Spring Movements of Paddlefish in a Prairie Reservoir System

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ABSTRACT

Paddlefish (*Polyodon spathula)* movements and habitat use were monitored in the Keystone Reservoir System, Oklahoma during 1996-1998 to determine reproductive activity patterns. Paddlefish spring spawning migrations were more dependent on water flows than water temperature or photoperiod. Paddlefish moved up the Cimarron River and Arkansas River in 1997 and 1998 when spring flows increased. However, they did not migrate up the rivers in 1996, a year with extremely low flows. Suitable spawning substrate was found in the Salt Fork River, a major tributary of the Arkansas River, and the tailwaters of Kaw Dam on the Arkansas River. Paddlefish were located over suitable spawning substrate in the Salt Fork River; however, no larvae were collected. Although paddlefish migrate up the Cimarron River in spring, minimal spawning habitat may limit successful spawning in that river. In 1998, paddlefish moved into the Salt Fork River rather than the Kaw Dam tailwaters, presumably because there was limited flow from Kaw Dam that spring. Paddlefish in the Keystone Reservoir system appear to have adapted to the high spring water temperatures and fluctuating flows enabling successful reproduction.

The paddlefish *(Polyodon spathula) is* native to large midwestern rivers in the central United States, including the Arkansas River and the Cimarron River, which combine to make Keystone Reservoir in northcentral Oklahoma. Paddlefish populations have diminished in numbers during the last century due in part to destruction of spawning grounds and dam construction (Graham 1997). Paddlefish traditionally migrate up rivers in spring (Unkenholz 1982, Russell 1986), where spawning occurs in flowing water over silt-free gravel (Purkett 1961) at water temperatures of 10-18° C (Pitman 1991). However, gravel is sparse in prairie rivers of the southcentral and southwestern U.S., and paddlefish may be required to spawn over other substrates (Bonislawsky 1977).

In the last 50 years, impoundments have, in many cases, diminished the size of paddlefish populations because they block fish from their spawning grounds or inundate the spawning areas altogether. In addition, river stage and discharge are usually highly regulated and may not mimic natural spring flow regimes (Unkenholz 1986), which may prohibit paddlefish spawning. However, some paddlefish populations, including the one in Keystone

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Reservoir, have survived and even flourished (Paukert 1998). Our objective was to determine spring movement patterns associated with reproductive activity of paddlefish in the Keystone Reservoir system, Oklahoma.

STUDY SITE

Keystone Reservoir is a 10,600-ha impoundment in northcentral Oklahoma with a self-sustaining, naturally-reproducing paddlefish population (Paukert 1998). Large water-level fluctuations are common due to the size of the watershed, power generation, and regulation of the Arkansas River and the Salt Fork River. The Arkansas River drains the southern plains of Kansas and is impounded by Kaw Dam 176 km upstream of Keystone Reservoir (Fig. 1). The Salt Fork River, a major tributary that enters the Arkansas River 152 km upstream from Keystone Reservoir, is impounded by Great Salt Plains Dam. The Cimarron River drains part of western Oklahoma and is unimpounded above Keystone Reservoir. All three rivers have predominantly sand substrate and highly fluctuating flows with braided channels. Few deepwater (>1 m) habitats are present; however, high spring water levels (e.g., >3 m) aid in spring migrations of paddlefish (Paukert 1998).

