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Adult paddlefish migrations in relation to spring river conditions of the Yellowstone and Missouri rivers, Montana and North Dakota, USA

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Summary

Migrations and movements of paddlefish (*Polyodon spathula*) into the regulated Missouri River and the largely unregulated Yellowstone River, North Dakota and Montana, USA were monitored with radio-telemetry to assess if (i) differential discharge between the Yellowstone River and the Missouri River influenced river selection, (ii) river conditions influenced directional movements in the Yellowstone River and (iii) inter-annual and sex-related migration patterns existed. In 2003 and 2004, telemetered upriver migrants selected the Yellowstone River rather than the Missouri River above its confluence with the Yellowstone River 34 of 54 times (63%). Fish typically ascended the river with flows that were increasing at a greater rate or decreasing at a lesser rate than the other river. Most (70%) upriver movements occurred when discharge and suspended sediment were increasing. Most (80%) downriver movements occurred when flows and suspended sediment were decreasing. Total migration distance was greater in 2004 than in 2003 for both sexes despite greater peak discharge in 2003. Movement of pre-spawn paddlefish into the Missouri River above its confluence with the Yellowstone River in response to attraction flows may have implications towards this stock's reproductive success. Accordingly, these implications should be taken into account when regulating spring Missouri River discharge levels upriver at Fort Peck Dam.

Introduction

The paddlefish (Order Acipenseriformes: *Polyodon spathula*) is a large, long-lived zooplanktivorous fish inhabiting major rivers of the Missouri and Mississippi river basins and selected Gulf Coast drainages of North America (Vasetskiy, 1971; Gengerke, 1986). Traditional habitats were large, free-flowing rivers with high floodplain connectivity and extensive backwaters; side-channels and other low-velocity areas provided productive feeding grounds (Russell, 1986). Mature paddlefish migrate up main river channels during the spring to spawn. These migrations historically extended 100s of kilometers to spawning areas (Paukert and Fisher, 2001). In northern populations, males typically delay sexual maturation until 9–11 years of age and females mature at 15–20 years (Scarnecchia et al., 1996). Males typically spawn every 1–2 years and females every 2–3 years (Scarnecchia et al., 2007).

Studies have shown that paddlefish require specific environmental conditions involving discharge, temperature and suspended sediment to cue migration and spawning (Pasch et al., 1980; Paukert and Fisher, 2001; Firehammer and Scarnecchia, 2006). As with many other riverine fishes, high flows may encourage reproductive success of paddlefish by scouring spawning substrates and facilitating dispersal of larvae (Russell, 1986). Increased sediment levels during spring runoff may also aid survival of paddlefish larvae and eggs by inhibiting sight-feeding predators as has been found in other large river fishes (Johnson and Hines, 1999; Gadomski and Parsley, 2005). Water temperature can influence the incubation time of paddlefish eggs; a typical incubation time is 7 days at 18–21°C (Purkett, 1961).

The creation of an extensive system of reservoirs and channel modifications on the Missouri and Mississippi rivers and their tributaries has resulted in regulated flow regimes and disconnected floodplains (White and Bramblett, 1993). Dams have blocked many paddlefish migrations and reduced the abundance of traditional rearing and spawning habitats (Sparrowe, 1986). During the past 100 years, paddlefish stocks in four states have been extirpated and abundance of several other populations has decreased (Graham, 1997). Habitat loss, especially for spawning, has been implicated as a major cause of many of the declines.

The lower-most reach of the Yellowstone River (hereafter YR), 114 river kilometers (rkm) in length, constitutes one of few major quasi-natural spawning areas remaining within the paddlefish's geographic range (White and Bramblett, 1993). Paddlefish in this reach rear in Lake Sakakawea, one of six large main-stem reservoirs on the Missouri River. Lake Sakakawea filled over a period of 13 years (December 1953 through 1966) during which a prolonged trophic upsurge increased paddlefish production (Scarnecchia et al., 1996). The Yellowstone-Sakakawea paddlefish stock has access to both productive rearing habitat (Lake Sakakawea) and free-flowing spawning areas (YR). This stock also has access to the highly regulated Missouri River (hereafter MR) below its confluence with the Yellowstone River (hereafter MRBC) as well as above the confluence (hereafter MRAC) during their upriver spawning migrations. These geographic qualities provide an unusual opportunity to study the migratory actions of a single stock under both highly regulated and quasi-natural environmental conditions.

Two important recreational fisheries exist for this stock, one in eastern Montana and the other in western North Dakota (Fig. 1). The Montana fishery located at Intake, immediately below a low-head dam 27 rkm downstream of Glendive, has yielded an annual harvest of between 1000 and 5000 fish since 1962. A second fishery centered at the confluence of the Missouri and Yellowstone rivers began in 1977 and provides an annual harvest of between 800 and 1500 fish (Scarnecchia et al., 1996). In 2006, annual harvest of paddlefish was limited by state regulations to no more than 1000 fish per state.

