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Fort Peck paddlefish population survival and abundance in the Missouri River

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Abstract

Excessive fishing pressure can induce population declines or complete collapse of fisheries. Unless commercial and recreational fisheries for K-selected fishes, or those with slow growth and late maturation, are carefully managed, declines in abundance or fishery collapse is probable. Paddlefish *Polyodon spathula*,are a K-selected species that experienced historical declines in abundance as a result of habitat degradation and overfishing. Mark-recapture studies are well-suited for long-lived fishes by providing information on population density and vital rates. For sustainable commercial or recreational fisheries targeting species such as the paddlefish, managers require accurate estimates of population vital rates including survival, abundance, and exploitation. We used a Montana Fish, Wildlife & Parks (MFWP) mark-recapture dataset and modified Jolly-Seber (POPAN) models to estimate survival, recapture, probability of entry, and abundance of 8,518 tagged paddlefish over a 25-year period. With many supporting estimates including stable survival (0.92 for females, mean of 0.82 for males), low exploitation rates (means of 2.6% for females and 2.9% for males), and stable abundance estimates (25-year mean of 12,309 individuals for both sexes), the Fort Peck paddlefish population appears to be stable and well-managed over the past 25 years. Presently, this is the only study focused on paddlefish in North America that has estimated survival and abundance for both male and female paddlefish using contemporary analyses. This research provided a unique opportunity to highlight that the effort exerted by management agencies to collect long-term field data is extremely useful to our understanding of fish populations and management.

KEYWORDS

fisheries ecology, fisheries resources

1 | INTRODUCTION

Excessive fishing pressure, whether commercial or recreational, can induce population declines or complete collapse of fisheries (Cooke & Cowx, 2006; Erisman et al., 2011; Froese, 2011; Hutchings & Reynolds, 2004; Sullivan, 2003). Responses to fishing pressure are often linked to life-history strategy. Life-history strategies are usually defined within the r-K continuum; that is r-selected species are thought to recover more quickly from harvest than K-selected species (Musick, 1999). However, overfishing can be consequential for r-selected fishes, exhibiting early maturity, high fecundity, and short life spans (Longhurst, 2002), such as Atlantic cod *Gadus morhua*, whose population collapse was attributed to high commercial fishing pressure (Hutchings & Myers, 1994). Winnemiller and

Rose (1992) redefined the r-K continuum to include three extreme life-history strategies: equilibrium (similar to K-selected), opportunistic (similar to r-selected), and periodic (K-selected with large clutches and little parental care). Within the three-end point strategy (Winnemiller & Rose, 1992), equilibrium and periodic life-history strategies are arguably less resilient to harvest than opportunistic strategists. Periodic species (Winemiller & Rose, 1992), such as Acipenseriformes, exhibit late age at maturation, long life spans, low natural mortality, and slow somatic growth rates (Stevens, Bonfil, Dulvy, & Walker Stevens, 2000) and can negatively respond to harvest rather quickly. Broadly, K-selected fishes are considered one of the most at-risk groups of fishes in the world (Olden, Poff, & Bestgen, 2008; Parent & Schriml, 1995; Pikitch, Doukakis, Lauck, Chakrabarty, & Erickson, 2005). Unless commercial and recreational fisheries for K-selected fishes are carefully managed, declines in abundance or fishery collapse is probable (Zhang et al., 2020).

Paddlefish *P. spathula*, are a K-selected or periodic species that is desirable in recreational and commercial fisheries. Unfortunately, many paddlefish populations experienced declines in abundance as a result of habitat degradation and overfishing between the late 1800s to mid 1990s (Bettoli, Kerns, & Scholten, 2009; Carlson & Bonislawsky, 1981; Combs, 1982; Graham, 1997; Zhang et al., 2020). Given that paddlefish are long-lived and late to mature, they are particularly vulnerable to overfishing—similar to other species in the order Acipenseriformes (Boreman, 1997). Paddlefish conservation efforts throughout North America were initiated by the mid 1990s and prioritized population monitoring and more conservative regulations to facilitate successful conservation (Bettoli et al., 2009; Scholten & Bettoli, 2005). For sustainable commercial or recreational fisheries targeting species such as the paddlefish, managers require accurate estimates of population metrics including survival, abundance, and exploitation. Once these metrics are available, the status of paddlefish populations can be put in context of harvest leading to more informed management decisions (i.e., harvest regulations) to conserve the population and ensure sustainable fisheries.

