Reviews in Fisheries Science, 17(2):241–266, 2009
Copyright © Taylor and Francis Group, LLC
ISSN: 1064-1262 print
DOI: 10.1080/10641260802621791

Riverine and Reservoir Influences on Year Class Strength and Growth of Upper Great Plains Paddlefish

DENNIS L. SCARNECCHIA,[1] L. FRED RYCKMAN,[2] YOUNGTAIK LIM,[1]
SHANNON E. MILLER,[1] BRAD J. SCHMITZ,[3] GREG J. POWER,[4]
and SHANE A. SHEFSTAD[2]

[1]Department of Fish and Wildlife Resources, University of Idaho, Moscow, Idaho, USA
[2]North Dakota Game and Fish Department, Williston, North Dakota, USA
[3]Montana Department of Fish, Wildlife, and Parks, Miles City, Montana, USA
[4]North Dakota Game and Fish Department, Bismarck, North Dakota, USA

A long-term investigation (1991–2006) was conducted on the relation between Yellowstone and Missouri River discharges, water level (elevation) changes of Lake Sakakawea, a Missouri River mainstem reservoir in western North Dakota, and the ecology of the Yellowstone-Sakakawea stock of paddlefish Polyodon spathula*, a zooplanktivorous Acipenseriform fish. After impoundment in December 1953, Lake Sakakawea filled gradually over a 13-year period (1953–1966). Water levels were lowered sharply and briefly in 1977 and 1981 and for much more prolonged periods of 1988–1993 and 2000–2006 associated with drought conditions in the central United States and water management decisions by the U.S. Army Corps of Engineers. The 1995 year class of paddlefish, by far the strongest in the 16-year study period, was associated with the sharp rise in water level from August 1993 through 1995, the longest continuous rise since the initial filling and the only period since initial filling when reservoir levels rose substantially in three consecutive years. High reservoir levels were associated with higher densities of zooplankton (all taxa combined and* Leptodora kindtii*, the primary food of age 0 paddlefish), stronger year classes (based on counts of age 0 fish along standard transects), greater mean weight and condition of age 0 fish in August, greater mean weights of recruits, higher growth rate of adult fish, and greater weight of gonadal fat bodies (GFBs), an indicator of energy storage, in absolute weight, as a percentage of gonad weight, and as a percentage of fish weight. Sixty-three percent of the variation in the ratio of GFB weight/gonad weight was explained by reservoir level. Fish tagged as adult migrants and recaptured in succeeding years after rearing in rising and high reservoir conditions gained an average of 0.04 kg/yr, whereas fish rearing in falling- and low-reservoir conditions lost an average of 0.19 kg/yr. Missouri River discharge during spring was significantly correlated with estimated age 0 year class strength, but a similar relationship did not hold for the Yellowstone River, which is the river used by most spawning paddlefish. Results of this study are consistent with studies from Lake Sakakawea and other reservoirs indicating that trophic upsurge in recently filled (and refilled) reservoirs favors the development of stronger year classes, faster growth, better condition, and larger size at maturity of fishes. Higher riverine discharges, thought to favor paddlefish reproductive success, were also typically associated with a rising or high reservoir. In contrast, low-reservoir levels over the period 2000–2006 have negatively affected paddlefish year class strength, growth, and energy storage. If, in succeeding years, Lake Sakakawea once again is allowed to rise to full pool as it did over the period 1993–1995, inundation of the shorelines and the vegetation can be expected to result in another upsurge period and a resulting benefit to paddlefish. Effective management of water levels in Lake Sakakawea for the benefit of paddlefish and other fishes will require a more balanced approach between upper basin and lower basin Missouri River interests.*

Keywords paddlefish, Polyodontidae, Missouri River, ecology, reservoir management

Address correspondence to Dennis L. Scarnecchia, Department of Fish and Wildlife Resources, University of Idaho, Moscow, ID 83844-1136. E-mail: scar@uidaho.edu

INTRODUCTION

In the past century, stocks of the paddlefish *Polyodon spathula*, an ancient (Grande and Bemis, 1991) zooplanktivorous

(Fredericks, 1994) Acipenseriform fish of the Missouri and Mississippi rivers (Gengerke, 1986), have experienced extensive changes in habitat conditions throughout much of their range. Most stocks have declined as riverine spawning habitat and natural sloughs, backwaters and oxbows formerly used as rearing habitat (Stockard, 1907) have been lost or degraded from dam building, channelization, and other large-river alterations (Sparrowe, 1986). Where adequate spawning habitat has been maintained, however, stock abundance has, in some instances, increased as the species has successfully used reservoirs constructed since the 1930s as productive feeding sites (Houser and Bross, 1959; Scarnecchia et al., 1996b; Paukert and Fisher, 2001).

Studies indicate that higher river discharge in spring and higher reservoir levels both favor greater year class strength and growth of paddlefish. Alexander and McDonough (1983) found that reproductive success of paddlefish rearing in Old Hickory Reservoir, Tennessee, as indicated by numbers of age 0 fish impinged at an electric plant facility, was higher during years of higher water temperature and higher discharge. Russell's (1986) conclusion that paddlefish spawn more effectively and produce stronger year classes in years with higher spring discharge is supported by other studies showing the aquatic production benefits of a higher flood pulse (Junk et al., 1989). His conclusion, although not extensively supported for paddlefish, is well supported by studies on closely related sturgeon species (*Acipenser transmontanus*: Miller and Beckman, 1993, Parsley et al., 1993; *Acipenser fulvescens*: Nilo et al., 1997). More rapid growth of age 0 paddlefish has also been associated with higher reservoir levels (Houser and Bross, 1959).

In the last half century, many large reservoirs used by paddlefish have exhibited extreme variations in size and habitat quality, resulting from factors such as climatic and weather fluctuations, variable river inflows, sedimentation, eutrophication, human water demands, and socioeconomic and political water use decisions. Numerous studies indicate that fish year class strength and growth in reservoirs may be influenced by a multitude of changes in abiotic (e.g., physical, hydrological, and chemical) aspects of habitat, as well as by biotic factors such as predation, competition, fishing, and other intra-specific and inter-specific relationships within and among species and trophic levels (see papers in American Fisheries Society, Southern Division, 1967; Hall, 1971; Hall and van den Avyle, 1986).

Water level and its changes have long been recognized as influencing fish populations and communities in reservoirs (Ellis, 1941). In various studies, water level or its changes have been shown to have significant impacts on fish abundance (several species; Paller, 1997), reproduction (carp *Cyprinus carpio*; Shields, 1957; Verrill and Berry, 1995), growth (largemouth bass *Micropterus salmoides*; Heman et al., 1969), recruitment (crappie *Pomoxis* spp.; Beam, 1983; Maceina, 2003), forage abundance (Noble, 1981), predator behavior (largemouth bass; Rogers and Bergersen, 1995), and other aspects of fish stocks. Because of the importance of water level in influencing reservoir fish communities, water level manipulation is considered a primary management tool for reservoir fisheries (Shields, 1958; Benson, 1982; Willis, 1986). Water level manipulations are used to both enhance desirable fish species and control undesirable ones (Bennett et al., 1985; Cooke et al., 1993; Verrill and Berry, 1995; Meronek et al., 1996).

In the Missouri River Basin of North America, periodic droughts and socioeconomic and political operational decisions (Bondurant and Livesey, 1967; Sveum, 1988) under the Missouri River Master Plan (U.S. Army Corps of Engineers, 2004) have resulted in highly variable water levels in upper basin mainstem reservoirs, including Lake Sakakawea in western North Dakota (Figure 1). Both high and increasing water levels in Lake Sakakawea have been linked to increases in reproductive success and abundance of numerous fish species (Power et al., 1994); conversely, low and decreasing water levels over the period 2000–2006 have been linked to lower reproductive success, lower abundance, and smaller fish size-at-age (Berard, 1989; Power et al., 1992; Hendrickson and Lee, 2000; Hendrickson et al., 2007).

The Yellowstone-Sakakawea paddlefish stock inhabits the Lower Yellowstone River, Missouri River, and Lake Sakakawea in the region including eastern Montana and western North Dakota (Scarnecchia et al., 2008; Figure 1). Evidence from migration studies indicates that the Yellowstone River is the primary spawning river for this stock (Firehammer and Scarnecchia, 2006, 2007). Fish rear primarily in Lake Sakakawea throughout their immature period as well as reside in the reservoir between spawning events (Scarnecchia et al., 2007). When Lake Sakakawea water levels began a steep decline after 1999, fisheries managers expressed concern that declining and low reservoir levels implicated in the declines of other species (Hendrickson et al., 2007) may also be negatively impacting year class strength and growth of paddlefish.

Under the cooperative, Montana-North Dakota Interstate Paddlefish Management Plan (Scarnecchia et al., 1995, 2008), fish stock assessment protocols have been implemented to monitor several aspects of the Yellowstone-Sakakawea paddlefish stock, including age structure, growth, and reproductive success. Physical and biological aspects of their habitat have also been monitored. In this study, we investigate if Yellowstone River or Missouri River discharges in spring and water level in Lake Sakakawea (and its changes) have had measurable impacts on paddlefish year class strength and growth, including fish condition and fish energy storage. We also attempt to identify possible mechanisms for any such impacts. Specifically, we hypothesized that higher Yellowstone River and Missouri River discharges in spring would be positively correlated with year class strength, as indicated by standard counts of age 0 fish in Lake Sakakawea (Fredericks and Scarnecchia, 1997). We also hypothesized that higher and increasing reservoir levels would be positively correlated with abundance of zooplankton (the primary paddlefish food; Fredericks, 1994), year class strength of paddlefish (expressed as counts of fish along standard transects and as the number of recruits in later years), growth (length-at-age and weight-at-age) of age 0 paddlefish, growth of newly

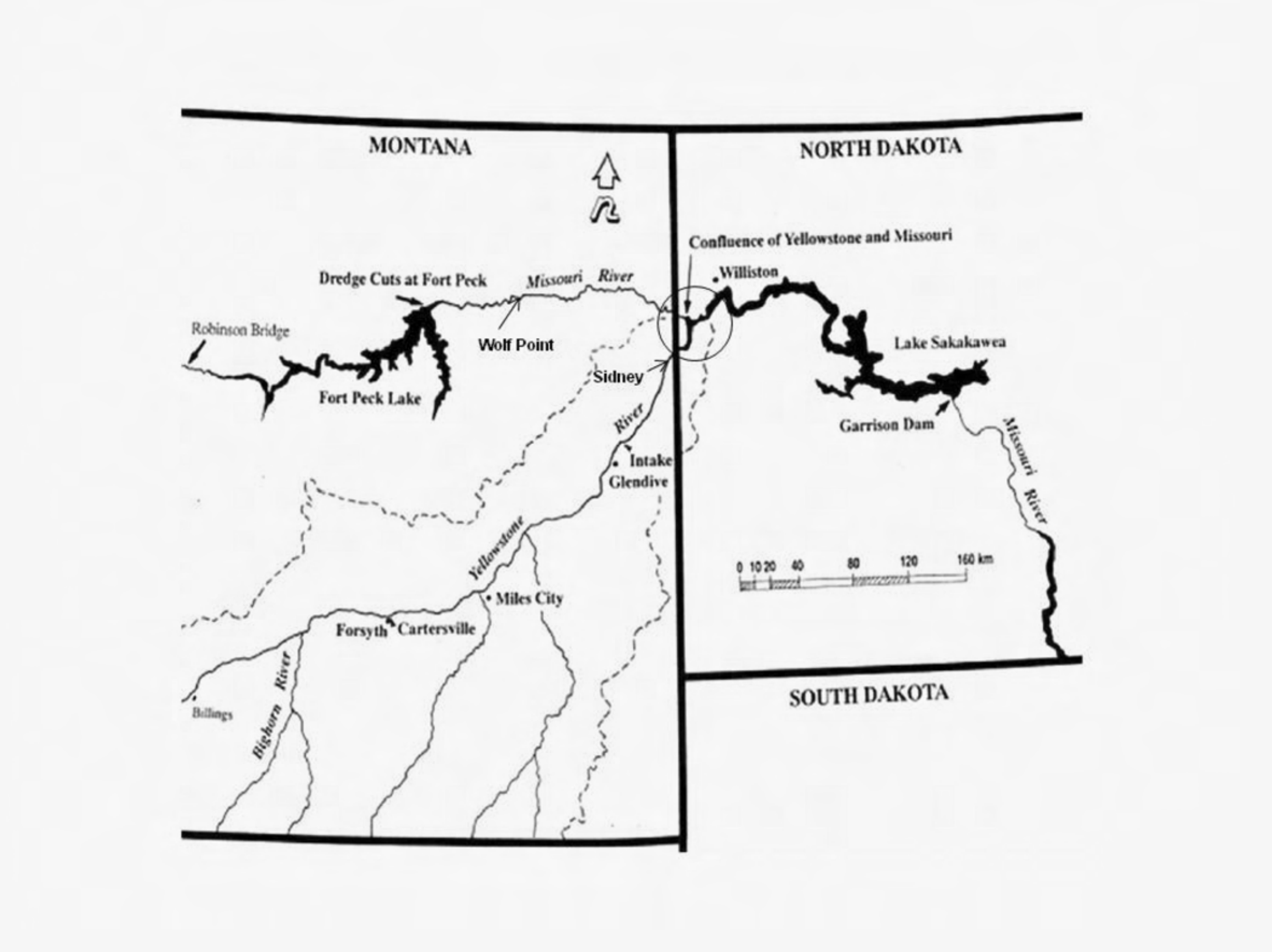


Figure 1 Map of Lake Sakakawea and upriver habitats of Yellowstone-Sakakawea paddlefish sampled in this study.

recruited paddlefish (expressed as size-at-age) of young male and female recruits), condition of age 0 and new recruits, and absolute and relative weights of gonadal fat bodies (GFBs), an indicator of energy storage, in young recruits (Scarnecchia et al., 2007). Knowledge of these relationships would be useful for managers in assessing the significance of future changes in river discharges and reservoir water levels on stock status and in implementing more favorable water management actions.

STUDY SITE

Before the 20th century, paddlefish had free access throughout most of the Mississippi and Missouri river basins, and migrations and movements extending hundreds of kilometers were documented (Russell, 1986). With the completion of a series of mainstem dams in the mid 20th century (Ridgeway, 1955; Hart, 1957; Hesse and Sheets, 1993), paddlefish movements were impeded. As of 2007, the range of the Yellowstone-Sakakawea paddlefish stock extended from Garrison Dam in the Missouri River up reservoir to the Lake Sakakawea headwaters, upriver to the confluence of the Missouri and Yellowstone rivers (a location hereafter called the Confluence), westward up the Missouri River 302 Rkm to the tailrace of Fort Peck Dam (MR Rkm 2,846, where the MR Rkm number indicates the distance above where the Missouri River merges with the Mississippi River at St. Louis), and southwestward up the Yellowstone River 114 Rkm to Intake, the site of a low-head irrigation diversion dam northeast of Glendive, Montana (Torrey and Kohout, 1956; Figure 1). In years of high spring discharge, some migratory paddlefish move either over or around the dam (via a flooded side-channel) past Intake as far as the Cartersville Diversion Dam at Forsyth (YR Rkm 382, where the YR Rkm number indicates distance above the Confluence). A small percentage of fish is stranded or rears volitionally in the Dredge Cuts, which are large, clear, flooded borrow pits immediately below Fort Peck Dam. Some of these fish periodically exit the Dredge Cuts and migrate downriver (Frazer, 1985).

Lake Sakakawea (area 156,000 Ha), the primary rearing habitat for this stock (Fredericks and Scarnecchia, 1997), is one of six large dam and reservoir projects on the Missouri River authorized by the Rivers and Harbors Act of 1935 and the Flood Control Act of 1944. The Pick-Sloan projects are managed as an integrated hydrosystem for multiple uses, including flood control, navigation, hydropower, water supply, water quality, recreation, and fish and wildlife (U.S. Army Corps of Engineers, 2004).

Since its origin, Lake Sakakawea has undergone wide fluctuations in water level under integrated management, a result of the merging of often conflicting socioeconomic and political interests between more arid upriver states and less arid downriver states (Ridgeway, 1955; Hart, 1957; Morris, 1992) and a highly variable continental climate in the Missouri and Mississippi river basins (Thornthwaite, 1941). After the initial filling of the reservoir over a 13-year period (1953–1966; Scarnecchia et al., 1996b), the water level reached its normal maximum elevation of 564.25 m in July 1969, dropped to 555.71 m in August 1990 during a drought period, rose to 564.58 m by August 1997 after a moist period, and dropped steadily over the period 1998–2004 during another drought to 553.72 m in August 2004 (U.S. Army Corps of Engineers, 2004). By mid 2007, the water level remained low at 552.08 m. In terms of reservoir levels during August, seven years—1991, 1992, and 2002–2006, early and late in the time series, were considered years of low water elevation (less than 558 m), six years, 1994–1999, in the middle of the time series, as years of high elevation (greater than 561 m), and three years (1993, 2000, 2001) as intermediate (558.8–560.1 m), one of the three years (1993) as intermediate and rising, and two of the three years (2000 and 2001) as intermediate and falling (Figure 2). The fish community, which consists of 58 species, has been monitored with a standardized sampling program by the North Dakota Game and Fish Department from soon after reservoir filling (Berard, 1989; Power et al., 1992; Hendrickson and Lee, 2000; Hendrickson et al., 2007).