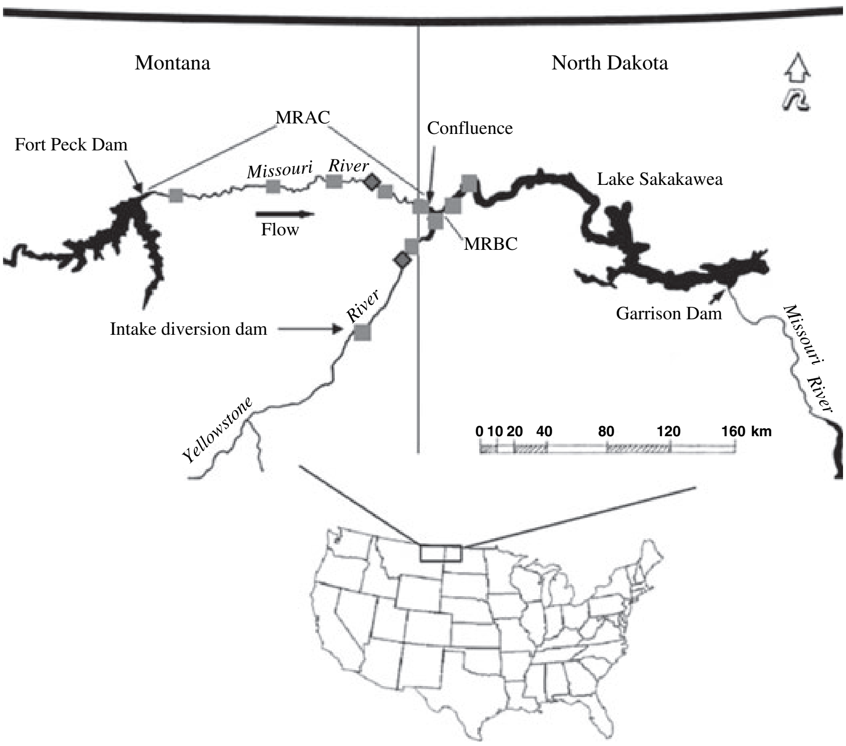

Fig. 1. Map of study area showing Missouri and Yellowstone rivers, Montana and North Dakota, USA. Diamonds = United States Geological Survey gauging station locations. Squares = locations of fixed telemetry receiving stations

Successful recruitment of the Yellowstone-Sakakawea paddlefish stock is thought to be closely related to environmental conditions of the Yellowstone and Missouri rivers during the spring spawning season. A thorough understanding of the relationships among flow conditions, paddlefish movements, and spawning events will therefore provide essential information needed for the long-term perpetuation of this stock. To meet these research needs, a multi-year study began in 1999 to examine the Yellowstone-Sakakawea paddlefish stock's migratory patterns and spawning activities (Firehammer and Scarnecchia, 2006). This paper is in part an extension of the study by Firehammer and Scarnecchia (2006). However, subsequent changes in the Lower Yellowstone-Missouri River complex allowed for expansion of previously addressed research objectives. First, the installation of several fixed radio-telemetry receiving stations in 2003 provided an opportunity to more thoroughly track spring paddlefish migrations. Fixed stations allowed for more precise information on when paddlefish moved in relation to flows and, because of the locations of the stations, when fish moved toward assumed spawning reaches. Second, considerable inter-annual variability in Yellowstone River flow regimes during the 2003–2004 study period compared to previous years provided an opportunity to further examine the influence of river conditions on paddlefish migrations and spawning events.

Although previous research on the YR and MR has indicated that paddlefish move further upriver during high flow years than during low flow years (Robinson, 1966; Rehwinkel, 1978), less is known concerning the collective influence of temperature, sediment and discharge on directional movements during the spring spawning migration. Previous migration studies (Firehammer and Scarnecchia, 2006) and harvest records (North Dakota Game and Fish Department, unpubl. data) suggest that during most years the majority of paddlefish originating in Lake Sakakawea that reach the MRBC ascend the YR rather than the MRAC. However, additional research is needed to better understand what role differential river dynamics between the YR and the MRAC may have on spawning river selection. The objectives of this study were to assess if (i) differential discharge between the YR and the MRAC influenced river selection, (ii) river conditions influenced directional movements in the YR and (iii) inter-annual and sex-related migration patterns existed.

