Transactions of the American Fisheries Society 135:200–217, 2006

DOI: 10.1577/T05-058.1

[Article]

Spring Migratory Movements by Paddlefish in Natural and Regulated River Segments of the Missouri and Yellowstone Rivers, North Dakota and Montana

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portant factor in determining the extent of the migration (Elser 1977; Purkett 1961). The influence of turbidity and fluctuating or low temperatures on migratory movements has not been investigated.

Studies conducted in regulated rivers, however, may not reveal the range of potential migratory behaviors in a stock. Dams tend to concentrate spawning adults in tailwater habitats during the spring and inhibit upriver movements (Southall and Hubert 1984; Stancill et al. 2002; Zigler et al. 2004). Regulated rivers have also been shown to exhibit highly modified and unnatural patterns of discharge, turbidity, and temperature (Poff et al. 1997). The suppression of rising spring discharge below dams may confound the interpretation of movements observed during the migration. In addition, reservoirs capture sediments moving downriver and release cold hypolimnetic waters, curbing the natural rise of both turbidity and temperature in the spring. In contrast, an investigation in an unregulated river with more natural levels of discharge, turbidity, and temperature may provide an assessment of natural migratory patterns in paddlefish.

The Yellowstone–Sakakawea paddlefish stock is one of the last naturally reproducing populations in the United States that sustains an annual harvest. This stock has persisted as a result of the productive rearing environment of Lake Sakakawea (Scarnecchia et al. 1996) and access to upriver spawning habitat in reaches of the Yellowstone and Missouri rivers (Gardner and Stewart 1987; Gardner 1995). Previous studies have indicated that the majority of paddlefish ascend the Yellowstone River rather than the Missouri River during the spawning migration, though the stimuli inducing river selection were not well understood (Robinson 1966; Rehwinkel 1978). The Yellowstone River, which has no large main-stem impoundments, has retained much of the natural variability in discharge, sediment, and temperature dynamics that have been considered important for successful paddlefish reproduction. In contrast, river dynamics along the segment of the Missouri River that is accessible to paddlefish have been altered by Fort Peck Dam. A valuable research opportunity thus exists to observe migratory patterns under both relatively natural and regulated river conditions.

A radiotelemetry study was conducted during 1999–2002 to examine the movements of Yellowstone–Sakakawea adult paddlefish during the spawning migration. The objective of the study was to determine how river conditions influence the temporal and spatial distribution of paddlefish along the Yellowstone and Missouri rivers. Based on relationships documented from the aforementioned studies, it was hypothesized that upriver movements would be associated with periods of increasing discharge, turbidity, and temperature along the river system. Additionally, it was hypothesized that paddlefish would be more likely to select the river with higher levels of discharge, turbidity, and temperature as they ascend upriver (i.e., the Yellowstone River rather than the Missouri River). Results from the study were then interpreted for their implications for reproductive success in this paddlefish population.

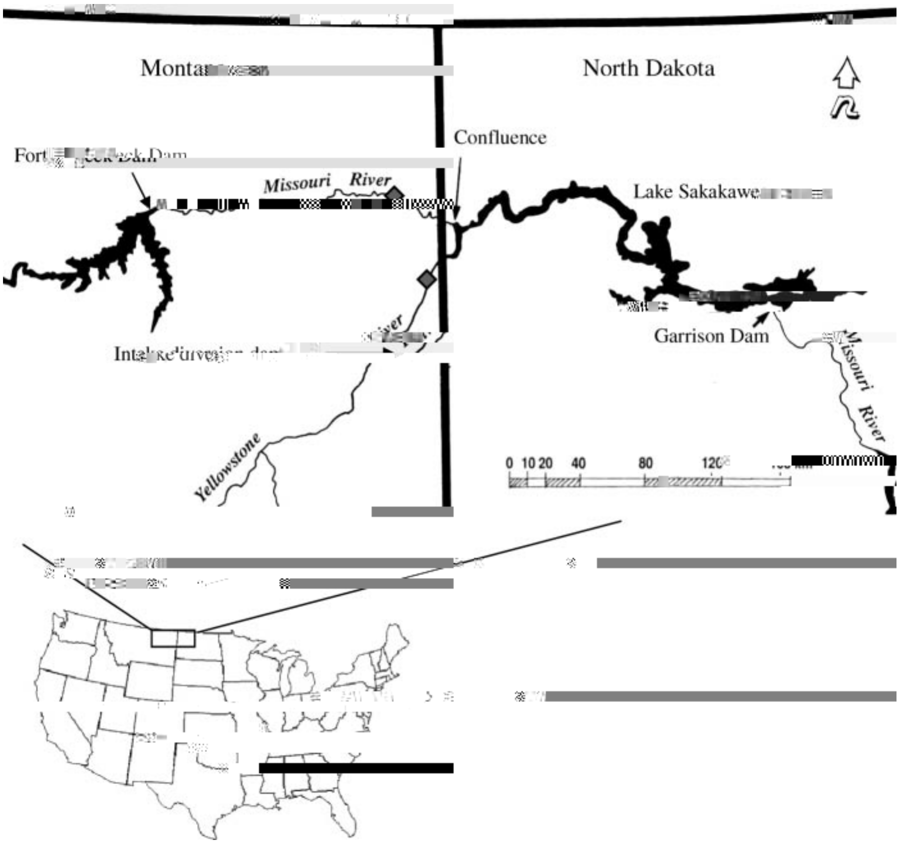

FIGURE 1.—Map of the study area, including the lower Yellowstone River and the Missouri River from Fort Peck Dam to Lake Sakakawea, Montana and North Dakota. The diamonds indicate the U.S. Geological Survey gauging stations at Culbertson (Missouri River river kilometer 63) and Sidney (Yellowstone River river kilometer 47), Montana.

tiple islands and alluvial channel bars, swift current and substrate consisting primarily of cobble and gravel, and an average slope of 0.046% (Koch et al. 1977). Although in-channel features remain common along the lowermost 40 km of the river, channel gradient declines and sand replaces gravel as the predominant substrate (Bramblett and White 2001).

