



Spawning related movement of shovelnose sturgeon in the Missouri River above Fort Peck Reservoir, Montana

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Summary

The hypotheses of this study were (i) that shovelnose sturgeon would make upstream movements to spawn, (ii) movement of spawning fish would be greater in a year with higher discharge, and (iii) that spawning fish would have greater movements than reproductively inactive fish. Shovelnose sturgeon *Scaphirhynchus platyrhynchus* (Rafinesque, 1820) in five reproductive categories (e.g. males, confirmed spawning females, potentially spawning females, atretic females, and reproductively inactive females) were tracked in 2008 and 2009. All reproductive categories, except reproductively inactive females, exhibited large-scale movements and had omnidirectional movements. No differences in movement rates were observed in confirmed spawning females between years despite a 45% higher peak discharge in 2008 ($839 \text{ m}^3 \text{ s}^{-1}$) than in 2009 ($578 \text{ m}^3 \text{ s}^{-1}$). A peak discharge was obtained at a faster rate in 2008 ($165 \text{ m}^3 \text{ s}^{-1} \text{ day}^{-1}$) than in 2009 ($39 \text{ m}^3 \text{ s}^{-1} \text{ day}^{-1}$), and high discharge was of greater duration in 2008. Reproductively inactive females did not exhibit large-scale movements and their movement rate differed from other reproductive categories. Shovelnose sturgeon spawned in both years, despite highly varying hydrographs between years.

Introduction

Many aquatic species have evolved life-history strategies in direct response to natural discharge regimes, with discharge linked to reproduction, larval survival, growth, and recruitment (Bunn and Arthington, 2002). Shovelnose sturgeon *Scaphirhynchus platyrhynchus* have been indigenous to the large, turbid rivers of the Missouri and Mississippi river basins for millions of years (Bailey and Cross, 1954) and have a life-history strategy that is dependent on the conditions of the environment (Wildhaber et al., 2011a). Dams and impoundments can fragment aquatic habitat, as well as alter and decouple natural discharge and water temperature regimes, reduce sediment transport, and disconnect the floodplain from the river channel (Junk et al., 1989; Sparks et al., 1990; Stanford et al., 1996; Poff et al., 1997). Although most shovelnose sturgeon populations are stable, some are in decline or extirpated (Koch and Quist, 2010). Discharge alteration due to dams is implicated as a primary cause (Keenlyne, 1997).

Changes in discharge and water temperature associated with the spring pulse are believed to cue spawning migrations in adult sturgeons (Becker, 1983; Keenlyne and Jenkins, 1993; DeLonay et al., 2009). Reproductively active sturgeon can fail

to spawn if the environmental cues of discharge and water temperature are absent (Auer, 2004), and in the Marias River, a tributary to the main stem Missouri River, shovelnose sturgeon have been shown to initiate spawning only when a threshold discharge was reached (Goodman, 2009). The construction and operation of dams on the Missouri River has altered and decoupled the putative environmental spawning cues of discharge and water temperature thought to initiate spawning in shovelnose sturgeon (Galat et al., 2001). Prior to dam construction, the Missouri River hydrograph was characterized by a large, highly variable spring pulse that is now more constant and reduced in magnitude and duration (Hesse and Mestl, 1993; Galat and Lipkin, 2000; Pegg et al., 2003).

The purpose of this study was to document spawning related movements of shovelnose sturgeon through the spring and early summer of the upper Missouri River and identify possible spawning locations relative to available larval drift distance. The specific objectives were to (i) compare the movements of spawning shovelnose sturgeon between years with differing spring hydrographs, (ii) compare movements among different reproductive categories, and (iii) document spawning locations of female shovelnose sturgeon relative to larval drift distance. Based on what is currently known and hypothesized regarding shovelnose sturgeon reproductive biology, we hypothesized that shovelnose sturgeon would make upstream movements to spawn, movement of spawning fish would be greater in a year with higher discharge, and that spawning fish would have greater movements than reproductively inactive fish.

Study area

The study area is located in north central Montana and includes the Missouri River from a point approximately 10 km upstream of Fort Benton, Montana (river kilometer [rkm] 3,350; all rkm measurements given as upstream distance from the nearest confluence), to approximately 40 km upstream of the headwaters of Fort Peck Reservoir (rkm 3,040) (Fig. 1). This section of the Missouri River was selected because it represents the majority of main stem shovelnose sturgeon habitat between Morony Dam (rkm 3,388) and the headwaters of Fort Peck Reservoir (rkm 3,000). Several dams exist in the Missouri River system upstream of the study area, with three dams operated by the U.S. Bureau of Reclamation (USBR) having the most effect on riverine flow and habitat (Gardner and Jensen, 2011). These include Canyon Ferry Dam on the Missouri River near Helena, MT (rkm 3,626),

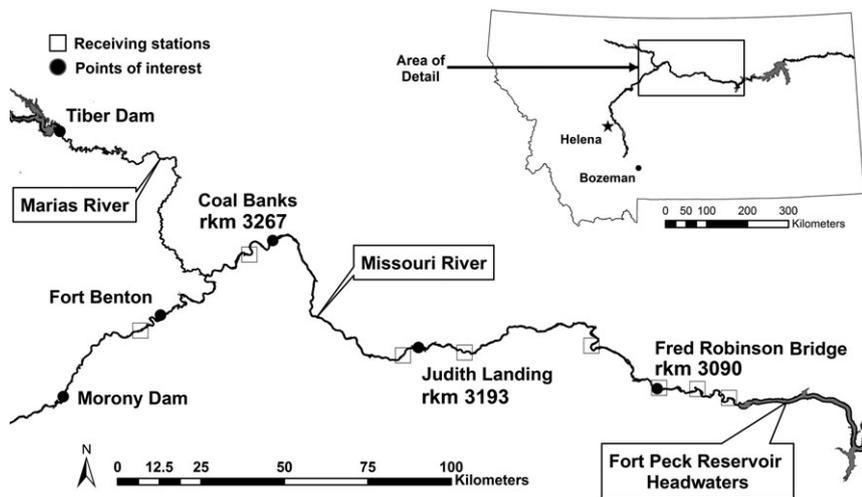


Fig. 1. Map of Missouri and Marias rivers in Montana, with study area in detail. River kilometer (rkm) measurements denote upstream distance from confluence with the Mississippi River.

Tiber Dam, on the Marias River near Chester, MT (rkm 129), and Gibson Dam (rkm 163) on the Sun River (Gardner and Jensen, 2011). Operation of these dams has altered the temperature and sediment transport regimes and moderated the peaks and troughs of the average hydrograph, but timing of peak discharge is similar to pre-impoundment conditions (Bellgraph et al., 2008). Although the peaks and troughs of the hydrograph are moderated by these dams, the Missouri River above Fort Peck Reservoir is considered the least hydrologically altered section of the Missouri River (Galat and Lipkin, 2000; Pegg et al., 2003; Galat et al., 2005). Further, the Missouri River above Fort Peck Reservoir has many of the natural features common to unregulated rivers including islands, alluvial bars, secondary channels, and backwaters. A combination of factors contribute to the retention of natural features in this river section including limited reservoir storage capacity, multi-use management of reservoirs, and numerous unregulated tributaries that limit the influence of upstream impoundments (Scott et al., 1997; Galat and Lipkin, 2000; Pegg et al., 2003).