Methods

Study area

Juvenile Yellowstone-Sakakawea paddlefish typically rear in Lake Sakakawea, a 156 000 ha, 270 km long main-stem impoundment of the MR located in western North Dakota, USA (Fig. 1). As paddlefish become sexually mature (typically 9–11 years for males and 15–20 years for females; Scarnecchia et al., 1996) they move toward the headwaters of Lake Sakakawea and into the MRBC in preparation for spawning. Besides the MRBC and the headwaters of Lake Sakakawea, migratory paddlefish can chose between two potential spawning reaches: (i) the lower 114 km of the YR from its confluence with the MR (the site of the confluence, hereafter referred to as the Confluence) to the Intake Diversion Dam near Glendive, Montana and (ii) the MRAC, a 300-km segment of the MR from the Confluence to the tail waters of Fort Peck Dam in Montana.

The YR and MRAC differ greatly in their physical characteristics. Large islands, side-channels, and irregular meanders characterize the lowermost 114 km of the YR. Gravels dominate the substrate in upper portions of the lower river and give way to sandy bottoms and isolated gravel bars in the lowermost 20 km (White and Bramblett, 1993). Mean annual discharge near Sidney, Montana is approximately 362 m^3 s^{-1} (United States Geological Survey, 2003).

Completion of Fort Peck Dam on the MRAC in 1937 resulted in stabilized discharges, reduced sediment loads, and lower average water temperatures in the MRAC than in the YR. Gravel and cobble substrates are common in the 50 km reach of the MRAC directly below Fort Peck Dam, with the lower 250 km having numerous sand bars due to increased sediment inputs from turbid tributaries. Mean annual discharge for the MRAC near Culbertson, Montana is approx. 291 m^3 s^{-1} (United States Geological Survey, 2003).

Tagging

Floating experimental gill nets 25 m in length (mesh sizes 7.6 cm, 10.2 cm, and 12.7 cm bar measure) were drifted in the MRBC to capture mature paddlefish during the autumn of 2002 and spring of 2004. Lotek Model 32_1s (Lotek Inc. Newmarket, ON, Canada) combined acoustic radio tags were surgically implanted into each fish following methods described in Ross and Kleiner (1982). Body lengths (front of eye to fork of caudal fin; Ruelle and Hudson, 1977) and weights were recorded and sex determined during tag implantation by visually observing the gonads through the incision. All fish were sexually mature at the time of tagging. In 2002, 10 male and 10 female paddlefish were tagged (Table 1). In 2004, 11 male and nine female paddlefish were tagged (Table 2).

Tracking

Tracking was conducted using fixed receiving stations and a powerboat (manual tracking) from April to October. Fixed stations were located on the YR at YR rkm 0, YR rkm 47 and YR rkm 113 (where numbers refer to the river distance in km above the Confluence), on the MRBC at MRBC rkm 2504, MRBC rkm 2531 and MRBC rkm 2554, and on the MRAC at MRAC rkm 2601, MRAC rkm 2657, MRAC rkm 2705 and MRAC rkm 2753 (where numbers refer to the river distance in km upriver of St Louis, Missouri; Fig. 1). Each station contained a solar-powered Lotek SRX 400 model receiver and a 512 kb memory data logger.

For manual tracking of paddlefish, an open-bow powerboat was equipped with a Lotek SRX 400 receiver and antenna. A global positioning unit was used to record latitude, longitude, and estimated rkm location of contact sites. United States Geological Survey (USGS) gauging stations at YR rkm 47 and MRAC rkm 2601 recorded daily river discharge. Daily suspended sediment levels (mg L^{-1}) were recorded at the YR gauging station. Daily water temperatures were recorded from April through October using remote temperature data loggers positioned near YR rkm 13.5 and MRAC rkm 2554.

Table 1
Biometric summary of paddlefish implanted with radio tags in autumn of 2002

Fish[a]	Length (cm)	Weight (kg)	Sex	Note[b]
51	112	30	F	Expelled tag at YRkm 60 on or around 5 May 2003
52	91	13.2	M	
55	97	17.7	M	Expelled tag at MRkm −95 on or around 10 July 03
56	91	12.2	M	Expelled tag at YRkm 48 on or around 28 June 2003
63	94	11.8	M	
64	107	26.8	F	
99	117	28.1	F	Expelled tag at YRkm 14 on or around 5 June 2003
100	91	10.4	M	Expelled tag at YRkm 30 on or around 12 June 2003
105	114	31.8	F	
111	84	10	M	Expelled tag at MR −103 on or around 10 July 2003
112	114	29	F	Expelled tag at YRkm 45 on or around 6 May 2003
123	104	11.3	M	
124	99	12.7	M	
131	99	12.7	M	
135	114	20.9	F	
136	109	21.3	F	Expelled tag at MRkm −105 on or around 10 August 2005
147	122	34	F	
148	114	27.7	F	
157	124	29.5	F	Expelled tag at MRkm 242 on or around 23 June 2003
158	97	12.7	M	

[a]Fish contacted above confluence of the Missouri and Yellowstone rivers in more than one spring in bold. All tags transmitted on a frequency of 149.760 kHz.
[b]Yellowstone River location in kilometers above Confluence denoted by YRkm; Missouri River location below Confluence denoted by negative km, above Confluence by positive km. Dates of tag expulsions are estimates. Tags expelled near headwaters of Lake Sakakawea (MRkm 90–105) may have drifted to those locations.

