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Timing of paddlefish spawning in the Upper Missouri River, Montana, USA in relation to river conditions

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Summary

Spawning activity of paddlefish *Polyodon spathula* in the Missouri River, Montana in 2008–2009 was examined to delineate spawning sites and times in relation to discharge, water temperature and turbidity. One hundred thirty-six eggs were collected at water temperatures ranging from 12.0 to 20.7°C (mean, 16.3°C; SD, 2.5). Only 12 of 89 (13%) congregations of radio-tagged adults observed during the spawning period coincided with egg captures. Six larvae were collected at water temperatures ranging from 19.1 to 21.7°C (mean, 20.5°C; SD, 0.86). Peak discharge in 2008 (903 m^3 s^{-1} on 14 June) was approximately 30% greater in magnitude and occurred 11 days later than peak discharge in 2009 (612 m^3 s^{-1} on 3 June). Despite these differences in the hydrograph, no significant differences in egg CPUE were found between years (ANOVA, $F = 0.69$, $P = 0.56$). Logistic regression identified no significant river condition variables associated with the presence or absence of eggs ($P > 0.14$ for all variables). However, in both years maximum egg CPUE was recorded within 3 days of the hydrograph peak and at similar water temperatures (17.5°C in 2008, 16.8°C in 2009). These results suggest an overall association of peaking discharge and seasonally warming water temperatures with egg deposition. Higher catches of eggs and larvae than observed in this study may be necessary to clarify short-term (day-to-day) effects of environmental changes on spawning activity. Continued investigation of the relationship between short-term changes in river conditions and paddlefish spawning activity is needed to understand the mechanics underlying the reproductive success of this species.

Introduction

During the last century, paddlefish *Polyodon spathula* abundance and distribution have declined throughout most of the species' range (Gengerke, 1986). Although overharvest has been a problem in many areas, habitat changes have been the major contributor to the declines. Large river modifications including flow regulation and impoundment have altered nursery and feeding habitats, inundated spawning grounds, and impeded spawning migrations (Carlson and Bonislawsky, 1981; Sparrowe, 1986; Unkenholz, 1986). Loss of spawning habitat has been a particularly widespread problem (Graham, 1997). Although several states have artificially propagated paddlefish and enhanced numbers of fish successfully in the past two decades (Bettoli et al., 2009), understanding the mechanisms behind the spawning success of wild fish may be essential for the long-term survival of the species.

Paddlefish respond to specific river conditions involving discharge, temperature and turbidity to initiate upriver movements and spawning (Stancill et al., 2002; Firehammer and Scarnecchia, 2006; Miller and Scarnecchia, 2008). It is thought that paddlefish spawn in loose groups where a female, attended by males, broadcasts her eggs over gravel bars (Purkett, 1961). Upon fertilization, the eggs develop an adhesive coating, lose buoyancy, adhere to hard substrates and typically hatch in six to 7 days at water temperatures of about 18–21°C (Jennings and Zigler, 2000). Photoperiod and water temperature may dictate the appropriate seasonal time of spawning but an increase in water flow may be necessary to trigger gamete release. If all environmental conditions are not satisfactory, female paddlefish may reabsorb their eggs (Russell, 1986; Jennings and Zigler, 2000).

Researchers have monitored paddlefish spawning congregations with radio-telemetry and netting techniques (Moen et al., 1989; Stancill et al., 2002; Firehammer and Scarnecchia, 2006). However, the strongest documented evidence of spawning was the visual observation by Purkett (1961), who observed a spawning 'rush' over inundated gravel bars in the Osage River, Missouri. Although congregations of paddlefish may indicate spawning sites and times, direct observation of spawning and collection of eggs or larvae may be useful in confirming spawning events. In most cases, the spawning season coincides with periods of high and turbid flows, making direct observations difficult (Russell, 1986). Instead, some researchers have collected eggs and larvae to locate spawning areas and document spawning success (Wallus, 1986; Firehammer et al., 2006; Miller et al., 2008).