Materials and methods

Fish capture and surgery

Shovelnose sturgeon were captured and implanted with radio transmitters at three locations in the upper Missouri River in 2008 and 2009 (Table 1; Fig. 1). The three sampling locations were chosen such that individuals from the upper, middle, and lower sections of the study area were represented. Shovelnose sturgeon were captured from 23 April to 15 May in 2008, and from 13 to 21 April in 2009 using drifting trammel nets (1.8 m deep \times 45.8 m long, 2.5 cm mesh inner panel, 25.4-cm mesh outer panels). Prior to transmitter implantation, gonads were visually inspected to determine sex and reproductive stage (DeLonay et al., 2007). Shovelnose sturgeon were selected for transmitter implantation if they were ≥ 1.9 kg and presumed to be either a male, gravid female (stage IV; Wildhaber et al., 2007), or reproductively inactive female (\leq stage III) after macroscopic inspection of the gonad. Transmitters were 16 \times 73 mm, weighed 26 g, and transmitted at a 5-s burst rate (Model MCFT-3L Lotek Wireless, Inc., Newmarket, ON, Canada). Transmitters were selected to be as light as possible while maximizing battery life ($\approx 1,624$ day) and did not exceed 2% of fish body weight (Winter, 1996). Transmitter-implantation surgery was

Table 1

Final sample size and original tagging location by reproductive category of telemetered shovelnose sturgeon, Missouri River above Fort Peck Reservoir, 2008–2009

Location	Year	
	2008	2009
Coal Banks (rkm 3,267)		
Male	5	5
Confirmed spawning female	2	3
Potentially spawning female	5	5
Atretic		1
Reproductively inactive female		5
Judith Landing (rkm 3,193)		
Male	3	3
Confirmed spawning female	2	6
Potentially spawning female	3	3
Atretic		1
Reproductively inactive female		6
Fred Robinson Bridge (rkm 3,090)		
Male	1	1
Confirmed spawning female	5	1
Potentially spawning female	2	8
Atretic	3	1
Reproductively inactive female		6

performed using methods modified from Ross and Kleiner (1982) and Summerfelt and Smith (1990). All fish were placed into a holding tank for 20 min to allow for recovery from the surgery, and were released near the capture location. During July–August in 2008 and 2009 an effort was made to recapture previously classified gravid females to determine egg deposition success; recapture was attempted with targeted drifting trammel nets after a fish was located via telemetry (see methods below).

Reproductive assessment

Ovarian tissue samples were collected from all females at the time of transmitter implantation to corroborate reproductive stage classifications made in the field, and samples were also collected from previously classified gravid females recaptured after the spawning period to determine spawning success. Ovarian tissue samples were preserved in 10% buffered formalin in the field and returned to the laboratory where they were embedded in paraffin, sectioned at 5 μ m, and stained by periodic acid Schiff stain (Luna, 1968). Slides were examined

under a compound scope (Olympus America Inc., model BX41 40–400×) and the germ cells scored for stage of maturation according to the protocol of Wildhaber et al. (2007).

Females were segregated into four categories based on stage of maturation and condition of the gonad: confirmed spawners (i.e. successful egg deposition), potential spawners, atretic, or reproductively inactive (Table 1). Indications of successful egg deposition include the presence of post-ovulatory follicles and an absence of atretic bodies. If post-ovulatory follicles were found in an ovarian tissue sample from a previously classified gravid female that was recaptured post-spawn, the fish was classified as a confirmed spawner (Crim and Glebe, 1990; Wildhaber et al., 2007). Previously classified gravid females that were not recaptured post-spawn were classified as potential spawners. If no post-ovulatory follicles were present and a large number of atretic bodies were observed the fish was classified as atretic. Female shovelnose sturgeon require multiple seasons between spawns for gonadal development (Billard and Lecointre, 2001; Colombo et al., 2007; DeLonay et al., 2009; Tripp et al., 2009); thus, female shovelnose sturgeon that were confirmed to have successfully deposited eggs in 2008 could not have spawned in 2009 and were included in the reproductively inactive female group (Table 1).

Hydrographs and water temperature profiles

To compare sturgeon movements through the course of the spring pulse, the hydrograph was partitioned into three phases based on the putative reproductive life-history requirements of shovelnose sturgeon. The pre-suitable spawning phase for each year was defined as the period between 1 May (arbitrarily selected based on when sampling started) until the peak of the hydrograph, which was on 28 May in 2008 and on 3 June in 2009. The suitable spawning phase was defined as the descending limb of the hydrograph, coincident to temperatures above 12°C, the lower threshold for spawning and embryonic survival, until water temperature in the river exceeded 24°C, the upper threshold of temperatures suitable for spawning and embryonic survival (K. Kappenman and M. Webb, U.S. Fish and Wildlife Service, unpubl. data). The discharge thresholds were based on shovelnose sturgeon spawning in the upper Missouri River that was documented to occur on the descending limb of the hydrograph, coincident to water temperatures within the suitable ranges for spawning and embryonic survival (Goodman, 2009). In 2008, suitable spawning conditions were from 29 May to 26 July, and in 2009 from 4 June to 22 July. The post-suitable spawning phase was defined as the period after water temperatures in the river exceeded 24°C until the end of tracking (31 August). Hydrographs were derived by averaging the mean daily discharge recorded at three USGS gauging stations on the Missouri River within the study site: Fort Benton (rkm 3,337), Virgelle Ferry (rkm 3,274), and Landusky (rkm 3,090). For comparison to average discharge, data from the same three USGS gauging stations were used to calculate the mean daily discharge averaged over the years 1935–2005. Water temperature data were derived by averaging the mean daily water temperature (°C) from two continuous-reading temperature loggers at rkm 3,092 and rkm 3,304 in 2008, and at rkm 3,092 and rkm 3,193 in 2009.

Tracking

Individual fish were tracked weekly from May through August in 2008 and 2009 to estimate the direction and extent of

movements associated with the pre-suitable spawning, suitable spawning, and post-suitable spawning phases of the hydrograph. Telemetered fish were located using a portable SRX-400 Lotek receiver (Lotek Wireless, Inc.) equipped with a boat-mounted, four-element Yagi antenna. More precise locations were determined by triangulation or by passing the boat directly over the fish using a three-element hand held Yagi antenna (Winter, 1996; Blanchfield et al., 2005). This method has been shown to be accurate to within five meters by means of blind tests using transmitters placed in the river (Bellgraph et al., 2008; Gerrity et al., 2008). Latitude, longitude, and river kilometer were measured at each fish location using a boat mounted GPS unit. Data from eight autonomous land-based, continuous recording radio-receiving stations (Fig. 1) were also incorporated into the data set. These stations were located on the bank adjacent to the river and each station consisted of a continuously recording, solar powered SRX-400 Lotek receiver attached to two-four-element Yagi antenna.

Movement and movement rates

Mean daily total and net movement rates were calculated for each fish for each phase of the hydrograph. Total daily movement rate was calculated for a given fish by dividing the distance in river kilometers between successive relocations by the number of days elapsed between relocations (White and Garrot, 1990). Net daily movement rate was calculated by dividing the difference in river kilometer between successive relocations by the number of days that elapsed between relocations such that a positive rate indicated upstream movement, a negative rate indicated downstream movement, and a rate of zero indicated no movement (Bramblett, 1996). Additional movement likely occurs between relocations; thus, all movement data represent a minimum for the period between relocations (Rogers and White, 2007). To identify possible spawning locations, shovelnose sturgeon movements were plotted by category through the hydrograph phases and visually assessed. In addition, mean river kilometer for locations of individual, confirmed spawning females during suitable spawning conditions were assessed.

