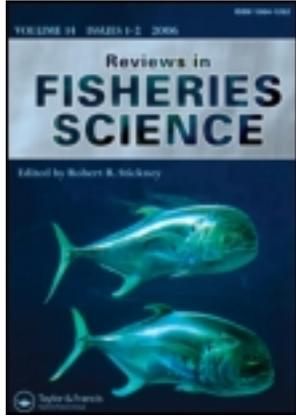


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# Virtual Population Analysis, Episodic Recruitment, and Harvest Management of Paddlefish with Applications to Other Acipenseriform Fishes

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*Virtual population analysis (i.e., cohort analysis) was conducted on the Yellowstone–Sakakawea paddlefish *Polyodon spathula* stock to evaluate recruitment patterns using a combined Montana–North Dakota dataset from the recreational snag fishery over the period 1993–2012. Distinct differences were found in the pattern of reconstructed virtual population sizes of the sexes. There existed a sharp increase in virtual male population size related to first recruitment only for the 1995 year-class. A much smaller increase was found in the female virtual population sizes because the female fish had just begun to recruit as of 2012. Episodic paddlefish recruitment seen in this study and elsewhere (e.g., Oklahoma) is probably common in other Acipenseriform stocks and may have an adaptive basis. However, adequate sex-specific age structure information is not available in many stocks for recruitment variations to be confirmed. Evidence suggests that episodic recruitment in the Yellowstone–Sakakawea paddlefish and other stocks is related to high spring discharge and resulting increasing reservoir water levels and subsequent trophic upsurge. Episodic recruitment poses some substantial challenges for harvest management, including the need to sustainably allot annual harvest until the occasional strong year-classes recruit. Knowledge of recruitment variations and its causes is critical for maintaining harvested stocks of paddlefish and other Acipenseriform species. Sustainable harvest for meat or caviar production in Acipenseriform species with episodic recruitment will require age- and sex-specific data allowing variations in annual recruitment success to be identified and harvest allotted accordingly.*

**Keywords** paddlefish, sturgeon, Missouri River, management, virtual population analysis, recruitment

## INTRODUCTION

Sustainable harvest management of paddlefish *Polyodon spathula* and other Acipenseriform fishes for meat and caviar is dependent on an understanding of the dynamics of individual

populations (stocks) or multi-stock harvest management units. For long-lived, late maturing, sexual-sized dimorphic species, such as paddlefish (Scarnecchia et al., 2007; Jennings and Zigler, 2009) and sturgeons, it is especially important to have an adequate understanding of population size, population age structure (Bruch, 1999), and inter-annual recruitment variability. Strong and weak year-classes can be identified in the harvest, and factors affecting year-class strength can be investigated (Scarnecchia et al., 2009). Acipenseriform species are often reproduction and recruitment limited (paddlefish: South Dakota,

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Unkenholz, 1986; Kootenai River white sturgeon *Acipenser transmontanus*, Anders et al., 2002; Ireland et al., 2002; pallid sturgeon *Scaphirhynchus albus*, Delonay et al., 2009), primarily because of alterations in their large river spawning and early rearing habitats, to the point where fisheries may no longer be viable or populations themselves are no longer sustainable even without harvest. In situations where fisheries remain an option but where reproductive success and recruitment are inconsistent or episodic, fishery managers can set regulations to parcel out annual harvest in a controlled and sustainable manner until new pulses of recruitment occur.

The largely zooplantivorous paddlefish (Eddy and Simer, 1929; Rosen and Hales, 1981; Fredericks, 1994) supports important recreational snag fisheries in the Yellowstone and Missouri Rivers of western North Dakota and eastern Montana (Scarnecchia et al., 2008). An interstate fishery harvests the Yellowstone–Sakakawea stock, a distinct group of fish largely isolated between Fort Peck Dam (completed 1940) and Garrison Dam (completed 1953) on the Missouri River. Fish from that stock typically spawn in the Yellowstone River and in the Missouri River below Fort Peck Dam, rearing to maturity and feeding between spawns in Lake Sakakawea, the Missouri River mainstem reservoir impounded by Garrison Dam (Figure 1). Although harvest of fish from this stock has been documented in the first half of the 20th century (Carufel, 1954; Scarnecchia et al., 1995a), the stock expanded greatly in abundance following the

closure of Garrison Dam in 1953 and the filling and resulting trophic upsurge of Lake Sakakawea from 1953 to 1966 (Scarnecchia et al., 1996, 2009). The recreational fisheries, which use heavy spinning rods and treble hooks and target mature pre-spawning fish, expanded concurrently and have been active in Montana since about 1962 (Robinson, 1966; Rehwinkel, 1978) and in North Dakota since the 1970s (Scarnecchia et al., 2008). As of 2012, the fisheries are managed under a Cooperative Interstate Paddlefish Management Plan (Scarnecchia et al., 1995b, 2008). Harvest is restricted to one fish per person per year in each state; mandatory retention of any snagged paddlefish is required during mandatory snag and harvest periods; and, as of 2012, each state caps the allowable annual harvest at 1,000 fish. Catch and release snagging (Scarnecchia and Stewart, 1997) is also permitted at specified times during and after the harvest season. A detailed chronology of the history and development of the fisheries and their management is in Scarnecchia et al. (2008).

The Yellowstone–Sakakawea paddlefish stock supports two roe donation programs, one begun in 1990 in Montana at Intake, the site of a low-head diversion dam near Glendive, and one begun in 1993 in North Dakota at the confluence of the Missouri and Yellowstone Rivers (hereafter, the Confluence). Under the programs, snaggers can receive free cleaning of fish of either sex for a donation of any fish roe present in their catch. The roe is processed into caviar on-site and later sold, with

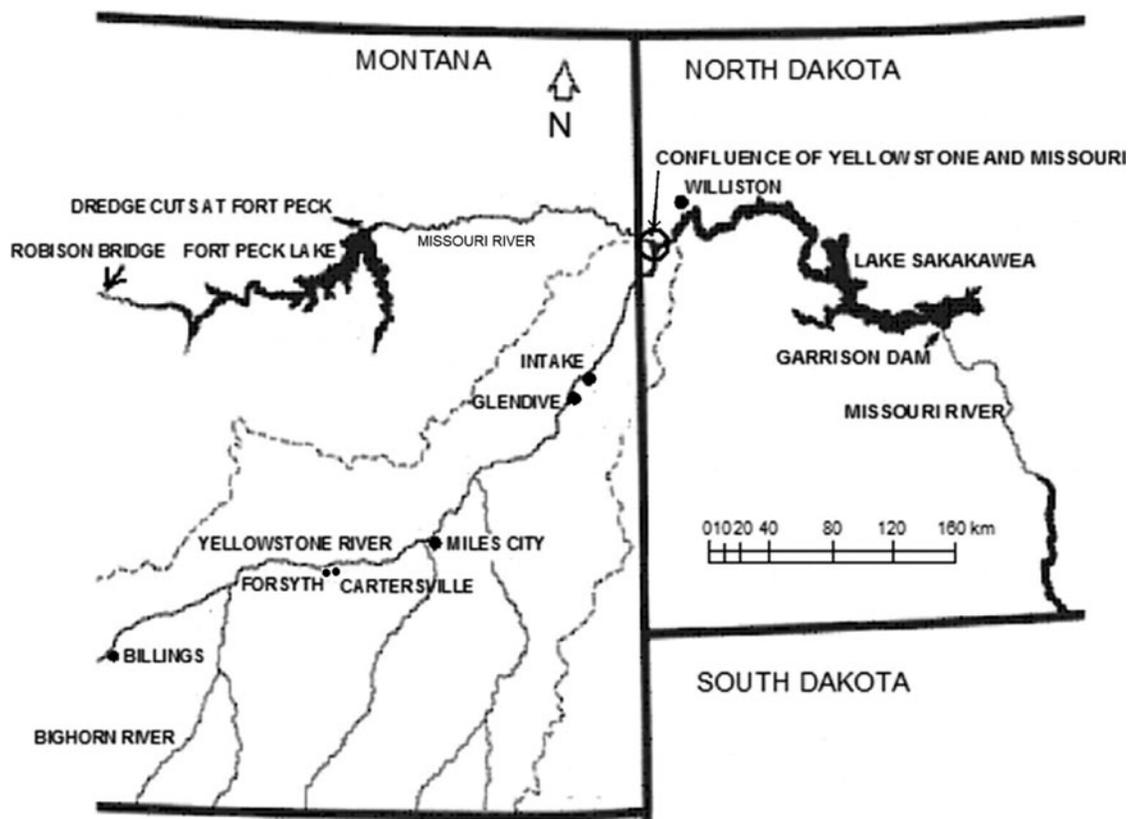


Figure 1 Region and study site associated with the Yellowstone–Sakakawea paddlefish stock.

proceeds going to programs of regional public benefit and to state agency conservation and enforcement efforts. The fish-cleaning operations at the two roe donation sites provide highly centralized locations for efficient collection of extensive fisheries data needed for stock assessment. In any given year, 70–95% of the fish in the total harvest in North Dakota and Montana are typically sampled for length, weight, sex, age, maturation status, and lipid reserves (Scarnecchia et al., 2007).

The harvest cap, a key element of harvest management, has historically been set cooperatively by state fisheries agencies in Montana and North Dakota, with the intent of maintaining the existing adult population size by adjusting harvest based on average five-year recruitment. Information on population sizes (from adult fish tagging and recovery; Fryda et al., 2010) and age structure of the catch (from counting validated annuli on dentary samples; Scarnecchia et al., 2006) is used to estimate the number of young male fish (ages 10–14) and young female fish (ages 17–21) recruiting to the fishery over the most recent five-year period (males recruit about seven years younger than females; Scarnecchia et al., 2007). With mandatory retention of snagged fish, nearly all of which are mature, age structure of the catch is assumed to be indicative of the recruited population age structure. This estimate has then been used to set an appropriate harvest cap such that allowable harvest plus an assumed low natural mortality for adult fish does not exceed recruitment. The harvest cap can be adjusted, annually if desired, to match the recruitment of young mature fish entering the stock over the prior five-year period. The regulations are designed to result in harvest of both males (which are typically smaller) and females similar to their composition in the adult population, the maintenance of a stable stock size, and the maintenance of a naturally protracted range of ages of spawning fish (as old as age 60; Scarnecchia et al., 2007). This conservative approach is warranted in this and other paddlefish stocks because the stock–recruitment relationships (*sensu* Ricker, 1954) and factors affecting recruitment variability are poorly understood, and where they are understood, they are often not controllable by harvest managers.

Although this simple method of setting a harvest cap has worked adequately over the past decade and continues to aid in setting harvest regulations, the accumulation of comprehensive catch data and recent evidence of highly erratic recruitment (including several year-class failures) made it desirable to develop more detailed approaches for assessing stock status. In circumstances with inconsistent or episodic recruitment, it is important to reconstruct effectively the historical stock dynamics to better assess historical recruitment variability and the frequency of strong year-classes and to then assess how long strong year-classes can be expected to support a harvest under various regulations.

