North American Journal of Fisheries Management 26:63–72, 2006

DOI: 10.1577/M05-012.1

[Management Brief]

Modification of a Passive Gear to Sample Paddlefish Eggs in Sandbed Spawning Reaches of the Lower Yellowstone River

JON A. FIREHAMMER* AND DENNIS L. SCARNECCHIA
Department of Fish and Wildlife Resources, University of Idaho, Moscow, Idaho 83844-1136, USA

STEVEN R. FAIN
National Fish and Wildlife Forensics Laboratory, 1490 East Main Street, Ashland, Oregon 97520, USA

Abstract.—A passive sampling technique was developed to collect eggs and confirm potential spawning sites for paddlefish *Polyodon spathula* in sandbed reaches of the lower Yellowstone River, Montana and North Dakota. In 2000, egg collectors modeled after the mats used in sturgeon research proved difficult to retrieve from the riverbed and did not collect eggs. In 2001 and 2002, tubular egg collectors designed to remain suspended off the bottom were successfully retrieved 97% of the time and collected 130 acipenseriform eggs along suspected spawning sites (99% of differentiable eggs were genetically confirmed as paddlefish). In both years, eggs were typically collected in mid-June after peak periods of Yellowstone River discharge and at river temperatures of 15–22°C. During collection periods in 2001 and 2002, 20% and 45% of retrieved tubes, respectively, had at least one egg, and 84% of all eggs were found on tubes retrieved from the channel thalweg. Although eggs were spatially distributed in a clumped manner at sample sites, the mean number of eggs per tube was low (<4), suggesting either collector inefficiency, the inability to deploy collectors in close proximity to concentrations of spawning paddlefish, or the widespread distribution of spawning effort over the lower Yellowstone River.

Paddlefish *Polyodon spathula* occupy large river habitats within the Mississippi River system and selected Gulf slope drainages. Although found within 22 states of the central and southeastern United States, their range and abundance have diminished from historic distributions, even in areas once considered strongholds (Hoxmeier and DeVries 1996; Graham 1997). The declines have been attributed mainly to large river modifications that have not only diminished productive rearing habitats but created conditions less favorable for successful reproduction (Sparrowe 1986). Impoundments have disrupted cues used by spawning paddlefish through the alteration of spring thermal and flow regimes and have inundated and blocked access to suitable spawning habitat (Unkenholz 1986; Hesse and Mestl 1993). Because of poor natural recruitment of many stocks and the potential for spawning reaches to be further altered through ongoing large river modifications, an understanding of habitat requirements for spawning paddlefish is needed.

The general requirements for successful reproduction in the wild have been described (Jennings and Zigler 2000). Paddlefish have been found to broadcast their eggs over well-swept gravel bars coincident with periods of rising temperature and discharge during the spring (Purkett 1961; Pasch et al. 1980; Russell 1986). Gravel–rubble substrate provides suitable attachment sites for the adhesive eggs, whereas adequate current velocity prevents siltation during the incubation period (6–12 d depending on temperature; Yeager and Wallus 1982). Spawning habitat has typically been identified within tailwater reaches, where dams tend to concentrate paddlefish during the spring (Pasch et al. 1980; Wallus 1986; Lein and DeVries 1998). However, detailed studies investigating spawning habitat along unregulated rivers are few, and spawning reaches have not been delineated for most stocks (Jennings and Zigler 2000).

Sexually mature, migratory paddlefish of the Yellowstone–Sakakawea stock of eastern Montana and western North Dakota are found along the lower Yellowstone River during the spring spawning period (Robinson 1966; Rehwinkel 1978). Although larval collections have demonstrated paddlefish reproduction in the lower river reaches (Gardner 1996; Liebelt 1996), spawning sites have not yet been identified. Whether sites are confined to specific reaches or are widely scattered is not known; however, preserving existing spawning habitat requires determining the distribution of these sites along the lower Yellowstone River.

Various techniques have been used to identify paddlefish spawning habitat. Purkett (1961) first identified spawning sites along the Osage River, Missouri, as receding water levels revealed exposed eggs along gravel bars. Active methods such as plankton nets or epibenthic sleds have also been used to identify spawning events along various river systems

* Corresponding author: fire0983@uidaho.edu

Received January 22, 2005; accepted September 27, 2005
Published online January 5, 2006

(Pasch et al. 1980; Wallus 1986; Hesse and Mestl 1993). However, these methods have been more successful in sampling larvae than eggs. In addition, the capture of larval fish may not accurately identify the location of spawning sites because of variable larval drift rates.

Artificial substrate mats have proven to be an effective technique for determining the fine-scale location of spawning sites for various sturgeon populations (Marchant and Shutters 1996; Sulak and Clugston 1998; Fox et al. 2000; Paragamian et al. 2001; Perrin et al. 2003; Duncan et al. 2004). Similar to paddlefish eggs, the highly adhesive sturgeon eggs sink after they are broadcast by spawning adults. As a result, eggs deposited on mats positioned along the river bottom presumably have been spawned in the vicinity of the mats. Mats may be more likely to detect spawning events than active sampling methods because they can be deployed continuously for periods as long as several days. In addition, mats may be less likely to get entangled along bottom obstructions, and can be deployed in areas where high current velocities may prevent the use of other sampling techniques. Although mats have proven effective in locations where substrate is relatively stable, it was unknown if they would be effective in the lower Yellowstone River, which is characterized by unstable, shifting substrate. This study was conducted along the lower Yellowstone River during paddlefish spawning periods of 2000 through 2002 to determine whether artificial substrate collectors could be used as an effective sampling technique to collect eggs and confirm suspected spawning reaches.