Mark-recapture techniques can provide a framework for statistical estimation of survival and abundance (Pine, Pollock, Hightower, Kwak, & Rice, 2003), which are key metrics used in species conservation (Williams, Nichols, & Conroy, 2002). Contemporary open-population mark-recapture studies and analyses (i.e., those that can include births, deaths, immigration, and emigration such as Jolly-Seber models [JS]; Jolly, 1965; Seber, 1965) are well-suited and valuable for conservation of long-lived fishes as they can also include environmental or management variables that may affect population vital rates. Moreover, individual capture histories within a mark-recapture framework can provide information on emigration and immigration; an important animal behavior that is overlooked in some closed-population models (e.g., Lincoln-Peterson, etc.).

Here, we used a 25-year mark-recapture dataset to estimate survival and abundance for the paddlefish fishery in the Missouri River and Fort Peck Reservoir, Montana, USA (hereafter termed the Fort Peck population). We evaluated whether the long-term dataset had sufficient information to use mark-recapture models (e.g., Jolly-Seber) and produce reliable estimates of adult survival rates and sex-specific adult abundance.

Despite the cultural, economic, and ecological value of this species, few peer-reviewed studies incorporate estimates of paddlefish population abundance (e.g., Pierce, Graeb, Willis, & Sorensen, 2015; Runstrom, Vondracek, & Jennings, 2001), though some include relative abundance (e.g., Lein & Devries, 1998; Scholten & Bettoli, 2005). Mark-recapture studies, such as those implemented by Runstrom et al. (2001), Pierce et al. (2015), and this study can provide valuable survival and abundance estimates. Prior estimates of survival and abundance have not been computed for the Fort Peck paddlefish population with contemporary methods. Furthermore, we used the abundance data to estimate exploitation for the targeted paddlefish fishery from 2005 through 2017 with the overarching goal of informing managers of a sustainable harvest level for the future.

2 | METHODS

Since 1993, paddlefish have been sampled using standardized methods in the Missouri River above Fort Peck Reservoir near Fred Robinson Bridge (river kilometer 3,091; Figure 1). Paddlefish are sampled during the spawning migration in the Missouri River during the ascending limb of the hydrograph when discharge is ≥226 $m^3 s^{-1}$ using floating gill nets that are drifted perpendicular to flow. Gill nets

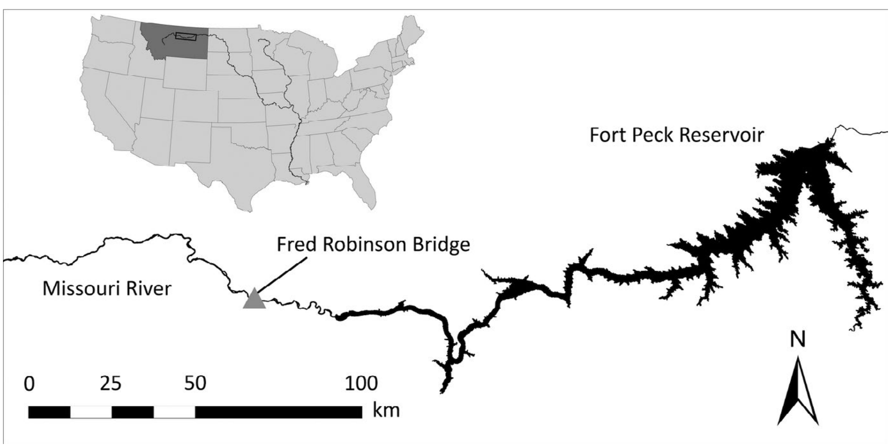

FIGURE 1 The complex of Fort Peck Reservoir, Montana, USA, and the Missouri River showing the extent of the sampling area for the Fort Peck population of paddlefish

are 45.7-m long, 2.4-m deep, and have 15.2-cm bar mesh. Weight, length (eye-fork length; EFL), sex, and tag number are recorded for all paddlefish sampled. Paddlefish without a tag are tagged using a numbered metal jaw tag, thus all paddlefish sampled are individually marked. Historical paddlefish live-recapture data were reformatted into an encounter history for each individual during each sampling occasion (one occasion per year, 1993–2017). In the encounter-history dataset, data regarding sex of the fish were included where available. Paddlefish live-recapture data also contained information on weight (kg) and EFL at time of capture, but was not consistent enough at the encounter-level to be included within the encounter-history dataset.

Phone-creel survey was used to estimate harvest from 2005 through 2017 (Figure 2). Each year, all paddlefish anglers were contacted by phone and asked if they harvested a paddlefish. Paddlefish harvested were also reported to creel clerks on site, but reporting was not mandatory; therefore, onsite harvest numbers are less than the number estimated from the phone-creel survey. On-site paddlefish harvest data did include weight (kg), EFL, sex, and age (years) at time of harvest. Thus, the ratio of males to females harvested from the on-site creel survey was applied to the phone-creel survey estimates to obtain the number harvested by sex.