Yellowstone-Sakakawea Paddlefish Stock Characteristics

The life history of the Yellowstone-Sakakawea paddlefish has been comprehensively described by Scarnecchia et al. (2007). Newly hatched larvae descend from the Yellowstone River, the primary spawning area, into the turbid headwaters of Lake Sakakawea (Fredericks and Scarnecchia, 1997), where, by July and August, as 150- to 250-mm fork length (tip of rostrum to fork of caudal fin) fish, they are feeding selectively on invertebrates, chiefly the large, predaceous cladoceran *Leptodora kindtii* (Fredericks, 1994). Fish detect their prey with a passive electrosensory system in their rostrum, head, and opercula, described by Wilkens et al. (2002). Observations of fish near the surface (Fredericks and Scarnecchia, 1997; Scarnecchia et al., 1997) indicate that age 0 fish are most concentrated near the reservoir headwaters. By late fall or the following summer, and for the rest of their life, paddlefish filter-feed on a wide variety of zooplankton and other invertebrates (Michaletz et al., 1982; Fredericks, 1994; Fredericks and Scarnecchia, 1997) with the aid of long, filamentous gill rakers (Kofoid, 1900; Imms, 1904). Visual observations and netting indicate that adult and sub-adult fish are widely distributed throughout the reservoir in summer

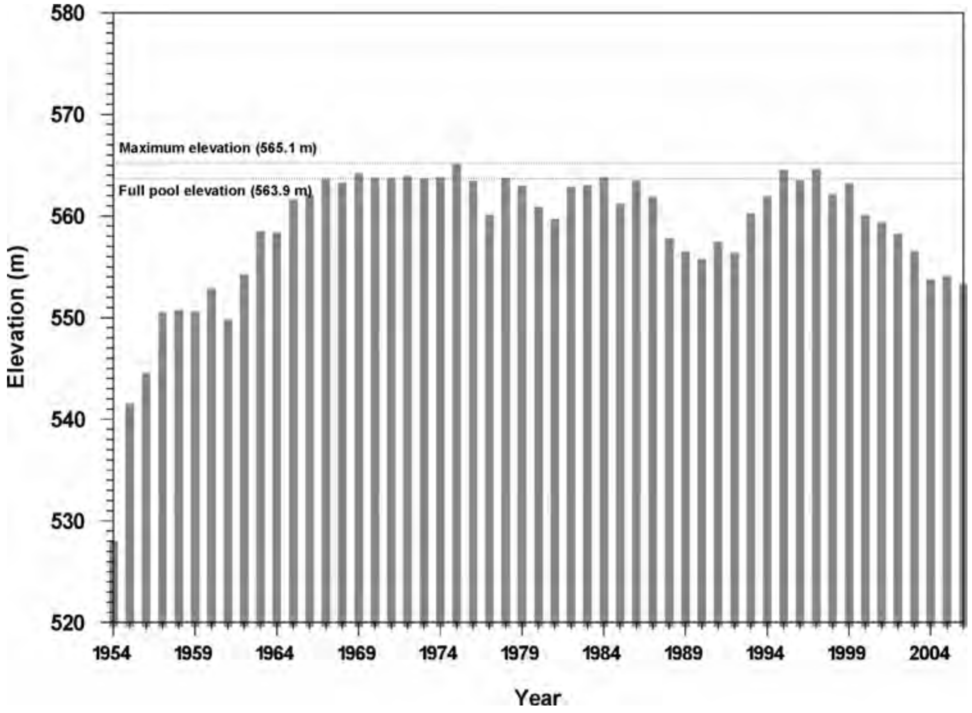


Figure 2 Mean August reservoir elevation, Lake Sakakawea, 1954–2006.

(North Dakota Game and Fish Department, Standard Adult Fish Population Sampling, unpublished data).

During the spring pre-spawning migration (May–June), a recreational snag fishery occurs in both Montana and North Dakota at several sites along the Missouri and Yellowstone rivers. The most important fishing sites are at the Confluence (MR Rkm 2,544) in North Dakota and at Intake (YR Rkm 114) in Montana. Additional details about the snag fishery as well as socioeconomic characteristics of the anglers are documented elsewhere (Scarnecchia et al., 1996a; Scarnecchia and Stewart, 1996, 1997a, 1997b; Scarnecchia et al., 2008).

MATERIALS AND METHODS

Data Sources

River Discharge

For the years 1992–2006, daily discharge data were obtained from two U.S. Geological Survey (USGS) gauging stations, located on the Yellowstone River near Sidney, Montana (YR Rkm 46.6; USGS 06329500) and the Missouri River near Wolf Point, Montana (MR Rkm 2,743.8; USGS 06177000). Daily records were combined over the period April 25 to July 15, the typical period when adult paddlefish would be migrating and spawning and larvae emerging in the rivers (Firehammer and Scarnecchia, 2006, 2007) to obtain annual time series for six variables: (1) median daily Yellowstone River discharge, (2) number of days in the period with Yellowstone River discharge at least 849.9 m^3/sec (30,000 ft^3/sec), (3) number of days with Yellowstone River discharge at least 1,132.7 m^3/sec (40,000 ft^3/sec), (4) median daily Missouri River discharge, (5) number of days with Missouri River discharge at least 354.9 m^3/sec (12,500 ft^3/sec), and (6) number of days with Missouri River discharge at least 424.7 m^3/sec (15,000 ft^3/sec). Indices 2, 3, 5, and 6 were established to more sharply distinguish years of persistently high discharge hypothesized to favor paddlefish spawning.

Reservoir Physical Characteristics and Zooplankton

For sampling of Lake Sakakawea's physical characteristics and zooplankton, horizontal (across-reservoir) transects were established at 4.8 km intervals from Rkm 2,476 down-reservoir to Rkm 2,404 in the headwater area of the reservoir. Sampling of habitat and zooplankton was concentrated in the upper third of the reservoir because observable concentrations of age 0 and age 1 paddlefish are highest in this portion of the reservoir (Fredericks, 1994; Fredericks and Scarnecchia, 1997; Scarnecchia et al., 1997). Roush et al. (2003) also found hatchery-reared age 0 paddlefish implanted with ultrasonic transmitters in Lake Francis Case, South Dakota, remained in the upper portion of that reservoir. Sampling typically was conducted weekly from the last week in July through early September, although some variation in the duration of the sampling season occurred among years.

Beginning in 1992, transects were sampled from Rkm 2,452 down-reservoir to Rkm 2,423. Wide fluctuations in water levels unfortunately made it impossible to sample any one transect every year. Transect sampling moved up-reservoir (Rkm 2,476 to Rkm 2,433) during the higher water years. After 2000, as reservoir levels dropped, upper transects became shallow or riverine and sampling moved down-reservoir, so that in 2006, sampling extended from Rkm 2,428 down-reservoir to Rkm 2,404. In 2004, sampling was able to be conducted only as far up-reservoir as Rkm 2,418. The longest available time series consisted of two transects (Rkm 2,438 and Rkm 2,433) sampled over the period 1992–2003. No comparable data were collected in 1994 and 1996. Analyses centered on these two transects. Data from the transects at Rkm 2,438 and Rkm 2,433 were collected over six weekly time periods (July 25–31, August 1–7, August 8–14, August 15–21, August 22–28, and August 29–September 4) over the period 1992–2003 and evaluated for trends in physical and biological conditions at a particular reservoir location.

Along each transect, three samples were taken, one at the center (midway across the reservoir) and one between the center and each shore. For each sample, depth was estimated to the nearest 0.1 m with a depth finder, and water transparency was estimated to the nearest centimeter with a Secchi disk. Each surface horizontal zooplankton tow (three per transect) was taken with a Wisconsin plankton net (80-μm mesh) equipped with a General Oceanics flow meter to estimate water volume. Zooplankton samples were preserved in 95% ethanol until analysis. In the laboratory, three replicate subsamples per sample (nine per transect) were enumerated and identified. Subsamples were diluted to known dilutions for identification and quantification if densities were too high for a complete enumeration. Plankton were enumerated with the aid of a counting maze and identified to genus or species (Pennak, 1953), depending on the taxon. Counts of each of the three subsamples were averaged and the total count expanded and combined with the estimate of total water volume sampled to obtain densities of each taxon in units of organisms per liter. Zooplankton were analyzed by combined two-week periods, August 1–14 and August 15–28 for (a) all taxa combined (i.e., similar to the typical food of age 1 and older paddlefish; Eddy and Simer, 1929; Rosen and Hales, 1981; Fredericks, 1994) and (b) for *Leptodora* only (i.e., the primary food for age 0 paddlefish in Lake Sakakawea; Fredericks, 1994).

Age 0 Fish

Year class strength. Relative abundance of age 0 fish, an indication of year class strength, was estimated based on counts of fish along the standard transects (Fredericks and Scarnecchia, 1997) and expressed as fish per kilometer based on the four highest weeks and transects. In 1996, sampling was conducted in only one week.

Growth and condition. Growth and condition of age 0 paddlefish were estimated from fish captured with dip nets during August (Fredericks and Scarnecchia, 1997; Scarnecchia et al., 1997). Catches in August were grouped into four weekly periods. Captured fish were measured for fork length, and the first 100 fish sampled each day were weighed to the nearest gram. Condition factor was calculated from the parameter (b) in a length-weight equation $W = aL^b$ (Lagler, 1956). Mean length, mean weight, and condition were calculated for all fish measured and weighed within each week.

Adult Fish

Growth of young recruits. Life history information for young recruits (typically ages 9 and 10 for males and ages 16–19 for females) and other adult fish was obtained over the 16-year period 1991–2006 from two fish cleaning stations, one each at the Confluence and Intake. A high percentage of harvested paddlefish was processed at these stations (from 65% to 98% of the annual harvest; North Dakota Game and Fish Department and Montana Department of Fish, Wildlife and Parks, Unpublished Data). From each fish, data collected included the date of harvest, harvest location (Rkm), body length (BL; anterior of eye to fork of caudal fin; Ruelle and Hudson, 1977) to the nearest 2.5-cm increment, weight to the nearest 0.5 kg, sex, maturation stage (Scarnecchia et al., 1996c), gonad weight, GFB weight (Scarnecchia et al., 2007), and dentaries (lower jaw bones) for age determination (Adams, 1942; Scarnecchia et al., 2006).

Age was estimated from dentaries collected over the period 1991–2006 (Scarnecchia et al., 2006). Dentaries were removed, cleaned of excess flesh, and stored dry in individual envelopes. The dentaries were later cleaned and sectioned as described in Scarneccchia et al. (1996b, 2006), and ages assessed by counting annuli (Adams, 1942; Meyer, 1960; Scarnecchia et al., 2006) using a Biosonics Optical Pattern Recognition System. From 1999 to 2006, a two-reader, double-blind protocol was used, along with a tolerance for minor disagreement as described in Scarnecchia et al. (2006). The accuracy of age determination using dentaries was validated for young recruits (males ages 9–10) based on recoveries of known-age, coded wire-tagged fish and partially validated for older recruits (females 16–19) based on jaw-tag recoveries (Scarnecchia et al., 2006). For the weight-at-age analysis, only male fish age 9–10 and female fish age 16–19 were utilized. Fish of these ages have nearly all reached sexual maturity and were considered new recruits to the fishery (Scarnecchia et al., 2007). The relative year class strength (an index of abundance) of young male recruits (Montana and North Dakota data combined) was expressed as the percentage of fish caught by age.

Condition of young recruits. Condition of newly recruited males (age 9 and 10 combined) over the period 1991–2006 was estimated by the relative weight, W_r, expressed as $W_r = 100\ (W/W_s)$, where W is the actual fish weight and W_s is the standard weight (g) for male paddlefish, calculated according to the empirical expression $W_s = –4.494 + 2.910 \log_{10} BL$, where BL is in mm (Brown and Murphy, 1993).

Gonadosomatic index (GSI) and gonadal fat body (GFB) weight of young recruits. The gonadosomatic index (GSI) was calculated as the weight of the gonads divided by the weight of the fish (De Vlaming et al., 1982). Each gonad (i.e., testis for males, roe for females) had associated with it a GFB—a discrete, consolidated, easily identifiable mass of fatty tissue (Scarnecchia et al., 2007). From 1992 through 2006, a random sample of GFBs was separated manually from the gonads of fish brought into the cleaning stations and weighed to the nearest gram. Weights of both GFBs (left and right sides) from a given fish were combined. GFB was expressed in three ways: as an absolute weight, as a ratio of GFB weight to total fish weight, and as the ratio of GFB weight to gonad weight.

Growth of adult fish. Records from jaw-tagged and recaptured paddlefish tagged since 1964 (Scarnecchia et al., 2007) allowed us to compare weight changes of fish at tagging and recapture to assess if rising or falling reservoir water levels affected growth of adult fish. For rising reservoir levels, the weight changes were based on individual fish jaw-tagged in 1991 through 1993 that were recaptured in 1998 through 2000 after water levels had risen. For falling reservoir levels, the weight changes were based on individual fish jaw-tagged in 1998 through 2000 that were recaptured in 2005 through 2007, after water levels had fallen.

ANALYSES

Year class strength (age 0 counts), river discharge, and reservoir elevation. Both correlation analysis and Spearman's rank correlation analysis (SAS Institute, 1989) were used to investigate interrelationships among year class strength (counts of age 0 paddlefish along standard transects) and the six defined variables of river discharge and reservoir elevation. Stepwise regression analysis was used to investigate relations between year class strength (dependent variable) and the six discharge variables (independent variables) and reservoir elevation (independent variable).

Physical characteristics, zooplankton, and age 0 fish. Analysis of variance was used to evaluate if annual differences existed in zooplankton (all species combined and *Leptodora* only) abundance, length, weight, and condition of age 0 paddlefish sampled at a given time. For the zooplankton, the null hypothesis was that there would be no differences among years. For the paddlefish, the null hypothesis was that even though the exact time of spawning and larval drift might vary with river discharge, there would be no differences among years in length, weight, and condition of age 0 fish in August. A Student Neuman-Keuls test (Ott, 1993) was used to evaluate differences among years.

Young adult fish weight, condition (relative weight), and gonadal fat body (GFB) weight. For age 9 and 10 male paddlefish, fish weight, gonad weight, GSI, GFB weight, ratio of GFB weight to fish weight, and ratio of GFB weight to gonad weight, the null hypotheses were that no significant differences would exist among years. Differences in mean weights, GFB weights, GFB weight/fish weight ratios, and GFB weight/gonad weight ratios among years were evaluated with analysis of variance methods (ANOVA) using PROC GLM in SAS (SAS Institute, 1989). Where significant differences among years were found, differences between years were evaluated with a Student Newman-Keuls test. When equality of variances was not achieved when tested for with Levene's test for homogeneity of variances, transformations were used: square roots for fish weights and GFB weights, arcsine of the square root for GFB weight/fish weight, and $\log_{10}$ for GFB weight/gonad weight, and the new variables were again tested for homogeneity of variances with Levene's test. If homogeneity of variances was still not achieved, annual data were ranked and tested with a Kruskal-Wallis non-parametric test. The same analyses of fish and GFB weights were conducted for females age 16–19, which represent typical ages of recruitment in the Yellowstone-Sakakawea paddlefish stock (Scarnecchia et al., 2007).

Regression analysis was used to compare mean weights of age 9 and 10 males with annual August reservoir level as well as annual increases or decreases in reservoir level (Snedecor and Cochran, 1967). Data from age 9 and 10 paddlefish were analyzed separately and together because a previous study (Scarnecchia et al., 2006) has shown that age estimation to these ages was for the most part exact, but in a minority of cases was in error by one year. It was hypothesized that the reservoir (elevation) level (E) and changes in reservoir elevation in the years (t) immediately before the return year would be correlated with the mean weights of age 9 and 10 male fish. Mean weights of age 9, age 10, and age 9 and 10 fish combined (dependent variable) were compared with six combinations of reservoir elevation level (E): (1) $E(t)$; (2) mean of $E(t)$ and $E(t-1)$; (3) mean of $E(t)$, $E(t-1)$, and $E(t-2)$; (4) mean of $E(t)$, $E(t-1)$, $E(t-2)$, and $E(t-3)$; (5) mean of $E(t)$, $E(t-1)$, $E(t-2)$, $E(t-3)$, and $E(t-4)$; (6) mean of $E(t-1)$, $E(t-2)$, and $E(t-3)$ and six combinations of changes in reservoir level, i.e., the sum of annual differences between $E(t)$, and (7) $E(t-1)$; (8) $E(t-2)$; (9) $E(t-3)$; (10) $E(t-4)$; (11) $E(t-5)$, and (12) between $E(t-1)$ and $E(t-2)$.

Weight changes in recruited adult fish. Weight changes in tagged fish at times of low elevation and recaptured at times of high elevation (i.e., tagged in 1991 through 1993 and recaptured in 1998 through 2000) were analyzed (known-sex and unknown-sex combined) against fish tagged at times of high elevation and recaptured at times of low elevation (i.e., tagged in 1998 through 2000 and recaptured in 2005 through 2007). Weight change from tagging to recovery was expressed as either increase or decrease per year. A t-test was used to compare growth rates of the two groups of fish. The null hypothesis was that annual weight changes in periods of rising and falling reservoir levels would be the same. In all statistical tests, $p < 0.05$ was required for significance.

RESULTS

Year class strength (age 0 counts), river discharge, and reservoir level. No significant correlations of year class strength, as indicated by the mean of the four highest counts of age 0 fish, were found for any discharge estimates for the Yellowstone River. Age 0 counts were significantly and positively correlated only with median Missouri River discharge ($r = 0.64$; $p = 0.0129$). Similarly, rank year class strength was significantly and positively correlated only with rank median Missouri River discharge ($r = 0.78$; $p = 0.0061$). In stepwise regression analyses, the two variable combination of rank median Missouri River discharge and reservoir level explained 46% of the variation in year class strength.

