

# Paddlefish Egg Deposition in the Lower Yellowstone River, Montana and North Dakota

SHANNON E. MILLER<sup>1</sup>, DENNIS L. SCARNECCHIA, and STEVEN R. FAIN

Department of Fish and Wildlife Resources, University of Idaho,  
Post Office Box 441136, Moscow, ID 83844 (SEM, DLS)  
National Fish and Wildlife Forensics Laboratory, 1490 East Main Street,  
Ashland, OR 97520 (SRF)

**ABSTRACT** -- We used passive egg collectors during May, June, and July of 2003 and 2004 in the lower 50 river kilometers (rkm) of the Yellowstone River, eastern Montana and western North Dakota, to detect egg deposition by spawning paddlefish (*Polyodon spathula*). Sampling yielded 292 eggs (46 in 2003 and 246 in 2004). All egg collections in 2003 occurred on the descending limb of the spring hydrograph but 99% of egg collections in 2004 occurred before the spring hydrograph began to descend. Catch-per-unit-effort (CPUE) in 2004 was about four times that of 2003. A combination of river conditions, in addition to rising or falling discharge levels, might have influenced the difference in timing of egg deposition between years. Water temperatures at time of peak egg CPUE were near 17.0°C in both years; however discharge and sediment levels were different. Although our study did not attempt to describe the entire spatial range of egg deposition, more eggs were found in lower reaches (rkm 13.7 and rkm 26.5) than in upper reaches (rkm 37.0 and rkm 40.2) of similar habitat character. The presence of adequate spawning substrate in the lower 27 rkm of the Yellowstone River might encourage egg deposition and successful paddlefish spawning if annual spring flood-pulses persist.

**Keywords:** paddlefish, *Polyodon spathula*, reproduction, spawning, Yellowstone River.

---

<sup>1</sup>Corresponding author. E-mail address: shannonmiller@vandals.uidaho.edu

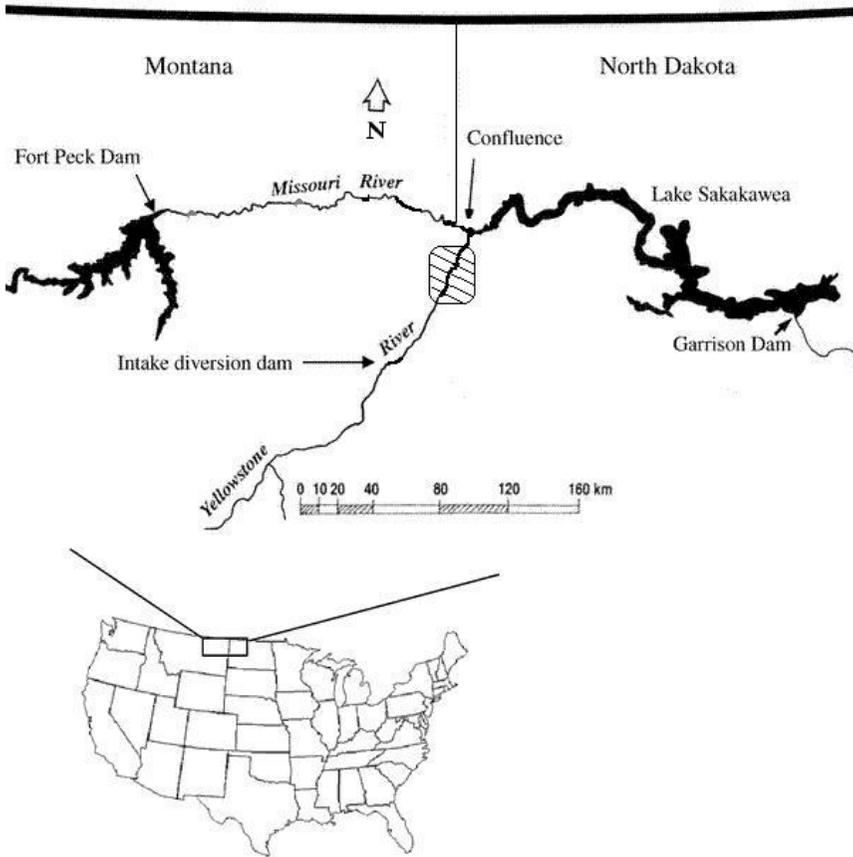
The paddlefish (*Polyodon spathula*) is widely distributed in major rivers of the Missouri and Mississippi basins and select Gulf Coast drainages of the United States (Gengerke 1986). During the past 100 years, the species has been extirpated in four states and has declined in several others. Loss of spawning habitat has been implicated as a major cause of many declines (Graham 1997). Although several states have artificially propagated paddlefish (Graham et al. 1986), locating and preserving the remaining spawning habitat for wild fish are essential for the long-term survival of the species (Carlson and Bonislawsky 1981).