The MRAC extends 305 rkm from the tailwaters of Fort Peck Dam downriver to the confluence. The completion of Fort Peck Dam in 1937 stabilized discharge, reduced sediment loads, and altered river temperatures along this reach of the Missouri River (Hesse et al. 1989). Since dam completion, average discharge during May and June at Culbertson, Montana (MRkm 63), has been 273 m

TABLE 1.—Summary statistics for Yellowstone–Sakakawea paddlefish radio-tagged in the Missouri River below its confluence with the Yellowstone River during 1999 and 2000. Mean lengths and weights for tagging groups are provided in parentheses.

Tagging group	Females			Males			Expelled tags	Harvested fish
	N	Length (cm)	Weight (kg)	*N*	Length (cm)	Weight (kg)		
Spring 1999	12	104–127 (117)	24.5–42.6 (32.7)	13	89–107 (97)	10.9–20.4 (15.3)	7	2
Fall 1999[a]	9	104–124 (117)	19.1–39.5 (30.4)	11	86–107 (99)	10.0–19.5 (15.4)	3	1
Fall 2000[b]	10	102–119 (114)	24.0–34.5 (30.5)	11	94–107 (101)	14.1–20.9 (16.4)	1	3
Total	31	102–127 (116)	19.1–42.6 (31.3)	35	86–107 (98)	10.0–20.9 (15.7)	11	6

[a] Excludes two additional fish of undetermined sex with lengths of 104 and 109 cm and weights of 20.9 kg.
[b] Excludes one additional fish of undetermined sex with a length of 97 cm and a weight of 20.9 kg.

with the MRAC, discharge and sediment levels along the MRBC are typically higher during the spring because of the influence of the YR. Sand bars are common along this reach, channel depths typically being greater than those along the YR and MRAC reaches.

Methods

Field procedures.—Paddlefish were captured along the MRBC by drifting modified gill nets (mesh sizes, 7.6, 10.2, and 12.7 cm) perpendicular to the channel current. Sampling below the confluence, rather than above, prevented selection of adults that had already migrated into one river over the other. Upon contact with nets, fish were removed and brought onboard the boat where length (eye-to-fork length [EFL]; Ruelle and Hudson 1977) and weight were recorded, and sex was noted during surgical implantation of radio transmitters (Ross and Kleiner 1982). Sixty-nine adult paddlefish received transmitters over the period April 1999 to September 2000: 25 during the spring (April 29–30) of 1999, 22 during the fall (September 30–October 5) of 1999, and 22 during the fall (September 27–28) of 2000. Females were typically longer and heavier than males (Table 1). Thirty-one of the 69 fish were females with lengths that ranged from 102 to 127 cm EFL (mean, 116 cm) and weights that ranged from 19.1 to 42.6 kg (mean, 31.3 kg). Thirty-five of the tagged fish were males with lengths that ranged from 86 to 107 cm EFL (mean, 98 cm) and weights that ranged from 10.0 to 20.9 kg (mean, 15.7 kg). The sex of three fish with lengths that ranged from 97 to 109 cm EFL (mean, 103 cm) and similar weights of 20.9 kg could not be determined. Mean lengths and weights were not significantly different among the three tagging groups for both females and males (analysis of variance [ANOVA]; P . 0.1). Although maturation stage was not determined for tagged fish during surgery, the presence of large, olive-gray eggs in females suggested that all were capable of spawning during the forthcoming spring migration.

Each of the radio transmitters (Advanced Telemetry Systems, Isanti, Minnesota) used in this study had a unique frequency between 49.011 and 49.930 Mhz and a life expectancy of 1,100 d (hereinafter fish will be identified by their abbreviated frequency; e.g., 49.011 as 011). All transmitters, running on a preprogrammed 12-h on–off cycle to conserve battery life, were activated to transmit between 0700 and 1900 hours. Transmitters of three different dimensions were implanted during the study. Sex-specific, large-diameter transmitters were used for fish tagged in the spring of 1999: large transmitters (14.5 cm long, 4.1 cm in diameter, and 265 g in weight) were implanted into females, whereas small transmitters (7.8 cm long, 4.1 cm in diameter, and 130 g in weight) were implanted into males. In comparison, the transmitters implanted into fish tagged in the fall of 1999 and 2000 were lighter (100 g), longer (17.0 cm), and of smaller diameter (2.0 cm) to accommodate a smaller incision and fewer sutures during surgeries. Radio transmitters weighed less than 2% of body weight for all tagged fish (Winter 1996).

Tracking was conducted by dividing the study area into four units: (1) YRkm 114–YRkm 47; (2) YRkm 47–confluence; (3) MRBC, a 40-km stretch extending downriver from the confluence; and (4) MRAC. The first three units were searched primarily by boat using a directional loop antenna. In addition, aerial surveys were conducted periodically, particularly along the MRAC because of its poor accessibility by boat. During early spring, units 2 and 3 were typically searched twice per week so that information could be obtained on short-term migratory movements that would more accurately reflect responses to rapidly changing river conditions (Southall 1982; Moen 1989; Curtis et al. 1997). The first 5–10 rkm of the MRAC above the confluence was also tracked during weekly searches to obtain information on river selection. When the distribution of fish was found to move further up the Yellowstone River as spring advanced, unit 1 was also searched 1–2 times per week. During spring searches, a tag that had been consecutively contacted in the same location along the river for a period longer than 30 d was assumed to have been expelled and not considered in analyses. Tracking was not conducted during the summer after fish were no longer contacted in the river (indicating movement back into the reservoir) because the radio transmitters were not easily detected at reservoir depths. Geographical coordinates were recorded for all contacted fish using a global positioning system receiver. These coordinates were later overlaid onto a digitized map of the river system using geographic information systems software (ARC–INFO, Environmental Systems Research Institute, Inc., Redlands, California), and each was assigned a positive or negative rkm indicating the distance above or below the confluence, respectively.