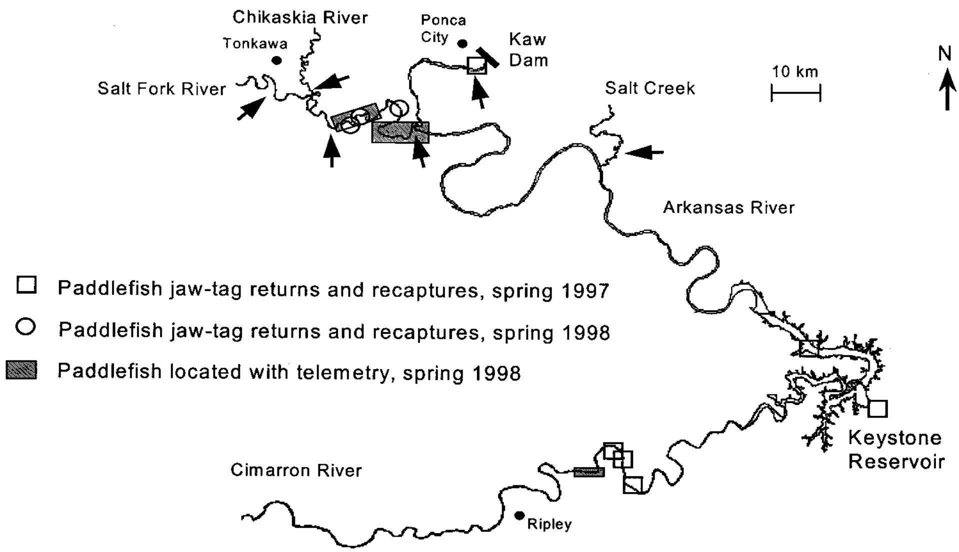

Figure 1. The Keystone Reservoir system in northcentral Oklahoma. Paddlefish spring recaptures, tag-return locations, and telemetry locations in the Keystone Reservoir system. Arrows indicate suitable spawning substrate for paddlefish. Great Salt Plains Dam is located on the Salt Fork River 165 km upstream from the mouth of the Arkansas River.

METHODS

Adult and juvenile paddlefish were collected from the Keystone Reservoir during winters 1996-1998 with monofilament gill nets (Paukert and Fisher 1999). Each fish was measured (nearest mm) from the anterior orbit of the eye to the fork of the tail (EFL; Ruelle and Hudson 1977), weighed (nearest 0.5 kg), tagged, and immediately released near its capture site.

To collect paddlefish larvae, conical plankton nets (0.5-m diameter, 2.5-m length, 0.5-mm bar mesh, and fitted with collecting buckets 10.2 cm in diameter and 30.5-cm long) were suspended for 10-20 min from bridges over three rivers (Cimarron, Arkansas and Salt Fork), and Salt Creek on 10 April 1996 and 15-26 April 1997. The samples were preserved in 10% formalin and enumerated in the laboratory. At each sampling site, water temperature, dissolved oxygen, and conductivity were measured with a multi-parameter meter (model H20, Hydrolab Inc., Austin, TX). Water flow data were obtained from the United States Geological Survey (USGS) gauging stations nearest each sampling site.

In March 1997, six male paddlefish (843 - 1,000 mm EFL) were implanted with ultrasonic transmitters (Sonotronics, Tuscon, AZ). (For specific implantation procedures, see Paukert 1998). In January-March 1998, an additional 18 fish (nine males and nine females, 974 - 1,290 mm EFL) were implanted with transmitters. Distribution and movement of transmitter-tagged fish were monitored from March to June 1997 (for the first six fish) and from February to June 1998 (for all 24 fish).

Paddlefish were tracked with a digital receiver (Sonotronics model USR 5W) and directional hydrophone (Sonotronics model DH-2). Beginning immediately after implantation, tracking was conducted about twice weekly in the reservoir and increased as fish moved near the upper reaches of the reservoir (an indication of staging to spawn). When fish left the reservoir, the Cimarron River, Arkansas River, and Salt Fork River were searched weekly. Early in the study, searches were conducted in all three rivers each week, beginning with the lower reaches near the reservoir. Later, tracking was conducted at known paddlefish concentrations and throughout the rivers when possible. Once a fish was located, its location coordinates were determined with a global positioning system (GPS) receiver. Substrate (gravel, sand, silt), habitat type (river bend, main river channel, scour hole), and depth (m) were recorded at sites where fish were located, and temperature, dissolved oxygen, and conductivity were recorded 1 m below the surface at these locations. We identified suitable spawning substrate (1.3 - 3.8 cm diameter gravel; Purkett 1961) by visual observation during our telemetry tracking in the rivers. When deeper (>0.5 m) water was encountered, we used a wooden rod to probe the bottom for gravel substrate. When gravel was encountered, we used a GPS receiver to determine the location of the upper and lower reaches of the gravel bar. Habitat type was defined as main channel (uniform depth with no defined river bends), scour hole (deepwater area caused by bridges, woody debris, incoming tributary, etc.), or bend (defined curvature of the river). Water flow data were obtained from USGS gauging stations nearest each fish location. River sections in which fish were located were searched more intensively for the remainder of the spring. Because of the vast extent of the rivers in this system, our efforts were focused on areas of known paddlefish locations or where adequate spawning substrate occurred. Tracking ended when the transmitter-tagged fish were located back in the reservoir after the spring migration. Periodically throughout spring 1997 and 1998, Keystone Reservoir was searched to determine if fish remained in the reservoir.

