RIVER RESEARCH AND APPLICATIONS

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SHOVELNOSE STURGEON SPAWNING IN RELATION TO VARYING DISCHARGE TREATMENTS IN A MISSOURI RIVER TRIBUTARY

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ABSTRACT

Many lotic fish species use natural patterns of variation in discharge and temperature as spawning cues, and these natural patterns are often altered by river regulation. The effects of spring discharge and water temperature variation on the spawning of shovelnose sturgeon *Scaphirhynchus platorynchus* have not been well documented. From 2006 through 2009, we had the opportunity to study the effects of experimental discharge levels on shovelnose sturgeon spawning in the lower Marias River, a regulated tributary to the Missouri River in Montana. In 2006, shovelnose sturgeon spawned in the Marias River in conjunction with the ascending, peak (134 m^3/s) and descending portions of the spring hydrograph and water temperatures from 16 °C to 19 °C. In 2008, shovelnose sturgeon spawned in conjunction with the peak (118 m^3/s) and descending portions of the spring hydrograph and during a prolonged period of increased discharge (28–39 m^3/s), coupled with water temperatures from 11 °C to 23 °C in the lower Marias River. No evidence of shovelnose sturgeon spawning was documented in the lower Marias River in 2007 or 2009 when discharge remained low (14 and 20 m^3/s) despite water temperatures suitable and optimal (12 °C−24 °C) for shovelnose sturgeon embryo development. A similar relationship between shovelnose sturgeon spawning and discharge was observed in the Teton River. These data suggest that discharge must reach a threshold level (28 m^3/s) and should be coupled with water temperatures suitable (12 °C−24 °C) or optimal (16 °C−20 °C) for shovelnose sturgeon embryo development to provide a spawning cue for shovelnose sturgeon in the lower Marias River. Copyright © 2012 John Wiley & Sons, Ltd.

KEY WORDS: shovelnose sturgeon; Missouri River; spawning; discharge; tributary; temperature; Teton River; Marias River

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INTRODUCTION

River regulation can alter natural river conditions and negatively affect lotic fishes, which are adapted to natural variation in discharge and water temperature (Galat *et al*., 1996; Stanford *et al*., 1996; Fausch and Bestgen, 1997; Poff *et al*., 1997). For example, discharge variation coupled with suitable water temperature can act as a cue for initiation of life-history events such as seasonal migrations (Chapman and Carr, 1995; Swanberg, 1997) and spawning (Nesler *et al*., 1988; Kieffer and Kynard, 1996; Schrank *et al*., 2001; Paragamian and Wakkinen, 2002). Decoupling of natural variation in discharge and water temperature through river regulation can result in the removal of cues or an absence of ideal conditions for spawning fish (Junk *et al*., 1989; Sparks *et al*., 1990; Galat *et al*., 1996; Bunn and Arthington, 2002).

Sturgeon (family Acipenseridae) can be influenced by river regulation because they rely on natural variation in discharge and water temperature for part or all of their life cycle requirements (Rochard *et al*., 1990; Kieffer and Kynard, 1996; Beamesderfer and Farr, 1997; Duke *et al*., 1999). Thus, given the global propensity to regulate rivers, natural river environments are disappearing, and most extant sturgeon populations are declining or endangered (Birstein, 1993; Birstein *et al*., 1997; Secor *et al*., 2002). However, the mechanisms by which river regulation causes declines in sturgeon are poorly understood (Secor *et al*., 2002). Shovelnose sturgeon *Scaphirhynchus platorynchus* and pallid sturgeon *Scaphirhynchus albus* are two North American species that have declined throughout their range (Dryer and Sandvol, 1993; Keenlyne, 1997). The intensive regulation of the Missouri River and many of its tributaries has been implicated in the declines of shovelnose sturgeon and pallid sturgeon (Dryer and Sandvol, 1993; Keenlyne, 1997). The regulation of the Missouri River and its tributaries has resulted in river

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fragmentation, reduced sediment transport, alteration of physical habitat, disconnection of the floodplain from the channel, altered water temperatures and decoupling of the natural variation in discharge and water temperature (Hesse and Sheets, 1993; Galat *et al.*, 1996).

We used shovelnose sturgeon as an indicator species to study the relationship between spawning and discharge–water temperature coupling, given the regional and global importance of understanding the effects of river regulation on sturgeon. Shovelnose sturgeon are a migratory species that live in the upper Missouri River and use main stem and tributary habitat (e.g. the Marias River) for spawning. The specific environmental conditions (e.g. discharge and water temperature levels) required by shovelnose sturgeon for spawning have not been previously documented (DeLonay *et al.*, 2007; Jacobson and Galat, 2008). If shovelnose sturgeon spawning is cued by pre-dam levels of spring discharge coupled with suitable spawning temperatures, then alterations of spring discharge from river regulation may negatively influence shovelnose sturgeon spawning migrations, gonadal maturation and release of gametes. Changes in dam operations to study the effects of varying discharge and water temperature on sturgeon are often difficult to implement because of economic and social constraints (Beamesderfer and Farr, 1997). However, large-scale manipulative studies are critical to the improvement of environmental management decisions because these studies can match the scale of management and provide results directly applicable to management problems (Carpenter, 1998). We had the opportunity to conduct a large-scale, manipulative experiment in the lower Marias River, Montana, to test the effects of varying discharge and water temperature on shovelnose sturgeon spawning as indexed by embryonic and larval shovelnose sturgeon density. Knowledge of the timing and location of shovelnose sturgeon spawning in relation to variation in discharge and water temperature can provide insight to natural resources managers about the ecological role of these fluctuations and how dams should be operated to optimize water use for environmental (e.g. native fish) and human needs (e.g. flood control). Thus, the objective of this study was to evaluate the effects of contrasting discharge treatments and water temperature variation on spatial and temporal variation in shovelnose sturgeon spawning as indexed by embryonic and larval density in the lower Marias and lower Teton Rivers.