The detailed long-term data collected by cohort for this stock are well suited for virtual population analysis (VPA), *i.e.*, cohort analysis. VPA, a retrospective approach to stock assessment, is “. . . an analysis of the catches of fisheries, obtained through fisheries statistics, combined with detailed information

on the contribution to the catch . . . usually obtained through sampling programmes and age readings. The ‘virtual’ population” is not the real population, but is the only one that is seen . . . The idea behind the method is to analyze what can be seen, the catch, in order to calculate the population that must have been in the water to produce this catch. . .” (Sparre and Venema, 1992, p. 153). Early efforts at the approach were described by Ricker (1971) and include references to early work by Derzhavin (1922) on stellate sturgeon *Acipenser stellatus* and Fry (1949) on lake trout *Salvelinus namaycush*. Many applications of the method are in the literature, especially in the last three decades of the 20th century, and the method remains widely used in making management decisions for marine species (*e.g.*, <http://nft.nefsc.noaa.gov/>). Although missing year-classes can often be seen from harvest or sampling in a given year, accurate cohort reconstruction provides a much more comprehensive assessment of the comparative strengths of year-classes. Information coming from the VPA on stock trends and year-class variability will better enable managers to model the predicted state of the stock in the future (Sparre and Venema, 1992) and to set appropriate regulations. This approach may be especially important for species that show inconsistent or episodic recruitment, as is evidenced in some stocks of paddlefish (Scarnecchia et al., 2008, 2011).

The objectives of this article are to develop a VPA of the Yellowstone–Sakakawea paddlefish stock, to use the reconstruction to evaluate recruitment periodicity, and to identify and discuss harvest and habitat management implications. Subsequent forward projections from this work in future works along with indices of reproductive success (Fredericks and Scarnecchia, 1997) will provide a better basis for setting appropriate annual harvest caps and sustainably managing the fisheries in both states.

## METHODS

### Data

The dataset used was the combined North Dakota and Montana harvest record for the years 1993 through 2012. Life history information was obtained over this period mainly from two fish cleaning stations, one in each state, at the Confluence and Intake. It was over this period, coinciding with the development of the roe donation programs, that data collection for the stock was comprehensive in both states. Almost no harvest or life-history data were available in North Dakota before 1993. Recreational snagging methods in the two states are the same with the exception of a bow and arrow fishery in Montana below Fort Peck Dam that harvests fewer than 50 fish per year. Commercial harvest is not allowed in either state. The only unaccounted-for legal harvest is from a tribal fishery that is unmonitored on the Missouri River near the towns of Wolf Point, Montana, and Frazer, Montana. Harvest is highly variable but ranges from negligible

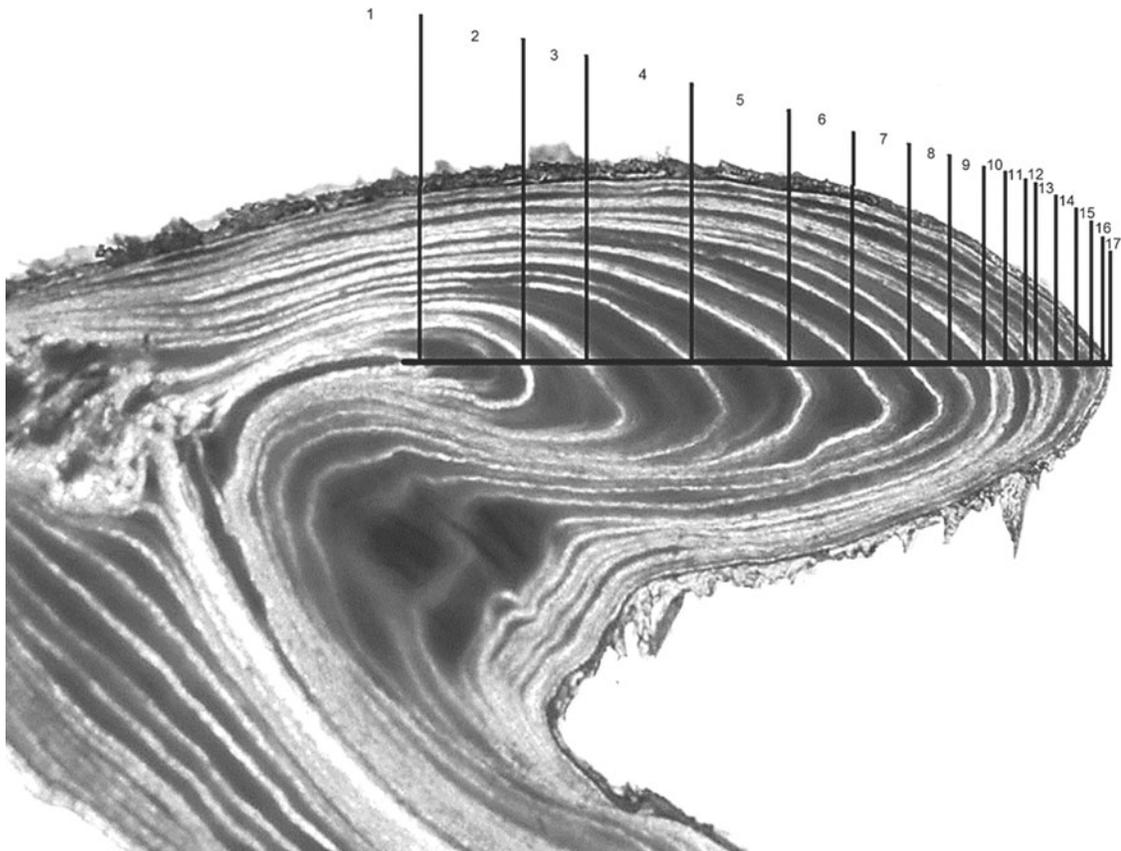
in many years to less than 100 fish per year in years of low Yellowstone River flows.

From each fish, data collected included the date of harvest, harvest location (river kilometer), body length (BL; anterior of eye to fork of caudal fin; Ruelle and Hudson, 1977) to the nearest 2.5 cm, weight to the nearest 0.5 kg, sex, maturation stage, gonad weight, gonadal fat weight, and dentaries (lower jaw bones) for age determination (Scarnecchia et al., 2007). With high-grading and release of fish prohibited and the prohibition enforced, the catch, which consists almost entirely of sexually mature pre-spawning migratory fish (Scarnecchia et al., 1996), is indicative of the actual composition of the spawning adult population.

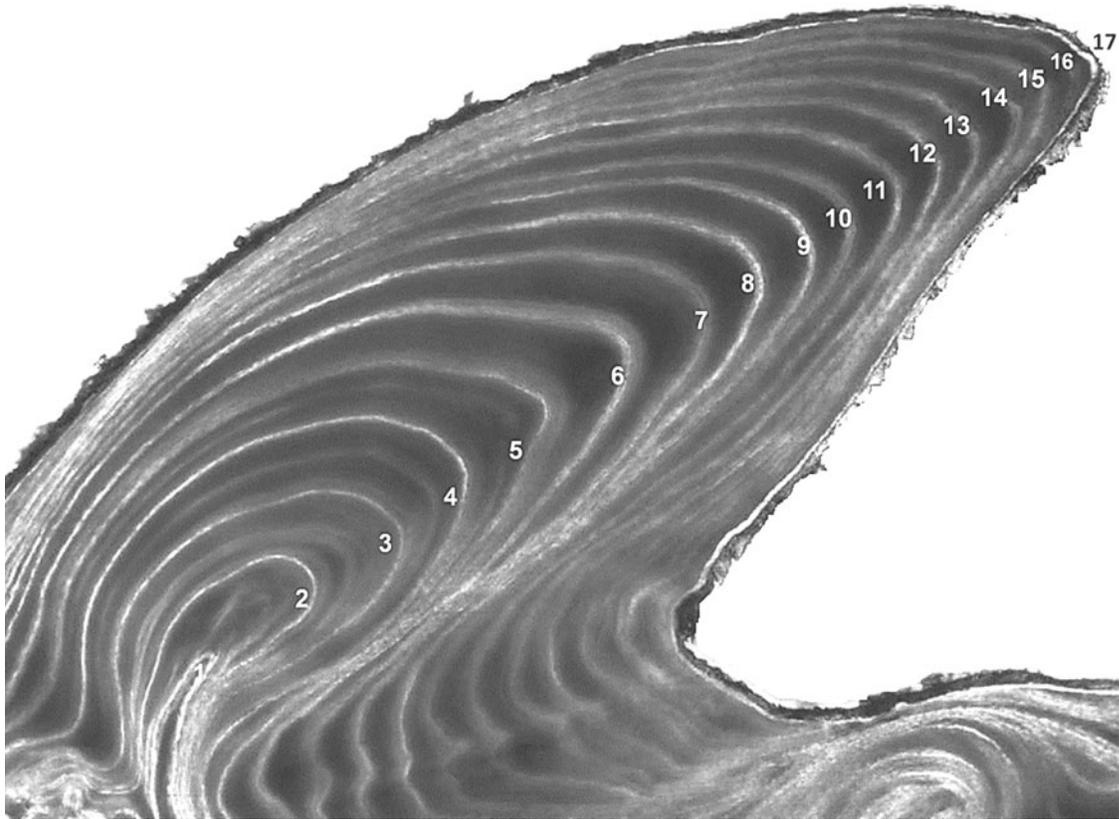
Age was determined by the use of dentaries using well-established methods (Adams, 1931, 1942; Scarnecchia et al., 2006). After removal, dentaries were stored dry in individual envelopes. The dentaries were later cleaned and sectioned and ages assessed by counting annuli (Meyer, 1960; Scarnecchia et al., 2006) using a Biosonics Optical Pattern Recognition System. Prior to 1999, fish were aged with one experienced reader. Starting in 1999, a two-reader double-blind protocol was used, along with a tolerance for minor disagreement. In this protocol, two persons (designated primary and secondary readers) aged the sections separately. If there was agreement (plus or minus one year for fish under age 20, plus or minus two years

for ages 20 to 34, and plus or minus three years for ages 35 and over), the final age was assigned by the primary reader. If the ages differed by more than the criteria, the sections were read independently again. If the age estimates still did not meet agreement criteria, the section was aged with both readers in consultation and a final age was assigned by the primary reader. The accuracy of age determination using dentaries was validated (Campana, 2001) for young recruits (age 10 and under) based on recoveries of known-age coded-wire tagged fish and partially validated for older recruits based on jaw-tag recoveries (Scarnecchia et al., 2006). The precision of age determination based on coefficients of variation (CV) between two readers ranged from 3.55 to 7.06%; these values were below the median CV (7.6%) reported by Campana (2001) from a summary of 117 published values over a variety of calcified structures, including scales, otoliths, fin rays, and spines (Scarnecchia et al., 2006). Accuracy and precision were thus interpreted to be within acceptable standards. Subsequent recovery of known-age fish has confirmed the accuracy of dentaries up to age 17 (D. L. Scarnecchia, unpublished data; Figures 2 and 3).