Study Area

Paddlefish from the Yellowstone–Sakakawea stock rear in Lake Sakakawea, a 156,000-ha Missouri River impoundment in western North Dakota created by the closure of Garrison Dam in 1953. Adults that are reproductively ripe migrate upriver out of the reservoir during spring; many ascend into the lowermost 110 km of the Yellowstone River, a quasi-natural stretch that extends upriver from its confluence with the Missouri River (hereafter referred to as the Confluence) to the Intake Diversion Dam near Glendive, Montana (Figure 1). The 70-km reach of the river below Intake contains multiple islands and alluvial channel bars with substrate consisting primarily of cobble and gravel. Along the lowermost 40 km of the river, sand replaces gravel as the predominant substrate, although in-channel features remain common (Bramblett and White 2001). Because the Yellowstone River remains unregulated, it has retained a natural hydrograph with high levels of discharge and sediment load during the spring freshet. Average discharge has been 707 m^3/s and average suspended sediment has been 1,231 mg/L at river kilometer (rkm) 47 over May and June for flow years 1972–1995, the maximum daily levels attaining 2945 m^3/s and 26,800 mg/L, respectively (U.S. Geological Survey, Montana water resource and streamflow data homepage [http://mt.water.usgs.gov/index], 2003).

Methods

Field techniques.—Because the intent of the study was to explore the effectiveness of egg collectors, sample sites were not randomly distributed over the entire length of the lower Yellowstone River but were chosen to maximize the likelihood of collecting eggs. Based on densities of larval paddlefish collected in bottom-drifted plankton nets along the lower 30 km (Gardner 1993, 1995, 1996), potential spawning sites were identified at rkm 9.5, 13.5, 21.5, and 25.5 (Figure 1). A summary of the physical characteristics of all four sites is provided in Table 1. Although substrate consisted primarily of sand along most of the lower 30 rkm, substrate samples indicated that gravel was present at all four sites, and tactile sampling with a long-handled wooden probe indicated that cobble, boulders, or bedrock was present at the three upriver sites (Figure 1). Additionally, during an ongoing radiotelemetry study, concentrations of paddlefish had been observed in the vicinity of all four sites, which supports the potential of these sites as spawning reaches.

Egg collectors were deployed from May 25 to June 16, from May 28 to June 22, and from May 24 to June 27 in 2000, 2001, and 2002, respectively. Dates of first deployment of egg collectors were determined by using a combination of the following information: (1) time periods when paddlefish larvae were first collected during previous years; (2) the rise of water temperatures above 10°C, the lower spawning threshold reported for paddlefish (Crance 1987; Jennings and Zigler 2000); and (3) the appearance of ovulated eggs in adult paddlefish harvested from Missouri and Yellowstone Rivers. Sampling was discontinued when tagged fish from an on-going telemetry study were no longer contacted in the river (indicating descent into the reservoir and probable cessation of spawning activity) and when water temperatures exceeded 23°C, the upper thermal limit reported for spawning paddlefish (Hoxmeier and DeVries 1997).

Egg collectors deployed in 2000 were mats of artificial substrate designed and used successfully by McCabe and Beckman (1990) for collecting white sturgeon *Acipenser transmontanus* eggs in the Columbia River. Furnace-filter material, which provided a rough surface for egg attachment, was fitted and