River discharge (m^3s^{-1}) data were compiled from the Missouri River at the U.S. Geological Survey (USGS) stream gage near Landusky, Montana (UTM Zone 12:673704.6 E, 5277926.9 N; USGS, 2018). Mean daily discharge from 1 April to 30 June during the study period (1993–2017) was summarized for maximum (mean daily), mean (mean daily), minimum (mean daily), and range (mean daily) discharge each year. Additionally, discharge data from 15 April to 15 May were summarized because this time period was identified as the consistent dates of sampling. For the 31 days of possible sampling (15 April–15 May), if the mean daily discharge was between 240 and 510 m^3s^{-1} (determined as ideal conditions for drifting gill nets), the day was assigned a one, if mean daily discharge was outside the minimum and maximum, the day was assigned a zero. For each year, the sum of the assigned values was calculated and divided by 31 (days of possible sampling) to obtain a metric defined as "discharge-days proportion."

Paddlefish mark-recapture data were analyzed using the superpopulation (the total number of individuals present during the

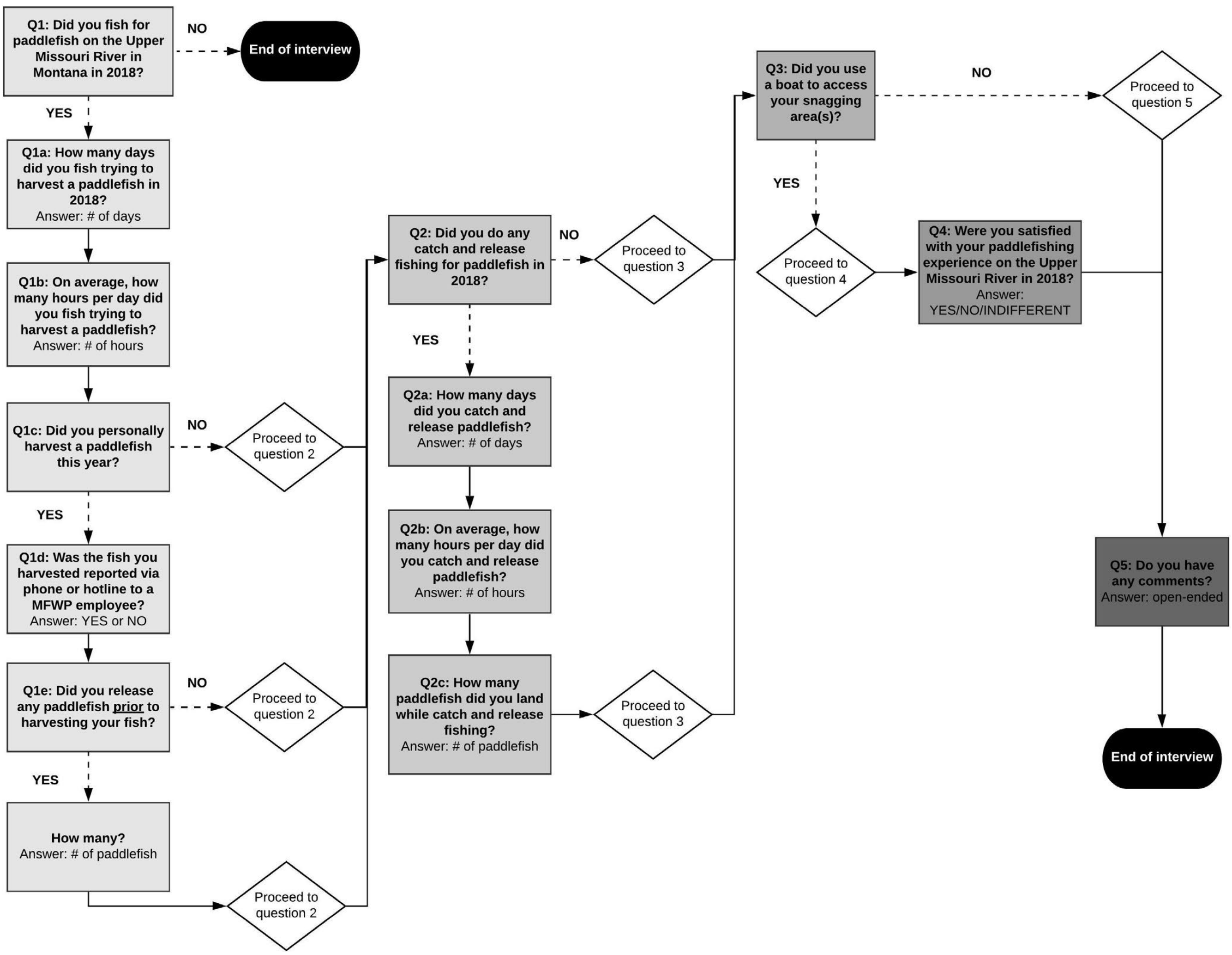

FIGURE 2 Flowchart depicting the phone-creel survey used to estimate harvest of the Fort Peck population of Paddlefish from 2005–2017