River conditions were assessed using information obtained from gauging stations or from data collected during weekly searches. Daily discharge (m^3/s) was obtained from U.S. Geological Survey (USGS) gauging stations near Sidney (YRkm 47) and Culbertson (MRkm 63), Montana. Peak levels of YR discharge were 1,509, 997, 680, and 1,093 m^3/s during migratory periods of 1999–2002. Compared with YR discharge, MRAC discharge was relatively stable with peak flows of 413, 382, 282, and 311 m^3/s during the four consecutive migratory periods. Daily MRBC discharge was estimated as the combined discharge from the YR and MRAC. River temperatures (°C) were obtained from data loggers positioned at YRkm 13.5 and MRkm 6. To estimate daily MRBC temperature, temperatures measured periodically along the MRBC during weekly searches were regressed on YR temperatures recorded by the logger to provide a predictive linear relationship ($R^2 = 0.98$). Daily YR suspended sediment (mg/L) data were also obtained from the USGS gauging station at Sidney. Because similar data were not available for the MRAC, turbidity (nephelometric turbidity units [NTU]) was used as a surrogate to estimate changing levels of suspended sediment (i.e., turbidity in the study area was abiotic) and was measured along both rivers above the confluence during surveys to permit comparisons between the two rivers.

Data analyses.—Movement patterns were analyzed to examine paddlefish responses to temporal changes in river conditions. Only data from spawning migrations of 2000 and 2001 were included in these analyses because of a lack of short-term movement data for 1999 and 2002. The relationship between directional movement and the change in discharge, suspended sediment, and temperature along the Yellowstone and Missouri rivers was evaluated by use of linear regression. Upriver and downriver movements for individual fish were expressed in regression models as positive and negative differences between successive contacts, respectively. Each movement was inversely weighted by the total number of movements by that fish to minimize bias toward fish that were frequently contacted during the migratory period. In addition, only movements during periods of monotonically increasing or decreasing river conditions were used in the analysis. For each movement, the change in discharge, suspended sediment, and river temperature was calculated as

$$\Delta X = \log_e(X_t/X_{t-d}), \qquad (1)$$

where X is the value of the river variable, t is the day of contact, and d is the number of elapsed days between successive contacts for an individual fish. The quotient, rather than the difference, was used to account for differential responses by paddlefish to similar increments or decrements in a river variable (e.g., an increase in discharge from 300 to 600 m^3/s may elicit a different response than an increase in discharge from 1,200 to 1,500 m^3/s). Quotients were log transformed to normalize their distribution. Changes in MRBC variables were calculated for movements along the MRBC, whereas changes in YR variables were calculated for movements along the YR and between the YR and MRBC. Movements along the MRAC were not included in the analysis because of infrequent contacts along this reach. Because multicollinearity was detected among the changes in the three river variables (variance inflation factor ≥ 2), a principal components analysis (PCA) was conducted (Table 2), and the principal components scores derived from the PCA were used as new explanatory variables in regression models (Graham 2003).

The information-theoretic approach was used to evaluate the relative plausibility of regression models that were derived to explain directional movement. This approach, which is well suited for drawing inferences from observational data, quantitatively compares a set of competing models to select those that are best supported by the data

TABLE 2.—Principal components analysis for river variables measured during migratory movements of radio-tagged paddlefish in the Yellowstone and Missouri rivers, 2000 and 2001. Included is the percent variation of the measured variables explained by each principal component (PC) and the component correlation vector, which describes the correlations between each PC and the measured variables.

		Component correlation vector		
Principal component	Variation explained (%)	Change in discharge	Change in suspended sediment	Change in temperature
PC-1	64	0.91	0.94	20.44
PC-2	30	0.28	0.15	0.89
PC-3	6	20.29	0.31	0.04

(Burnham and Anderson 1998). The candidate set comprised the full model with all newly created explanatory variables and reduced models, which included those with all possible subsets of explanatory variables and a model with no explanatory variables (i.e., directional movement was not related to changing river conditions). Akaike's information criterion, corrected for small sample bias (AIC_c), was used to rank and select models that accounted for the most variation in the data with the fewest number of parameters (Burnham and Anderson 1998). The model with the smallest AIC_c value was considered best at approximating the data, whereas models with AIC_c values of more than 10 units greater than the best model's AIC_c provided strong evidence against their consideration (Burnham and Anderson 1998). To measure the relative weight of evidence for each model under consideration, Akaike weights (w_i) were computed as follows:

$$w_i \ 5 \ \frac{\exp(2\,0.5 \cdot \mathrm{DAIC}_c)}{\sum [\exp(2\,0.5 \cdot \mathrm{DAIC}_c)]},$$

where DAIC_c was the difference between a given model's AIC_c and the best model's AIC_c (only models with a DAIC_c less than 10 were considered and included in the summation term in the equation; Burnham and Anderson 1998). A model's Akaike weight can be interpreted as the probability that the given model is best at approximating the data. In addition, the relative importance of a given explanatory variable in determining directional movement was evaluated by summing Akaike weights over those models in which the variable appeared. A variable's index of relative importance could range from 0 (i.e., the variable was not included in any model under consideration) to 1 (i.e., the variable was included in every model under consideration).