In Montana, the completion of Fort Peck Dam in the late 1930s resulted in the physical isolation of the Fort Peck paddlefish stock from other stocks down river. A popular recreational snag fishery occurs each year in the Missouri River above Fort Peck Reservoir (MRAFP) when adult paddlefish migrate out of the reservoir toward riverine spawning reaches. In recent years, harvest of Fort Peck paddlefish has ranged between 300 and 1,000 fish. In 2008, a harvest cap of 500 fish was placed on the stock primarily as a response to concerns of recently low recruitment.

An understanding of the relationship between river conditions and paddlefish spawning in the MRAFP will provide information needed for the long-term perpetuation of this stock and perhaps other wild stocks elsewhere. In addition, identifying spawning locations and times may help guide future habitat protections and aid managers in understanding paddlefish reproductive ecology. In this paper the collective evidence of congregations of telemetered paddlefish, egg

deposition and larval fish captures in 2008–2009 was examined to delineate spawning sites and times in the MRAFP, and to assess the relationship between spawning events and river conditions.

Study area

The Fort Peck paddlefish stock inhabits the MRAFP between Fort Peck Dam 336 km upriver to Morony Dam, 24 km downstream of Great Falls, Montana (Fig. 1). Two major tributaries enter the river in this reach, the Marias River from the north near river kilometer (rkm) 3305 (where numbers refer to kilometers above the mouth of the Missouri River at St Louis, Missouri) and the Judith River from the south near rkm 3192. Berg (1981) described the riverine areas as consisting of two fishery zones. The upper zone is a coldwater / warmwater transitional zone extending from Morony Dam to the mouth of the Marias River. Sauger *Sander canadensis* is the predominant game fish in the upper zone. Paddlefish are more common in the lower zone, a warmwater reach extending from the mouth of the Marias River downstream to the headwaters of Fort Peck Reservoir. Areas of the lower zone below rkm 3088 are characterized by a wide meandering channel with numerous sand bars, large islands, side channels and backwaters. Areas of the lower zone above rkm 3088 have more constricted channels and coarser substrate types than areas below rkm 3088.

Methods

Fish capture and tag implantation

Paddlefish spawning congregations were monitored during May and June of 2008 and 2009 using radio-telemetry. Drifted, floating gill nets 25 m in length (mesh size 12.7 cm) were used to capture migratory adult paddlefish during April and May of 2006 through 2009 in the lower zone of the study area (rkm 3097–3034). Lotek Model 3L Microprocessor coded radio transmitters (4.5 year battery-life; Lotek Inc. Newmarket, Ontario, Canada) were surgically implanted into each fish. A 3–4 cm incision was made midway between the pelvic and pectoral fins along the ventral midline of the fish. At that time, sex and maturation stage were determined by observing the gonads through the incision. A large bore catheter needle created an exit point for the antennae about five cm posterior of the incision. After tag implantation, the incision was closed with 6–8 non-absorbable sutures. Each surgery took less than five minutes during which time river water was pumped across the gills to enable the fish to respire. After implantation, fish were held in the river and released when swimming movements suggested recovery. All release sites were within one km of the point of capture.

Fixed station and manual tracking

Tracking was conducted with fixed receiving stations and searching by boat. In 2008, there were eight fixed stations continuously operating at rkms 3075, 3088, 3117, 3192, 3171, 3273, as well as at the mouth of the Marias River and five rkm up the Marias River. In 2009, three more fixed stations were installed: one 5 rkm up the Judith River, one at rkm 3268, and one at rkm 3337. Manual tracking was conducted approximately 5 days a week during daylight hours using an open-bow motorboat. Once a radio-tagged fish was located, a global positioning unit (GPS) recorded latitude, longitude, and the approximate rkm of contact sites. The United States Geological Survey gauging station near Landusky (Station Number 06115200) recorded mean daily river discharge. A temperature data logger positioned near the gauging station recorded daily water temperatures. Turbidity levels in Nephlometric Turbidity Units (NTU) were recorded during manual tracking events using a Hach 2100P portable turbidity meter.

