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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 Þsheries may no longer be viable or populations themselves are no longer sustainable even without harvest. In situations where Þsheries remain an option but where reproductive success and recruitment are inconsistent or episodic, Þshery managers can set regulations to parcel out annual harvest in a controlled and sustainable manner until new pulses of recruitment occur.

The largely zooplantivorous paddleÞsh (Eddy and Simer, 1929; Rosen and Hales, 1981; Fredericks, 1994) supports important recreational snag Þsheries in the Yellowstone and Missouri Rivers of western North Dakota and eastern Montana (Scarnecchia et al., 2008). An interstate Þshery harvests the YellowstoneÐSakakawea stock, a distinct group of Þsh 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 Þsh from this stock has been documented in the Þrst 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 Þlling and resulting trophic upsurge of Lake Sakakawea from 1953 to 1966 (Scarnecchia et al., 1996, 2009). The recreational Þsheries, which use heavy spinning rods and treble hooks and target mature prespawning Þsh, 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 Þsheries are managed under a Cooperative Interstate PaddleÞsh Management Plan (Scarnecchia et al., 1995b, 2008). Harvest is restricted to one Þsh per person per year in each state; mandatory retention of any snagged paddleÞsh is required during mandatory snag and harvest periods; and, as of 2012, each state caps the allowable annual harvest at 1,000 Þsh. Catch and release snagging (Scarnecchia and Stewart, 1997) is also permitted at speciÞed times during and after the harvest season. A detailed chronology of the history and development of the Þsheries and their management is in Scarnecchia et al. (2008).

The YellowstoneÐSakakawea paddleÞsh 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 conßuence of the Missouri and Yellowstone Rivers (hereafter, the Conßuence). Under the programs, snaggers can receive free cleaning of Þsh of either sex for a donation of any Þsh roe present in their catch. The roe is processed into caviar on-site and later sold, with

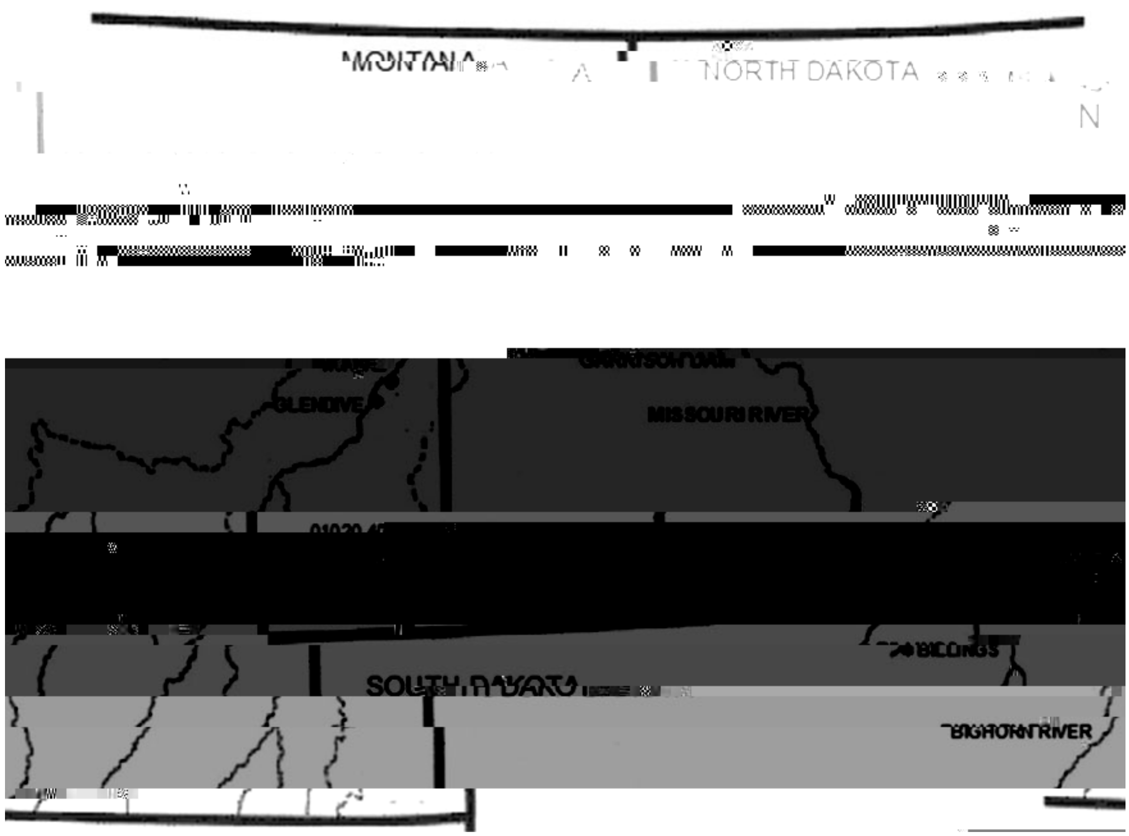

Figure 1 Region and study site associated with the YellowstoneÐSakakawea paddleÞsh stock.