Methods of cohort reconstruction based on ages of individual fish were outlined in Sparre and Venema (1992) and Lassen and Medley (2001). Over the period from 1993 to 2012, where nearly complete age data were available for both states, total numbers



**Figure 2** Validated age-17 male Yellowstone-Sakakawea paddlefish (BL 940 mm, weight 9.98 kg) of the 1995 year-class.



**Figure 3** Validated age-17 female Yellowstone-Sakakawea paddlefish (BL 1,067 mm, weight 21.32 kg) of the 1995 year-class.

of fish caught by age were able to be expanded in proportion to the age structure of the aged sample from information obtained from phone creel censuses on the number of fish known to be processed at the Confluence and Intake cleaning stations and the percentage of the harvested fish that were brought to those stations for processing. In this approach, in each year, the observed age frequency distribution for the observed harvested fish was scaled up in number by age to meet the total estimated harvest. Because of the high intensity sampling program, these expansions were modest, typically less than 25% (Table 1) but resulted in an estimate of the total harvest of fish by age over the period.

### VPA

VPA uses a deterministic, recursive algorithm to calculate stock size based on fish harvest by age. Given a terminal fishing mortality ( $F_T$ ), from which a terminal virtual cohort size is obtained, all other fishing mortality values and corresponding virtual population sizes at younger ages (i.e., earlier years) are calculated. In VPA, catch-at-age data are accepted as exact. The data transformation performed by VPA, however, is not unique, because there are choices in terminal fishing mortality. The catches are converted into a set of equivalent virtual population sizes and fishing mortalities. Any aging or other errors in the

original data therefore affect the population and fishing mortality estimates. Natural mortality ( $M$ ) cannot be estimated by the analysis; it is usually set as a constant or a function of age. Using an inappropriate value for  $M$  can lead to overestimation or underestimation of cohort sizes. Estimates of fishing mortalities and population size for earlier years and younger ages become progressively less sensitive to the starting assumptions about terminal fishing mortality  $F_T$  (Sparre and Venema, 1992; Lassen and Medley, 2001).

VPA is based on two equations: the exponential decay or stock equation,

$$N_t = N_{t-1} \cdot e^{-Z_{t-1}} = N_{t-1} \cdot e^{-(F_{t-1} + M_{t-1})},$$

and Baranov's catch equation,

$$C_t = \frac{F_t}{Z_t} N_t (1 - e^{-Z_t}) = \frac{F_t}{F_t + M_t} N_t (1 - e^{-(F_t + M_t)}),$$

where  $N_t$  is the number of fish in a cohort at time  $t$ ,  $C_t$  is the catch from  $N_t$ ,  $Z_t$  is total mortality, and  $F_t$  and  $M_t$  are fishing and natural mortality, respectively. The decomposition of the total mortality into natural and fishing mortality is required because only catch  $C_t$  is observed.

**Table 1** Ratio of processed paddlefish to total estimated harvest, Montana and North Dakota, 1993–2012

Year	North Dakota			Montana		
	Actual	Estimated	(Actual/estimated)Ratio	Actual	Estimated	(Actual/estimated)Ratio
1993	121	2,039	0.059	1,941	1,635	1.0
1994	859	1,429	0.601	361	278	1.0
1995	1,151	1,724	0.667	1,523	1,657	0.919
1996	667	975	0.684	1,160	1,199	0.967
1997	623	800	0.778	815	1,075	0.758
1998	1,453	1,970	0.737	601	717	0.838
1999	948	1,309	0.724	1,412	1,706	0.827
2000	1,545	2,205	0.700	547	666	0.821
2001	1,407	1,566	0.898	349	360	0.969
2002	1,305	1,364	0.956	727	1,208	0.601
2003	798	1,041	0.766	845	1,060	0.797
2004	822	1,076	0.763	226	329	0.686
2005	916	1,100	0.832	1,082	1,323	0.817
2006	899	1,059	0.848	1,195	1,194	1.0
2007	690	829	0.832	867	998	0.868
2008	985	1,114	0.884	946	1,102	0.858
2009	716	982	0.729	802	967	0.829
2010	912	947	0.963	822	1,027	0.800
2011	841	1,095	0.768	715	949	0.753
2012	703	856	0.821	468	599	0.781

**Selection of Terminal Mortality Values**

Terminal mortality values were selected using catch-curve methods based on 1993–2010 combined Montana and North Dakota catch-at-age data. Sums of cross-sectional catch for each age were used for estimating  $Z$  of male and female paddlefish. Catch-curve regression equations were

$$\begin{aligned} \text{male paddlefish: } \text{Log}(N_t) &= 9.660 - 0.159 T \text{ for } 10 \leq T \\ &\leq 49 (R^2 = 0.899); p\text{-value} \\ &< 0.001; \text{ Figure 4)} \end{aligned}$$

and

$$\begin{aligned} \text{female paddlefish: } \text{Log}(N_t) &= 11.603 - 0.192 T \text{ for } 20 \leq T \\ &\leq 53 (R^2 = 0.888); p\text{-value} \\ &< 0.001; \text{ Figure 4)} \end{aligned}$$

where  $N_t$  and  $T$  are catch at age =  $t$  and fish age, respectively. The 95% confidence limits for  $Z$  were (0.1419, 0.1771) for male fish and (0.1670, 0.2161) for female fish.

Values for male and female  $Z_T$  in this study were first selected using limits of corresponding 95% CI: 0.14 and 0.18 for male  $Z_T$  (age  $\geq 10$ ), and 0.16 and 0.22 for female  $Z_T$  (age  $\geq 20$ ). Younger male (age  $\leq 9$ ) and female (age  $\leq 19$ ) recruits were assumed to have  $Z_T = 0.1$ . To perform VPA with selected values for  $Z_T$ , corresponding values for terminal fishing mortality or  $F_T$  must be set such that  $Z_T = F_T + M$ . Because of difficulties in estimating natural mortality,  $M$  is usually assumed to be a known constant. For VPA, however, some investigators recommend  $M$

$< F_T$  and thereby  $0.5 \leq F_T/Z_T$  (Sparre and Venema, 1992; Lassen and Medley, 2001). This is because the influence of  $M$  increases as cohort sizes are back-calculated toward the younger ages (i.e.,  $N_{t-1} = N_t \cdot e^{(F_{t-1}+M)}$ ). Two values for  $F_T/Z_T$  were subjectively selected for this study:  $F_T/Z_T = 0.5$  and 0.8. With the above eight sets of terminal mortality, values were selected separately for male and female paddlefish cohorts to cover the possible range of virtual sizes (Table 2).

**“Exact” VPA Methodology**

With each set of terminal mortality values (Table 2), virtual sizes of each cohort were first calculated separately using male and female catch-at-age data. By adding male and female virtual sizes of the same cohort, virtual sizes of the cohort at each age were obtained.

For example, if under a particular terminal fishing mortality, calculated size of 1995 male cohort in 2001 (age = 6) was 12,694 and size of 1995 female cohort was 2,123, the virtual size of 1995 cohort was  $12,694 + 2,123 = 14,817$ . Cross-sectional sums of virtual sizes were then obtained as virtual population sizes for each year from 1993 to 2012.

Virtual sizes of a given cohort were calculated using the following steps. The “terminal” virtual size or  $N_T$  of the cohort was first calculated using given estimates of  $M$  and  $F_T$ :

$$N_T = \frac{C_T}{\frac{F_T}{F_T+M} (1 - e^{-(F_T+M)})} = \frac{C_T}{\frac{F_T}{Z_T} (1 - e^{-Z_T})}$$

Based on results of catch curves, the eight sets of terminal fishing mortalities  $F_T$  and total mortalities  $Z_T$  were used

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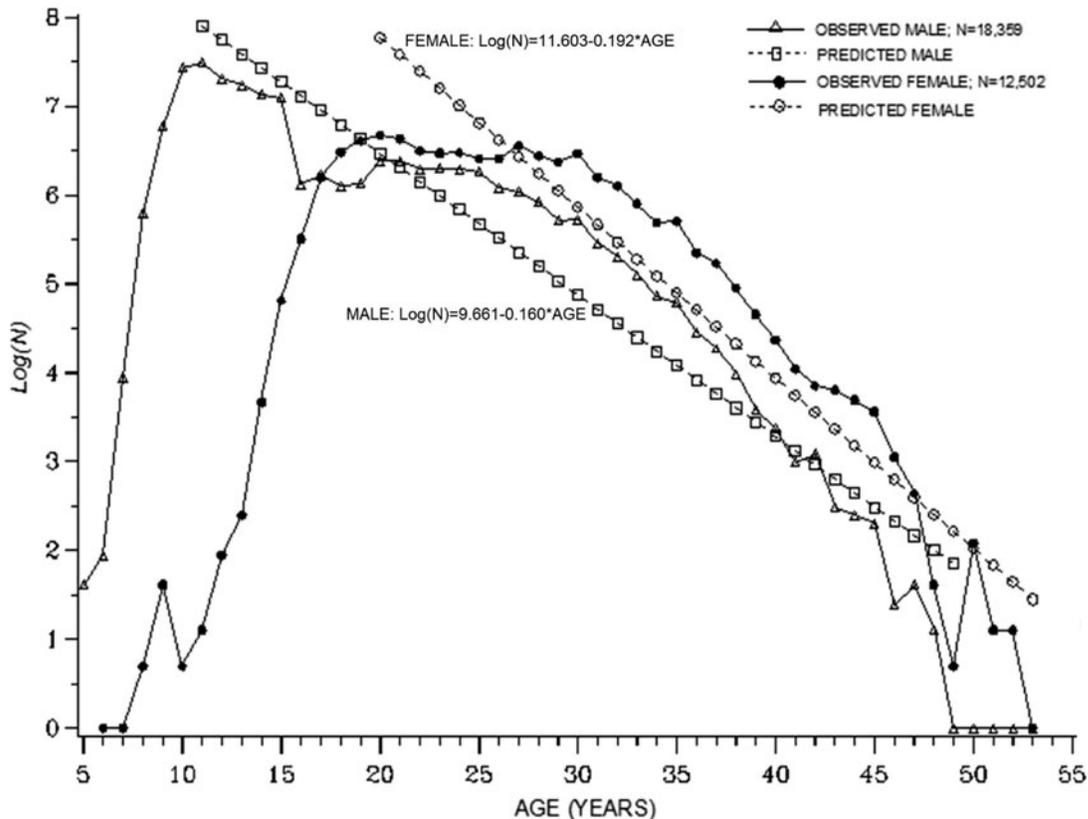
**Table 2** Eight sets of terminal fishing mortality ( $F_T$ ) and total mortality ( $Z_T$ ) values used in VPA with 1993–2012 combined Montana and North Dakota male and female catch-at-age data