Several studies have used radio-telemetry and mark-recapture techniques to locate paddlefish spawning congregations (Moen et al. 1989, Stancill et al. 2002, Firehammer and Scarnecchia 2006). The strongest documented evidence of spawning is the visual observation by Purkett (1961), who observed a spawning 'rush' over inundated gravel bars in the Osage River, Missouri. Eggs and larvae subsequently were collected after receding water levels exposed the gravel bars. When fertilized, paddlefish eggs develop an adhesive coating, lose buoyancy, adhere to hard substrates, and typically hatch in seven days at water temperatures of about 16°C (Russell 1986).

A combination of environmental factors including discharge, suspended sediment, and water temperature are thought to provide cues for migration and spawning of paddlefish (Pasch et al. 1980, Paukert and Fisher 2001, Firehammer and Scarnecchia 2006). In northern populations, upriver migration of mature paddlefish and subsequent spawning typically is associated with increasing discharges, increasing suspended sediment levels, and water temperatures of 14 to 20°C (Firehammer and Scarnecchia 2006, Miller and Scarnecchia 2008). If an appropriate combination of these factors does not occur, female paddlefish might fail to spawn and reabsorb their eggs (Russell 1986, Scarnecchia et al. 2007).

Although congregations of paddlefish might be indicative of spawning sites and times, direct observation of spawning and collection of eggs or larvae are more reliable means of confirming spawning events. In most cases, the spawning season coincides with periods of high and turbid flows, making direct observations difficult (Russell 1986). Instead, most researchers have collected larvae and eggs to locate spawning areas and document spawning success (Pasch et al. 1980, Wallus 1986).

The Yellowstone River (YR) in eastern Montana and western North Dakota is one of few major quasi-natural spawning areas remaining within the species' geographic range (White and Bramblett 1993; Fig. 1). Penkal (1981) reported 14 paddlefish eggs collected from an 8 km reach of the YR below the Intake Diversion Dam in 1980. Firehammer et al. (2006) collected 84 genetically identified paddlefish eggs at YR river kilometer (rkm) 9.5 and YR rkm 13.5 (where numbers refer to kilometers above the mouth). During the mid 1990's, Gardner (1996) conducted four years of larval paddlefish sampling in the lowermost 114 rkm to the confluence with the Missouri River (a site hereafter referred to as the Confluence) and caught a total of 266 larvae at eight locations.



**Figure 1.** Map of the study area, eastern Montana and western North Dakota. The hatched area indicates that portion of the river sampled for paddlefish eggs in 2003 and 2004.

Paddlefish larvae might move downstream at speeds similar to ambient flows (Wallus 1986). Thus, although larval capture is useful in confirming general spawning areas, egg collection at deposition sites can more accurately identify specific spawning locations. Our study described an effort to identify paddlefish egg deposition in the lower YR during 2003 and 2004. We hypothesized that egg deposition in the YR would not be limited to one area and that river conditions (i.e., discharge, suspended sediment, and water temperature) would be associated with the timing of egg captures.

## STUDY AREA

Total length of the YR is 1,091 km from its headwaters in Yellowstone Park, Wyoming to the Confluence in North Dakota. The drainage basin encompasses 182,325 km<sup>2</sup> of Wyoming, Montana, and North Dakota (White and Bramblett 1993). Large islands, side-channels, and irregular meanders characterize the lowermost 114 km. Sinuosity values range from 1.14 to 1.36 and slope is approximately 0.046% near the Confluence. Gravels dominate the substrate in upper portions of the lower river and give way to sandy bottoms and isolated gravel bars in the last 20 km (White and Bramblett 1993). The hydrograph typically is characterized by a moderate discharge rise in March and April followed by a peak discharge in late May or early June. Mean annual discharge near Sidney, Montana is approximately 362 m<sup>3</sup>/s; maximum recorded instantaneous flow was estimated at 4,502 m<sup>3</sup>/s on June 2, 1921 (United States Geological Survey 2003).

Egg sampling was restricted to the lowermost 50 km of the YR for three reasons. First, larval fish collections made by Gardner (1996) indicated most paddlefish spawning occurs in this portion of the YR. Second, previous migration studies (Firehammer and Scarnecchia 2006) and harvest records (North Dakota Game and Fish Department and Montana Department of Fish, Wildlife, and Parks, unpublished data) suggested that during most years the majority of migrating paddlefish ascend the YR rather than the Missouri River above the Confluence. Third, it was not logistically practical with existing resources to sample both rivers simultaneously.

## METHODS

Our egg collectors consisted of a 0.75 m wide strip of furnace filter material secured around PVC cylinders 0.75 m long and 0.15m in diameter (McCabe and Beckman 1990, Firehammer et al. 2006). A 5.0 kg grappling anchor was attached 0.5 m from one side of the cylinder with a 15 m buoyed float-line trailing the opposite side.