proceeds going to programs of regional public beneÞt and to state agency conservation and enforcement efforts. The Þsh-cleaning operations at the two roe donation sites provide highly centralized locations for efÞcient collection of extensive Þsheries data needed for stock assessment. In any given year, 70Ð95% of the Þsh 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 Þsheries agencies in Montana and North Dakota, with the intent of maintaining the existing adult population size by adjusting harvest based on average Þve-year recruitment. Information on population sizes (from adult Þsh 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 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 consultTJ 0 -1..1(r)-36.8(f)-.7dm(i)ahigh-g220.9(t(s)-300.5(a).i70r

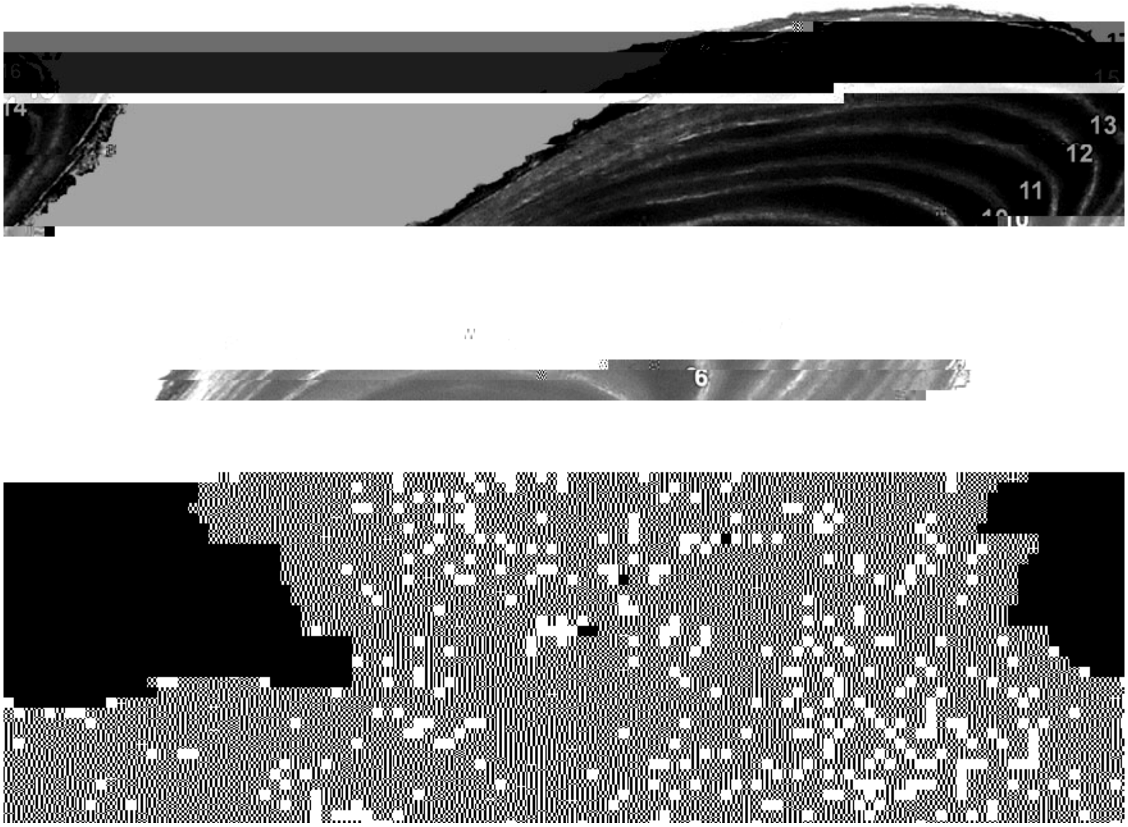

Figure 3 Validated age-17 female YellowstoneÐSakakawea paddleÞsh (BL 1,067 mm, weight 21.32 kg) of the 1995 year-class.

of Þsh 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 Þsh known to be processed at the Conßuence and Intake cleaning stations and the percentage of the harvested Þsh that were brought to those stations for processing. In this approach, in each year, the observed age frequency distribution for the observed harvested Þsh 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 Þsh by age over the period.