In spring 1997 and 1998, gill netting and snagging with rod-and-reel were used to collect paddlefish in the rivers to determine their distribution and reproductive status. Gill nets (set for 24 h and checked about every 3 h) were also used in the reservoir in spring 1997 to determine when paddlefish returned to the reservoir from the rivers after the spawning migration. Throughout the rivers, gill nets were drifted through deep holes and bends, and snagging was used when concentrations of paddlefish were located. Each paddlefish collected was inspected for a jaw tag, weighed, and measured. Sex was determined by biopsy or the presence of milt or eggs observed after squeezing the abdomen.

To determine age structure of the paddlefish population and to estimate year-class strength, dentary bones of paddlefish that died in our gill nets were sectioned and aged by methods described by Adams (1942). Ages of unaged fish were assigned using the mean length at age data from the aged fish.

Paddlefish year-class strength was evaluated using catch-curve data from 1984-1997. Only ages fully recruited to our gill nets (age 2; Paukert 1998) were used in the catch-curve. In addition, only age groups with five or more individuals were used in the analysis (Ricker 1975).

River discharges for each river were recorded from USGS stations on the Cimarron River at Ripley, the Arkansas River at Ponca City, and the Salt Fork River at Tonkawa.

A Kolmogorov-Smirnov two-sample test was used to detect difference in length distribution of paddlefish collected in the river and reservoir (Zar 1996). A chi-square test was used to compare habitat use and substrate differences between males and females. When the expected values of some of the cells in the chi-square test were less than 5.0, Fisher's exact test was used (Zar 1996). Multiple regression was used to assess year-class strength (Maceina 1997). This method involves using a catch-curve plus an environmental variable as an additional independent variable in the model:

$$\log_e \text{abundance} = \text{age} + \text{environmental effect}$$

with the environmental effect being mean monthly discharge for February to May for the Salt Fork River, Cimarron River, and Arkansas River. All statistical analyses were performed in SAS (SAS Institute 1996) with a alpha level of 0.05.

RESULTS

We jaw-tagged 1,138 paddlefish (588 - 1,291 mm EFL) during the winters of 1996-1998. In addition, we collected dentary bones from 106 (323 - 1,323 mm EFL) paddlefish for age and growth analysis. The oldest paddlefish was 14 years and at least 11 age groups were represented in each year of the three-year study.

Spring 1996 movements. Paddlefish remained in Keystone Reservoir the entire spring. Paddlefish staged in the upper reaches of the Cimarron River Arm of the reservoir, as indicated by high gill net catch-per-effort in this tributary arm in February (Paukert 1998), suggesting they were preparing for their upriver spawning migration. Discharge was 8-52 m^3/s in the Cimarron River and Arkansas River during this period (Figure 2). River and upper reservoir reach water temperatures in February-March were 6-11°C. No tags were returned by anglers in 1996.

Spring 1997 movements. Spawning migrations occurred in spring 1997, based on gill-net catches and tag returns from the rivers. Paddlefish did not appear to stage in the upper ends of the reservoir in 1997, based on little change in gill net catch-per-effort in the upper reaches of the reservoir (Paukert 1998); however, they left the reservoir during high flows (>750 m^3/s) despite relatively low water temperatures (6-8°C). Paddlefish were located in the Cimarron River, Arkansas River and Salt Fork River from 1 March to11 April (Table 1; Figure 1).

Table 1. Locational statistics of paddlefish sampled in the Keystone Reservoir system, Oklahoma during spring 1997 and 1998. Total fish represents the number of fish collected by both gill netting and by angler tag returns (1997) and the total number of telemetry observations (1998). Recaptures indicate the number of jaw-tagged fish collected in Keystone Reservoir (1997) and the number of different telemetry-tagged fish located (1998). No telemetry tagged fish were located in the Arkansas River in 1998. Eleven transmitter-tagged male paddlefish remained in Keystone Reservoir throughout spring 1998.

	1997 gill netting and tag returns			1998 telemetry locations		
	Cimarron River	Arkansas River	Salt Fork River	Cimarron River	Arkansas River	Salt Fork River
First date located	15 March	1 March	22 March	10 April	22 March	2 April
Last date located	5 April	11 April	2 April	10 April	15 May	21 May
Total fish	18	23	18	1	0	21
Recaptures	2	1	0	1	0	10

In the Cimarron River, 11 paddlefish were gill netted on 15 March. An additional four paddlefish were gill netted from 27 March to 1 April 60 km upstream of Keystone Reservoir. No fish were collected on 24 and 27 April in gill netting and snagging efforts. Three tags from 60 km upstream of the reservoir were returned by anglers from the Cimarron River from 23 March to 5 April (Figure 1).