STUDY AREA

The study was conducted near the confluence of the Marias and Teton Rivers near Loma, Montana (Figure 1). The Marias River originates at the confluence of Two Medicine River and Cut Bank Creek approximately 80 km east of Glacier National Park, Montana, and flows 275 km southeast through north-central Montana where it enters the Missouri River at 3302 river kilometers (rkm; as measured from its mouth). The Marias River basin drains 18 485 km^2. Construction of Tiber Dam (129 rkm) on the Marias River was completed in 1957, forming Lake Elwell (USBR, 2010). This reservoir has a storage capacity of 1.920 km^3 and was constructed for flood control, irrigation, recreational use and municipal water supply (Gardner and Berg, 1983). Before impoundment of the Marias River, discharge peaked in the spring (e.g. May or June) because of mountain snowmelt and minimum discharge occurred in late fall and winter (Scott *et al.*, 1997). Currently, discharge in the lower Marias River is almost entirely controlled by the operation of Tiber Dam, and water temperatures downstream from Tiber Dam are reduced from historical levels because of hypolimnetic releases (Gardner and Berg, 1983). However, water releases from Tiber Dam can be a mixture of reservoir surface water (i.e. spillway release), near-surface water (i.e. auxiliary outlet release) and subsurface water (i.e. hypolimnetic river outlet release). The maximum release possible from the hypolimnetic river outlet is 28 m^3/s. Therefore, during high discharge events (i.e. discharge > 60 m^3/s), most of the water released is surface and near-surface water that is closer to ambient temperature than hypolimnetic releases. Peak annual discharge in the lower Marias River has been reduced in nearly every year on record since Tiber Dam was constructed [US Geological Survey (USGS), 2010]. This reduction in peak discharge in the spring allows for augmented discharge during late summer and fall (Rood and Mahoney, 1995).

The Teton River originates at the confluence of the North Fork Teton and South Fork Teton rivers and flows 296 km in a path roughly parallel to that of the Marias River through northcentral Montana. The Teton River drains 5206 km^2 before entering the lower Marias River (1.6 rkm) (Garvin and Botz, 1975; USGS, 2010) (Figure 1). The Teton River is used for irrigation but remains undammed and has historically produced large flood pulses (e.g. 1546 m^3/s in 1964) associated with naturally occurring hydroclimatic variables (Bovee and Scott, 2002; USGS, 2010).

METHODS

Hydrograph treatments

We worked with water managers of Tiber Dam (i.e. US Bureau of Reclamation) to manipulate discharge in the Marias River from 2006 through 2009. Four hydrograph treatments were designed to test the effect of discharge on the timing and location of shovelnose sturgeon spawning: a pulse treatment, a sustained-pulse treatment and two normal treatments. The specific treatment possible in each

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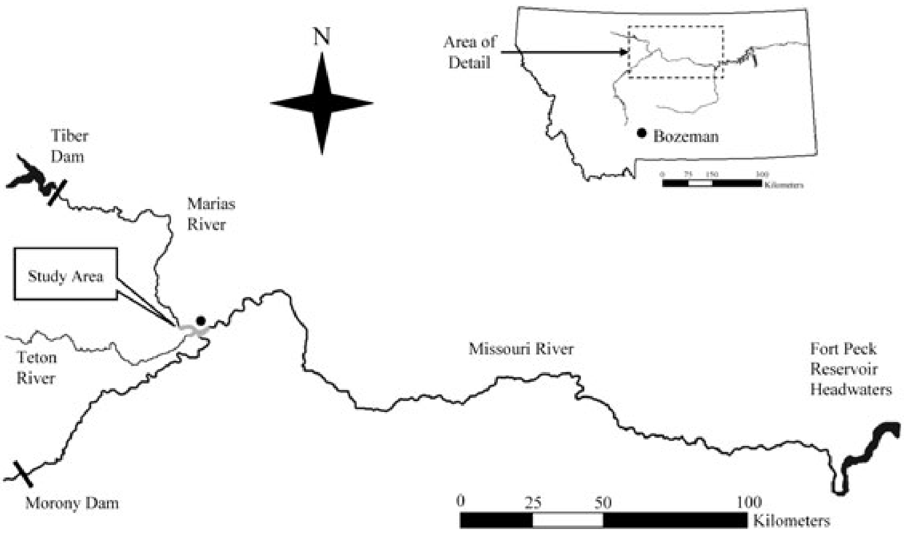

Figure 1. Map of the upper Missouri River, lower Marias River, lower Teton River and the study area (denoted by the grey line)

year was dependent on water availability as determined by reservoir storage. The original plan was to design at least one pulse treatment, taking advantage of a year with ample reservoir storage, and to contrast this treatment with normal dam operations (i.e. normal treatments) where discharge remained low to save water for late-summer irrigation. The planned Marias River hydrograph treatment in 2006 (‘pulse treatment’) represented an increase in the magnitude and duration of elevated discharge relative to normal Tiber Dam operations. The planned timing and magnitude of elevated discharge in 2006 was modelled after the 1982 hydrograph upstream of Tiber Reservoir (USGS, 2010). This hydrograph was selected because it best represented the average of several years of hydrograph data. In 2008, a fortuitous increase in late-spring precipitation allowed for planning an additional experimental hydrograph treatment similar to the 2006 pulse treatment, but with a decreased magnitude of peak discharge and a protracted duration of increased discharge after the peak (‘sustained-pulse treatment’). The 2007 and 2009 planned hydrograph treatments (‘normal treatments’) represented normal operation of Tiber Dam. Hydrograph treatments could not be implemented on the Teton River because it is unregulated. Discharge variation in the Teton River was caused by annual variation in hydroclimatic variables and irrigation withdrawals.