25-year study in the Fort Peck population; POPAN) parameterization of the Jolly-Seber model, which uses multi-year mark-recapture data to estimate annual rates of apparent survival (φ) and detection (p), annual probabilities of entry to the superpopulation (*pent*), and the size of the superpopulation, which is the total number of individuals ever in the population during the multi-year study (N) (Crosbie & Manly, 1985; Jolly, 1965; Schwarz & Arnason, 1996; Seber, 1965). From those quantities, the number of individuals present at the beginning of the study (N_1), the number of new entrants each year (b_i, where i refers to a given year), and the number of individuals present in each subsequent year of the study (N_i) were obtained as derived quantities. Here, probability of entry is defined as the probability that an adult (i.e., sexually mature) paddlefish that has not been encountered enters the population. The abundance estimated here is for adult paddlefish.

We fit separate models for males and females to provide an opportunity for models to converge and because sex-specific spawning periodicity was not apparent in our data due to low recapture rates over the 25-year period. Sex-specific differences in spawning periodicity are well described in paddlefish populations and to adequately account for this variation we chose to model males and females separately. Though this approach is unconventional, ignoring variation in sex-specific survival and abundance from year to year would have important implications for harvest management strategies.

For φ, two model structures were considered where φ was held constant or allowed to vary by year. For p, six model structures were considered where p was held constant among years, allowed to vary each year with confounding years constrained ($p_1 = p_2$ and $p_{24} = p_{25}$), allowed to vary with yearly maximum discharge, yearly mean discharge, yearly minimum discharge, yearly range of discharge, or yearly discharge-days proportion. For *pent*, six model structures were considered in which *pent* was held constant among years, allowed to vary by year, yearly maximum discharge, yearly mean discharge, yearly minimum discharge, yearly range of discharge, or yearly discharge-days proportion. The possible combinations of structures for φ, p, *pent*, and N resulted in 72 models for each sex.

We estimated φ, p, *pent*, and N using Program MARK (White & Burnam, 1999) via RMark (Laake, 2013) using the R software system (R Core Team, 2017). Akaike's Information Criterion adjusted for sample size (AIC_c) was used to evaluate support among the competing models (Burnham & Anderson, 1998; Burnham & Anderson, D. R., White, G. C., Brownie, C., and Pollock, 1987). Goodness of fit was assessed using Program RELEASE as implemented through Program MARK. We conducted model selection using a threshold of 2 AIC_c to determine the top model for female and male paddlefish. All confidence intervals reported are 95%.

Exploitation was estimated for each sex using the abundance estimates per year from the POPAN models and harvest estimates from phone creel surveys. Exploitation was estimated as the quotient of the proportion of paddlefish harvested and abundance of paddlefish in that year. Confidence intervals for exploitation were estimated as the quotient of the proportion of paddlefish harvested in a year and the confidence intervals for the abundance estimate for that year.

3 | RESULTS

From 1993 through 2017, Montana Fish, Wildlife & Parks (MFWP) tagged 8,518 individuals in the Missouri River above Fort Peck Reservoir: 2,469 females and 6,049 males. The maximum number of individual paddlefish encountered was 834 paddlefish in 2017 and the minimum was 34 in 2001. Few tagged paddlefish were recaptured; of the 2,469 adult females tagged, 184 (7.5%) were recaptured and of 6,049 males tagged 624 (10.3%) were recaptured. Mean adult female EFL was 110.5 cm (minimum 82.4–maximum 175.3 cm) and weight was 29.7 kg (minimum 9.1–maximum 56.7 kg), and mean male EFL was 90.3 cm (minimum 54.8–maximum 144.8 cm) and weight was 13.4 kg (minimum 4.9–maximum 39 kg). The distribution of EFL and weight for females and males was relatively stable for the 25-year period (coefficients of variation [CV] for length among years was 1.7% for females and 1.7% for males; CV for weight among years was 8.9% for females and 8.0% for males).

Mean river discharge from 1 April through 30 June was 340 m^3s^{-1} during the 25-year study. Maximum spring river discharge was 2018 m^3s^{-1} in 2011 and minimum spring river discharge was 119 m^3s^{-1} in 2001. Discharge-days proportion varied from 0 to 1 during the 25-year study with 7 years having all discharge days between 240 and 510 m^3s^{-1} and 7 years with no discharge days between 240 and 510 m^3s^{-1} (Figure 3).