Data analysis

Individual radio-tagged fish were the experimental unit for all applicable statistical tests, and normality for all variables was assessed using residual and normal probability plots. To reduce the chance of making a type II error, an $\alpha = 0.1$ was established *a priori* for all analyses. Discharge, water temperature, and rates of change for each hydrograph phase were compared between years using a two-sample *t*-test after data were \log_{10} transformed to correct for non-normal distribution. Repeated measures (with individual fish as the repeated variable) analysis of variance (ANOVA) was used to test the hypotheses that there were no differences in total and net movement rates between confirmed spawning females in 2008 and 2009. If movement rates did not differ significantly, years were pooled to increase statistical power and repeated measures ANOVA was used to test the hypotheses that there were no differences in total and net movement rates among hydrograph phases.

Repeated measures ANOVA was also used to test the hypotheses that there were no differences in total and net movement rates among reproductive categories (i.e. males, potentially spawning females, confirmed spawning females,

atretic females, and reproductively inactive females) within each year. If movement rates did not differ significantly, reproductive categories were pooled to increase statistical power and repeated measures ANOVA was used to test the hypotheses that there were no differences in total and net movement rates among hydrograph phases for each year. Bonferroni multiple-comparisons test was used to control the experiment-wise error rate for all repeated measures ANOVAs (Rogers and White, 2007). Sample sizes within reproductive categories were relatively small; however, the repeated measures ANOVA used to analyze the data takes into consideration the variation within individuals, thus offering high statistical power relative to sample size (Ott, 1993; Kutner et al., 2004).

Results

Hydrographs and water temperature profiles

Daily discharge during the pre-suitable spawning phase was significantly higher in 2008 than in 2009 ($t = -6.54$, $P < 0.001$), and peak discharge was 45% higher in 2008 than in 2009 (Fig. 2; Table 2). Daily discharge was also significantly higher during the suitable spawning phase in 2008 than in 2009 ($t = 7.18$, $P < 0.001$), but daily discharge did not differ significantly between years during the post-suitable spawning phase ($t = -0.11$, $P = 0.91$). Rate of change in daily discharge differed between years for the pre-suitable spawning phase ($t = 1.84$, $P = 0.07$), and was significantly higher in 2008. Rate of change in daily discharge did not differ significantly between years for the suitable spawning phase ($t = -1.14$, $P = 0.26$), or the post-suitable spawning phase ($t = 0.27$, $P = 0.78$) (Fig. 2; Table 2). In addition to higher peak discharge achieved at a higher rate, discharge levels remained high for a greater duration in 2008 than in 2009. For example, in 2008 discharge remained above the highest rate observed in 2009 ($578 \text{ m}^3 \text{ s}^{-1}$) for 28 days, while discharge in 2009 began to decrease sharply immediately after the peak was achieved (Fig. 2). Discharge in 2008 was higher than average discharge during the pre-suitable and suitable spawning phases, while discharge in 2009 during these hydrograph phases more closely approximated average values. However, the duration of increased discharge in 2008 more closely resembled that of the average discharge, while the peak in discharge in 2009 was of a shorter duration. During the post-suitable spawning phases discharge in both years was similar to the average discharge values (Fig. 2).

Daily water temperature did not differ significantly between years for the pre-suitable spawning phase ($t = 0.14$, $P = 0.89$) or the post-suitable spawning phase ($t = -1.56$, $P = 0.62$). However, daily water temperature differed significantly between years during the suitable spawning phase ($t = -2.33$, $P = 0.02$), and was lower for a longer period in 2008. The difference observed in water temperature between years during the suitable spawning phase is likely a function of the prolonged period of high discharge in 2008 (Fig. 2). Rate of change in daily water temperature did not differ significantly between years for the pre-suitable spawning phase ($t = -1.56$, $P = 0.13$), suitable spawning phase ($t = 0.43$, $P = 0.66$), and post-suitable spawning phase ($t = 0.05$, $P = 0.96$) (Fig. 2; Table 2).

Movement and movement rates

Shovelnose sturgeon movement patterns were highly variable with respect to capture location but similar between years (Figs 3 and 4). For example, shovelnose sturgeon initially

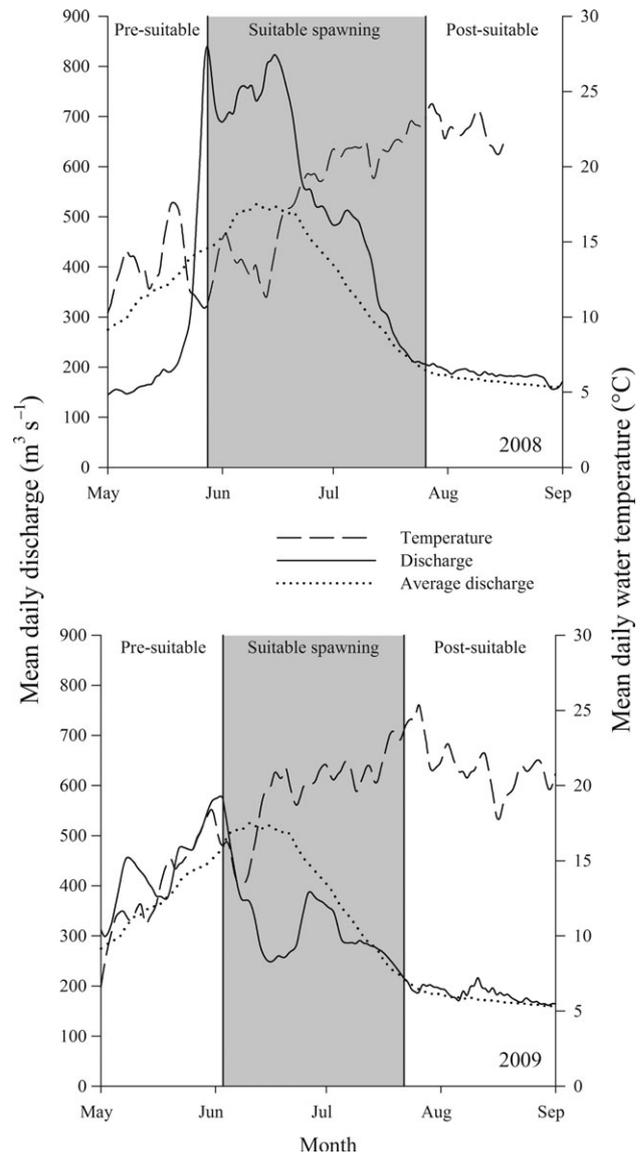


Fig. 2. Hydrograph phases for Missouri River upstream of Fort Peck Reservoir, 2008 and 2009 as defined by discharge and water temperature relative to shovelnose sturgeon (*Scaphirhynchus platyrhynchus*) putative reproductive life history. Average discharge represents mean daily discharge averaged over 1935–2005. Hydrograph phases include pre-suitable, suitable (shaded), and post-suitable spawning conditions (see text for hydrograph phase definitions).