Sampling sites

In 2006 and 2007, embryonic and larval shovelnose sturgeon were sampled at five fixed sites in the lower 11 rkm of the Marias River. Sampling was conducted at river bends that were selected subjectively to evaluate spatial variation in embryonic and larval sturgeon density relative to suspected shovelnose sturgeon spawning locations (i.e. large riffles). Shovelnose sturgeon spawning locations have not been previously documented; however, riffles were suspected as spawning habitat because other sturgeon species are known to spawn in river locations with gravel, cobble, boulder or bedrock substrate (Wildhaber *et al.*, 2007) and with high relative velocity (e.g. Parsley *et al.*, 1993). Sampling locations were immediately upstream and downstream of two large riffles representing potential shovelnose sturgeon spawning locations. In addition, sampling was conducted upstream and downstream of the Teton River confluence to estimate spatial and temporal variation in embryonic and larval sturgeon density in the Marias River relative to input from the Teton River. In 2008 and 2009, sampling was only conducted at two of the five Marias River sampling sites (i.e. the sites immediately upstream and downstream of the Teton River) because of logistical constraints. Two subsamples were conducted per sampling occasion at each fixed site in the Marias River: one subsample in the outside bend and one subsample mid-channel.

From 2006 through 2009, embryonic and larval shovelnose sturgeon were sampled at one fixed site located at the first bend in the Teton River (0.2 rkm) to compare spatial and temporal variation in embryonic and larval fish density between the Marias and the Teton Rivers. During part of 2006 and all of 2007, discharge in the Teton River was too low to acquire accurate measures of density because water velocities were outside the velocity range for the flowmeters used (i.e. General Oceanics, Model 2030R). However, no embryonic or larval sturgeon were sampled on dates when discharge was too low to accurately measure; therefore, all nonzero density measurements were accurate.

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Embryonic and larval sturgeon collection

Embryonic and larval shovelnose sturgeon density in the Marias and Teton Rivers was used as an index to shovelnose sturgeon spawning and was estimated using plankton net sampling. Shovelnose sturgeon spawn in the upper Missouri River basin from late May to mid-July (Berg, 1981). Thus, from 2006 through 2009, plankton net samples were collected about every 3 to 4 days at fixed sampling locations from late May to mid-July in the Marias and Teton Rivers. The 3- to 4-day intervals between sampling occasions were selected because typical hatch times for shovelnose sturgeon are from 4 to 8 days at water temperatures from 16 °C to 20 °C (K. M. Kappenman and M. A. H. Webb, US Fish and Wildlife Service, unpublished data; Colombo *et al*., 2007). Thus, if shovelnose sturgeon spawned, then it was likely that either embryos or larvae would be present during the following sampling event.

Sampling gear consisted of two plankton nets: one conical plankton net (0.20-m^2 opening) and one rectangular plankton net (0.20-m^2 opening), each with 1.5 m of 750-μm mesh with an attached 750-mL collection cup and weighted with a 4.5-kg lead weight. Nets were set near the riverbed to increase efficiency of sampling for larval shovelnose sturgeon and pallid sturgeon because their density is greatest in the lower 0.5 m of the water column (Braaten *et al*., 2008). The efficiency of plankton nets for sampling shovelnose sturgeon embryos before hatching is unknown, but it is likely less than for larval sturgeon because prehatched embryos become adhesive after fertilization and typically adhere to the substrate rather than drift (Jacobson and Galat, 2008). However, the embryos sampled in this study were often coated in fine substrate (e.g. sand) or debris, which likely allowed them to drift along the riverbed. Density data from paired samples using different net types were pooled for all data analyses. The pooled sample was considered a subsample for each fixed site sample. Sampling duration was inversely proportional to the water velocity and the rate of debris accumulation and varied from 2 to 20 min among samples. Each net was fitted with a flowmeter (Model 2030R; General Oceanics, Inc., Miami, FL, USA) to estimate water velocity and volume of water sampled. Subsamples were placed in Whirl-Pak® bags (Nasco, Fort Atkinson, WI, and Modesto, CA, USA), preserved in 10% formalin and dyed with Phloxine B dye. Shovelnose sturgeon larvae and embryos were removed from the debris and placed in vials containing 70% ethanol. Shovelnose sturgeon counts were converted to density at a fixed site using volume estimates from the flowmeters and net dimensions.

Estimates of daily discharge (m^3/s) in the Marias and Teton Rivers were provided by the USGS gauging stations at Loma, Montana. Water temperature (°C) was measured hourly from April to August during 2006–2009 using a continuous-reading temperature logger placed in the Marias River (2 rkm). Estimates of mean daily water temperature in the Teton River were also provided by the USGS gauging station at Loma, Montana.

Spawning date estimation

Sampled embryos and larvae were used to estimate shovelnose sturgeon spawning dates. Spawning dates were estimated by subtracting the time required to reach the observed stage of development at a given temperature from the time of collection. An interval of time required to reach the observed stage of development was estimated based on the rates of embryonic shovelnose sturgeon development (K. M. Kappenman and M. A. H. Webb, unpublished data). The stage of embryonic and larval development was determined using descriptions of developmental stages from Dettlaff *et al*. (1993) and Colombo *et al*. (2007). Chorions were removed from sampled shovelnose sturgeon embryos to facilitate identification of development stage.

Laboratory studies suggest that water temperatures from 12 °C to 24 °C are suitable for successful shovelnose sturgeon spawning and embryo survival in natural conditions (K. M. Kappenman and M. A. H. Webb, unpublished data). In addition, embryonic development rate and metabolic efficiency (conversion of yolk sac to tissue) in shovelnose sturgeon embryos were greatest from 16 °C to 20 °C, suggesting that these water temperatures are optimal for shovelnose sturgeon spawning and embryo development (K. M. Kappenman and M. A. H. Webb, unpublished data). These water temperature thresholds were used to estimate the availability of suitable and optimal water temperatures for shovelnose sturgeon spawning during hydrograph treatments.