The most-supported POPAN models for female paddlefish estimated constant survival, recapture rate varying through time, and probability of entry being best estimated by either discharge days or held constant over time (Table 1). We describe the similarities or differences between those models in more detail below because the two models were within the 2 AIC_c threshold. The most-supported POPAN model for male paddlefish estimated survival varying through time, recapture rate varying through time, and probability of entry varying through time (Table 1). The most-supported model was selected based on a delta AICc of 9.7 between the top and second model. For males, no support was given to include discharge covariates in the model.

Survival was estimated to be constant in the best-competing models for females. The top model for females estimated φ as constant at 0.92 (CI 0.89–0.94) over the 25-year period and p as time varying with a mean rate of 0.01 (CI 0.00–0.03). Survival was estimated to vary among years for the best-competing models for males. The top model for males estimated φ as time varying with a mean of 0.82 (CI 0.53–0.94) over the 25-year period and p as time varying with a mean rate of 0.03 (CI 0.00–0.08 CI).

The superpopulation of adult females, the total number of individuals present during the entire 25-year study in the Fort Peck population, was estimated to be 24,531 individuals. The proportion of those individuals present at the beginning of the study was estimated to be 0.18 of the superpopulation estimate or 4,416

FIGURE 3 Proportion of days from 15 April through 15 May (31 days) when discharge was from 240 to 510 cubic meters per second (cms; m^3s-1)

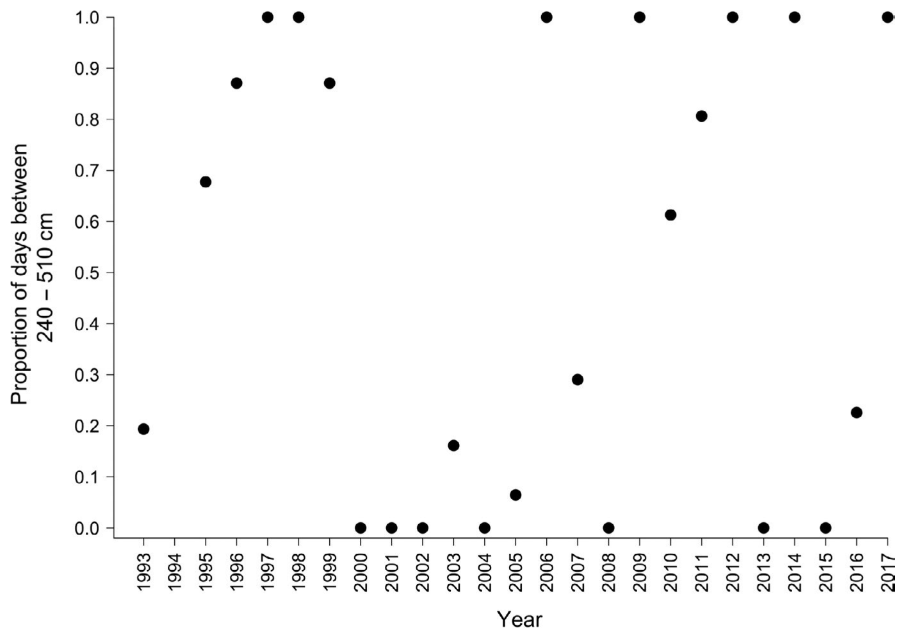

TABLE 1 Jolly-Seber (POPAN) model results for adult paddlefish. Only top five models displayed for each sex

Model structure	Number of parameters	AICc	Delta AICc	Weight
Females				
φ (constant) p (time) pent (discharge days) *N* (constant)	27	2,559.7	0.0	0.3
φ (constant) p (time) pent (constant) *N* (constant)	26	2,560.2	0.5	0.2
φ (constant) p (time)pent (mean discharge) *N* (constant)	50	2,561.2	1.5	0.1
φ (constant) p (time) pent (minimum discharge) *N* (constant)	49	2,561.8	2.1	0.1
φ (constant) p (time) pent (maximum discharge) *N* (constant)	49	2,562.2	2.5	0.1
Males				
φ (time) p (time) pent (time) *N* (constant)	72	7,249.2	0.0	0.9
φ (constant) p (time) pent (time) *N* (constant)	49	7,258.9	9.7	0.0
φ (time) p (time) pent (minimum discharge) *N* (constant)	50	7,281.9	32.7	0.0
φ (time) p (time) pent (maximum discharge) *N* (constant)	50	7,285.4	36.2	0.0
φ (time) p (time) pent (mean discharge) *N* (constant)	50	7,286.7	37.5	0.0

Note: Symbols: φ, survival; p, recapture; pent, probability of entry; *N*, abundance; AICc, small-sample corrected Akaike Information Criterion.

individuals. The top model for females estimated a mean *pent* of 0.03 (mean SE 0.009). We compared *pent* rates for the top two models, where *pent* was a function of annual values for "discharge days" or held constant; confidence intervals overlapped for all *pent* estimates for the top two models (Figure 4). Combinations of entry rates described above and losses due to mortality resulted in annual abundance estimates between 4,488 (CI 1698–11,860) and 10,254 (CI 7,287–14,431); the confidence intervals for the top two models overlapped for every estimate over the 25-year study (Figure 5).