Egg sampling was delineated with a stratified random sample design. A stratum was based on a specific morphological characteristic in which the main channel was constricted into an hourglass shaped riffle-pool sequence. Dredging indicated that these areas provided an abundance of gravel and cobble, substrates previously shown to provide incubation sites for paddlefish eggs (Purkett 1961, Firehammer 2004). Four strata were identified and transects within these areas were then sampled at random. Egg collectors were deployed at YR rkm 9.7, 13.7, 22.5, 26.5, 37.0, and 40.2 from 19 May to 1 July 2003. A typical set of collectors consisted of three collectors evenly spaced perpendicular to the shoreline across the width of the channel with three remaining collectors set in a similar fashion 50

m downstream. Effort at each stratum was increased in 2004 in an attempt to increase the number of eggs collected. Sets of six to twenty collectors were deployed at rkm 13.7, 22.5, 26.5, and 40.2 from 25 May to 2 July 2004.

Depth and time at deployment were recorded for each set of collectors. Due to logistical constraints, deployment of collectors varied from 24 to 72 hours. However, during periods of rapidly increasing discharge, collectors were set for a maximum of 24 hours to avoid entanglement in river debris.

Collectors were inspected visually for the presence of eggs immediately after retrieval. Potential paddlefish eggs were distinguished from most other species by their distinct steel-gray coloration. However, paddlefish eggs are visually indistinguishable from sturgeon (*Scaphirhynchus* spp.) eggs (Pasch et al. 1980). Therefore, potential paddlefish eggs were preserved in 80% ethanol and sent to the National Fish and Wildlife Forensics laboratory in Ashland, Oregon, for genetic identification.

A United States Geological Survey gauging station at YR rkm 47 recorded daily river discharge and suspended sediment levels. Daily water temperatures were recorded with a remote temperature data logger positioned near YR rkm 13.5.

Sampling effort (collector day) was calculated as the number of collectors successfully retrieved from each transect multiplied by hours set divided by 24. Sample day was recorded as the date of retrieval. An attempt was made to set and retrieve collectors on the same dates during 2003 and 2004; however, sampling began approximately one week later in 2004. Collectors were reset immediately after inspection.

Two sets of variables related to river conditions were recorded for each retrieval day: 1) values of suspended sediment, water temperature, and discharge recorded at the gauging station and the temperature logger on the day of collector retrieval, and 2) the absolute value of the difference of these variables between the day of retrieval and day of deployment. We hypothesized positive linear relationships among suspended sediment, discharge, and egg catch-per-unit-effort (CPUE), but a non-linear relationship between water temperature and egg CPUE. Therefore, water temperatures were assigned a ranking based on the optimum temperatures for paddlefish spawning reported in the literature (Pasch et al. 1980, Wallus et al. 1990, Pitman 1991, Mims et al. 1999). Optimum temperatures in the range from 16 to 18°C were assigned the highest rank (3). Temperatures two degrees above or below the optimum were assigned the second highest rank (2). Temperatures more than two degrees higher or lower than the optimum range were assigned the lowest rank (1).

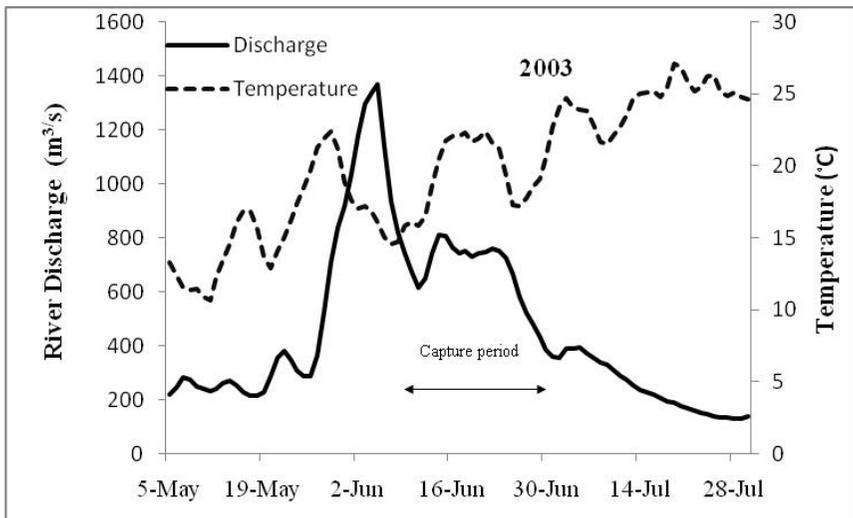
The non-normal distribution of the catch data and presence of both continuous independent variables (discharge and suspended sediment) and an ordinal independent variable (ranked water temperature) did not allow for testing the data with parametric regression models. Therefore, we treated egg CPUE as presence or absence data and used step-wise logistic regression to test for associations

between egg catches and river conditions. In the event that logistic regression would not identify any significant associations between river conditions and egg catches at the  $\alpha = 0.05$  level of significance, a higher significance level (0.35) was established in the stepwise procedure as suggested by Hosmer and Lemeshow (2000). This relaxation of significance level in the stepwise procedure increased the probability that marginally significant variables could enter the model and the relative importance of the variables could be evaluated. However, only variables that met the 0.05 level of significance were allowed to remain in the model for hypothesis testing.