There is a possibility that some of the embryos and larvae called shovelnose sturgeon in this study were actually pallid sturgeon or paddlefish. The chondrostean fishes present in the Missouri River basin include shovelnose sturgeon, pallid sturgeon and paddlefish. Embryos of these fishes cannot be distinguished by morphology, and all of our samples were preserved in formalin, which eliminates the possibility of using genetics to identify species. However, we are confident that all chondrostean embryos collected in the current study are *Scaphirhynchus* spp. embryos (i.e. shovelnose sturgeon or pallid sturgeon) because previous studies have found no evidence of paddlefish spawning in, or use of, the study reach (Berg, 1981; Gardner, 1997), and all larval chondrosteans collected in the current study were identified as *Scaphirhynchus* spp. Further, it is unlikely that embryonic and larval *Scaphirhynchus* spp. are pallid sturgeon as evidence of natural recruitment to the pallid sturgeon population in this river section has not been documented for more than 30 years and abundance has been estimated at 50 adults (Gardner, 1997). In addition, no radio-tagged adult

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pallid sturgeon came within 100 km of the Marias River during a concurrent pallid sturgeon telemetry study (Gardner and Jensen, 2007; Gardner and Jensen, 2008; Jensen and Gardner, 2009). In contrast, radio-tagged adult shovelnose sturgeon were located in the Marias River throughout this study (Gardner and Jensen, 2007; Gardner and Jensen, 2008; Jensen and Gardner, 2009).

RESULTS

Hydrograph treatments

In the 2006 pulse treatment, spring discharge reached the greatest magnitude of the 4 years (Figure 2), but the duration of increased magnitude was relatively short (i.e. 17 days). Peak discharge was 184% (134 m^3/s; 2006), 19% (14 m^3/s; 2007), 162% (118 m^3/s; 2008) and 27% (20 m^3/s; 2009) of the average of peak annual discharge for the Marias River from 1958 to 2005 (i.e. after the construction of Tiber Dam) (USGS, 2010). The mean discharge values from 1 June to 31 July were 78% (2006), 31% (2007), 98% (2008) and 42% (2009) of the average discharge from 1 June to 31 July in the Marias River from 1958 to 2005 (USGS, 2010).

The mean daily water temperature during the Marias River hydrograph treatments varied among 2006 (mean, 20 °C; range, 13 °C – 24 °C), 2007 (mean, 22 °C; range, 14 °C–27 °C), 2008 (mean, 19 °C; range, 11 °C–23 °C) and 2009 (mean, 20 °C; range, 12 °C–24 °C). The 2006 hydrograph peaked later (16 June) than that in 2008 (9 June), and the mean water temperature in conjunction with peak discharge was greater in 2006 (16 °C) than that in 2008 (14 °C) (Figure 2). In addition, water temperature decreased in conjunction with both peaks in discharge (Figure 2). The annual number of days that suitable and optimal spawning temperatures were present in the Marias River varied among treatments. From 29 May to 17 July (i.e. the shovelnose sturgeon spawning date range observed in this study), suitable shovelnose sturgeon spawning temperatures (i.e. 12 °C–24 °C) occurred for 50 days in 2006, 38 days in 2007, 49 days in 2008 and 50 days in 2009, and optimal shovelnose sturgeon spawning temperatures (i.e. 16 °C–20 °C) occurred for 21 days in 2006, 17 days in 2007, 15 days in 2008 and 17 days in 2009 (Figure 2).

Contrasting patterns of annual discharge occurred in the Teton River from 2006 to 2009 (Figure 3). Similar to the Marias River annual hydrographs, noticeable spikes in spring discharge (i.e. ≥10 m^3/s) occurred in the Teton River in early June in 2006 and 2008, whereas discharge remained low (i.e. <5 m^3/s) in 2007 and 2009 (Figure 3). Historical discharge data for this portion of the Teton River are unavailable. Discharge reached 0 m^3/s in 2006 and 2007 when portions of the river channel were dry (Figure 3).

Water temperature in the Teton River when discharge was greater than zero varied among 2006 (mean, 21 °C; range, 14 °C–26 °C), 2007 (mean, 19 °C; range, 12 °C–25 °C), 2008 (mean, 19 °C; range, 11 °C–26 °C) and 2009 (mean, 21 °C; range, 13 °C–24 °C) (Figure 3). The 2006 hydrograph peaked

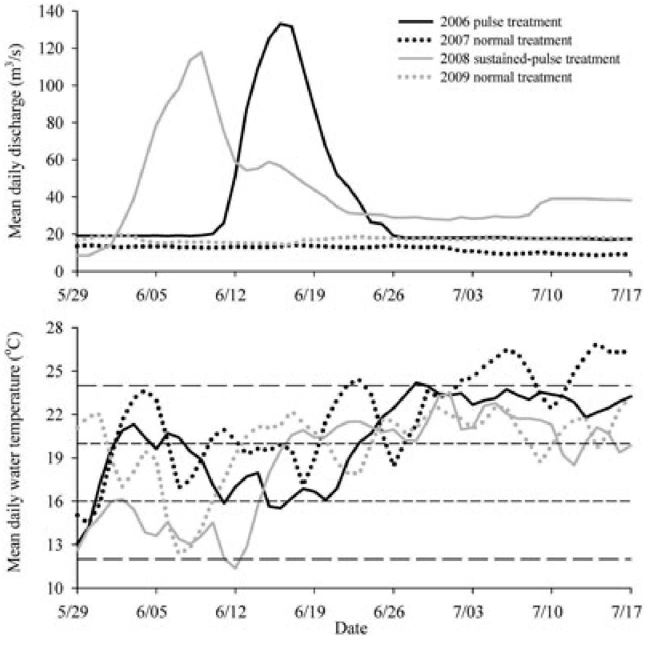

Figure 2. Mean daily discharge (top) and water temperature (bottom) in the Marias River at Loma, Montana (2 rkm), from 29 May to 17 July in 2006, 2007, 2008 and 2009. Dashed lines denote optimal (short dash) and suitable (long dash) shovelnose sturgeon spawning temperature ranges