located near Coal Banks did not exhibit extensive upstream movements while those initially located near Fred Robinson Bridge did not move downstream (Figs 3 and 4). Movement patterns within reproductive categories were similar between years; for example most males initially located near Judith Landing (rkm 3,193) either moved upstream or downstream (Figs 3 and 4). Movements of confirmed spawning females initially located near Coal Banks were similar between years (Figs 3 and 4). Confirmed spawning females initially located near Judith Landing in 2008 moved upstream or downstream, while confirmed spawning females in 2009 did not move or moved downstream. Most confirmed spawning females initially located near Fred Robinson Bridge in both years made no movements (Figs 3 and 4). Movement patterns of potentially spawning females initially located near Coal Banks and Judith Landing were similar to those of confirmed spawners from the same areas. However in both

Table 2

Minimum, maximum, and mean (SD) daily discharge, daily water temperature, and rates of change (ROC), Missouri River upstream of Fort Peck Reservoir for all hydrograph phases, 2008–2009. See text for hydrograph phase definitions

Variable	Year	Phase	Minimum	Maximum	Mean (SD)
Discharge ($\text{m}^3 \text{s}^{-1}$)	2008	Pre-suitable	145	839	259 (192)
		Suitable	206	823	542 (200)
		Post-suitable	156	207	185 (12)
	2009	Pre-suitable	299	578	440 (78)
		Suitable	215	530	313 (66)
		Post-suitable	161	216	185 (14)
Discharge ROC ($\text{m}^3 \text{s}^{-1} \text{day}^{-1}$)	2008	Pre-suitable	-4	165	26 (46)
		Suitable	-65	45	-10 (20)
		Post-suitable	-11	11	-1 (4)
	2009	Pre-suitable	-15	39	8 (17)
		Suitable	-49	36	-7 (17)
		Post-suitable	-18	18	-1 (4)
Water temperature ($^{\circ}\text{C}$)	2008	Pre-suitable	10.26	17.59	13.28 (2.11)
		Suitable	11.33	23.25	18.21 (3.63)
		Post-suitable	20.88	24.12	22.50 (0.97)
	2009	Pre-suitable	6.58	18.39	13.46 (2.97)
		Suitable	13.54	23.67	19.54 (2.66)
		Post-suitable	17.88	25.37	21.32 (1.65)
Water temperature ROC ($^{\circ}\text{C} \text{day}^{-1}$)	2008	Pre-suitable	-2.20	1.82	0.02 (0.96)
		Suitable	-1.61	1.38	0.20 (0.63)
		Post-suitable	-1.34	0.60	-0.13 (0.55)
	2009	Pre-suitable	-1.18	1.51	0.21 (0.63)
		Suitable	-1.33	1.22	0.15 (0.68)
		Post-suitable	-1.68	1.01	-0.09 (0.72)

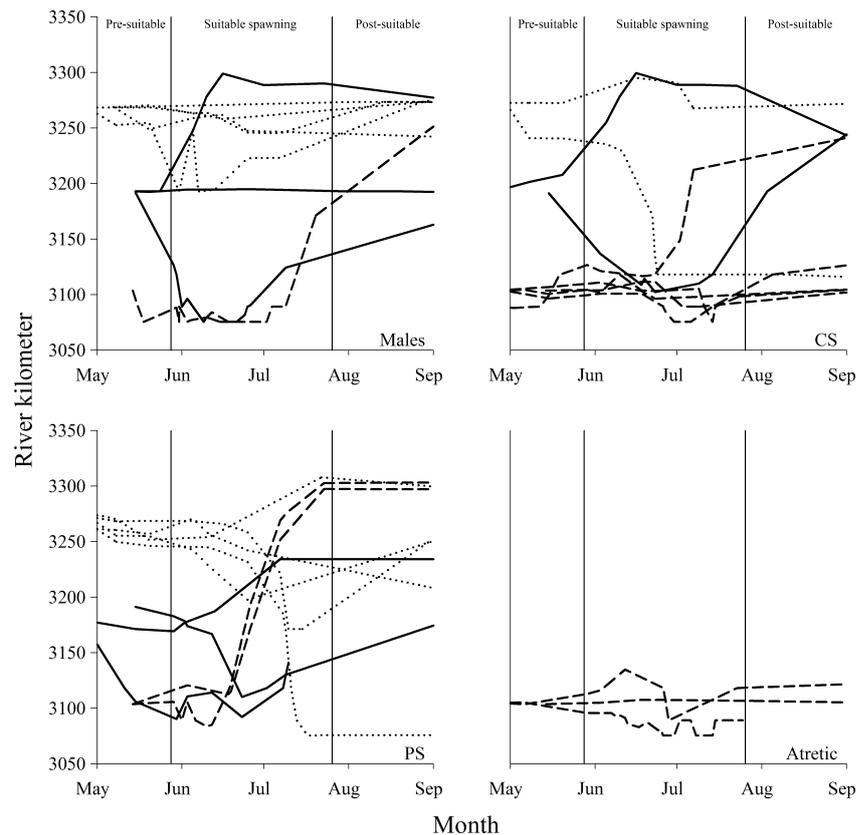


Fig. 3. Movement patterns of male, confirmed spawning female (CS), potentially spawning female (PS), and atretic female shovelnose sturgeon, Missouri River above Fort Peck Reservoir, 2008. River kilometer designates distance upstream from the confluence with Mississippi River (rkm 0). In all panels, dotted lines = fish initially captured at Coal Banks (rkm 3,267), solid lines = fish initially captured at Judith Landing (rkm 3,193), dashed lines = fish initially captured at Fred Robinson Bridge (rkm 3,090).

years, potentially spawning females initially located near Fred Robinson Bridge made extensive upstream movements (Figs 3 and 4), indicating that some gravid females from this area likely spawn at upstream locations. Atretic females exhibited similar movements to confirmed spawning females (Figs 3 and 4). Reproductively inactive females did not

exhibit the extensive movements observed in the other reproductive categories (Fig. 4).

Despite the higher, more prolonged discharge and the lower water temperature in 2008, mean total movement rate ($F_{1,17} = 1.69$, $P = 0.21$) and mean net movement rate ($F_{1,17} = 0.24$, $P = 0.63$) of confirmed spawning female shovelnose