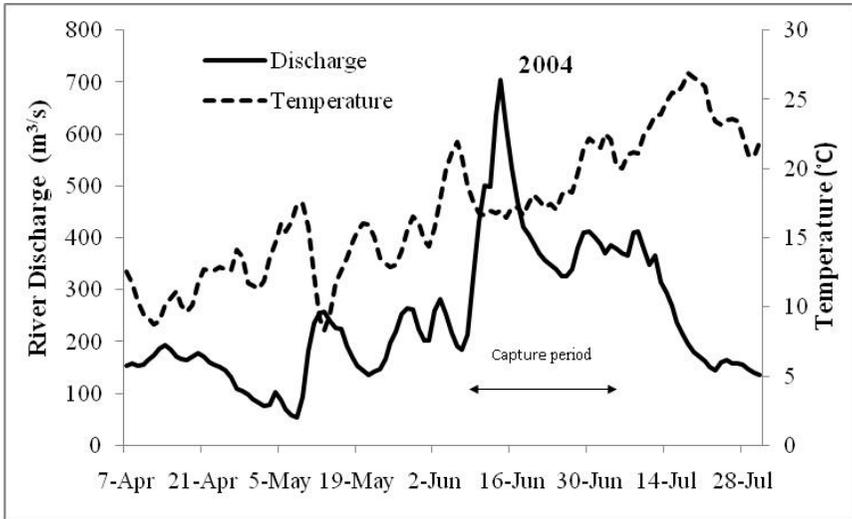
## RESULTS

Spring discharge during 2003 peaked at 1,370 m<sup>3</sup>/s on 5 June (Fig. 2). Peak discharge in 2004 (14 June) occurred nine days later than in 2003 and was approximately half the magnitude (705 m<sup>3</sup>/s) of the previous year (Fig. 3). Low flow conditions were especially pronounced during May 2004 when mean daily discharge (167.5 m<sup>3</sup>/s) was at its lowest recorded level for May since 1961 (95 year average = 512.0 m<sup>3</sup>/s).

Higher mean daily water temperatures were recorded during May and June 2003 (mean = 17.0°C) than in May and June 2004 (mean = 15.9°C). Suspended



**Figure 2.** Spring discharges (m<sup>3</sup>/s) and temperatures (°C) during 2003 for the Yellowstone River (YR) near river kilometer 40.2. The horizontal arrow indicates period during which paddlefish eggs were collected.



**Figure 3.** Spring discharges ( $m^3/s$ ) and temperatures ( $^{\circ}C$ ) during 2004 for the Yellowstone River (YR) near river kilometer 40.2. The horizontal arrow indicates period during which paddlefish eggs were collected.

sediment levels were greater in 2003 than in 2004 (Fig. 4 and Fig. 5). Mean daily suspended sediment measurements for May and June 2003 (860.0 mg/l) were nearly twice that for the same months in 2004 (433.0 mg/l).

Of the 57 acipenseriform eggs collected during 2003, 46 were identified genetically as paddlefish and one as a sturgeon. Genetic differentiation of 10 eggs was not possible. Of the 289 acipenseriform eggs collected during 2004, 246 were identified positively as paddlefish and four as *Scaphirhynchus* spp. Genetic differentiation of 31 eggs was not possible. All captured eggs exhibited an adhesive coating and probably had been fertilized prior to adhering to the collectors.

A four-fold increase in total egg CPUE was observed in 2004 (0.22 eggs per collector-day) compared to 2003 (0.05 eggs per collector-day). In 2003, transects at rkm 26.5 yielded the highest CPUE at 0.13 eggs per collector-day. Sample transects at rkm 9.7, 13.7, 37.0, and 40.2 yielded CPUE values of 0.06, 0.09, 0.01 and 0.01, respectively. In 2004, transects at rkm 13.7 yielded the highest CPUE at 0.41 eggs per collector-day. No paddlefish eggs were collected from rkm 40.2 during 2004 (Table 1).