The superpopulation of spawning males in the Fort Peck population was estimated to be 49,912 individuals. The proportion of those individuals present at the beginning of this study was estimated to

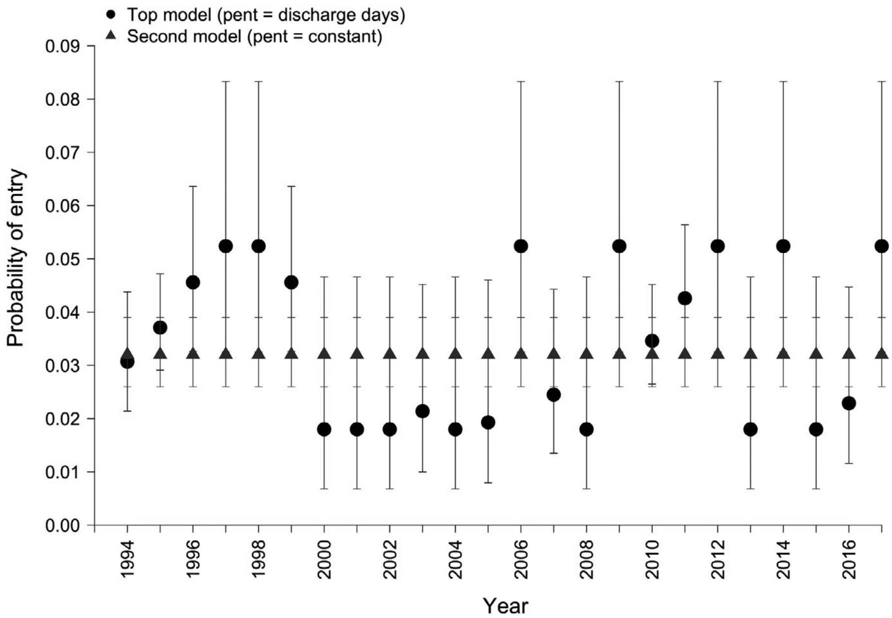

FIGURE 4 Probability of entry (pent) estimates for females estimated by Jolly-Seber (POPAN) models. Bars delineate 95% confidence intervals

be 0.23 of the superpopulation estimate or 11,480 individuals. The top model for males estimated a mean *pent* rate of 0.03 (mean SE 0.01). Combinations of entry rates described above and losses due to mortality resulted in annual abundance estimates between 4,337 (CI 2,889–6,512) and 22,757 (CI 18,525–27,956; Figure 6) over the 25-year study.

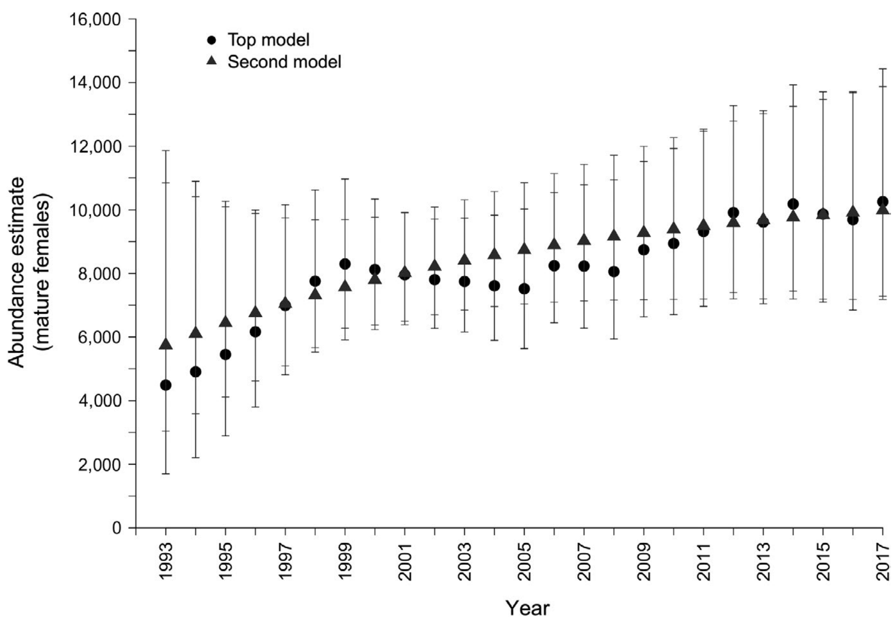

FIGURE 5 Abundance estimates for the Fort Peck Reservoir population of spawning female paddlefish. Bars indicate 95% confidence intervals

Exploitation estimates for males or females never exceeded 10% from 2005 through 2017 (Figure 7). Mean exploitation rate for all years was 2.6% (CI 2.0–3.5) for females and 2.9% (CI 2.2–4.0) for males (Figure 7). Maximum exploitation rate was 5.0% (CI 3.9%–6.6%) for females in 2006 and 6.7% (CI 5.2%–8.7%) for males in 2006 (Figure 7).