Year class strength (young recruits) and water levels. The strength of the 1995 year class became evident in plots of age frequency distributions of combined Montana and North Dakota catches from 2003 to 2006 (Figure 3). The 1995 year class constituted 45% of the total catch of males over the period 2003–2006, and was the strongest year class seen since detailed sampling began in 1991. The 1995 year class was also associated with the sharp rise in reservoir level beginning in August 1993 and extending through 1995. This period was the longest and greatest period of rising reservoir since the initial filling (Figure 2) and the only period since the reservoir filled when reservoir levels rose substantially in three consecutive years (Figure 2). In 2006, recruitment from the combined 1996 and 1997 year classes, when the reservoir was near its maximum, was less than one-sixth as strong as the 1995 year class (Figure 3).

Physical characteristics and zooplankton. Mean densities of total zooplankton (all taxa combined) at both Rkm 2,433 and 2,438 were highest during the mid period of highest reservoir levels and lowest during the early and late periods of low reservoir levels. This result was found for the first two weeks of August (August 1–14) and the second two weeks (August 15–28; Figure 4a and 4b; Table 1). Densities of *Leptodora* were very low compared to other important taxa in all years, but tended to be highest during middle period years of high reservoir levels during both two-week periods in August (Figure 4c and 4d; Table 1).

Age 0 fish counts. Mean counts of age 0 fish per kilometer along transects were highest during the period of high reservoir levels. The five highest annual count indices occurred from 1996 to 2000. Four of these five years were years of high reservoir levels (1996–1999) and one year (2000) had intermediate but declining water levels (Figure 5; Table 1).

Age 0 fish lengths and weights. Over the period 1996–2006, significant yearly differences were found in the lengths of age 0 fish caught in August during Week 1 (ANOVA; $F = 175.28$; $p < 0.0001$), Week 2 (ANOVA; $F = 173.42$; $p < 0.0001$), Week 3 (ANOVA; $F = 42.90$; $p < 0.0001$), and Week 4 (ANOVA; $F = 13.54$; $p < 0.0001$). For the two weeks (1 and 2) with the most available data, multiple comparisons indicated a pattern of greater lengths in high reservoir years (Figure 6a; Table 1).

Weights were more closely associated with reservoir level than were lengths with reservoir level. Overall weights of age 0 fish in August were higher in years of high reservoir levels

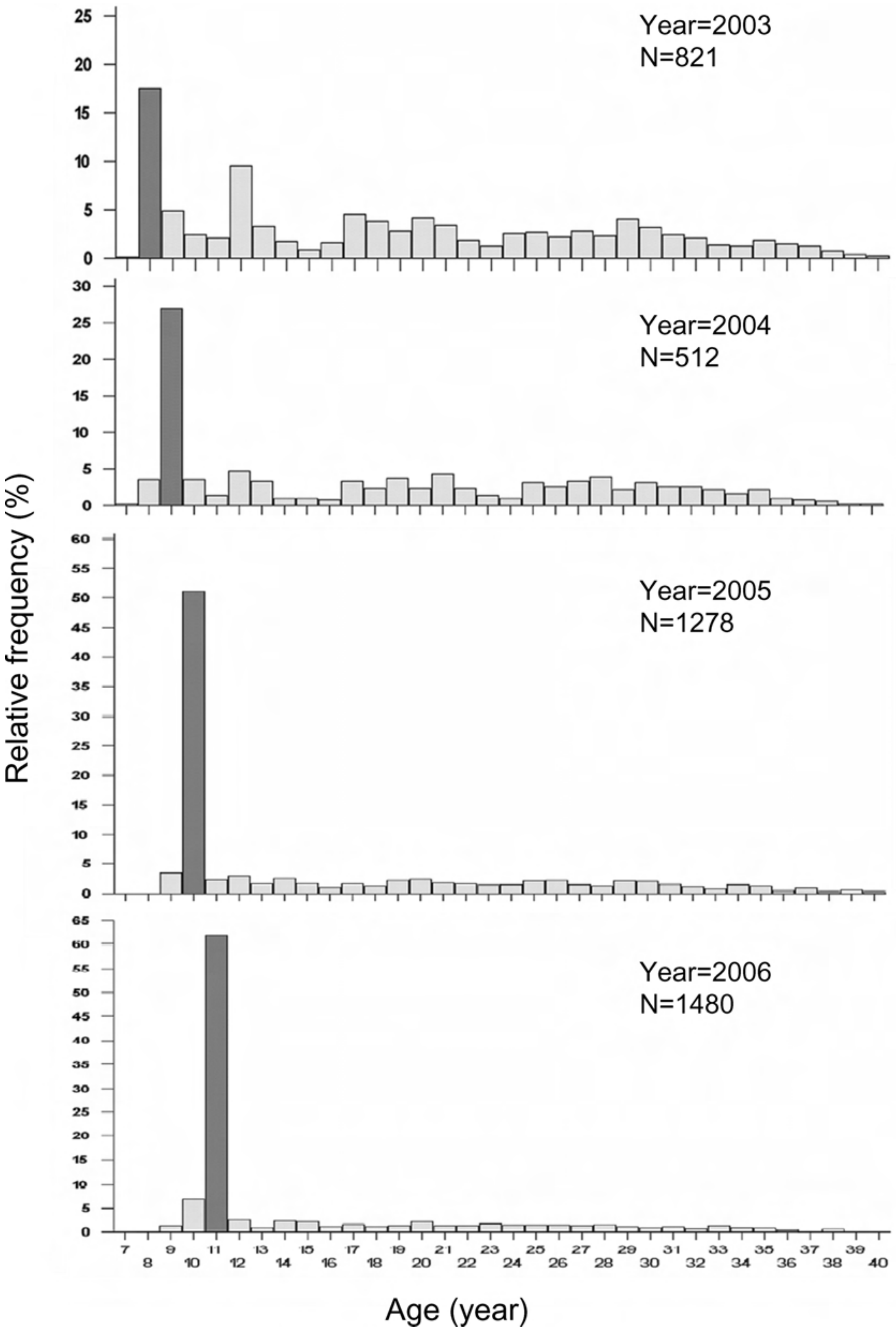


Figure 3 Age composition of combined Montana and North Dakota male paddlefish harvest, 2003–2006, showing dominance of the 1995 year class (shaded columns).

than in years of low reservoir levels (Figure 6b). Over the period 1996–2006, significant differences were found in the weights of age 0 fish caught in August weekly during Week 1 (ANOVA; $F = 71.48$; $p < 0.0001$), Week 2 (ANOVA; $F = 42.48$; $p < 0.0001$), Week 3 (ANOVA; $F = 16.74$; $p < 0.0001$), and Week 4 (ANOVA; $F = 9.56$; $p < 0.0001$). In multiple comparisons for the two weeks with the most data (1 and 2), for Week 1 the three years of heaviest fish (1996, 1997, and 1999) and the year of lightest fish (1998) were years of high reservoir levels. In Week 2, the pattern of larger fish with high reservoir levels was more pronounced, with heaviest fish in 1996, 1998, and 1999, three high reservoir years (none were measured in Week 2 in

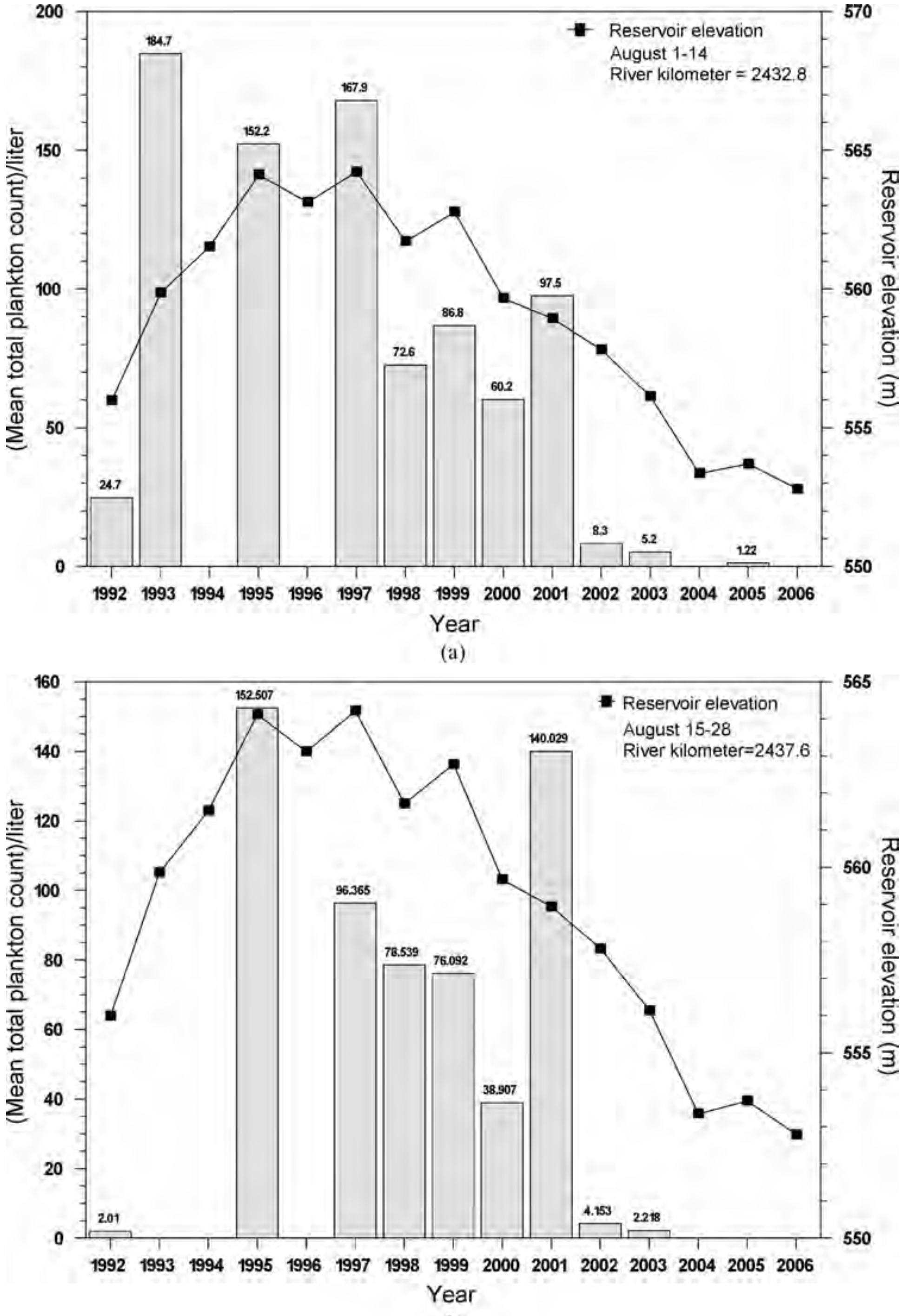
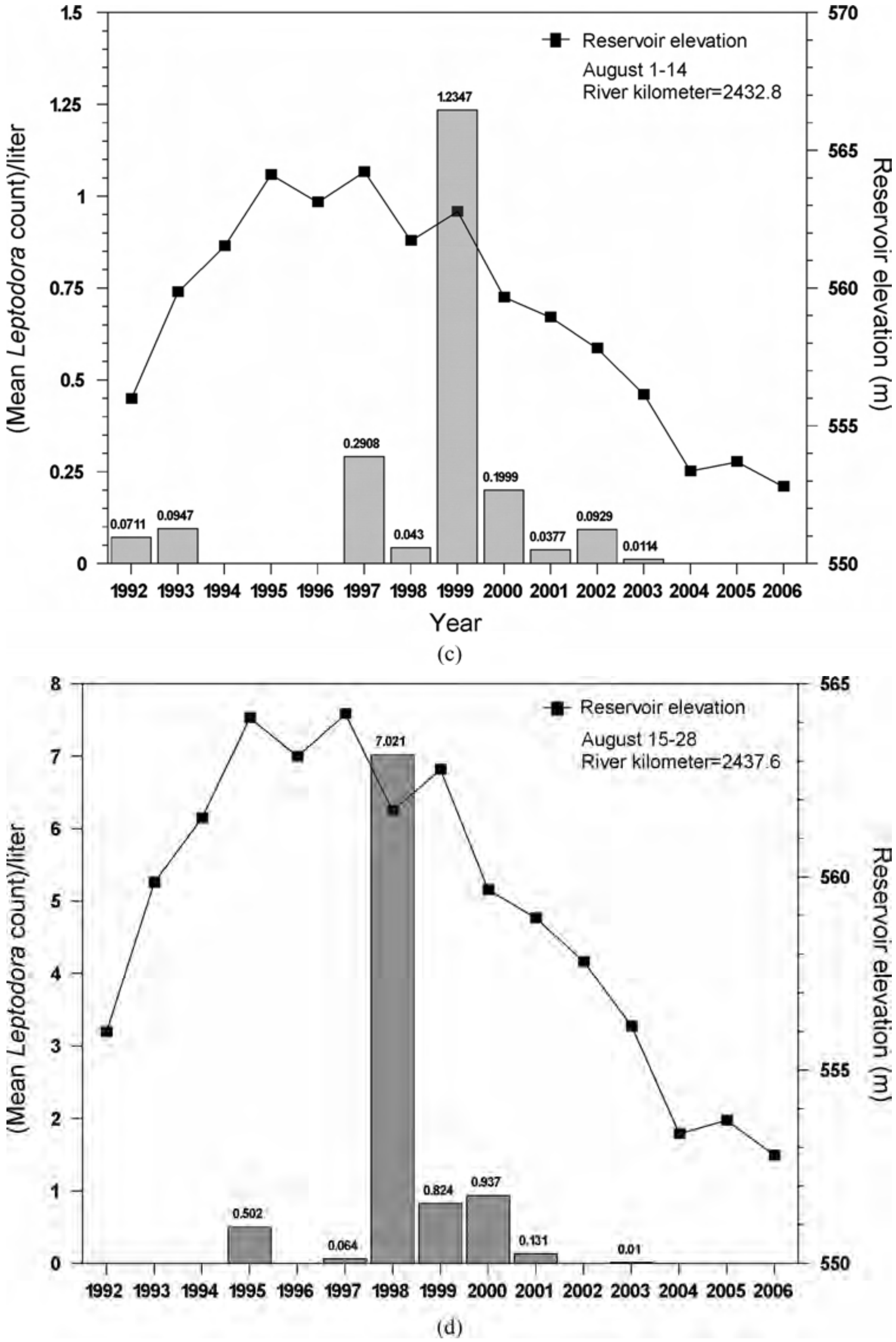


Figure 4 Mean density of zooplankton (organisms/l) for (a) all species combined during the period August 1–14, 1992–2005, at Rkm 2,433; (b) all species combined during the period August 15–28, 1992–2003, at Rkm 2,438; (c) *Leptodora kindtii* during the period August 1–14, 1992–2003, at Rkm 2,433; and (d) *Leptodora kindtii* during the period August 15–28, 1995–2003, at Rkm 2,438. Reservoir elevation over the period 1992–2006 is also plotted on the right vertical axis. *(Continued)*



(c)

(d)

Figure 4 (Continued).

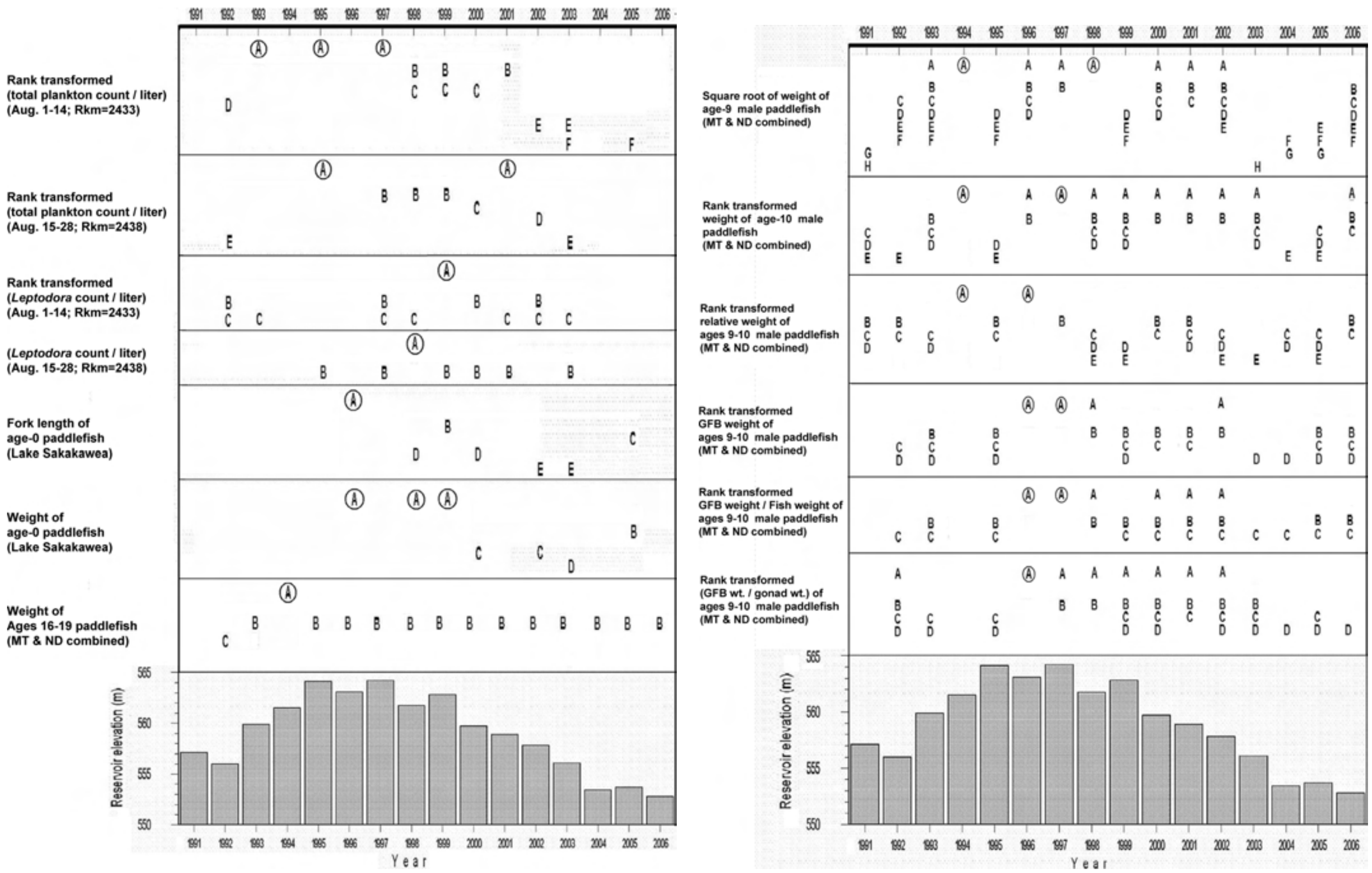
1997), and lightest fish in 2000, 2002, 2003, and 2005, four low reservoir years (Figure 6b; Table 1).