In 2003, all egg captures occurred during the descending limb of the spring hydrograph (Fig. 4). However, debris in the river from 31 May to 4 June, 2003

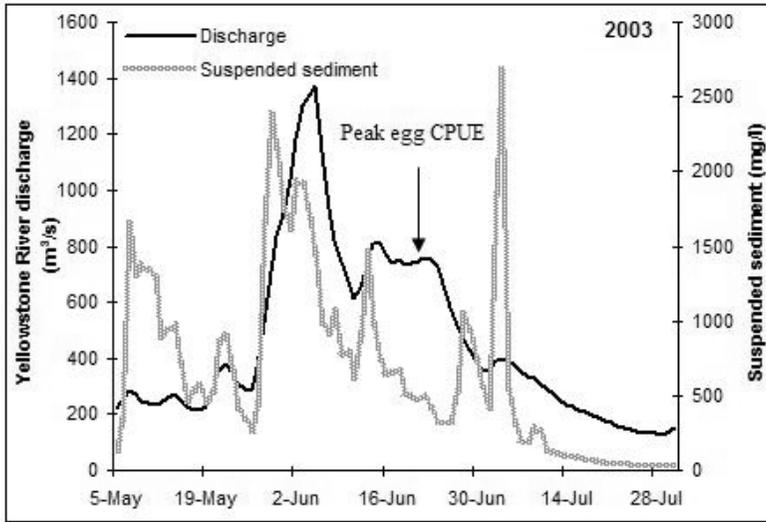


Figure 4. Spring discharges (m<sup>3</sup>/s) and suspended sediment (mg/l) for the Yellowstone River near river kilometer 40.2 during 2003 with peak paddlefish egg collection date indicated.

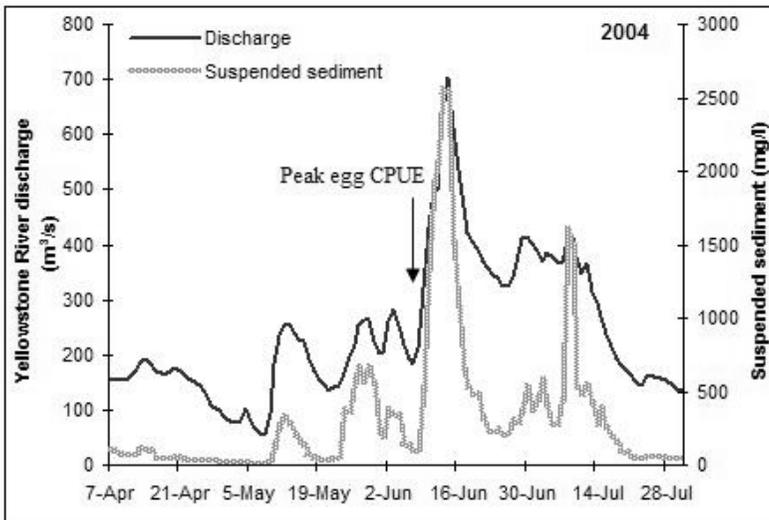


Figure 5. Spring discharges (m<sup>3</sup>/s) and suspended sediment (mg/l) for the Yellowstone River near river kilometer 40.2 during 2004 with peak paddlefish egg collection date indicated.

prevented sampling during this period. Egg CPUE peaked on 26 June when discharge was approximately 580 m<sup>3</sup>/s and suspended sediment was 322 mg/l. Eggs were first collected on 13 June shortly after discharge declined sharply from a peak of over 1,360 m<sup>3</sup>/s. Eggs were last captured on 1 July when discharge was 360 m<sup>3</sup>/s. In contrast to the 2003 season, 99% of eggs in 2004 were captured before the spring hydrograph began to descend (Fig. 5). Egg CPUE peaked on 11 June when discharge was approximately 500 m<sup>3</sup>/s and suspended sediment was 1920 mg/l. Eggs were first collected on 1 June when discharge was 201 m<sup>3</sup>/s. Eggs were last captured on 2 July when discharge was 391 m<sup>3</sup>/s.

Mean daily water temperatures during the 2003 capture period ranged from 17.2 to 22.7°C. Peak CPUE occurred on 26 June when mean daily water temperature was at its lowest point during the capture period (17.2°C). The thermal regime during the 2004 capture period exhibited a broader range of temperatures (14.4 to 22.2°C) than that of 2003. However, water temperature at peak CPUE in 2004 (16.8°C) was similar to the temperature at peak CPUE in 2003 (17.2°C).

Specific discharge, suspended sediment, and temperature characteristics were associated with the highest paddlefish egg captures in both 2003 and 2004. In most cases, egg captures occurred during periods of rapidly changing flows and suspended sediment loads and declining temperatures. In contrast, most catch rates of zero were made during periods of stable river conditions (Table 2). Significant, positive correlations existed between suspended sediment and discharge ( $N = 25$ ,  $r = 0.54$ ,  $p < 0.01$ ) and between changes in discharge and changes in suspended sediment ( $N = 25$ ,  $r = 0.42$ ,  $p = 0.037$ ). Change in discharge (logistic regression;  $p = 0.13$ ) and change in temperature ( $p = 0.32$ ) had stronger associations with egg catches than did other measures of river conditions such as ranked temperatures, discharges, suspended sediment, and changes in suspended sediment ( $p > 0.40$ ). However, none of the variables remained in the model at the 0.05 significance level.