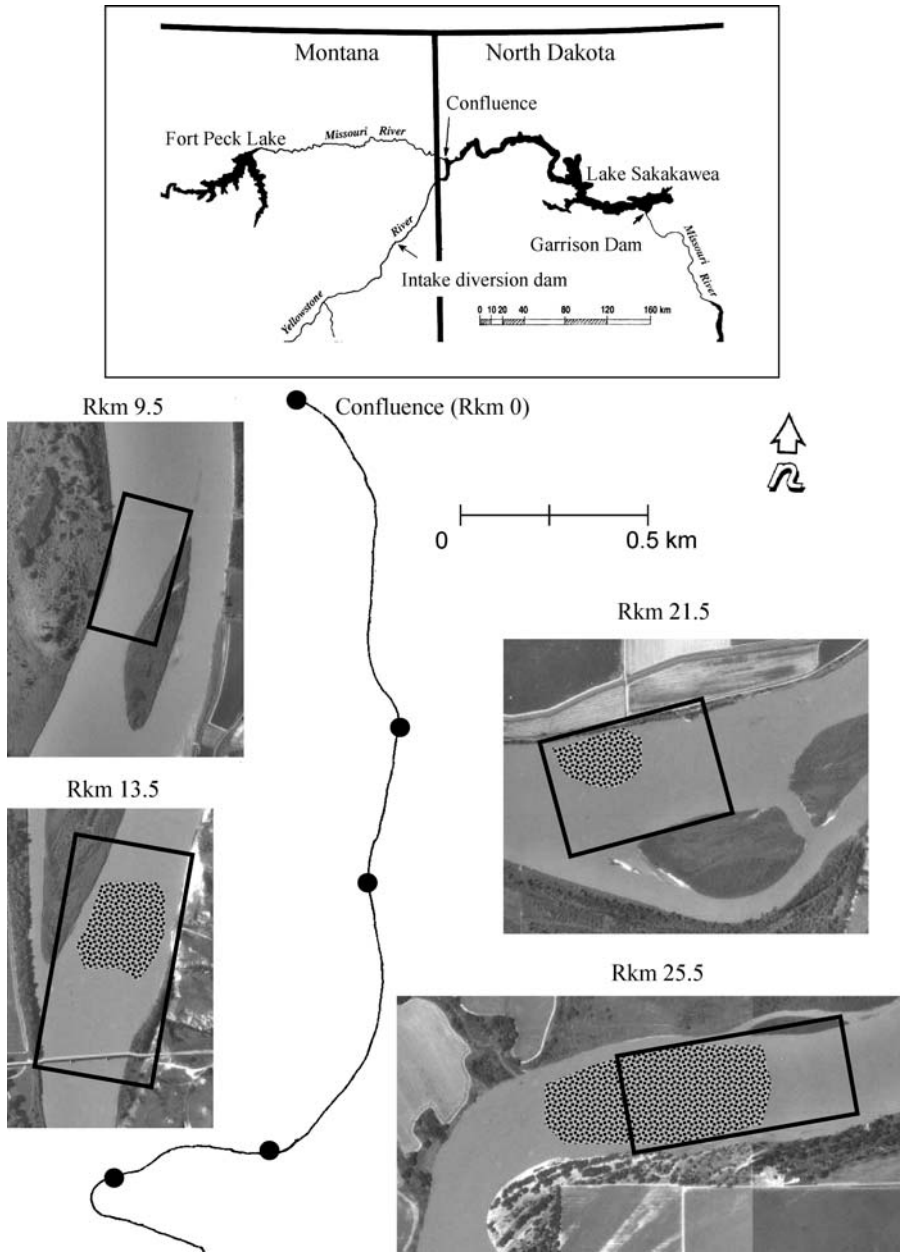

FIGURE 1.—Map of the lower Yellowstone and Missouri rivers, Montana and North Dakota (top) and inset showing the locations along the Yellowstone River (solid circles) where acipenseriform eggs were sampled during 2000–2002. Rectangular boxes on the enlarged aerial photos designate the areas in which egg collectors were deployed; the stippled areas indicate the locations of gravel–rubble shoals within sample sites. The distance scale applies to the aerial photos.

secured between complementary 0.60 × 0.75 m angle-iron frames. Each mat was equipped with a 4.5–5.0-kg rebar grapple anchor and a buoyed hauling line. Mats were deployed at rkm 13.5, 21.5, and 25.5 in the spring of 2000. The use of this mat design was permanently discontinued after June 16 because many of the mats were buried by sand or silt and could not be retrieved.

In 2001 and 2002, a tubular type of collector was constructed that would minimize prolonged contact with the river bottom and reduce the possibility that fine sediments would bury the collector. A single strip

TABLE 1.—Summary of the physical characteristics of the four river sites sampled for paddlefish eggs along the lower Yellowstone River during 2000–2002.

Sample site	Rkm	Length (km)	Average width (km)	Range of sample depths (m)[a]	Comments
1	9.5	0.35	0.20	1.5–4.9	Gravel present in deep channel thalweg along the west bank
2	13.5	0.75	0.35	0.9–4.6	Wide midchannel thalweg; shallow gravel, rubble shoal located downriver
3	21.5	0.45	0.30	0.9–2.5	Shallow gravel, rubble shoal located along the north bank
4	25.5	0.65	0.25	0.9–3.8	Shallow gravel, rubble shoal located throughout the upriver segment

[a] Depths varied depending on river stage.

of furnace filter material (0.75 m wide) was fitted and secured around an open-ended PVC cylinder 0.75 m long × 0.15 m diameter. A 4.5–5.0-kg anchor was secured to one end of the tube with a 0.20-m-long anchor line, and a buoyed hauling line was attached to the other end of the tube. The intent of this design was to suspend the collector off the riverbed while maintaining a sampling position near the bottom of the water column. To determine the effectiveness of the newly designed tubes, only rkm 13.5 was sampled in 2001 and rkm 9.5 and 13.5 in 2002.

Three to five egg collectors were deployed equidistantly as a set across the river channel. Depending on the apparent size of the potential egg deposition area, two or three sets, separated by distances of 200–300 m, were deployed within each site. Depth and channel position were recorded for each deployed collector. Every 2–5 d, collectors were retrieved and examined for presence of eggs. Acipenseriform eggs, identified by color and size, were removed and preserved in 80% ethanol. Collectors were then rinsed thoroughly before redeployment into the river. Because sturgeon (*Scaphirhynchus* sp.) were also present in the study area, the eggs collected were sent to the National Fish and Wildlife Forensics Laboratory in Ashland, Oregon, for species identification. Mitochondrial DNA sequences from a region of the cytochrome *b* gene were obtained from eggs and compared with reference sequences from paddlefish, pallid sturgeon *S. albus*, and shovelnose sturgeon *S. platorhynchus*. The genetic methods and analyses used are described in Straughan et al. (2002).

Data analyses.—Sampling effort expended at each site (collector days) was calculated as the number of retrieved collectors multiplied by set duration summed over all sample periods. Catch per unit effort (CPUE; eggs·collector^{-1}·d^{-1}) at each site was used to draw comparisons among years and to relate collection of eggs to Yellowstone River conditions. Daily Yellowstone River discharge (m^3/s) data were obtained from the U.S. Geological Survey gauging station near Sidney, Montana (USGS 06329500; rkm 47), and river temperatures (°C) were obtained from a temperature logger positioned at rkm 13.5.