Age 0 fish condition factor. Condition factor of age 0 fish did not differ significantly among years and ranged between 2.49 and 2.81, except for 1997, the year of highest reservoir levels, when condition (3.13) was significantly higher than in the other years (Figure 7; Table 1).

Adult Fish Weights—Males

Interannual comparisons. In general, the pattern of changes in male mean weights over the years 1991–2006 was dome shaped, with lowest weights at the beginning and end of the interval, (i.e., low reservoir years), and highest weights near the middle of the interval (i.e., high reservoir years; Figure 10). For age

Table 1 Summary of relations among Lake Sakakawea reservoir level and 13 potential biotic indicators of reservoir production. A circled letter A indicates those years that had significantly higher values for that biotic indicator than other years. Years with the same letters were not significantly different from each other: (1) rank transformed total zooplankton count per liter at Rkm 2,433, August 1–14; (2) rank transformed total zooplankton count per liter at Rkm 2,438, August 15–28; (3) rank transformed *Leptodora* count per liter, Rkm 2,433, August 1–14; (4) *Leptodora* count per liter, Rkm 2,438, August 15–28; (5) fork length of age 0 paddlefish, August 8–14; (6) weight of age 0 paddlefish, August 8–14; (7) weight of age 16–19 female paddlefish; (8) square root of weight of age 9 male paddlefish; (9) rank transformed weight of age 10 male paddlefish; (10) rank transformed relative weight of age 9–10 male paddlefish; (11) rank transformed GFB weight of age 9–10 male paddlefish; (12) rank transformed GFB weight/fish weight of age 9 and age 10 male paddlefish; (13) rank transformed GFB weight/gonad weight of age 9–10 male paddlefish.



9 males, significant differences in mean weights of fish existed among years from 1991 through 2006 (square-root transformed data; ANOVA; $F = 16.98$; $p < 0.0001$). In multiple comparisons, significantly higher weights predominated in high reservoir years over low reservoir years (square-root transformed data; Student Newman-Keuls test; $p < 0.05$; Table 1). In the three years of highest mean weights of age 9 fish (all high reservoir years), the weights were 9.87, 9.58, and 9.90 kg, whereas in years of lowest weights (both low reservoir years), the weights were 6.93 and 6.60 kg, or as much as 3.3 kg less (Figure 8).

In general, the pattern of changes in mean weights for age 10 males over the years 1991–2006 was also dome shaped, with lowest weights at the beginning and end of the interval, (low reservoir levels) and highest near the middle of the interval (high reservoir levels; Figure 9; Table 1). For age 10 males, significant differences in mean weights of fish also existed among years from 1991 through 2006 (ranked data; Kruskal-Wallis; $F = 24.15$; $p < 0.0001$). In multiple comparisons, significantly higher weights predominated in high reservoir years over low reservoir years (ranked data; Student Newman-Keuls test; $p < 0.05$; Table 1). In the two years of highest mean weights of age 10 fish (both high reservoir years), the weights were 10.52 and 10.21 kg, whereas in the two years of lowest weights (both low reservoir years), the weights were both 7.74 kg, or 2.78 and 2.47 kg less (Figure 9).

For age 9 and age 10 fish combined, significant differences in mean weights of fish also existed among years from 1991 through 2006 (ranked data; Kruskal-Wallis; $F = 41.66$; $p < 0.0001$). In multiple comparisons, five years of highest weights (1994, 1996, 1997, 1998 (all high reservoir years)) and 2002 (a low reservoir year) had significantly higher weights than 1991–1993 and 2003–2005, all low reservoir years

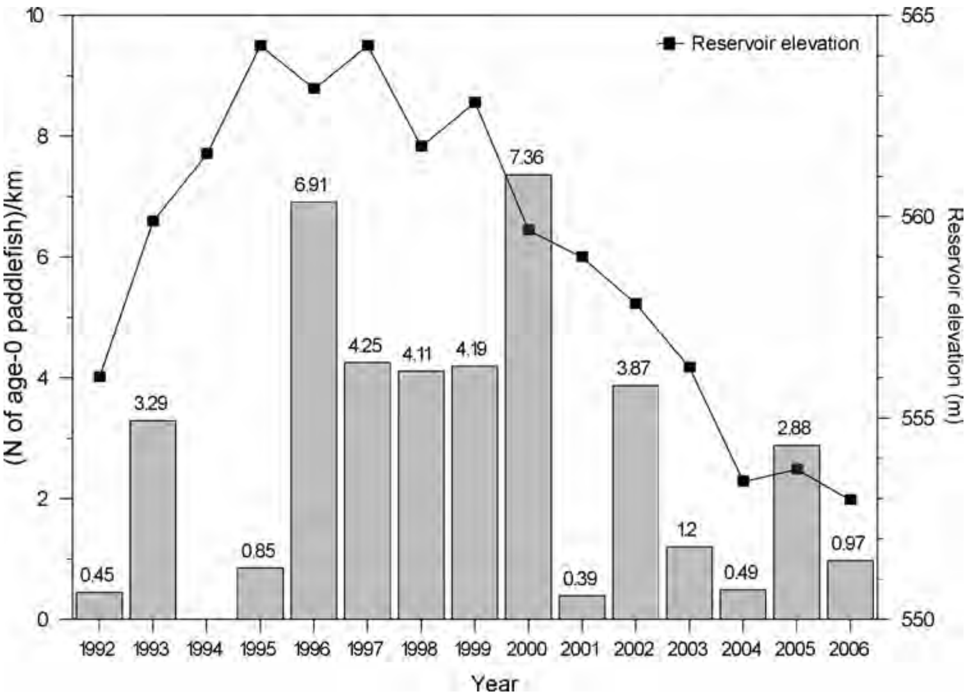


Figure 5 Number of age 0 paddlefish counted per kilometer during the four weeks and transects with the highest counts, 1992–2006.

(ranked data; Student Newman-Keuls test; $p < 0.05$; Table 1).

Yearly, combined, and lagged reservoir levels versus fish weights. For age 9 males, among 12 models tested for relations between fish weight and reservoir level, the closest relation was found between weight of fish in year t and reservoir level that year (t) and the previous year (t – 1) ($r^2 = 0.35$; $p = 0.016$; Figure 10; Table 2). Five other correlations between fish weight and reservoir level were also significant, however ($p < 0.05$; Table 2). Three models included reservoir levels in one or more years, and two models included the sum of changes in reservoir levels (Table 2).

Table 2 Simple linear relationships and correlation coefficients between mean weight of age 9, age 10, and ages 9 and 10 combined Yellowstone-Sakakawea paddlefish and water level (elevation, E) of Lake Sakakawea in year t 1991–2006. The first model elevation $E(t)$ refers to reservoir elevation in the same year (t). The other models compare mean paddlefish weight in year (t) with six combinations of mean reservoir elevation levels (E) in August: (1) $E(t)$; (2) mean of $E(t)$ and $E(t-1)$; (3) mean of $E(t)$, $E(t-1)$, and $E(t-2)$; (4) mean of $E(t)$, $E(t-1)$, $E(t-2)$, and $E(t-3)$; (5) mean of $E(t)$, $E(t-1)$, $E(t-2)$, $E(t-3)$, and $E(t-4)$; (6) mean of $E(t-1)$, $E(t-2)$, and $E(t-3)$, and six combinations of changes in reservoir level, i.e., the sum of annual differences between $E(t)$ and (7) $E(t-1)$; (8) $E(t-2)$; (9) $E(t-3)$; (10) $E(t-4)$; (11) $E(t-5)$, and (12) between $E(t-1)$ and $E(t-2)$. Significant relationships ($p < 0.05$) are in bold.

Model Mean of	Age 9 r (p-value)	Age 10 r (p-value)	Age 9 and 10 r (p-value)
E(t)	**0.54 (0.031)**	**0.51 (0.045)**	**0.51 (0.046)**
E(t), E(t-1)	**0.59 (0.016)**	**0.55 (0.028)**	**0.54 (0.029)**
E(t), E(t-1), E(t-2)	**0.55 (0.026)**	**0.53 (0.033)**	**0.51 (0.044)**
E(t), E(t-1), E(t-2), E(t-3)	**0.54 (0.029)**	**0.56 (0.024)**	**0.51 (0.042)**
E(t), E(t-1), E(t-2), E(t-3), E(t-4)	0.45 (0.083)	**0.52 (0.038)**	0.43 (0.099)
E(t-1), E(t-2), E(t-3)	0.49 (0.050)	**0.53 (0.035)**	0.47 (0.066)
Sum of annual differences between			
E(t) and E(t-1)	–0.05 (0.855)	–0.02 (0.955)	–0.01 (0.972)
E(t) and E(t-2)	0.25 (0.349)	0.18 (0.515)	0.24 (0.361)
E(t) and E(t-3)	0.24 (0.373)	0.11 (0.683)	0.19 (0.482)
E(t) and E(t-4)	**0.53 (0.035)**	0.34 (0.201)	0.48 (0.058)
E(t) and E(t-5)	**0.52 (0.041)**	0.44 (0.090)	**0.50 (0.048)**
E(t-1) and E(t-2).	0.40 (0.125)	0.26 (0.329)	0.35 (0.182)

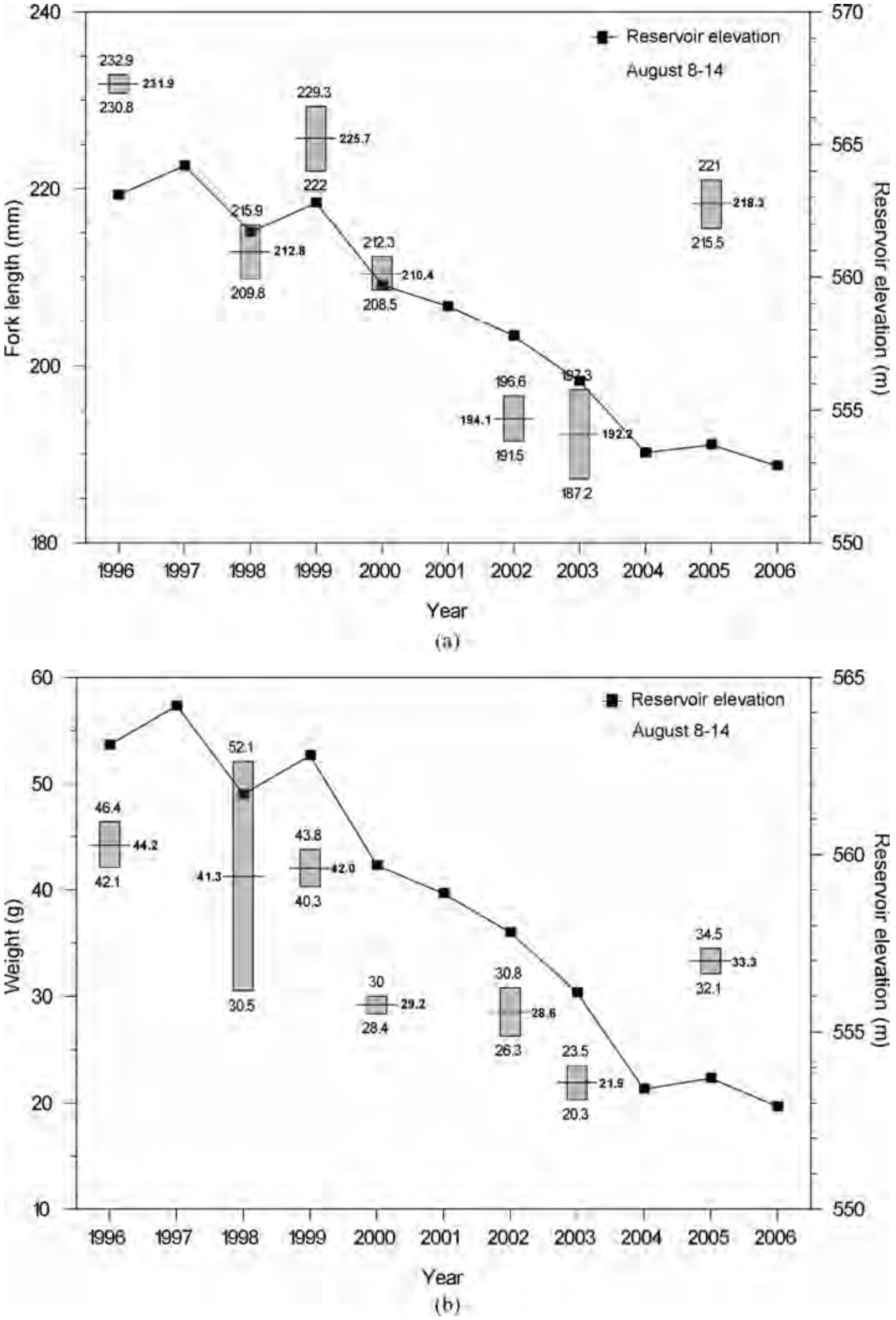


Figure 6 Mean and 95% confidence interval for (a) fork length (N = 3,139) and (b) weight (N = 926) of age 0 paddlefish caught during August (Week 2) versus reservoir elevation, 1996–2006. No fish were weighed or measured in Week 2 in 1997, 2004, and 2006.

For age 10 males, among 12 models tested for relations between fish weight and reservoir level, significant relations were found for six models, each involving reservoir levels in one or more consecutive years (Table 2). None of the models including changes in reservoir levels in consecutive years were significant ($p > 0.05$; Table 2).

For age 9 and 10 males combined, among 12 models tested for relations between fish weight and reservoir level, significant relations were found for five models ($p < 0.05$), four involving reservoir levels in one or more consecutive years, and one involving the sum of reservoir level changes in consecutive years (Table 2).

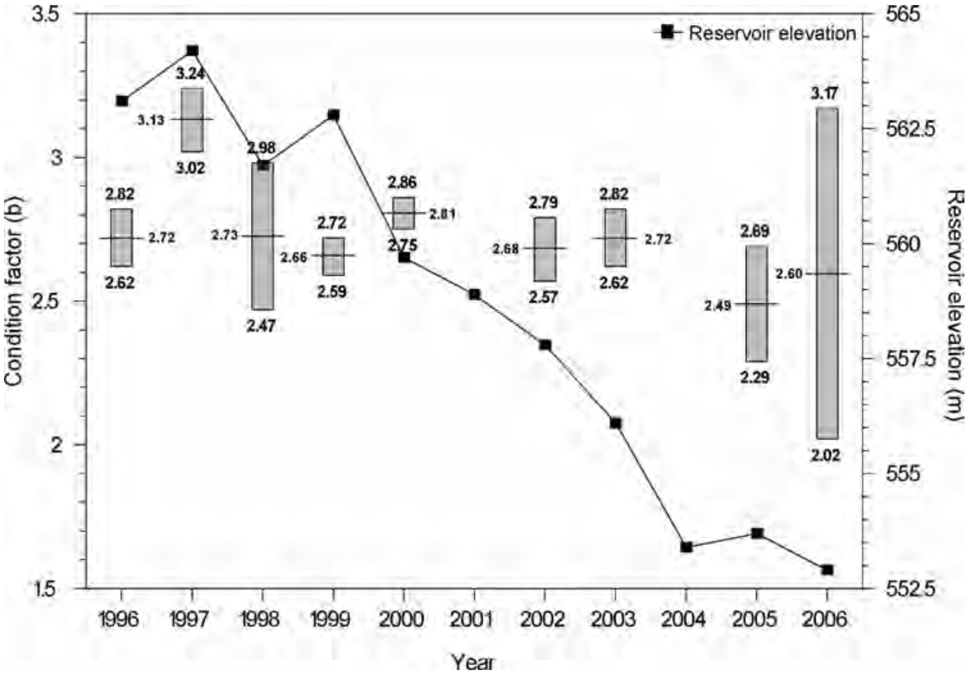


Figure 7 Condition factor of age 0 paddlefish in August versus reservoir elevation, 1996–2006 (N = 3,062).

Condition (Relative Weight)—Males

For age 9 and 10 males combined, significant differences were found in condition, expressed as relative weight, over the years 1991–2006 (ANOVA; $F = 22.01$; $p < 0.0001$). The four highest relative weights occurred over the period 1994–1997, during the high reservoir period. Two years, 1994 and 1996, were significantly higher than any of the other years (Student Newman-Keuls test; $p < 0.05$; Table 1).

