 and 16) associated with their lack of vulnerability to any harvest may be compensated for later in life, as larger females, even if migrating less often upriver, are preferentially targeted for harvest by snaggers (Scarnecchia et al. 2000).

The low total annual mortality of Fort Peck Paddlefish is also consistent with, and a necessary aspect of, life as a late-maturing, iteroparous spawner subjected to fishing. With the protracted life history of the stock and the trade-offs between reproduction and mortality, an evolved low natural mortality rate on recruits would be anticipated for species persistence (Williams 1966; Bell 1980; Jørgensen and Holt 2013). The tendency for declines of both Paddlefish and sturgeon stocks (Boreman 1997) rangewide typically results not only from poor reproductive success and its ecological reasons (Scarnecchia et al. 2019b), but also from a combination of excessive harvest of recruited fish and increased natural mortality of adults from a variety of anthropogenic factors, such as catch-and-release mortality, entrainment at dams, and boat propeller strikes (Bettoli et al. 2019; Hoover et al. 2019).

Recruitment

Transect counts conducted for the Fort Peck stock are used as indicators of reproductive success and recruitment. In most years, the typically low transect counts of age-0 and subadult (age-1 and age-2) fish and other nonrandom, nontransect searches for age-0 and subadult fish indicate that some reproduction seems to occur in most or all years. However, recruitment is stronger with higher spring flows in the Missouri River and rising reservoir levels (e.g., late 1990s, 2008, and 2011; Figure 11) and weaker in years of drought (Berg 1981; Nagel 2017). The same pattern has been seen in the Yellowstone–Sakakawea stock (Scarnecchia et al. 2019b, 2021).

However, transect counts for the Fort Peck stock have been much less successful, perhaps an order of magnitude so, than those for the Yellowstone–Sakakawea stock immediately downriver (Scarnecchia et al. 2009, 2021). Although interannual recruitment variation in the Fort Peck stock has been detected, the amount of variation in recruitment has been less than that in the Yellowstone–Sakakawea stock, where one year-class (1995) has dominated the fishery for two decades, and in the Grand Lake (Oklahoma) stock, where the 1999 year-class has dominated the fishery for the following decade or more (Scarnecchia et al. 2011). These results suggest to us that the Fort Peck stock is characterized by less overall recruitment than the Yellowstone–Sakakawea stock over the past 25 years.

Recruitment of year-classes can also be discerned, at least approximately, from the frequency of young males in the harvest, much as is done for the Yellowstone–Sakakawea stock (Scarnecchia et al. 2014). Analysis of dentaries since 1992 indicates that some recruitment occurs in all years. However, results from 2007, the only year with mandatory retention (Figure 12), indicate that recruitment of the Fort Peck stock over the study duration has not matched the episodically high recruitment exhibited in the Yellowstone–Sakakawea stock (e.g., in 1995; Scarnecchia et al. 2014, 2019b). For comparison between the stocks, using 2007 data, catches of young male recruits (ages 10–14) in the Fort Peck stock constituted only 26% of the total catch of males and only 12% of the total aged catch of both sexes ($n = 127$). In contrast, catches of young male recruits (ages 10–14) in the Yellowstone–Sakakawea stock constituted 78% of the male harvest (Montana and North Dakota combined) and 58% of the total aged catch of both sexes ($n = 1{,}472$; University of Idaho, unpublished data). The difference in proportion of young male recruits was attributed to a strong year-class in the Yellowstone–Sakakawea stock (Scarnecchia et al. 2014), which was not seen in the Fort Peck stock. A similar pattern of higher versus lower age-0 and subadult counts by year has been associated with comparable patterns of higher versus lower river discharges and reservoir elevation level fluctuations in both Fort Peck Reservoir (Figure 2) and Lake Sakakawea (Scarnecchia et al. 2021). However, the Fort Peck stock has not experienced nearly the magnitude of recruitment as the Yellowstone–Sakakawea stock. Understanding specific factors leading to Paddlefish recruitment