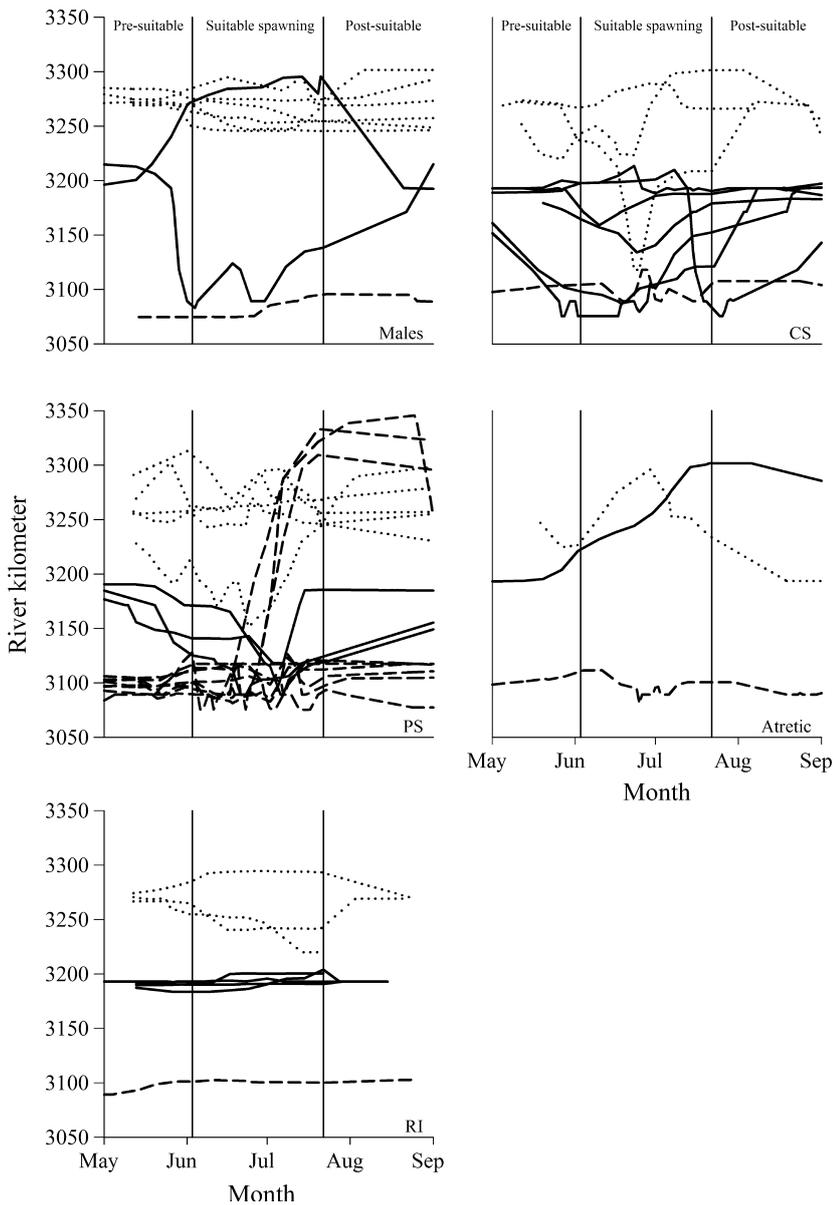


Fig. 4. Movement patterns of male, confirmed spawning female (CS), potentially spawning female (PS), atretic, and reproductively inactive female (RI) shovelnose sturgeon, Missouri River above Fort Peck Reservoir, 2009. River kilometer designates distance upstream from the confluence with the Mississippi River (rkm 0). In all panels, dotted lines = fish initially captured at Coal Banks (rkm 3,267), solid lines = fish initially captured at Judith Landing (rkm 3,193), and dashed lines = fish initially captured at Fred Robinson Bridge (rkm 3,090).

sturgeon did not differ significantly between years within hydrograph phases. When years were pooled, mean total movement rate ($F_{2,36} = 9.49$, $P < 0.001$) and mean net movement rate ($F_{2,36} = 2.99$, $P = 0.06$) of confirmed spawning female shovelnose sturgeon differed significantly among hydrograph phases. Mean total movement rate was highest during the suitable spawning period at water temperatures between 18 and 22°C; at temperatures below 18°C and above 22°C total movement rates decreased (Fig. 5). Net movement rate of confirmed spawning females was negative during the pre-suitable spawning phase indicating overall downstream movement, while upstream movement was highest during the post-suitable spawning phase. Net movement rate during the suitable spawning phase was near zero, with upstream and downstream movements nearly equal.

In 2008, mean total movement rate ($F_{3,27} = 0.94$, $P = 0.44$) and mean net movement rate ($F_{3,27} = 0.03$, $P = 0.99$) did not differ significantly among reproductive categories within hydrograph phases (Table 3). Although no significant differences were observed in mean total movement rates among reproductive categories, the highest weekly mean total

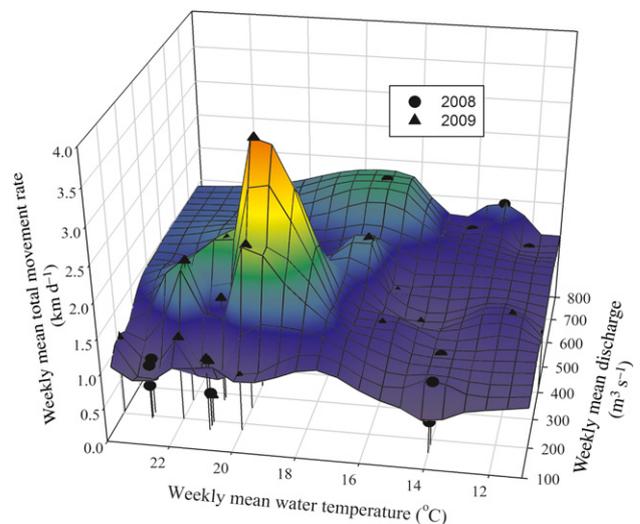


Fig. 5. Weekly mean total movement rates of confirmed spawning female shovelnose sturgeon, Missouri River upstream of Fort Peck Reservoir 2008–2009 as a function of weekly mean discharge and water temperature.

Table 3

Minimum, maximum, and mean \pm 90% confidence interval (CI) net and total movement rates (km per day) for reproductive categories of shovelnose sturgeon, Missouri River upstream of Fort Peck Reservoir for all hydrograph phases, 2008. Positive net movement rates represent overall upstream movement, negative rates represent downstream movement. Reproductive categories include males, confirmed spawning females (CS), potentially spawning females (PS), and atretic females. See text for hydrograph phase definitions

Variable	Category	Phase	Minimum	Maximum	Mean \pm 90% CI
Net movement rate	Male	Pre-suitable	-4.69	1.63	-0.78 \pm 0.97
		Suitable	-0.16	1.64	0.39 \pm 0.36
		Post-suitable	-0.32	1.86	0.41 \pm 0.37
	CS	Pre-suitable	-2.88	1.37	-0.09 \pm 0.70
		Suitable	-2.03	1.63	0.02 \pm 0.54
		Post-suitable	-1.12	2.16	0.29 \pm 0.47
	PS	Pre-suitable	-2.35	0.86	-0.42 \pm 0.44
		Suitable	-2.88	3.34	0.39 \pm 1.01
		Post-suitable	-0.50	1.69	0.29 \pm 0.37
	Atretic female	Pre-suitable	-0.33	0.30	0.01 \pm 0.30
		Suitable	-0.11	0.10	0.01 \pm 0.10
		Post-suitable	-0.04	0.09	0.02 \pm 0.10
	Pooled	Pre-suitable	0.07	4.69	-0.39 \pm 0.37
		Suitable	1.12	1.17	0.25 \pm 0.37
		Post-suitable	0.50	0.60	0.31 \pm 0.21
Total movement rate	Male	Pre-suitable	0.07	4.69	1.44 \pm 0.86
		Suitable	0.05	2.94	1.17 \pm 0.61
		Post-suitable	0.01	1.86	0.50 \pm 0.33
	CS	Pre-suitable	0.05	2.88	0.86 \pm 0.50
		Suitable	0.34	2.10	1.29 \pm 0.36
		Post-suitable	0.06	2.16	0.55 \pm 0.38
	PS	Pre-suitable	0.11	2.35	0.68 \pm 0.33
		Suitable	0.85	5.19	2.53 \pm 0.79
		Post-suitable	0.00	1.69	0.45 \pm 0.31
	Atretic female	Pre-suitable	0.07	0.36	0.26 \pm 0.16
		Suitable	0.07	1.64	1.00 \pm 0.78
		Post-suitable	0.04	0.09	0.06 \pm 0.03
	Pooled	Pre-suitable	0.05	4.69	0.91 \pm 0.32
		Suitable	0.05	5.19	1.63 \pm 0.37
		Post-suitable	0.00	2.16	0.47 \pm 0.18