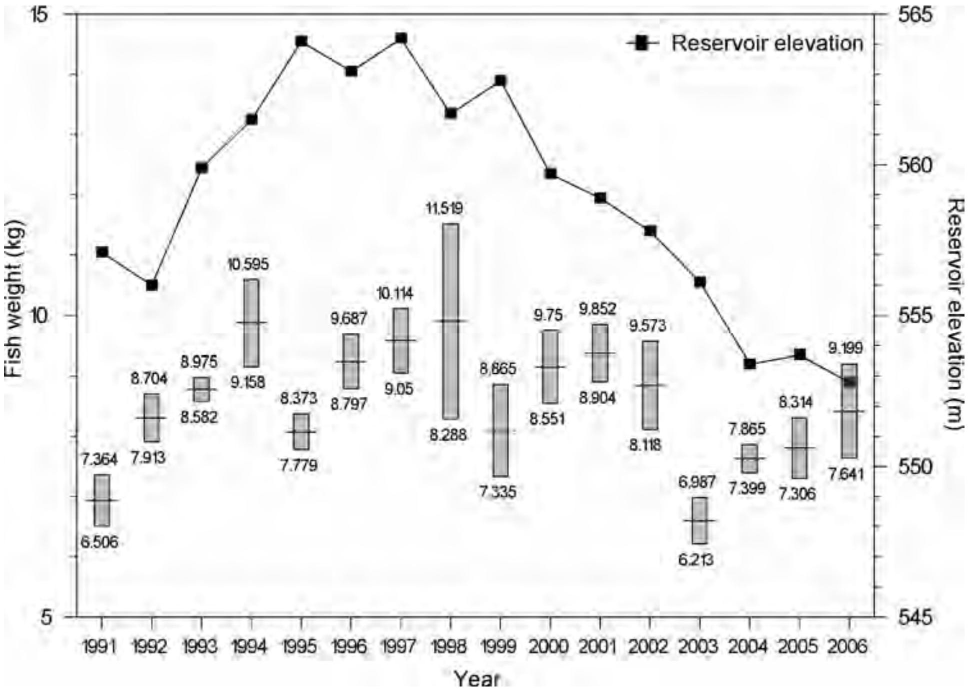


Figure 8 Mean weight and 95% confidence intervals for age 9 male paddlefish, 1991–2006 (N = 955).

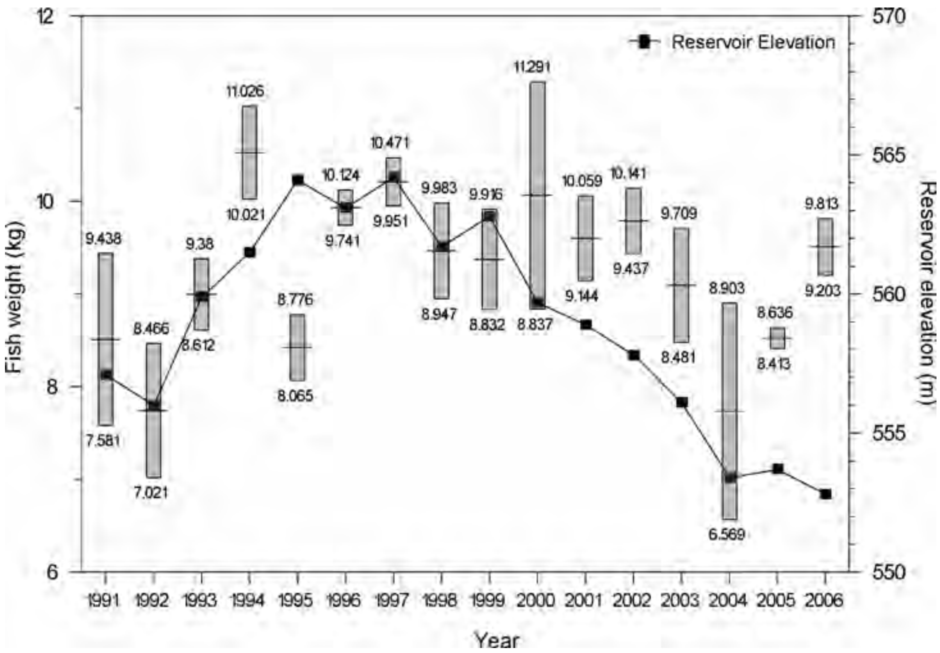


Figure 9 Mean weight and 95% confidence intervals for age 10 male paddlefish, 1991–2006 (N = 1,697).

Gonad Weight and GSI—Males

Mean annual gonad (testes) weight (age 9 and 10 fish combined) showed no correlation with reservoir level (r^2 =0.001; $n = 14$; $p = 0.27$). Similarly, GSI showed no correlation with reservoir level ($r^2 = 0.0000$; $n = 14$; $p = 0.98$).

GFB Weight—Males

For age 9 and 10 males combined, GFB weights exhibited a dome-shaped response, with lowest GFB weights at the beginning and end of the interval, (i.e., low reservoir years) and highest weights near the middle of the interval (i.e., high reservoir

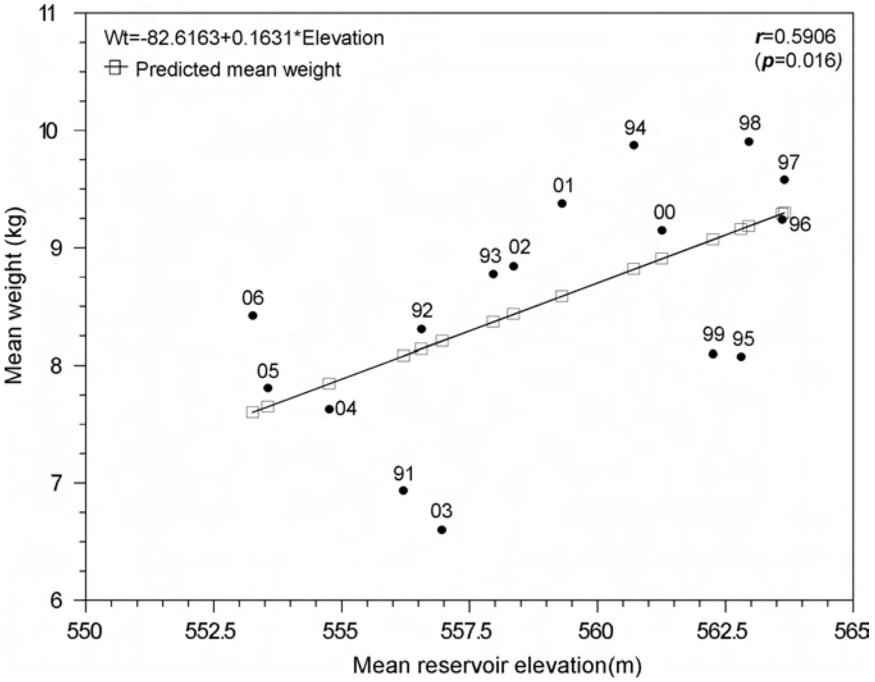


Figure 10 Mean weight of age 9 male paddlefish in year t versus mean August reservoir elevation in year t and year $t - 1$, 1991–2006.

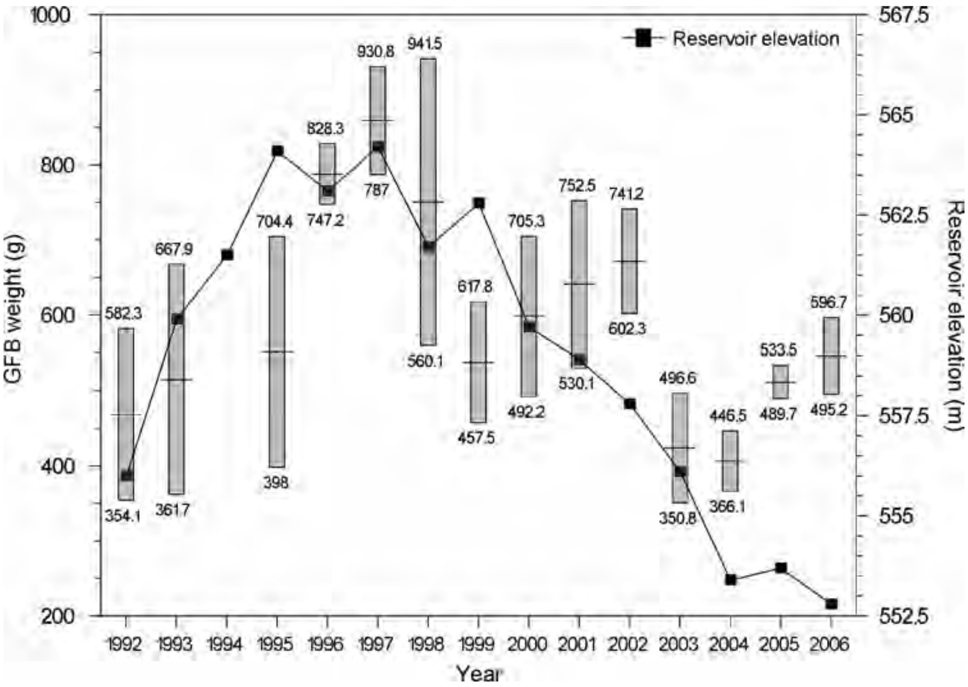


Figure 11 Mean gonadal fat body (GFB) weight and 95% confidence intervals for age 9 and age 10 male paddlefish, 1992–2006 (N = 1,700).

years; Figure 11; Table 1). GFB weights also exhibited significant differences among years (ranked data; Kruskal-Wallis; $F = 24.49$; $p < 0.0001$). In multiple comparisons, significantly higher GFBs were found in high reservoir years (1996–1998) than in low reservoir years (1992, 2003–2004) (ranked data; Student Newman-Keuls test; $p < 0.05$; Table 1).

A similar domed-shaped response was found when GFBs were expressed as the ratio of GFB weight/fish weight, with lowest ratios at the beginning and end of the interval, (i.e., low reservoir years) and highest weights near the middle of the interval (i.e., high reservoir years; Figure 12; Table 1). Ratios were significantly different among years (ranked data; Kruskal-Wallis; $F = 16.69$; $p < 0.0001$). In multiple comparisons, higher ratios still predominated in high reservoir years over low reservoir years (Table 1). The same response was found when GFBs were expressed as GFB weight/gonad weight, with lowest ratios at the beginning and end of the interval (i.e., low reservoir years) and highest weights near the middle of the interval (i.e., high reservoir years; Figure 13). Combined age 9 and age 10 males also exhibited significant differences among years (ranked ratios; Kruskal-Wallis; $F = 17.94$; $p < 0.0001$). In multiple comparisons, higher ratios predominated in years of high reservoir levels over low reservoir levels (Table 1). Sixty-three percent of the variation in the ratio of GFB weight/gonad weight was explained by reservoir level ($r^2 = 0.63$; $n = 14$; $p = 0.0007$; Figure 14). Overall, results with GFBs for males indicated that, in high reservoir years, age 9 and age 10 recruits tended to be heavier and also tended to have larger GFBs in absolute weights as a percentage of fish weight and as a percentage of gonad weight.

Adult Fish Weights—Females

Results of weight-at-age differences for the young female recruits (age 16–19) were much less pronounced than for young males. Although significant inter-annual differences among years were found for the square root of weight (ANOVA; $F = 8.97$; $p < 0.0001$), in multiple comparisons, 13 of 15 years had no differences among them, with only 1994 being significantly higher and 1992 being significantly lower than the other years (Student Newman-Keuls test; $p < 0.05$; Figure 15).

GFB Weights—Females

Results of GFB weight differences by reservoir level for the young female recruits (age16–19) were also less pronounced than for young males. Significant differences among years were found for the square root of GFB weight (ANOVA; $F = 5.95$; $p < 0.0001$), but the differences did not appear to be related to reservoir levels. GFB weights in 1993 and 1997 were significantly higher than in 1992 and 2006. The square root of mean GFB weight in 1993 was significantly higher than in 1992 (Student Newman-Keuls test; $p < 0.05$).

When GFBs were expressed as the ratio of GFB weight/fish weight, the ratios also indicated significant differences among years for the arcsine of the ratio (ANOVA; $F = 3.30$; $p < 0.0001$). In multiple comparisons among years, arcsine ratios were significantly higher in 1993 than in 1992 (Student Newman-Keuls test, $p < 0.05$).

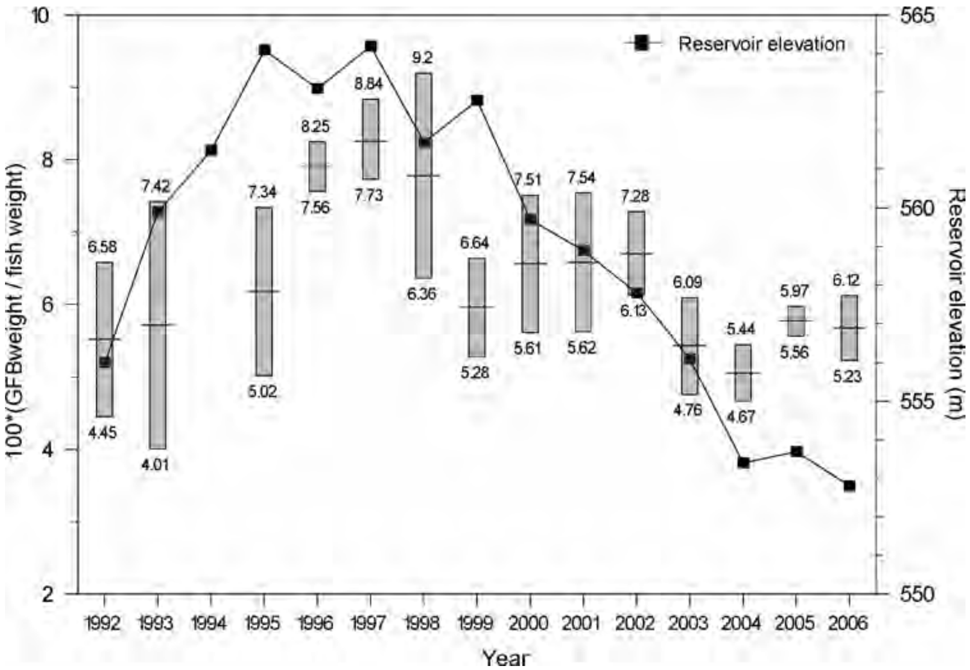


Figure 12 Mean GFB weight/fish weight and 95% confidence interval for age 9 and age 10 male paddlefish, 1992–2006 (N = 1,700).

When GFBs were expressed as GFB weight/gonad weight, the square root of the ratios also exhibited significant differences among years (ANOVA; $F = 6.14$; $p < 0.0001$). In multiple comparisons involving the square root of the ratios, 1993 was significantly higher than two other low reservoir years, 1992 and 2006 (Student Newman-Keuls test; $p < 0.05$).

Overall, results with GFBs for young female recruits (age 16–19) indicated that reservoir level tended to have less association with weight of recruits and weight of GFBs, expressed as absolute weights, as a percentage of fish weight, or as a percentage of gonad weight, than for the younger male recruits (age 9–10).

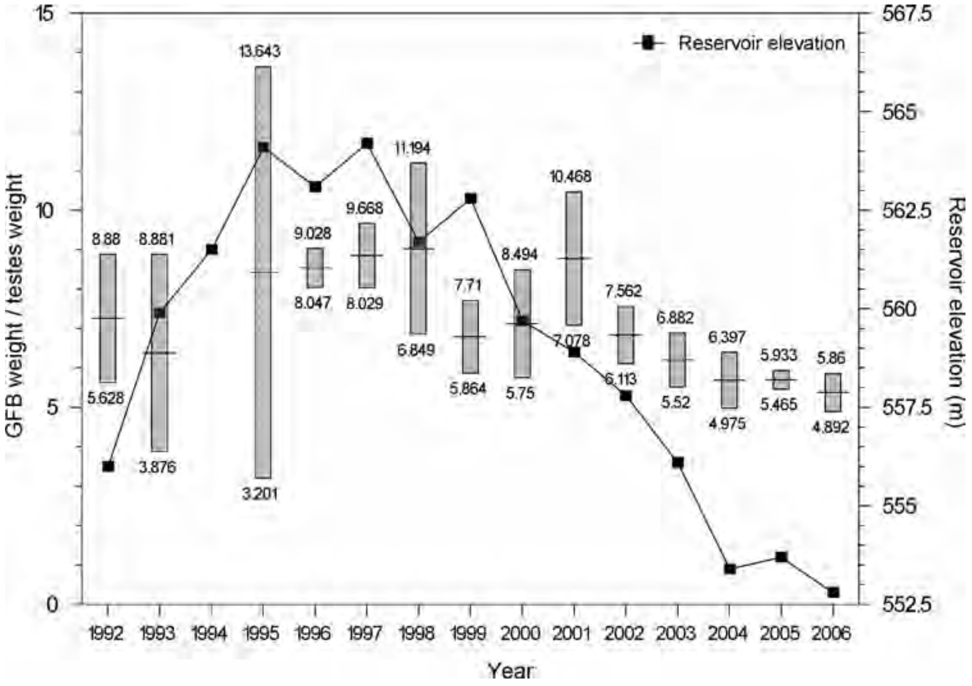


Figure 13 Mean GFB weight/testes weight and 95% confidence intervals for age 9 and age 10 male paddlefish, 1992–2006 (N = 1,696).