Table 2
Biometric summary of paddlefish implanted with radio tags in spring of 2004

Fish[a]	Length (cm)	Weight (kg)	Sex
5	99	17	M
9	109	23.5	F
47	109	27.5	F
48	96.5	13	M
49	89	13	M
70	119	24.5	F
71	114	32	F
72	101	15	M
74	114	30	F
83	101.5	17	M
84	122	31	F
85	96.5	17	M
92	96.5	16	M
94	117	33	F
98	114	32	F
103	104	17	M
110	109	28.5	F
120	104	20	M
143	94	12.7	M
146	94	14	M

[a]Fish with tags transmitting on 149.680 kHz in bold, all others transmitting on 149.760 kHz.
Harvested on 5 May 2004; tag re-implanted 15 May 2004. Demographic data is for second implantation.

Data analysis

Binomial logistic regression was used to test the hypothesis that differential discharge between the YR and the MRAC influenced river selection (Ott and Longnecker, 2001). The response variable was a new entry by a fish into either river above the Confluence. A new entry was defined as the presence of a fish in these reaches when prior contact was in the MRBC within the previous 3 days.

The difference in the rate of change and the difference in the magnitude of discharge between the two rivers were used as predictor variables. The difference in the rate of change in discharge between rivers was calculated as:

$$Q_{y-m} = (X_{\Delta y} - X_{\Delta m})/d$$

where Q_{y-m} is the difference in the rate of change in discharge between rivers, $X_{\Delta y}$ is the change in discharge for the YR, $X_{\Delta m}$

is the change in discharge for the MRAC, and d equals number of days between contacts. The difference in the magnitude of discharge between rivers was calculated as:

$$D_{y-m} = \log_{10}(D_y/D_m)$$

where D_{y-m} is the difference in the magnitude of discharge between rivers, D_y is YR discharge, and D_m is MRAC discharge.

Telemetry contacts were assigned a river kilometer with positive and negative values indicating distance upstream or downstream of the Confluence. Changes in discharge, suspended sediment, or temperature (X_Δ) during the period elapsed between contacts were calculated as:

$$X_\Delta = \log_{10}(X_{t2}/X_{t1})$$

where X_{t2} is discharge, suspended sediment, or water temperature on latter day of contact and X_{t1} is discharge, suspended sediment, or water temperature on former day of contact.

Multiple regression models were used to evaluate which river variable(s) were most closely associated with directional movements. Principal components analysis (PCA) was used to create subsets of explanatory variables (Johnson and Wichern, 2002). All principal component scores were then used as new explanatory variables in multiple regression models.

Analysis of variance was used to examine sex-related influence on movement rates and total distance traveled during migration. The main factor in the model was sex with individual fish treated as sampling units to avoid problems associated with serial correlation (Kenward, 1992).

Results

All 20 fish (10 males, 10 females) tagged in 2002 were relocated during the 2003 field season. A total of 513 contacts was made between 9 April and 22 October 2003. Contact occurrence was highest in May (148 relocations). Transmitters of four females and one male were determined to be stationary by October 2003, indicating that these fish died or their tags were expelled. Expulsion of these tags occurred after the date of peak discharges and probably did not alter interpretation of directional movement or river selection data. In 2004, a total of 840 contacts was made between 4 April and 8 November. Contact occurrence was highest in May (301 relocations). At the beginning of the 2004 tracking season, 35 paddlefish retained active CART tags.

River conditions

Spring river dynamics for the YR and MRAC showed marked inter-annual differences in terms of timing and relative magnitudes of discharge and temperature (Figs 2 and 3). Spring discharge for the YR during 2003 peaked at 1370 m^3 s^{-1} on 5 June. Peak discharge in 2004 occurred 9 days later (14 June) and was approx. half the magnitude (705 m^3 s^{-1}) of peak flow in 2003. Mean daily YR discharge for the period 1 May–30 June 2003 was 559 m^3 s^{-1}. In 2004, mean daily discharge for the same period was considerably lower (271 m^3 s^{-1}). Low flow conditions were especially pronounced during May 2004, when mean daily discharge (167.5 m^3 s^{-1}) was at its lowest recorded level for that month since 1961 (95 year average = 512 m^3 s^{-1}).