To assess the likelihood of sample sites as spawning reaches, models were constructed that examined the spatial distribution of the collected eggs. A highly contagious distribution would provide evidence that eggs were spawned in close proximity to collectors (Sulak and Clugston 1998). We hypothesized that eggs would be more highly clumped on collectors set immediately downriver of spawning activity than collectors set further downriver or upriver within a sample site. Accordingly, egg counts were fit by the negative binomial distribution, which is described by the mean (m) and a dispersion parameter (k) that measures degree of clumping (i.e., as k decreases, clumping increases) (Bliss and Fisher 1953; White and Bennetts 1996). Conversely, eggs spawned at distant upriver sources were hypothesized to have dispersed during downriver drift and to be more randomly distributed on collectors within a site. Paddlefish eggs have been found to be swept downriver of gravel bars before adhering onto substrate (Purkett 1961). According to this hypothesis, egg counts would be better fit by the Poisson distribution, which is described by the mean parameter, λ. Because eggs were collected in sufficient numbers during only four sample periods during June 8–25 in 2002 (denoted as periods *a*, *b*, *c*, and *d*), modeling was restricted to this time period. In addition, only eggs collected along the thalweg were included in models because differences in current velocities between the thalweg and channel margins could affect egg interception and deposition rates and thus confound interpretation of results. Model construction and parameter estimation were performed using version 7 of Matlab (The MathWorks, Inc., Natick, Massachusetts).

The information-theoretic approach was used to evaluate the relative plausibility of the models derived to examine the spatial distribution of egg counts. This approach, which is well-suited for drawing inferences from observational data, quantitatively compares a set of competing models to select those that are best supported by the data (Burnham and Anderson 1998).

Because it was assumed that intensity of spawning activity may vary over time and between sites, the candidate set included models with spatial parameters (m and k, or λ) unique to each site and sample period, in addition to reduced models with parameters held constant across sites, sample periods, or both. Akaike's information criterion, corrected for small sample bias (AIC_c), was used to rank and select the models that accounted for the most variation in the data with the fewest parameters (Burnham and Anderson 1998). The model with the smallest AIC_c value was considered best at approximating the data; models with AIC_c values not more than 4 units greater than the AIC_c of the best model (i.e., $\Delta AIC_c \leq 4$) were also considered to receive support as best models, whereas models with ΔAIC_c values greater than 10 provided strong evidence against their consideration as best (Burnham and Anderson 1998). Uncertainty in the best model is incorporated into parameter estimates by calculating a weighted average across selected models (Burnham and Anderson 1998); however, model averaging was not used to derive estimates of spatial parameters in this analysis because the intent of the study was descriptive rather than predictive.

Results

During the study period, 326 collectors were deployed for a total of 1,179 collector days (Table 2). Less effort was expended in 2000 than in 2001 and 2002 because of the foreshortened sample period and number of mats lost. During 2000, 56 of the 71 (79%) mats were recovered during initial retrieval attempts. Three mats were later recovered after elapsed periods of 29–37 d. Mats were most likely temporarily buried by sand because they were difficult to dislodge from the riverbed. Conversely, 97% of tubes were retrieved successfully during both 2001 (88 of 91) and 2002 (159 of 164; Table 2). Although tubes typically were retrieved from the location where they had been deployed, debris accumulated along hauling lines during periods of rising discharge and tubes were occasionally recovered downriver from point of deployment. As a result, tubes were temporarily removed from the river for a period of 2 d in 2001 (June 17–18) and 5 d in 2002 (June 3–7) because of large amounts of debris transported downriver at these times.

We collected 130 acipenseriform eggs over the study period (Table 2). In 2001 and 2002, 17 and 105 eggs, respectively, were collected on tubes, whereas no eggs were found on mats at any sample site during 2000. However, eight eggs were collected on a mat deployed in 2000 at rkm 13.5 in 2002. Eighty-nine of 90 differentiable eggs (99%) were genetically confirmed as paddlefish eggs; 1 egg was determined to be either shovelnose sturgeon or pallid sturgeon. Eggs were typically collected after the first week in June and were found on 20% and 45% of tubes retrieved during these peak collection periods in 2001 and 2002, respectively (Figure 2). In 2001, egg CPUE peaked during sample period June 19–22 (0.21 eggs·collector^{-1}·d^{-1}) after discharge had peaked on June 17 (680 m^3/s). In 2002, egg CPUE peaked during sample period June 13–17 at both rkm 9.5 (0.46 eggs·collector^{-1}·d^{-1}) and rkm 13.5 (0.65 eggs·collector^{-1}·d^{-1}) after discharge had peaked on June 6 (1206 m^3/s). Average daily river temperature ranged between 15°C and 22°C during periods in which eggs were collected in both years.

The eggs collected at both sites were most often found in low numbers and on tubes retrieved from the channel thalweg (Figure 3). In 2001, seven of the nine tubes with eggs were retrieved from the mid-channel thalweg at rkm 13.5, and these seven tubes accounted for 65% of eggs collected that year. Only one or two eggs were found on all but one of the nine tubes. During June 8–25 in 2002, 17 of the 25 (68%) tubes with eggs at rkm 13.5 were retrieved from the mid-channel thalweg, and these 17 accounted for 83% of

TABLE 2.—Effort and catch information for collectors used to sample acipenseriform eggs at four sites on the lower Yellowstone River in 2000–2002 (see Methods for descriptions of collector types). Parenthetic values are the number of eggs genetically confirmed as paddlefish.

Year	Collector type	Site (rkm)	Number of collectors deployed	Number of collectors retrieved	Sampling effort (collector days)	Number of eggs
2000	Mat	13.5	35	31[a]	185[b]	0
		21.5	13	10	26	0
		25.5	23	18	42	0
2001	Tube	13.5	91	88	338	17 (14)
2002	Tube	9.5	50	48	176	34 (19)
		13.5	114	111	412	79 (56)[c]

[a] Three collectors were retrieved in midsummer after initial attempts failed.
[b] Includes 103 d from the three collectors retrieved in midsummer.
[c] Eight eggs were found on a recovered mat deployed in 2000.