## DISCUSSION

The success of collecting paddlefish eggs (20 of 46 eggs in 2003 and 182 of 246 eggs in 2004) in the lowermost 13.7 rkm of the YR was consistent with previous investigations. Gardner (1996) conducted larval paddlefish sampling in the lower YR and reported the greatest larval densities below rkm 20. Firehammer et al. (2006) used a similar egg collection technique as in the present study and collected 84 eggs at two locations (YR rkms 9.5 and 13.7). They considered rkm 13.7 to be a probable egg deposition site because the clumped distribution of eggs captured at this site indicated the eggs likely were released by nearby females. In the first year (2003) of our study, however, CPUE was highest upriver at rkm 26.5 rather than at rkm 13.7. Paddlefish egg deposition probably also occurred at several other lower river locations.

**Table 1.** Summary of paddlefish and sturgeon egg collections from the Yellowstone River, Montana and North Dakota during 2003 and 2004.

River kilometer	Stratum	Year	Number of eggs collected	Effort (collector-days)	Eggs per collector-day (SE)
9.7	1	2003	11	176.4	0.06 (0.13)
9.7	1	2004	0	0	NA
13.7	1	2003	20	228.5	0.09 (0.33)
13.7	1	2004	182	445.9	0.41 (0.88)
22.5	2	2003	0	78.0	0.00
22.5	2	2004	0	0	NA
25.0	2	2003	0	81.1	0.00
25.0	2	2004	12	132.3	0.09 (0.15)
26.5	3	2003	13	97.5	0.13 (0.25)
26.5	3	2004	52	366.9	0.14 (0.21)
37.0	4	2003	1	118.3	0.01 (0.03)
37.0	4	2004	0	0	NA
40.2	4	2003	1	85.1	0.01 (0.19)
40.2	4	2004	0	67.7	0.00

Results from our study indicated egg deposition following an increase in spring discharge as previously suggested by Firehammer et al. (2006). However, a definitive link between egg deposition and the timing and magnitude of the YR hydrograph was difficult to establish. In 2003, for example, all paddlefish eggs were collected on the descending limb of the hydrograph whereas in 2004 nearly all eggs were collected on the ascending limb (Fig. 4 and Fig. 5). Several possible explanations exist for this difference. First, the sampling might have failed to adequately characterize the entire temporal range of spawning. This interpretation is not supported, however, by larval paddlefish captures reported in a concurrent study (Montana Department of Fish Wildlife and Parks 2005), where larval captures peaked near the mouth of the YR 13 days after the peak egg CPUE observed in our study. Given the range of water temperatures during this period and the out-migration distance between larval capture locations and egg capture locations, the elapsed time between peak egg capture and peak larval capture is consistent with hatching and drift times previously reported for paddlefish (Purkett 1961, Russell 1986). These data suggested that our collection of eggs did occur at the peak period of the spawn.

A second possibility is that factors other than rising or falling discharges such as temperature might have influenced the timing of egg deposition. For example, water temperatures at time of peak egg CPUE were similar for both years (17.2 in 2003, 16.8 in 2004), but discharge and suspended sediment levels were substantially different. Water temperature might thus have a separate but critical influence on the timing of spawning.

**Table 2.** Association between presence or absence of paddlefish eggs and changes in river conditions ( $\Delta$  discharge, suspended sediment, or temperature) in the Yellowstone River, Montana and North Dakota during 2003 and 2004.

Sample Date	Year	Presence of eggs (Y/N)	$\Delta$ Discharge (+/-)	$\Delta$ Suspended sediment (+/-)	$\Delta$ Temperature (+/-)
23 May	2003	N	+	+	+
27 May	2003	N	+	-	+
30 May	2003	N	+	+	+
5 June	2003	N/A	N/A	N/A	N/A
10 June	2003	N	-	-	-
13 June	2003	Y	+	+	+
17 June	2003	N	no change	-	+
20 June	2003	Y	-	-	-
26 June	2003	Y	-	no change	-
1 July	2003	Y	-	+	+
23 May	2004	N/A	N/A	N/A	N/A
28 May	2004	N	+	+	+
1 June	2004	Y	-	-	-
5 June	2004	Y	+	-	+
8 June	2004	N	-	-	-
11 June	2004	Y	+	+	-
15 June	2004	N	-	-	no change
23 June	2004	N	-	-	+
28 June	2004	Y	-	+	+
2 July	2004	Y	+	+	+

A third possibility is that a change in discharge reached an appropriate threshold to cue spawning, and subsequent discharge levels were of less importance. In this scenario, the hydrograph continued upward after spawning occurred in 2004, whereas it descended after spawning occurred in 2003. The direction of the hydrograph when the eggs were sampled would therefore not be of any causal significance.

A fourth possible reason that egg captures occurred on the hydrograph ascendancy in 2004 but the decendancy in 2003 is that an initial rise in discharge might not result in immediate, complete spawning. Fractional spawning has been reported in paddlefish (Friberg 1972) and fish might not have completed spawning before discharge began to drop in 2003.