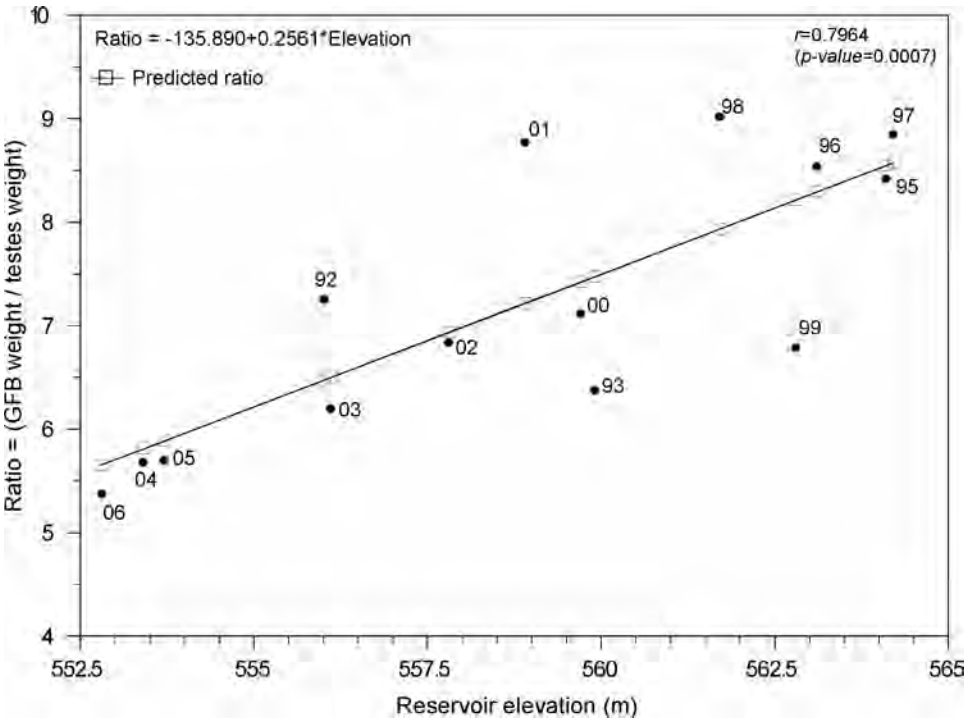


Figure 14 Mean GFB weight/testes weight versus reservoir water level, 1992–2006.

Weight Change of Recruited Adults and Reservoir Level

Adult fish tagged at the end of the low reservoir years (1990–1992) and recaptured in 1998 and 1999 after living several years in high reservoir levels showed significantly greater weight gain (or less weight loss) than fish tagged at the end of high reservoir years and lived several years in low reservoir levels (t-test; $t = -2.57$; $p = 0.012$). Fish rearing in rising and high reservoir conditions ($n = 29$) gained an average of 0.04 kg/yr, whereas fish rearing in falling and low reservoir conditions ($n = 66$) lost an average of 0.19 kg/yr.

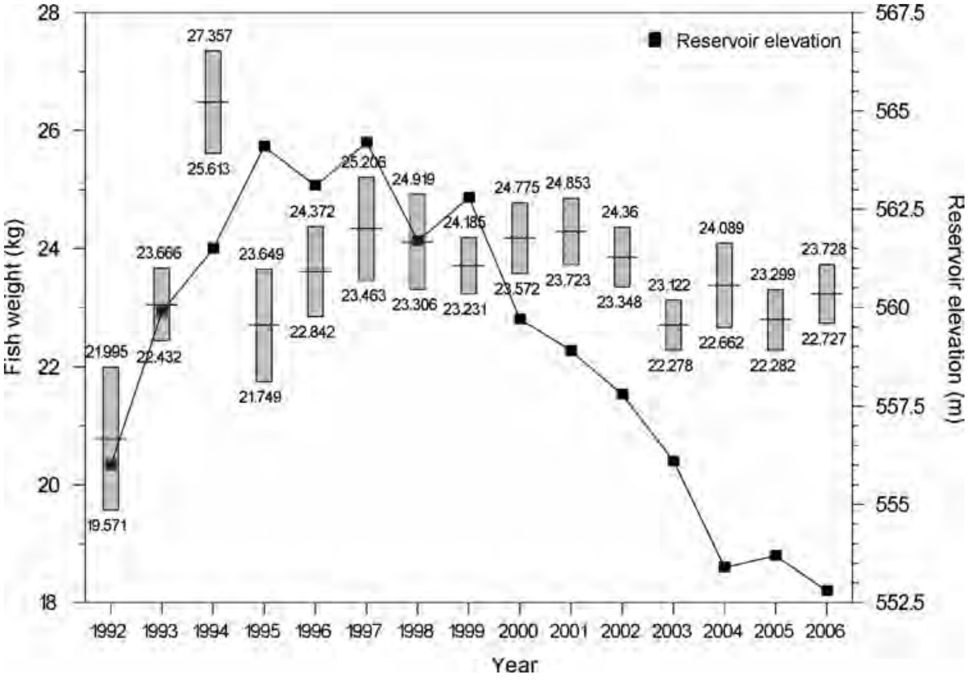


Figure 15 Mean weight and 95% confidence intervals for age 16–19 female paddlefish, 1992–2006 (N = 1,934).

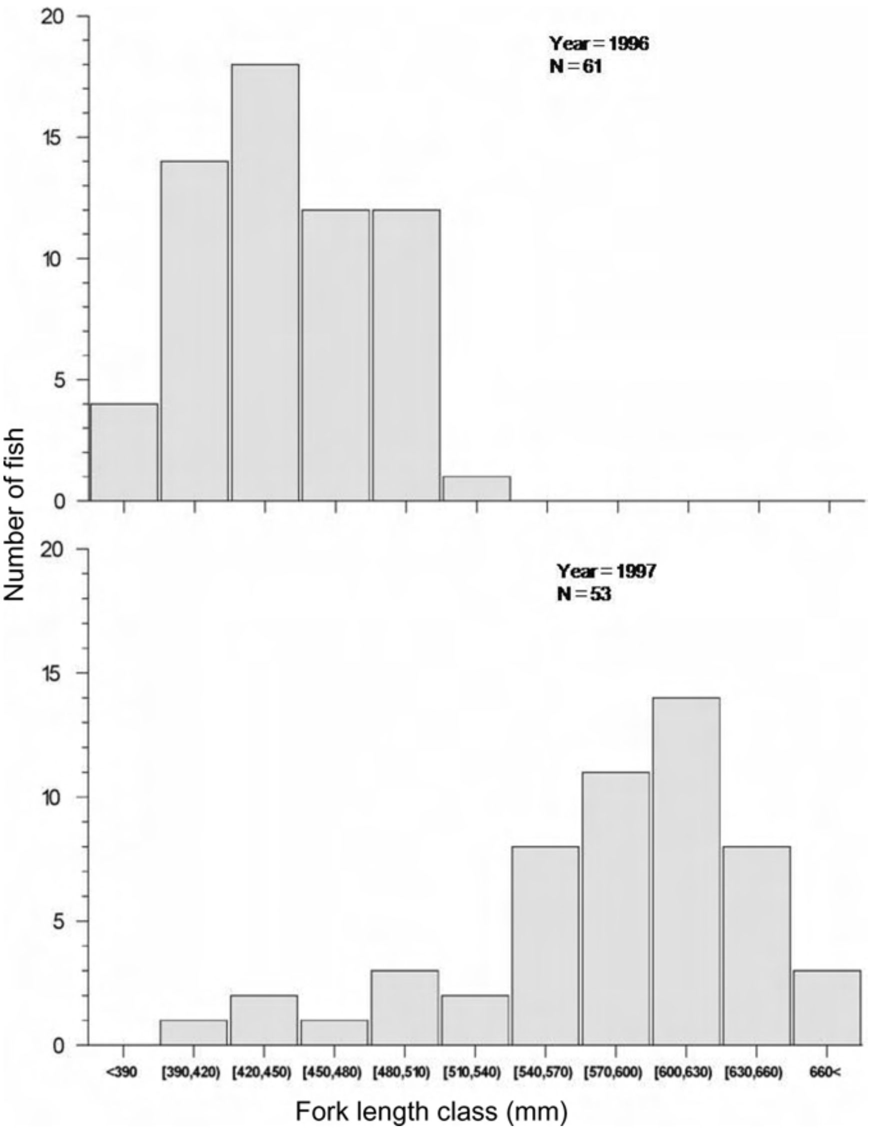


Figure 16 Length-frequencies of all age 1 and older paddlefish dip netted in Lake Sakakawea headwaters in (a) 1996 and (b) 1997.

DISCUSSION

Reservoir levels and Yellowstone-Sakakawea paddlefish. Results of this investigation showed that the reservoir levels of Lake Sakakawea, as well as inter-annual increases and decreases in those levels, were highly associated with differences in zooplankton densities and with several aspects of year class strength, growth, and condition of Yellowstone-Sakakawea paddlefish. In general, rising and high reservoir levels were associated with stronger year classes (Figure 5), higher growth rates of immature fish (Figures 6b and 8), greater condition (Figure 7), greater storage of energy as GFBs in young recruits (Figures 11–14), and higher growth rates of adult fish than were falling and low reservoir levels (Table 1). The rising and high reservoir levels were also correlated with higher discharge levels from the two major rivers discharging into Lake Sakakawea.

Reservoir levels and year class strength. A key result of this investigation was the identification of the strong 1995 year class observed in the harvests from 2002 to 2006 (Figure 3) and its association with the three years of reservoir water level increases from mid 1993 through 1995 (Figure 2). This initial rise in mid 1993 was a result of wet climatic conditions throughout much of the north central United States in 1993, when the U.S. Army Corps of Engineers found it necessary to retain water in Lake Sakakawea and other Missouri River mainstem reservoirs to reduce flooding impacts downriver (Perry, 1993). We had anticipated the strength of the 1995 Yellowstone-Sakakawea paddlefish year class as early as 1996, seven years before recruitment. Over the period August 2–15, 1996, 60 juvenile paddlefish ranging in fork length (FL) from 373 to 518 mm were dip-netted in the upper reaches of Lake Sakakawea (Figure 16). Yearling paddlefish are occasionally encountered in Lake Sakakawea during transect counts, but not in numbers where more than one per day might be dip-netted. These fish were too large to be age 0 fish (which were all less than 300 mm FL at that time) and were assumed to be yearlings. In August 1997, fish of this year class were again captured in the upper reservoir; by this time they had exceeded 500 mm FL (Figure 16). By 1998, they had become too large to be vulnerable to capture with dip nets. Males of this strong year class were occasionally encountered in the period 2000–2002 as unusually young recruits to the snag fisheries, but were not encountered in large numbers until many of them began to mature and recruit to the fisheries from 2003–2006 (Figure 3). As of 2007, females of this year class had remained in Lake Sakakawea and had not yet recruited to the snag fisheries.

The development of the strong 1995 year class associated with the rise in reservoir level starting in 1993 is similar to a past response of Yellowstone-Sakakawea paddlefish. Although a few paddlefish had been caught in North Dakota and at Intake for a century or more, a substantial snag fishery began about 1962 in Montana when large numbers of young, sexually mature males ascended to Intake (Robinson, 1966; Scarnecchia et al., 1996b). The fishery developed nine years after the closure of Garrison Dam in 1953. Robinson (1966) reported that sex ratios of the harvested fish at Intake were at least 97% male each year from 1963 to 1965, which is the expected outcome if strong year classes of males produced immediately after initial reservoir filling began to make their first upriver migrations (Scarnecchia et al., 1996b); females of the same brood years were immature and remained in the reservoir. Elser (1975) reported that both the paddlefish run and fishery at Intake were strong in 1974; most males were age 10–13 and most females 17–19 (Rehwinkel, 1978). By 1974, the sex ratio of creeled fish had reached 50–50; by 1976, it had reached more than two-thirds females (Elser, 1977). Scarnecchia et al. (1996b) reviewed this evidence and concluded, as Elser (1977) had suggested, that upon the filling of Lake Sakakawea (1953–1966), the paddlefish population increased substantially. The stock expansion supported the development of important fisheries in both Montana and North Dakota in the ensuing decades (Scarnecchia et al., 2008).

The initial stock expansion in the 1950s and 1960s and the strength of the 1995 year class are best viewed as responses to trophic upsurge in Lake Sakakawea. The largest upsurge and the largest population increase occurred upon initial filling (1953–1966), and a smaller upsurge and a smaller population increase occurred upon refilling (1993–1995).

Several investigators have described trophic upsurge (Baranov, 1961; Benson, 1982) and the resulting ecological changes within reservoirs in the years soon after impoundment (Eschmeyer and Jones, 1941; Abell and Fisher, 1953; Chamberlain, 1972, Popp and Hoagland, 1995, Popp et al., 1996; Holz et al., 1997). Ellis (1941) and Kimmel and Groeger (1986) summarized the increases in habitat, increased nutrient loading, increased availability of detritus, and higher primary and secondary production associated with the process of reservoir filling. Trophic upsurge after impoundment has also been observed through its effects on fish production (Eschmeyer and Jones, 1941; Abell and Fisher, 1953; Chamberlain, 1972; Benson, 1982); strong year classes and high growth rates of many species are common (Ploskey, 1981; Benson, 1982), although they may be delayed from initial primary and secondary production surges. Beckman and Elrod (1971) reported that the initial filling of Lake Oahe, a Missouri River mainstem reservoir, resulted in strong year classes of several species, including northern pike *Esox lucius*, carp, and buffalofishes (*Ictiobus bubalus* and *Ictiobus cyprinellus*). In particular, production of sport fish species such as centrarchids may increase soon after the upsurge (Abell and Fisher, 1953; Kimmel and Groeger, 1986; Bonneau, 1999).

Trophic upsurge is typically short lived, however, and within a few years after a reservoir is filled, primary production declines, along with production at higher trophic levels as the reservoir ages (Benson, 1982), a response referred to as trophic depression (Popp and Hoagland, 1995; Popp et al., 1996; Holz et al., 1997). According to Kimmel and Groeger (1986), several factors are associated with or contribute to trophic depression, including "decreased internal nutrient loading, . . . declines in biologically labile organic detritus, . . . cessation of habitat expansion . . . and a reduction in favorable habitat" (p. 105). Fish species vary widely in their responses. Centrarchids may decrease following their initial increase in numbers (Bonneau, 1999). Although some species (e.g., benthic omnivores; Bonneau, 1999) may increase as the reservoir ages, the overall fish production typically declines (Ploskey, 1981). Trophic depression can also be exacerbated in many instances by a declining reservoir level. Paller (1997) reported that the drawdown of a small (10.5 km^2) South Carolina reservoir to less than 50% of its former surface area and 35% of its former volume resulted in declines in abundance of several fish species, including largemouth bass. The exact response of water level changes on reservoir fish and fisheries are often indirectly mediated through effects on the food web. Benson and Hudson (1975) found that a reduction in the extent of autumn drawdown in Lake Francis Case, a Missouri River mainstem reservoir, from depths of 10–12 m to 6–7 m resulted in a threefold increase in benthos density over previous drawdowns. Manifestations of trophic upsurge followed by trophic depression on short-lived species such as centrarchids can be observed as rapid increases in abundance and subsequent declines within 10 years or less.

The effects of trophic upsurge and depression can be protracted in long-lived residents such as the paddlefish in slowly filling reservoirs such as Lake Sakakawea. With a lifespan reaching 50 or more years (Scarnecchia et al., 2007) and the gradual filling of Lake Sakakawea (Figure 2), Yellowstone-Sakakawea paddlefish manifested the effects of upsurge much longer into the future than most other species, many years after the initial increase in productivity. A series of strong year classes has contributed to the adult population and snag fisheries for decades (Scarnecchia et al., 1996b).

The relations between paddlefish year class strength and reservoir water levels are in agreement with past and present studies on the broader fish community of Lake Sakakawea, in which increasing reservoir levels during initial and subsequent filling periods, as well as sustained periods of high reservoir levels, have been linked to higher reproductive success and higher abundance of fish (Cassity, 1979; Berard, 1989; Power et al., 1992). Cassity (1979) reported that buffalofishes in Lake Sakakawea benefited greatly from the initial filling of Lake Sakakawea by producing large year classes, but that year classes weakened after the reservoir filled and new vegetated spawning areas were no longer being created. Conversely, decreasing and low water levels in the late 1980s, early 1990s, and over the period 2000–2007 have been linked to lower reproductive success and lower abundance (Power et al., 1992; Hendrickson and Lee, 2000; Hendrickson et al., 2007). In a recent summary, Hendrickson et al. (2007) reported that as reservoir levels fell over the period 2000–2007, declines in abundance (based on catch per effort with standardized gears) occurred for walleye *Sander vitreus*, sauger *Sander canadensis*, yellow perch *Perca flavescens*, northern pike, Chinook salmon *Oncorhynchus tshawytscha*, and rainbow smelt *Osmerus mordax*. Similar increases in reproductive success and stronger year class strength with higher water levels and poorer reproductive success and year classes with declining water levels have been reported in other localities in the Missouri River basin (Lake Francis Case; Gasaway, 1970) and elsewhere (Sammons et al., 1999; Allen et al., 2003).

Reservoir levels and paddlefish growth and condition. The strong correlation between weight-at-age of young (age 9 and age 10) male recruits and Lake Sakakawea water levels (Figures 8–10) is in agreement with studies elsewhere indicating that growth rates and condition may be higher at higher reservoir levels than at lower levels, especially for fishes low in food webs that can benefit from recent upsurge. Houser and Bross (1959) reported that the total length (TL) of age 0 paddlefish (721 mm) at the end of their first growing season in 1957 in Fort Gibson Reservoir, Oklahoma, was nearly as great as their length after three growing seasons (812 mm TL) in earlier years. They attributed the more rapid growth in 1957 to maintenance of a flood pool elevation for more than six weeks, resulting in more than a doubling of reservoir surface area, extensive inundation of vegetation, and large plankton blooms in bays, all conditions not present during years of slower paddlefish growth. Reservoir habitat often produces larger and faster-growing paddlefish than strictly riverine habitat, especially in areas with few backwaters and side channels containing zooplankton. At the time of reservoir closure in 1953, no significant fishery for paddlefish existed in North Dakota, and the few fish present in the riverine habitat were smaller than today, ranging from 4.5 to 13.6 kg, with occasional fish as large as 22.7 kg (Carufel, 1954). Similarly, higher water levels in a given reservoir may lead to more rapid paddlefish growth.