In the Arkansas River, 22 paddlefish were netted in the Kaw Dam tailwaters from 12 March to 11 April. In addition, an angler caught a jaw-tagged paddlefish in the Kaw Dam tailwaters on 1 March (Table 1). No paddlefish were collected in the lower Arkansas River (up to 24 km upstream of Keystone Reservoir) on 18 March. Gill netting on 30 April in the Kaw Dam tailwaters collected no paddlefish. However, an angler caught a paddlefish previously tagged in the Kaw Dam tailwaters in the tailwaters on 9 June (Figure 1).

Eighteen paddlefish were netted or snagged in the Salt Fork River from 22 March to 2 April, 167 km upstream from Keystone Reservoir. Gill netting on 6 May in the Salt Fork River collected no paddlefish. In addition, no jaw tags were returned from anglers from the Salt Fork River in 1997.

Six male paddlefish (implanted with transmitters in March 1997) remained in and made extensive movements within the reservoir during spring. Five of the six fish, which were implanted in the Cimarron River arm of Keystone Reservoir on 2 and 7 March 1997, moved from the Cimarron River in early March to the Arkansas River in April and May. These fish did not return to the Cimarron River arm throughout the summer 1997 (Paukert 1998).

Paddlefish returned to the reservoir from the rivers in mid-May. Length distributions from reservoir gill netting in winter compared to May gill netting in the reservoir indicated paddlefish length distributions were similar beginning 16 May (Kolmogorov-Smirnov two-sample test; $P = 0.270$).

Spring 1998 movements. Paddlefish migrated up the Cimarron River and Salt Fork River in 1998, based on transmitter-tagged fish locations and jaw tag returns in the rivers. High water flows ($>1400\ m^3/s$) likely prompted paddlefish to migrate up the rivers in mid-March (Figure 2). Paddlefish staged in the upper ends of the reservoir in spring 1998. Of 17 fish located on 17 March, 10 were in the upper reaches of the Arkansas River and three were in the upper reaches if the Cimarron River. On 21 March, only two male paddlefish were located in the upper reaches of Keystone Reservoir; the remainder of the fish (92%) presumably moved upriver to spawn, although water temperatures were low (6-7°C).

In searches of 138 km of the Cimarron River, only one transmitter-tagged fish was located on 10 April (a female at river km 95). However, eight female and two male transmitter-tagged paddlefish were located in the Salt Fork River from 2 April to 21 May (Table 1). No paddlefish were located in the Salt Fork River on 27 May. In contrast, five searches of the Kaw Dam tailwaters from 29 March to 15 May located no transmitter-tagged fish. In addition, no tag returns from anglers were from the Arkansas River and poor snagging success was reported in the Kaw Dam tailwaters in spring 1998 (Figure 1).

On 16 sampling trips from 2 April to 21 May, paddlefish were located in the Salt Fork River from river km 0 to river km 40. Movement of five of these eight fish was highly variable in spring 1998; however, paddlefish tended to move upriver when flows increased. In addition to the transmitter-tagged fish, we snagged 35 paddlefish (mostly small males; mean length 890 mm EFL, SD = 103 mm) in the Salt Fork River from 17 April to 21 May. Two of the fish were recaptures of fish jaw-tagged in the reservoir. In addition, one tag was