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TABLE 3.—Principal components analysis for river variables measured during periods of river selection by migratory radio-tagged paddlefish in the Yellowstone and Missouri rivers, 2000–2002 (see text for an explanation of river variables). Included is the percent variation of the measured variables explained by each principal component (PC) and the component correlation vector, which provides the correlations between each PC and the measured variables.

Principal component	Variation explained (%)	Component correlation vector: Difference in rate of change in discharge	Difference in discharge	Difference in turbidity
PC-1	74	0.77	0.88	0.91
PC-2	18	0.62	20.36	20.19
PC-3	8	0.07	0.31	20.39

in 2000, 2001, and 2002 were used because of lengthy elapsed periods between contacts for fish

TABLE 4.—Summary of migratory movement indices for radio-tagged Yellowstone–Sakakawea paddlefish contacted during May 2–June 29, March 22–July 5, April 19–June 21, and April 23–July 1, 1999–2002. The subheadings under the heading ''ascend confluence'' indicate the number of fish that never ascended past the confluence of the Yellowstone and Missouri rivers (0) or that moved upriver of the Confluence either once (1) or several times (. 1).

Migration year	Contacted fish	Total contacts	Contacts per fish			Ascend confluence		
			Median	Minimum	Maximum	0	1	. 1
1999	23	135	4.0	1	13	3	15	5
2000	20	226	10.5	1	23	8	5	7
2001	26	224	8.5	4	16	3	9	14
2002	22	111	4.5	1	10	3	8	11

in 2000 (median, 10.5 contacts) and 2001 (median, 8.5 contacts) than in 1999 (median, 4 contacts) and 2002 (median, 4.5 contacts). Many of the fish that were infrequently contacted were those that eventually expelled their tags or were harvested. Eleven fish presumably expelled their transmitters during the study period (Table 1). Seven of these 11 fish had been fitted with the large-diameter tags implanted during the spring of 1999. Although 7 of the 11 fish moved upriver during the spring following implantation and before repeated tag contact indicated probable expulsion, the other four fish were not found to move upriver during telemetry searches suggesting tag loss soon after implantation. Five males and one female were harvested throughout the study period; two fish were never contacted during the spring after tag implantation.

The distribution of radio-tagged paddlefish generally moved upriver as spring advanced in all four study years. During periods of relatively stable YR discharge in April, fish were typically contacted in reaches below the confluence (Figure 2). Yellowstone River temperatures were generally increasing during this time and in excess of 14°C by the end of April in most years. Movement above the confluence was typically first detected during initial periods of rising YR discharge and suspended sediment in May of all four years; YR temperatures generally ranged between 10°C and 18°C during these periods (Figure 2). At this time, contacted fish were typically distributed between MRkm −35 and YRkm 50. During periods of high YR discharge and suspended sediment in June of all years, 82% of the contacts were distributed above the confluence along the lowermost 50 rkm of the YR; few fish were contacted below the confluence (Figure 2). By late June and early July in all years, few fish were contacted in the Yellowstone or Missouri rivers; river temperatures typically exceeded 20°C at this time.*tged padde5sT* Pefir(duf)-riod-346351(above.)](sprspende55(temper-346Co548*

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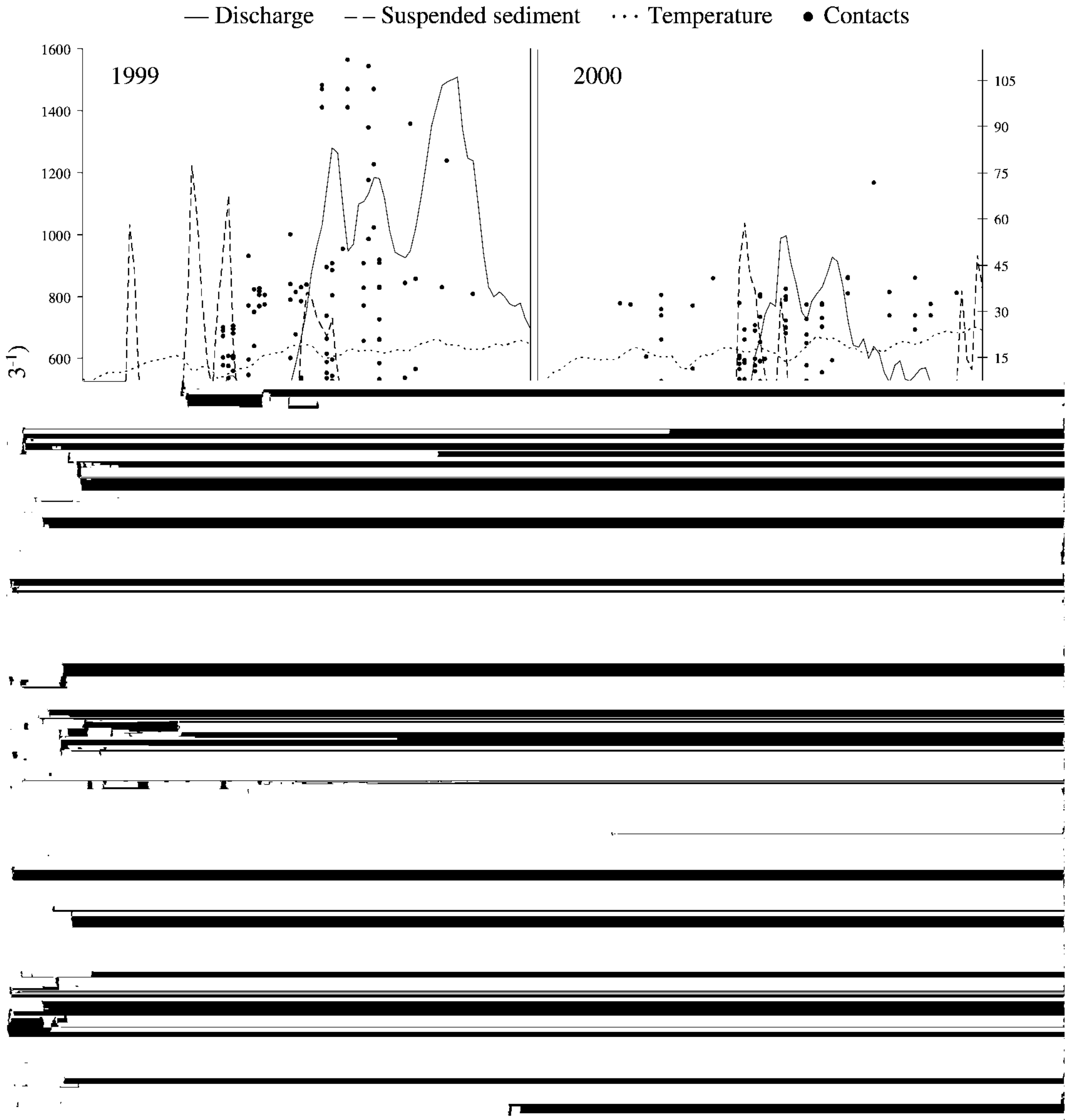