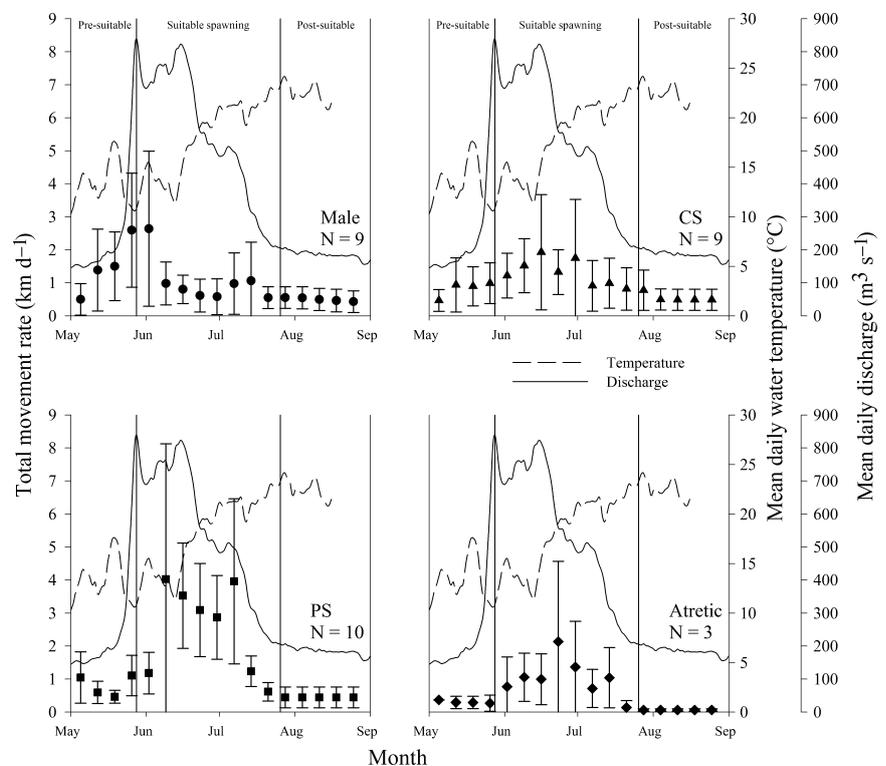


Fig. 6. Mean total movement rates for male, confirmed spawning female (CS), potentially spawning female (PS), and atretic female shovelnose sturgeon by hydrograph phase in 2008. Symbols = weekly mean total movement rates; error bars = 90% confidence intervals.

movement rates of males occurred 3–4 weeks before the highest weekly mean total movement rates of females (Fig. 6). Both total movement rate ($F_{2,58} = 14.12$, $P < 0.001$)

and net movement rate ($F_{2,58} = 3.58$, $P = 0.03$) differed among hydrograph phases when reproductive categories were pooled (Table 3). Overall, total movement rates were highest

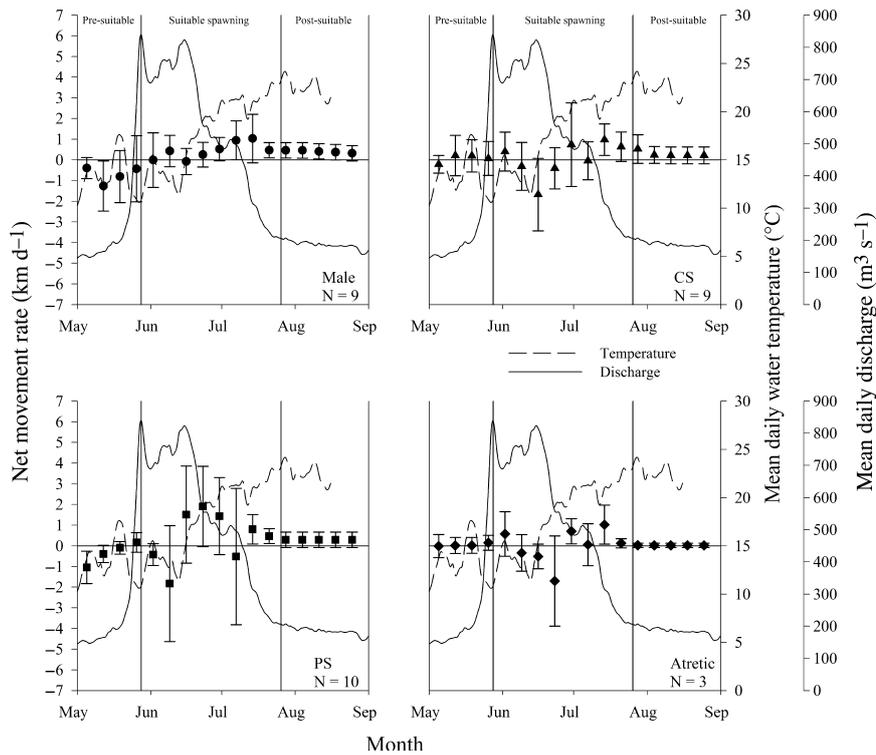


Fig. 7. Mean net movement rates for male, confirmed spawning female (CS), potentially spawning female (PS), and atretic female shovelnose sturgeon by hydrograph phase in 2008. Symbols = weekly mean net movement rates; error bars = 90% confidence intervals. Values greater than zero = movement upstream; values less than zero = movement downstream.

Table 4

Minimum, maximum, and mean \pm 90% confidence interval (CI) net and total movement rates (km per day) for reproductive categories of shovelnose sturgeon, Missouri River upstream of Fort Peck Reservoir for all hydrograph phases, 2009. Positive net movement rates represent overall upstream movement, negative rates represent downstream movement. Reproductive categories include males, confirmed spawning females (CS), potentially spawning females (PS), atretic females, and reproductively inactive females (RI). See text for hydrograph phase definitions

Variable	Category	Phase	Minimum	Maximum	Mean \pm 90% CI
Net movement rate	Male	Pre-suitable	-3.88	2.27	-0.32 ± 0.88
		Suitable	-0.46	1.15	0.13 ± 0.27
		Post-suitable	-2.42	1.89	0.05 ± 0.61
	CS	Pre-suitable	-2.24	0.25	-0.69 ± 0.45
		Suitable	-2.38	1.16	0.09 ± 0.54
		Post-suitable	-1.16	1.64	0.44 ± 0.43
	PS	Pre-suitable	-1.77	0.78	-0.16 ± 0.20
		Suitable	-1.05	4.76	0.75 ± 0.67
		Post-suitable	-1.76	1.16	0.02 ± 0.25
	Atretic female	Pre-suitable	-0.89	0.90	0.13 ± 0.87
		Suitable	-0.22	1.59	0.45 ± 0.94
		Post-suitable	-0.97	-0.25	-0.54 ± 0.36
RI	Pre-suitable	-0.68	0.72	0.05 ± 0.14	
	Suitable	-0.71	0.38	-0.05 ± 0.10	
	Post-suitable	-1.83	0.78	-0.22 ± 0.27	
Pooled	Pre-suitable	-3.88	2.27	-0.20 ± 0.19	
	Suitable	-2.38	4.76	0.27 ± 0.25	
	Post-suitable	-2.42	1.89	0.01 ± 0.17	
Total movement rate	Male	Pre-suitable	0.01	3.88	1.16 ± 0.74
		Suitable	0.07	8.74	1.66 ± 1.49
		Post-suitable	0.02	2.42	0.65 ± 0.48
	CS	Pre-suitable	0.22	3.04	1.18 ± 0.53
		Suitable	0.85	4.43	1.92 ± 0.58
		Post-suitable	0.09	2.28	0.92 ± 0.45
	PS	Pre-suitable	0.14	3.35	1.05 ± 0.38
		Suitable	0.02	6.15	2.47 ± 0.74
		Post-suitable	0.01	2.75	0.46 ± 0.27
	Atretic female	Pre-suitable	0.41	1.92	1.08 ± 0.73
		Suitable	1.31	2.59	1.83 ± 0.64
		Post-suitable	0.39	0.97	0.59 ± 0.31
RI	Pre-suitable	0.04	0.74	0.32 ± 0.09	
	Suitable	0.04	0.71	0.27 ± 0.09	
	Post-suitable	0.00	1.83	0.40 ± 0.22	