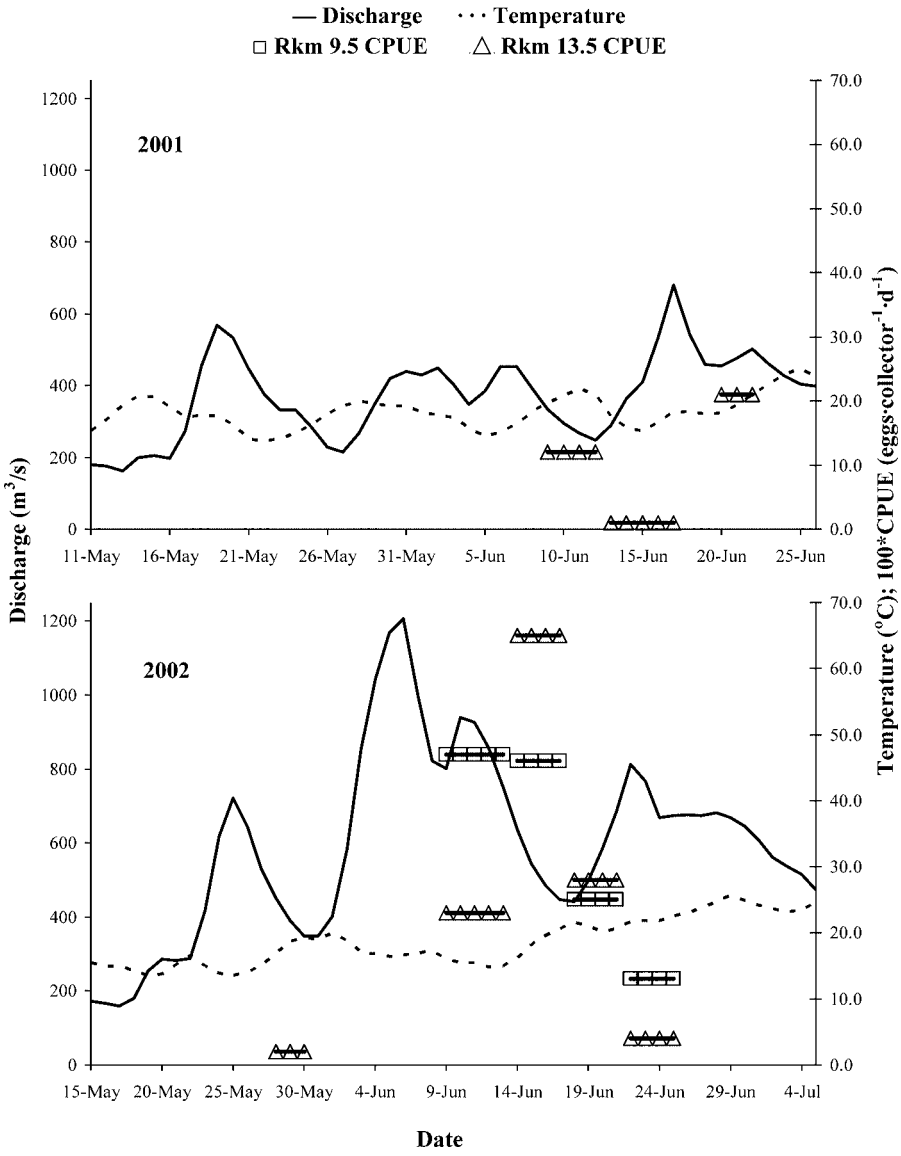

FIGURE 2.—Catch per unit effort (CPUE) of acipenseriform eggs at rkm 9.5 and 13.5 in relation to Yellowstone River discharge and temperature during the spring of 2001 and 2002. The number of symbols along each horizontal CPUE bar indicates the duration of the sample period in days.

collected eggs at that site. At rkm 9.5, 9 of the 11 (82%) tubes with eggs were retrieved along the thalweg near the west bank and accounted for 94% of eggs collected at that site. Estimates of mean egg counts over collection periods in 2002 were low, ranging between 0.42 and 3.55 eggs/collector for distribution models that received support in model selection (Table 3). Fewer than four eggs were found on 27 of the 36 (75%) tubes that had collected eggs at both sites in 2002 (Figure 3).

A clumped distribution of eggs was suggested by the finding of nine or more eggs on several tubes in combination with a lack of eggs on many tubes during collection periods in 2002 (Figure 3). Accordingly, the three models that received support as "best" in model selection were fit by a negative binomial distribution (Table 3). Conversely, large ΔAIC_c values calculated for Poisson models provided strong evidence against a random distribution of eggs. In addition, though selected models did not support a difference in mean