Egg and larval fish collection

Delineation of potential paddlefish spawning sites was addressed using two additional methods: artificial substrate egg collectors described by McCabe and Beckman (1990) and

Fig. 1. Map of study area including fixed telemetry stations and approximate *Polyodon spathula* egg sampling sites, Missouri River above Fort Peck Reservoir, Montana

Firehammer et al. (2006); and larval fish captures using conical larval nets.

Rectangular egg collectors were constructed of 0.60 by 0.75 m angle-iron frames with furnace filter fitted into the frames. Collectors were secured to the substrate with a 5.0 kg grapple anchor with a 12.0–15.0 m buoyed float line affixed to the collector for retrieval. There is no commercial shipping traffic in the upper Missouri River and thus buoys were in little danger of being snagged by barges.

Egg sampling sites were chosen based on three criteria. First, telemetry data from 2006–2007 and catch data reported in Berg (1981) identified potential spawning sites. Second, sample sites provided an abundance of gravel and cobble, substrates previously shown to provide incubation sites for paddlefish eggs (Purkett, 1961; Miller et al., 2010). Third, sample sites were restricted to areas below rkm 3112.5 because telemetry data from 2006–2007 indicated few fish made prolonged movements above this area and logistical restraints prevented sampling of the entire free flowing reach of the MRAFP. In each year, egg sampling began when rising discharge levels and telemetry monitoring indicated sustained upriver movement of fish. Egg sampling ceased when telemetry monitoring indicated a majority of fish had exited the river. In 2008, egg collectors were deployed at rkms 3099.5, 3112.5 and 3119 from 5 to 27 June. In 2009, egg collectors were deployed at rkms 3084, 3099.5, 3112.5, 3119 and 3127 from 27 May to 15 June. However, shifting sand substrates at rkm 3084 made retrieval of egg collectors difficult and little sampling effort (eight collector-days) was applied at this site. A typical set of collectors consisted of 12 individual collectors, with six collectors evenly spaced perpendicularly to the shoreline across the width of the channel and with six more collectors set in a similar fashion 50 m downstream. Egg collectors were deployed continuously throughout the sample period in each year. However, the duration of deployment between inspections varied from 24 to 72 h.

Upon retrieval, collectors were visually inspected immediately for the presence of eggs. Paddlefish eggs are distinguished from most other species by their distinct steel-gray coloration but are not easily distinguishable from Missouri River sturgeons *Scaphirynchus* spp. (DeSalle and Birstein, 1996). Putative paddlefish eggs were preserved in 80% ethanol and sent to the U.S. Fish and Wildlife Service Forensics Laboratory in Ashland, Oregon for genetic identification.

Larval fish were sampled using 0.5×1.8 m^2 conical nets (750 μm Nitex mesh) with attached buckets and weighted with 4.5 kg lead weights. A General Oceanics 230 OR flow meter was suspended in the mouth of the net to permit estimation of total water volume sampled. In 2008, larval fish samples were taken weekly during daylight hours from 2 to 25 June at six locations: rkms 3084, 3090, 3099.5, 3111, 3119 and 3127. In 2009, sampling in lower reaches of the MRAFP (i.e. below rkm 3084) was included to provide larval distribution data not collected in 2008. This change was made because restricting larval sampling to areas that were simultaneously sampled for eggs yielded no larvae captures in 2008. Larval sampling in 2009 occurred from 9 to 23 June at nine locations: rkms 3028, 3035, 3050, 3059, 3062, 3084, 3099.5, 3111 and 3119.