Mean daily discharge for the MRAC during 2003 peaked at 340 m^3 s^{-1} on 15 May. Similar to the YR, peak discharge for the MRAC in 2004 occurred later (29 May) than in 2003, but

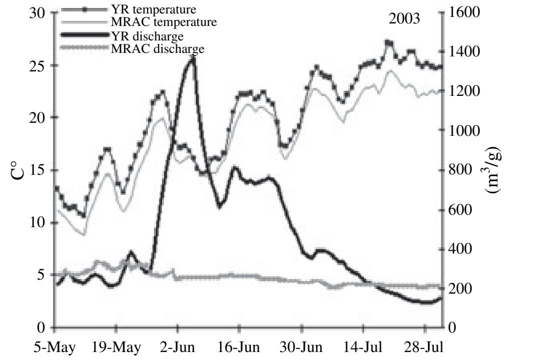

Fig. 2. Spring river conditions for Yellowstone River (YR) and Missouri River above the confluence (MRAC) during 2003. Discharges and temperatures are for Yellowstone River near Sidney, Montana and the Missouri River near Culbertson, Montana

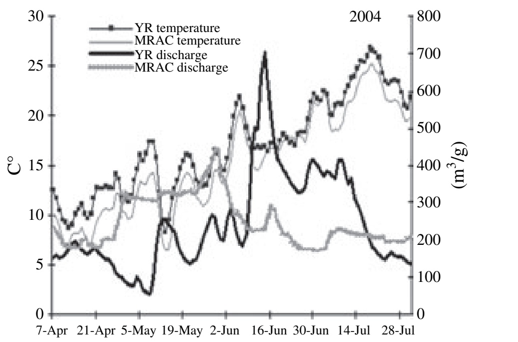

Fig. 3. Spring river conditions for Yellowstone River (YR) and Missouri River above the Confluence (MRAC) during 2004. Discharges and temperatures are for Yellowstone River near Sidney, Montana and the Missouri River near Culbertson, Montana, USA

peak flow for the MRAC was greater in 2004 (445 m^3 s^{-1}) than in 2003 (340 m^3 s^{-1}). In both years, the MRAC exhibited greater discharges than the YR during most of May.

Thermal regimes for both rivers were characterized by higher mean daily water temperatures during May and June 2003 than in May and June 2004. Mean daily water temperature for the YR during this period was 17°C in 2003 compared to 15.9°C in 2004. May and June water temperatures in the MRAC averaged 15.7°C in 2003 and 14.4°C in 2004. Mean daily water temperatures were consistently lower in the MRAC than in the YR by 0.5°C to 2.0°C during both years.

YR suspended sediment levels were greater in 2003 than in 2004 (Figs 4 and 5). Mean daily suspended sediment measurements for May and June 2003 (860 mg L^{-1}) were nearly twice that for the same period during 2004 (433 mg L^{-1}). Insufficient data on MRAC suspended sediment were collected to draw meaningful comparisons between years.

River selection

In 2003, 16 of 20 fish (10 males, six females) were relocated in the YR at least once. Seven females and one male were found in the MRAC at least once. No males and two females were found to enter one river then subsequently enter the other river at least once. First entry into the YR peaked at four fish (20% of total migrants) on 27 May when discharge and water temperature were 365 m^3 s^{-1} and 21.3°C, respectively. First entry into the MRAC peaked at two fish (10% of total

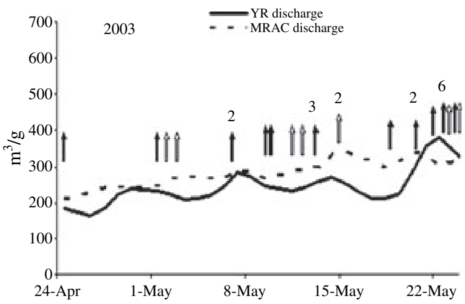

Fig. 4. Number of paddlefish that selected either Yellowstone River (closed arrows) or Missouri River (open arrows) during 2003. Each arrow = one fish unless noted by a number; height of arrow is arbitrary. Discharge is for Yellowstone River near Sidney, Montana and the Missouri River near Culbertson, Montana, USA

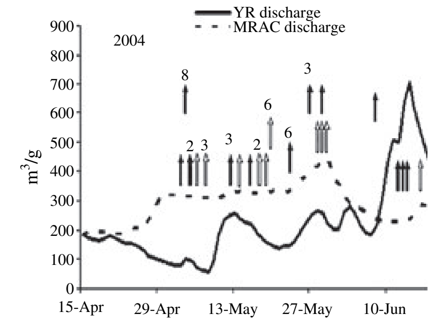

Fig. 5. Number of paddlefish that selected either Yellowstone River (closed arrows) or the Missouri River (open arrows) during 2004. Each arrow = one fish unless noted by a number; height of arrow is arbitrary. Discharge is for Yellowstone River near Sidney, Montana and the Missouri River near Culbertson, Montana, USA

migrants) on 14 May when discharge was 331 $m^3 s^{-1}$ and mean daily water temperature was 12.4°C.