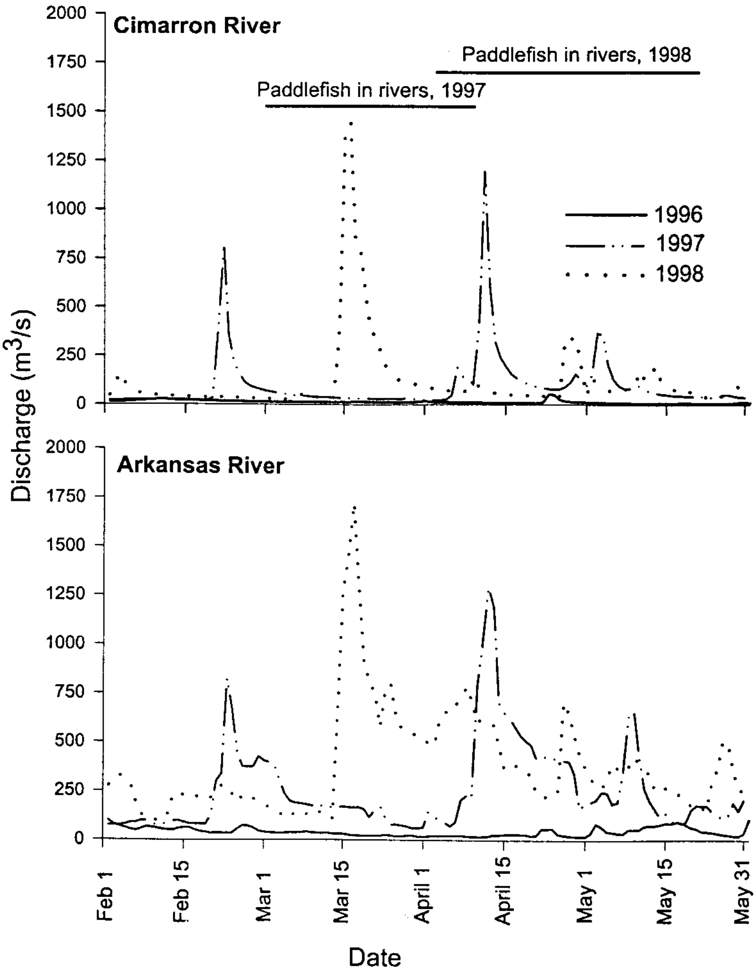

Figure 2. Discharge (m^3/s) for the Arkansas and Cimarron rivers, spring 1996 - spring 1998. Horizontal bars indicate dates that paddlefish were located in either river in 1997 and 1998, the two years paddlefish migrated up the rivers to spawn.

returned by an angler from the Salt Fork River (Figure 1). One gravid female (1,256 mm EFL) was caught on 21 May, in 27°C water temperature. Searches of Keystone Reservoir on 15 April and 2 May indicated that 11 male transmitter-tagged paddlefish (890-1,132 mm EFL) did not make the spring spawning migration.

Transmitter-tagged paddlefish located in the rivers during spring 1998 were first located back in the reservoir on 18 May (one female last found in the Cimarron River and a 1,260 mm male last located in the Salt Fork River). All five females located in the Salt Fork River on 20-21 May were among the 21 fish located in Keystone Reservoir on 29 May, which occurred after a high flow event (>300 m^3/s) in the Salt Fork River on 25-28 May.

Habitats. During spring 1998, transmitter-tagged paddlefish were located over gravel substrate 14% of the time, 36% over sand, and 50% over silt. There was no difference in substrate use between males and females (Fisher's exact test; $P = 0.321$). Although some fish were located over suitable spawning substrate (gravel), we found no other direct evidence of paddlefish spawning. Paddlefish were primarily located in river bends (47%), the main river channel (30%), and scour holes (20%). There were no differences in location between males and females (Fisher's exact test; $P = 0.378$). Paddlefish were generally in shallow water (median depth 3.0 m) but were never shallower than 1.7 m. However, deep water was rare, except in scour holes where depth could reach 7 m. Most deepwater river bends were <3.5 m in depth.

Year-class strength. There was no relationship among year-class strength and water flows for the Cimarron River, Arkansas River, or Salt Fork River (all Ps >0.10). Therefore, river flows indicated little statistical significance with year-class strength. However, strong year classes were evident in 1993 and 1995, whereas weak year classes were evident in 1994 and 1996. The Salt Fork River flows (percent of mean flows from February to May) were 375% in 1993 and 129% in 1995 but were lower in 1994 (62%) and 1996 (25%). The Cimarron River also had above normal flows in 1993 (280%) but lower in 1994-1996 (<88%). The Arkansas River had high flows in 1993 (386%) and 1996 (144%) but lower flows in 1994 (93%) and 1995 (73%).

Reproduction. Sampling for early life stages of paddlefish in 1996 and 1997 produced no paddlefish larvae. Low flows (8-92 m^3/s) precluded sampling beyond mid-April in 1996. However, water temperatures (10-18°C) and discharge (75-269 m^3/s) in 1997 were within the range suitable for paddlefish spawning.

River comparisons. In the two years that paddlefish migrated up the rivers, it appeared that there was limited use of the Cimarron River. No spawning substrate was found in that river, and few paddlefish were located (either by tag returns or telemetry tracking; Figure 1). In contrast, paddlefish migrated up the Arkansas River in both 1997 and 1998, extensively using the Kaw Dam tailwaters in 1997 and the Salt Fork River in 1998. Large expanses of suitable gravel were located in the Kaw Dam tailwaters. Smaller patches (usually <50 m in length) of marginal spawning substrate (usually 5 cm - 15 cm dia. gravel) were located in the Salt Fork River. However, the Chikaskia River, which enters the Salt Fork at river km 40, has gravel shoals throughout its lower reach. Paddlefish moved up to the Kaw Dam tailwaters in 1997 presumably because high flows from Kaw Dam directed their movement. In contrast, paddlefish migrations were directed toward the high flows of the Salt Fork River in 1998 (Figure 3). Water temperatures in the Kaw Dam tailwaters were relatively stable and well within the suitable paddlefish spawning range of 10-18°C in spring 1998, whereas the Salt Fork River water temperatures were highly variable in spring 1998 and fluctuated in and out of suitable spawning range (Figure 4).