FIGURE 2.—The distribution of radio-tagged paddlefish contacts along the Yellowstone and Missouri rivers in relation to Yellowstone River discharge, suspended sediment, and temperature during migratory periods, 1999–2002. Positive and negative river kilometers (rkm) indicate the number of kilometers above and below the confluence (represented by the solid horizontal line), respectively. One fish was contacted at Missouri River rkm 198 on June 3, 2000, but not displayed in the graph. Open circles indicate river kilometers along the Missouri River above its confluence with the Yellowstone River, where fish were aerially contacted during 2002.

Of those fish that had moved above the confluence, 58% (7 of 12) of fish in 2000 and 61% (14 of 23) of fish in 2001 had been found to ascend the confluence more than once (Table 4). As a result of these directional changes, the cumulative distances traversed by female (mean, 162 rkm) and male (mean, 179 rkm) paddlefish were extensive but similar in both years (ANOVA: $F_{3,21}$ 5 0.3, P 5 0.82). The two greatest cumulative movements of 310 and 292 km were recorded from females. Though coordinated directional movements occurred in response to changing river conditions, there were few cases in which individual fish were found to move together as a unit. On only three

TABLE 5.—Regression models used to explain directional movement in 2000–2001 and river selection in 2000–2002 for radio-tagged paddlefish in the Yellowstone and Missouri rivers. Model variables comprised combinations of the principal components (PCs) derived from a principal components analysis (see Tables 2 and 3). One hundred eighty-one movements were used from 41 fish (mean, 4.4 movements/fish) for the directional movement analysis, and 26 ascensions above the confluence of the Yellowstone and Missouri rivers were used from 19 fish (mean, 1.4 ascensions/fish) for the river selection analysis. Akaike's information criterion, corrected for small sample size (AIC_c), was used to rank the competing models. The difference in AIC_c between the best and subsequent models (ΔAIC_c) and Akaike weights (w_i) provide an index of the relative weight in favor for each model. Akaike weights and PC coefficients were computed only for models receiving support as the best ($\Delta AIC_c < 10$). The relative importance of a model variable can be assessed by summing the w_is over the models in which the variable occurs.

Model variables	Number of parameters[a]	AIC_c	ΔAIC_c	w_i	Estimated coefficients
Directional movement					
PC-1, PC-3[b]	4	797.27	0.00	0.616	8.99, −12.82
PC-1, PC-2, PC-3	5	798.24	0.97	0.379	8.94, 1.7, −12.92
PC-1	3	807.09	9.82	0.005	8.80
PC-1, PC-2	4	808.29	11.03		
PC-3	3	855.64	58.38		
PC-2, PC-3	4	856.30	59.03		
No variables	2	860.27	63.01		
PC-2	3	861.13	63.86		
River selection					
PC-1[c]	2	26.88	0.00	0.559	1.71
PC-1, PC-3	3	28.97	2.09	0.197	1.78, 1.16
PC-1, PC-2	3	29.09	2.21	0.185	1.80, −0.37
PC-1, PC-2, PC-3	4	31.40	4.52	0.058	1.89, −0.38, 1.22
No variables	1	37.59	10.71		
PC-3	2	39.69	12.81		
PC-2	2	39.83	12.95		
PC-2, PC-3	3	42.15	15.27		

[a] Parameters include variable coefficients, intercepts, and variance (directional analysis only).
[b] Model statistics: $P < 0.0001$; $R^2 = 0.31$.
[c] Model statistics: $P < 0.001$; $R^2 = 0.40$.

occasions were two fish contacted within the same river kilometer on the same date after a previous contact together within an upriver or downriver river kilometer.

The rate of upriver movement by paddlefish was positively associated with the rate of increase in discharge and suspended sediment during migratory periods in 2000 and 2001 (Table 6). In 2001, individual-specific movement rates were significantly greater during the rapid increase in both river variables from May 14 to May 19 than during their gradual increase from May 1 to May 6 (Wilcoxon signed rank test: median difference, 9.7 km/d; $P = 0.01$). Although a significant difference in movement rates was not detected for the 2000 data (Wilcoxon signed rank test: median difference, 0.2 km/d; $P = 0.16$), movement rates for seven of the nine fish were greater during the rapid rise in discharge and suspended sediment that occurred from May 20 to June 2 than during the gradual rise in both variables that occurred from April 26 to May 9.