VPA

VPA uses a deterministic, recursive algorithm to calculate stock size based on Þsh harvest by age. Given a terminal Þshing mortality (F_T), from which a terminal virtual cohort size is obtained, all other Þshing 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 Þshing mortality. The catches are converted into a set of equivalent virtual population sizes and Þshing mortalities. Any aging or other errors in the original data therefore affect the population and Þshing 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 Þshing mortalities and population size for earlier years and younger ages become progressively less sensitive to the starting assumptions about terminal Þshing 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 BaranovÕs catch equation,

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

where N_t is the number of Þsh 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 Þshing and natural mortality, respectively. The decomposition of the total mortality into natural and Þshing mortality is required because only catch C_t is observed.

Table 1 Ratio of processed paddleÞsh to total estimated harvest, Montana and North Dakota, 1993Ð2012

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,		

Table 2 Eight sets of terminal Þshing mortality (F)

(Table 1). Second, for t Ð 1, $F_{t\ Ð\ 1}$

Figure 5 Virtual populations for 1993Ð2012 combined Montana and North Dakota male paddleÞsh: (A) processed Þsh and (B) expanded total harvest.

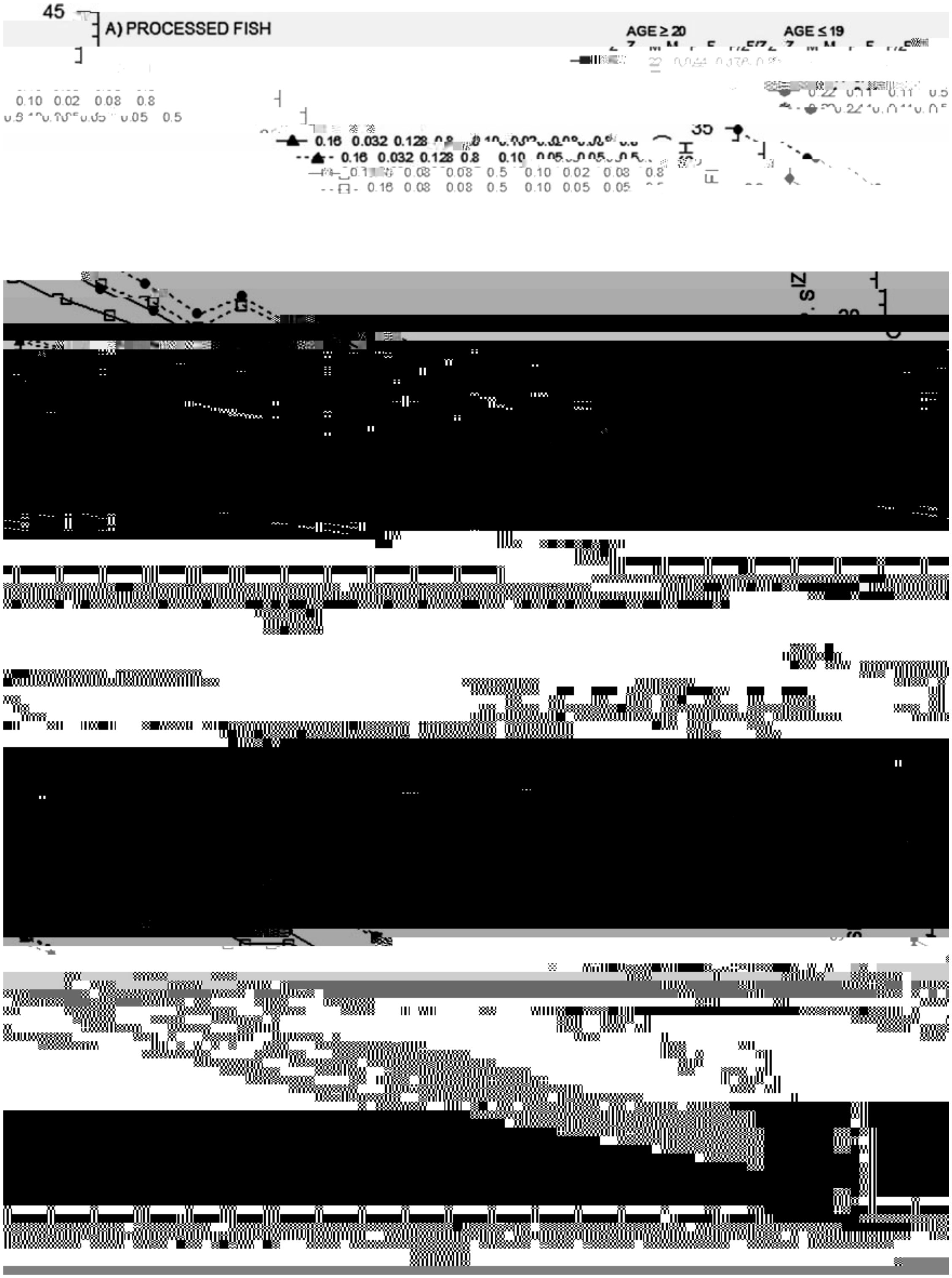

Figure 6 Virtual populations for 1993Ð2012 combined Montana and North Dakota female paddleÞsh: (A) processed Þsh and (B) expanded total harvest.