We observed greater egg CPUE in 2004, a low-flow year, than in 2003, a high-flow year. These results contrast with previous research (Wallus 1986) suggesting better paddlefish reproduction in high-flow years than low-flow years. The four-fold increase in egg CPUE observed in 2004 might have been the result of more efficient sampling during a year of lower peak flow. Lower water levels in 2004 might have encouraged paddlefish to spawn in fewer areas rather than in widespread areas where perhaps no collectors were deployed. Moreover, effort was considerably less (80 collector-days versus 226 collector-days) during the five day period of highest discharge in 2003 (June 2-6) than in 2004 (June 11-15). These differences were due to a larger amount of debris in the YR during 2003 that dislodged and damaged many collectors during peak flows.

Possibly greater reproduction actually occurred in 2003, the high-flow year, but was not limited to areas below YR rkm 50. Distributions of telemetered paddlefish from a concurrent study (Miller and Scarnecchia 2008) did not indicate substantial congregations of fish below YR rkm 50 during the period of highest egg collections in either year. In 2003, 70% of all telemetered paddlefish were contacted in the Missouri River above the Confluence (MRAC), not the YR during this period. Likewise, only one telemetered female was contacted within 20 rkm of egg sample transects immediately preceding or during the four day period of highest egg CPUE in 2004. In addition, juvenile monitoring along standard transects in the headwaters of Lake Sakakawea observed higher densities of young-of-year paddlefish in 2003 (87 fish) than 2004 (30 fish; North Dakota Game and Fish Department, unpublished data). Future research should also consider the reproductive contribution of fish entering the MRAC in addition to fish entering the lower YR.

Results from our study provided useful base-line information for future studies on paddlefish reproductive ecology. First, total egg catches (292 eggs), though low in comparison to catch rates of other life stages, were higher than documented in previous studies on paddlefish egg collections in the YR and elsewhere (e.g., 17 eggs, Pasch et al. 1980; 14 eggs, Penkal 1981; 41 eggs, Wallus 1986; 84 eggs, Firehammer et al. 2006). This suggests that the tubular egg collectors described by Firehammer et al. (2006) are an effective gear for collecting paddlefish eggs in the YR. Second, results did confirm greater egg deposition in lower reaches (rkm 13.7 and rkm 26.5) than in higher reaches (rkm 37.0 and rkm 40.2) with similar habitat characteristics. Third, our results showed an association among changes in river conditions (discharges, suspended sediment levels, and water temperatures) and egg catch rates. Further study of this relationship would provide beneficial information for the long-term perpetuation of the Yellowstone River-Lake Sakakawea paddlefish population and paddlefish populations elsewhere.

### ACKNOWLEDGMENTS

We thank G. Power, F. Ryckman, and S. Shefstad of the North Dakota Game and Fish Department, K. McDonald and B. Snyder of the Montana Department of Fish, Wildlife, and Parks, and J. Firehammer of the University of Idaho for providing logistical support and technical insight. T. Larsen and T. Miller assisted in fieldwork. We also thank K. Cain, D. Graden, J. Nagler, and J. Osiensky for reviewing our manuscript. Our project was funded by the Montana Department of Fish, Wildlife, and Parks with additional logistical support provided by the North Dakota Game and Fish Department.

### LITERATURE CITED

- Carlson, D. M., and P. S. Bonislawsky. 1981. The paddlefish (*Polyodon spathula*) fisheries of the Midwestern United States. *Fisheries* 6(2):17-27.
- Firehammer, J. A. 2004. Spawning migration of adult paddlefish *Polyodon spathula* of the Yellowstone-Sakakawea stock in the Yellowstone and Missouri rivers, North Dakota and Montana. Ph.D. Dissertation, University of Idaho, Moscow.
- Firehammer, J. A., and D. L. Scarnecchia. 2006. Spring migratory movements by paddlefish in natural and regulated segments of the Missouri and Yellowstone rivers, North Dakota and Montana. *Transactions of the American Fisheries Society* 135:200-217.
- Firehammer, J. A., D. L. Scarnecchia, and S. R. Fain. 2006. Modification of a passive gear to sample paddlefish eggs in sandbed reaches of the lower Yellowstone River. *North American Journal of Fisheries Management* 26:63-72.
- Friberg, A. 1972. Investigation of paddlefish populations in South Dakota and development of management plans. South Dakota Department of Game, Fish, and Parks, Federal Aid in Fish Restoration Project F-15-R-7, Study 9, Pierre, South Dakota.
- Gardner, W. M. 1996. Yellowstone River paddlefish spawning study. Montana Department of Fish, Wildlife and Parks. Job Progress Report, Project F-78-R-2, Job III-E, Helena, Montana.
- Gengerke, T. W. 1986. Distribution and abundance of paddlefish in the United States. Pp. 22-35 in *The paddlefish: status, management and propagation*. (J. G. Dillard, L. K. Graham, and T. R. Russell, editors). American Fisheries Society, North Central Division, Special Publication 7, Bethesda, Maryland.
- Graham, K. 1997. Contemporary status of the North American paddlefish, *Polyodon spathula*. *Environmental Biology of Fishes* 48:279-289.