River Selection and River Conditions

Paddlefish primarily chose the Yellowstone River over the Missouri River during their spawning migration. Radio-tagged fish were found to ascend the YR 105 of the 128 times (82%) when consecutive contacts indicated upriver movement from below the confluence. However, 2, 4, 6, and 10 fish were contacted along the MRAC during the four consecutive spring migrations (Figure 4). Although fish were typically contacted within the lowermost 5 rkm of the MRAC, one fish was contacted at MRkm 198 on June 3 in 2000 and four fish were contacted further than MRkm 60 in 2002.

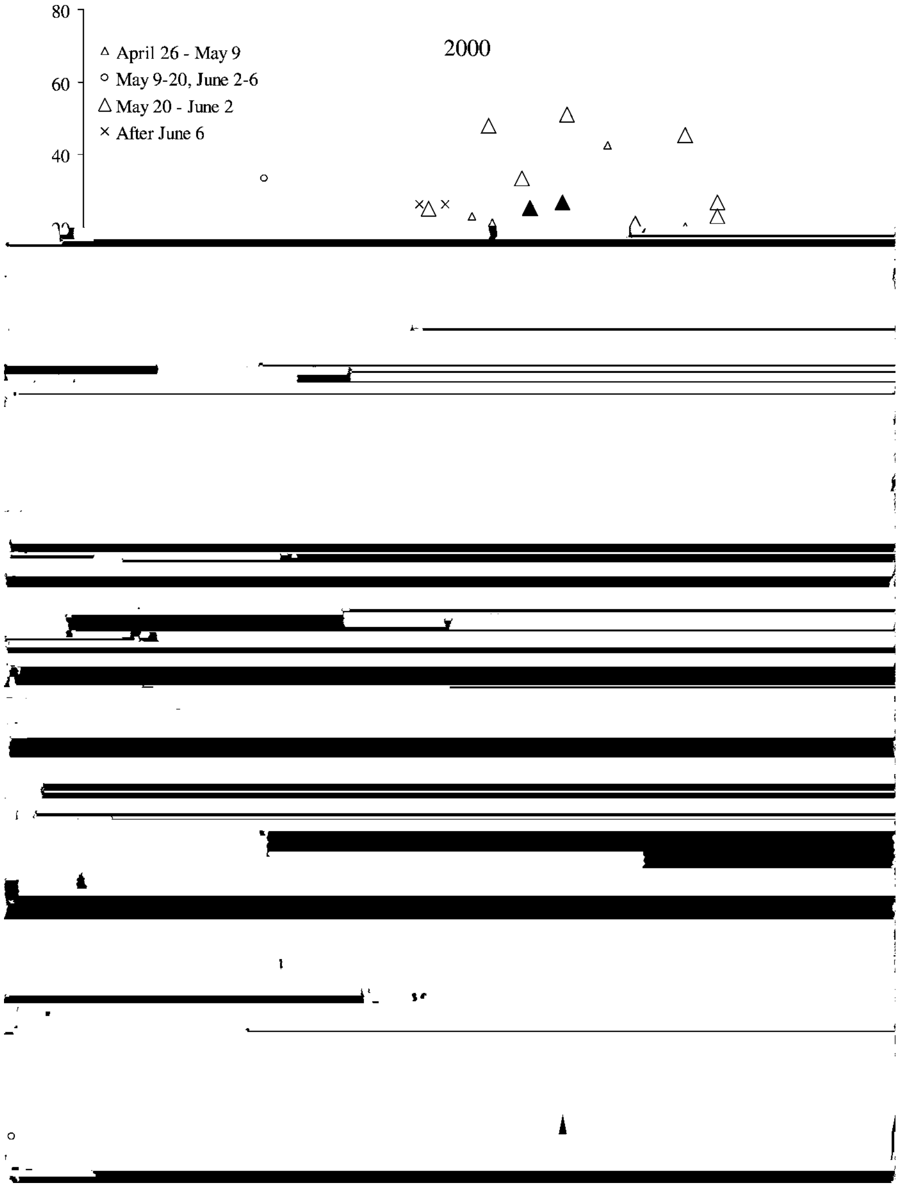

FIGURE 3.—Relationship between movement and the change in discharge (see text for calculation) for migratory radio-tagged paddlefish in the Yellowstone and Missouri rivers, 2000 and 2001. Upriver (positive) and downriver (negative) movements are highlighted during periods of gradually increasing discharge (small triangles), rapidly increasing discharge (large triangles), and decreasing discharge (small circles). Darkened triangles indicate movements during a period when discharge was increasing but suspended sediment was decreasing in 2000 and a period when discharge was relatively stable but suspended sediment was rapidly increasing in 2001.

was PC-1 the only covariate included in the best model, but it was considered four times as important in predicting river selection than other principal components (relative importance: PC-1 5 1.00, PC-2 5 0.24, PC-3 5 0.25; Table 5). The positive coefficient estimate for PC-1 indicated that paddlefish selected the river that had a greater rate of increasing discharge and higher average discharge and turbidity than the other river when ascending past the confluence. For example, contacts of fish along the MRAC often occurred during brief periods of increasing MRAC discharge and

TABLE 6.—Comparison of upriver movement rates for radio-tagged paddlefish contacted during periods of increasing Yellowstone River discharge and suspended sediment in 2000 and 2001. In 2000, the first period occurred from April 26 to May 9 and the second from May 20 to June 2; in 2001, the first period occurred from May 1 to May 6 and the second from May 14 to May 19. There was a significant difference in movement rates between the first and second periods in 2001 but not in 2000 (Wilcoxon signed rank test: $P \leq 0.05$).