4 | DISCUSSION

We were able to estimate survival and abundance for the Fort Peck population of adult paddlefish using capture histories from the 25-year mark-recapture dataset. No apparent long-term patterns in the survival and abundance estimates existed, though any potential long-term patterns were likely masked by the uncertainty in our models. Despite the uncertainty, these data provide useful benchmarks for managing the paddlefish population. For example, the average lower confidence limits for female paddlefish from 1993 through 2017 was 5,846. Thus, an estimate of 5,846 adult female paddlefish could be implemented as a conservative population estimate to guide sustainable management. Less uncertainty existed

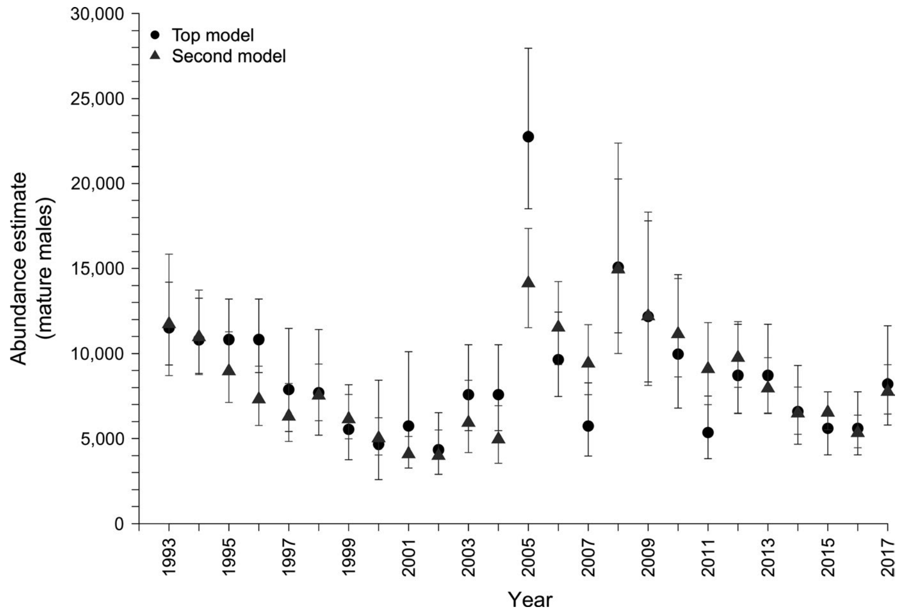

FIGURE 6 Abundance estimates for the Fort Peck Reservoir population of spawning male paddlefish. Bars indicate 95% confidence intervals

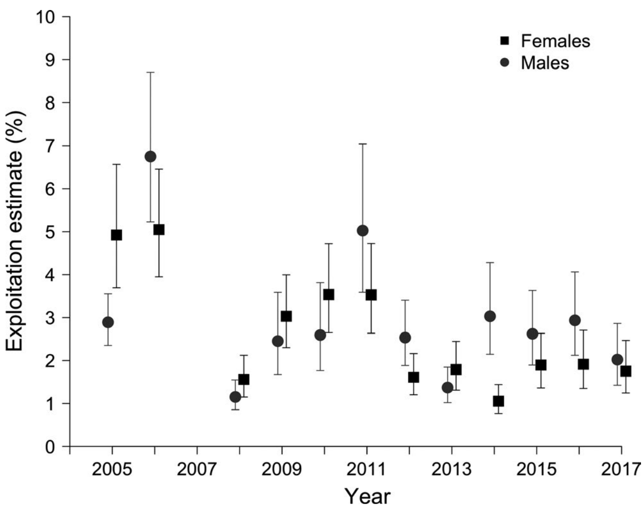

FIGURE 7 Exploitation estimates for the Fort Peck Reservoir population of male and female paddlefish. Bars indicate 95% confidence intervals

in abundance estimates for adult male paddlefish because recapture rates were slightly higher for male paddlefish relative to female paddlefish. The variation in point estimates for males observed is likely a function of year-class strength resulting from abiotic conditions during spawning, reservoir conditions during age-0 and age-1 life stages, or both. The long-term average of the abundance at the lower confidence limit for the Fort Peck adult paddlefish population was 12,309 (sexes combined). The estimate of 12,309 is conservative but may be useful when considering management actions as it would provide a cautious approach to managing this valuable fishery, especially given the uncertainty in the estimates as a result of low recapture rates.