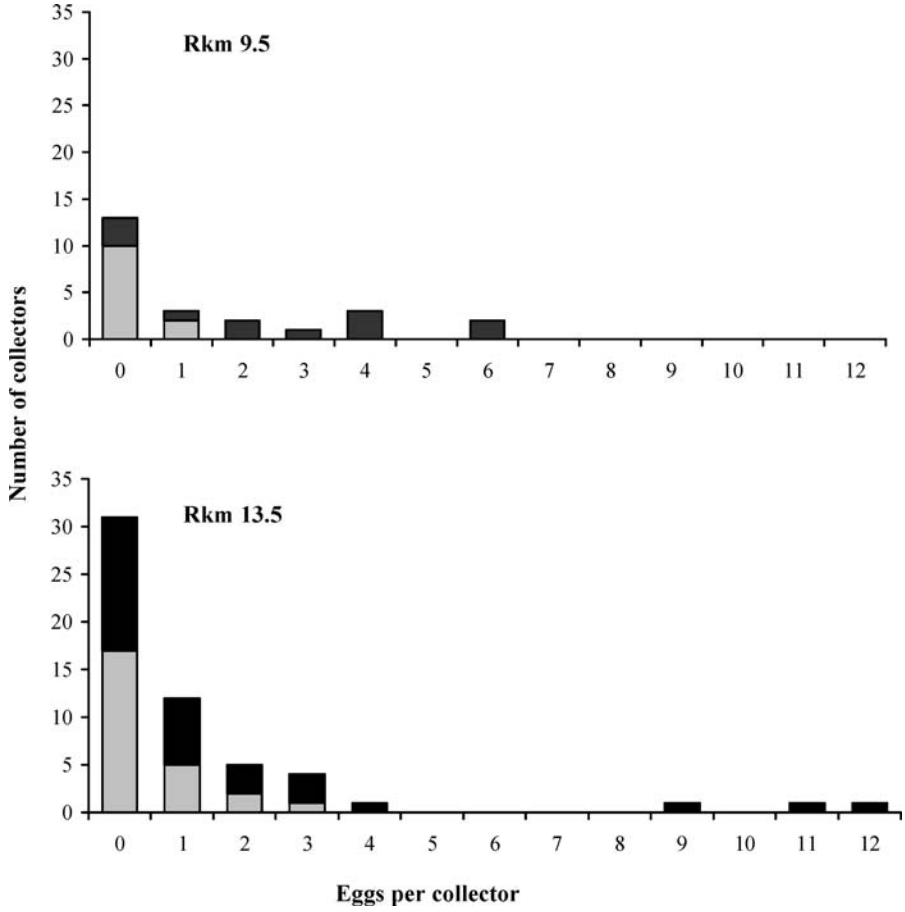

FIGURE 3.—Distribution of acipenseriform eggs found on tubes retrieved from within (black bars) and outside of (gray bars) the channel thalweg at rkm 9.5 and 13.5 in the lower Yellowstone River during June 8–25, 2002.

TABLE 3.—Comparison of negative binomial and Poisson models describing the spatial distribution of acipenseriform eggs found on collectors retrieved along the thalweg at rkm 9.5 (site 1) and 13.5 (site 2) in the lower Yellowstone River from June 8 to 25, 2002. Subscripts in means (m or λ) and dispersion parameters (k) refer to sites (1 and 2) and time periods (a–d); a period indicates a common estimated parameter across sites or time periods. The column headed ΔAIC_c indicates the difference between the model's AIC_c and the best model's AIC_c (model 1; AIC_c 178.4). The set of models receiving support as best approximating the egg count data included those where ΔAIC_c was ≤ 4.

Model	ΔAIC_c	Parameters	Parameter estimates for best models
1	0.00	$m_{.a}, \ldots, m_{.d}, k$	2.08, 3.55, 1.75, 0.42, 0.92
2	1.90	$m_{.a}, \ldots, m_{.d}, k_{1.}, k_{2.}$	2.22, 3.37, 1.71, 0.44, 1.58, 0.74
3	3.67	$m_{..}, k$	1.92, 0.61
4	4.53	$m_{..}, k_{1.}, k_{2.}$	
5	5.93	$m_{1.}, m_{2.}, k$	
6	6.89	$m_{1.}, m_{2.}, k_{1.}, k_{2.}$	
7	9.34	$m_{1a}, \ldots, m_{1d}, m_{2a}, \ldots, m_{2d}, k$	
8	11.64	$m_{1a}, \ldots, m_{1d}, m_{2a}, \ldots, m_{2d}, k_{1.}, k_{2}$	
9	35.20	$\lambda_{.a}, \ldots, \lambda_{.d}$	
10	41.11	$\lambda_{1a}, \ldots, \lambda_{1d}, \lambda_{2a}, \ldots, \lambda_{2d}$	
11	61.59	λ	
12	63.67	$\lambda_{1.}, \lambda_{2.}$	

egg counts between sites, the second best model indicated a higher degree of clumping at rkm 13.5 ($k = 0.74$) than at rkm 9.5 ($k = 1.58$).

Discussion

The tubular collectors deployed during 2001 and 2002 along the lower Yellowstone River proved to be a viable passive technique for collecting paddlefish eggs in spawning reaches characterized by predominantly sandy substrate. Tubes were successfully retrieved over 95% of the time, whereas the mats often became buried and were difficult to dislodge from the riverbed. Paragamian et al. (2001), in their efforts to document white sturgeon spawning events in the Kootenai River, Idaho, also found that egg mats became buried by shifting sand during high-flow events. Although mats that are temporarily buried may later be recovered, the sample design and interpretation of results are compromised. Tubes collected eggs during both years of deployment, whereas eggs were not found on retrieved mats in 2000. However, the effectiveness of the two types of collectors could not be directly compared because they were not deployed in concert. The discontinuation of sampling by mid-June of 2000 may have prevented the collection of eggs by mats in that year. Nonetheless, the sampling efficiency of mats that become covered by shifting sands decreases, whereas tubes suspended off the bottom retain an exposed surface area for egg attachment.

The collection and genetic confirmation of eggs at rkm 9.5 and 13.5 support the existence of spawning and egg deposition habitat for paddlefish within this stretch of the lower Yellowstone River. These results are consistent with previous larval collections, as paddlefish have been regularly collected along the lower 30 rkm with high densities found around rkm 13.5 (Gardner 1993, 1995, 1996). On the other hand, our positive results might be attributed only to interception of drifting eggs and not to egg deposition, as suggested by the high percentage of eggs collected along the thalweg. However, the finding of eight eggs on a retrieved egg mat, which presumably lay flush with the riverbed, supports the supposition of egg deposition at rkm 13.5. Additionally, the presence of cobble and bedrock at this site would provide suitable attachment sites for adhesion of eggs. The role of other physical characteristics at rkm 13.5, such as eddy currents that might facilitate egg deposition and adhesion, needs further investigation (Sulak and Clugston 1998; Perrin et al. 2003).