Eight sets for male cohorts in catch-at-age data													
Age $\geq 10$							Age $\leq 9$						
$M$	$F_T$	$Z_T$	$F_T/Z_T$	$A = 1 - e^{-Z}$	$u$ (%)	$v$ (%)	$M$	$F_T$	$Z_T$	$F_T/Z_T$	$A = 1 - e^{-Z}$	$u$ (%)	$v$ (%)
0.028	0.112	0.14	0.8	0.1306	10.45	2.61	0.02	0.08	0.1	0.8	0.0952	7.61	1.90
0.028	0.112	0.14	0.8	0.1306	10.45	2.61	0.05	0.05	0.1	0.5	0.0952	4.76	4.76
0.07	0.07	0.14	0.5	0.1306	6.53	6.53	0.02	0.08	0.1	0.8	0.0952	7.61	1.90
0.07	0.07	0.14	0.5	0.1306	6.53	6.53	0.05	0.05	0.1	0.5	0.0952	4.76	4.76
0.036	0.144	0.18	0.8	0.1647	13.18	3.29	0.02	0.08	0.1	0.8	0.0952	7.61	1.90
0.036	0.144	0.18	0.8	0.1647	13.18	3.29	0.05	0.05	0.1	0.5	0.0952	4.76	4.76
0.09	0.09	0.18	0.5	0.1647	8.24	8.24	0.02	0.08	0.1	0.8	0.0952	7.61	1.90
0.09	0.09	0.18	0.5	0.1647	8.24	8.24	0.05	0.05	0.1	0.5	0.0952	4.76	4.76

Eight sets for female cohorts in catch-at-age data													
Age $\geq 20$							Age $\leq 19$						
$M$	$F_T$	$Z_T$	$F_T/Z_T$	$A = 1 - e^{-Z}$	$u$ (%)	$v$ (%)	$M$	$F_T$	$Z_T$	$F_T/Z_T$	$A = 1 - e^{-Z}$	$u$ (%)	$v$ (%)
0.032	0.128	0.16	0.8	0.1479	11.83	2.96	0.02	0.08	0.1	0.8	0.0952	7.61	1.90
0.032	0.128	0.16	0.8	0.1479	11.83	2.96	0.05	0.05	0.1	0.5	0.0952	4.76	4.76
0.08	0.08	0.16	0.5	0.1479	7.39	7.39	0.02	0.08	0.1	0.8	0.0952	7.61	1.90
0.08	0.08	0.16	0.5	0.1479	7.39	7.39	0.05	0.05	0.1	0.5	0.0952	4.76	4.76
0.044	0.176	0.22	0.8	0.1975	15.80	3.95	0.02	0.08	0.1	0.8	0.0952	7.61	1.90
0.044	0.176	0.22	0.8	0.1975	15.80	3.95	0.05	0.05	0.1	0.5	0.0952	4.76	4.76
0.11	0.11	0.22	0.5	0.1975	9.87	9.87	0.02	0.08	0.1	0.8	0.0952	7.61	1.90
0.11	0.11	0.22	0.5	0.1975	9.87	9.87	0.05	0.05	0.1	0.5	0.0952	4.76	4.76

Note:  $M$  = natural mortality;  $F_T$  = terminal fishing mortality;  $Z_T$  = terminal total mortality =  $M + F_T$ ;  $u$  (%) =  $F * A/Z$  (expected death from fishing);  $v$  (%) =  $M * A/Z$  (expected death from natural causes).



**Figure 4** Catch curves for male and female paddlefish based on 1993–2010 combined Montana and North Dakota catch-at-age data.

(Table 1). Second, for  $t - 1$ ,  $F_{t-1}$  was estimated using

$$C_{t-1} = \frac{F_{t-1}}{F_{t-1} + M} N_t (e^{(F_{t-1}+M)} - 1)$$

with known  $C_{t-1}$ ,  $N_t$ , and  $M$ . Since  $f(F_{t-1}) = C_{t-1} - \frac{F_{t-1}}{F_{t-1}+M} N_t (e^{(F_{t-1}+M)} - 1)$  is not a linear function of  $F_{t-1}$ , the solution can be obtained using a numerical method. In this study, the standard Newton-Raphson method was used:

$$x_{n+1} = x_n - \frac{f(x_n)}{f'(x_n)}, \text{ where } x_{n+1} = (F_{t-1})_{n+1}.$$

An iterative solution for  $F_{t-1}$  of the equation was found:

$$(F_{t-1})_{n+1} = (F_{t-1})_n$$

$$= \frac{(F_{t-1})_n N_t (e^{((F_{t-1})_n + M)} - 1) - (F_{t-1})_n N_t - (F_{t-1})_n C_{t-1} - M C_{t-1}}{N_t e^{(F_{t-1})_n} (1 + (F_{t-1})_n) - N_t - C_{t-1}}.$$

Using an obtained value for  $F_{t-1}$  from this equation, the following was calculated:

$$N_{t-1} = N_t \cdot e^{(F_{t-1}+M)}.$$

The previous two steps were then repeated for  $(F_{T-2}, N_{T-2})$ ,  $(F_{T-3}, N_{T-3})$ , and so on. The results of male cohort sizes calculated using the above exact VPA methodology for male catch-at-age data, female catch-at-age data, and combined males and females were calculated for each set of selected terminal mortality values (Table 2).

## RESULTS

There were 49 male cohorts in catch-at-age data from the combined 1993–2012 Montana and North Dakota paddlefish data, the first cohort in 1949, and the last cohort in 2005. There was no documented catch from the 1950 cohort. There were 49 female cohorts in the catch-at-age data from the combined 1993–2012 Montana and North Dakota paddlefish data, the first female cohort in 1946, followed by the 1950 cohort, and the last cohort in 1997.

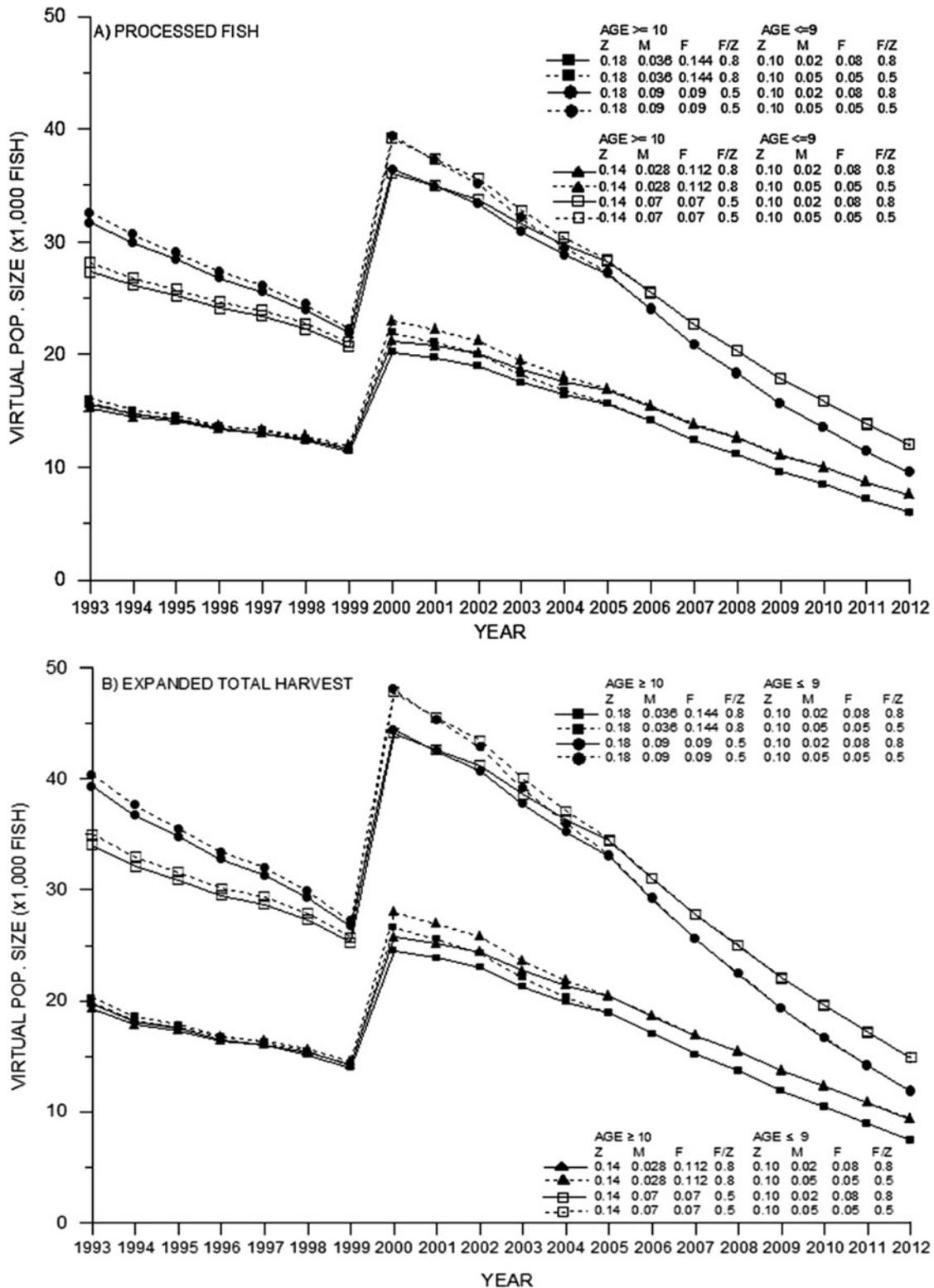
There were distinct differences in the pattern of virtual population sizes of the sexes. There existed a sharp increase in virtual male population size from 1999 to 2000 (Figure 5), related to first recruitment of the 1995 year-class (i.e., the first recruitment to the fishery of that cohort was at age 5). This was the only year of all cohorts examined when a noticeable increase in virtual population size was noted. In contrast to the males, only a small increase in virtual population size was found in the female dataset (Figure 6). As of 2012, a few females of the 1995 cohort had recruited. When virtual population sizes from combined male and female size were plotted (Figure 7), the sharp increase in virtual population size from 1999 to 2000 was also clearly shown, mainly due to male recruitment of the 1995 year-class. In no other years did recruitment spike upward. Plots of four selected cohorts from four different decades (1995, 1986, 1977,

and 1968) generally showed the predictable declines through time (Figures 8 and 9). In those two figures, the 1995 cohort, consisting almost entirely of males, was much higher so that a separate scale for 1995 male cohort sizes was necessary in both figures. In both figures, the recruitment of males of the 1986 cohort to the fishery is clearly evident in their sharp decline in the early 1990s, as opposed to the females of that cohort, which had not yet recruited to the fishery at that time. Overall, VPA results strongly indicated that one major recruitment episode in 1995 dominated the stock over the period analyzed.

## DISCUSSION

VPA indicates that overall recruited stock size of Yellowstone–Sakakawea paddlefish has shown a consistent pattern of decrease since 1993, in which mortality of paddlefish has either approximately met or exceeded annual recruitment. The one important exception has been the effects of the strong 1995 year-class. This cohort greatly increased the male recruitment and harvestable stock size starting in 2000 but, as of 2012, had just begun to increase the female recruitment (Figure 6) because nearly all females take at least 15 years to recruit (Scarnecchia et al., 2007).