Sustainable fisheries can be established for K-selected or periodic species despite the potential issues stemming from life-history characteristics, such as late age at maturity. Several studies have recommended that exploitation of paddlefish should not exceed 15% (Combs, 1982; Pasch & Alexander, 1986) — exploitation did not exceed 10% in this study from 2005 through 2017. Some riverine paddlefish populations can sustain 6%–20% exploitation with little detrimental effect to survival (Combs, 1982; Pasch & Alexander, 1986; Rehwinkel, 1978), supporting the sustainability of K-selected or periodic fisheries when properly managed. Lake sturgeon *Acipenser fulvescens* fisheries established in the St. Lawrence River and Lake Winnebago (Bruch, 1999; Mailhot, Dumont, & Vachon, 2011) are recognized as sustainable fisheries with exploitation less than 5% of population abundances (Haxton, Whelan, & Bruch, 2014). Similarly, a sustainable paddlefish fishery in the Mississippi River had exploitation of about 4% (Kramer, Phelps, Tripp, & Herzog, 2019). Additionally, the life-history strategy of male paddlefish spawning more often than females may provide a unique opportunity for increased harvest of male paddlefish. In general, the survival rates from our models corroborated the low exploitation rates estimated from the abundance and harvest data. Thus, it appears that the Fort Peck paddlefish fishery is within the general recommendations of exceedingly low exploitation rates for a K-selected species.

The survival, abundance, and calculated exploitation rates inherently include model assumptions. With any models, assumptions need to be carefully evaluated to determine if any were violated. We were unable to determine the prevalence of tag loss for this population; tag loss can be incorporated into models to increase precision in survival and abundance estimates (Arnason & Mills, 1981). The unique life history of this paddlefish population also introduces potential violations of assumptions. The Fort Peck adult paddlefish population spends a majority of the year in the reservoir and only migrates into the river during the spawning season. Additionally, males and females exhibit differing spawning periodicities. Therefore, two "populations" of marked and unmarked paddlefish exist simultaneously: marked and unmarked paddlefish exist in the reservoir and the river during the same sampling period. Therefore, only paddlefish that are in the river are susceptible to harvest and the assumption of homogenous survival may be violated. The same concern exists for catchability; the paddlefish in the reservoir are unsusceptible to recapture if they are not in the sampling area, possibly violating the assumption of homogeneous catchability. Little research exists regarding how those assumption violations may bias estimates of abundance and survival for the superpopulation parameterization of the Jolly-Seber model. Thus, conducting simulations to provide insight into how violating model assumptions could influence survival and abundance estimates could be helpful in future investigations.

Since the initiation of conservation efforts for paddlefish nearly 30 years ago, research has been conducted on paddlefish life history (e.g., Hoxmeier & Devries, 1997; Kozfkay & Scarnecchia, 2002; Miller & Scarnecchia, 2011; Reed, Kelso, & Rutherford, 2004) and fisheries management (e.g., Billard & Lecointre, 2000; Boreman, 1997; Graham, 1997; Jennings & Zigler, 2009; Miranda & Bettoli, 2007; Pikitch et al., 2005; Scholten & Bettoli, 2005; Wirgin, Stabile, & Waldman, 1997). The historical research surrounding paddlefish harvest has identified important changes in the way exploitation goals should be established and changed the paradigm surrounding the management of commercial and recreational paddlefish fisheries (e.g., Combs, 1982; Kramer et al., 2019; Pasch & Alexander, 1986; Rehwinkel, 1978). Though the implementation of those changes caused apparent positive responses in paddlefish population abundance or overall stability, few quantitative studies exist to substantiate those responses (e.g., Pierce et al., 2015; Runstrom et al., 2001). Our research is the first to estimate sex-specific survival and abundance for a harvested paddlefish population. This research provided a unique opportunity to highlight the effort by management agencies to collect long-term field data. We support the collection of long-term fisheries data when driven by testable and clearly articulated objectives and encourage the periodic review and analysis of any long-term inland fisheries datasets to guide management. The results from this analysis indicate that uncertainty in estimates could be reduced by increasing recapture rates. Thus, Montana Fish, Wildlife & Parks is considering various sampling designs to improve recapture rates. Increasing estimate precision will ensure that the Fort Peck paddlefish fishery is sustainably managed.

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CONFLICT OF INTEREST

The authors of this manuscript have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Shared data are not included with this manuscript.

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