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 Þlling period was in 1995, as three years of Þlling 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

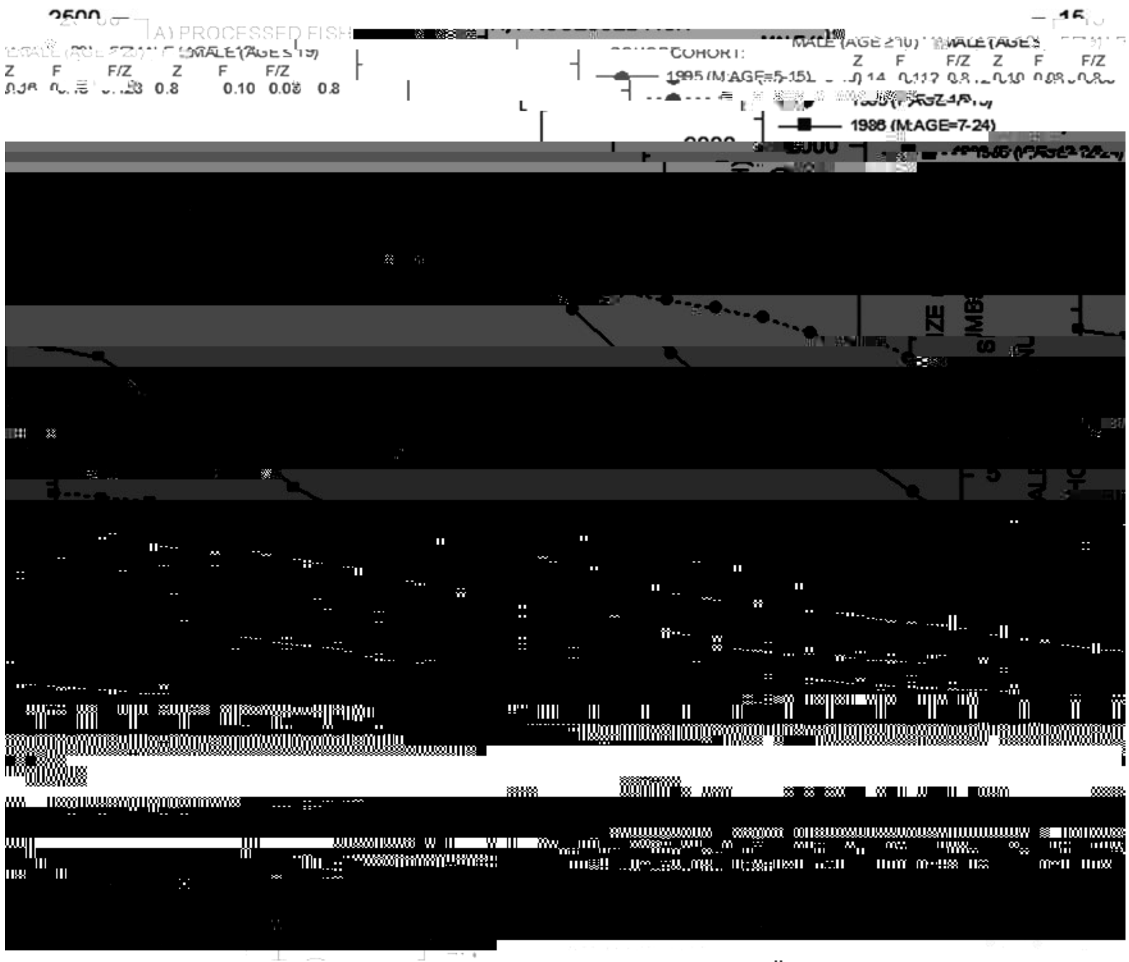

Figure 8 Virtual population sizes for male and female paddleÞsh, Montana and North Dakota combined, of four selected cohorts (1968, 1977, 1986, 1995),
F/Z = 0.8: (A) processed Þsh and (B) expanded total harvest.