In each sampling event, two nets were suspended on either side of the bow of the boat for 10 min. Nets were towed upstream at a rate of 1–2 km h^{-1} without dredging bottom sediment. Net contents were then preserved in 10% formalin. Phloxene-B, a chemical dye, was also added to the net contents to stain larval fishes and thereby reduce their crypticness when being sorted.

Sampling effort for eggs was expressed in units of collector day, calculated as the number of egg collectors successfully retrieved from each transect multiplied by the number of hours the mats were deployed divided by 24. Sample date was recorded as the date of retrieval. Catch-per-unit-effort (CPUE) for eggs was then expressed as eggs per collector-day. Larval paddlefish were identified using keys from Auer (1982), Holland-Bartels et al. (1990), Wallus et al. (1990), and Kay et al. (1994). Larval fish CPUE was expressed as the number of larvae per 100 m^3 of filtered water.

Data analysis

Telemetry contacts were quantified into a grid system of individual cells (Kieffer and Kynard, 1996). Cells were 6.4 km in length and bound by rkm 3192 as the upriver limit of analysis and rkm 3038 as the downriver limit. These cell boundaries were selected because telemetry contacts made in 2006–2007 indicated that this area represented the migratory range of most paddlefish entering the MRAFP during spawning migration. Cell length was selected to provide a buffer of approx. 3 km around each egg sample site. A congregation of fish was defined as the presence of at least 5% of a given year's total migrating telemetered fish in the same cell on the same day. Under this restriction, three or more fish represented a congregation in 2008, and four or more fish in 2009.

The influence of explanatory variables (water temperature, discharge, turbidity and fish congregations) on the response variable (daily presence or absence of eggs) was examined with logistic regression (Cooke and Leach, 2004; Miller et al., 2008). A possible non-linear relationship was hypothesized between water temperature and egg presence/absence. In addition to observed water temperatures in °C, temperatures were also 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 ranking (3). Temperatures within two degrees above or below the optimum were assigned the second highest ranking (2). Temperatures more than two degrees higher or lower of the optimum range were assigned the lowest rank (1). Observed discharges, temperatures and turbidities on the day of collector retrieval, and the relative change in these variables between the day of retrieval and day of deployment were also used as explanatory variables. Changes in river conditions during the elapsed period between deployment and retrieval were calculated using the equation:

$$X_{\Delta} = \mathrm{Log}_{10}(X_{t2}/X_{t1})$$

where X_{t2} equals river variable on day of retrieval and X_{t1} equals river variable on day of deployment. The fish congregation response variable was standardized as a percentage of each year's total migrating telemetered fish. Differences in egg CPUE among sites and between years were examined with a rank-transformed, main effects two-way analysis of variance (ANOVA; Conover, 1999). The statistical analysis software program SAS 9.1 and a significance level of 0.05 were used to perform all analyses (SAS Institute Inc., Cary, NC).

Results

One hundred fifty-one Acipenseriform eggs were collected during the 2-year study period (72 in 2008 and 79 in 2009). Of

the 72 eggs collected in 2008, five eggs were identified as shovelnose sturgeon, *Scaphirynchus platorynchus,* two eggs did not yield conclusive results, and the remaining 65 eggs were positively identified as paddlefish. The two eggs that did not yield conclusive species origin results were captured with groups of positively identified paddlefish eggs and were included in analyses of paddlefish egg CPUE. Of the 79 eggs collected in 2009, five eggs did not yield conclusive results, three eggs did not yield DNA, and the remaining 71 eggs were positively identified as paddlefish. The five eggs that did not yield conclusive species origin results were captured with groups of positively identified paddlefish eggs and included in analyses of paddlefish CPUE.