The strong recruitment event in 1995 for the Yellowstone–Sakakawea stock was identified and discussed by Scarnecchia et al. (2009), who found it to be associated with increased reservoir water levels. Evidence since reservoir construction in 1953 indicates that it is in periods of substantial reservoir filling that strong recruitment is most likely to occur. The first strong recruitment was associated with the initial reservoir filling; during this phase (1953–1966; Figure 10), trophic upsurge (Kimmel and Groeger, 1986) was associated with a large population expansion (Scarnecchia et al., 2009). Strong year-classes of paddlefish resulted in a large male-dominated harvest (97%) at Intake in the early 1960s (Robinson, 1966), as the males migrated up the Yellowstone River in unprecedented numbers. By 1973–1974, the sex ratio of harvested fish had equalized (Rehwinkel, 1978) as females had begun to undertake spawning migrations and enter the harvest, and by the early 1990s, the sex ratio had shifted strongly to females, fostering the development of the roe donation programs (Scarnecchia et al., 2008). This complete shift in sex ratio indicated that this early expansion was by far the strongest recruitment pulse prior to the early 1990s, although some modest recruitment was noted based on young males in the early and mid-1990s. The stock has been in a long decline, however, since its rapid expansion following reservoir construction (Scarnecchia et al., 1996, 2009) as a result of fishing and natural mortality. The decline in population size during the 1980s and early 1990s was probably unavoidable, as reservoir productivity for the species declined and a new fish community, including potential predators on larval and age-0 paddlefish, became established. This pattern of rapid population expansion followed by a decline is common for many



**Figure 5** Virtual populations for 1993–2012 combined Montana and North Dakota male paddlefish: (A) processed fish and (B) expanded total harvest.

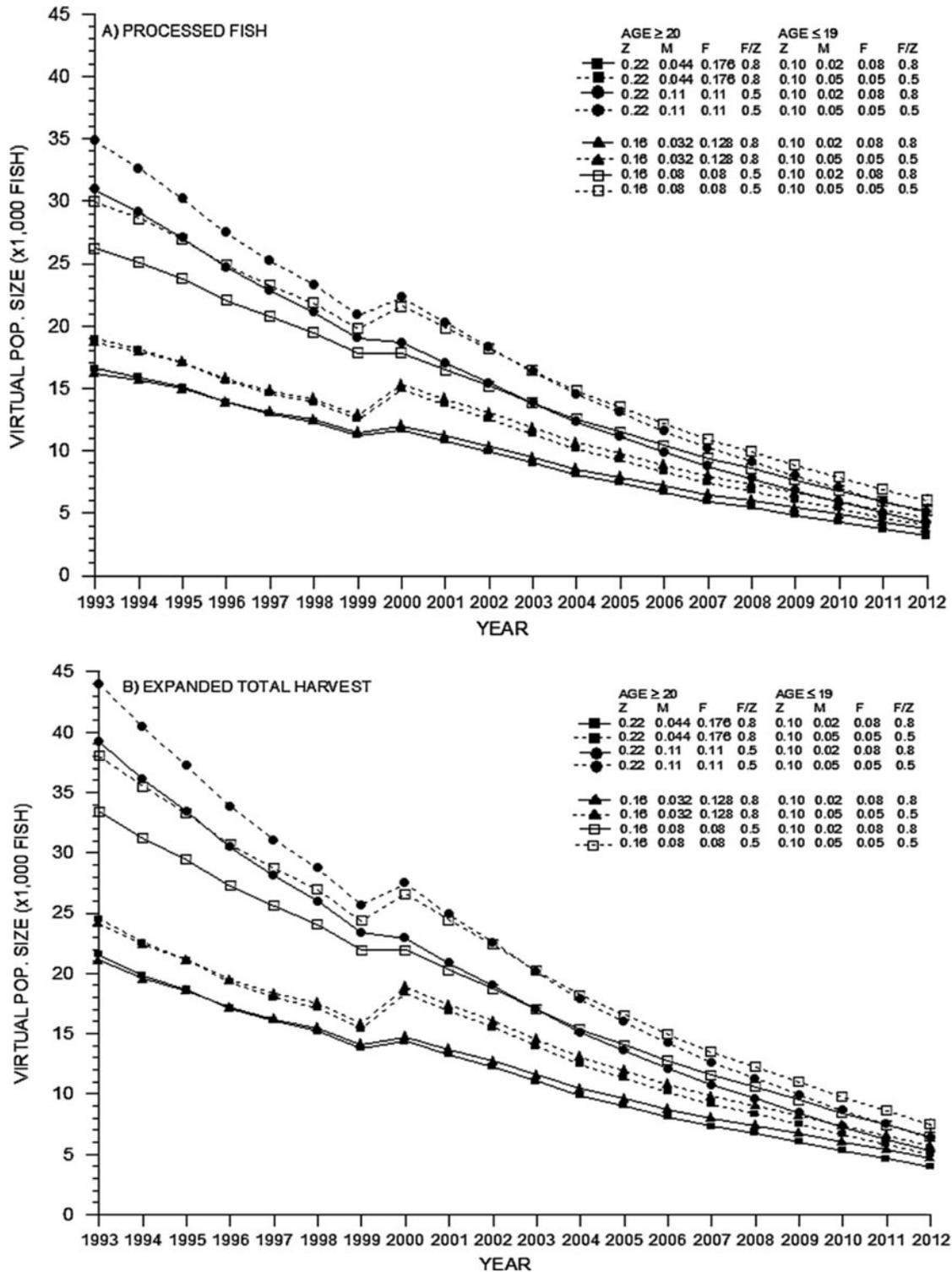


Figure 6 Virtual populations for 1993–2012 combined Montana and North Dakota female paddlefish: (A) processed fish and (B) expanded total harvest.

reservoir-rearing species (Kimmel and Groeger, 1986) but much more protracted in this late maturing, long-lived species than would have been seen in shorter lived species such as Centrarchidae or Percidae typically associated with North American reservoirs.

The clearest evidence of a temporary reversal in this declining trend since the initial filling period was in 1995, as three years of filling following a protracted drought and low reservoir water levels in the late 1980s and early 1990s (Figure 10), led to another smaller trophic upsurge and the

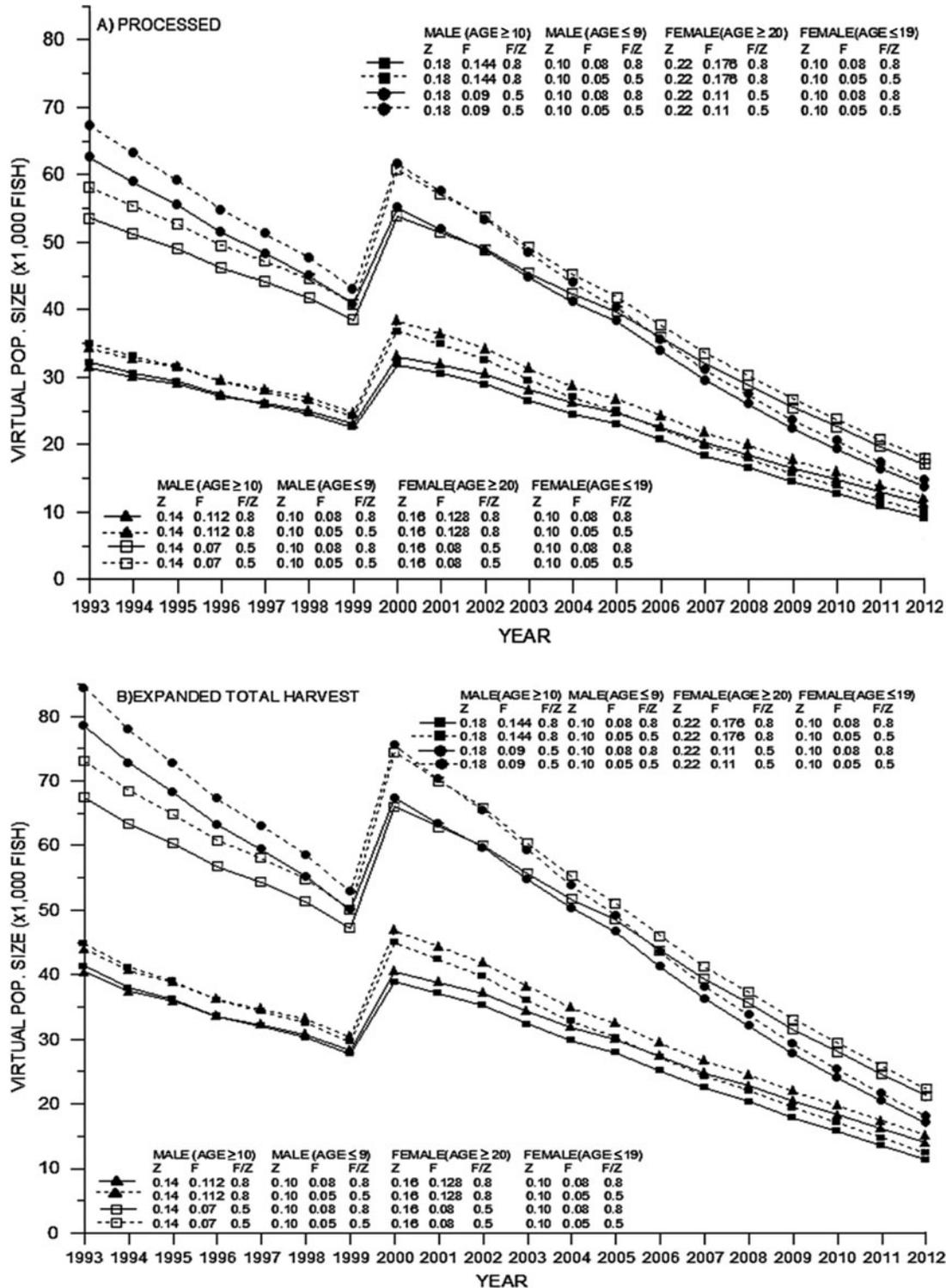


Figure 7 Virtual populations for 1993–2012 combined Montana and North Dakota male and female paddlefish: (A) processed fish and (B) expanded total harvest.

strong 1995 year-class whose males have contributed to the fishery since 2000 (Scarnecchia et al. 2009; Figure 11). However, since reservoir re-filling in 1993–1995, recruitment has become much less (Figure 12) following several years of drought and declining reservoir levels (Figure 10). Observations in 2012 in-

dicate that following record high Yellowstone River discharges and high reservoir levels in 2011, for the first time since 1996, numerous age-1 paddlefish were seen along standard transects in 2012 (D. L. Scarnecchia and L. F. Ryckman, unpublished data; Figure 13), indicating that another substantial year-class