Fish	First period movement rate (km/d)	Second period movement rate (km/d)	Movement rate difference (km/d)
2000 migration data			
701	2.4	11.1	8.7
721	1.9	4.3	2.4
730	7.6	7.8	0.2
741	4.8	2.9	21.9
821	9.2	5.5	23.7
841	0.5	0.7	0.2
870	3.0	8.4	5.4
900	1.5	6.0	4.5
910	4.6	4.8	0.2
2001 migration data			
51	3.3	22.2	18.9
151	4.0	6.4	2.4
191	10.7	12.0	1.3
331	11.8	19.7	7.9
571	4.0	22.4	18.4
591	5.5	3.2	22.3
621	2.2	22.7	20.5
881	1.2	10.9	9.7
930	3.4	14.0	10.6

decreasing YR discharge; turbidity and discharge were also typically higher along the MRAC than the YR during this time (Figure 4). Because recorded temperatures along the MRAC were never higher and averaged 2.08C lower than those along the YR when fish ascended either river past the confluence, temperature was not considered a discriminatory variable in river selection.

When using the best approximating model to predict river selection, fish were correctly classified 11 of 15 (73%) times for those that ascended the YR and 9 of 11 (82%) times for those that ascended the MRAC. Incorrect classifications occurred when flow regimes between the two rivers were similar to each other. For example, three incorrectly classified fish that had ascended the YR moved above the confluence from May 4 to May 5, 2001. Although discharge and turbidity were slightly higher along the YR than the MRAC during this time, the MRAC was slightly increasing whereas the YR was temporarily decreasing (Figure 4). In addition, two other fish had ascended the MRAC during the same 2-d period.

Discussion

Radio-tagged adult paddlefish of the Yellowstone–Sakakawea stock moved extensively upriver and downriver during the spring migration coincident with periods of increasing and decreasing discharge and suspended sediment. Previous findings along free-flowing reaches of the Yellowstone River (Rehwinkel 1978) and Missouri River above Fort Peck Dam (Berg 1981) have also noted an association between upriver movement and peaking levels of river discharge. Similar results have been reported along regulated river systems as well. Paddlefish have been found to move upriver and concentrate in tailwater reaches below dams under periods of increasing discharge along the Osage River, Missouri (Purkett 1961); Cumberland River, Tennessee (Pasch et al. 1980); lower Alabama River system (Hoxmeier and DeVries 1997); and Arkansas River, Oklahoma (Paukert and Fisher 2001). However, none of these studies mentioned the incidence of extensive downriver movements corresponding to intermittent periods of declining discharge during the spawning migration.

In contrast to our study, several studies conducted along navigation pools of the upper Mississippi River did not detect a relationship between change in discharge and synchronized directional movement (Southall 1982; Moen et al. 1992; Zigler et al. 2003). This difference may have been because of differences in the maturation status of tagged paddlefish among studies. The presence of large, olive-gray eggs in females tagged in this study suggested that all were capable of spawning during the forthcoming spring migration. Povedundence6(the