In 2008, eggs were first collected on 10 June and last collected on 25 June (Table 1). Temperatures during the capture period ranged from 12.0 to 20.7°C (mean, 16.6°C; SD, 3.1), discharges ranged from 586 to 903 $m^3 s^{-1}$ (mean, 792 $m^3 s^{-1}$; SD, 112.9), and turbidity ranged from 45 to 1066 NTU (mean, 199 NTU; SD, 286.6). Egg CPUE, for all sites combined, peaked at 2.95 eggs per-collector-day on 17 June 2008, 3 days after spring discharge had peaked at 903 $m^3 s^{-1}$ (Fig 2). Discharge at time of peak egg CPUE was approximately 875 $m^3 s^{-1}$, water temperature was 17.5°C and turbidity 134.3 NTU. The sample site at rkm 3119.0 yielded the highest egg CPUE (0.46 eggs per-collector-day) followed by the site at rkm 3112.5 (0.33 eggs per-collector-day) and at rkm 3099.5 (0.32 eggs per-collector-day; Table 2). No paddlefish larvae were collected in 2008.

In 2009, eggs were first collected on 29 May and last collected on 12 June. Temperatures during the egg capture period ranged from 13.5 to 18.7°C (mean, 16.0°C; SD, 1.8), discharges ranged from 382 to 612 $m^3 s^{-1}$ (mean, 506 $m^3 s^{-1}$; SD, 89.8), and turbidity ranged from 21 to 84 NTU (mean, 54 NTU; SD, 20.9). Egg CPUE, for all sites combined, peaked at 2.5 eggs per-collector-day on 2 June, one day before spring discharge peaked at 612 $m^3 s^{-1}$ (Fig 2). Discharge at time of peak egg CPUE was approximately 579 $m^3 s^{-1}$, water temperature 16.8°C and turbidity 74.5 NTU. The sample site at rkm 3084 (2.0 eggs per-collector-day) yielded the highest egg CPUE followed by the sites at rkm 3099.5 (0.23 eggs per-collector-day), rkm 3112.5 (0.23 eggs per-collector-day), rkm 3119 (0.02 eggs per-collector-day) and rkm 3127 (0 eggs per-collector-day).

Six paddlefish larvae were collected in 2009. Paddlefish larvae were first collected on 17 June and last collected on 23 June. One paddlefish larvae was captured at rkm 3050 on 17 June, one at rkm 3099.5 on 22 June, one at rkm 3028 on 23 June, one at rkm 3035 on 23 June, and two at rkm 3059 on 23 June. Temperatures during the larval capture period ranged from 19.1 to 21.7°C (mean, 20.5°C; SD, 0.86), discharges from 261 to 297 $m^3 s^{-1}$ (mean, 278 $m^3 s^{-1}$; SD, 10.9), and turbidity from 40 to 238 NTU (mean, 117 NTU; SD, 71.3).

One hundred nine fish (65 males and 44 females) were implanted with radio tags during the course of a concurrent, multi-year migration study. Males ranged in body length (BL; front of eye to fork of caudal fin; Ruelle and Hudson, 1977) from 82.5 to 116.8 cm (mean, 95.0 cm; SD, 7.1) and in weight from 5.7 to 24.1 kg (mean, 13.1 kg; SD, 3.6). Females ranged in BL from 100.3 to 134.6 cm (mean, 117.7 cm; SD, 7.2) and in weight from 18.6 to 43.3 kg (mean, 28.3 kg; SD, 4.9).

In 2008 contacts were made with 43 telemetered *P. spathula* (33 males and 10 females) migrating in the MRAFP. Cell counts indicated 23 congregations of telemetered paddlefish during the spawning period; seven of these congregations occurred in cells that contained egg sampling sites. Three of these seven congregations coincided with egg captures.