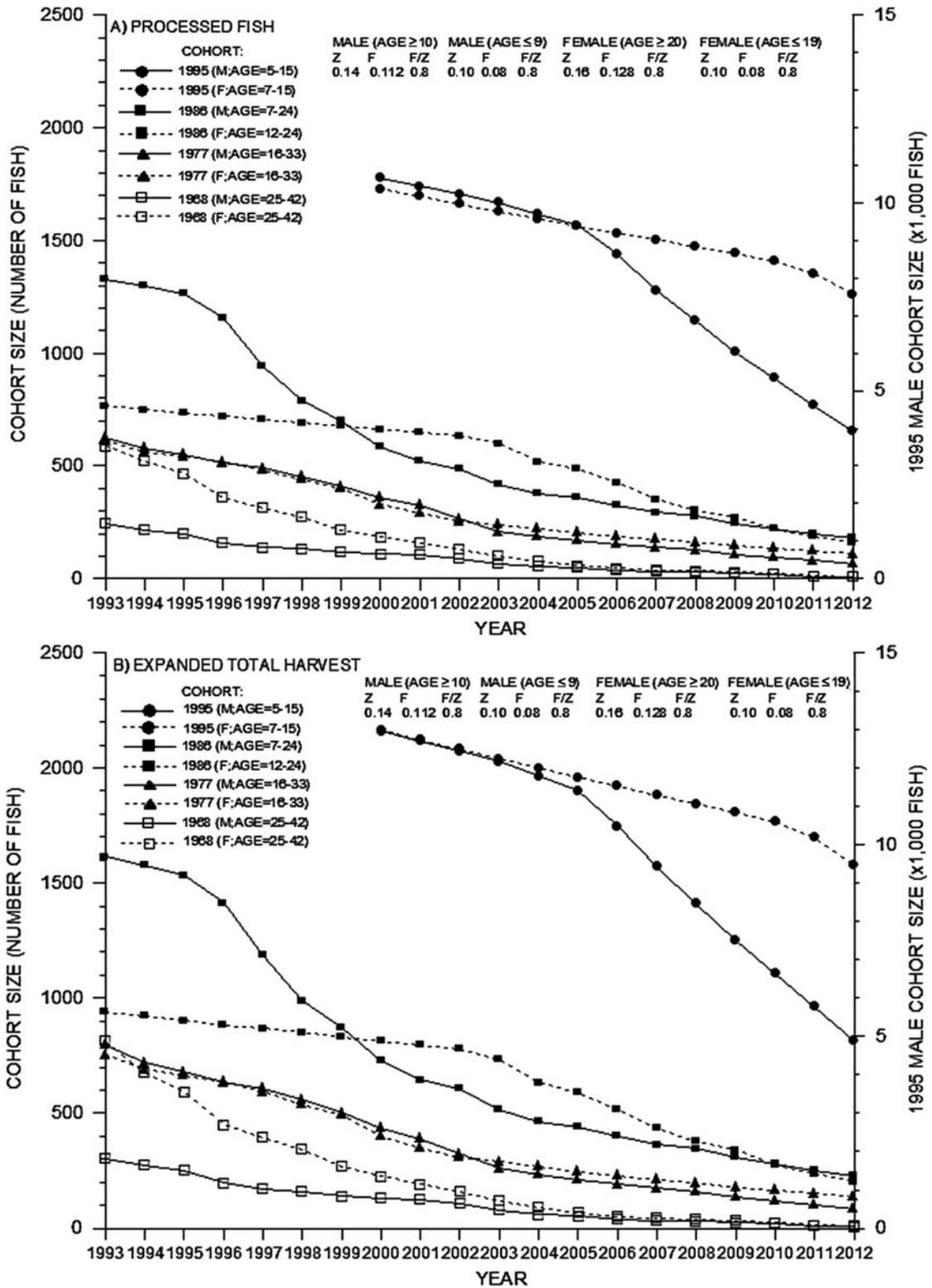


Figure 8 Virtual population sizes for male and female paddlefish, Montana and North Dakota combined, of four selected cohorts (1968, 1977, 1986, 1995), for  $F/Z = 0.8$ : (A) processed fish and (B) expanded total harvest.

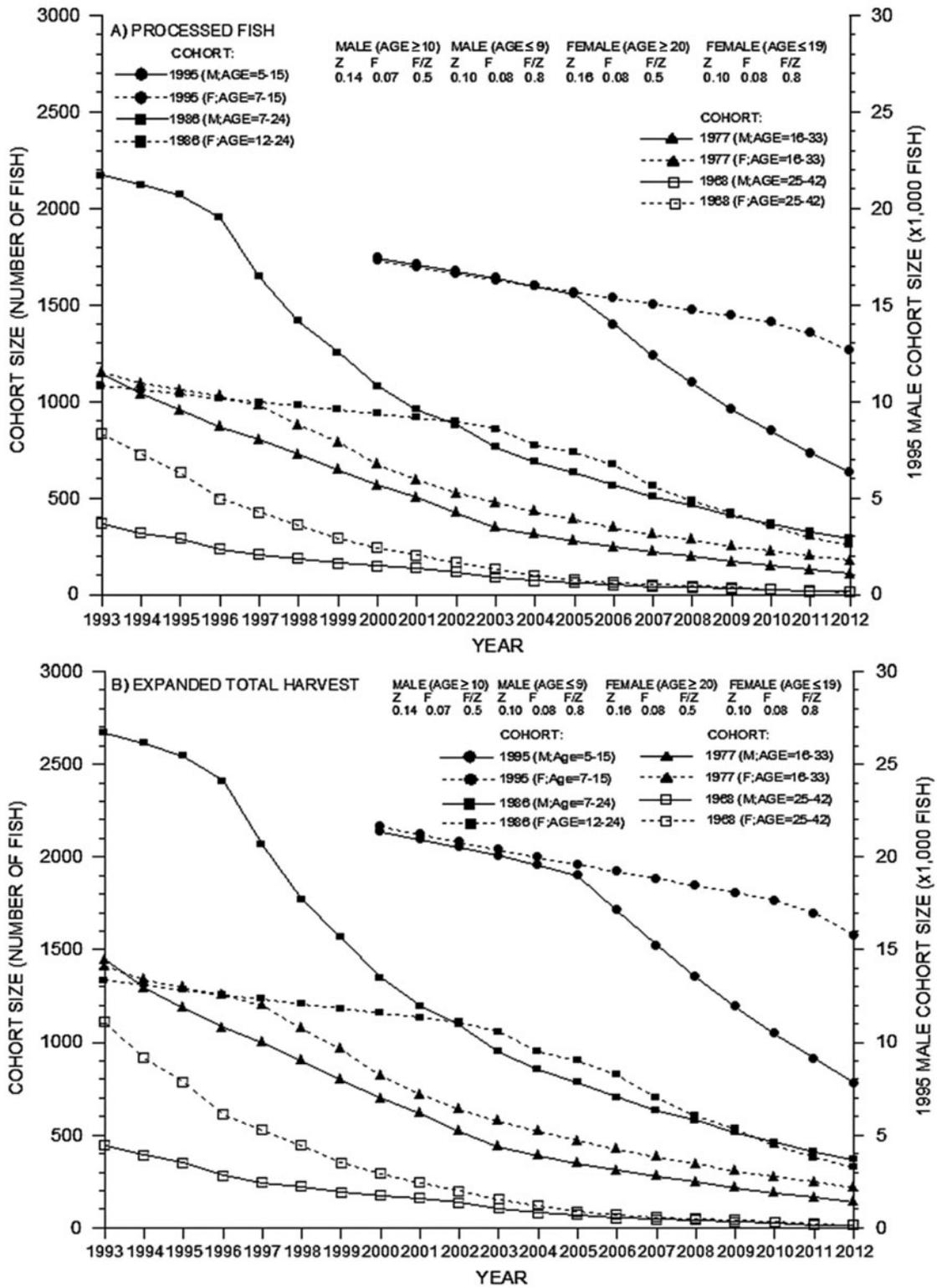


Figure 9 Virtual population sizes for male and female paddlesh, Montana and North Dakota combined, of four selected cohorts (1968, 1977, 1986, 1995), for  $F/Z = 0.5$ : (A) processed fish and (B) expanded total harvest.

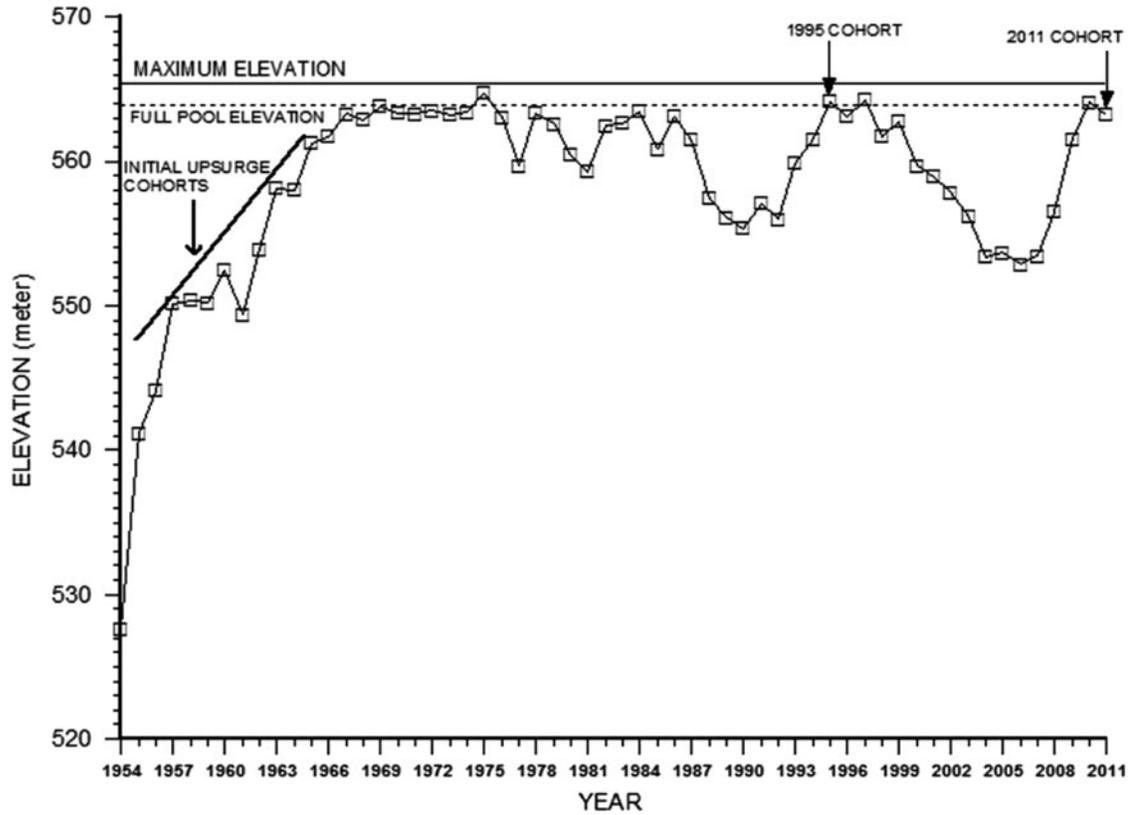


Figure 10 Mean water levels in August, Lake Sakakawea, North Dakota, 1954–2011, and associated strong year-classes of Yellowstone–Sakakawea paddlefish.