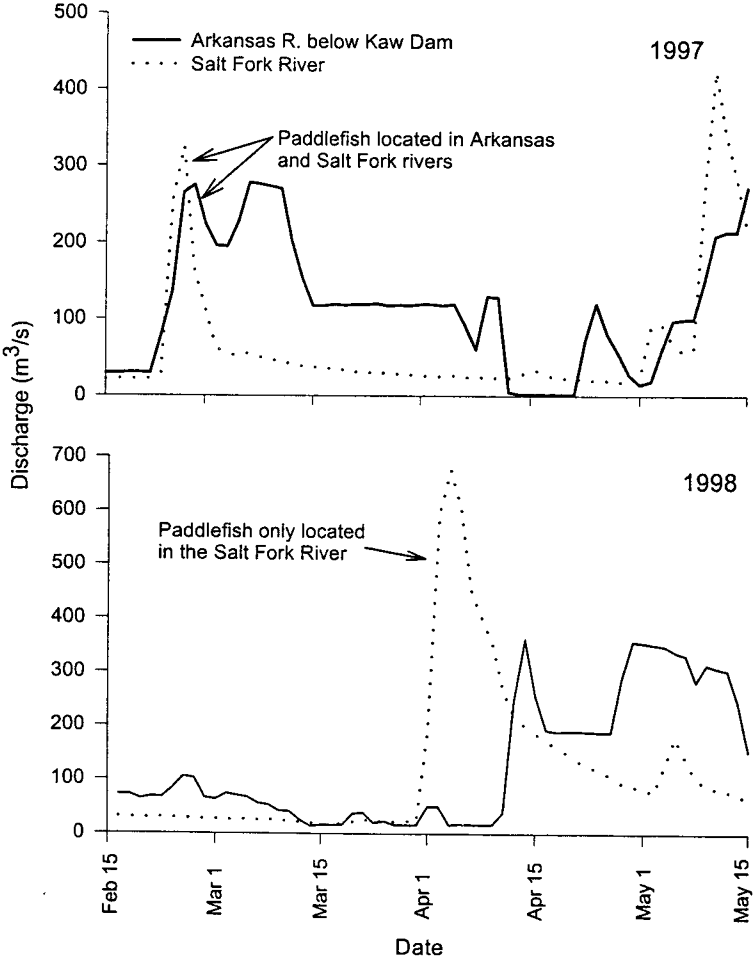

Figure 3. Spring river flows for the Salt Fork and Arkansas rivers (below Kaw Dam) in 1997 and 1998. Arrows indicate that paddlefish were located in both rivers in 1997 and only in the Salt Fork River in 1998.

DISCUSSION

Water flow from tributaries of Keystone Reservoir appear to direct paddlefish migrations. Paddlefish did not migrate upriver to spawn in 1996, presumably because of low river flows. In contrast, paddlefish migrated up the rivers with increased flows in February 1997 and March 1998. In 1998, paddlefish were not found in the Kaw Dam tailwaters. This may have been the result of low discharge from Kaw Dam in mid-March when fish left the reservoir and moved up the Arkansas River. Concurrently, high flows occurred in the Salt Fork River. In addition, anglers report that a snag fishery developed below

Great Salt Plains Dam. In 1997 paddlefish migrated up the Arkansas River and Salt Fork River as flows increased in February in both rivers. Transmitter-tagged paddlefish remained in the rivers until high flows triggered downstream movements back to the reservoir in May and June.

For paddlefish to spawn successfully, there needs to be a suitable combination of water flows, water temperature, spawning substrate (Russell 1986), and possibly photoperiod (Lein and DeVries 1998). In the Keystone Reservoir system, neither water temperatures nor photoperiod appeared to strongly influence paddlefish spring migrations. In 1996, water temperatures were suitable for the fish to move up the rivers in February and March, but low flow and apparently shallow water prevented their migration. In contrast, water temperatures were low (7-8°C) in 1997 and 1998, but paddlefish moved upstream with increased flows. Tag returns in 1997 from the Kaw Dam tailwaters revealed that these fish moved 176 km to Kaw Dam in just a few days. Other studies suggest paddlefish movement rates can be high, exceeding 45 km per day (Russell 1986, Filipek 1990, Paukert 1998).