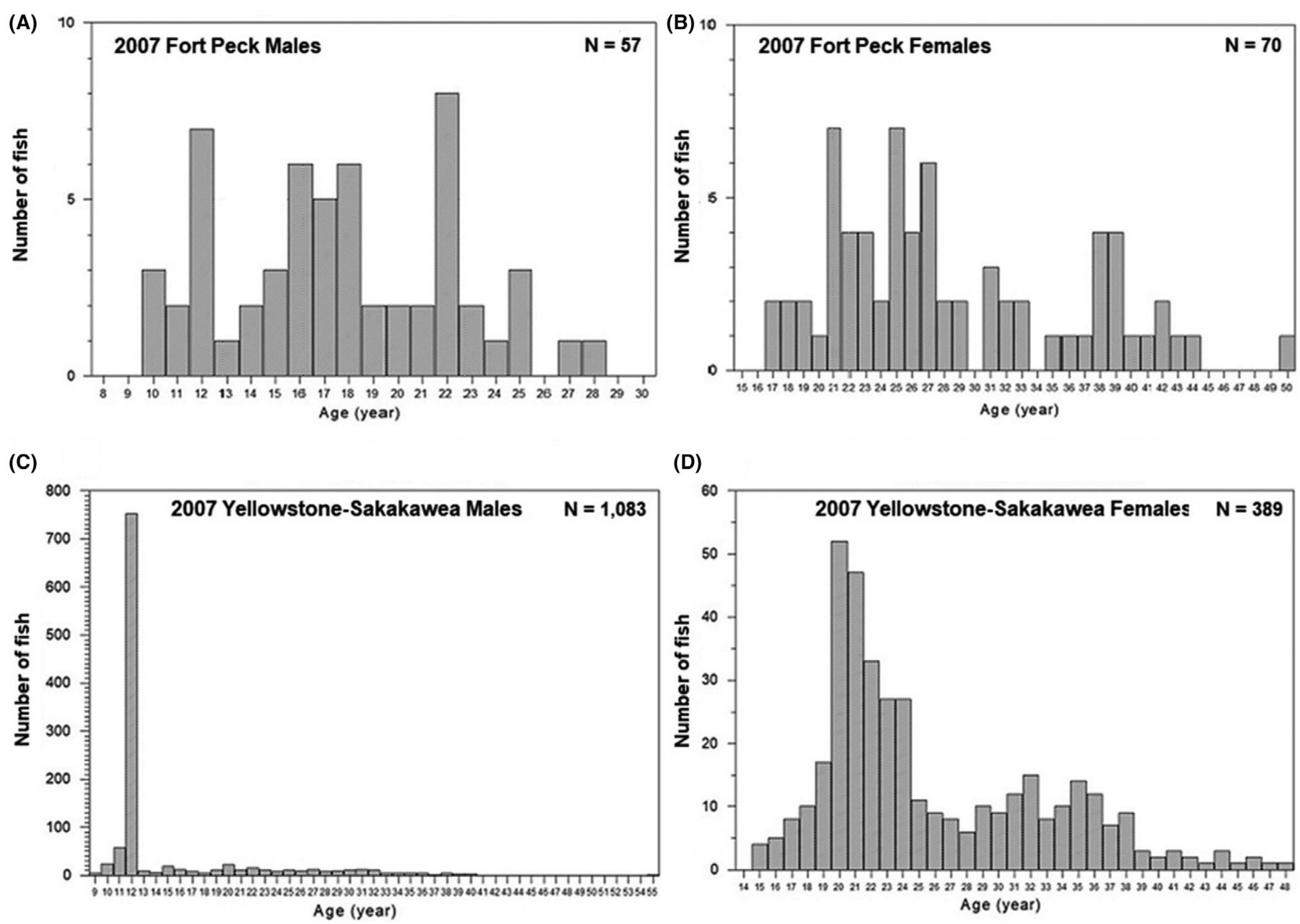

FIGURE 12. Age structure of harvested Paddlefish under mandatory retention in 2007 for **(A)** Fort Peck stock (Montana) males, **(B)** Fort Peck stock females, **(C)** Yellowstone–Sakakawea (Montana–North Dakota) males, and **(D)** Yellowstone–Sakakawea females. A strong year-class from 1995 in Lake Sakakawea is evident for males in panel C; females had not yet recruited to the fishery.

has long been identified as a critical but widely unfulfilled need in their conservation (Russell 1986; Jennings and Zigler 2009; Scarnecchia et al. 2019b). In the neighboring Yellowstone–Sakakawea stock, recruitment of the strongest year-classes has been fairly well documented. Initial high recruitment was associated with the trophic upsurge following initial reservoir filling (Scarnecchia et al. 1996) and, thereafter, with smaller upsurges following reservoir refilling after the cessation of drought periods (Kimmel and Groeger 1986; Scarnecchia et al. 2009, 2019b). After initial reservoir filling, however, it was concluded that even in years of higher recruitment, survival to age 1 was always low, even in years of stronger year-classes (Scarnecchia et al. 2009, 2019b).

Harvest Management Considerations

The low total mortality, low natural mortality, and modest recruitment of the Fort Peck Paddlefish stock provide both limitations and opportunities for sustainable harvest management. In long-lived species that are difficult to age as they grow older, errors in age estimation can lead to erroneous estimates of natural and harvest mortality (Campana 2001). Small errors in estimates can propagate in a cohort through decades, leading to large overall errors. One simple way of dealing with this common (if often unrecognized) problem is to assume that ages are probably underestimated (Scarnecchia et al. 2006) and set the allowable harvest based on the numbers of recruited young, more easily aged fish into the fishery. This approach ("fish in" [recruitment] – "fish out" [harvest plus natural mortality]) can serve to maintain stock size (Ricker 1975, Figure 1.2). The same approach has also been used to set a harvest cap for the Yellowstone–Sakakawea stock (balancing 5-year recruitment of age-10–14 males and age-17–21 females against harvest; Scarnecchia et al. 2021).

Age data from this study indicate that despite the absence of a mandatory retention requirement (except in 2007), management actions, in particular the low harvest rate, have had the intended result of maintaining older fish in the population and avoiding a skewed sex ratio toward males. This result is especially important toward the goal of maintaining old females (Francis et al. 2007; Kuparinen and Merilä 2007; Gwinn et al. 2015), the largest of all Paddlefish taken (Scarnecchia et al. 2014).

As of 2021, harvest of the Fort Peck Paddlefish stock has been managed based on the conservative approach of maintaining population size, age structure, and sex ratios and allowing harvest consistent with its modest recruitment. Glassic et al. (2020:559) concluded that "the Fort Peck Paddlefish population appears to be stable and well-managed over the past 25 years." Efforts are planned to continue obtaining information from fishery monitoring of harvest and anglers to maximize the benefits of the limited number of fish available for capture and harvest (Scarnecchia et al. 2021). In addition, Paddlefish management will be evaluated within the broader context of fisheries management and stocking programs for other species within Fort Peck Reservoir (Dalbey et al. 2012).

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