The clumped distribution of eggs collected at both sites also provides evidence that paddlefish spawned in the vicinity of deployed tubes. It is difficult to determine whether there were different groups of spawning adults upriver of both sites, or if any eggs collected at rkm 9.5 were the result of residual drift from rkm 13.5. Although a less clumped distribution at rkm 9.5 may indicate residual drift, model selection yielded ambiguous evidence for a detectable difference in dispersion parameters between sites. In addition, site-specific clumping patterns could be due to differences in near-bed current velocities or in the proximity of collectors to spawners between sites.

The overall low number of eggs collected per tube at both sites, however, suggests a low collector efficiency (i.e., collecting a small percentage of available eggs). Although published accounts of passive egg collection techniques for paddlefish are scarce, collector efficiency comparisons may be drawn with regard to similar studies in which sturgeon spawning sites had been identified. Sulak and Clugston (1998) found groups of up to 63 gulf sturgeon *A. oxyrinchus desotoi* eggs on individual samplers deployed along the Suwanee River in Florida. McCabe and Beckman (1990) recorded counts of 423 white sturgeon eggs on individual mats set below Bonneville Dam on the Columbia River. During lake sturgeon egg sampling efforts on the Wolf River, Kempinger (1988) calculated seasonal means of 1035–8805 on 1-m^2 trays set along spawning areas. In contrast to these studies, Perrin et al. (2003) collected only 77 white sturgeon eggs on 221 deployed mats along the unregulated Fraser River and posited that this was the result of the widespread distribution of both spawners and spawning habitat. Similarly, only 42 gulf sturgeon eggs were collected at widely distributed sites along the Choctawhatchee River system, where previous knowledge of specific sturgeon spawning areas was unavailable (Fox et al. 2000). In general, egg collection efficiency increased when fish were either highly concentrated (e.g., below dams) or efforts were focused along spawning areas previously identified through telemetry, visual observation, or other sampling techniques.

The low number of paddlefish eggs collected in our study may be due to a lack of information concerning specific paddlefish spawning sites as well as the widespread distribution of spawners. The low sampling effort relative to the size of potential spawning areas probably contributed to our inability to deploy collectors in close proximity to concentrations of spawning paddlefish. Telemetry data have also indicated that fish are not concentrated within a few reaches during the spawning season and that upriver movements do not cease at specific sites but are extensive and bi-directional throughout the spawning migration (Firehammer 2004). Such a broad distribution of spawning effort would not be an unexpected

tactic in a spatially unpredictable reproductive environment such as the lower Yellowstone River (den Boer 1968). On the other hand, low egg counts may be representative of typical egg densities along Yellowstone River deposition sites. Because where in the water column paddlefish spawn is not known, eggs released in the upper portion of the water column may be dispersed by current before their adherence onto substrate (Purkett 1961).

The collection of eggs after peak periods of Yellowstone River flow in June of 2001 and 2002 implies an influential relationship between high levels of spring discharge and spawning activity consistent with that reported previously in this system (Gardner 1996; Liebelt 1996) and in other paddlefish rivers (Purkett 1961; Wallus 1986; Lein and DeVries 1998). Though eggs were collected at higher rates in the higher flow year of 2002, insufficient sampling effort precluded further conclusions regarding the effect of the freshet's profile on spawning cues. In addition, the near absence of eggs on collectors after lesser freshets in late May of both years suggests that, though discharge may be the triggering stimulus, photoperiod and temperature as factors regulating gamete maturation are also important preparatory cues in controlling the timing of spawning (Russell 1986; Wallus 1986; Pasch et al. 1980). The long, cold winters in northern latitudes may explain the detection of spawning along the Yellowstone River at dates later than those reported for paddlefish along more southerly river systems (Pasch et al. 1980; Wallus 1986; Hoxmeier and DeVries 1997; Lein and DeVries 1998).

The objective of this study was to develop an egg collection technique that would confirm paddlefish spawning sites in sandbed river reaches. Despite low collection rates, we believe the tubes proved effective in sampling eggs and suggest that more intensive sampling than was applied in this study would achieve a better spatial resolution of spawning activity within suspected reaches. In addition, our results indicate that predominant substrate type is an important factor to consider when choosing an appropriate passive gear for sampling eggs. Although tubes were effective at sand-dominated sites sampled in this study, mats may work equally well or better in reaches further upriver along the Yellowstone River, where gravel and cobble predominate. Using collector types that are suitable for riverbed conditions will increase sampling success and aid in identifying the spatial distribution of spawning sites for paddlefish.

Acknowledgments

Funding for this research was provided by the North Dakota Game and Fish Department. We thank G. Power and F. Ryckman of the North Dakota Game and Fish Department for their advice throughout this project; D. Straughan of the U.S. Fish and Wildlife Service National Forensics Laboratory in Ashland, Oregon, for conducting genetic analyses; and the Nez Perce tribe for providing field materials for egg mats. We are also grateful to S. Shefstad, B. Bowersox, and S. Koerner for their assistance in the field. We also thank anonymous reviewers for their constructive comments on the manuscript.

References

Bliss, C. I., and R. A. Fisher. 1953. Fitting the negative binomial distribution to biological data. Biometrics 9:176–200.