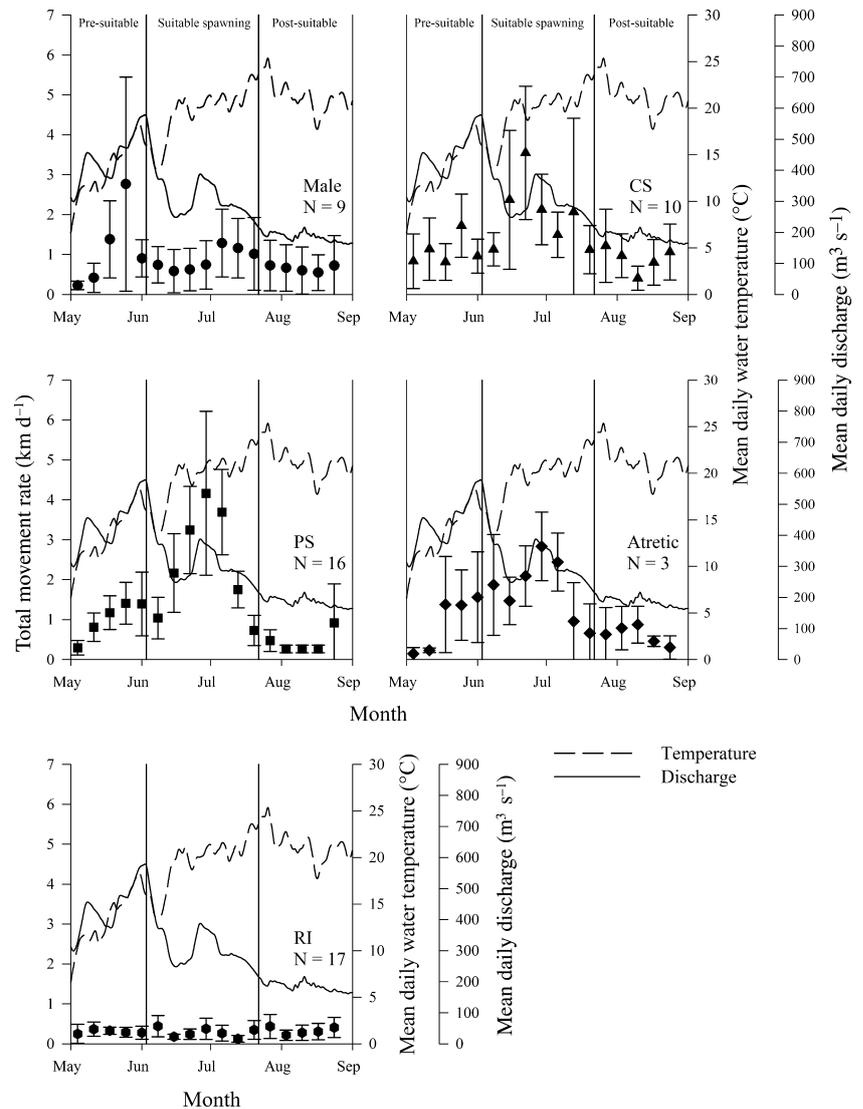


Fig. 8. Mean total movement rates for male, confirmed spawning female (CS), potentially spawning female (PS), atretic female, and reproductively inactive female (RI) shovelnose sturgeon by hydrograph phase in 2009. Symbols = weekly mean total movement rates; error bars = 90% confidence intervals.

during the suitable spawning phase at 1.63 km day^{-1} , compared to 0.91 km day^{-1} during the pre-suitable spawning phase, and 0.47 km day^{-1} during the post-suitable spawning phase (Table 3). This corresponds with the high variation observed in weekly mean net movement rates during the suitable spawning phase as fish increased movement upstream and downstream (Fig. 7).

Mean total movement rates in 2009 differed among reproductive categories within hydrograph phases ($F_{4,51} = 3.76$, $P = 0.01$) with reproductively inactive females moving significantly less than other reproductive categories (Table 4). As in the previous year, weekly mean total movement rates of males peaked earlier than females, with the highest total movement rates of males occurring 4–5 weeks prior to the highest female total movement rates (Fig. 8). Mean net movement rate data were similar to those in 2008, with net movement rates having no significant differences among reproductive categories within hydrograph phases ($F_{4,51} = 0.65$, $P = 0.63$), but differing among hydrograph phases when reproductive categories were pooled ($F_{2,107} = 3.51$, $P = 0.03$) (Table 4). While no significant differences were observed in mean net movement rates among reproductive categories within hydrograph phases in 2009, weekly mean net movement rates of reproductively inactive females did not exhibit the variation observed in the other categories (Fig. 9). Weekly mean

net movement rates of reproductively inactive females were centered on zero for all hydrograph phases and had little variation, indicating a lack of movement upstream or downstream.

Discussion

We rejected the hypothesis that shovelnose sturgeon in the upper Missouri River would only move upstream to spawn because shovelnose sturgeon had variable movement patterns during the spawning period, with some fish displaying no movement and others moving upstream or downstream. This is in contrast to research results in the Missouri River below Gavins Point Dam where gravid female shovelnose sturgeon that move downstream or do not move fail to spawn, with only females that move upstream spawning successfully (DeLonay et al., 2007, 2009). The differences between our results and DeLonay et al. (2007, 2009) may be related to differences in the availability of suitable habitat. For example, it is possible that shovelnose sturgeon resident to the furthest upstream extent of suitable shovelnose sturgeon habitat near Coal Banks cannot make upstream movements without encountering unsuitable conditions. Conversely, shovelnose sturgeon resident to the area near Fred Robinson Bridge cannot make extensive movements downstream without