- Graham, L. K., E. J. Hamilton, T. R. Russell, and C. Hicks. 1986. The culture of paddlefish: a review. Pp. 78-94 in *The paddlefish: status, management and propagation*. (J. G. Dillard, L. K. Graham, and T. R. Russell, editors). American Fisheries Society, North Central Division, Special Publication 7, Bethesda, Maryland.
- Hosmer, D. W., and S. Lemeshow. 2000. *Applied logistic regression*, Second edition. John Wiley and Sons, Hoboken, New Jersey.
- McCabe, G. T., and L. G. Beckman. 1990. Use of an artificial substrate to collect white sturgeon eggs. *California Fish and Game* 76:225-234.
- Miller, S. E., and D. L. Scarnecchia. 2008. Adult paddlefish migrations in relation to spring river conditions of the Yellowstone and Missouri rivers, Montana and North Dakota, USA. *Journal of Applied Ichthyology* 24:221-228.
- Mims, S., W. Shelton, F. Wynne, and R. Onders. 1999. Production of paddlefish. Southern Regional Aquaculture Center, Stoneville, Mississippi.
- Moen, C. T., D. L. Scarnecchia, and J. S. Ramsey. 1989. Paddlefish movements and habitat use in Pool 13 of the Upper Mississippi River during abnormally low river stages and discharges. *North American Journal of Fisheries Management* 12:744-751.
- Montana Department of Fish, Wildlife and Parks. 2005. Annual Report for 2004 of the Upper Basin Pallid Sturgeon Recovery Workgroup, Helena, Montana.
- Pasch, R. W., P. A. Hackney, and J. A. Holbrook Jr. 1980. Ecology of paddlefish in Old Hickory Reservoir, Tennessee, with emphasis on first-year life history. *Transactions of the American Fisheries Society* 109:157-167.
- Paukert, C. P., and W. L. Fisher. 2001. Spring movements of paddlefish in a prairie reservoir system. *Journal of Freshwater Ecology* 16:113-123.
- Penkal, R. F. 1981. Life history and flow requirements of paddlefish, shovelnose sturgeon, channel catfish and other fish in the lower Yellowstone River system. Job Progress Report, Montana Department of Fish, Wildlife and Parks, Helena, Montana.
- Pitman, V. 1991. Synopsis of paddlefish biology and their utilization and management in Texas. Special Report. Texas Parks and Wildlife Department, Fisheries and Wildlife Division, Inland Fisheries Branch, Austin, Texas.
- Purkett, C. A. 1961. Reproduction and early development of the paddlefish. *Transactions of the American Fisheries Society* 90:125-129.
- Russell, T. R. 1986. Biology and life history of the paddlefish - a review. Pp. 2-18 in *The paddlefish: status, management and propagation*. (J. G. Dillard, L. K. Graham, and T. R. Russell, editors). American Fisheries Society, North Central Division, Special Publication 7, Bethesda, Maryland.
- Scarnecchia, D. L., L. F. Ryckman, Y. Lim, G. J. Power, B. J. Schmitz, and J. A. Firehammer. 2007. Life history and the costs of reproduction in northern Great Plains paddlefish (*Polyodon spathula*) as a potential framework for other acipenseriform fishes. *Reviews in Fisheries Science* 15:211-263.

- Stancill, W., G. R. Jordan, and C. P. Paukert. 2002. Seasonal migration patterns and site fidelity of adult paddlefish in Lake Francis Case, Missouri River. *North American Journal of Fisheries Management* 22:815-824.
- United States Geological Survey. 2003. Water resources data for the Yellowstone River near Sidney MT. <http://waterdata.usgs.gov/mt/nwis/uv?06329500>.
- Wallus, R. 1986. Paddlefish reproduction in the Cumberland and Tennessee river systems. *Transactions of the American Fisheries Society* 115:424-428.
- Wallus, R., B. Yeager, and T. Simon. 1990. Reproductive biology and early life history of fishes in the Ohio River drainage, Volume I: Acipenseridae through Esocidae. Tennessee Valley Authority, Chattanooga, Tennessee.
- White, R. G., and R. G. Bramblett. 1993. The Yellowstone River - its fish and fisheries. Pp. 396-413 *in* Restoration planning for the rivers of the Mississippi River ecosystem. (L. Heese, C. Stalnaker, N. Benson, and J. Zuboy, editors). United States Department of the Interior, National Biological Survey, Washington, District of Columbia.

*Received: 25 February 2008*

*Accepted: 17 August 2009*

*Associate Editor for Ichthyology: Brian Blackwell*