Bramblett, R. G., and R. G. White. 2001. Habitat use and movements of pallid and shovelnose sturgeon in the Yellowstone and Missouri rivers in Montana and North Dakota. Transactions of the American Fisheries Society 130:1006–1025.

Burnham, K. P., and D. R. Anderson. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York.

Crance, J. H. 1987. Habitat suitability index curves for paddlefish, developed by the Delphi technique. North American Journal of Fisheries Management 7:123–130.

den Boer, P. J. 1968. Spreading of risk and stabilization of animal numbers. Acta Biotheoretica 18:165–194.

Duncan, M. S., J. J. Isely, and D. W. Cooke. 2004. Evaluation of shortnose sturgeon spawning in the Pinopolis Dam tailrace, South Carolina. North American Journal of Fisheries Management 24:932–938.

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. Doctoral dissertation. University of Idaho, Moscow.

Fox, D. A., J. E. Hightower, and F. M. Paruka. 2000. Gulf sturgeon spawning migration and habitat in the Choctawhatchee River system, Alabama–Florida. Transactions of the American Fisheries Society 129:811–826.

Gardner, W. M. 1993. Yellowstone River paddlefish spawning study. Montana Department of Fish, Wildlife and Parks, Federal Aid in Sport Fish Restoration, Project F-46-R-6, Job 3-E, Helena.

Gardner, W. M. 1995. Yellowstone River paddlefish spawning study. Montana Department of Fish, Wildlife and Parks, Federal Aid in Sport Fish Restoration, Project F-78-R-1, Job 3-E, Helena.

Gardner, W. M. 1996. Yellowstone River paddlefish spawning study. Montana Department of Fish, Wildlife and Parks, Federal Aid in Sport Fish Restoration, Project F-78-R-2, Job 3-E, Helena.

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

Hesse, L. W., and G. E. Mestl. 1993. The status of Nebraska fishes in the Missouri River, 1. Paddlefish (Polyodonti-

dae: *Polyodon spathula*). Transactions of the Nebraska Academy of Sciences 20:53–65.

Hoxmeier, R. J. H., and D. R. DeVries. 1996. Status of paddlefish in the Alabama waters of the Tennessee River. North American Journal of Fisheries Management 16:935–938.

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

Jennings, C. A., and S. J. Zigler. 2000. Ecology and biology of paddlefish in North America: historical perspectives, management approaches, and research priorities. Reviews in Fish Biology and Fisheries 10:167–181.

Kempinger, J. J. 1988. Spawning and early life history of lake sturgeon in the Lake Winnebago system, Wisconsin. Pages 110–122 *in* R. D. Hoyt, editor. Eleventh annual larval fish conference. American Fisheries Society, Symposium 5, Bethesda, Maryland.

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.

Liebelt, J. E. 1996. Lower Missouri River and Yellowstone River pallid sturgeon study. Montana Fish, Wildlife, and Parks, Western Area Power Administration grant agreement BAO-709, Helena.

Marchant, S. R., and M. K. Shutters. 1996. Artificial substrates collect gulf sturgeon eggs. North American Journal of Fisheries Management 16:445–447.

McCabe, G. T. Jr., and L. G. Beckman. 1990. Use of an artificial substrate to collect white sturgeon eggs. California Fish and Game 76:248–250.

Paragamian, V. L., G. Kruse, and V. Wakkinen. 2001. Spawning habitat of Kootenai River white sturgeon, post-Libby Dam. North American Journal of Fisheries Management 21:22–33.

Pasch, R. W., P. A. Hackney, and Holbrook A II.. 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.

Perrin, C. J., L. L. Rempel, and M. L. Rosenau. 2003. White sturgeon spawning habitat in an unregulated river: Fraser River, Canada. Transactions of the American Fisheries Society 132:154–165.

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

Rehwinkel, B. J. 1978. The fishery for paddlefish at Intake, Montana, during 1973 and 1974. Transactions of the American Fisheries Society 107:263–268.

Robinson, J. W. 1966. Observations on the life history, movement, and harvest of the paddlefish, *Polyodon spathula*, in Montana. Proceedings of the Montana Academy of Sciences 26:33–44.

Russell, T. R. 1986. Biology and life history of the paddlefish: a review. Pages 2–20 *in* J. G. Dillard, L. K. Graham, and T. R. Russell, editors. The paddlefish: status, management, and propagation. American Fisheries Society, North Central Division, Special Publication 7, Bethesda, Maryland.

Sparrowe, R. D. 1986. Threats to paddlefish habitat. Pages 36–45 *in* J. G. Dillard, L. K. Graham, and T. R. Russell, editors. The paddlefish: status, management, and propagation. American Fisheries Society, North Central Division, Special Publication 7, Bethesda, Maryland.

Straughan, D. J., M. B. Burnham-Curtis, and S. R. Fain. 2002. Experimental search for forensically useful markers in the genus *Scaphirhynchus*. Journal of Applied Ichthyology 18:621–628.

Sulak, K. J., and J. P. Clugston. 1998. Early life history stages of gulf sturgeon in the Suwanee River, Florida. Transactions of the American Fisheries Society 127:758–771.

Unkenholz, D. G. 1986. 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. American Fisheries Society, North Central Division, Special Publication 7, Bethesda, Maryland.

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

White, C. C., and R. E. Bennetts. 1996. Analysis of frequency count data using the negative binomial distribution. Ecology 77(8):2549–2557.

Yeager, B., and R. Wallus. 1982. Development of larval *Polyodon spathula* (Walbaum) from the Cumberland River in Tennessee. Pages 73–77 *in* C. F. Bryan, J. V. Conner, and F. M. Truesdale, editors. Proceedings of the fifth annual larval fish conference. Louisiana State University, Baton Rouge.