In 2009 contacts were made with 62 telemetered *P. spathula* (43 males and 19 females) migrating in the MRAFP. Cell counts indicated 66 congregations of telemetered paddlefish during the spawning period; 26 of these congregations

Table 1
Association between presence or absence of paddlefish (*Polyodon spathula)* eggs captured by rectangular egg mats and river conditions (temperature and discharge), changes in river conditions (Δ discharge or temperature), and observed congregations of telemetered adult paddlefish near egg capture sites, Missouri River above Fort Peck Reservoir, Montana, 2008 and 2009

Sample date	Year	Presence of eggs (Y / N)	Temperature (°C)	Δ Temperature (+ / −)	Discharge ($m^3 s^{-1}$)	Δ Discharge (+ / −)	Congregation (% of total radio-tagged migrants)
6 June	2008	N	14.6	0.0005	807	0.0267	0
10 June		Y	13.9	0.0225	844	−0.0044	9
11 June		Y	13.2	−0.0227	883	0.0199	7
13 June		Y	12.0	−0.0412	881	−0.0014	0
17 June		Y	17.5	0.0466	875	−0.0084	0
18 June		Y	18.4	0.0219	847	−0.0143	0
19 June		Y	18.4	0.0017	813	−0.0178	0
20 June		N	18.5	0.0008	779	−0.0186	0
23 June		N	19.7	0.0291	620	−0.0989	0
25 June		Y	20.7	0.0201	586	−0.0245	7
27 June		N	20.0	−0.0155	549	−0.0282	0
27 May	2009	N	16.7	0.0177	501	0.0049	37
28 May		N	17.3	0.0156	527	0.0219	31
29 May		Y	17.8	0.0124	538	0.0089	29
1 June 1		Y	17.8	0.0000	603	0.0495	53
2 June 2		Y	16.8	−0.0251	597	−0.0043	8
3 June 3		Y	16.2	−0.0146	612	0.0108	39
5 June 5		N	16.2	−0.0029	552	−0.0448	0
8 June 8		Y	13.6	−0.0747	416	−0.1229	6
10 June		Y	14.2	0.0174	394	−0.0236	6
11 June		N	15.5	0.0391	399	0.0055	9
12 June		Y	16.6	0.0286	382	−0.0189	0
15 June		N	19.6	0.0748	286	−0.1257	0

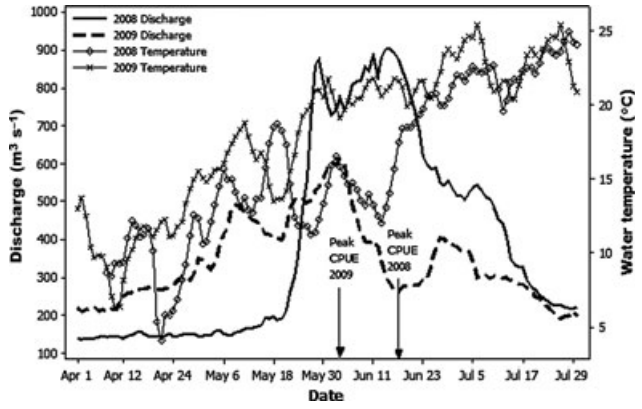

Fig. 2. Spring discharges ($m^3 s^{-1}$) and water temperatures (°C), Missouri River, Montana near rkm 3091 in 2008 and 2009. Vertical arrows = date of *P. spathula* peak egg catch-per-unit-effort in 2008 (2.95 eggs-per-collector-day) and 2009 (2.5 eggs-per-collector-day)

Table 2
Paddlefish (*P. spathula*) eggs captured by rectangular egg collectors, Missouri River above Fort Peck Reservoir, Montana, 2008 and 2009. River kilometers = above Missouri River mouth, St Louis, Missouri

Year	River kilometer	Eggs (N)	Effort (collector-days)	Catch-per-unit-effort
2008	3099.5	22	67.1	0.32
	3112.5	25	75.6	0.33
	3119.0	18	39.0	0.46
2009	3084.0	4	8.0	2.00
	3099.5	44	188.6	0.23
	3112.5	23	104.1	0.22
	3119.0	4	169.7	0.02
	3127.0	0	83.9	0.00

occurred in cells that contained egg sampling sites. Nine of these 26 congregations coincided with egg captures.