Paddlefish spawn at water temperatures between 10-20°C (Purkett 1961, Wallus 1986). We did not document paddlefish reproduction in the Keystone Reservoir system. This may have been a reflection of our low sampling effort in this large river system. In South Dakota, Unkenholz (1982) collected only 46 larval paddlefish in 1,122 hours of netting from 1975 to 1981, and Wallus (1986) collected 269 larval paddlefish in eight years of sampling. Despite our failure to collect paddlefish eggs or larvae, we are certain they spawn, or attempt to do so, throughout the system when environmental conditions permit. Mature male and female paddlefish moved up the rivers in the

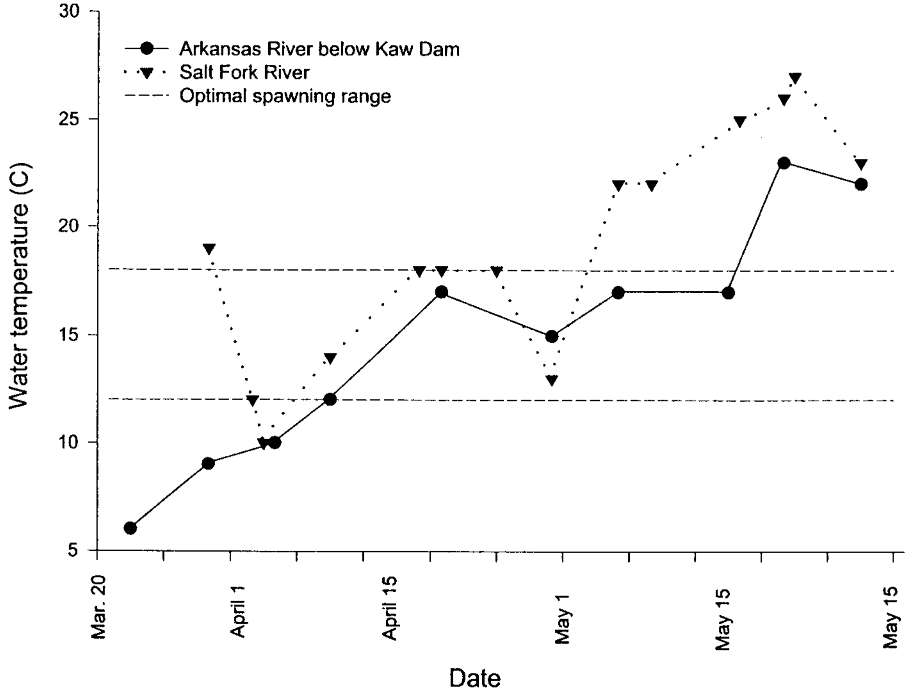

Figure 4. Water temperature for the Salt Fork and Arkansas rivers (below Kaw Dam) during spring 1998. Dashed lines indicate range of suitable temperatures for paddlefish spawning.

Keystone Reservoir system in 1997 and 1998 and remained there for up to two months. Water temperatures were within the suitable spawning range for paddlefish in both years.

Paddlefish migrations indicated high use of the Arkansas River in 1997, a year when high flows from Kaw Dam directed their movements to areas with suitable spawning substrate and presumably more suitable water temperatures. In contrast, high water flows in 1998 directed the paddlefish to the Salt Fork of the Arkansas River, a river with less suitable spawning substrate and water temperatures.

Increased water flows during spring apparently trigger paddlefish to spawn. Wallus (1986) suggested that water flows >275 m^3/s were needed for successful reproduction in Tennessee. Water level rises of 3 - 6 m have also been shown to allow a successful spawn (Purkett 1961, Hoxmeier and DeVries 1997). The Keystone Reservoir system is typical of other prairie river systems throughout the southwest, with highly fluctuating spring flows regulated by impoundments. However, high flows of the duration typically needed for paddlefish spawning do not occur every year. Based on our spring migration studies and year-class evaluations, paddlefish in the Keystone Reservoir system need sustained periods of high water and cooler water temperatures for successful reproduction. In addition, strong year-classes in 1993 and 1995 indicate that the Salt Fork River may have an influence on the reproductive success of paddlefish in the system. In years with strong year classes, the Salt Fork River always had above normal flows. In contrast, weak year-classes were associated with low flows from the Salt Fork River.