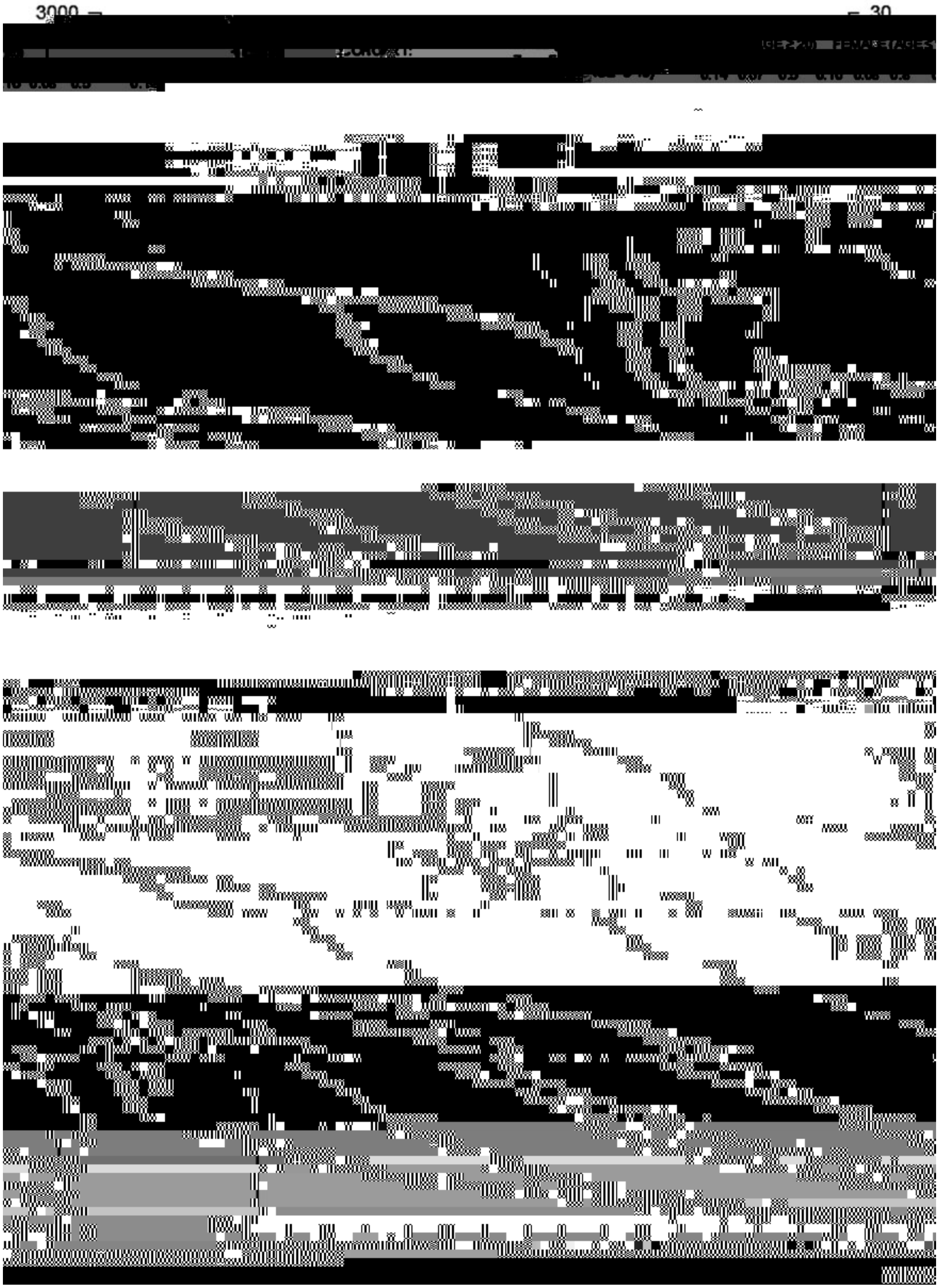

Figure 9 Virtual population sizes for male and female paddleÞsh, Montana and North Dakota combined, of four selected cohorts (1968, 1977, 1986, 1995), for F/Z = 0.5: (A) processed Þsh and (B) expanded total harvest.