In 2004, of the 21 fish that moved above the Confluence, 19 (10 males, nine females) were contacted in the YR at least once. Eight female and 10 male fish were contacted in the MRAC at least once. Five males and six females were found to enter one river then subsequently enter the other river at least once. First entry into the YR peaked at eight fish (38% of total migrants) on 10 May when discharge and water temperature were 182 $m^3 s^{-1}$ and 15.8°C, respectively. First entry into the MRAC peaked at four fish (19% of total migrants) on 21 May when discharge was 334 $m^3 s^{-1}$ and mean daily water temperature was 14°C.

For 2003 and 2004 data combined, fish selected the YR 34 of 54 times (63%) when the prior contact was below the Confluence in the previous 3 days (Figs 4 and 5). A higher percentage of fish selected the YR in 2003 (80%) than in 2004 (59%). Timing of entrance into the MRAC in 2004 was similar among fish, with 13 of 18 (72%) selections occurring in the 10-day period between 19 May and 28 May when mean daily discharge for the MRAC (355 $m^3 s^{-1}$) was nearly twice that of the YR (182 $m^3 s^{-1}$).

The difference in the rate of change in discharge between rivers (Q_{y-m}) was found to be a significant explanatory variable for river selection (logistic regression $P = 0.0232$) but the difference in the magnitude of discharge between rivers (D_{y-m}) was not ($P = 0.0925$). Over 70% of new entrances into the YR occurred when YR discharge was increasing at a greater rate or decreasing at a lesser rate than MRAC discharge. Likewise, 80% of MRAC selections occurred when MRAC discharge was either increasing at a greater rate or decreasing at a lesser rate than YR discharge. The influence of different magnitudes of discharge between rivers was less clear. Nearly 90% (30 of 34 relocations) of new entrances into the YR occurred when MRAC discharge was greater than YR discharge. However, all new entrances into the MRAC occurred when MRAC discharge was greater than YR discharge.

Once fish selected the MRAC they were unlikely to be contacted in the YR as spring progressed. For example, four out of 10 female fish entered the MRAC during mid-May 2003 and were not subsequently found in the YR during the remainder of the 2003 tracking period. Regardless of the number of days between contacts, 48% of MRAC entries were not followed by a subsequent telemetry contact in the YR.

Directional movements

Two general migratory patterns were reconstructed for telemetered paddlefish as spring progressed in both 2003 and 2004. Pattern 1 was for fish that selected the Yellowstone River and was characterized by four phases: (i) pre-spawn staging 1–30 rkm below the Confluence during base flows, (ii) short bi-directional movements during periods of fluctuating flows, (iii) sustained upriver movements on the ascending limb of the spring hydrograph, and (iv) rapid downriver movement by females and gradual downriver movement by males on the descending limb of the hydrograph. Pattern 2 was seen in fish that made prolonged ascents into the MRAC and was characterized by three phases: (i) staging below the Confluence in early spring, (ii) sustained upriver movements in early to mid-May when MRAC discharge exceeded that of the Yellowstone River, and (iii) variable descending movements through late June.

Directional movements in the YR were associated with changes in both discharge and suspended sediment. In 2003, 23 of 33 (70%) upriver movements greater than 10 rkm occurred during periods of increasing discharge. Twenty-one of 33 (64%) upriver movements greater than 10 rkm occurred during periods of increasing suspended sediment during 2003. A similar relationship was seen in 2004, with 33 of 46 (72%) upriver movements greater than 10 rkm occurring during rising flows. Fewer of these upriver movements (50%) were coupled with increasing suspended sediment levels in 2004.

Downriver movements were associated with decreasing flows and decreasing suspended sediment levels in both years. In 2003, 14 of 18 (78%) downriver movements greater than 10 rkm occurred during decreasing discharges and 11 of 14 (79%) downriver movements greater than 10 km occurred during decreasing suspended sediment levels. In 2004, 29 of 36 (81%) downriver movements greater than 10 rkm occurred during periods of both decreasing discharge and decreasing suspended sediment. Directional movements were significantly correlated with discharge (multiple regression, $P < 0.0001$) and suspended sediment ($P = 0.0013$) but not with water temperature ($P = 0.6082$). Model selection analysis indicated that upriver or downriver movements were most likely to occur when discharge and suspended sediment were either increasing or decreasing jointly. No obvious relationship between directional movement and changes in YR water temperature was observed in either year.

Differences between sexes

No significant difference was found between mean total migration distance of males and females (ANOVA, P = 0.894). However, mean total migration distance was significantly greater (ANOVA, P = 0.04) in 2004 than in 2003 for both males (415 km vs 245 km) and females (365 km vs 279 km).