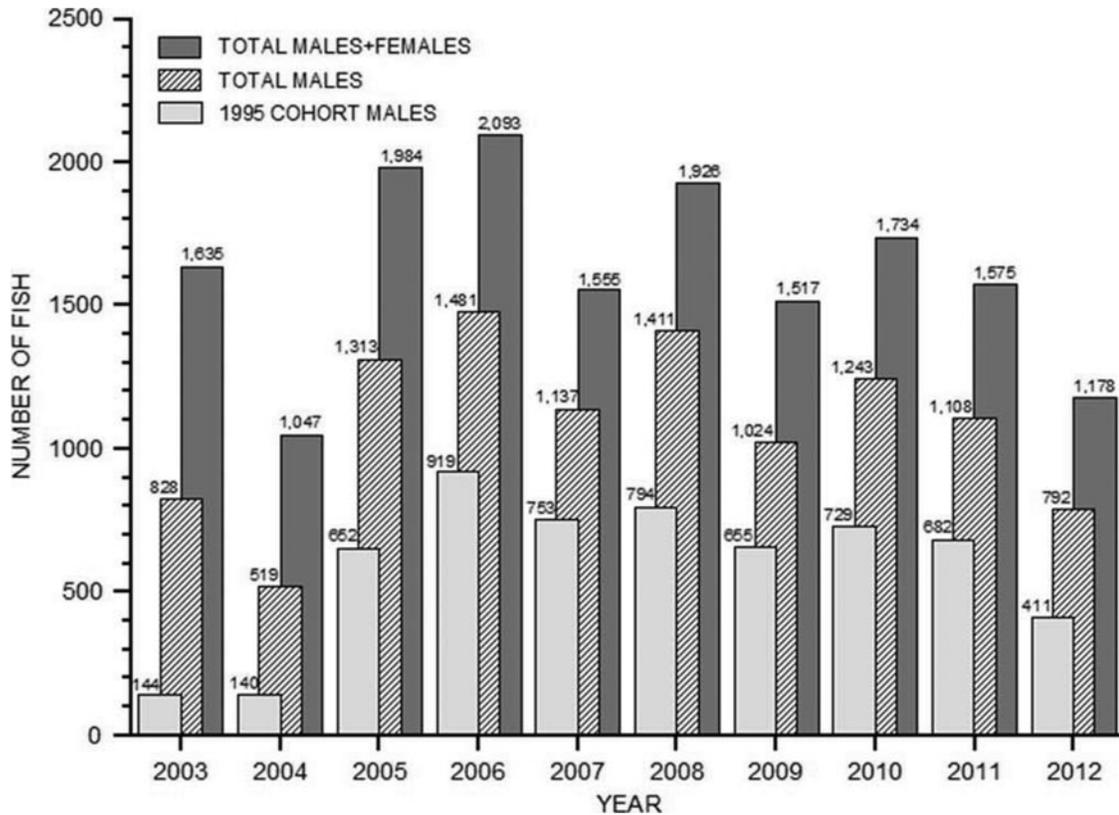
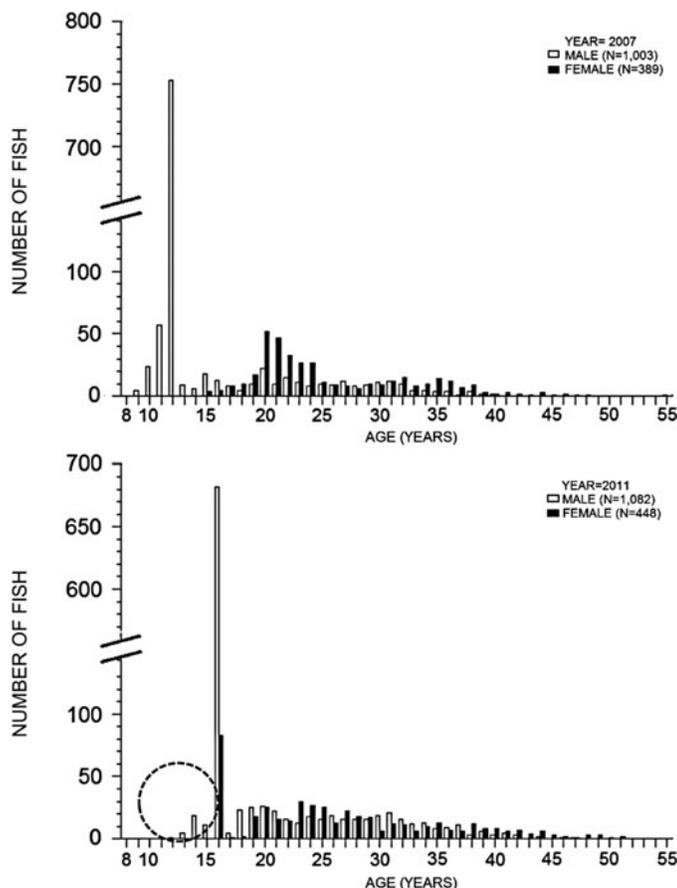


Figure 11 Contribution of the 1995 cohort of male paddlefish to total processed fish at Intake, Montana, and the Confluence, North Dakota, 2003–2012.



**Figure 12** Age structure of the processed paddlefish of Yellowstone–Sakakawea paddlefish harvest under mandatory retention regulations, 2011, showing absence or near absence of several year-classes of male fish (circled) in contrast to harvest when the strong 1995 year-class was recruiting to the fishery, 2007.

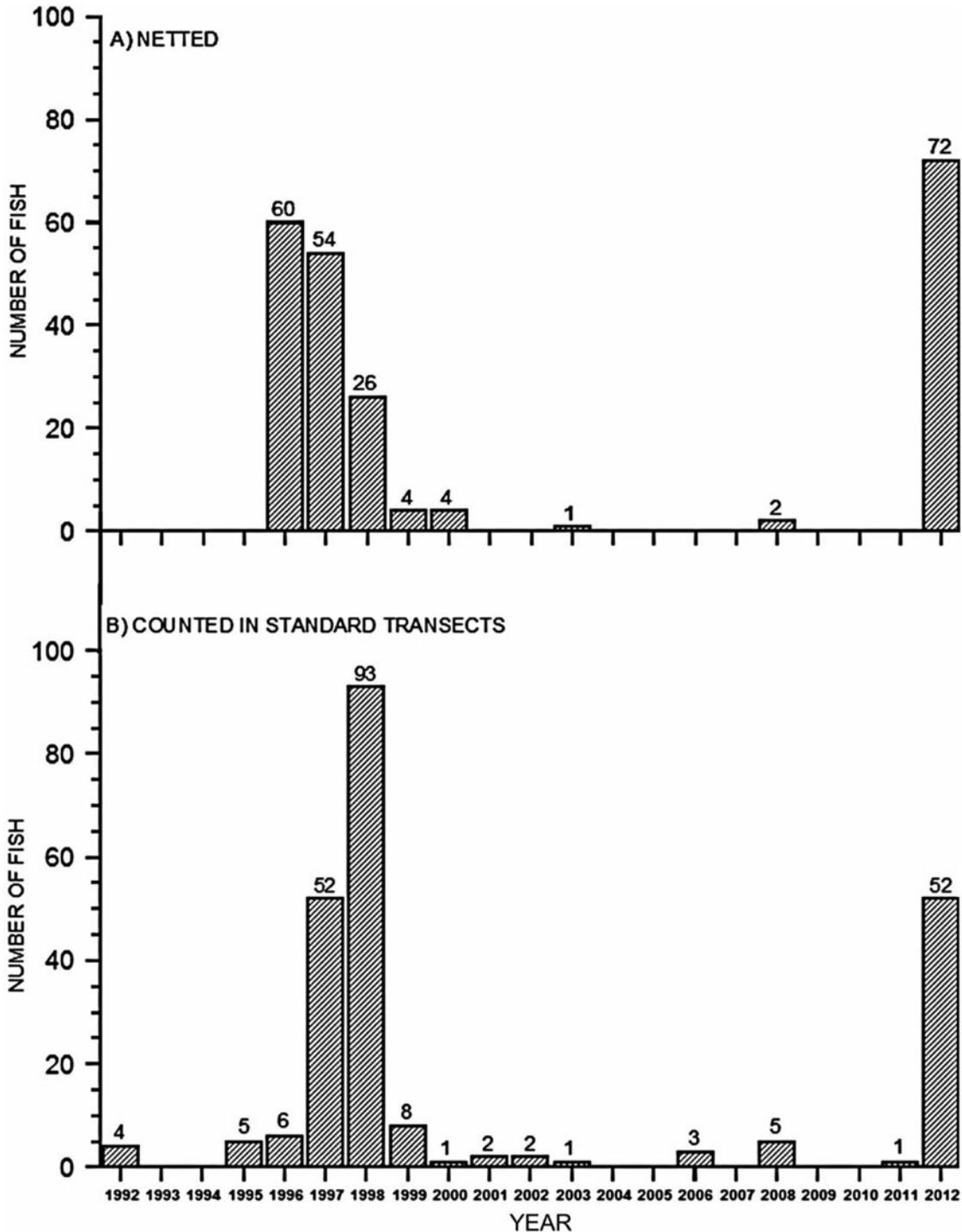
may exist in the 2011 cohort. After initial reservoir filling, strong recruitment of this stock can thus be characterized as episodic. A similar presence of an episodic strong year-class has also been found in the Grand Lake, Oklahoma, stock of paddlefish (Scarnecchia et al., 2011), which was not suspected of showing this recruitment pattern before the intensive sampling began.

Episodic recruitment of the Yellowstone–Sakakawea paddlefish stock exists even though standard transect counts of age-0 fish (Fredericks and Scarnecchia, 1997; Scarnecchia et al., 1997) indicate that reproduction occurs in nearly all years (all but two years documented over the period 1992–2012; unpublished data). Cohorts with large numbers of age-0 fish in a given year may produce few age-1 fish the following year. Survival past age 0 is thus the critical issue not only for this stock but for some other Acipenseriform fish, sometimes leading to hatchery releases to circumvent the age-0 survival bottleneck (Ireland et al., 2002).

It is suggested, from both environmental and evolutionary perspectives, that erratic or episodic recruitment may be much more prevalent in paddlefish, sturgeon, and many other long-lived fish than is recognized. It may be pervasive in many long-

lived, late maturing, non-annual, high-fecundity, oviparous, broadcast spawners. Large upriver migrations of paddlefish and strong year-classes have been associated with episodic environmental events, e.g., high spring discharges and high reservoir water levels (Russell, 1986; Scarnecchia et al., 2009). Reproductive synchrony among fish in such years, when early life-history habitat is more abundant and more productive (Kimmel and Groeger, 1986), may provide recruitment benefits. Large age-0 year-classes of paddlefish and other prey species benefitting from the upsurge may swamp potential predators (Horn, 1978), perhaps before the predator populations respond to the upsurge with larger numbers of large fish able to eat the prey. More research is needed in the exact mechanisms associated with upsurge that might favor recruitment. Regardless of the mechanism, however, when fishes with evolved long lifespans and iteroparity exist in episodically favorable environmental conditions, the outcome will often be episodic recruitment. They produce very large numbers of tiny offspring with highly uneven annual results, with a few good recruitment years adequate to compensate for the preponderance of poor recruitment years. In contrast, other late maturing long-lived species, such as various sharks and rockfishes *Sebastes* spp., address the recruitment issue through viviparity (Wourms and Lombardi, 1992; Gunderson, 1997), producing small numbers of large highly viable offspring in a much less episodic, more predictable pattern. That reproductive approach will typically result in a slow but steady recruitment pattern more buffered from environmental vicissitudes. Both strategies can be effective in long-lived fishes if adult mortality (e.g., from harvest) is not too high and the fish are allowed to survive to the advanced age they are physiologically capable of attaining.