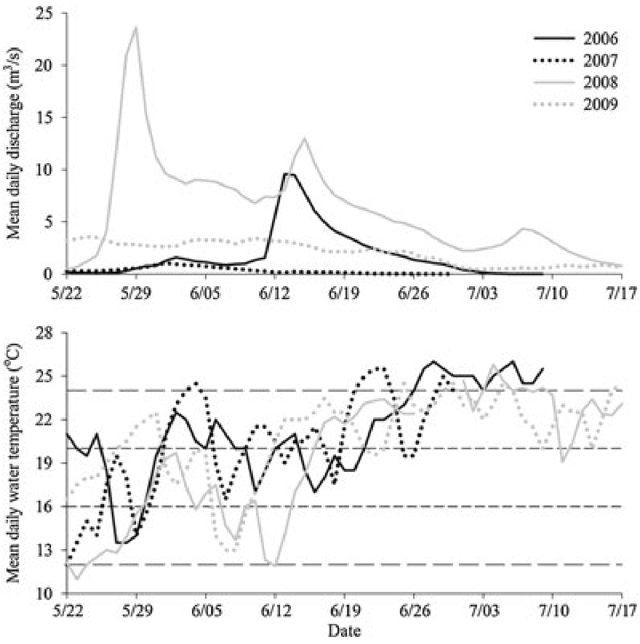

Figure 3. Mean daily discharge (top) and water temperature (bottom) in the Teton River at Loma, Montana (0.7 rkm), from 22 May to 17 July in 2006, 2007, 2008 and 2009. Dashed lines denote optimal (short dash) and suitable (long dash) shovelnose sturgeon spawning temperature ranges

at a later date (13 June) than the 2008 hydrograph (29 May), and water temperature was greater in conjunction with the 2006 peak (21 °C) than the 2008 peak (16 °C) (Figure 3). During the secondary discharge spike in 2008 (15 June), mean daily water temperature was 18 °C (Figure 3). In the Teton River, decreases in water temperature did not coincide with hydrograph peaks (Figure 3). From 29 May to 17 July (or the day when discharge reached zero) in each sampling year, water temperatures were suitable for shovelnose sturgeon spawning for 30 days (2006), 22 days (2007), 43 days (2008) and 46 days (2009), and water temperatures were optimal for shovelnose sturgeon spawning for 15 days (2006), 9 days (2007), 16 days (2008) and 13 days (2009).

Shovelnose sturgeon density and timing of spawning

During the 2006 pulse treatment, two shovelnose sturgeon embryos and 23 shovelnose sturgeon larvae were sampled in the Marias River (Table 1). Both shovelnose sturgeon embryos were sampled on 18 June in 2006 and were at developmental stages 26–29 (Table 1; Figure 4). All shovelnose sturgeon larvae collected in the Marias River in 2006 were aged at 0–24 h after hatch (i.e. protolarval) and were captured 4 to 8 days after the shovelnose sturgeon embryos were collected (Table 1; Figure 4). Mean larval shovelnose sturgeon density was greatest on 22 June, 6 days after peak discharge. The sampling period during each year included approximately 50 days (i.e. late May to mid-July). Water temperatures were optimal for shovelnose sturgeon spawning (i.e. 16 °C–20 °C) on 21 of 50 days during the pulse treatment and occurred in conjunction with the discharge pulse (i.e. 5 days before and 7 days after peak discharge) (Figure 4). It was estimated that shovelnose sturgeon spawned in conjunction with the ascending, peak and descending portions of the pulse treatment (11 June to 22 June) coupled with water temperatures optimal for shovelnose sturgeon spawning (16 °C to 19 °C) in the Marias River in 2006 (Figure 4).

In contrast to the pulse treatment in 2006, no shovelnose sturgeon embryos or larvae were sampled in the Marias River during the 2007 and 2009 normal treatments. Embryos and larvae were absent from samples despite the occurrence of water temperatures suitable (38 of 50 days in 2007 and all 50 days in 2009) and optimal (17 of 50 days in 2007 and 2009) for shovelnose sturgeon spawning (Figure 2).

In 2008, four shovelnose sturgeon embryos were collected in the Marias River during the sustained-pulse treatment from 3 July to 16 July (Table 1; Figure 4). In addition, 78 shovelnose sturgeon protolarvae were collected from 20 June to 16 July (Table 1; Figure 4). The density of shovelnose sturgeon embryos peaked on 3 July, whereas larval density peaked on 7 July (Figure 4). An early spike in larval shovelnose sturgeon density occurred on 20 June, 11 days after peak discharge. In addition, a late spike in larval density occurred on the last sampling occasion (16 July) after a late-season increase in discharge (i.e. from 29 m^3/s on 7 July to 39 m^3/s on 10 July). Estimated fertilization dates indicate that shovelnose sturgeon spawned in the Marias River during the sustained-pulse treatment from 9 June to16 July. Water temperatures were suitable (49 of 50 days) and optimal (15 of 50 days) for shovelnose sturgeon spawning on fewer days in 2008 compared with 2006 (Figure 4). Nonetheless, an evidence of shovelnose sturgeon spawning was found on more sampling occasions and was associated with increased discharge (relative to normal treatments) and with mean daily water temperatures from 11 °C to 23 °C (Table 1; Figure 4).

For all years in the Marias River, mean water temperatures during development of all larval shovelnose sturgeon sampled varied from 16 °C to 22 °C (Table 1). On the basis of development rates at temperatures from 16 °C to 22 °C, shovelnose sturgeon spawning events that produced these larvae likely occurred 3 to 9 days before collection. Shovelnose sturgeon larvae were absent from all 33 samples collected when mean discharge in the Marias River (for the period 3 to 9 days prior) was from 10 to 27 m^3/s, despite the occurrence of suitable and optimal shovelnose sturgeon spawning temperatures in conjunction with these discharge

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Table I. Estimates of fertilization timing for shovelnose sturgeon embryos and larvae collected in the Marias and Teton Rivers in 2006 and 2008

Location	Year	Day	Mean temperature (°C)	Embryos	Developmental stage	Larvae	Developmental stage	Hours after fertilization
Marias River	2006	6/18	16.4	2	26–29	0		52–95
		6/22	16.8	0		18	0–24 h after hatch	87–264
		6/23	17.0	0		4	0–24 h after hatch	87–264
		6/26	18.9	0		1	0–24 h after hatch	87–225
	2008	6/20	17.7	0		7	0–24 h after hatch	87–264
		6/23	19.8	0		2	0–24 h after hatch	87–225
		7/3	22.1; 21.5	3	14–32	2	0–24 h after hatch	17–174
		7/7	22.2	0		28	0–24 h after hatch	72–174
		7/10	21.8	0		8	0–24 h after hatch	72–174
		7/16	19.6; 20.2	1	12	17	0–24 h after hatch	11–174
Teton River	2006	6/23	19.3	0		1	0–24 h after hatch	87–225
	2008	6/9	16.7	0		1	0–24 h after hatch	87–264
		6/16	15.5	0		1	0–24 h after hatch	153–351
		6/20	18.8	0		10	0–24 h after hatch	87–225
		6/23	21.8	0		2	0–24 h after hatch	72–174