Female paddlefish may not spawn annually but may only spawn every four-five years (Russell 1986). Our data indicate that most female paddlefish migrate up the rivers each year during the spawning migration, but they may not successfully spawn. In spring 1997, no paddlefish >1,000 mm EFL were collected in the reservoir. In spring 1998, none of the nine transmitter-tagged females was located in the reservoir, while seven of these females were located in the rivers; all nine were located back in the reservoir in late May. Male paddlefish are capable of spawning every year, but may remain in the reservoir during the spring spawning migration. All six of the transmitter-tagged male paddlefish remained in the reservoir in 1997, and 11 of 15 transmitter-tagged male paddlefish remained in the reservoir in 1998. However, several smaller males were located in the rivers, indicating that there is no distinct difference in the size of males that made the spawning migration.

Although recruitment is variable, it appears that paddlefish reproductive success in the Keystone Reservoir system may be influenced primarily by the Arkansas and Salt Fork rivers. With the regulation of the Arkansas River by Kaw Dam (which alters spring spawning migrations), the Salt Fork River appears to play a vital role in the maintenance of the paddlefish population in the Keystone Reservoir system, and protection of its flow regime and habitat seems important to the survival of the population.

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LITERATURE CITED

Adams, L. A. 1942. Age determination and rate of growth in *Polyodon spathula* by means of the growth rings of the otolith and dentary bone. American Midland Naturalist 28:617-630.

Bonislawsky, P. 1977. Paddlefish investigations. Kansas Forestry, Fisheries, and Game Commission, Dingell-Johnson Final Report, Project F-15-R-30, Topeka.

Filipek, S. 1990. Arkansas paddlefish investigations. Arkansas Game and Fish Commission, Federal Aid in Sport Fish Restoration Project F-42-6 Final Report, Little Rock.

Graham, K. 1997. Contemporary status of the North American paddlefish, *Polyodon spathula.* Environmental Biology of Fishes 48:279-289.

Hoxmeier, R. J. H., and D. R. DeVries. 1997. Habitat use, diet, and population size of adult and juvenile paddlefish in the lower Alabama River. Transactions of the American Fisheries Society 126:288-301.

Lein, G. M., and D. R. DeVries. 1998. Paddlefish in the Alabama River drainage: population characteristics and the adult spawning migration. Transactions of the American Fisheries Society 127:441-454.

Maceina, M. J. 1997. Simple application of using residuals from catch curve regressions to assess year-class strength in fish. Fisheries Research 32:115-121.

Paukert, C. P. 1998. Population ecology of paddlefish in the Keystone Reservoir System, Oklahoma. Master's thesis, Oklahoma State University, Stillwater.

Paukert, C. P., and W. L. Fisher. 1999. Evaluation of paddlefish length distributions and catch rates in three mesh sizes of gill nets. North American Journal of Fisheries Management 19:599-604.

Pitman, V. M. 1991. Synopsis of paddlefish biology and their utilization and management in Texas. Texas Parks and Wildlife Department, Special Report, Austin.

Purkett, C. A. 1961. Reproduction and early development of the paddlefish. Transactions of the American Fisheries Society 90:125-129.

Ricker, W. L. 1975. Computation and interpretation of biological statistics if fish populations. Fisheries Research Board of Canada Bulletin No. 191, Ottawa.

Ruelle, R. and P. Hudson. 1977. Paddlefish (*Polyodon spathula*): growth and food of young of the year and a suggested technique for measuring length. Transactions of the American Fisheries Society 106:609-613.

Russell, T. R. 1986. The biology and life history of the paddlefish - a review. Pages. 2-21 *in* J. G. Dillard, L. K. Graham, and T. R. Russell, editors. The paddlefish: status, management, and propagation. North Central Division, American Fisheries Society Special Publication Number 7, Columbia, Missouri.

SAS Institute. 1996. SAS/STAT user's guide, version 6.11. SAS Institute, Cary, North Carolina.

Unkenholz, D. G. 1982. Paddlefish spawning movements and reproductive success in the Missouri River below Fort Randall Dam, 1979-81. South

Dakota Department of Game, Fish, and Parks, Completion Report, Number 82-3, Pierre.

Unkenholz, D. G. 1986. The effects of dams and other habitat alterations on paddlefish sport fisheries. Pages 54-61 *in* J. G. Dillard, L. K. Graham, and T. R. Russell, editors. The paddlefish: status, management, and propagation. North Central Division, American Fisheries Society Special Publication Number 7, Columbia, Missouri.

Wallus, R. 1986. Paddlefish reproduction in the Cumberland and Tennessee river systems. Transactions of the American Fisheries Society 115:424-428.

Zar, J. H. 1996. Biostatistical analysis, 3rd edition. Prentice-Hall, Inc., Upper Saddle River, New Jersey.

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