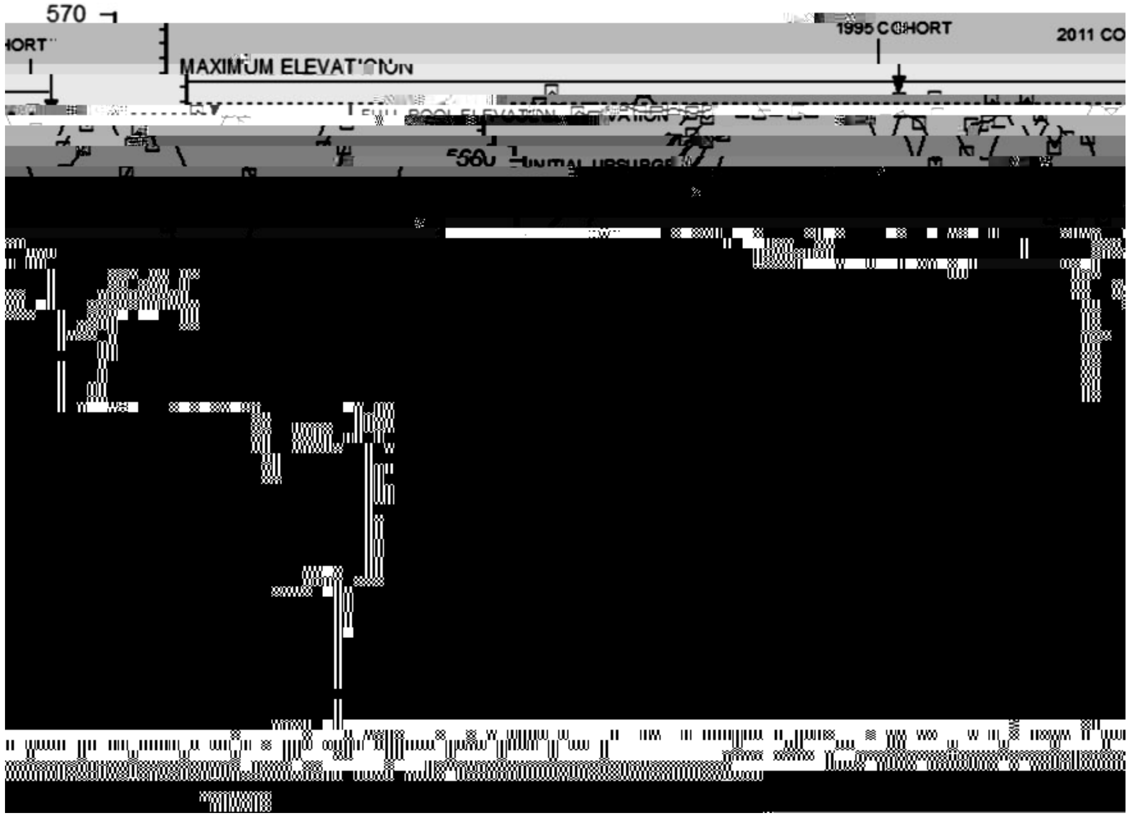

Figure 10 Mean water levels in August, Lake Sakakawea, North Dakota, 1954Ð2011, and associated strong year-classes of YellowstoneÐSakakawea paddl