Developmental stages of embryos and larvae were estimated using descriptions of development from Dettlaff *et al*. (1993) and Colombo *et al*. (2007).

levels (Figure 5). However, when suitable and optimal spawning temperatures occurred in conjunction with mean discharge from 28 to 112 m^3/s in the Marias River, larval shovelnose sturgeon were sampled (i.e. evidence of spawning was found) on 8 of 15 sampling occasions (Figure 5). The greatest mean density of larval shovelnose sturgeon in the Marias River occurred after the period of greatest mean discharge was coupled with optimal shovelnose sturgeon spawning temperatures (Figure 5).

One shovelnose sturgeon protolarva (0–24 h after hatch) was sampled in the Teton River on 23 June 2006, 10 days after the occurrence of peak discharge (Table 1; Figure 6). The estimated fertilization date for this larva (14 June to 19 June) indicates that shovelnose sturgeon spawned in conjunction with the descending limb of the spring hydrograph coupled with water temperatures suitable or optimal for shovelnose sturgeon spawning (17 °C–21 °C) (Table 1; Figure 6). In 2007, no embryonic or larval shovelnose

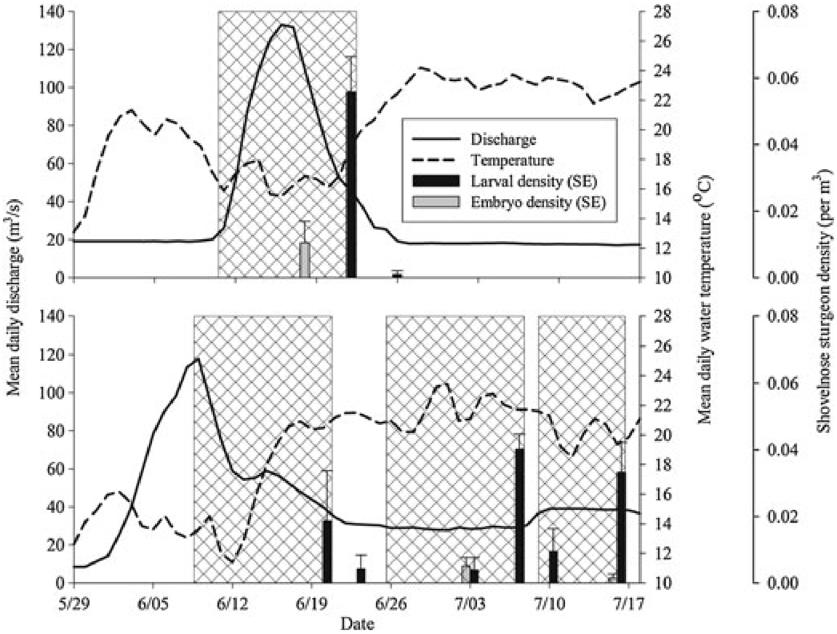

Figure 4. Mean daily discharge, water temperature and larval sturgeon density in the Marias River at Loma, Montana (2 rkm), in 2006 (top panel) and 2008 (bottom panel). The crosshatched areas delineate the spawning periods for shovelnose sturgeon estimated from analysis of developmental stages of shovelnose sturgeon embryos and larvae

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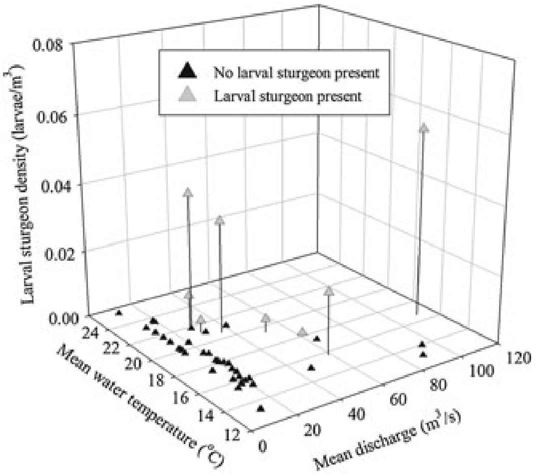

Figure 5. Mean daily larval shovelnose sturgeon density in the Marias River (all years) as a function of mean discharge and water temperature. Means of discharge and water temperature are from the period 3 to 9 days before each sampling day

sturgeon were sampled in the Teton River; however, sampling only occurred on 4 days because of low discharge. Conversely, discharge was relatively high in the Teton River in 2008, and 14 shovelnose sturgeon protolarvae (0 to 24 h after hatch) were collected from 9 June to 23 June (Table 1). Larval shovelnose sturgeon were first sampled on 9 June after peak discharge (Figure 6). Larval density peaked on 20 June, 5 days after a secondary spike in discharge (Figure 6). Estimated fertilization dates indicate that shovelnose sturgeon spawned in the Teton River in 2008 (30 May to 20 June) in conjunction with the descending limb of the spring hydrograph coupled with water temperatures suitable or optimal for shovelnose sturgeon spawning (12 °C–22 °C) (Table 1; Figure 6). Similar to 2007, no embryonic or larval shovelnose sturgeon were sampled in the Teton River in 2009 when discharge remained <5 m^3/s. Embryos and larvae were absent from samples despite water temperatures suitable (46 of 50 days) and optimal (13 of 50 days) for shovelnose sturgeon spawning (Figure 3).