Although the two transects used in this article are clearly not sufficient to fully characterize trends in zooplankton production, we believe that they indexed overall zooplankton production in the upper reservoir. Higher zooplankton densities were associated with years of higher water levels (Table 1), which also tended to be years of clearer water in the two long-term transects (D. L. Scarnecchia, unpublished data). As water levels dropped, reservoir headwaters moved down-reservoir, as did comparable locations of depths and water clarity. The two up-reservoir transects became shallower, water became less clear, and zooplankton densities decreased. A decrease in food for paddlefish in the upper reservoir was also associated with the smaller size-at-age of age 0 paddlefish in August in most years of low water levels (Figure 6a and 6b), and also associated with the smaller size-at-age (Figures 8 and 9) among young male recruits rearing primarily in years of low reservoir levels. Paddlefish are in continuous motion during the foraging season, undertaking particulate feeding (typically for age 0 fish; Michaletz et al., 1982; Fredericks, 1994) or filter feeding (for older fish; Rosen and Hales, 1981; Smith, 2004) and gaining the obligatory benefits of ram ventilation in the process (Burggren and Bemis, 1991; Sanderson et al., 1994). They also have the ability to move considerable distances in the reservoirs in search of food. In 1997, for example, we found that tagged age 0 fish moved up reservoir as far as 47 km within a 2-week period as part of their feeding activities (L. F. Ryckman, letter to D. L. Scarnecchia, October 22, 1997). The paddlefish's foraging habits make weight-at-age, an indicator of growth opportunity, an excellent indicator of overall food availability resulting from the zooplankton production. Increasing and high water levels resulted in a greater volume of productive rearing habitat, more food, and more rapid growth of paddlefish, whereas decreasing and low water levels resulted in a lower volume of productive rearing habitat, less food, and slower growth.

Results for growth for other species in Lake Sakakawea and elsewhere also support our results. Chinook salmon in Lake Sakakawea have also declined greatly in size-at-age in association with declines in smelt, an important forage species, and reduction in coldwater habitat (Hendrickson et al., 2007). Gasaway (1970) reported that growth of 13 species in Lake Francis Case, South Dakota, increased soon after filling but later decreased.

Relationships of reservoir level to growth of young female recruits (age 16–19) were not nearly as pronounced as for young male recruits (ages 9 and 10) because of the longer periods of time needed for female maturation. Over a period of 16–19 years, most trends in growth average out across the many years of both high and low reservoir levels. We therefore did not expect to see as well defined a relationship for females as for males.

Reservoir levels and paddlefish energy accumulation and storage (GFBs). The strong correlations between reservoir level and GFBs (total weight, in proportion to fish weight, and in proportion to gonad weight; Figures 11–13) support the premise that paddlefish were able to acquire and store more energy during increasing and high reservoir levels than decreasing and low reservoir levels. Scarnecchia et al. (2007) demonstrated how GFBs, as indicators of energy acquisition and storage, are accumulated mainly during the immature life history period and depleted (gradually in males; more rapidly, within 2–3 spawns, in females) for maintenance, maturation, and spawning as the fish age. Results from the present article indicate that, in addition to larger fish size and greater condition, the size of the GFB, in absolute weight, in relation to fish weight, and in relation to gonad (testes) weight is larger in newly recruited males during higher reservoir levels.

Cumulative effects of reservoir levels on paddlefish. The faster growth, greater condition, and greater energy storage associated with higher reservoir levels may have functioned cumulatively, favoring the development of greater reproductive success and stronger year classes. For example, increased growth rate may have resulted in a decreased period of time in which paddlefish remained small enough to be preyed upon by other fishes. Age 0 paddlefish are commonly eaten by walleye and sauger in Lake Sakakawea (Mero et al., 1995), with larger predators eating more and larger young paddlefish (Parken and Scarnecchia, 2002). The more rapidly young paddlefish grow past a size where they are vulnerable to predation, the better their survival and the stronger the year class. Faster-growing fish will also be larger at sexual maturity and throughout their lives, with generally higher fecundity than the slower-growing fish (Scarnecchia et al., 2007). Similarly, greater energy storage through accumulation of larger GFBs provides a more reliable energy source for maintenance, maturation, and spawning. All of the above factors would in turn contribute to greater reproductive success and stronger year classes of paddlefish.

Conversely, any density-dependent effects that may exist in paddlefish growth may be exacerbated by low water levels. Strong year classes such as that of 1995 might be especially prone to density dependence. Although our study did not investigate density dependence, if the declines in size of age 9 and 10 paddlefish observed in this study are associated with density-dependent space or food limitations, such limitation would be less likely at high reservoir levels than at low reservoir levels. Density-independent and density-dependent effects could thus act cumulatively, resulting in the decline in growth rates observed in our study.

Influence of combined high river discharges and rising and high reservoir levels. Results of this study do not provide a strong indication of the importance of higher river discharges for paddlefish year class success, in contrast to other studies on Acipenseriform fishes, where high discharge in spring has been found to correlate positively with estimates of year class strength in several situations (Russell, 1986; Miller and Beckman, 1993; Parsley et al., 1993; Nilo et al., 1997). Only Missouri River discharge was positively correlated with the index of year class strength, not Yellowstone River discharge. However, most Yellowstone-Sakakawea paddlefish ascend the Yellowstone River rather than the Missouri River to spawn (Miller and Scarnecchia, 2008). Evidence indicates that the largely unregulated Yellowstone River provides much more suitable spawning conditions than the highly regulated Missouri River, including a more natural hydrograph, higher natural levels of suspended sediment, and a more appropriate thermal profile for spawning (Miller and Scarnecchia, 2008).

The specific reasons for the lack of relation between Yellowstone River discharge and the index of age 0 paddlefish year class strength are not known, but a few possibilities exist. First, our age 0 index, although generally indicative of year class strength (Fredericks and Scarnecchia, 1997) may not be sufficiently sensitive. In particular, the strong 1995 year class, based on age 1 and 2 samples (Figure 16) and later by recruitment to the fishery (Figure 3) was not detected in the age 0 index. Because of an undetermined amount of mortality (including over winter) before age 1, year class strength is not likely to be completely established by August of the first year. More information on mortality of age 0 paddlefish, especially over winter, would be beneficial. Overall, however, the age 0 index remains the best available estimate of year class strength prior to recruitment. Larval sampling has not yet proven as useful for realistically representing year class strength (D. Fuller, Montana Department of Fish Wildlife and Parks, unpublished data), nor, with the exception of the large 1995 year class (Figure 16) has sampling of age 1 and older immature paddlefish from Lake Sakakawea (our unpublished data). Second, within prevailing river discharges and reservoir levels encountered in this study, the effects of river discharges on year class strength may be dominated by the reservoir influences, which were shown in this article to be highly important for this stock (Table 1). For example, during the high reservoir period of the mid 1990s, the Missouri River was backed up to near Williston, North Dakota, creating considerable backwater and slough rearing habitat. In the low reservoir period (since 2003 in particular), the river has had to cut through large sediment deposits for up to 65 Rkm before meeting the reservoir. For newly emerged paddlefish drifting downriver from riverine to reservoir habitat and shifting from endogenous to exogenous feeding, the high reservoir results in a much more favorable transition zone than does a low reservoir. Further studies are needed to clarify the factors affecting year class strength of paddlefish in the riverine-reservoir transition area.

Management implications. Results of this study indicated that for the Yellowstone-Sakakawea paddlefish stock, year class strength, recruitment, juvenile growth, adult growth, and energy storage accumulation (GFBs) are favored at high reservoir levels compared to low levels. In particular, a rising reservoir and resulting trophic upsurge, followed by a period of high reservoir elevation, favors the development of strong year classes. The rapid rise in the reservoir in 1993 following the drought and resulting low water period of 1988–1993 provided much needed recruitment to the paddlefish stock and the snag fisheries in Montana and North Dakota. Continued low reservoir levels, whether a result of drought or persistent unfavorable socioeconomic and political decisions, or both, have had and will continue to have highly detrimental effects on the year class strength, growth, and recruitment of Yellowstone-Sakakawea paddlefish and many other fish species rearing in Lake Sakakawea (Hendrickson, 2003; Hendrickson et al., 2007).

If wetter climatic conditions such as occurred in 1992–1993 (Perry, 1993) reoccur, or if more equitable upriver versus downriver water management objectives are implemented, so that Garrison Dam discharges are reduced and Lake Sakakawea rises toward full pool, inundation of shoreline substrates and their associated vegetation can be expected to result in another trophic upsurge, and an increase in Yellowstone-Sakakawea paddlefish year class strengths, growth, condition, and energy storage. As of August 2008, floods in the lower Missouri and Mississippi river basins have resulted in retention of water and rising water levels in Missouri Basin reservoirs, including Lake Sakakawea.

As summarized by Bennett et al. (1985), "properly timed and regulated water level fluctuations can enhance the fishery resource . . . by impairing the spawning of undesirable species and enhancing the spawning and survival of desirable species. . . . However, unregulated fluctuations have generally been found to have deleterious effects" (p. 12). Periodic drawdowns and refilling are inevitable in all large multi-purpose reservoirs; in its half century of existence, Lake Sakakawea's level has undergone many fluctuations, from the long-term, high-volume changes of initial filling to mid-term, mid-volume changes in the period 1993–1995 to short-term (seasonal or shorter), low-volume changes several times per year. Important responses of Lake Sakakawea's fish stocks have been reported as a result of the initial filling (paddlefish, Scarnecchia et al., 1996a; several species, Hendrickson and Power, 1999), the mid-term response of 1995 (several species, Hendrickson et al., 2007; paddlefish, this paper) and short-term, small-volume changes (Hendrickson, 2003). These fluctuations of differing magnitude and duration will have different effects on paddlefish recruitment. Shorter-term (1–3 yr) partial drawdowns and refilling within an elevation range of 557–563 m would be expected to provide an acceptable range of habitat conditions for paddlefish, resulting in periodic habitat contraction and expansion (and resulting trophic upsurge). It is not yet clear if it would be preferable for paddlefish recruitment to have one rapid rise in the reservoir to full pool (e.g., in a year) or a step-like annual series of three increases to full pool (e.g., over three years). Although shoreline vegetation along Lake Sakakawea has often had difficulty remaining established amid rapid fluctuations in water levels (Hoffman, 1978), the long period of low water levels from 2002 to 2007 has resulted in extensive revegetation of the dried lake bed. Drawdown and refilling within this time period (three years) and elevation (557–563 m) may result in a favorable combination of beneficial upsurge without the strongly negative impacts of several consecutive years of low recruitment.

Future habitat management for paddlefish and other fishes will require a more balanced approach than currently exists. For example, with the frequent droughts associated with the upper Great Plains, the current emphasis on preferentially releasing reservoir water and thereby lowering reservoir levels for navigation benefits downriver would need to be balanced more equitably against economic, recreational, and ecological benefits associated with fuller reservoirs (Morris, 1992; Rounds, 2007). Similarly, future maintenance of adequate river flows, especially in the Yellowstone River, under increasing demand for irrigation and industrial uses may require a more comprehensive approach that considers not only traditional short-term economic benefits but also long-term ecological sustainability (Jager and Smith, 2008).

ACKNOWLEDGMENTS

Funding for this work was provided by the North Dakota Game and Fish Department and the Montana Department of Fish, Wildlife, and Parks. We thank the many fisheries biologists and technicians of those agencies for their efforts, including P. Stewart, V. Riggs, D. Fuller, and T. Crutchfield. S. Gangl and J. W. Quinn provided helpful comments on the manuscript. We also thank the fish cleaning and caviar processing programs at Intake and the Confluence for their cooperation.

REFERENCES

Abell, D. L., and C. K. Fisher. Creel census at Millerton Lake, California, 1942–1952. *Calif. Fish Game,* **39:** 463–484 (1953).

Adams, L. A. Age determination and rate of growth in *Polyodon spathula*, by means of the growth rings of the otoliths and dentaries. *Am. Midl. Nat.*, **28:** 617–630 (1942).

Alexander, C. M., and T. A. McDonough. Effect of water conditions during spawning on paddlefish year-class strength in Old Hickory Reservoir, Tennessee. Tennessee Valley Authority TVA/ONR/WRF-83/4(a), Knoxville, TN (1983).

Allen, M. S., W. Tate, K. I. Tugend, M. Rogers, and K. J. Dockendorf. Effects of water-level fluctuations on the fisheries of Lake Tarpon. Pinellas County Department of Environmental Management, Clearwater, FL (2003).

American Fisheries Society, Southern Division. *Reservoir Fishery Resource Symposium*. April 5–7, 1967. Reservoir Committee, Washington, DC (1967).

Baranov, I. V. Biohydrochemical classification of reservoirs in the European USSR. **In:** *The Storage Lakes of the USSR and Their Importance for Fishery* (P. V. Tyurin, Ed., pp. 139–183). Tel Aviv, Israel: Israel Program for Scientific Translations (1961).

Beam, J. H. The effect of annual water level management on population trends of white crappie in Elk City Reservoir, Kansas. *N. Am. J. Fish. Manage.*, **3:** 34–40 (1983).

Beckman, L. G., and J. H. Elrod. Apparent abundance and distribution of young-of-year fishes in Lake Oahe, 1965–1969. **In:** *Reservoir Fisheries and Limnology* (G. E. Hall, Ed., pp. 333–347) Washington, D C: American Fisheries Society Special Publication 8 (1971).

Bennett, D. H., O. E. Maughan, and D. B. Jester, Jr. Generalized model for predicting spawning success of fish in reservoirs with fluctuating water levels. *N. Am. J. Fish. Manage.*, **5:** 12–20 (1985).

Benson, N. G. Some observations on the ecology and fish management of reservoirs in the United States. *Can. Water Resour. J.*, **7:** 2–23 (1982).

Benson, N. G., and P. L. Hudson. Effects of a reduced fall drawdown on benthos abundance in Lake Francis Case. *Trans. Am. Fish. Soc.*, **104:** 526–528 (1975).

Berard, E. Ecological investigations of the Missouri mainstem reservoirs in North Dakota. North Dakota Game and Fish Department, Division of Fisheries Report A-1156, Bismarck (1989).

Bondurant, D. C., and R. H. Livesey. Operational problems associated with a basin reservoir system. **In:** *Reservoir Fishery Resources Symposium*, pp. 47–55. Washington, D C: American Fisheries Society, Southern Division (1967).

Bonneau, J. L. Ecology of a fish biomanipulation in a Great Plains reservoir. Doctoral dissertation. University of Idaho, Moscow (1999).

Brown, M. L., and B. R. Murphy. Management evaluation of body condition and population size structure for paddlefish: A unique case. *Prairie Natural.*, **25:** 93–108 (1993).

Burggren, W. W., and W. E. Bemis. Metabolism and ram gill ventilation in juvenile paddlefish, *Polyodon spathula*, (Chondrostei: Polyodontidae). *Physiol. Zool.*, **65:** 515–539 (1991).

Carufel, L. Paddlefish. *North Dakota Outdoors.* **July:** 6–7 (1954).

Cassity, R. L. Age, growth, and reproduction of buffalofishes in Lake Sakakawea, North Dakota, 1978. North Dakota Game and Fish Department, Division of Fisheries, Report 1311, Bismarck (1979).

Chamberlain, L. L. Primary productivity in a new and an older California reservoir. *Calif. Fish Game*, **58:** 254–267 (1972).

Cooke, G. D., E. B. Welch, S. A. Peterson, and P. R. Newroth. *Restoration and Management of Lakes and Reservoirs*, 2nd edition. Boca Raton, FL: Lewis Publishers (1993).

De Vlaming, V., G. Grossman, and F. Chapman. On the use of the gonadosomatic index. *Comp. Biochem. Phys.*, **73A:** 31–39 (1982).

Eddy, S., and P. H. Simer. Notes on the food of the paddlefish and the plankton of its habitat. *Trans. Ill. Acad. Sci.*, **25:** 59–68 (1929).

Ellis, M. M. Fresh-water impoundments. *Trans. Am. Fish. Soc.*, **71:** 80–93 (1941).

Elser, A. A. Paddlefish investigations. Montana Department of Fish and Game, Federal Aid to Fish Restoration Project F-30-R-11, Helena (1975).

Elser, A. A. Paddlefish investigations. Montana Department of Fish and Game, Federal Aid to Fish Restoration Project F-30-R-13, Helena (1977).

Eschmeyer, R. W., and A. M. Jones. The growth of game fishes in Norris Reservoir during the first years of impoundment. *Trans. Sixth N. Am. Wildl.Conf.*, 222–240 (1941).

Frazer, K. J. Evaluation of the fishery in the Fort Peck tailwater/Dredge Cut area and assessment of potential impacts from increased hydropower production at Fort Peck Dam on this fishery. Montana Department of Fish, Wildlife and Parks, Helena (1985).

Firehammer, J. A., and D. L. Scarnecchia. Spring migratory movements by paddlefish in natural and regulated river segments of the Missouri and Yellowstone Rivers, North Dakota and Montana. *Trans. Am. Fish. Soc.*, **135:** 200–217 (2006).

Firehammer, J. A., and D. L. Scarnecchia. The influence of discharge on duration, ascent distance, and fidelity of the spawning migration for paddlefish of the Yellowstone-Sakakawea stock. *Environ. Biol. Fishes*, **78:** 23–36 (2007).