Harvest and management of the Montana and North Dakota recreational snag fisheries since 2004 have been strongly influenced by the episodic recruitment success of the 1995 year-class. Recruitment greatly exceeded natural and harvest mortality for several years as males, which start to mature at about age 8 and are mostly mature by ages 10–12 (Scarnecchia et al., 2007), recruited to the fishery over the period 2003–2008 and continued to dominate harvest through 2012 (Figure 11). Under mandatory retention regulations and a harvest cap (Scarnecchia et al., 2008), males from the 1995 year-class have buffered older males and all females from harvest, as harvest has consisted of a high percentage of young males. As of 2012, the females, which start to mature at about age 15 and thus recruit nearly a decade later than the males of the same cohort (Scarnecchia et al., 2007), had just begun to enter the harvest (D. L. Scarnecchia, unpublished data; Figure 6). Looking ahead, results of age determination indicated that several year-classes of Yellowstone–Sakakawea paddlefish from 1998 through 2003 are extremely weak, as indicated by the absence of recruited males of ages 8–13 (Figure 12). Harvest management of the Yellowstone–Sakakawea paddlefish stock must therefore be conducted with the understanding that several year-classes have failed and that almost no males or females will recruit from these cohorts. With such episodic recruitment and year-class failures, male and female fish of the abundant



**Figure 13** Catches and counts of age-1 paddlefish in Lake Sakakawea: (A) netted throughout upper end of reservoir and (B) counted along standard transects, 1992–2012. (Most fish caught and counted in 1997 and 1998 are age-2 and age-3 fish; Scarnecchia et al. 2009.)

1995 year-class will need to be carefully allotted to harvest until recruitment improves. Episodic recruitment as clearly demonstrated by VPA in the Yellowstone–Sakakawea stock thus poses some substantial challenges for harvest management. Under these conditions, in most years, the optimal harvest may consist of mining fish, i.e., harvesting at levels that exceed recruitment,

under the assumption that future episodic recruitment, which must be monitored for detection, will repopulate the stock and re-vitalize the fishery. In this approach, the harvest would be allotted mainly as dictated by episodic recruitment. A much more conservative approach for this long-lived stock might involve more closely matching the harvest to mean or median observed

recruitment from the VPA, not including episodic years such as 1995 (i.e., leveling out the virtual population size trends in Figures 5–7 rather than permitting the observed progressive declines). Regardless of the approach, paddlefish stock status must continue to be monitored for harvest and recruitment information; future efforts will involve using the results of this VPA to predict future conditions of the stock based not only on past performance and a deterministic future (Sparre and Venema, 1992) but on unforeseen future conditions (Walters and Punt, 1993; Virtala et al., 1998).

Since the development of the first Cooperative Interstate Management Plan (Scarnecchia et al., 1995b) and the revised plan 13 years later (Scarnecchia et al., 2008), the clearly stated emphasis has been on maintaining natural recruitment of wild fish. The tacit assumption has been that the wild Yellowstone–Sakakawea paddlefish would adequately recruit under existing conditions on their own. This assumption of adequate recruitment of wild fish is not assured. It may be necessary to more actively manage physical and ecological aspects of such regulated rivers and their reservoirs to improve recruitment conditions. However, this approach presents challenges. Although there is evidence that reproductive success may be favored by increasing water levels following low water level periods (Scarnecchia et al., 2009; Figure 12), the Missouri River reservoir water levels, including those of Lake Sakakawea, are managed by the U.S. Army Corps of Engineers under the Master Plan, with flood control its highest priority (<http://www.nwd-mr.usace.army.mil/rcc/reports/pdfs/MissouriRiverFloodingUpdate1-Aug.pdf>). Water levels are thus not under the jurisdiction of the state of North Dakota.

Predation may also be a problem for recruitment. There is evidence that paddlefish are subject to predation by piscivorous fish, such as the walleye *Sander vitreus*, sauger *Sander canadensis*, and northern pike *Esox lucius* (Mero et al., 1994; Parken and Scarnecchia, 2002). A review of stocking records from Lake Sakakawea since Garrison Dam was closed indicates that walleye and northern pike have each been stocked in 25 different years (Fryda et al., 2010). Most fish stocked from 1954 through 1978 were northern pike, with walleye increasing in emphasis since then. Although no northern pike have been stocked since 1993, the population is self-sustaining and fluctuates with reservoir levels, typically increasing after years of high or rising water levels. Chinook salmon *Oncorhynchus tshawytscha* have also been stocked in 32 different years since 1976 (Fryda et al., 2010), and their potential effects on age-0 paddlefish are not known. All three of these stocked piscivorous species are highly popular with anglers, and until the exact effects of predation on recruitment success are clearly shown, predator control actions will be difficult to justify and gain public support. In addition to piscivorous predators, gulls (Laridae) and other birds have been observed eating age-0 paddlefish on Lake Sakakawea; their impacts are unknown. More food web research is needed into understand how predation affects recruitment.

With natural changes in productivity associated with reservoir aging (Kimmel and Groeger, 1986), including sedimenta-

tion of the upper end of the reservoir heavily used by age-0 paddlefish (Fredericks and Scarnecchia, 1997) and stocking of paddlefish predators, wild paddlefish recruitment may decrease in the future. To better understand factors affecting recruitment of wild paddlefish, more consideration should thus be given to issues of river discharges (including the inflowing plume in the reservoir headwaters), reservoir conditions (including water levels and trophic upsurge; Scarnecchia et al., 2009), and food web issues with predators (Parken and Scarnecchia, 2002; Naiman et al., 2012).

As a last resort, hatchery production and stocking to improve long-term paddlefish recruitment remains an option. Occasional experimental paddlefish stockings have been conducted, including a successful stocking in 1995 (D. L. Scarnecchia and L. F. Ryckman, unpublished data). Stocking has been designed mostly for obtaining scientific information validating annuli of dentaries (Scarnecchia et al., 2006) and obtaining information on factors affecting survival (Scarnecchia et al., 2009). Potential concerns with hatchery fish on wild stocks are well documented for other fish species and detailed in Scarnecchia et al. (2008). At this time, however, a preferable approach would be to improve conditions for wild paddlefish recruitment; this effort should be given a much higher priority. Factors affecting strong episodic recruitment such as in 1995 and probably 2011 (very high spring discharges and strongly increasing reservoir levels after drought and reservoir drawdowns) may be outside of state or regional control. However, other options, such as altering food web interactions, should be investigated for their potential to provide modest but consistent increases in average recruitment in other more typical years.

The recruitment issue has relevance to the ecology of paddlefish, other Acipenseriform species, and other fish taxa worldwide. Managing for episodic recruitment may be increasingly necessary in this and other locations because of dam construction, habitat fragmentation, and resulting stock separation in large rivers. Historically, paddlefish, sturgeons *Scaphirhynchus* spp., blue suckers *Cycleptus elongatus*, and other large river species were able to undertake long unimpeded migrations (Russell, 1986). Considerable evidence from Montana and Oklahoma indicates that more paddlefish migrate farther upriver for spawning during high-water years than low-water years (e.g., Neosho River flows at Commerce, Oklahoma, and Grand Lake stock paddlefish catches upriver at Chetopa, Kansas [D. L. Scarnecchia, unpublished data]; Yellowstone River flows at Sidney, Montana, and catches upriver at Intake, Montana [Scarnecchia et al., 2008]). Large numbers of newly hatched young would then populate downriver areas, rearing in flooded habitat. Under such conditions, the lack of successful spawning in a particular river segment at regular intervals may not have been crucial to species survival in that area. Under the fragmented habitat brought about by the mainstem dams, however, stocks may be more isolated, necessarily more self-sustaining, and more dependent on successful episodic recruitment events, even though regulated flows may not only impede migrations but impede successful spawning (Sparrowe, 1986; Unkenholz, 1986).

Several aspects of the Yellowstone–Sakakawea research program may also be worth emulating for sustainable harvest management of other wild paddlefish and sturgeon stocks for meat or caviar production. First, reliable sex-specific age structure trends should form the basis of the harvest management strategy in any recreational or commercial situation. Obtaining a thorough understanding of sex-specific age structure and development of an historical VPA will show stock trends, allow the identification of strong and weak year-classes, and set the stage for predictive models to guide harvest management. Because validating ages of very old fish is often difficult, the recommended approach is to identify the strong year-classes as early as possible (e.g., as pre-recruits or as early recruits to the adult spawning population) to allow for the use of more easily validated ages (Scarnecchia et al., 2006). Strong cohorts can then be followed more reliably based on dentaries or other aging structures, or tagging, as they age. Recruitment problems can be identified as they arise rather than in hindsight, when such knowledge may come after stock abundance has declined and it is too late for an effective response (Crouse, 1999).

By implementing time-area closures, mandatory retention, and harvest cap regulations, fisheries will harvest a limited number of both males (which are smaller and recruit younger) and females. With fisheries that focus harvest on mature fish (i.e., fish that are at least making their first spawning migration), harvest of the mature males can be used effectively to herald future abundance of mature female spawners of the same cohort, the same approach used with jack coho salmon *Oncorhynchus kisutch* (Gunsolus, 1978) or Atlantic salmon *Salmo salar* grilse to forecast future years' abundance of older salmon of the same cohort (Jacobsson and Johansen, 1921; Peterman, 1982; Scarnecchia, 1984). Males can be used as an effective tool to forecast and, if necessary, protect female spawners until males from strong cohorts will protect them under mandatory retention and harvest cap regulations (Scarnecchia et al., 2008; Figure 12).

In order to permit paddlefish to achieve their evolved life history strategy, including delayed maturity and a long lifespan, it is recommended that all paddlefish harvests be managed to mimic the natural mortality pattern, similar to the catch-curve pattern resulting from a mandatory retention fishery (e.g., Figure 4). Eliminating excessive high-grading will avoid the all-too-common practice of overharvesting the largest and oldest fish, typically females. In that way, the stock of paddlefish or other species will be able, as it has adapted to through evolutionary time, to take advantage of favorable recruitment conditions, even if they are episodic.

All of these harvest management approaches are much simpler for managers and better for the paddlefish stocks if mandatory retention fisheries with defined harvest caps are parts of the harvest management strategy. If harvest caps are met, some catch-and-release recreational snag fisheries can also be implemented in specific situations where they can be monitored (Scarnecchia and Stewart, 1997).

Obtaining and assessing more information on physical and chemical factors (e.g., river discharges, reservoir water levels,

nutrients) and ecological factors (food webs, predators) affecting Acipenseriform reproductive success and recruitment are critical to long-term sustainability. Such knowledge may preferably lead to attempts to improve recruitment, avoiding the use of hatcheries except as a last resort. More consistent and predictable recruitment will be more favorable than episodic recruitment in terms of providing options for harvest management and sustainability of the stocks.

The controlled mining approach described above for the Yellowstone–Sakakawea stock may become necessary for other Acipenseriform species once their age structure and recruitment patterns are better understood if their harvests are to be managed sustainably for meat and caviar production. Currently, most paddlefish fisheries and sturgeon fisheries worldwide lack adequate information on validated ages to determine if such episodic recruitment exists, and most harvest models, however sophisticated, are based on poor data. For paddlefish and sturgeon worldwide, which are some of our most ancient and highly-valued species, harvest managers must become more focused on enacting and enforcing regulations so that their fisheries act as instruments of sound public policy and provide high-quality data that can be used to document recruitment patterns and improve harvest management.

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