DISCUSSION

The results of this study suggest that shovelnose sturgeon spawning is influenced by discharge in the Marias and Teton Rivers, tributaries to the Missouri River. Shovelnose sturgeon spawning in both rivers was initiated in conjunction with peak spring discharge, suggesting that increased discharge provided a spawning cue. The lack of shovelnose sturgeon spawning in the Marias and Teton Rivers in 2007 and 2009 when discharge was low provides further evidence that discharge influences spawning. The timing of peak shovelnose sturgeon spawning relative to peak discharge varied between treatments in the Marias River and was likely related to water temperature. During the pulse treatment, larval shovelnose sturgeon density peaked 6 days

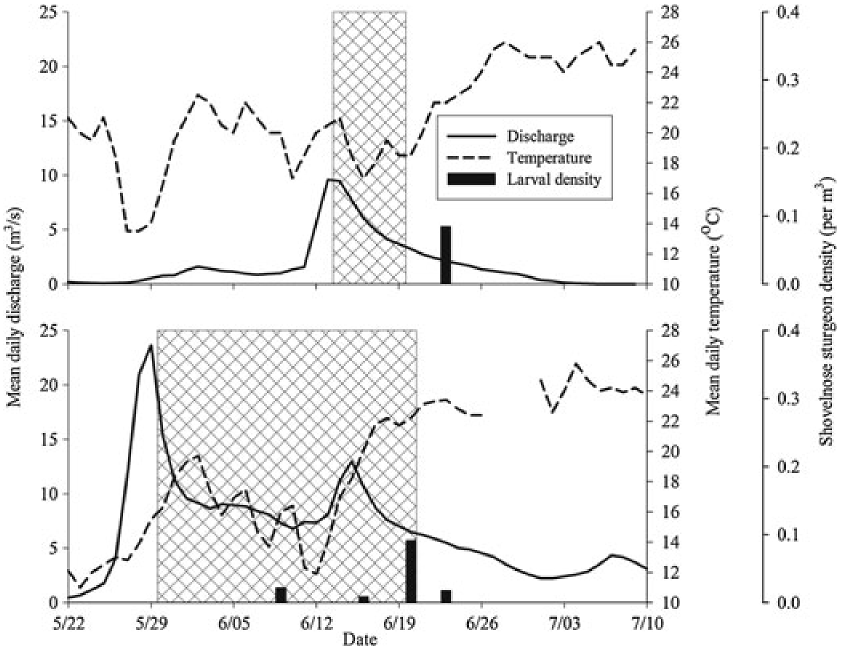

Figure 6. Mean daily discharge and water temperature (gap represents missing data) in the Teton River (0.7 rkm) from 29 May to 10 July in 2006 (top panel) and 2008 (bottom panel). The crosshatched areas delineate the spawning periods for shovelnose sturgeon estimated from analysis of developmental stages of shovelnose sturgeon larvae

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after peak discharge. In contrast, larval shovelnose sturgeon density peaked later during the sustained-pulse treatment when water temperature had stabilized and elevated discharge was maintained. Colder water temperatures during peak discharge and immediately after peak discharge during the sustained-pulse treatment may have contributed to the later peak in shovelnose sturgeon spawning. Interestingly, water temperature in the Marias River was suitable for shovelnose sturgeon spawning for most the normal treatments but was not coupled with an increase in discharge. This decoupling was likely the mechanism for the lack of shovelnose spawning in the Marias River during the normal treatments. Thus, these data suggest that there is an interaction between discharge and water temperature in their effects on shovelnose sturgeon spawning (i.e. without the necessary level of discharge, temperature alone does not cue spawning in the Marias River). Previous studies have indirectly linked shovelnose sturgeon spawning with increased spring discharge (Elser *et al*., 1977; Berg, 1981; Mayden and Kuhajda, 1997) and water temperature (Christenson, 1975; Elser *et al*., 1977; Moos, 1978; Berg, 1981); however, a direct link between shovelnose sturgeon spawning and coupling of increased discharge with suitable water temperature has not been previously documented (DeLonay *et al*., 2007; Wildhaber *et al*., 2007; Jacobson and Galat, 2008). This is the first study we are aware of that used discharge treatments to experimentally test the effects of discharge on shovelnose sturgeon spawning.

As a result of the association between increased discharge and increased density of shovelnose sturgeon embryos and larvae, the question arises as to whether this association was a sampling artefact resulting from augmented discharge increasing sampling efficiency rather than evidence of increased spawning activity. Although sampling efficiency for shovelnose sturgeon embryos and larvae was not directly measured in this study, an alteration of sampling efficiency caused by increased discharge is an unlikely explanation for the observed increases in embryonic and larval shovelnose sturgeon density. Larval density in the Marias and Teton Rivers peaked after the peak in discharge and on the descending limb of the hydrograph in 2006. Further, the peak larval density in the Marias River in 2008 was at the lowest level of discharge available in 2008 rather than at the peak. In addition, it seems more likely that increased discharge would decrease sampling efficiency rather than increase it as the area available for embryos and larvae to bypass plankton nets increases with increasing discharge. Further, the increased use of the Marias River for spawning by shovelnose sturgeon during the pulse and sustained-pulse treatments in this study is also corroborated by the results of a concurrent radio-telemetry study of adult shovelnose sturgeon. In this concurrent study, a greater proportion of radio-tagged adult shovelnose sturgeon moved into the Marias River during the pulse treatment (9 of 34; 26%) and the sustained-pulse treatment (11 of 88; 13%) than during the 2007 normal treatment (2 of 55; 4%) (Gardner and Jensen, 2007; Gardner and Jensen, 2008; Jensen and Gardner, 2009). In addition, experiments in both laboratory (Kynard *et al*., 2002) and field (Braaten *et al*., 2008) conditions suggest that shovelnose sturgeon larvae (especially 0- to 2-day posthatch shovelnose sturgeon larvae) drift in the lower 0.5 m of the water column at various water velocities. Thus, although it is possible that sampling efficiency was affected by varying discharge, the increases in embryonic and larval density during the pulse and sustained-pulse treatments were most likely caused by increased spawning activity than by changes in sampling efficiency.