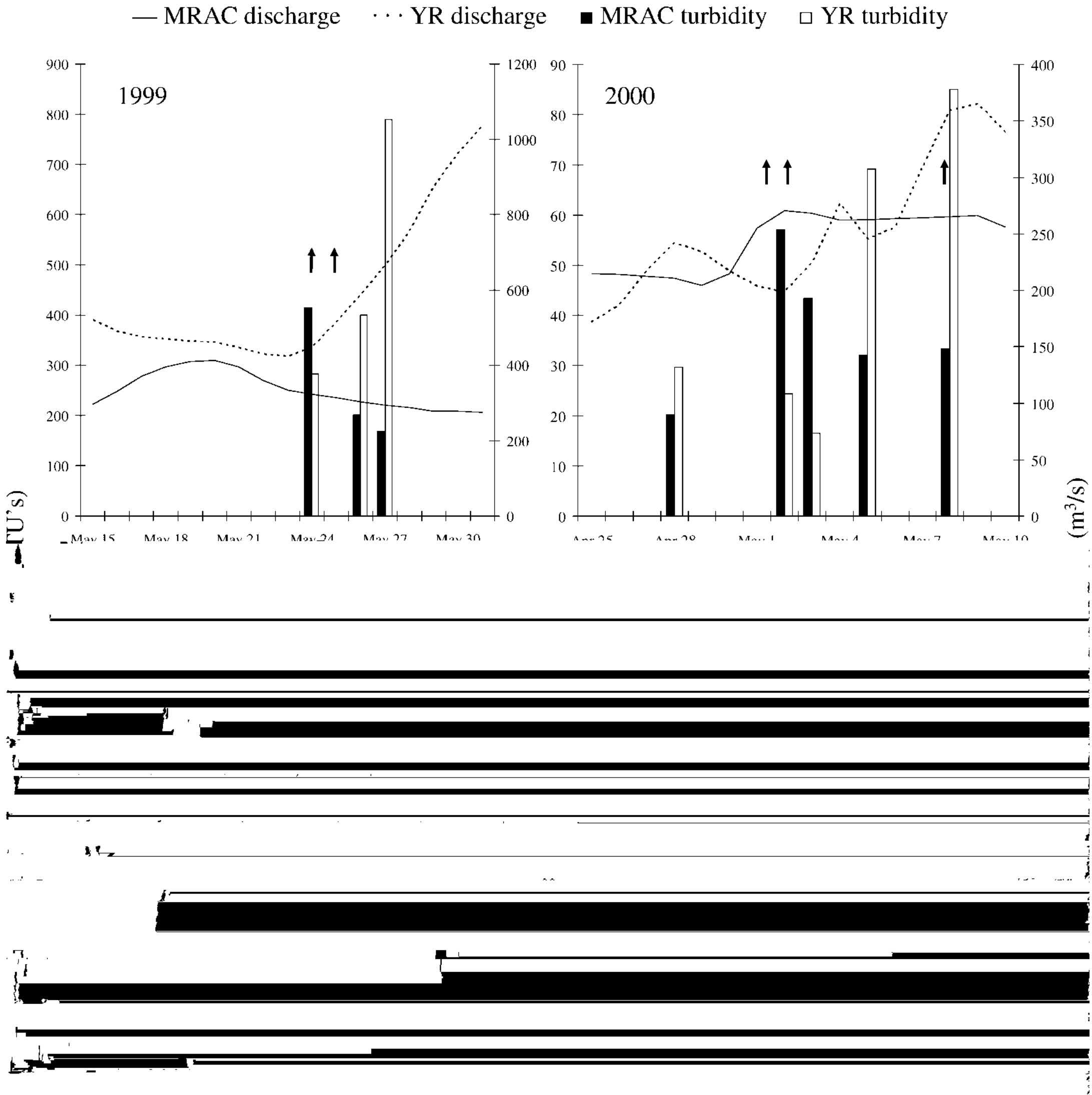

FIGURE 4.—Comparison of discharge and turbidity (nephelometric turbidity units) along the Yellowstone River (YR) and the Missouri River above its confluence with the Yellowstone River (MRAC) during time periods in which radio-tagged paddlefish were contacted along the MRAC, 1999–2002. Arrows indicate the dates when fish were contacted up the MRAC after a previous contact either along the Missouri River below its confluence with the Yellowstone River (MRBC) or the YR. Not displayed in 2000 was a fish contacted on June 3 after a previous contact along the MRBC on April 25. In 2001, arrows at May 18 and May 25 belong to one fish that was contacted at the confluence during the intervening time period. In 2002, the number underneath the arrow indicates the number of fish that were contacted along the MRAC on the survey date.

during our study occurred in the unobstructed lower 50 rkm and in reaches below the confluence. In contrast, paddlefish in other studies were often concentrated below dams during spring and thus were prevented from moving upriver during periods of increasing discharge (Southall 1982; Moen 1989). Zigler et al. (2003) also suggested that the presence of Prairie du Sac Dam, which prevented upriver movement of fish staging in its tailwaters, may have been a factor contributing to the unusual downriver movement noted during periods of high spring discharge along the Wisconsin River. However, migratory patterns in these other studies may have been obfuscated during low-water years in which discharge was considered insufficient to stimulate upriver movement (Moen et al. 1992).

differing spring flow regimes to influence river selection in migratory paddlefish. They suggested that the earlier peak in discharge along the Salt Fork River contributed to fish ascending the Salt Fork River rather than the Arkansas River. Differences in the flow regime between the YR and MRAC have also been found to influence river selection by other large migratory fish. Bramblett and White (2001) found radio-tagged pallid sturgeon *Scaphirhynchus albus* to ascend the Yellowstone River on 28 of 31 occasions when moving above the confluence. Additionally, movements into both rivers were associated with a higher level of discharge in the river that was ascended.

The observed patterns of river selection may provide insight into potential behavior by paddlefish under proposed water releases from Fort Peck Reservoir that increase Missouri River discharge during the spring (U.S. Fish and Wildlife Service, Denver, Colorado, letter to U.S. Army Corps of Engineers, Omaha, Nebraska, containing a final biological opinion on the operation of the Missouri River main-stem reservoir system, 2000). Paddlefish that ascended the MRAC during our study did not remain long in this reach as many were later contacted in the YR after MRAC discharge receded. Evidently, the relatively stable, regulated flows along the MRAC did not provide the cues necessary to sustain upriver movement. However, any prolonged increases in MRAC spring discharge, as proposed in the changes to Missouri River management (USFWS 2000), may keep paddlefish in this reach throughout the spawning period. It is unclear if such water releases would result in better spawning success or merely draw paddlefish into less favorable habitats for spawning and rearing of early life history stages.

The results from this study indicated that river temperature was not as influential as discharge and suspended sediment in determining the directional movement of prespawning fish. Not only was river selection not associated with temperature differences between the two rivers, but fish also exhibited stationary behavior before initial rises in discharge even though river temperatures typically exceeded 148C and were increasing. Paukert and Fisher (2001) also noted a lack of upriver movement out of Keystone Reservoir, Oklahoma, during one of their study seasons, even though temperatures were in excess of 108C. Other studies, in contrast, have found upriver movements to be associated with increasing temperatures above 108C (Purkett 1961; Russell 1986; Lein and DeVries 1998). On the other hand, Hoxmeier and DeVries (1997) found paddlefish to move downriver away from spawning grounds as river temperatures exceeded 248C. Temperatures in excess of 208C may approach the thermal limit for spawning paddlefish (Crance 1987) and thus elicit an avoidance, rather than a migratory, response. River temperatures during migratory periods in this study, however, were typically below 208C. As has been suggested for other migratory fishes, temperature is more likely to be instrumental in affecting the timing of the general migratory response to other stimuli rather than influencing immediate directional movements (Northcote 1984; Leggett 1985; Smith 1985; Whalen et al. 1999).

The changes in direction and, to a lesser extent, rate of movement observed in this study can be evaluated in t1997) 5(D(groK17(t1997))(migrator)-43(y)-34
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