Males did not ascend above the Confluence earlier than females. In 2003, for example, four of 10 males and five of 10 females ascended above the Confluence before 15 May. However, males lingered in the YR and were contacted there considerably later in the migration season than were females. In 2003, all but one female that had ascended the YR earlier that year had also descended below the Confluence by the end of June. However, 30% of males remained in the YR until the end of July. In 2004, females were last contacted in the YR on 17 June whereas up to 10% of males were found in the YR nearly a month later.

Discussion

In this study, migratory, pre-spawning paddlefish ascending from Lake Sakakawea were faced with a choice to move into either the highly regulated MRAC or the quasi-natural YR during the spawning season. The greater frequency of paddlefish ascensions into the YR (63%) than the MRAC (37%) found in our study is consistent with the consistently higher catch rates of paddlefish in the YR than in the MRAC (North Dakota Game and Fish Department and Montana Department of Fish, Wildlife, and Parks, unpubl. data). Our results were also consistent with those of Firehammer and Scarnecchia (2006) who reported that 82% of telemetered fish selected the YR during 1999–2002. Bramblett and White (2001) reported that 90% of telemetered pallid sturgeon (*Scaphirhynchus albus*) and 80% of shovelnose sturgeon (*Scaphirhynchus platorynchus*) chose the YR over the MRAC when previous radio-telemetry contact was in the MRBC during the spring migration period.

The preferential selection of the YR during the spawning migration over the MRAC is consistent not only with higher paddlefish catches on the YR, and with previous studies at this location, but also with studies on other species elsewhere. Bowen et al. (2003) concluded that regulated flows and reduced sediment transport in the MRAC have led to reductions in nutrient cycling in areas of inundated vegetation, and in abundance and diversity of areas of slow current velocity compared to the lower YR. The physical attributes of the quasi-natural YR (i.e. natural flow variations, suspended sediment or turbidity, and water temperature profiles) have been shown to be associated with increased production and abundance of other large river fishes. The lack of a natural hydrograph and low water temperatures in the highly regulated Missouri River below Garrison Dam, North Dakota were associated with lower growth rates of shovelnose sturgeon in that river segment than in the YR (Everett et al., 2003). Dieterman and Galat (2004) reported that increased distance to upstream impoundment, high flow variability, and high mean turbidity were significantly associated with presence of endangered sicklefin chub (*Macrhybopisis meeki*) in the YR and upper and middle Missouri River.

Although a majority of tagged fish selected the YR in 2003 and 2004, there were substantial differences in the degree of preference for the YR over the MRAC between our study and that of Firehammer and Scarnecchia (2006). More fish ascended the MRAC and utilized this river section longer than reported by Firehammer and Scarnecchia (2006). Combining the 2003 and 2004 data, telemetered paddlefish selected the MRAC 20 of 54 times (37%) and typically made prolonged forays into this river section by remaining there at least 1 week. In contrast, Firehammer and Scarnecchia (2006) found that only 18% of telemetered paddlefish selected the MRAC between 1999 and 2002. Moreover, the few fish that did select the MRAC prior to 2003 typically made short distance movements and were subsequently contacted in the YR within a week.

Differential river discharge is one factor that may explain why a higher percentage of paddlefish utilized the MRAC in our study than in Firehammer and Scarnecchia (2006). In 2003, 40% of tagged females entered the MRAC during mid-May and were not subsequently found in the YR during the remainder of the tracking period. These fish were first contacted in the MRAC during a 13-day period in which mean discharge in this river section was greater than for the YR (291 $m^3 s^{-1}$ vs 246 $m^3 s^{-1}$). Firehammer and Scarnecchia (2006) also reported that most MRAC selections were made when the MRAC had a greater rate of increase in discharge and ⁄ or a higher average discharge than the YR. However, in none of the 4 years of their study did MRAC discharge exceed that of YR discharge for more than four consecutive days during the month of May. These results suggest that prolonged, high MRAC discharge early in the migration provides attraction flows that may encourage paddlefish to move into this river segment.

Another mechanism that may influence river selection is site fidelity through homing. Stancill et al. (2002) found that 31% of male paddlefish tagged near assumed spawning reaches of the White River, South Dakota returned to these areas in later years of both limited and peak flows. Homing capabilities have been suggested in Gulf sturgeon (*Acipenser oxyrinchus desotoi*; Heise et al., 2004), lake sturgeon (*Acipenser fluvescens*; Knights et al., 2002) and Atlantic sturgeon (*Acipenser oxyrinchs*; Waldman and Wirgin, 1998). If Yellowstone-Sakakawea paddlefish have natal homing tendencies, greater reproduction in the YR would lead to a greater proportion of fish selecting the YR. Too few fish made consecutive year migrations to ascertain the importance of site fidelity or the existence of homing. However, one male migrated 50 km up the Yellowstone River in 2003 but made a prolonged foray into the MRAC in 2004.