Distinct differences in the MRAFP spring hydrograph were evident between years. Peak discharge in 2008 (903 $m^3 s^{-1}$ on 14 June) was approx. 30% greater in magnitude and occurred approximately 2 weeks later than peak discharge in 2009 (612 $m^3 s^{-1}$ on 3 June). The number of days above 396 $m^3 s^{-1}$, which is the minimum flow required for sustained upriver movement postulated by Berg (1981), was also lower in 2009 (37 days) compared to 2008 (50 days). Despite differences in the hydrograph between years, no significant differences in egg CPUE were identified between years or among sites (ANOVA, $F = 0.69$, $P = 0.56$). For both years combined, logistic regression did not identify any significant explanatory variables (water temperature, discharge, turbidity, fish congregations and relative changes in water temperature, discharge and turbidity) for the presence or absence of eggs ($P > 0.14$ for all variables).

Discussion

Although peak discharge was greater in 2008 (903 $m^3 s^{-1}$ on 14 June) and occurred 11 days later than in 2009 (612 $m^3 s^{-1}$ on 3 June), maximum egg CPUE in both years was observed within one to 3 days of the hydrograph peak (17 June 2008; 2 June 2009). These results support the idea that spawning is closely linked to strongly and steadily rising flows typically preceding a spring discharge peak, regardless of the exact magnitude or exact timing of the actual peak or whether that peak turns out to be the highest discharge level that spring. This link between spawning and strongly rising flows is consistent with the spawning of *P. spathula* and other Acipenseriform fishes elsewhere. Miller et al. (2008) reported maximum paddlefish egg captures occurring within 3 days of peak spring discharge in the lower Yellowstone River but that relative changes in discharge were more closely associated with egg captures than were absolute magnitudes of discharge. Firehammer et al. (2006) observed maximum paddlefish egg captures in the lower Yellowstone River within two to 5 days of peak discharge, but did not evaluate the influence of discharge magnitude on spawning events. O'Keefe et al. (2007) found that 95% of paddlefish egg captures in the regulated Tennessee-Tombigbee waterway were associated with a substantial rise in water levels. Caroffino et al. (2010) found that a heavy rainfall event and the associated rapid rise in discharge triggered a spawning event of lake sturgeon *Acipenser fulvescens* in a Wisconsin river but that no significant relationship between magnitude of discharge and presence of eggs was evident.

The widespread tendency for paddlefish and other Acipenseriform fishes to have evolved a spawn timing associated with strongly and steadily increasing flows may have several ecological advantages. First, sustained high flows both during and after the spawn would decrease the risk of egg desiccation (Purkett, 1961). Second, higher flows would increase the likelihood and rate of downstream dispersal of larvae (Braaten et al., 2008). Third, because higher flows are typically linked with higher turbidities in this river section and in other nearby localities (Lower Yellowstone River: Firehammer, 2004; Missouri River below Fort Peck Reservoir: Braaten et al., 2009), predation by sight feeding predators on newly hatched larvae may be reduced. For example, sauger *Sander canadensis* and walleye *S. vitreus*, two known paddlefish predators (Parken and Scarnecchia, 2002) may feed less effectively in more turbid waters (Abrahams and Kattenfeld, 1997). Fourth, the spring rise in discharge and associated nutrient inputs to rivers from floodplains (Junk et al., 1989) may result in improved exogenous feeding opportunities for paddlefish larvae, resulting in higher early survival and stronger year classes. The overall pattern of egg deposition corresponding to strongly and steadily rising discharge found in the present study is thus not only well supported in other studies, but is also consistent with the ecological and habitat preferences of paddlefish.