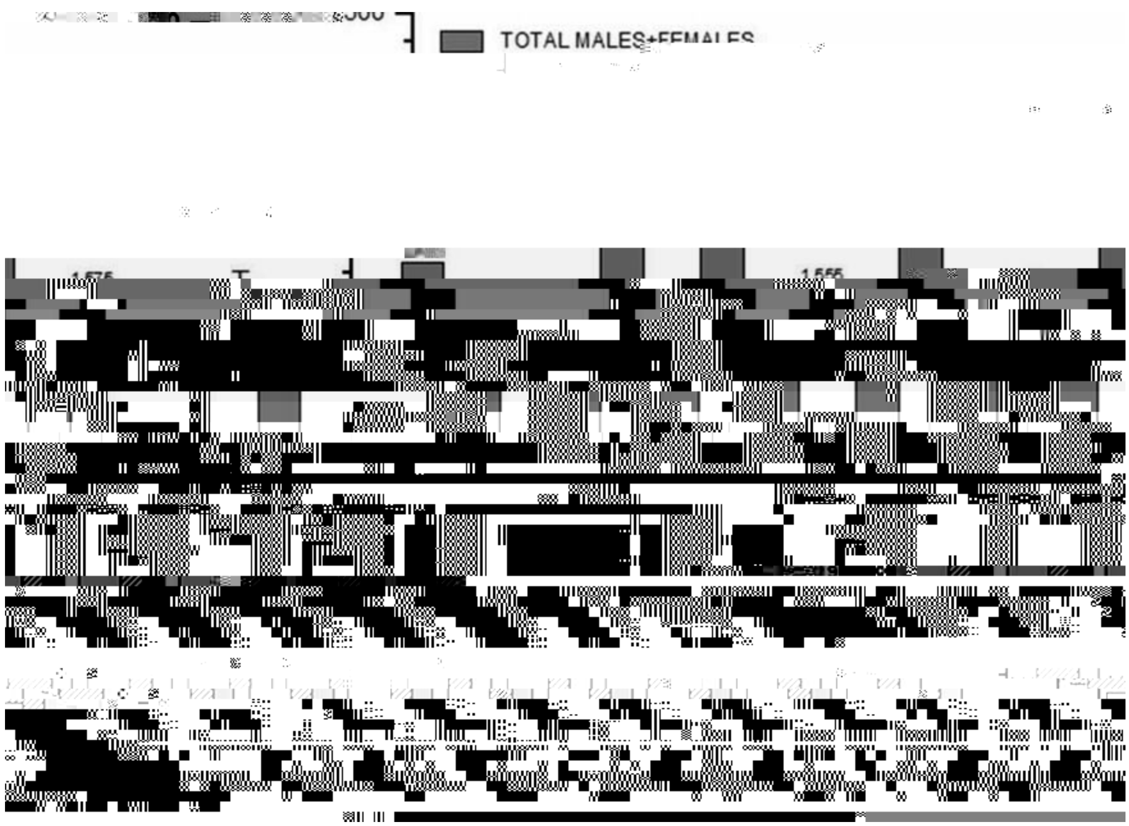

Figure 11 Contribution of the 1995 cohort of male paddleÞsh to total processed Þsh at Intake, Montana, and the Conßuence, North Dakota, 2003Ð2012.

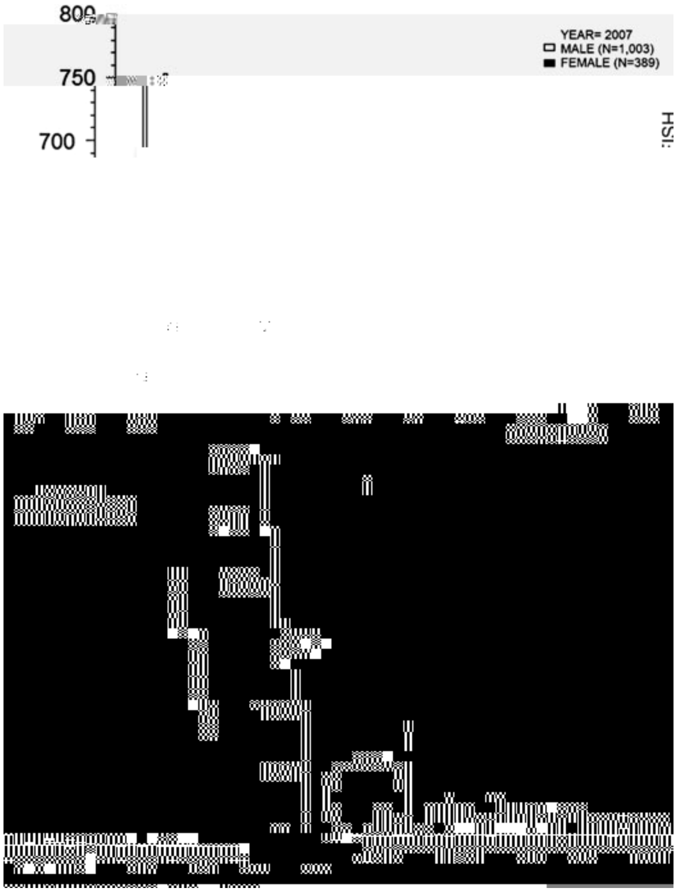

Figure 12 Age structure of the processed paddleÞsh of YellowstoneÐ Sakakawea paddleÞsh harvest under mandatory retention regulations, 2011, showing absence or near absence of several year-classes of male Þsh (circled) in contrast to harvest when the strong 1995 year-class was recruiting to the Þshery, 2007.