As of 2007, there are plans to provide artificially increased water releases from Fort Peck Dam to aid pallid sturgeon spawning (United States Fish and Wildlife Service, 2003). Based on the results of our study, any such releases have the potential to immediately impact paddlefish spawning migrations and reproductive success. For example, if Fort Peck water releases attract paddlefish into the MRAC when they would have otherwise entered the YR, it would also be important that suspended sediment, temperature and other characteristics of good spawning habitat known to be important for paddlefish and sturgeon spawning were also present (Russell, 1986). The MRAC is clearer, colder and has more stable flows in the spring than the YR (United States Geological Survey, 2003). Hypolimnetic discharge from Fort Peck Reservoir in late spring lowers water temperatures and in turn may delay spawning and incubation time of eggs (Purkett, 1961; Sparrowe, 1986). Moreover, stabilized flows and lower sediment loads may increase out-migration times of larvae and increase predation on larvae by clear-water adapted predators, as has been shown in other species (Johnson and Hines, 1999; Gadomski and Parsley, 2005; Bestgen et al., 2006). A lack of empirical data regarding differential hatching rates and larval survival rates between the MRAC and YR makes it difficult to draw definitive conclusions. If suitable spawning conditions are not met, attraction flows could serve as an ecological trap, drawing paddlefish into the more altered MRAC and hindering rather than aiding successful reproduction of paddlefish and possibly other species, including the pallid sturgeon.

Results from this study indicate a strong relationship between directional movements of paddlefish in the YR and discharge and suspended sediment. The overall upstream movement of paddlefish with increasing discharge observed in 2003 and 2004 is consistent with the idea that increases in discharge may trigger fish to move out of staging sites in the MRBC and into either the YR or the MRAC. These results are consistent with other studies. Firehammer and Scarnecchia (2006) reported that directional movements in the Yellowstone River 1999–2002 were positively related to changes in discharge and turbidity but not temperature. Paukert and Fisher (2001) used jaw tag recoveries and biotelemetry to investigate spawning migrations of paddlefish in Keystone Reservoir, Oklahoma. High flows ($>1400\ m^3\ s^{-1}$) from tributaries appeared to direct paddlefish migrations whereas water temperatures and photoperiod had little influence.

Paddlefish exhibited greater cumulative movement in 2004 (a low water year) than in 2003 (a high water year). A possible explanation for this unexpected result may be found in differences in movement rates between fish in the YR and fish in the MRAC. Directional movement analysis indicated that paddlefish respond strongly to abrupt changes in discharge. A greater proportion of fish utilized the MRAC in 2003 than in 2004, and inter-annual movement rates may have been biased by differential river dynamics. In both years, the MRAC showed less variation in discharge (coefficient of variation = 0.26) between 1 April and 1 July than the YR (coefficient of variation = 0.58). The controlled spring hydrograph of the MRAC removed the stimuli of sudden rises and falls in discharge and in turn may not have favored repeated upriver and downriver movements as seen in the YR.

The combination of fixed radio-telemetry receiving stations and manual tracking used in this study provided more timely and precise data on movements and migrations than did the exclusive manual tracking used in a previous study on Yellowstone-Sakakawea paddlefish (Firehammer and Scarnecchia, 2006). The mean number of days elapsed between telemetry contacts of individual fish in our study was nearly two times less (4.3 days) than in the previous study (7.9 days; Firehammer and Scarnecchia, 2006). Moreover, the mean number of contacts per fish was approx. 28% times higher in our study (21.7 contacts ⁄ fish) than in the previous study (16.9 contacts ⁄ fish; Firehammer and Scarnecchia, 2006).

This increased timeliness and precision with fixed stations enabled us to document several important paddlefish movements over spans of 4 days or less that would not have been detected by manual tracking alone. For example, in 2004 one fish was contacted at the fixed station near the YR mouth 1 day, detected at a fixed station 48 km up the YR 2 days later, then detected back near the mouth on the fourth day. A second fish made an upriver movement of 35 km in 2 days, then moved 76 km downriver the following day in association with a sudden decrease in YR discharge. A third fish was repeatedly detected by a fixed station on the Milk River (a tributary of the MRAC 18 km downstream of Fort Peck Dam), the first documented movement of a telemetered paddlefish into that river. Manual tracking had not been conducted on that tributary. Several other fish demonstrated rapid short-term movements. Future advances in technology such as satellite-monitored radio tracking may enable us to monitor even more thoroughly the migrations and movements of Yellowstone-Sakakawea paddlefish in response to environmental cues.

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