Fredericks, J. P. Distribution, abundance, and feeding ecology of paddlefish in Upper Lake Sakakawea, North Dakota. Master of Science Thesis, University of Idaho, Moscow, ID (1994).

Fredericks, J. P., and D. L. Scarnecchia. Use of surface visual counts for estimating relative abundance of age 0 paddlefish in Lake Sakakawea. *N. Am. J. Fish. Manage.*, **17:** 1014–1018 (1997).

Gasaway, C. R. Changes in fish populations in Lake Francis Case in South Dakota in the first 16 years of impoundment. Washington, D C: U.S. Department of the Interior, Bureau of Sport Fisheries and Wildlife Technical Paper 56 (1970).

Gengerke, T. W. Distribution and abundance of paddlefish in the United States. **In:** *The Paddlefish: Status, Management and Propagation.* (J. G. Dillard, L. K. Graham, and T. R. Russell, Eds., pp. 22–35). Bethesda, MD: American Fisheries Society, North Central Division (1986).

Grande, L., and W. E. Bemis. Osteology and phylogenetic relationships of fossil and Recent paddlefishes (Polyodontidae) with comments on the interrelationships of Acipenseriformes. *J. Vert. Paleontol.*, **11(Suppl. 1):** (1991).

Hall, G. E. (Ed.). *Reservoir Fisheries and Limnology*. Washington, DC: American Fisheries Society Special Publication 8 (1971).

Hall, G. E., and M. J. Van Den Avyle (Eds.). *Reservoir Fisheries Management, Strategies for the 80s.* Bethesda, MD: American Fisheries Society, Southern Division, Reservoir Committee (1986).

Hart, H. C. *The Dark Missouri.* Madison: University of Wisconsin Press (1957).

Heman, M. L., R. S. Campbell, and L. C. Redmond. Manipulation of fish populations through reservoir drawdown. *Trans. Am. Fish. Soc.*, **98:** 293–304 (1969).

Hendrickson, J. Depth of spawning of rainbow smelt in Lake Sakakawea, North Dakota. North Dakota Game and Fish Department Fisheries Investigations Report 51, Bismarck (2003).

Hendrickson, J., and J. Lee. Aquatic investigations of the Missouri mainstem in North Dakota. North Dakota Game and Fish Department, Fisheries Investigations Report 36, Bismarck (2000).

Hendrickson, J., J. Lee, and F. Ryckman. Aquatic investigations of the Missouri mainstem in North Dakota. North Dakota Game and Fish Department, Fisheries Investigations Report 67, Bismarck (2007).

Hendrickson, J. C., and G. Power. Changes in fish species abundance in a Missouri River mainstem reservoir during its first 45 years. *J. Freshwat. Ecol.*, **14:** 407–416 (1999).

Hesse, L. W., and W. Sheets. The Missouri River hydrosystem. *Fisheries*, **18**(5): 5–14 (1993).

Hoffman, G. R. Shore vegetation of Lakes Oahe and Sakakawea, mainstem Missouri River reservoirs. Vermillion: University of South Dakota, Biology Department (1978).

Holz, J. C., K. D. Hoagland, R. L. Spawn, A. Popp, and J. L. Andersen. Phytoplankton community response to reservoir aging, 1968–92. *Hydrobiologia*, **346:** 183–192 (1997).

Houser, A., and M. G. Bross. Observations on the growth and reproduction of paddlefish. *Trans. Am. Fish. Soc.*, **88:** 50–52 (1959).

Imms, A. D. Notes on the gill rakers of the spoonbill sturgeon, *Polyodon spathula*. *Proc. Zool. Soc. Lond.*, **(Part 2):** 22–35 (1904).

Jager, H. I., and B. T. Smith. Sustainable reservoir operation: can we generate hydropower and preserve ecosystem values? *River Res. Applic.*, **24:** 340–352 (2008).

Junk, W. J., P. B. Bayley, and R. E. Sparks. The flood pulse concept in river-floodplain systems. **In:** *Proceedings of the International Large River Symposium* (D. P. Dodge, Ed., pp. 110–127). *Can. Spec. Publ. Fish. Aquat. Sci.*, **106:** Ottawa, Ontario, Canada (1989).

Kimmel, B. L., and A. W. Groeger. Limnological and ecological changes associated with reservoir aging. **In:** *Reservoir Fisheries Management, Strategies for the 80s* (G. E. Hall and M. J. van den Avyle, Eds., pp. 103–109). Bethesda, MD: American Fisheries Society, Southern Division, Reservoir Committee (1986).

Kofoid, C. A. Notes on the natural history of *Polyodon. Science (new series).* **11:** 252 (1900).

Lagler, K. F. *Freshwater Fishery Biology*, 2nd edition. Dubuque, IA: Wm. C. Brown Company Publishers (1956).

Maceina, M. J. Verification of the influence of hydrologic factors on crappie recruitment in Alabama reservoirs. *N. Am. J. Fish. Manage.*, **23:** 470–480 (2003).

Mero, S. W., D. W. Willis, and G. J. Power. Walleye and sauger predation on paddlefish in Lake Sakakawea, North Dakota. *N. Am. J. Fish. Manage.*, **14:** 226–227 (1995).

Meronek, T. G., P. M. Bouchard, E. R. Buckner, T. M. Burri, K. K. Demmerly, D. C. Hatleli, R. A. Klumb, S. H. Schmidt, and D. W. Coble. A review of fish control projects. *N. Am. J. Fish. Manage.*, **16:** 63–74 (1996).

Meyer, F. P. Life history of *Marsipometra hastata* and the biology of its host, *Polyodon spathula*. Ph.D. Dissertation, Iowa State University, Ames (1960).

Michaletz, P. H., C. F. Rabeni, W. W. Taylor, and T. R. Russell. Feeding ecology and growth of young-of-the-year paddlefish in hatchery ponds. *Trans. Am. Fish. Soc.*, **111:** 700–709 (1982).

Miller, A. I., and L. G. Beckman. A recruitment index for white sturgeon in the Columbia River downstream from McNary Dam. **In:** *Status and Habitat Requirements of the White Sturgeon Population in the Columbia River Downstream from McNary Dam*, Volume 2 (R. C. Beamesderfer and A. A. Nigro, Eds., pp. 141–163). Portland, OR: Bonneville Power Administration (1993).

Miller, S, E., and D. L. Scarnecchia. Adult paddlefish migrations in relation to spring river conditions of the Yellowstone and Missouri Rivers, Montana and North Dakota, USA. *J. Appl. Icthyol.*, **24:** 221–228 (2008).

Morris, B. Unanswered prayers: The upper Missouri River basin states take on the U.S. Army Corps of Engineers. *N. Dakota Law Rev.*, **68:** 897–935 (1992).

Nilo, P., P. Dumont, and R. Fortin. Climatic and hydrologic determinants of year-class strength of St. Lawrence River lake sturgeon (*Acipenser fulvescens*). *Can. J. Fish Aquat. Sci.*, **54:** 774–780 (1997).

Noble, R. L. Management of forage fishes in impoundments of the southern United States. *Trans. Am. Fish. Soc.*, **110:** 738–750 (1981).

Ott, R. L. *An Introduction to Statistical Methods and Data Analysis*, 4th edition. Belmont, CA: Duxbury Press (1993).

Paller, M. H. Recovery of a reservoir fish community from drawdown related impacts. *N. Am. J. Fish. Manage.*, **17:** 726–733 (1997).

Parken, C., and D. L. Scarnecchia. Predation on age 0 paddlefish by walleye and sauger in a Great Plains reservoir. *N. Am. J. Fish. Manage.*, **22:** 750–759 (2002).

Parsley, M. J., P. J. Anders, A. I. Miller, L. G. Beckman, and G. T. McCabe, Jr. Factors affecting spawning and recruitment of white sturgeon in the Columbia River downstream from McNary Dam. **In:** *Status and Habitat Requirements of the White Sturgeon Population in the Columbia River Downstream from McNary Dam*, Volume 1 (R. C. Beamesderfer and A. A. Nigro, Eds., pp. 61–79). Portland, OR: Bonneville Power Administration (1993).

Paukert, C. P., and W. L. Fisher. Characteristics of paddlefish in a southwestern U.S. reservoir, with comparisons of lotic and lentic populations. *Trans. Am. Fish. Soc.*, **130:** 634–643 (2001).

Pennak, R. W. *Fresh-Water Invertebrates of the United States.* New York: The Ronald Press Company (1953).

Perry, C. A. *Effects of Reservoirs on Flood Discharges in the Kansas and Missouri River Basins, 1993*. Washington, DC: United States Geological Survey Circular 1120-E (1993)

Ploskey, G. R. *Factors Affecting Fish Production and Fishing Quality in New Reservoirs, with Guidance on Timber Clearing, Basin Preparation, and Filling.* Vicksburg, MS: U.S. Army Corps of Engineers Waterways Experiment Station Technical Report E-81-11 (1981).

Popp, A., and K. D. Hoagland. Changes in benthic community composition in response to reservoir aging. *Hydrobiologia*, **306:** 159–171 (1995).

Popp, A., K. D. Hoagland, and G. L. Hergenrader. Zooplankton community response to reservoir aging. *Hydrobiologia*, **339:** 13–21 (1996).

Power, G. J., J. C. Hendrickson, B. L. Kreft, and L. K. McGregor. *Aquatic Investigations of the Missouri Mainstem in North Dakota*. North Dakota Game and Fish Department, Fisheries Investigations Report 1, Bismarck (1992).

Power, G. J., J. C. Hendrickson, J. D. Lee, and F. Ryckman. *Missouri River System Fishery Reference and Operational Management Document*. North Dakota Game and Fish Department, Fisheries Investigations Report 10, Bismarck (1994).

Rehwinkel, B. J. The fishery for paddlefish at Intake, Montana, during 1973 and 1974. *Trans. Am. Fish. Soc.*, **107:** 263–268 (1978).

Ridgeway, M. E. *The Missouri Basin's Pick-Sloan Plan.* Urbana: University of Illinois Press (1955).

Robinson, J. W. Observations on the life history, movement, and harvest of the paddlefish, *Polyodon spathula*, in Montana. *Proc. Montana Acad. Sci.*, **26:** 33–44 (1966).

Rogers, K. B., and E. P. Bergersen. Effects of a fall drawdown on movement of adult northern pike and largemouth bass. *N. Am. J. Fish. Manage.*, **15:** 596–600 (1995).

Rosen, R. A., and D. C. Hales. Feeding of paddlefish, *Polyodon spathula*. *Copeia*, **1981:** 441–455 (1981).

Rounds, M. M. Missouri River: A view from upstream. Letter to J. P. Woodley, Assistant Secretary of the Army. *Prairie Fire*, December (2007).

Roush, K. D., C. P. Paukert, and W. Stancill. Distribution and movement of juvenile paddlefish in a mainstem Missouri River reservoir. *J. Freshwat. Ecol.*, **18:** 79–87 (2003).

Ruelle, R., and P. L. Hudson. Paddlefish (*Polyodon spathula*): Growth and food of young of the year and a suggested technique for measuring length. *Trans. Am. Fish. Soc.*, **106:** 609–613 (1977).

Russell, T. R. Biology and life history of the paddlefish—A review. **In:***The Paddlefish: Status, Management, and Propagation* (J. G. Dillard, L. K. Graham, and T. R. Russell, Eds., pp. 2–20). Bethesda, MD: American Fisheries Society, North Central Division, Special Publication 7 (1986).

Sammons, S. M., L. G. Dorsey, P. W. Bettoli, and F. C. Fiss. Effects of reservoir hydrology on reproduction by largemouth bass and spotted bass in Normandy Reservoir, Tennessee. *N. Am. J. Fish. Manage.*, **19:** 78–88 (1999).

Sanderson, S. L., J. J. Cech, Jr., and A. Y. Cheer. Paddlefish buccal flow velocity during ram suspension feeding and ram ventilation. *J. Exp. Biol.*, **186:** 145–156 (1994).

SAS Institute. *SAS Users guide*. Cary, NC (1989).

Scarnecchia, D. L., L. F. Ryckman, and J. Lee. Capturing and tagging of wild age 0 and age 1 paddlefish in a Great Plains reservoir. *N. Am. J. Fish. Manage.*, **17:** 800–802 (1997).

Scarnecchia, D. L., L. F. Ryckman, Y. Lim, G. Power, B. Schmitz, and V. Riggs. A long-term program for validation and verification of dentaries for age estimation in the Yellowstone-Sakakawea paddlefish stock. *Trans. Am. Fish. Soc.*, **135:** 1086–1094 (2006).

Scarnecchia, D. L., L. F. Ryckman, Y. Lim, G. Power, B. J. Schmitz, and J. A. Firehammer. Life history and the costs of reproduction in northern Great Plains paddlefish (*Polyodon spathula*) as a potential framework for other Acipenseriform fishes. *Rev. Fish. Sci.*, **15:** 211–263 (2007).

Scarnecchia, D. L., L. F. Ryckman, B. J. Schmitz, S. Gangl, W. Wiedenheft, L. L. Leslie, and Y. Lim. Management Plan for the Montana and North Dakota Paddlefish Stocks and Fisheries. A Cooperative Interstate Plan. Helena, MT, and Bismarck, ND: Montana Department of Fish, Wildlife, and Parks and North Dakota Game and Fish Department (2008).

Scarnecchia, D. L., P. Stewart, and L. F. Ryckman. Management Plan for the Paddlefish Stocks in the Yellowstone River, upper Missouri River, and Lake Sakakawea. Bismarck, ND, and Helena, MT: North Dakota Game and Fish Department and Montana Department of Fish, Wildlife, and Parks (1995).

Scarnecchia, D., and P. Stewart. Managing Montana's paddlefish: New approaches. *Montana Outdoors*, **26**(3): 10–14 (1996).

Scarnecchia, D. L., P. A. Stewart, and Y. Lim. Profile of recreational paddlefish snaggers on the lower Yellowstone River, Montana. *N. Am. J. Fish. Manage.*, **16:** 872–879 (1996a).

Scarnecchia, D. L., P. A. Stewart, and G. J. Power. Age structure of the Yellowstone-Sakakawea paddlefish stock, 1963–1993, in relation to reservoir history. *Trans. Am. Fish. Soc.*, **125:** 291–299 (1996b).

Scarnecchia, D. L., P. A. Stewart, L. F. Ryckman, and K. Gilge. Montana-North Dakota paddlefish sampling procedures. Montana Department of Fish, Wildlife, and Parks and North Dakota Game and Fish Department. Helena, MT, and Bismarck, ND (1996c).

Scarnecchia, D. L., and P. A. Stewart. Implementation and evaluation of a catch-and-release fishery for paddlefish. *N. Am. J. Fish. Manage.*, **17:** 795–799 (1997a).

Scarnecchia, D. L., and P. A. Stewart. Angler response to harvest regulations in Montana's Yellowstone River paddlefish (*Polyodon spathula*) fishery. *Intermountain J. Sci.*, **3:** 94–100 (1997b).

Shields, J. T. Experimental control of carp reproduction through water drawdowns in Fort Randall Reservoir. *Trans. Am. Fish. Soc.*, **87:** 23–33 (1957).

Shields, J. T. Fish management problems of large impoundments on the Missouri River. *Trans. Am. Fish. Soc.*, **87:** 356–362 (1958).

Smith, N. A. Feeding ecology and morphometric analysis of paddlefish, *Polyodon spathula*, in the Mermentau River, Louisiana. Master of Science Thesis, Louisiana State University, Baton Rouge (2004).

Snedecor, G. W., and W. G. Cochran. *Statistical Methods*, 6th edition. Iowa State University, Ames (1967).

Sparrowe, R. D. Threats to paddlefish habitat. **In:***The Paddlefish: Status, Management, and Propagation* (J. G. Dillard, L. K. Graham, and T. R. Russell, Eds., pp. 36–45). Bethesda, MD: American Fisheries Society, North Central Division, Special Publication 7 (1986).

Stockard, C. R. Observations on the natural history of *Polyodon spathula*. *Am. Nat.*, **41:** 753–766 (1907).

Sveum, D. J. Regulation of Missouri River main stem reservoirs. **In:** *The Missouri River: The Resources, Their Uses and Values* (N. G. Benson, Ed., pp. 51–66) Bethesda, MD: American Fisheries Society, North Central Division, Special Publication 8 (1988).

Thornthwaite, C. W. Climate and settlement in the Great Plains. **In:** *Yearbook of Agriculture*, pp. 177–187. Washington, DC: U.S. Department of Agriculture (1941).

Torrey, A. E., and F. A. Kohout. *Geology and groundwater resources of the Lower Yellowstone River Valley, between Glendive and Sidney, Montana.* Water Supply Paper 1355. Washington, DC: United States Geological Survey (1956).

U.S. Army Corps of Engineers. *Missouri River Mainstem Reservoir System Master Water Control Manual.* Omaha, NE: Missouri River Basin, Northwestern Division. (2004).

Verrill, D. D., and C. R. Berry, Jr. Effectiveness of an electrical barrier and lake drawdown for reducing common carp and bigmouth buffalo abundances. *N. Am. J. Fish. Manage.*, **15:** 137–141 (1995).

Wilkens, L. A., M. H. Hofmann, and W. Wojtenek. The electric sense of the paddlefish: A passive system for the detection and capture of zooplankton prey. *J. Physiol., Paris*, **96:** 363–377 (2002).

Willis, D. W. Review of water level management on Kansas reservoirs. **In:** *Reservoir Fisheries Management: Strategies for the 80s* (G. E. Hall and M. J. van den Avyle, Eds., pp 110–114). Bethesda, MD: American Fisheries Society, Southern Division, Reservoir Committee (1986).