Although the overall pattern of egg deposition and timing of larval catches in this study suggests a general relationship among discharge, water temperature and spawning, our range of sampling and statistical analyses were unable to identify particular river conditions (observed discharges, temperatures and turbidities or their relative changes) as significant explanatory variables for egg deposition (Table 1). The main factor leading to this discrepancy may be that our catches of eggs and larvae, while clearly indicative of the general time of spawning, were too few to quantitatively characterize short-term (e.g. day-to-day) variations in spawning activity in relation to short-term variations in environmental conditions. There is no guarantee that the capture of a few eggs in a given day, even if that day had the highest egg catches, represented the day of peak spawning. Secondly, the sampling design was focused on a seasonal period presumed to be suitable for paddlefish spawning based on the current literature and previous observations in the Missouri River drainage (Firehammer et al., 2006; Miller et al., 2008; Braaten et al., 2009). Increased

sampling earlier or later in the year outside this range of conditions may have increased the number of null observations in the model and thus led to statistical results closer to significance. However, expanding the sampling season in this manner would not necessarily have clarified the short-term influences of the environmental conditions on spawning that are of interest. Increased resolution would require much higher catches of eggs and larvae than observed in this study.

Larval catches in 2009 yielded the first paddlefish larvae (N = 6) observed during three years of sampling effort. This result may be explained by a change in the larval sampling design made during 2009. In addition to assumed upriver spawning sites sampled in previous years, additional downriver areas were sampled during 2009. These downriver sample sites were presumed *a priori* to be staging areas based on telemetry data from adult spawners collected in a concurrent study. Five of six paddlefish larvae collected in 2009 were found in these downriver sites. These five larvae were collected 15–21 days after peak egg CPUE was observed. Drift rates for larval paddlefish have yet to be clearly defined. However, drift rates of Missouri River sturgeon larvae *Scaphyrinchus* sp. suggest that these fishes may move downstream at speeds similar to ambient flows shortly after hatching (Braaten et al., 2008). Although the present study did not attempt to quantify larval drift rates or hatch times of paddlefish, the presence of larvae downstream of suspected egg sites is useful for clarifying the timing of the spawn.

Fish congregations were not a significant explanatory variable for the presence or absence of eggs. This lack of a consistent association between fish congregations and egg captures is a phenomenon also reported for paddlefish spawning in the Yellowstone River. Miller et al. (2008) reported no substantial congregations of telemetered fish in association with egg deposition. Several possible explanations exist for this result. One factor may be, as previously mentioned, the inadequacy of the low numbers of egg captures to effectively characterize short-term (day-to-day) spawning activity. A second factor may be that only a small fraction of the overall population was monitored by radio-telemetry. It is not clear if the number of tagged fish monitored in the present study (43 in 2008, 62 in 2009) adequately depicted the overall spawning congregations of the larger population of several thousand fish. Another explanation may be related to possible diel preferences in paddlefish spawning. Other large river fishes have been shown to preferentially spawn at night rather than during the day (Duncan et al., 2004; Tiffan et al., 2005). In addition, Fort Peck paddlefish have been observed moving at average rates of up to 13 km day^{-1} during their migrations (Miller and Scarnecchia, 2011). It is possible that some telemetered fish congregated at night to spawn in areas outside the range of fixed receiving stations and then rapidly dispersed before being detected by daytime manual tracking.

The number of genetically confirmed paddlefish eggs captured in this study (136 eggs) was less than may be expected given the abundance of spawning adults in the study area, which is estimated to be as high as several thousand fish (D. Scarnecchia, unpubl. data). However, the number of eggs in the present study (136 eggs, 0.20 eggs-per-collector-day) was similar to those reported for paddlefish in similar studies (Wallus, 1986, 41 eggs, no CPUE reported; O'Keefe et al., 2007, 106 eggs, 0.23 eggs-per-collector-day; Miller et al., 2008, 292 eggs, 0.15 eggs-per-collector-day). Based on current success rates of capturing eggs, egg sampling methods seem to be inadequate for accurately indicating annual reproductive success of Fort Peck paddlefish. However, these methods can provide valuable information on the timing of spawning events. Continued modification of egg sampling methods and further investigations of the relationships between short-term river conditions and paddlefish spawning is needed to understand the mechanics underlying the reproductive success of this species.

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