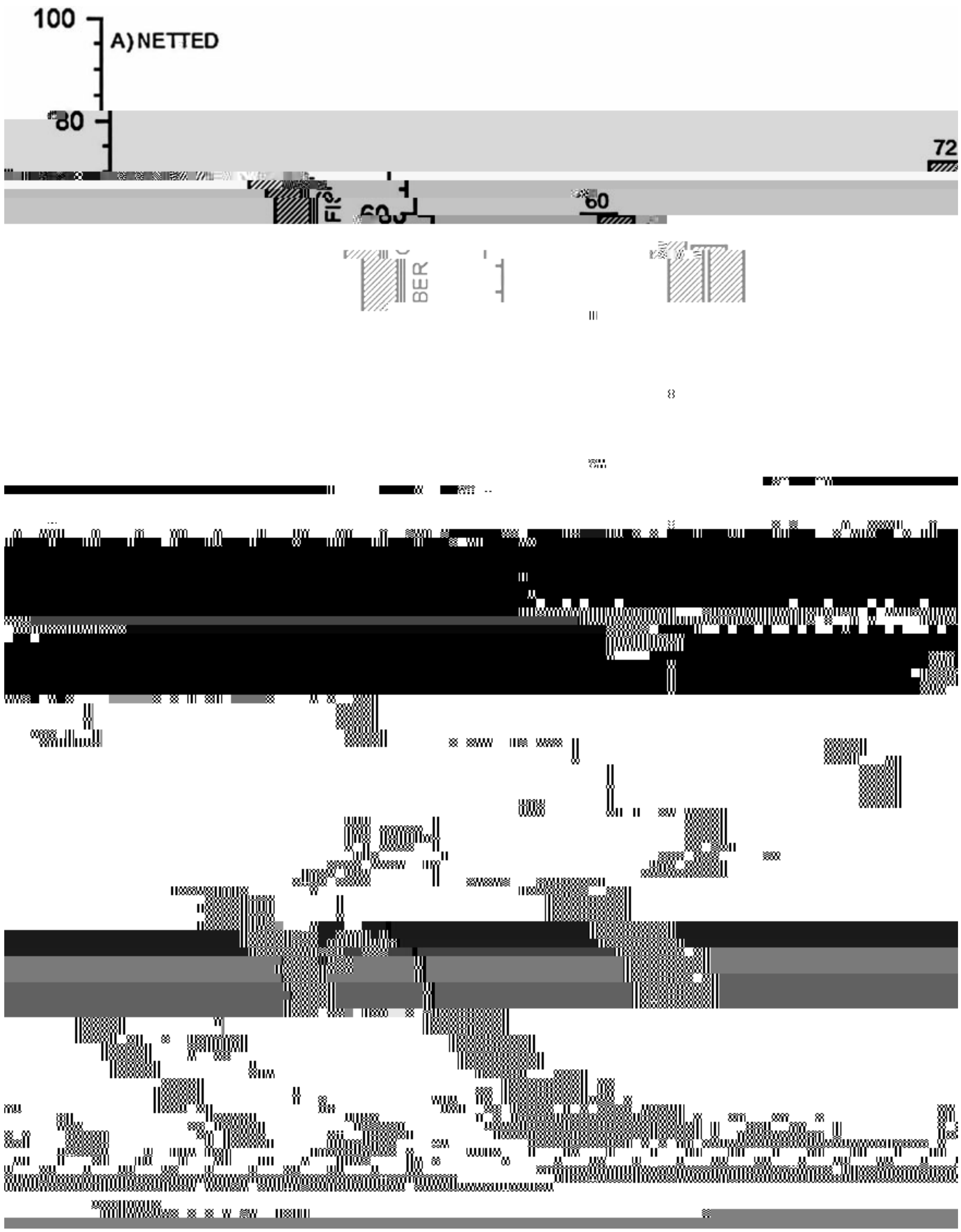

Figure 13 Catches and counts of age-1 paddleÞsh in Lake Sakakawea: (A) netted throughout upper end of reservoir and (B) counted along standard trans 1992Ð2012. (Most Þsh caught and counted in 1997 and 1998 are age-2 and age-3 Þsh; Scarnecchia et al. 2009.)

1995 year-class will need to be carefully allotted to harvest until recruitment improves. Episodic recruitment as clearly demonstrated by VPA in the YellowstoneÐSakakawea stock thus poses some substantial challenges for harvest management. Under these conditions, in most years, the optimal harvest may consist of mining Þsh, 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 revitalize the Þshery. 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 5Ð7 rather than permitting the observed progressive declines). Regardless of the approach, paddleÞsh stock status must continue to be monitored for harvest and recruitment information; future efforts will involve using the results of this VPA to

Several aspects of the YellowstoneÐSakakawea research program may also be worth emulating for sustainable harvest management of other wild paddleÞsh and sturgeon stocks for meat or caviar production. First, reliable sex-speciÞc age structure trends should form the basis of the harvest management strategy in any recreational or commercial situation. Obtaining a thorough understanding of sex-speciÞc age structure and development of an historical VPA will show stock trends, allow the identiÞcation of strong and weak year-classes, and set the stage for predictive models to guide harvest management. Because validating ages of very old Þsh is often difÞcult, 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 identiÞed 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, Þsheries will harvest a limited number of both males (which are smaller and recruit younger) and females. With Þsheries that focus harvest on mature Þsh (i.e., Þsh that are at least making their Þrst 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 yearsÕ 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 paddleÞsh to achieve their evolved life history strategy, including delayed maturity and a long lifespan, it is recommended that all paddleÞsh harvests be managed to mimic the natural mortality pattern, similar to the catch-curve pattern resulting from a mandatory retention Þshery (e.g., Figure 4). Eliminating excessive high-grading will avoid the all-too-common practice of overharvesting the largest and oldest Þsh, typically females. In that way, the stock of paddleÞsh 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 paddleÞsh stocks if mandatory retention Þsheries with deÞned harvest caps are parts of the harvest management strategy. If harvest caps are met, some catch-and-release recreational snag Þsheries can also be implemented in speciÞc 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 YellowstoneÐSakakawea 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 paddleÞsh Þsheries and sturgeon Þsheries 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 paddleÞsh 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 Þsheries act as instruments of sound public policy and provide high-quality

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