The cause of the temporal gaps between estimated spawning periods reported in this study (e.g. two gaps during the sustained-pulse treatment) are unknown. During the sustained-pulse treatment in the Marias River, the early spike in larval shovelnose sturgeon density may have been influenced by spawning in the Teton River as the density of larval shovelnose sturgeon was greater downstream of the Teton River than upstream (Goodman, 2009). In addition, the density of larval shovelnose sturgeon in the Teton River peaked on the same day as the early spike in larval shovelnose sturgeon density in the Marias River. The late peak in larval shovelnose sturgeon density (mid-July) in conjunction with water temperatures at the upper end of the optimal spawning temperature range during the sustained-pulse treatment may have been related to the rapid increase in water temperature that occurred in conjunction with the descent from peak discharge. For example, lake sturgeon spawning is often delayed until water temperature reaches the upper end of their optimal spawning temperature range in years with a rapid increase in water temperature (Bruch and Binkowski, 2002). In addition, some female lake sturgeon are predisposed to spawn at the lower end of the optimal spawning temperature range, whereas others are predisposed to spawn at the middle or upper end of this range (Bruch and Binkowski, 2002). Such temporal variation in spawning may be related to variation in endogenous reproductive rhythm among individual females (e.g. Webb *et al*., 2001).

The lack of embryonic and larval shovelnose sturgeon in the Marias River during the normal hydrograph treatment suggests that there is a discharge threshold that cues shovelnose sturgeon spawning in the Marias River. Shovelnose sturgeon spawned in the Marias River when discharge ≥ 28 m^3/s was coupled with suitable and optimal spawning temperatures. The occurrence of suitable and optimal spawning temperatures during the normal hydrograph treatment and the corresponding absence of larval shovelnose sturgeon suggest that water temperature alone does not provide a cue for shovelnose sturgeon spawning in the Marias River. Rather, these results suggest that suitable or optimal shovelnose sturgeon spawning temperatures must be coupled with a threshold level of discharge (e.g. 28 m^3/s) to provide a spawning cue. The Marias River may not be suitable for shovelnose sturgeon spawning use when discharge is less than 28 m^3/s. Interestingly, shovelnose sturgeon spawned in the Teton River when discharge was less than 28 m^3/s (i.e. as low as 4 m^3/s in 2006 and 7 m^3/s in 2008). These data suggest that the discharge threshold for shovelnose sturgeon spawning is river specific (e.g. a percentage of bankfull discharge). For example, it is possible that low discharge may render spawning adults more vulnerable to predation and stranding, or that suitable spawning habitat is not available at baseflows. Another possibility is that the changes in water velocity or turbidity associated with increased discharge influence spawning habitat selection by shovelnose sturgeon. For example, white sturgeon spawn in the swiftest water available in the Columbia River (Parsley *et al*., 1993).

Shovelnose sturgeon also spawned in the section of the Missouri River adjacent to the Marias River (Goodman, 2009). In the Missouri River upstream of the Marias River, larval shovelnose sturgeon density was greater in 2007 than that in 2006 despite similar patterns of variation in discharge and water temperature between years (Goodman, 2009). In addition, shovelnose sturgeon spawned in the upper Missouri River above Fort Peck Reservoir under highly different discharge patterns in 2008 and 2009, suggesting that discharge is less important as a cue for spawning in the main stem Missouri River (Richards, 2011). The decoupling of increased discharge and suitable spawning temperature in the Marias River in 2007 may have caused an increase in the use of the Missouri River for spawning by shovelnose sturgeon. Thus, the selection of tributary rather than main stem habitat for spawning by shovelnose sturgeon in the upper Missouri River basin may be dependent on the coupling of increased discharge with suitable spawning temperatures. The use of tributaries for spawning by shovelnose sturgeon has been reported elsewhere (e.g. Cross, 1967; Elser *et al*., 1977; Berg, 1981; Bramblett and White, 2001; Engel *et al*., 2006). However, the effects of discharge and water temperature coupling on use of tributaries for spawning by shovelnose sturgeon have not been previously documented (Jacobson and Galat, 2008).

The relative use of the Marias River compared with the Missouri River for spawning by shovelnose sturgeon is unknown. Recent data suggest that larval shovelnose sturgeon drift for long periods before settling out in their preferred habitat (e.g. Braaten *et al*., 2008). The uppermost portions of the upper Missouri River basin allow for the greatest drift distances before arrival at Fort Peck Reservoir headwaters where the survival of passively drifting larvae may be compromised. Thus, it is possible that the Marias River and the Missouri River upstream of the Marias River contain the most important spawning habitat for shovelnose sturgeon upstream of Fort Peck Reservoir.

Shovelnose sturgeon spawning at mean discharge from 28 to 112 m^3/s in the Marias River, coupled with suitable shovelnose sturgeon spawning temperatures, suggests that discharge must reach a threshold level in the Marias River to provide a cue for shovelnose sturgeon spawning. Maintaining spring discharge above this threshold level in the Marias River may increase the duration of shovelnose sturgeon spawning activity. These results suggest that water management in regulated tributaries in the Missouri River basin should include the coupling of an increase in discharge with suitable spawning temperatures for shovelnose sturgeon, if maintaining shovelnose sturgeon spawning is a management goal for these rivers. River regulation that reduces spring discharge can decrease the amount of available spawning habitat for shovelnose sturgeon and may negatively affect the spawning success of shovelnose sturgeon. River managers and fishery managers can also use the information from this study to better manage multiple resources. Shovelnose sturgeon are a long-lived species and do not necessarily require annual recruitment to persist. Even periodic spring discharge that provided intermittent recruitment could be beneficial to a shovelnose sturgeon population. Managers could take advantage of years when precipitation is high and water is readily available for multiple uses to discharge water at the levels we suggest. In addition, managers may wish to provide a sustained pulse when possible to extend the spawning season. An extended spawning season may allow early, middle and late spawners (e.g. fish with different endogenous cycles) an opportunity to produce offspring. Furthermore, the conditions that promote shovelnose sturgeon spawning might be beneficial to other coevolved fish species of the Missouri River basin (e.g. pallid sturgeon).

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