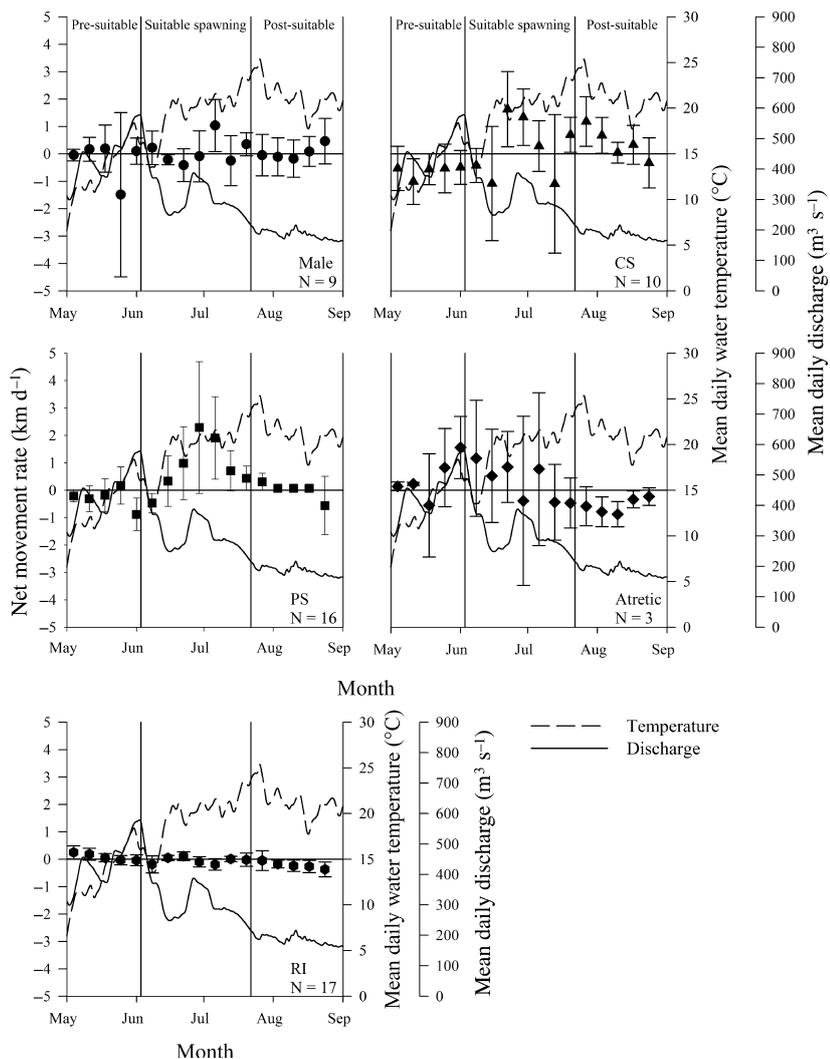


Fig. 9. Mean net movement rates for male, confirmed spawning female (CS), potentially spawning female (PS), atretic female, and reproductively inactive female (RI) shovelnose sturgeon by hydrograph phase in 2009. Symbols = weekly mean net movement rates; error bars = 90% confidence intervals. Values greater than zero = movement upstream; values less than zero = movement downstream.

encountering the headwaters of Fort Peck Reservoir. Thus, shovelnose sturgeon spawning movements are constrained. This is further illustrated by the point estimates of distance travelled by confirmed spawning female shovelnose sturgeon in the upper Missouri River (mean, 141.39 km; SD, 85.78) which are less than in shovelnose sturgeon downstream (mean, 215.68 km; SD, 148.01; DeLonay et al., 2007).

The hypothesis that movement of spawning shovelnose sturgeon would be greater in a year with higher discharge was rejected. Despite differences in discharge and water temperature between years, movement rates and movement patterns were similar. How discharge outside of those observed in this study affects spawning movements and how discharge affects recruitment of shovelnose sturgeon in the upper Missouri River is unknown and requires further investigation. We failed to reject the hypothesis that spawning shovelnose sturgeon would have greater movements than reproductively inactive females. Reproductively inactive female shovelnose sturgeon did not exhibit the extensive movements observed in other reproductive categories and had significantly lower total movement rates. As the impetus for movement is lacking (e.g. spawning), reproductively inactive females do not expend energy moving long distances. These results argue for always knowing the reproductive status of fishes when conducting telemetry studies during the spawning period.

Total movement rates and the variation in net movement rates of confirmed spawning, potentially spawning, and atretic females were highest during suitable spawning conditions, and then declined during post-suitable spawning conditions to similar values as observed in pre-suitable conditions. In both years, movements of males were highest 3–5 weeks earlier than females. This is consistent with reported spawning behavior of males in other sturgeon species; males arrive at spawning sites prior to females, and stay longer as they attempt to maximize the opportunity for successful mating (Fox et al., 2000; Paragamian and Kruse, 2001; Bruch and Binkowski, 2002). The timing of increased movements in female shovelnose sturgeon in the upper Missouri River coincides with the increase in the proportion of mature (stage IV) female shovelnose sturgeon observed in the Mississippi River, which was concurrent with increasing discharge and temperatures between 17–21°C (Tripp et al., 2009). The increase in the proportion of mature females observed in the Mississippi River was followed by an increase in the proportion of spent (stage VI) females approximately 1–2 months later (Tripp et al., 2009). Movements of atretic females in the upper Missouri River were similar to confirmed and potentially spawning. Female sturgeon can fail to spawn and undergo follicular atresia when the appropriate cues for spawning are lacking (Auer, 1996, 2004; Webb et al., 1999, 2001; Linares-Casenave et al., 2002; Wildhaber et al., 2011b).

Reproductively inactive females did not make large-scale spawning movements in the upper Missouri River. Reduced movements in reproductively inactive adult shovelnose sturgeon compared to spawners were also observed in the Missouri River below Gavins Point Dam (DeLonay et al., 2009).

Shovelnose sturgeon spawned at multiple locations throughout the upper Missouri River. Spawning at several locations over large patches of river has also been documented in shovelnose sturgeon populations downstream in the Missouri River (DeLonay et al., 2007, 2009; Wildhaber et al., 2011a). The highest densities of confirmed spawning females during suitable spawning conditions were from rkm 3,125 to rkm 3,200. Confirmed spawning female shovelnose sturgeon did not appear to use an approximately 50 km stretch of river between Coal Banks and Judith Landing. Confirmed spawning female shovelnose sturgeon made movements through this reach prior to suitable spawning conditions, but none remained there during suitable spawning conditions.

Shovelnose sturgeon larvae drift for 6 days post hatch (dph) and cover distances from 94 to 250 km (Braaten et al., 2008). Using the minimum estimate of shovelnose sturgeon larval drift distance, spawning would need to take place upstream of rkm 3,094 for larvae to avoid settling in the headwaters of Fort Peck Reservoir (rkm 3,000). In the 2 years examined, 95% of confirmed spawning females had mean locations during suitable spawning conditions that were above this threshold.

Recently, the hypothesis that discharge initiates spawning of shovelnose sturgeon has been under increased scrutiny. Currently it is thought that reproductive maturation in shovelnose sturgeon is initiated many months prior to spawning with day length as the environmental cue, while spawning is initiated by the proximate cue of water temperature (DeLonay et al., 2009; Papoulias et al., 2011; Wildhaber et al., 2011a). Our results support this hypothesis given that we observed confirmed spawning females in 2 years with highly differing discharge regimes. *Scaphirhynchus* spp. were observed successfully spawning in the Mississippi River in both low and high water years at suitable temperatures (Phelps et al., 2010), and multi-year studies on the lower Missouri River have shown no discharge associated differences in physiological measures of spawning readiness despite high variation in discharge between years and study sections (DeLonay et al., 2009; Papoulias et al., 2011). However, extended periods of high discharge have been shown to result in protracted spawning and in turn a greater abundance of larval and age-0 *Scaphirhynchus* spp. (Goodman, 2009; Phelps et al., 2010).

Conservation actions for shovelnose sturgeon in the upper Missouri River need to be conducted on a large scale given their observed large-scale movements in this study. Understanding how movement and recruitment dynamics relate to management actions (varying discharge regimes) is the next logical step in better understanding the ecology of shovelnose sturgeon. Improved knowledge of shovelnose sturgeon ecology may provide insight into the ecology of the endangered pallid sturgeon *Scaphirhynchus albus* in the upper Missouri River.

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